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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Authorization to Submit Thesis

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Abstract

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

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Thank you.

Dedication

¿Qué sería del hombre, si todos los secretos decidieron revelarse?

—Hernando Guerra Tovar

For Liz, Violet and Fifes to come

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Chapter 1: Introduction

1.1 Research context

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 (Aguilar et al. 2013, Martin 2008, Knowlton and Thomas 1934, Liefting et al. 2008, Liefting et al. 2009 Wallis 1955).

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

Publications regarding the psyllid initially emerged from 1926-1928, due a condition affecting solanaceous plants known as 'psyllid yellows' (Eyer and Crawford 1933, Richards 1928, Richards and Blood 1973).

Potato psyllids have recently been identified as vectors of "*Candidatus* Liberibacter solanacearum" (Lso) (Rhizobiaceae; Alphaproteobacteria) (Cicero et al. 2016, Goolsby et al. 2007, Liefting at al. 2009, Munyaneza et al. 2007). Lso is an uncultured gram-negative α-proteobacterium (Liefting et al. 2009) that infects solanaceous plants. *Candidatus* Liberibacter solanacearum is transmitted to the plant's phloem by the psyllid's saliva while feeding (Cooper and Bamberg 2014).

Symptoms 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 which char and blacken when fried (Alvarado et al. 2012, Buchman et al. 2012, Navarre et al. 2009). This

condition is known as 'zebra chip' disease (ZC) (Crosslin et al. 2011, Hansen et al. 2008, Liefting et al. 2009, Lin et al. 2009). Zebra chip-affected tubers are unmarketable, which results in large economic losses for growers (Munyaneza et al. 2007, Rosson et al. 2006). 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 was 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 (Murphy et al. 2012, Crosslin et al. 2012). Since 2011, Lso and ZC have remained a continuing threat to potato production in the PNW and contribute substantively to production costs (Greenway 2014, Greenway and Rondon 2018, Guenthner et al. 2012, Wenninger et al. 2017).

Various pest management practices have been investigated for management of Lso and ZC. Psyllid management traditionally relies on insecticides (Echegaray and Rondon 2017), to manage vector populations, using chemicals such as abamectin, imidacloprid, spiromesifen, thiamethoxam and dinotefuran (Gharalari et al. 2009, Goolsby et al. 2007, Guenthner et al. 2012, Vega-Gutiérrez et al. 2008). Psyllid populations have the potential to develop resistance to common insecticides such as neonicotinoids and abamectin (Hernández-Bautista et al. 2013, Chávez et al. 2015 Liu and Trumble 2004, Prager et al. 2013).

Multiple pesticide applications also increase production costs (Greenway 2014, Guenthner et al. 2012). Around half of Eastern Idaho growers' insecticide expenditures were related to ZC control in 2018 (Greenway and Rondon 2018). The difficulty and large expense of psyllid control emphasizes the need for alternative and improved pest management strategies such as host plant resistance.

Host plant resistance is a valuable part of integrated pest management (Butler et

al. 2012, Diaz-Montano et al. 2013, Kogan 1988, Munyaneza 2012). Even a small amount of resistance or tolerance of a plant to a pathogen or a vector may help reduce damage below action thresholds and reduce pesticide applications (Kennedy et al. 1987). Host plant resistance also increases pesticide efficiency and helps to delay insecticide resistance (Gharalari et al. 2009). Currently, no commercial potato varieties have been found with acceptable resistance to Lso. (Anderson et al. 2012, Munyaneza et al. 2011).

Potatoes which have been bred with potato relatives 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. These plants have special traits which can be bred or cloned into commercial cultivars, conferring them the same resistance to the disease (Casteel et al. 2006, 2007, Kaloshian 2004). However, it remains unclear whether these genotypes are resistant or tolerant to Lso or to the psyllid vector (Butler et al. 2011, Putten et al. 2001, Kennedy et al. 1987).

