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

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**Abstract**

The potato/tomato psyllid *Bactericera cockerelli* (Šulc) (Hemiptera: Triozidae) transmits “*Candidatus* Liberibacter solanacearum” (Lso) (also known as “*Candidatus* Liberibacter psyllaurous”), the bacterium associated with zebra chip disease (ZC) in potato. When disease incidence is high, ZC causes large economic losses through reductions in potato yield and tuber quality. No commercial potato variety has been found resistant to the pathogen. We evaluated host acceptance behaviors using no-choice assays on three breeding clones derived from *Solanum chacoense* Bitter with putative resistance to Lso and/or ZC as part of an effort to determine if the resistance observed in those breeding clones was related to effects on psyllid settling behavior. We also counted the number of eggs laid and nymphs hatched on the different genotypes to observe any differences in reproduction. The potato variety ‘Russet Burbank’ was used as a susceptible control. Probing frequency and female walking duration were greater on Russet Burbank than the other genotypes. Oviposition did not differ among genotypes. However, female psyllids on two of the putatively resistant genotypes displayed reduced fertility 18-24 days after confinement with a male, relative to females on Russet Burbank. These results suggest that although the germplasms display minor abiotic activity on psyllid fertility, putative resistance to Lso may be more strongly linked with resistance to the pathogen rather than effects on settling behaviors.

**Resumen**

El psílido de la papa y tomate *Bactericera cockerelli* (Šulc) (Hemiptera: Triozidae) transmite la bacteria "Candidatus *Liberibacter solanacearum*" (Lso) (conocida también como "Candidatus *Liberibacter psyllaurous*"), la cual ha sido asociada con la enfermedad ‘punta morada’ (PM) de la papa. Cuando la incidencia de la enfermedad es alta, PM causa grandes pérdidas económicas ya que produce severas reducciones en el rendimiento y la calidad del tubérculo de la papa. Hasta el momento, no se ha encontrado ninguna variedad comercial de papa resistente al patógeno causante de PM. Nosotros evaluamos la aceptación del psílido de papa a su huésped mediante ensayos de no-elección en clones reproductores derivados de *Solanum chacoense* Bitter. Ya que dichos clones han sido reportados con resistencia putativa a Lso y / o PM, nosotros quisimos investigar si tal resistencia estaba relacionada con cambios en el comportamiento de aceptación del psílido a dichos clones. También registramos el número de huevos puestos y el número de ninfas producidas por la eclosión dichos huevos, esta evaluación se realizó con el fin de observar alguna diferencia en la reproducción del psílido debido genotipo del huésped. La variedad de papa "Russet Burbank" se utilizó como control susceptible. Los resultados mostraron que la frecuencia de prueba del tejido huésped y la duración de la caminata de las hembras fueron mayores en Russet Burbank que en los otros genotipos. La oviposición fue similar en todos los genotipos; sin embargo, se observó una reducida fertilidad de los huevos 18-24 días después del apareamiento, en los genotipos considerados como resistentes a PM. La eclosión de huevos fue mayor durante el último período de observación (18-20 días después del apareamiento) en Russet Burbank que en los genotipos considerados como resistentes a PM. Estos resultados sugieren que, aunque los genotipos evaluados muestran una actividad abiótica menor en la fertilidad del psílido de papa, esta putativa resistencia no se debe a la reducción de los comportamientos de alimentación del psílido, sino que puede estar más fuertemente relacionada con la resistencia al patógeno.

**Key Words** *Solanum tuberosum*, *Solanum chacoense,* host plant resistance, tomato psyllid

# 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, Wallis 1955, Martin 2008, Aguilar et al. 2013). First discovered in Colorado (Šulc 1909), potato psyllids have a history closely tied to potato growing regions in North America to and to potato diseases (Richards and Blood 1973). The geographical distribution of *B. cockerelli* ranges from southern Canada to Central America, throughout the Western United States (Munyaneza et al. 2007, Rehman et al. 2010, Butler and Trumble 2012) and a recent introduction to New Zealand (Martin 2008, Liefting et al. 2009, Teulon et al. 2009).

Interest in potato psyllids grew during the 1920s due to the apparent association of this insect with a condition affecting solanaceous plants known as ‘psyllid yellows’ (Richards 1928, Eyer and Crawford 1933, Richards and Blood 1973). More recently, potato psyllids have been identified as vectors of “*Candidatus* Liberibacter solanacearum” (Lso) (also known as “*Candidatus* Liberibacter psyllaurous”) (Rhizobiaceae: Alphaproteobacteria) (Goolsby et al.  2007b, Hansen et al. 2008, Munyaneza et al. 2007, Liefting et al. 2009, Cicero et al. 2016). Lso is an uncultured gram-negative -proteobacterium (Liefting et al. 2009) that infects solanaceous plants. Lso is transmitted to the plant’s phloem by the psyllid’s saliva while feeding (Cooper and Bamberg 2014).

Symptoms of Lso infection in potato include stunting, swollen axillary buds, aerial tubers, leaf purpling, chlorosis and reduced yield (Munyaneza et al. 2007, 2008). Infection also alters tuber sugars and phenolics, resulting in brown stripes that char and blacken when fried (Navarre et al. 2009, Alvarado et al. 2012, Buchman et al. 2012). This condition is known as zebra chip disease (ZC) (Munyaneza et al. 2007). ZC-affected tubers are unmarketable, which results in large economic losses for growers (Rosson et al. 2006, Munyaneza et al. 2007). Yield reduction from Lso infection has ranged from 43% to 93% in some cases (Munyaneza et al. 2008, 2011).

Lso and ZC symptoms were first described in 1994 in Mexico and first detected in the United States in 2000 (Secor and Rivera-Varas 2004). Lso and ZC were first detected in the Pacific Northwest (PNW) states of Idaho, Washington and Oregon in 2011 (Crosslin et al. 2012). Since 2011, Lso and ZC continue to threaten potato production in the PNW, increasing production costs for growers (Guenthner et al. 2012, Greenway 2014, Wenninger et al. 2017, Greenway and Rondon 2018).

Management of ZC primarily targets the potato psyllid vector, usually relying on multiple applications of insecticides (Guenthner et al. 2012, Greenway 2014, Echegaray and Rondon 2017). In 2018, around half of Eastern Idaho growers’ insecticide expenditures were related to ZC control (Greenway and Rondon 2018). Chemicals such as abamectin, imidacloprid, spiromesifen, thiamethoxam and dinotefuran (Goolsby et al. 2007a, Vega-Gutiérrez et al. 2008, Gharalari et al. 2009, Guenthner et al. 2012) are commonly used but, some psyllid populations are starting to develop resistance to common neonicotinoids and abamectin (Liu and Trumble 2004, Hernández-Bautista et al. 2013, Prager et al. 2013, Chávez et al. 2015). The difficulty and large expense of psyllid control emphasizes the need for alternative and improved pest management strategies such as host plant resistance to control ZC.

Host plant resistance to Lso or the potato psyllid would provide growers with a valuable tool for integrated pest management (Kogan 1988, Butler and Trumble 2012, Munyaneza 2012, Diaz-Montano et al. 2013). Even a small amount of resistance or tolerance of a plant to a vector or its pathogen can reduce damage below action thresholds and reduce pesticide applications (Kennedy et al. 1987). Host plant resistance also increases pesticide efficiency and helps to delay development of insecticide resistance (Gharalari et al. 2009). Currently no commercial potato varieties have been found with acceptable resistance to Lso (Munyaneza et al. 2011, Anderson et al. 2012).

