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Research

Potato Psyllid (Hemiptera: Triozidae) Behavior on Three Potato Genotypes With Tolerance to '*Candidatus* Liberibacter solanacearum'

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Abstract

The potato/tomato psyllid *Bactericera cockerelli* (Šulc) 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 totally resistant to the pathogen. We evaluated host acceptance behaviors using no-choice assays on three breeding clones derived from *Solanum chacoense* Bitter with putative tolerance to Lso and/or ZC as part of an effort to determine whether the disease tolerance 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 Lso-tolerant genotypes displayed reduced fertility 18–24 d 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, tolerance to Lso may be more strongly linked with plant tolerance to the pathogen rather than effects on host acceptance 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 tolerancia putativa a Lso y / o PM, nosotros quisimos investigar si tal tolerancia 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 tolerantes 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 tolerancia no

se debe a la reducción de los comportamientos de alimentación del psílido, sino que puede estar más fuertemente relacionada con la tolerancia al patógeno.

Key words: *Solanum tuberosum*, *Solanum chacoense*, host plant resistance, tomato psyllid

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 and to potato diseases in North America (Richards and Blood 1973). The geographical distribution of *B. cockerelli* ranges from southern Canada to Central America, throughout the Western United States, New Zealand, and Australia (EPPO 2013).

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 Lso (also known as '*Candidatus* Liberibacter psyllaurous') (Rhizobiaceae: Alphaproteobacteria) (Goolsby et al. 2007b, Hansen et al. 2008, Li et al. 2009, Liefting et al. 2009). Lso is an unculturable gram-negative α-proteobacterium (Liefting et al. 2009), 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 blacken when fried (Navarre et al. 2009, Alvarado et al. 2012, Buchman et al. 2012). The condition associated with these symptoms 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 or tolerance to control ZC.

Host plant resistance/tolerance 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 plant tolerance to a vector or its pathogen can reduce damage below action thresholds and consequently require fewer pesticide applications (Kennedy et al. 1987). Host plant resistance also increases the efficiency of pesticide use and helps to delay the development of insecticide resistance (Gharalari et al. 2009). Currently, no potato varieties have been found with total resistance to Lso (Munyaneza et al. 2011, Anderson et al. 2012), though some varieties exhibit varying degrees of tolerance to the pathogen (Levy et al. 2015, Rubio-Covarrubias et al. 2017, Say 2012, Wallis et al. 2015).

Some of these tolerant potato varieties have been bred with closely related solanaceous plants such as *Solanum chacoense* Bitter (Rashidi et al. 2017) and *Solanum berthaultii* Hawkes (Butler et al. 2011), thereby conferring the offspring with greater tolerance to Lso infection. These clones have been demonstrated to have lower Lso titer than other genotypes tested and exhibited less severe browning/blackening when scoring cut and fried tubers (Prager et al. 2013, Rashidi et al. 2017). By determining whether these tolerant genotypes resist or tolerate the psyllid vector itself, provide the plant additional protection from Lso infection in the field (Kennedy et al. 1987, Putten et al. 2001, Butler et al. 2011). Subsequently, breeders can identify and use these traits to improve these potato cultivars (Kaloshian 2004; Casteel et al. 2006, 2007).

The A07781 family of genotypes derived from *S. chacoense* exhibit high tolerance to Lso (Rashidi et al. 2017). However, these genotypes also had a high degree of variance for Lso transmission (7–58%) (Rashidi et al. 2017). This variance in transmission rate may be related to either resistance or tolerance to the psyllid vector in addition to the tolerance of Lso itself. Focusing on psyllid host selection behaviors (i.e., walking and time spent on the leaf), as well as feeding behaviors (probing), can help us understand if a plant-induced change in psyllid behavior is causing the observed reduction of Lso transmission. The purpose of our studies was to test if this tolerance of the A07781 genotypes is correlated with resistance to psyllid feeding/host acceptance behaviors. In order to quantify putative resistance to the psyllid, we examined psyllid host acceptance behaviors as well as oviposition and egg fertility on three potato breeding clones in the A07781 family: 'A07781-10LB' ('10LB'), 'A07781-3LB' ('3LB'), and 'A07781-4LB' ('4LB') (Rashidi et al. 2017). 'Russet Burbank' was used as a susceptible control. Our results will help to clarify potato plant-psyllid interactions on these genotypes, which will assist plant breeders to develop Lso-resistant/tolerant potatoes (Kennedy et al. 1987).

