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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, comparado a hembras puestas en papas de la variedad Russet Burbank. Estos resultados sugieren que, aunque los genotipos evaluados muestran una actividad abiótica menor en la fertilidad del psílido de papa, esta putativa resistencia al no se debe a la reducción de los

52 comportamientos de alimentación del psílido, sino que puede estar más fuertemente
53 relacionada con la resistencia al patógeno.

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

55

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 α-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,

122 walking and time spent on the leaf can help us understand if a plant-induced change in
123 psyllid behavior is part of why we observed any reduction in Lso transmission and/or ZC
124 symptoms. Our results will help to clarify potato-psyllid interactions on these genotypes,
125 which will help plant breeders to develop Lso-resistant potatoes (Kennedy et al. 1987).

126 **Materials and Methods**

127 **Experimental insects**

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

134 **Experimental plants**

135 Potato clones were provided by the USDA-ARS, Small Grains and Potato Germplasm
136 Research Unit Aberdeen, ID, USA. The selected potatoes were grown in cages in the same
137 greenhouse as described above (25-32°C, 32% RH, 16:8 (L:D)). We used three sibling
138 clones derived from *Solanum chacoense* Bitter with putative relative resistance and/or
139 tolerance to Lso: A07781-3LB, A07781-4LB and A07781-10LB (Rashidi et al. 2017). Russet
140 Burbank was used as control because it is susceptible to Lso (Munyaneza et al. 2011) and
141 because of its prevalence in potato production in the Pacific Northwest (NASS Northwest
142 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 °C. 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

208 were replaced with each new plant and washed and dried at 90°C before reuse to prevent
209 potential volatile accumulation. Recordings were done with a L3CMOS C-mount USB
210 camera and ToupView recording software (L3CMOS14000KPA, Hangzhou ToupTek
211 Photonics Co., Ltd, Hangzhou, Zhejiang, China).

212 **No-Choice Behavior Assays**

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

223 **Oviposition Assays**

224 Oviposition assays were conducted with the same greenhouse conditions, plants and
225 insects as previously described. A female + male pair of recently emerged (teneral) psyllids,
226 identified by their green body color, was introduced to a plant covered with an insect
227 rearing sleeve (MegaView Science Co., Ltd., Taiwan). These rearing sleeves were supported
228 over the plant using two lengths of galvanized steel wire with a diameter of 1.63 mm. Each
229 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 χ^2 tests, followed by least-squares means with Tukey's HSD adjustments to test for multiple comparisons. Statistical significance was considered at $\alpha = 0.05$.

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).

293 **Oviposition Assays**

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

306 **Discussion**

307 It is difficult to separate the mechanisms of host plant resistance or tolerance and how
308 these correlate with psyllid host acceptance (Diaz-Montano et al. 2006, Butler et al. 2011).
309 Our visual observations of settling behavior lack the precision of electrical penetration
310 recordings used in similar studies (Butler et al. 2012, Sandanayaka et al. 2014, Mustafa et
311 al. 2015), but require less expensive equipment. Our results are similar to those of other
312 investigations of putatively resistant potato genotypes. Our analysis of the video recordings
313 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

337 and settling (Davis et al. 2012) – a behavior which has been seen in other insect-plant-
338 vector relationships (Cao et al. 2016, Eigenbrode et al. 2018). In the present study it may be
339 that this phenomenon encouraged greater acceptance of genotypes that would be rejected
340 by an uninfected psyllid. A high percentage of the psyllids in our colony were infected and
341 our plants were all uninfected, so psyllid infection may not entirely explain the patterns we
342 observed. Infection status also would not explain the minor trend we saw between male
343 and female probing on Russet Burbank.

344 Another possible explanation for differences between genotypes is that the female psyllids
345 are more influenced by familiar cues while selecting host plants for oviposition or feeding
346 (Prager et al. 2014). Russet Burbank was one of the plants used to rear our colonies, so it is
347 possible that the volatiles from this genotype were more stimulating for female psyllids.
348 Further studies into potato psyllid's attraction to plant volatiles while Lso positive and Lso
349 negative can help clarify if these possible explanations correlate with host plant
350 acceptance.