Potatoes that have been bred with closely related plants such as *Solanum chacoense* Bitter (Rashidi et al. 2017) and *Solanum berthaultii* Hawkes (Butler et al. 2011) have shown less Lso infection and/or ZC symptoms than other genotypes tested. By determining how these genotypes resist or tolerate either Lso or the psyllid vector itself (Kennedy et al. 1987, Putten et al. 2001, Butler et al. 2011), we can decide which traits should be bred or cloned into commercial cultivars to develop resistant potato cultivars (Kaloshian 2004, Casteel et al. 2006, 2007).

We examined psyllid host acceptance behaviors as well as oviposition and egg fertility on three potato breeding clones derived from *Solanum chacoense*: ‘A07781-10LB’ (‘10LB’), ‘A07781-3LB’, (‘3LB’) and ‘A07781-4LB’ (‘4LB’) (Rashidi et al. 2017). ‘Russet Burbank’ was used as a susceptible control (Munyaneza et al. 2011). The A07781 family of genotypes exhibits high tolerance and low susceptibility to Lso (Rashidi et al. 2017). This low susceptibility to Lso may be due to either resistance or tolerance to the psyllid vector or the bacteria itself. Focusing on psyllid host selection and settling behaviors such as probing, walking and time spent on the leaf can help us understand if a plant-induced change in psyllid behavior is part of why we observed any reduction in Lso transmission and/or ZC symptoms. Our results will help to clarify potato-psyllid interactions on these genotypes, which will help plant breeders to develop Lso-resistant potatoes (Kennedy et al. 1987).

# Materials and Methods

## Experimental insects

A Lso-positive potato psyllid colony was reared in colonies with free access to both Russet Burbank potatoes and ‘Yellow Pear’ tomatoes (*Solanum lycopersicum* L.). Colonies were kept in a greenhouse maintained between 25-32°C, 32% RH, with a photoperiod of 16:8 (L:D). Colony plants were fertilized once weekly with approximately 4.5 g of 24:8:16 NPK fertilizer per liter of water (MiracleGro All Purpose Plant Food, Scotts Company, Marysville, OH). Plants were replaced as needed.

## Experimental plants

Potato clones were provided by the USDA-ARS, Small Grains and Potato Germplasm Research Unit Aberdeen, ID, USA. The selected potatoes were grown in cages in the same greenhouse as described above (25-32°C, 32% RH, 16:8 (L:D)). We used three sibling clones derived from *Solanum chacoense* Bitter with putative relative resistance and/or tolerance to Lso: A07781-3LB, A07781-4LB and A07781-10LB (Rashidi et al. 2017). Russet Burbank was used as control because it is susceptible to Lso (Munyaneza et al. 2011) and because of its prevalence in potato production in the Pacific Northwest (NASS Northwest Regional Field Office 2017). 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, 1984). We used plants in their vegetative growth stage (growth stage II) (Dwelle et al. 2003) for all experiments.

## Psyllid Haplotype and Lso Detection

Idaho harbors four haplotypes of the potato psyllid: Northwestern, Western, Central and Southwestern as well as Lso haplotypes A and B (Dahan et al. 2017, Wenninger et al. 2017). Our lab colony was comprised of ‘Central’ psyllids infected with Lso ‘B’, verified via the methods described in Swisher and Crosslin (2014). The infection status of psyllids was verified in a sample of 40 psyllids collected from our Lso-positive colony. Each psyllid tested positive for Lso, suggesting a 100% rate of infection for the colony.

Lso incidence was determined by the analysis of Lso presence in individual potato psyllids at the Entomology Laboratory in the Aberdeen Research and Extension Center (Aberdeen, ID, USA). Forty adults’ psyllids were collected from the positive colony and transferred to individual microcentrifuge tubes containing 70% ethanol. Ethanol was removed completely from psyllids before DNA extraction. DNA extraction was based on the methods described by Marzachi et al. (1998). Tissue was ground in 500 μl of Cetyl Trimethylammonium Bromide 2% solution (Alpha Teknova, Inc., Hollister, CA, Cat. No. C2190) (Composition: 2% CTAB, 100 mM Tris-HCl, pH 8.0, 20 mM EDTA, pH 8.0, 1.4M Sodium Chloride (NaCl) by a homogenizer (Omni International Inc., Kennesaw, GA). Samples were then incubated at 60°C for 30 minutes and gently mixed by inversion every 10 minutes while incubating. Tubes were centrifuged at 14000 rpm for 5min, then the supernatant was transferred to new tube of 2ml. One volume of chloroform:isoamyl alcohol (24:1 v:v) (Sigma-Aldrich, Inc., Atlanta, GA: Catalog number C0549) was added and then tubes mixed by vortex for 20 seconds and centrifuged at 14,000 rpm for 10 minutes at 4 ℃. The supernatant was collected into a new 2 ml tube, then cold isopropanol (Sigma-Aldrich, Inc., Atlanta, GA: Catalog number I9516) was added at a rate of 2/3 of the volume of the supernatant. The mixture was then stored at -20°C for 30 minutes. DNA was precipitated by centrifuging the mixture for 20 minutes at 14,000 rpm at 4°C, then isopropanol was gently removed. Finally, 300 μL of 70% ethanol was added to the pellet and centrifuged for 5 minutes at 10,000 rpm. After ethanol was completely removed, the pellet was resuspended in 30 μL of nuclease-free water (Sigma-Aldrich, Inc., Atlanta, GA: Catalog number W4502) and stored at -20°C. DNA was used to detect the presence of Lso in psyllid tissue using qPCR SYBR Green analysis using a CFX Real-Time PCR System (Biorad, Hercules, CA). The qPCR reaction contained primers 150 nM of HLBr (5’-GCG TTA TCC CGT AGA AAA AGG TAG-3’) and LsoF (5’-GTC GAG CGC TTA TTT TTA ATA GGA-3’) primers (Li et al. 2006, 2009); 1X SsoAdvanced Universal SYBR Green Supermix (Biorad, Hercules, CA), and 1 ul of DNA template. The program cycle was as follows: one cycle at 98°C for 2 minutes followed by 40 cycles of 95°C for 10 sec and 62°C for 20 sec. The melt curve was 65 to 95 °C, with increments of 0.5 sec-1. DNA of a healthy tuber was used as a negative control. DNA of a healthy psyllids was used as a negative control and water was used as a no-template control in all tests.

## No-Choice Arena Design

No-choice assays were conducted in a climate-controlled lab closet maintained at 26°C. 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), but modified to use leaflets of intact, potted plants as in Butler et al. (2011). This permitted us to observe the psyllids with minimal interference to plant physiology and avoided altering plant volatiles or chemical defenses that might be activated by damaging plant tissues (Klingler et al. 2005). 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 cut 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, allowing the psyllid access to the lower (abaxial) surface of the leaf. We used leaves from the upper canopy of the plants for trials. The filter paper was discarded between observations to avoid cross contamination. The glass pane and foam were replaced with each new plant and washed and dried at 90°C before reuse to prevent 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).