In order to asses these genotypes for possible antibiosis and antixenosis against the psyllid vector, we examined psyllid probing, walking and cleaning behaviors as well as female oviposition and egg fertility on three potato breeding clones: 'A07781-10LB' ('10LB'), 'A07781-3LB', ('3LB') and 'A07781-4LB' ('4LB') (Rashidi et al. 2017). These genotypes were derived from a potato relative *Solanum chacoense* and exhibit high tolerance and low susceptibility to Lso (Rashidi et al. 2017). Russet Burbank was used as a susceptible control (Munyaneza et al. 2011). The results will help clarify the mechanisms of resistance found in these genotypes and help inform plant breeders in the development of Lso-resistant potatoes (Kennedy et al. 1987).

Chapter 2: Materials and methods

2.1 Plant characteristics and living conditions

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

2.2 Insect characteristics and living conditions

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

2.3 Lso Detection

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

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

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

2.4 No-choice behavior assays

No-choice assays were conducted in a climate-controlled room 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 (Figure 2.1a) was modeled after the design described by Liu et al. (2004), but modified to use leaflets of intact, potted plants like 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 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 in the center (28 mm diameter). The arena was held together with two clips. This arena was then suspended by a suction cup held by an adjustable burette clamp. We used leaves from the upper canopy of the plants. The filter paper was discarded between observations. The glass pane and foam were replaced with each new plant and washed and dried at 90°C before reuse to remove potential volatile accumulation. Recordings were done with a L3CMOS C-mount USB camera and ToupView recording software (L3CMOS14000KPA, Hangzhou ToupTek Photonics Co., Ltd, Hangzhou, Zhejiang, China).

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

2.5 Oviposition assays

Oviposition assays were conducted with greenhouse conditions, plants, and insects as previously described section 2.1 and section 2.2, above). A female/male pair of teneral psyllids (identified by their green body color) was introduced to a plant covered with an insect rearing sleeve (MegaView Science Co., Ltd., Taiwan). Rearing sleeves were supported over the plant using two lengths of galvanized steel wire with a diameter of 1.63 mm. Each wire was curved into a parabolic shape and each end of the wire was inserted into the soil on opposite corners of the plant pot (Figure 2.1b). Plants were blocked by germplasm accession in rows of four and placed inside 60 cm length × 60 cm width × 60 cm height mesh-covered PVC-framed cages. Plants were watered on alternating days by soaking pots in 56 cm length × 28 cm width × 6 cm height plastic trays until the soil became saturated (approximately 45 mins). After a period of six to eight days the males were removed from the plants and the female transferred to a new plant of the same accession. The female psyllid was then transferred to a new plant every four days at three intervals. Eggs were counted on each plant after the female was removed. Nymphs were counted four days, eight days and twelve days later to allow time for hatching (Knowlton and Janes 1931). Each nymph was removed as it was counted. The number of nymphs that hatched was considered an indicator of egg fertility. Fertility percentages were calculated as the ratio of nymphs divided by egg

counts for each sample.

2.6 Statistical Analysis

Statistical analysis was performed using R Version 3.5.1 (R Core Team 2013) Assumptions of normality were investigated 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 modeling techniques (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 germplasm accession, sex and the interaction of accession $\times$ sex. Psyllid replicate was treated as a random factor. The interaction of accession $\times$ sex was excluded from the off-leaf model to low occurrences (n = 20 out of 181 observations), which did not allow an interaction to be estimated by the model. Oviposition models had fixed factors of accession, period and accession $\times$ period. Psyllid replicate was considered the random factor. Egg fertility was modeled with accession and period as fixed factors and individual psyllids as the random factor. All data were tested with Wald's χ^2 tests, followed by least-squares means with Tukey's adjustments to test for multiple comparisons. Statistical significance was considered at $\alpha = 0.05$.

(a) No-choice arena used for behavioral recordings

(b) Sleeve cage with potato used in oviposition assays

Figure 2.1: Testing arena and sleeve cage

Chapter 3: Results

3.1 No-choice assays

The number of probing events observed was significantly different among genotypes (Table 5.1). Psyllids probed more frequently on Russet Burbank than on A07781-10LB and A07781-3LB, which did not differ between each other (Table 5.2); 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 5.2); however, the genotype × sex interaction was not significant (Table 5.1). Probing frequency did not was not affected by sex (Table 5.1). Overall, psyllids spent more time engaged in probing behavior than in the other activities recorded (Tables 5.2-5); however, probing duration did not differ among genotypes, between sexes or by their interaction (Table 5.1).

