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

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Abstract The potato/tomato psyllid *Bactericera cockerelli* (Šulc) (Hemiptera: Triozidae) transmits "*Candidatus* Liberibacter solanacearum" (Lso), the causal agent of zebra chip disease (ZC) in potato. ZC creates large economic losses when disease incidence is high. No commercial potato variety has been found resistant to the pathogen or the disease symptoms. We observed host acceptance behaviors using no-choice assays on breeding clones derived from *Solanum chacoense* Bitter with putative resistance to Lso and/or ZC. We also compared oviposition and egg fertility for psyllids held on these genotypes. Probing frequency and female walking duration were highest on 'Russet Burbank,' suggesting greater activity on this variety than on the three resistant genotypes. The number of eggs did not differ among genotypes but declined on all genotypes during the last period of observation (18-20 days after confinement with a male). Egg fertility did not differ among genotypes for the first three observation periods (16-18 days after confinement with a male) but more eggs were fertile on Russet Burbank than on 10LB or 3LB during the last observation period (18-20 days after confinement with a male). We discuss the modality of resistance in context of these genotypes.

Key Words *Bactericera cockerelli*, Candidatus *Liberibacter solacearum*, behavior, host plant resistance

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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, 2009, 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) (Rhizobiaceae: Alphaproteobacteria) (Cicero et al. 2016, Goolsby et al. 2007, Munyaneza et al. 2007, Liefting et al. 2009). 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) (Hansen et al. 2008, Liefting et al. 2009, Lin et al. 2009, Crosslin et al. 2011). 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 (Secor and Rivera-Varas 2004, Munyaneza et al. 2009) 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, Murphy 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).

Current management of ZC 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, Adamczyk, et al. 2007, 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

89 emphasizes the need for alternative and improved pest management strategies such as
90 host plant resistance.

91 Host plant resistance is a valuable part of integrated pest management (Kogan 1988, Butler
92 and Trumble 2012a, Munyaneza 2012b, Diaz-Montano et al. 2013). Even a small amount of
93 resistance/tolerance of a plant to a vector or its pathogen can reduce damage below action
94 thresholds and reduce pesticide applications (Kennedy et al. 1987). Host plant resistance
95 increases pesticide efficiency and helps to delay insecticide resistance (Gharalari et al.
96 2009). Currently no commercial potato varieties have been found with acceptable
97 resistance to Lso (Munyaneza et al. 2011, Anderson et al. 2012).

98 Potatoes which have been bred with closely related plants such as *Solanum chacoense*
99 Bitter (Rashidi et al. 2017) and *Solanum berthaultii* Hawkes (Butler et al. 2011) have shown
100 less Lso infection and/or ZC symptoms than other genotypes tested. By determining how
101 these genotypes resist or tolerate either Lso or the psyllid vector itself (Kennedy et al.
102 1987, Putten et al. 2001, Butler et al. 2011), we can decide which traits should be bred or
103 cloned into commercial cultivars to develop resistant potato cultivars (Kaloshian 2004,
104 Casteel et al. 2006, 2007).

105 We examined psyllid host acceptance behaviors as well as oviposition and egg fertility on
106 three potato breeding clones derived from *Solanum chacoense*: 'A07781-10LB' ('10LB'),
107 'A07781-3LB', ('3LB') and 'A07781-4LB' ('4LB') (Rashidi et al. 2017). These genotypes
108 exhibit high tolerance and low susceptibility to Lso (Rashidi et al. 2017), possibly due to
109 resistance or tolerance to the psyllid vector. Russet Burbank was used as a susceptible
110 control (Munyaneza et al. 2011). Our results will help clarify potato psyllid interactions on
111 these genotypes, which will help plant breeders to develop Lso-resistant potatoes
112 (Kennedy et al. 1987).

113 **Materials and Methods**

114 **Plant Characteristics and Living Conditions**

115 Potato clones were provided by the USDA-ARS, Small Grains and Potato Germplasm
116 Research Unit Aberdeen, ID, USA. We used three sibling clones derived from *Solanum*
117 *chacoense* Bitter with putative tolerance/resistance to Lso: A07781-3LB, A07781-4LB, and
118 A07781-10LB (Rashidi et al. 2017). 'Russet Burbank' was used because it is susceptible to
119 Lso (Munyaneza et al. 2011) and because of its large impact on potato production in the
120 Pacific Northwest (NASS Northwest Regional Field Office 2017). The selected potatoes
121 were grown in a greenhouse maintained between 25-32°C, 32% RH, with a photoperiod of
122 16:8 (L:D). Plants were grown in pots of approximately 8.5 cm length × 8.5 cm width × 9.5
123 cm height, with a soil mixed in ratios of 4:4:4:1 peat moss: compost: coconut coir: perlite.
124 Fertilizer was not used on experimental plants to avoid nitrogen increases which may alter
125 insect feeding behaviors (Pfeiffer and Burts 1983, 1984). We used plants in their vegetative
126 growth stage (growth stage II) (Dwelle et al. 2003).