## No-Choice Behavior Assays

We collected psyllids from the colony using an aspirator and transferred them to 8 × 35 mm glass shell vials. All psyllids were tested within 90 minutes from the time of collection from the colony. For each experimental replicate, a single psyllid was introduced to the arena, and its behaviors recorded for five minutes. Psyllid sex was identified, and psyllids were preserved in 95% ethanol for later testing for Lso by qPCR. (see Psyllid Haplotype and Lso Detection, above). We recorded behaviors similar to Butler et al. (2011): probing, walking, cleaning and whether the psyllid was on or off the leaf. These behaviors have putative significance with disease transmission and host selection (Prager et al. 2014a,b). These behaviors were scored using CowLog3 (Hänninen and Pastell 2009), which records behavioral incidences with timestamps from prerecorded video.

## Oviposition Assays

Oviposition assays were conducted with the same greenhouse conditions, plants and insects as previously described. A female + male pair of recently emerged (teneral) psyllids, identified by their green body color, was introduced to a plant covered with an insect rearing sleeve (MegaView Science Co., Ltd., Taiwan). These 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 arranged in a randomized complete block in rows of four and placed inside mesh-covered PVC-framed cages (60 cm length × 60 cm width × 60 cm height). Plants were watered on alternating days by soaking pots in plastic trays (56 cm length × 28 cm width × 6 cm height) until the soil became saturated (approximately 45 mins).

The oviposition experiment used two different mating access periods (Period 1): six days and eight days. Period 1 involved maintaining a male and female psyllid in the same cage on a plant, after which the male was removed, and the female transferred to a new plant of the same genotype. After the mating access period, the females were transferred to a new plant of the same genotype every four days (Periods 2-4, 18 - 20 days total)

Eggs were counted on each plant after the female was removed using 10× headband magnifiers. Nymphs were counted four days, eight days and twelve days later to allow time for hatching (Knowlton and Janes 1931). Each nymph was removed as it was counted. Egg fertility percentages were calculated as the ratio of nymphs divided by egg counts for each sample × 100.

## Statistical Analysis

Statistical analysis was performed using R Version 3.5.1 (R Core Team 2013). Assumptions of normality were examined with qqplots and Cullen and Frey graphs from the R package fitdistrplus (Delignette-Muller and Dutang 2015). No-choice experiments and egg count data were analyzed using generalized linear mixed model (GLMM) (Stroup 2015) from the glmer function (Bates et al. 2015). 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 plant genotype, psyllid sex and the interaction of plant genotype × psyllid sex. Psyllid replicate (n=181) was treated as random factor. Model formula: Behavior ~ Genotype + Sex + Sex \* Genotype + (1 | Psyllid). There were not enough psyllids that left the leaf (n = 20 out of 181 psyllids) to analyze an interaction between genotype × sex, so this interaction was excluded in the off-leaf model. Oviposition models had fixed factors of genotype, time period and genotype × time period. Psyllid replicate was considered the random factor. Model formula: Eggs ~ Genotype \* Period + (1 | Psyllid). Egg fertility was modeled with genotype and time period (days between plant rotations) as fixed factors and individual psyllids as the random factor. Model formula: Hatch Rate ~ Genotype \* Period + (1 | Psyllid). All data were tested with Wald’s χ2 tests, followed by least-squares means with Tukey’s HSD adjustments to test for multiple comparisons. Statistical significance was considered at α = 0.05.

**Results**

## No-Choice Assays

Overall, psyllids spent more time engaged in probing behavior than in the other activities recorded (Tables 1-5). 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 from 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 was not affected by sex (Table 1). 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 on 10LB (Table 3). Female psyllids on Russet Burbank walked significantly more often than males and females on 10LB and females on 3LB (Table 3). 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 occurred infrequently. 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 time period and the interaction of genotype × time 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 period (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, Butler et al. 2011). Our visual observations of settling behavior lack the precision of electrical penetration recordings used in similar studies (Butler et al.  2012, Sandanayaka et al. 2014, Mustafa et al. 2015), but require less expensive equipment. Our results are similar to those of other investigations of putatively resistant potato genotypes. Our analysis of the video recordings showed more probing and walking on Russet Burbank than on the putatively resistant genotypes, which is consistent with results reported by Butler et al. (2011) and Prager et al. (2014b). However, in contrast to Butler et al. (2011), 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) and Mustafa et al (2015) both suggest that it takes *B. cockerelli* approximately two hours to access the phloem and acquire Lso. This suggests that very long observations may be necessary to determine when probing becomes true feeding. Limited observations of 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 (Buchman et al. 2011; Rashed et al. 2012) and the disease progresses independently of bacterial titer (Rashed et al. 2012). 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 and feeding 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) have examined how host plant volatiles can alter psyllid behaviors (Wenninger et al. 2009, Davidson et al. 2014). Plant volatiles can induce probing in combination with visual and chemical cues from host plants (Patt et al. 2011). It is possible that Lso infection alters *B. cockerelli*’s attraction to leaf volatiles (Mayer et al. 2008) and their settling behavior as well (Mas et al. 2014). Lso infection can increase psyllid preferences for undamaged, uninfected hosts for oviposition and settling (Davis et al. 2012) – a behavior which has been seen in other insect-plant-vector relationships (Cao et al. 2016, Eigenbrode et al. 2018). In the present study it may be that this phenomenon encouraged greater acceptance of genotypes that 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 may not entirely explain the patterns we observed. Infection status also would not explain the minor trend we saw between male and female probing on Russet Burbank.

Another possible 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). Russet Burbank was one of the plants used to rear our colonies, so it is possible that the volatiles from this genotype were more stimulating for female psyllids. Further studies into potato psyllid’s attraction to plant volatiles while Lso positive and Lso negative 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, Diaz-Montano et al. 2013, Cooper and Bamberg 2014, Rubio-Covarrubias et al. 2017) our study showed similar oviposition rates among genotypes, consistent with results reported by (Prager et al. 2017). Other studies have found psyllids will oviposit on a variety of hosts (Diaz-Montano et al. 2013, Thinakaran et al. 2015), even when it is not beneficial for their survival (Prager et al. 2014b). Psyllids oviposited on every type of potato offered, showing 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,) and Yang et al. (2010, 2013). 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 in fertility may have a cumulative effect on psyllid populations, which could contribute to integrated pest management. Longer observation periods could help to better quantify these effects.

It is possible that Lso infection status played a role in the egg fertility observed; Lso has been reported to negatively impact female fertility (Frias et al. 2018, Nachappa et al. 2012a, 2012b, 2014, Yao et al. 2016). The evidence of antibiotic effects we observed on egg fertility of psyllids housed on putatively resistant genotypes might manifest differently for 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, Wenninger and Hall 2008, Arnqvist and Rowe 2013). Abdullah (2008), Yang and Liu (2009) and Yang et al. (2013) 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 mating over time to maintain egg fertility (Wenninger and Hall 2008, Arnqvist and Rowe 2013). Knowlton and Janes (1931) 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), which all influence how long females are able to remain fertile (Qazi and Hogdal 2010, Schnakenberg et al. 2011, Wolfner 2011, Abe and Kamimura 2015).

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 putatively 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) is not likely related to psyllid settling behaviors, but rather that reduced ZC symptoms may be due to resistance to Lso development itself or presence of mechanisms that limit symptom expression. Further work will be required to clarify the modality of resistance to Lso in the A07781 genotypes.