The number of walking events differed significantly among genotypes as well as by the interaction of genotype × sex (Table 5.1). Psyllids walked more on Russet Burbank than 10LB (Table 5.3). Female psyllids on Russet Burbank walked significantly more often than males and females on 10LB and females on 3LB (Table 5.3). 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 5.1). Female psyllids walked significantly longer on Russet Burbank than for all other genotype × sex combinations (Table 5.3).

Cleaning behaviors generally were uncommon and of short duration. The frequencies and durations of cleaning behaviors were not significantly different among genotypes, betweeen sexes, or in their interaction terms (Table 5.1, Table 5.4).

Off-leaf behaviors also tended to occur rarely. Frequency of off-leaf behaviors did not differ among genotypes, betweeen sexes or by their interaction (Table 5.1).

However, the duration of off-leaf behaviors differed significantly among genotypes (Table 5.1). 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 5.5). Off-leaf duration did not differ by sex (Table 5.1). 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).

3.2 Oviposition assays

Neither the number of eggs laid nor percent viable eggs differed significantly among genotypes (Table 5.6). However, both the number of eggs laid and egg fertility were significantly different by period and the interaction of genotype × period (Table 5.6). 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 5.7). 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 5.7). There were no significant differences among genotypes within periods 1-3 (Table 5.7). Overall oviposition (with genotype pooled) was significantly lower during period 4 than for the first (Table 5.7). Similarly, egg fertility (with genotype pooled) tended to decline during the last observation period for all genotype except for Russet Burbank (Table 5.7).

Chapter 4: Discussion

It is difficult to separate the mechanisms of host plant resistance or tolerance and how they to correlate with psyllid host acceptance (Diaz-Montano et al. 2006, Butler et al. 2011). Furthermore, visual observation of settling behavior lacks the precision of electrical penetration recordings used in similar studies (Butler et al. 2012, Mustafa et al. 2015, Sandanayaka et al. 2014). Nevertheless, the results presented here were comparable with similar investigations of putatively resistant potato genotypes. Our study found more probing and walking on Russet Burbank than on the putatively resistant genotypes, which is consistent with results reported by Butler et al. (2011) and Prager et al. (2014). However, in contrast to Butler et al. (2011), we found cleaning and leaf-leaving behaviors to be rare. Although Russet Burbank received more probes than two other genotypes, 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 recordings may be necessary to determine when probing becomes true feeding. Minimal overnight recordings revealed little activity besides apparent feeding on the genotype where they were placed (ANF, unpublished data). A single psyllid is enough to transmit Lso and the disease progresses independently of bacterial titer (Buchman et al. 2011, Rashed et al. 2012). Therefore, it is unlikely that we were observing phloem feeding that would result in pathogen transmission within the span of our short observation periods. These factors underscore that psyllid probing behavior would have to be nearly eliminated to truly reduce the risk of Lso transmission. We found no evidence for such reductions in probing behavior on these genotypes. A possible explanation for the higher probing and walking frequencies observed is that some phytoplasmas (including Lso) can alter psyllid attraction to leaf volatiles (Mayer et al. 2008) and affect settling behavior (Mas et al. 2014). The psyllids used in our experiment were taken from a Lso-positive colony with a high percentage of

infected psyllids. Lso-infected psyllids have increased 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). However, such phenomena likely do not fully explain the patterns observed here because all observations in our experiments featured likely Lso-positive psyllids on Lso-negative plants, regardless of genotype. Studies on the Asian citrus psyllid, *Diaphorina citri* Kuwayama (Hemiptera: Liviidae), a vector of other liberibacter pathogens (Teixeira et al. 2005) have examined how host plant volatiles can alter psyllid behavior (Davidson et al. 2014, Wenninger et al. 2009), including increased probing in response to visual and chemical cues from host plants (Patt et al. 2011). This is a possible explanation for the minor trend we saw with female psyllids probing more often than male psyllids. Given that Russet Burbank was the natal plant host from our colonies, it is possible that the volatiles from this variety were more stimulating, especially for female psyllids, which may be more influenced by familiar cues while selecting host plants for oviposition or feeding (Prager et al. 2014). Further studies into volatile attractiveness in potato psyllids would help to clarify how these results relate with host plant acceptance. Although leaf-leaving duration differed statistically significant 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 our observation arena. On a plant in the field there is a much larger surface area for a psyllid to explore, so the leaf-leaving events might represent questing behavior rather than host rejection. It also is possible that the duration between a psyllid's initial encounter and settling behaviors or eventual plant rejection is longer than the time we allotted for recording.