Materials and Methods

Experimental Insects

Lso-positive potato psyllid colonies of the 'Central' biotype (Swisher et al. 2012) were reared in PVC-framed cages (60 cm length × 60 cm width × 60 cm height) covered with econet mesh (U.S. Global Resources Inc., Florida, TX) with a mesh size sufficient to prevent psyllid escape and cross contamination. Psyllids were reared in a

cage that allowed free access to both Russet Burbank potatoes and 'Yellow Pear' tomatoes (*Solanum lycopersicum* L.). Colonies were kept in a greenhouse maintained between 25 and 32°C, 32% RH, with a photoperiod of 16:8 (L:D) h. 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.

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 psyllids of the 'Central' biotype infected with Lso 'B', verified via the methods described in Swisher and Crosslin (2014). The infection status of psyllids was verified from a subset of 40 psyllids of the 182 psyllids used for choice tests. All psyllids used in experiments were collected from a colony known to have a rate of near 100% Lso infection.

Lso incidence in the colonies used 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). Forty adult psyllids were collected from the positive colony and transferred to individual microcentrifuge tubes after choice tests were conducted. Microcentrifuge tubes were filled with 95% ethanol to preserve the psyllids prior to DNA extraction. Ethanol was removed completely from psyllids before DNA extraction. DNA extraction was based on the methods described by Marzachi et al. (1998).

Each of the 40 psyllids tested was positive for Lso, suggesting a 100% rate of infection for the colony.

Experimental Plants

Potato clones were provided by the USDA-ARS, Small Grains and Potato Germplasm Research Unit, Aberdeen, ID. The selected potatoes were grown in cages in the same greenhouse as described above (25–32°C, 32% RH, 16:8 (L:D) h). We used three sibling clones derived from *S. chacoense* Bitter with tolerance to Lso: A07781-3LB, A07781-4LB, and A07781-10LB (Rashidi et al. 2017). Russet Burbank was used as a 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 rectangular 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). All experiments used plants of a similar size in their vegetative growth stage (growth stage II) (Dwelle et al. 2003). There were no apparent morphological differences between genotypes and Russet Burbank plants.

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 sheet of diffusion material (Rosco Laboratories Inc., Stamford, CT). 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, United Kingdom) 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).

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

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 min from the time of collection from the colony. 181 behavior assays were conducted. For each experimental replicate, a single psyllid was introduced to the arena, and its behaviors recorded for 5 min. Leaves used for choice assays were stained and cleared using the methods of Backus et al. 1988 to reveal any salivary sheaths left from probing/feeding. Psyllid sex was determined, 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 for pathogen transmission and/or host selection (Prager et al. 2014a, b). These behaviors were scored using CowLog3 (Hänninen and Pastell 2009), which records behavioral incidences with timestamps from a 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 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 bottom-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 min).

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

The oviposition experiment used two different mating access durations: 6 d and 8 d. 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 initial mating access period, the females were transferred to a new plant of the same genotype every 4 d (designated Periods 2–4, 18–20 d total).

Eggs were counted on each plant after the female was removed using 10× headband magnifiers. Nymphs were counted 4 d, 8 d, and 12 d 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 a 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 a random factor. Model formula: Hatch Rate ~ Genotype * Period + (1 | Psyllid). All data were tested with Wald's chi-square tests, followed by least-squares means with Tukey's HSD adjustments to test for multiple comparisons. Statistical significance was considered at $\alpha = 0.05$. Psyllid mortality and loss were recorded and analyzed with contingency tables and chi-square tests.

Results

No-Choice Assays

Overall, psyllids spent more time engaged in probing behavior than in other activities recorded (Tables 2–4). The number of probing events observed was significantly different among genotypes (Tables 1 and 2). Psyllids probed more frequently on Russet Burbank than on A07781-10LB and A07781-3LB, which did not differ from each other (Table 2). 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).

Table 1. Wald's chi-square tests comparing psyllid behaviors between sexes and among four potato 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	—	—	—	—

*represents significantly different ($\alpha = 0.05$).

[a]The 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 potato genotypes: A07781-10LB, A07781-3LB, A07781-4LB, and 'Russet Burbank'

Genotype	Sex	Sample size	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 ($\alpha = 0.05$). Capital letters indicate differences among genotypes with sex pooled.

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 (Tables 1 and 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). Stained leaves did not reveal any salivary sheaths left from psyllids during choice tests.