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**Statement of Author Contributions**

Austin N. Fife: Collected data, performed statistical analyses, helped write the manuscript

Arash Rashed: Helped write the manuscript, provided psyllid haplotypes, assisted with molecular analysis, provided funding

Karin Cruzado: Tested psyllid haplotypes, assisted with molecular analysis

Richard G. Novy: Helped write the manuscript, developed A07781 breeding clones and provided plant materials, helped write the manuscript

Erik J. Wenninger: Conceived and designed the experiments, helped write the manuscript, provided funding

**References Cited**

**Abdullah, N. M. H.** **2008**. Life history of the potato psyllid *Bactericera cockerelli* (Homoptera: Psyllidae) in controlled environments agriculture in Arizona. Afr. J. Agric. Res. 3: 60–67.

**Abe, J., and Y. Kamimura**. **2015**. Sperm economy between female mating frequency and male ejaculate allocation. Am. Nat. 185: 406–416.

**Aguilar, E., V. G. Sengoda, B. Bextine, K. F. McCue, and J. E. Munyaneza**. **2013**. First report of "*Candidatus* Liberibacter solanacearum" on tobacco in Honduras. Plant Dis. 97: 1376–1376.

**Alvarado, V. Y., D. Odokonyero, O. Duncan, T. E. Mirkov, and H. B. Scholthof**. **2012**. Molecular and physiological properties associated with zebra complex disease in potatoes and its relation with *Candidatus* Liberibacter contents in psyllid vectors. PLoS ONE. 7: e37345.

**Anderson, J. A. D., G. P. Walker, P. A. Alspach, M. Jeram, and P. J. Wright**. **2012**. Assessment of susceptibility to zebra chip and *Bactericera cockerelli* of selected potato cultivars under different insecticide regimes in New Zealand. Am. J. Potato Res. 90: 58–65.

**Arnqvist, G.,** **and L. Rowe**. **2005.** Sexual conflict (Monographs in Behavior and Ecology). Princeton University Press (New Jersey).

**Bates, D., M. Mächler, B. Bolker, and S. Walker**. **2015**. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67.

**Buchman, J. L., T. W. Fisher, V. G. Sengoda, and J. E. Munyaneza**. **2012**. Zebra chip progression: From inoculation of potato plants with Liberibacter to development of disease symptoms in tubers. Am. J. Potato Res. 89: 159–168.

**Buchman, J. L., V. G. Sengoda, and J. E. Munyaneza**. **2011**. Vector transmission efficiency of Liberibacter by *Bactericera cockerelli* (Hemiptera: Triozidae) in zebra chip potato disease: Effects of psyllid life stage and inoculation access period. J. Econ. Entomol. 104: 1486–1495.

**Butler, C. D., B. Gonzalez, K. L. Manjunath, R. F. Lee, R. G. Novy, J. C. Miller, and J. T. Trumble**. **2011**. Behavioral responses of adult potato psyllid, *Bactericera cockerelli* (Hemiptera: Triozidae), to potato germplasm and transmission of *Candidatus* Liberibacter psyllaurous. Crop Prot. 30: 1233–1238.

**Butler, C. D., and J. T. Trumble**. **2012**. The potato psyllid, *Bactericera cockerelli* (Šulc) (Hemiptera: Triozidae): Life history, relationship to plant diseases, and management strategies. Terrestrial arthropod reviews. 5: 87–111.

**Butler, C. D., G. P. Walker, and J. T. Trumble**. **2012**. Feeding disruption of potato psyllid, *Bactericera cockerelli*, by imidacloprid as measured by electrical penetration graphs. Entomol. Exp. Appl. 142: 247–257.

**Cao, H., H. Liu, Z. Zhang, and T. Liu**. **2016**. The green peach aphid *Myzus persicae* perform better on pre-infested chinese cabbage *Brassica pekinensis* by enhancing host plant nutritional quality. Sci. Rep. 6.

**Casteel, C. L., L. L. Walling, and T. D. Paine**. **2006**. Behavior and biology of the tomato psyllid, *Bactericerca cockerelli*, in response to the mi-1.2 gene. Entomol. Exp. Appl. 121: 67–72.

**Casteel, C. L., L. L. Walling, and T. D. Paine**. **2007**. Effect of mi-1.2 gene in natal host plants on behavior and biology of the tomato psyllid *Bactericerca cockerelli* (Sulc) (Hemiptera: Psyllidae). J. Entomol. Sci. 42: 155–162.

**Chávez, E. C., O. H. Bautista, J. L. Flores, L. A. Uribe, and Y. M. O. Fuentes**. **2015**. Insecticide-resistance ratios of three populations of *Bactericera cockerelli* (Hemiptera: Psylloidea: Triozidae) in regions of northern Mexico. Fla. Entomol. 98: 950–953.

**Cicero, J. M., T. W. Fisher, and J. K. Brown**. **2016**. Localization of “*Candidatus* Liberibacter solanacearum” and evidence for surface appendages in the potato psyllid vector. Phytopathology. 106: 142–154.

**Cooper, W. R., and J. B. Bamberg**. **2014**. Variation in *Bactericera cockerelli* (Hemiptera: Triozidae) oviposition, survival, and development on *Solanum bulbocastanum* germplasm. Am. J. Potato Res. 91: 532–537.

**Crosslin, J. M., H. Lin, and J. E. Munyaneza**. **2011**. Detection of “*Candidatus* Liberibacter solanacearum” in the potato psyllid, *Bactericera cockerelli* (Sulc), by conventional and real-time PCR. Southwest. Entomol. 36: 125–135.

**Crosslin, J. M., N. Olsen, and P. Nolte**. **2012**. First report of zebra chip disease and *Candidatus* Liberibacter solanacearum on potatoes in Idaho. Plant Dis. 96: 453–453.

**Dahan, J., E. J. Wenninger, B. Thompson, S. Eid, N. Olsen, and A. V. Karasev**. **2017**. Relative abundance of potato psyllid haplotypes in southern Idaho potato fields during 2012 to 2015, and incidence of “*Candidatus* Liberibacter solanacearum” causing zebra chip disease. Plant Dis. 101: 822–829.

**Davidson, M. M., R. C. Butler, N. M. Taylor, M. C. Nielsen, C. E. Sansom, and N. B. Perry**. **2014**. A volatile compound, 2-undecanone, increases walking, but not flying, tomato potato psyllid movement toward an odour source. New Zealand plant protection. 67: 184–190.

**Davis, T. S., D. R. Horton, J. E. Munyaneza, and P. J. Landolt**. **2012**. Experimental infection of plants with an herbivore-associated bacterial endosymbiont influences herbivore host selection behavior. PLoS ONE. 7: e49330.

**Delignette-Muller, M. L., and C. Dutang**. **2015**. fitdistrplus: An R package for fitting distributions. J. Stat. Softw. 64.

**Diaz-Montano, J., J. C. Reese, W. T. Schapaugh, and L. R. Campbell**. **2006**. Characterization of antibiosis and antixenosis to the soybean aphid (Hemiptera: Aphididae) in several soybean genotypes. J. Econ. Entomol. 99: 1884–1889.

**Diaz-Montano, J., B. G. Vindiola, N. Drew, R. G. Novy, J. C. Miller, and J. T. Trumble**. **2013**. Resistance of selected potato genotypes to the potato psyllid (Hemiptera: Triozidae). Am. J. Potato Res. 91: 363–367.