351 Although leaf-leaving duration differed significantly among genotypes, the incidence and
352 duration of leaf-leaving behaviors was very small and probably not biologically significant.
353 It is also important to note that leaf-leaving was defined in the context of leaving the leaf in
354 our small observation arena. On a plant in the field there is a much larger surface area for a
355 psyllid to explore, so the leaf-leaving events might represent questing behavior rather than
356 host rejection. It also is possible that the duration between a psyllid's initial encounter and
357 settling behaviors or eventual plant rejection is longer than the time we allotted for
358 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

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738 **Table 1.** Wald's χ^2 tests comparing psyllid behaviors between sexes and among four
739 genotypes: A07781-10LB, A07781-3LB, A07781-4LB and Russet Burbank.

Behavior	Factors		Incidence		Duration	
		df	χ^2	Pr > χ^2	χ^2	Pr > χ^2
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 [a]	Genotype	3	1.15	0.765	2.23	0.023*
	Sex	1	0.71	0.401	0.48	0.832
	Genotype × Sex	3	—	—	—	—

740 [a]The interaction genotype × sex was unable to be analyzed due to the low number of
741 psyllids that left the leaf (n = 20 out of 181)

742 **Table 2.** Least-square mean ± SEM incidence and duration of potato psyllid probing
743 behaviors recorded during 300-s no-choice tests on four different genotypes: A07781-
744 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

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

747

748 **Table 3.** Least-square mean ± SEM incidence and duration of potato psyllid walking
749 behaviors recorded during 300-s no-choice tests on four different genotypes: A07781-
750 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

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

754

755 **Table 4.** Least-square mean ± SEM incidence and duration of potato psyllid cleaning
756 behaviors recorded during 300-s no-choice tests on four different genotypes: A07781-
757 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

758

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

Genotype[a]	Sex	N	Incidence	Duration (s)	
A07781-10LB	Female	21	0.03 ± 0.02	$1449.9 \pm 2934.1 \times 10^{-7}$	AB
	Male	25	0.05 ± 0.03	$1873.6 \pm 3716.9 \times 10^{-7}$	
A07781-3LB	Female	27	0.06 ± 0.03	$2229.5 \pm 4272.9 \times 10^{-7}$	B
	Male	21	0.09 ± 0.05	$2881.0 \pm 5700.0 \times 10^{-7}$	
A07781-4LB	Female	25	0.05 ± 0.04	$10.6 \pm 31.6 \times 10^{-7}$	A
	Male	18	0.08 ± 0.06	$13.7 \pm 41.6 \times 10^{-7}$	
Russet Burbank	Female	26	0.03 ± 0.02	$9.1 \pm 27.1 \times 10^{-7}$	A
	Male	18	0.05 ± 0.03	$11.7 \pm 35.7 \times 10^{-7}$	

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

765 [a]Off-leaf sex × genotype interactions were unable to be analyzed statistically due to low
766 numbers of replicates (n = 20 out of 181).

767

768 **Table 6.** Wald's χ^2 tests comparing psyllid oviposition and fertility among four genotypes:

769 A07781-10LB, A07781-3LB, A07781-4LB and Russet Burbank.

	Total Eggs			Egg Fertility		
Factors	χ^2	df	Pr > χ^2	χ^2	df	Pr > χ^2
Genotype	0.84	3	0.840	0.21	3	0.976
Time Period	70.23	3	0.000	25.60	3	0.000
Genotype × Time Period	51.00	9	0.000	81.93	9	0.000

770

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

A. Total Eggs

Genotype	N	Period 1[a]	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

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

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

779

780

781 Figure captions

782

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

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

785

786 Fig. 1

787

788

789 Fig. 2

790

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

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