Contrary to previously published studies (Butler et al. 2011, Cooper and Bamberg 2014, Diaz-Montano et al. 2013, 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. 2014). Psyllids oviposited on every type of potato offered, similar to observations by Prager et al. (2017), giving little evidence of antixenosis.

We selected the number of days for our observations to correlate with the periods of maximum oviposition reported in the life history tables of Abdullah (2008), 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 may have a cumulative effect on psyllid populations. Longer observation periods could help to better quantify these effects.

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

We saw a large degree of variability in fertility for psyllids on all genotypes. We only permitted male access to the female psyllids during the initial period to increase female longevity by preventing possible harassment (Abdullah 2008, Arnqvist 2013, Wenninger and Hall 2008). Abdullah (2008) and 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 matings over time to maintain egg fertility (Arnqvist 2013, Wenninger and Hall 2008). 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 physiological interactions of male spermatophores, female spermathecae and/or spermatodose (Marchini et al. 2011) formation, which influence how long females are able to remain fertile (Abe and Kamimura 2015, Qazi

and Hogdal 2010, Schnakenberg et al. 2011, Wolfner 2011).

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

Chapter 5: Tables

Table 5.1: Wald's χ^2 tests comparing psyllid behaviors among four genotypes: A07781-10LB, A07781-3LB, A07781-4LB and Russet Burbank

Behavior	**Incidence**			**Duration**		
Factors	χ^2	df	Pr > χ^2	χ^2	df	Pr > χ^2
Probing						
Genotype	27.46	3	0.000*	2.51	3	0.473
Sex	3.24	1	0.072	0.00	1	0.959
Genotype × Sex	6.49	3	0.090	4.74	3	0.192
Walking						
Genotype	16.17	3	0.001*	4.66	3	0.199
Sex	1.65	1	0.200	0.036	1	0.850
Genotype × Sex	11.13	3	0.011*	10.73	3	0.013*
Cleaning						
Genotype	5.98	3	0.113	2.23	3	0.525
Sex	0.45	1	0.503	0.48	1	0.490
Genotype × Sex	0.33	3	0.955	0.09	3	0.993
Off-Leaf						
Genotype	1.15	3	0.765	2.23	3	0.023*
Sex	0.71	1	0.401	0.48	1	0.832
Genotype × Sex	—	—	—	—	—	—

* indicates values which are significant at P > 0.05

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

Table 5.2: Potato psyllid probing behaviors recorded during 300 s no-choice tests on four different genotypes: A07781-10LB, A07781-3LB, A07781-4LB and Russet Burbank

Probing		Incidence		Duration (s)
Genotype	N	Mean ± SEM		Mean ± SEM
10LB	21 ♀	1.40 ± 0.26	**A**	182.0 ± 28.2
	25 ♂	1.30 ± 0.23		242.0 ± 34.0
3LB	27 ♀	1.50 ± 0.24	**A**	248.0 ± 33.6
	21 ♂	1.40 ± 0.26		183.0 ± 28.2
4LB	25 ♀	1.70 ± 0.27	**AB**	244.0 ± 34.1
	18 ♂	1.90 ± 0.34		215.0 ± 35.6
Russet Burbank	26 ♀	3.40 ± 0.38	**B**	250.0 ± 34.4
	18 ♂	1.80 ± 0.32		285.0 ± 47.0

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

Table 5.3: Potato psyllid walking behaviors recorded during 300 s no-choice tests on four different genotypes: A07781-10LB, A07781-3LB, A07781-4LB and Russet Burbank