**Dwelle, R. B., J. M. Alvarez, P. Bain, C. R. Baird, E. J. Bechinski, W. H. Bohl, D. L. Corsini, C. V. Eberlein, L. L. Ewing, B. F. Finnigan, B. D. Geary, J. F. Guenthner, S. L. Hafez, P. J. S. Hutchinson, W. B. Jones, B. A. King, G. E. Kleinkopf, J. S. Miller, P. Nolte, R. Novy, N. Olsen, S. Palanisamy, P. E. Patterson, L. E. Sandvol, R. L. Stoltz, D. T. Westermann, and J. C. Whitmore**. **2003**. Potato production systems, pp. 12–14. *In*. The University of Idaho agricultural communications.

**Echegaray, E. R., and S. I. Rondon**. **2017**. Incidence of *Bactericera cockerelli* (Hemiptera: Triozidae) under different pesticide regimes in the lower Columbia Basin. J. Econ. Entomol. 110: 1639–1647.

**Eigenbrode, S. D., N. A. Bosque-Pérez, and T. S. Davis**. **2018**. Insect-borne plant pathogens and their vectors: Ecology, evolution, and complex interactions. Annu. Rev. Entomol. 63: 169–191.

**Eyer, J. R., and R. F. Crawford**. **1933**. Observations on the feeding habits of the potato psyllid (*Paratrioza cockerelli* Sulc.) and the pathological history of the "psyllid yellows" which it produces. J. Econ. Entomol. 26: 846–850.

**Frias, A. A. T., F. Ibanez, A. Mendoza, W. M. de Carvalho Nunes, and C. Tamborindeguy**. **2018**. Effects of "*Candidatus* Liberibacter solanacearum" (haplotype b) on *Bactericera cockerelli* fitness and vitellogenesis. Insect Sci.

**Gharalari, A. H., C. Nansen, D. S. Lawson, J. Gilley, J. E. Munyaneza, and K. Vaughn**. **2009**. Knockdown mortality, repellency, and residual effects of insecticides for control of adult *Bactericera cockerelli* (Hemiptera: Psyllidae). J. Econ. Entomol. 102: 1032–1038.

**Goolsby, J. A., J. Adamczyk, B. Bextine, D. Lin, J. E. Munyaneza, and G. Bester**. **2007a**. Development of an IPM program for management of the potato psyllid to reduce incidence of zebra chip disorder in potatoes. Subtropical Plant Science. 59: 85–94.

**Goolsby, J. A., B. Bextine, J. E. Munyaneza, M. Setamou, J. Adamczyk, and G. Bester**. **2007b**. Seasonal abundance of sharpshooters, leafhoppers, and psyllids associated with potatoes affected by zebra chip disorder. Subtropical Plant Science. 59: 15–23.

**Greenway, G.** **2014**. Economic impact of zebra chip control costs on grower returns in seven US states. Am. J. Potato Res. 91: 714–719.

**Greenway, G. A., and S. Rondon**. **2018**. Economic impacts of zebra chip in Idaho, Oregon, and Washington. Am. J. Potato Res.

**Guenthner, J., J. Goolsby, and G. Greenway**. **2012**. Use and cost of insecticides to control potato psyllids and zebra chip on potatoes. Southwest. Entomol. 37: 263–270.

**Hansen, A. K., J. T. Trumble, R. Stouthamer, and T. D. Paine**. **2008**. A new huanglongbing species, "*Candidatus* Liberibacter psyllaurous," found to infect tomato and potato, is vectored by the psyllid *(*Bactericera cockerelli) (Sulc). Appl. Environ. Microbiol. 74: 5862–5865.

**Hänninen, L., and M. Pastell**. **2009**. CowLog: Open-source software for coding behaviors from digital video. Behav. Res. Methods. 41: 472–476.

**Hernández-Bautista, O., E. Cerna-Chávez, J. Landeros-Flores, Y. Ochoa-Fuentes, J. Chacón-Hernández, and S. Castillo-Arriaga**. **2013**. Resistance proportion of *Bactericera cockerelli* (Sulc) in regions from Villa de Arista, San Luis Potosí and Saltillo, Coahuila. Entomología mexicana.

**Kaloshian, I.** **2004**. Gene-for-gene disease resistance: Bridging insect pest and pathogen defense. J. Chem. Ecol. 30: 2419–2438.

**Kennedy, G. G., F. Gould, O. M. B. Deponti, and R. E. Stinner**. **1987**. Ecological, agricultural, genetic, and commercial considerations in the deployment of insect-resistant germplasm. Environ. Entomol. 16: 327–338.

**Klingler, J., R. Creasy, L. Gao, R. M. Nair, A. S. Calix, H. S. Jacob, O. R. Edwards, and K. B. Singh**. **2005**. Aphid resistance in *Medicago truncatula* involves antixenosis and phloem-specific, inducible antibiosis, and maps to a single locus flanked by NBS-LRR resistance gene analogs. Plant Physiol. 137: 1445–1455.

**Knowlton, G. F., and M. J. Janes**. **1931**. Studies on the biology of *Paratrioza cockerelli* (Sulc). Ann. Entomol. Soc. Am. 24: 283–292.

**Knowlton, G. F., and W. L. Thomas**. **1934**. Host plants of the potato psyllid. J. Econ. Entomol. 27: 547–549.

**Kogan, M.** **1988**. Integrated pest management theory and practice. Entomol. Exp. Appl. 49: 59–70.

**Levy, J., A. Ravindran, D. Gross, C. Tamborindeguy, and E. Pierson**. **2011**. Translocation of “*Candidatus* Liberibacter solanacearum”, the zebra chip pathogen, in potato and tomato. Phytopathology. 101: 1285–1291.

**Li, W., J. A. Abad, R. D. French-Monar, R. J., A. Wen, N. C. Gudmestad, G. A. Secor, I. M. Lee, Y. Duan, and L. Levy**. **2009**. Multiplex real-time PCR for detection, identification and quantification of “*Candidatus* Liberibacter solanacearum” in potato plants with zebra chip. J. Microbiol. Methods. 78: 59–65.

**Li, W., J. S. Hartung, and L. Levy**. **2006**. Quantitative real-time PCR for detection and identification of *Candidatus* Liberibacter species associated with citrus huanglongbing. J. Microbiol. Methods. 66: 104–115.

**Liefting, L. W., B. S. Weir, S. R. Pennycook, and G. R. G. Clover**. **2009**. ‘*Candidatus* Liberibacter solanacearum’, associated with plants in the family Solanaceae. Int. J. Syst. Evol. Microbiol. 59: 2274–2276.

**Lin, H., H. Doddapaneni, J. E. Munyaneza, E. L. Civerolo, V. G. Sengoda, J. L. Buchman, and D. C. Stenger**. **2009**. Molecular characterization and phylogenetic analysis of 16S rRNA from a new "*Candidatus* Liberibacter" strain associated with zebra chip disease of potato (*Solanum tuberosum* l.) and the potato psyllid (*Bactericera cockerelli* Sulc). J. Plant Pathol. 91: 215–219.

**Liu, D., and J. T. Trumble**. **2004**. Tomato psyllid behavioral responses to tomato plant lines and interactions of plant lines with insecticides. J. Econ. Entomol. 97: 1078–1085.

**Marchini, D., G. D. Bene, R. Viscuso, and R. Dallai**. **2011**. Sperm storage by spermatodoses in the spermatheca of *Trioza alacris* (Flor, 1861) Hemiptera, Psylloidea, Triozidae: A structural and ultrastructural study. J. Morphol. 273: 195–210.