Insect Characteristics and Living Conditions

140 A Lso-positive potato psyllid colony was reared in the same greenhouse conditions as
141 described above to avoid phenological asynchrony (Hodkinson et al. 2015). Psyllids were
142 allowed free access to both Russet Burbank potatoes and 'Yellow Pear' tomatoes (*Solanum*
143 *lycopersicum* L.). Colony plants were fertilized once weekly with approximately 17 g of
144 24:8:16 NPK fertilizer per gallon of water (MiracleGro All Purpose Plant Food, Scotts
145 Company, Marysville, OH). Plants were replaced as needed.

Lso Detection

147 Idaho harbors four haplotypes of the potato psyllid: Northwestern, Western, Central and
148 Southwestern and two haplotypes of Lso: Lso A and Lso B (Dahan et al. 2017, Wenninger et
149 al. 2017). Our lab colony was determined to be comprised of 'Central' psyllids infected with
150 Lso 'B' via the methods described in Swisher and Crosslin (2014 a). A sample of forty
151 psyllids taken from the colony were transferred to individual microcentrifuge tubes filled
152 with 70% ethanol. Lso incidence was tested at the Aberdeen Research and Extension
153 Center (Aberdeen, ID, USA). DNA extraction was based on the methods described by
154 Marzachi et al. (1998). Individual psyllids were ground by a homogenizer (Omni
155 International Inc., Kennesaw, GA), macerating each psyllid for 1 minute at high speed and
156 an additional minute at medium speed in 500 of Cetyl Trimethylammonium Bromide 2%
157 (Alpha Teknova, Inc., Hollister, CA, Cat. No. C2190) (Composition: 2% CTAB, 100mM Tris-
158 HCl, pH 8.0, 20mM EDTA, pH 8.0, 1.4M Sodium Chloride (NaCl). Microcentrifuge tubes were
159 then incubated at 60 for 30 minutes and gently mixed by inversion every 10 minutes while
160 incubating. Tubes were then spun in a centrifuge at 14,000 rpm for 5 minutes and then the
161 supernatant was transferred to clean 2 ml tubes. The supernatant was vortexed for
162 approximately 20 seconds with 500 ml of chloroform:isoamyl alcohol (24:1 v:v) (Sigma-
163 Aldrich, Inc., Atlanta, GA: Catalogue number C0549), then centrifuged at 14,000 rpm for 5-
164 10 minutes at 4. The clean supernatant was transferred to a new tube, then refrigerated
165 isopropanol (Sigma-Aldrich, Inc., Atlanta, GA: Catalogue number I9516) was added at a rate
166 of 2/3 of the volume of the supernatant. The mixture was then refrigerated at -20 for 20-30
167 minutes. DNA was precipitated by centrifuging the mixture for 20 minutes at 14,000 rpm at
168 4, gently pouring off the supernatant and keeping the precipitated DNA pellet. The pellet
169 was washed in 300 of 70% ethanol and centrifuged for 5 mins at 10,000 rpm. The pellet
170 was then dried overnight in a fume hood. Once dry, 30 of nuclease-free water was added.
171 DNA was stored at -20.

172 Extracted DNA samples were then processed using a Sybgreen method. SsoAdvanced
173 Universal SYBR Green Supermix (Biorad, Hercules, CA) was mixed in a CFX Connect Real-
174 Time PCR Detection System (Biorad, Hercules, CA). HLBr (5'-GCG TTA TCC CGT AGA AAA
175 AGG TAG-3') and LsoF (5'-GTC GAG CGC TTA TTT TTA ATA GGA-3') were used as primers
176 (Li et al. 2006, 2009) and 10 of Sybgreen supermix was added to 150 nM of each primer
177 with 1 of DNA template. The program cycle was as follows: one cycle at 98 for 2 mins
178 followed by 40 cycles of 95 for 10 sec and 62 for 20 sec. The melt curve was 65 to 95, with
179 increments of 0.5 sec^{-1}. DNA of a healthy tuber was used as a negative control. DNA of a
180 Lso-infected tuber was used as a positive control and water was used as a no-template
181 control in all tests. pIDTSmart Kan (Synthetic Genomics, SGI-DNA, CA) with a 250 bp region

182 was amplified with the primer HLBr. The plasmid was diluted 10-fold and used with the
183 following dilutions: 1×10^{-2}, 1×10^{-3}, 1×10^{-4}, 1×10^{-6}, 1×10^{-7}, and 1×10^{-8} ng. Pathogen
184 quantity was reported as copy number of Lso, copy numbers were determined using the
185 methods of (Levy et al. 2011).