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

Similar studies of psyllid feeding and acceptance behaviors (Butler et al. 2012, Sandanayaka et al. 2014, Mustafa et al. 2015) have traditionally relied on electrical penetration graphs (EPG) to record psyllid feeding and probing. Although EPG analysis allows for accurate interpretation of different stages of feeding, these tests require expensive equipment, delicate specimen manipulation, and skilled interpretation of waveform data, which results in a large time investment to replicate ratio. In contrast, scoring of video requires less expensive equipment, with the option to fast-forward during periods of limited activity and avoids interpretation of waveforms. This makes data processing possible by inexperienced technicians and reduces the time between tests. This allows for faster screening

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

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

Means in the same column that share a letter are not significantly different ($\alpha = 0.05$). 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 potato genotypes: A07781-10LB, A07781-3LB, A07781-4LB, and 'Russet Burbank'

Genotype	Sex	Sample size	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

Effects without significance letters are not significantly different ($\alpha = 0.05$) based on Wald's chi-square tests.

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 potato genotypes: A07781-10LB, A07781-3LB, A07781-4LB, and Russet 'Burbank'

Genotype[a]	Sex	Sample size	Incidence	Duration (s)	
A07781-10LB	Female	21	0.03 ± 0.02	$1{,}449.9 \pm 2{,}934.1 \times 10^{-7}$	AB
	Male	25	0.05 ± 0.03	$1{,}873.6 \pm 3{,}716.9 \times 10^{-7}$	
A07781-3LB	Female	27	0.06 ± 0.03	$2{,}229.5 \pm 4{,}272.9 \times 10^{-7}$	B
	Male	21	0.09 ± 0.05	$2{,}881.0 \pm 5{,}700.0 \times 10^{-7}$	
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	$11.7 \pm 35.7 \times 10^{-7}$	

Means in the same column that share a letter are not significantly different ($\alpha = 0.05$). Capital letters indicate differences among genotypes with sex pooled.
[a]Off-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 chi-square tests comparing psyllid oviposition and fertility among four potato genotypes: 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
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

of plant rejection by psyllids. Our analysis of the video recordings showed more probing and walking on Russet Burbank than on the tolerant 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 2 h to access the phloem and acquire Lso. In addition, clearing and staining the leaves using the methods of Backus et al. 1988 revealed no salivary sheaths in leaves where psyllid probing occurred. This suggests

Table 7. Mean ± SEM (A) total eggs laid and (B) egg fertility for psyllids on four different potato 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 ± 2.0a
A07781-3LB	13	65.9 ± 12.8	61.0 ± 12.6	55.7 ± 13.3	11.9 ± 6.8ab
A07781-4LB	19	62.3 ± 10.5	64.1 ± 10.1	49.6 ± 12.2	29.2 ± 10.4bc
Russet Burbank	14	47.0 ± 13.0	50.9 ± 12.7	63.9 ± 11.9	70.1 ± 10.9c
Overall	66	61.3 ± 5.9A	58.9 ± 5.9AB	57.8 ± 6.1AB	20.3 ± 4.7B

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 (the mating access period) comprised of 6 or 8 d, 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 4-d time periods (Periods 2–4, 18–20 d total).

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 (A. N. Fife, unpublished data), but cleared and stained leaves from overnight recordings revealed salivary sheaths near probing/feeding sites. 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 feeding 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 feeding/host acceptance behaviors 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 (estimated at 100%) of the psyllids in our colony were infected and our plants were grown from clean (putatively uninfected) seed pieces, 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. 2014a). 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 psyllid feeding/host acceptance 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 d from the mating period). Fertility declined on the tolerant 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 for reduced egg fertility of psyllids housed on these 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). 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. Diaphorina *citri* require multiple mates to remain fertile over time, otherwise they experience a decrease in fertility (Wenninger and Hall 2008). Potato psyllids may also need to mate multiple times to maintain egg fertility. 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. 2012), 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).

Psyllids exhibit host acceptance behaviors with greater frequency on their natal host plant when compared to a novel host (Prager et al. 2014a). The psyllids used in our experiments were selected at random from a colony that allowed free access to both Russet Burbank potatoes as well as Yellow Pear tomatoes. Familiarity with Russet Burbank potatoes may explain the higher number of probes seen, although the apparent differences between potato plant volatiles, physiology, and morphology are possibly minor. It is also possible that psyllids born on tomato exhibited fewer behaviors than psyllids born on potatoes, but this reduction should be evenly distributed among the different genotypes and varieties used and would be minimized by a large number of replicates per plant.

In conclusion, we found little evidence of host rejection or psyllid mortality with respect to psyllid feeding/host acceptance behaviors, but we saw a reduction in egg fertility on these genotypes 18–24 d after mating. Taken together, these results suggest that psyllid feeding/host acceptance behaviors likely play a minor role in the variance in Lso transmission for A07781 genotypes. Further work will be required to clarify the modality of tolerance to Lso in the A07781 genotypes.

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