**Martin, N. A.** **2008**. Host plants of the potato/tomato psyllid: A cautionary tale. The Weta. 35: 12–16.

**Marzachi, C., F. Beratti, and D. Bosco**. **1998**. Direct PCR detection of phytoplasmas in experimentally infected insects. Ann. Appl. Biol. 133: 45–54.

**Mas, F., J. Vereijssen, and D. M. Suckling**. **2014**. Influence of the pathogen *Candidatus* Liberibacter solanacearum on tomato host plant volatiles and psyllid vector settlement. J. Chem. Ecol. 40: 1197–1202.

**Mayer, C. J., A. Vilcinskas, and J. Gross**. **2008**. Phytopathogen lures its insect vector by altering host plant odor. J. Chem. Ecol. 34: 1045–1049.

**Munyaneza, J. E.** **2012**. Zebra chip disease of potato: Biology, epidemiology, and management. Am. J. Potato Res. 89: 329–350.

**Munyaneza, J. E., J. L. Buchman, V. G. Sengoda, T. W. Fisher, and C. C. Pearson**. **2011**. Susceptibility of selected potato varieties to zebra chip potato disease. Am. J. Potato Res. 88: 435–440.

**Munyaneza, J. E., J. L. Buchman, J. E. Upton, J. A. Goolsby, J. M. Crosslin, G. Bester, G. P. Miles, and V. G. Sengoda**. **2008**. Main content area impact of different potato psyllid populations on zebra chip disease incidence, severity, and potato yield. Subtropical plant science. 60: 27–37.

**Munyaneza, J. E., J. M. Crosslin, and J. E. Upton**. **2007**. Association of *Bactericera cockerelli* (Homoptera: Psyllidae) with ’zebra chip,’ a new potato disease in southwestern United States and Mexico. J. Econ. Entomol. 100: 656–663.

**Murphy, A. F., S. I. Rondon, and A. S. Jensen**. **2012**. First report of potato psyllids, *Bactericera cockerelli*, overwintering in the Pacific Northwest. Am. J. Potato Res. 90: 294–296.

**Mustafa, T., D. R. Horton, W. R. Cooper, K. D. Swisher, R. S. Zack, H. R. Pappu, and J. E. Munyaneza**. **2015**. Use of electrical penetration graph technology to examine transmission of “*Candidatus* Liberibacter solanacearum” to potato by three haplotypes of potato psyllid (*Bactericera cockerelli*; (Hemiptera: Triozidae). PLoS ONE. 10: e0138946.

**Nachappa, P., J. Levy, and C. Tamborindeguy**. **2012a**. Transcriptome analyses of *Bactericera cockerelli* adults in response to "*Candidatus* Liberibacter solanacearum" infection. Mol. Genet. Genomics. 287: 803–817.

**Nachappa, P., A. A. Shapiro, and C. Tamborindeguy**. **2012b**. Effect of “*Candidatus* Liberibacter solanacearum” on fitness of its insect vector, *Bactericera cockerelli* (Hemiptera: Triozidae), on tomato. Phytopathology. 102: 41–46.

**Nachappa, P. J. Levy, E. Pierson, and C. Tamborindeguy**. **2014**. Correlation between "*Candidatus* Liberibacter solanacearum" infection levels and fecundity in its psyllid vector. J. Invertebr. Pathol. 115: 55–61.

**NASS Northwest Regional Field Office, U. S. D. A.** **2017**. Potato size and grade summary – 2017 crop. United States Department of Agriculture - National Agricultural Statistics Service.

**Navarre, D. A., R. Shakya, J. Holden, and J. M. Crosslin**. **2009**. LC-MS analysis of phenolic compounds in tubers showing zebra chip symptoms. Am. J. Potato Res. 86: 88–95.

**Patt, J. M., W. G. Meikle, A. Mafra-Neto, M. Sétamou, R. Mangan, C. Yang, N. Malik, and J. J. Adamczyk**. **2011**. Multimodal cues drive host-plant assessment in asian citrus psyllid (*Diaphorina citri*). Environ. Entomol. 40: 1494–1502.

**Pfeiffer, D. G., and E. C. Burts**. **1983**. Effect of tree fertilization on numbers and development of pear psylla (Homoptera: Psyllidae) and on fruit damage. Environ. Entomol. 12: 895–901.

**Pfeiffer, D. G., and E. C. Burts**. **1984**. Effect of tree fertilization on protein and free amino acid content and feeding rate of pear psylla (Homoptera: Psyllidae). Environ. Entomol. 13: 1487–1490.

**Prager, S. M., I. Esquivel, and J. T. Trumble**. **2014a**. Factors influencing host plant choice and larval performance in *Bactericera cockerelli*. PLoS ONE. 9: e94047.

**Prager, S. M., O. M. Lewis, J. Michels, and C. Nansen**. **2014b**. The influence of maturity and variety of potato plants on oviposition and probing of *Bactericera cockerelli* (Hemiptera: Triozidae). Environ. Entomol. 43: 402–409.

**Prager, S. M., B. Vindiola, G. S. Kund, F. J. Byrne, and J. T. Trumble**. **2013**. Considerations for the use of neonicotinoid pesticides in management of *Bactericera cockerelli* (Šulk) (Hemiptera: Triozidae). Crop Prot. 54: 84–91.

**Prager, S. M., C. M. Wallis, M. Jones, R. Novy, and J. T. Trumble**. **2017**. Examining the potential role of foliar chemistry in imparting potato germplasm tolerance to potato psyllid, green peach aphid, and zebra chip disease. J. Econ. Entomol. 111: 327–336.

**Putten, W. H. V. der, L. E. M. Vet, J. A. Harvey, and F. L. Wäckers**. **2001**. Linking above - and belowground multitrophic interactions of plants, herbivores, pathogens, and their antagonists. Trends in Ecology & Evolution. 16: 547–554.

**Qazi, M. C. B., and L. Hogdal**. **2010**. Hold on: Females modulate sperm depletion from storage sites in the fly *drosophila melanogaster*. J. Insect Physiol. 56: 1332–1340.

**Rashed, A., T. D. Nash, L. Paetzold, F. Workneh, and C. M. Rush**. **2012**. Transmission efficiency of “*Candidatus* Liberibacter solanacearum” and potato zebra chip disease progress in relation to pathogen titer, vector numbers, and feeding sites. Phytopathology. 102: 1079–1085.

**Rashidi, M., R. G. Novy, C. M. Wallis, and A. Rashed**. **2017**. Characterization of host plant resistance to zebra chip disease from species-derived potato genotypes and the identification of new sources of zebra chip resistance. PLoS ONE. 12: e0183283.

**R Core Team**. **2013**. R: A language and environment for statistical computing. R foundation for statistical computing, Vienna, Austria.

**Rehman, M., J. C. Melgar, C. J. M. Rivera, A. M. Idris, and J. K. Brown**. **2010**. First report of "*Candidatus* Liberibacter psyllaurous" or "*ca.* Liberibacter solanacearum" associated with severe foliar chlorosis, curling, and necrosis and tuber discoloration of potato plants in Honduras. Plant Dis. 94: 376–376.

**Richards, B. L.** **1928**. A new and destructive disease of the potato in Utah and its relation to the potato psylla. Phytopathology. 18.