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

No-Choice Behavior Assays

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

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

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

Oviposition Assays

221 Oviposition assays were conducted with greenhouse conditions, plants, and insects as
222 previously described. A female/male pair of teneral psyllids (identified by their green body

223 color) was introduced to a plant covered with an insect rearing sleeve (MegaView Science
224 Co., Ltd., Taiwan). Rearing sleeves were supported over the plant using two lengths of
225 galvanized steel wire with a diameter of 1.63 mm. Each wire was curved into a parabolic
226 shape and each end of the wire was inserted into the soil on opposite corners of the plant
227 pot (*Fig. 2*). Plants were blocked by germplasm accession in rows of four and placed inside
228 60 cm length × 60 cm width × 60 cm height mesh-covered PVC-framed cages. Plants were
229 watered on alternating days by soaking pots in 56 cm length × 28 cm width × 6 cm height
230 plastic trays until the soil became saturated (approximately 45 mins). After a period of six
231 to eight days the males were removed from the plants and the female transferred to a new
232 plant of the same accession. The female psyllid was then transferred to a new plant every
233 four days at three intervals. Eggs were counted on each plant after the female was
234 removed. Nymphs were counted four days, eight days and twelve days later to allow time
235 for hatching (Knowlton and Janes 1931). Each nymph was removed as it was counted. The
236 number of nymphs that hatched was considered an indicator of egg fertility. Fertility
237 percentages were calculated as the ratio of nymphs divided by egg counts for each sample.

238 **Statistical Analysis**

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

255

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

257
258   **Fig. 2.** Sleeve cage with potato used in oviposition assays

Results

No-Choice Assays

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

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

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

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

Oviposition Assays

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

299   tended to decline during the last observation period for all genotypes except for Russet
300   Burbank (*Table 7*).

301   **Discussion**

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

324   Studies on the Asian citrus psyllid, *Diaphorina citri* Kuwayama (Hemiptera: Liviidae), a
325   vector of a similar liberibacter pathogen (Teixeira et al. 2005) have examined how host
326   plant volatiles can alter psyllid behaviors (Wenninger et al. 2009, Davidson et al. 2014).
327   Plant volatiles can induce probing in combination to visual and chemical cues from host
328   plants (Patt et al. 2011).

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

338   Another explanation for differences between genotypes is that the female psyllids are more
339   influenced by familiar cues while selecting host plants for oviposition or feeding (Prager et

340 al. 2014). Russet Burbank was one of the plants used to rear our colonies, so it is possible
341 that the volatiles from this variety were more stimulating for female psyllids. Further
342 studies into potato psyllid's attraction to plant volatiles while infected can help clarify if
343 these possible explanations correlate with host plant acceptance.

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

352 Contrary to previously published studies (Butler et al. 2011, Diaz-Montano et al. 2013,
353 Cooper and Bamberg 2014, Rubio-Covarrubias et al. 2017) our study showed similar
354 oviposition rates among genotypes, consistent with results reported by (Prager et al.
355 2017). Other studies have found psyllids will oviposit on a variety of hosts (Diaz-Montano
356 et al. 2013, Thinakaran et al. 2015), even when it is not beneficial for their survival (Prager,
357 Lewis, et al. (2014) b). Psyllids oviposited on every type of potato offered, like observations
358 by Prager et al. (2017), giving little evidence of antixenosis.

359 We selected the number of days for our observations to correlate with the periods of
360 maximum oviposition reported in the life history tables of Abdullah (Knowlton and Janes
361 1931, 2008) and Yang et al. (2010, 2013). Therefore, it was surprising to see the large
362 reduction of egg fertility for some psyllids in period four (18-24 days). Fertility declined on
363 the resistant genotypes as opposed to the Russet Burbank variety, which suggests that
364 these genotypes may have antibiotic effects over time. Over the course of a growing season,
365 these reductions may have a cumulative effect on psyllid populations. Longer observation
366 periods could help to better quantify these effects.

367 It is possible that Lso infection status played a role in the fertility observed: Lso has been
368 reported to negatively impact female fertility (2012 a, Nachappa, Shapiro, et al. 2012, 2014,
369 Yao et al. 2016, Frias et al. 2018). The antibiotic effects we observed may have different
370 effects on uninfected psyllids.