**Richards, H. L., and H. L. Blood**. **1973**. Psyllid yellows of the potato. Readings in insect-plant disease relationships. 46: 139.

**Rosson, P., M. Niemeyer, M. Palma, and L. Ribera**. **2006**. Economic impacts of zebra chips on the Texas potato industry. Center for North American studies, department of agricultural economics, Texas A&M university, College Station, TX.

**Rubio-Covarrubias, O. A., M. A. Cadena-Hinojosa, S. M. Prager, C. M. Wallis, and J. T. Trumble**. **2017**. Characterization of the tolerance against zebra chip disease in tubers of advanced potato lines from Mexico. Am. J. Potato Res. 94: 342–356.

**Sandanayaka, W. R. M., A. Moreno, L. K. Tooman, N. E. M. Page-Weir, and A. Fereres**. **2014**. Stylet penetration activities linked to the acquisition and inoculation of *Candidatus* Liberibacter solanacearum by its vector tomato potato psyllid. Entomol. Exp. Appl. 151: 170–181.

**Schnakenberg, S. L., W. R. Matias, and M. L. Siegal**. **2011**. Sperm-storage defects and live birth in *drosophila* females lacking spermathecal secretory cells. PLoS Biology. 9.

**Secor, G. A., and V. V. Rivera-Varas**. **2004**. Emerging diseases of cultivated potato and their impact on latin america. Revista Latinoamericana de la Papa (Suplemento). 1: 1–8.

**Stroup, W. W.** **2015**. Rethinking the analysis of non-normal data in plant and soil science. Agron. J. 107: 811.

**Swisher, K. D., and J. M. Crosslin**. **2014**. Restriction digestion method for haplotyping the potato psyllid, *Bactericera cockerelli*. Southwest. Entomol. 39: 49–56.

**Šulc, K.** **1909**. *Trioza cockerelli* n. Sp., a novelty from North America, being also of economic importance. Acta Societatis Entomologicae Bohemiae. 6: 102–108.

**Teixeira, D. do C., C. Saillard, S. Eveillard, J. L. Danet, P. I. da Costa, A. J. Ayres, and J. Brové**. **2005**. ’*Candidatus* Liberibacter americanus’, associated with citrus huanglongbing (greening disease) in Sao Paulo State, Brazil. Int. J. Syst. Evol. Microbiol. 55: 1857–1862.

**Teulon, D. A. J., P. J. Workman, K. L. Thomas, and M. C. Nielsen**. **2009**. *Bactericera cockerelli*: Incursion, dispersal and current distribution on vegetable crops in New Zealand. New Zealand Plant Protection. 62: 136–144.

**Thinakaran, J., E. A. Pierson, M. Longnecker, C. Tamborindeguy, J. E. Munyaneza, C. M. Rush, and D. C. Henne**. **2015**. Settling and ovipositional behavior of *Bactericera cockerelli* (Hemiptera: Triozidae) on solanaceous hosts under field and laboratory conditions. J. Econ. Entomol. 108: 904–916.

**Vega-Gutiérrez, M. T., J. C. Rodríguez-Maciel, O. Díaz-Gómez, R. Bujanos-Muñiz, D. Mota-Sánchez, J. L. Martínez-Carrillo, A. Lagunes-Tejeda, and J. A. Garzón-Tiznado**. **2008**. Susceptibility to insecticides in two Mexican population of tomato-potato psyllid, *Bactericera cockerelli* (Sulc.) (Hemiptera: Triozidae). Agrociencia. 42: 463–471.

**Wallis, R. L.** **1955**. Ecological studies on the potato psyllid as a pest of potatoes. U.S. Department of Agriculture; US Deptartment of Agriculture.

**Wenninger, E. J., A. Carroll, J. Dahan, A. V. Karasev, M. Thornton, J. Miller, P. Nolte, N. Olsen, and W. Price**. **2017**. Phenology of the potato psyllid, *Bactericera cockerelli* (Hemiptera: Triozidae), and “*Candidatus* Liberibacter solanacearum” in commercial potato fields in Idaho. Environ. Entomol. 46: 1179–1188.

**Wenninger, E. J., and D. G. Hall**. **2008**. Importance of multiple mating to female reproductive output in *Diaphorina citri*. Physiol. Entomol. 33: 316–321.

**Wenninger, E. J., L. L. Stelinski, and D. G. Hall**. **2009**. Roles of olfactory cues, visual cues, and mating status in orientation of *Diaphorina citri* Kuwayama (Hemiptera: Psyllidae) to four different host plants. Environ. Entomol. 38: 225–234.

**Wolfner, M. F.** **2011**. Precious essences: Female secretions promote sperm storage in *Drosophila*. PLoS Biology. 9.

**Yang, X. B., and T. X. Liu**. **2009**. Life history and life tables of *Bactericera cockerelli* (Homoptera: Psyllidae) on eggplant and bell pepper. Environ. Entomol. 38: 1661–1667.

**Yang, X. B., Y. M. Zhang, D. C. Henne, and T. X. Liu**. **2013**. Life tables of *Bactericera cockerelli* (Hemiptera: Triozidae) on tomato under laboratory and field conditions in southern Texas. Fla. Entomol. 96: 904–913.

**Yang, X. B., Y. M. Zhang, L. Hua, and T. X. Liu**. **2010**. Life history and life tables of *Bactericera cockerelli* (Hemiptera: Psyllidae) on potato under laboratory and field conditions in the Lower Rio Grande Valley of Texas. J. Econ. Entomol. 103: 1729–1734.

**Yao, J., P. Saenkham, J. Levy, F. Ibanez, C. Noroy, A. Mendoza, O. Huot, D. F. Meyer, and C. Tamborindeguy**. **2016**. Interactions of "*Candidatus* Liberibacter" solanacearum - *Bactericera cockerelli*: Haplotype effect on vector fitness and gene expression analyses. Front. Cell. Infect. Microbiol. 6.

**Table 1.** Wald’s χ2 tests comparing psyllid behaviors between sexes and among four genotypes: A07781-10LB, A07781-3LB, A07781-4LB and Russet Burbank.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| Behavior | Factors |  | Incidence | | Duration | |
|  |  | df | χ2 | Pr > χ2 | χ2 | Pr > χ2 |
| Probing | Genotype | 3 | 27.46 | 0.000\* | 2.51 | 0.473 |
|  | Sex | 1 | 3.24 | 0.072 | 0.00 | 0.959 |
|  | Genotype × Sex | 3 | 6.49 | 0.090 | 4.74 | 0.192 |
| Walking | Genotype | 3 | 16.17 | 0.001\* | 4.66 | 0.199 |
|  | Sex | 1 | 1.65 | 0.200 | 0.036 | 0.850 |
|  | Genotype × Sex | 3 | 11.13 | 0.011\* | 10.73 | 0.013\* |
| 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 | 0.023\* |
|  | Sex | 1 | 0.71 | 0.401 | 0.48 | 0.832 |
|  | Genotype × Sex | 3 | — | — | — | — |

aThe interaction genotype × sex was unable to be analyzed due to the low number of psyllids that left the leaf (n = 20 out of 181)

**Table 2.** Least-square mean ± SEM incidence and duration of potato psyllid probing behaviors recorded during 300-s no-choice tests on four different genotypes: A07781-10LB, A07781-3LB, A07781-4LB and Russet Burbank.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| Genotype | Sex | N | Incidence |  | Duration (s) |  |
| A07781-10LB | Female | 21 | 1.4 ± 0.26 | A | 182 ± 28.2 |  |
|  | Male | 25 | 1.3 ± 0.23 | 242 ± 34.0 |  |
| A07781-3LB | Female | 27 | 1.5 ± 0.24 | A | 248 ± 33.6 |  |
|  | Male | 21 | 1.4 ± 0.26 | 183 ± 28.2 |  |
| A07781-4LB | 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 |  |

Means in the same column that share a letter are not significantly different (α = 0.05). Capital letters indicate differences among genotypes with sex pooled.