371 We saw a large degree of variability in fertility for psyllids on all genotypes. We only
372 permitted male access to the female psyllids during the initial period to increase female
373 longevity by preventing possible harassment (Abdullah 2008, Wenninger and Hall 2008,
374 Arnqvist 2013). Abdullah (2008, and Yang and Liu 2009, and Yang et al. 2013) all kept
375 female and male psyllids together to freely mate for the duration their observations, which
376 may explain why they observed greater fertility than we did. It is possible that potato
377 psyllids may require multiple mates and/or multiple matings over time to maintain egg
378 fertility (Wenninger and Hall 2008, Arnqvist 2013). Knowlton and Janes (1931) reported
379 (with a limited number of observations) reductions in egg fertility over time after a single
380 mating. There also may be some variability in female reproductive output created by the
381 physiological interactions of male spermatophores, female spermathecae and/or

382   spermatodose (Marchini et al. 2011), which all influence how long females are able to
383   remain fertile (Qazi and Hogdal 2010, Schnakenberg et al. 2011, Wolfner 2011, Abe and
384   Kamimura 2015).

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

392

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

Behavior	Factors		Incidence		Duration	
		df	χ^2	$Pr > \chi^2$	χ^2	$Pr > \chi^2$
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 †	Genotype	3	1.15	0.765	2.23	0.023*
	Sex	1	0.71	0.401	0.48	0.832
	Genotype × Sex	3	—	—	—	—

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

398

408 Table 2. Least-square mean ± SEM incidence and duration of potato psyllid probing
409 behaviors recorded during 300-s no-choice tests on four different genotypes: A07781-
410 10LB, A07781-3LB, A07781-4LB and Russet Burbank

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

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

414

446 Table 3. Least-square mean ± SEM incidence and duration of potato psyllid walking
447 behaviors recorded during 300-s no-choice tests on four different genotypes: A07781-
448 10LB, A07781-3LB, A07781-4LB and Russet Burbank

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

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

452

477 Table 4. Least-square mean ± SEM incidence and duration of potato psyllid cleaning
478 behaviors recorded during 300-s no-choice tests on four different genotypes: A07781-
479 10LB, A07781-3LB, A07781-4LB and Russet Burbank

Genotype	Sex	N	Incidence	Duration (s)
10LB	Female	21	0.34 ± 0.15	0.008 ± 0.017
	Male	25	0.33 ± 0.13	0.023 ± 0.048
3LB	Female	27	0.13 ± 0.07	0.002 ± 0.003
	Male	21	0.20 ± 0.10	0.003 ± 0.005
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

480

494 Table 5. Least-square mean ± SEM incidence and duration of potato psyllids leaving the leaf
495 surface during 300-s no-choice tests on four different genotypes: A07781-10LB, A07781-
496 3LB, A07781-4LB and Russet Burbank

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

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

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

502

514 Table 6. Wald's χ^2 tests comparing psyllid oviposition and fertility among four genotypes:
515 A07781-10LB, A07781-3LB, A07781-4LB and Russet Burbank

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

516

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

A. Total Eggs

Genotype	N	Period 1[a]	Period 2	Period 3	Period 4
10LB	20	6.3 ± 1.5	7.0 ± 1.7	9.4 ± 2.3	3.8 ± 1.0
3LB	13	4.8 ± 1.4	9.5 ± 2.8	9.1 ± 2.7	4.3 ± 1.3
4LB	19	8.4 ± 2.0	10.5 ± 2.6	8.0 ± 2.0	6.9 ± 1.8
Russet Burbank	14	5.8 ± 1.7	7.6 ± 2.2	7.0 ± 2.0	6.6 ± 1.9
Overall	66	9.5 ± 1.6	12.5 ± 1.8	12.5 ± 2.0	8.2 ± 1.5

B. Percent Fertility

Genotype	N	Period 1	Period 2	Period 3	Period 4
10LB	20	68.8 ± 9.2	59.5 ± 10.9	61.8 ± 10.7	3.2 ± 2.0 a
3LB	13	65.9 ± 12.8	61.0 ± 12.6	55.7 ± 13.3	11.9 ± 6.8 ab
4LB	19	62.3 ± 10.5	64.1 ± 10.1	49.6 ± 12.2	29.2 ± 10.4 bc
Russet Burbank	14	47.0 ± 13.0	50.9 ± 12.7	63.9 ± 11.9	70.1 ± 10.9 c
Overall	66	66.8 ± 4.2 A	68.2 ± 4.0 AB	66.0 ± 5.5 AB	43.8 ± 6.2 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).

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

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