**Table 3.** Least-square mean ± SEM incidence and duration of potato psyllid walking behaviors recorded during 300-s no-choice tests on four different genotypes: A07781-10LB, A07781-3LB, A07781-4LB and Russet Burbank.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| Genotype | Sex | N | Incidence |  | Duration (s) |  |
| A07781-10LB | Female | 21 | 0.7 ± 0.19 a | A | 0.9 ± 0.8 a |  |
|  | Male | 25 | 0.3 ± 0.12 a | 0.6 ± 0.5 a |  |
| A07781-3LB | Female | 27 | 0.5 ± 0.15 a | AB | 0.4 ± 0.4 a |  |
|  | Male | 21 | 0.8 ± 0.21 ab | 4.0 ± 3.3 a |  |
| A07781-4LB | Female | 25 | 0.9 ± 0.21 ab | AB | 1.6 ± 1.3 a |  |
|  | Male | 18 | 1.1 ± 0.28 ab | 5.7 ± 5.0 a |  |
| Russet Burbank | Female | 26 | 1.8 ± 0.33 b | B | 10.5 ± 7.5 b |  |
|  | Male | 18 | 0.6 ± 0.20 ab | 0.6 ± 0.6 a |  |

Means in the same column that share a letter are not significantly different (α = 0.05). Differences among sex × genotype are indicated by lowercase letters; capital letters indicate differences among genotypes with sex pooled.

**Table 4.** Least-square mean ± SEM incidence and duration of potato psyllid cleaning behaviors recorded during 300-s no-choice tests on four different genotypes: A07781-10LB, A07781-3LB, A07781-4LB and Russet Burbank.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| Genotype | Sex | N | Incidence |  | Duration (s) |  |
| A07781-10LB | Female | 21 | 0.34 ± 0.15 |  | 0.008 ± 0.017 |  |
|  | Male | 25 | 0.33 ± 0.13 |  | 0.023 ± 0.048 |  |
| A07781-3LB | Female | 27 | 0.13 ± 0.07 |  | 0.002 ± 0.003 |  |
|  | Male | 21 | 0.20 ± 0.10 |  | 0.003 ± 0.005 |  |
| A07781-4LB | Female | 25 | 0.20 ± 0.10 |  | 0.002 ± 0.003 |  |
|  | Male | 18 | 0.26 ± 0.13 |  | 0.008 ± 0.018 |  |
| Russet Burbank | Female | 26 | 0.09 ± 0.05 |  | 0.001 ± 0.001 |  |
|  | Male | 18 | 0.13 ± 0.08 |  | 0.001 ± 0.002 |  |

**Table 5.** Least-square mean ± SEM incidence and duration of potato psyllids leaving the leaf surface during 300-s no-choice tests on four different genotypes: A07781-10LB, A07781-3LB, A07781-4LB and Russet Burbank.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| Genotypea | Sex | N | Incidence |  | Duration (s) |  |
| A07781-10LB | Female | 21 | 0.03 ± 0.02 |  | 1449.9 ± 2934.1 × 10-7 | AB |
|  | Male | 25 | 0.05 ± 0.03 |  | 1873.6 ± 3716.9 × 10-7 |
| A07781-3LB | Female | 27 | 0.06 ± 0.03 |  | 2229.5 ± 4272.9 × 10-7 | B |
|  | Male | 21 | 0.09 ± 0.05 |  | 2881.0 ± 5700.0 × 10-7 |
| A07781-4LB | Female | 25 | 0.05 ± 0.04 |  | 10.6 ± 31.6 × 10-7 | A |
|  | Male | 18 | 0.08 ± 0.06 |  | 13.7 ± 41.6 × 10-7 |
| Russet Burbank | Female | 26 | 0.03 ± 0.02 |  | 9.1 ± 27.1 × 10-7 | A |
|  | Male | 18 | 0.05 ± 0.03 |  | 11.7 ± 35.7 × 10-7 |

Means in the same column that share a letter are not significantly different (α = 0.05). Differences among sex × genotype are indicated by lowercase letters; capital letters indicate differences among genotypes with sex pooled.

aOff-leaf sex × genotype interactions were unable to be analyzed statistically due to low numbers of replicates (n = 20 out of 181).

**Table 6.** Wald’s χ2 tests comparing psyllid oviposition and fertility among four genotypes: A07781-10LB, A07781-3LB, A07781-4LB and Russet Burbank.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
|  | Total Eggs | | |  | Egg Fertility | | |
| Factors | χ2 | df | Pr > χ2 |  | χ2 | df | Pr > χ2 |
| Genotype | 0.84 | 3 | 0.840 |  | 0.21 | 3 | 0.976 |
| Time Period | 70.23 | 3 |  |  | 25.60 | 3 |  |
| Genotype × Time Period | 51.00 | 9 |  |  | 81.93 | 9 |  |

**Table 7.** Mean ± SEM (A) total eggs laid and (B) egg fertility of psyllids on four different genotypes.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| A. Total Eggs |  |  |  |  |  |
| Genotype | N | Period 1a | Period 2 | Period 3 | Period 4 |
| A07781-10LB | 20 | 6.3 ± 1.5 | 7.0 ± 1.7 | 9.4 ± 2.3 | 3.8 ± 1.0 |
| A07781-3LB | 13 | 4.8 ± 1.4 | 9.5 ± 2.8 | 9.1 ± 2.7 | 4.3 ± 1.3 |
| A07781-4LB | 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 |
| Overall | 66 | 6.2 ± 0.8 | 8.5 ± 1.1 | 8.3 ± 1.1 | 5.2 ± 0.7 |
|  |  |  |  |  |  |
| B. Percent Fertility |  |  |  |  |  |
| Genotype | N | Period 1 | Period 2 | Period 3 | Period 4 |
| A07781-10LB | 20 | 68.8 ± 9.2 | 59.5 ± 10.9 | 61.8 ± 10.7 | 3.2 ± 2.0 a |
| A07781-3LB | 13 | 65.9 ± 12.8 | 61.0 ± 12.6 | 55.7 ± 13.3 | 11.9 ± 6.8 ab |
| A07781-4LB | 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 |
| Overall | 66 | 61.3 ± 5.9 A | 58.9 ± 5.9 AB | 57.8 ± 6.1 AB | 20.3 ± 4.7 B |

Means for individual genotypes within a time period that share a letter or overall means within a row that share a letter are not significantly different (P > 0.05).

aPeriod 1 (the mating access period) comprised of six or eight days, during which a female + male pair of psyllids was held on a caged plant. At the end of Period 1, the male was removed and the remaining female was transferred to a new plant of the same genotype over three successive four-day time periods (Periods 2-4, 18-20 days total).

Figure captions

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

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

Fig. 1



Fig. 2



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