Walking		Incidence		Duration (s)
Genotype	N	Mean ± SEM		Mean ± SEM
10LB	21 ♀	0.70 ± 0.19 **a**	**A**	0.9 ± 0.8 **a**
	25 ♂	0.30 ± 0.12 **a**		0.6 ± 0.5 **a**
3LB	27 ♀	0.50 ± 0.15 **a**	**AB**	0.4 ± 0.4 **a**
	21 ♂	0.80 ± 0.21 **ab**		4.0 ± 3.3 **a**
4LB	25 ♀	0.90 ± 0.21 **ab**	**AB**	1.6 ± 1.3 **a**
	18 ♂	1.10 ± 0.28 **ab**		5.7 ± 5.0 **a**
Russet Burbank	26 ♀	1.80 ± 0.33 **b**	**B**	10.5 ± 7.5 **b**
	18 ♂	0.60 ± 0.20 **ab**		0.6 ± 0.6 **a**

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

Table 5.4: Potato psyllid cleaning behaviors recorded during 300 s no-choice tests on four different genotypes: A07781-10LB, A07781-3LB, A07781-4LB and Russet Burbank

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

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

Table 5.5: Potato psyllids leaving the leaf surface during 300 s no-choice tests on four different genotypes: A07781-10LB, A07781-3LB, A07781-4LB and Russet Burbank

Off-leaf‡		Incidence	Duration (s)	
Genotype	N	Mean ± SEM	Mean ± SEM	
10LB	21 ♀	0.03 ± 0.02	$1449.9 \pm 2934.1 \times 10^{-7}$	**AB**
	25 ♂	0.05 ± 0.03	$1873.6 \pm 3716.9 \times 10^{-7}$	
3LB	27 ♀	0.06 ± 0.03	$2229.5 \pm 4272.9 \times 10^{-7}$	**B**
	21 ♂	0.09 ± 0.05	$2881.0 \pm 5700.0 \times 10^{-7}$	
4LB	25 ♀	0.05 ± 0.04	$10.6 \pm 31.6 \times 10^{-7}$	**A**
	18 ♂	0.08 ± 0.06	$13.7 \pm 41.6 \times 10^{-7}$	
Russet Burbank	26 ♀	0.03 ± 0.02	$9.1 \pm 27.1 \times 10^{-7}$	**A**
	18 ♂	0.05 ± 0.03	$11.7 \pm 35.7 \times 10^{-7}$	

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

‡ Off-leaf interactions were unable to be analyzed statistically due to low numbers of replicates (n = 20 out of 181).

Table 5.6: Wald's χ^2 tests comparing psyllid oviposition among four genotypes: A07781-10LB, A07781-3LB, A07781-4LB and Russet Burbank

	Eggs Laid			**Egg fertility**		
Factors	χ^2	df	$\Pr > \chi^2$	χ^2	df	$\Pr > \chi^2$
Genotype	0.84	3	0.84	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*

Table 5.7: Mean (± SEM) Eggs laid and egg fertility of psyllids on four different genotypes. A mating pair of female and male psyllids were placed on a caged plant for six to eight days after which the male was removed. The remaining female was transferred every four days to a new plant of the same genotype until 12 more days had elapsed.

Eggs Laid	**N**	**Period 1**	**Period 2**	**Period 3**	**Period 4**
10LB	**20**	6.3 ± 1.5	7.0 ± 1.7	9.4 ± 2.3	3.8 ± 1.0
3LB	**13**	4.8 ± 1.4	9.5 ± 2.8	9.1 ± 2.7	4.3 ± 1.3
4LB	**19**	8.4 ± 2.0	10.5 ± 2.6	8.0 ± 2.0	6.9 ± 1.8
Russet Burbank	**14**	5.8 ± 1.7	7.6 ± 2.2	7.0 ± 2.0	6.6 ± 1.9
Overall†	**66**	9.5 ± 1.6	12.5 ± 1.8	12.5 ± 2.0	8.2 ± 1.5
Percent Fertile					
10LB		68.8 ± 9.2	59.5 ± 10.9	61.8 ± 10.7	3.2 ± 2.0 **a**
3LB		65.9 ± 12.8	61.0 ± 12.6	55.7 ± 13.3	11.9 ± 6.8 **ab**
4LB		62.3 ± 10.5	64.1 ± 10.1	49.6 ± 12.2	29.2 ± 10.4 **bc**
Russet Burbank		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**

† Letters represent differences among periods ($P > 0.05$)
Means in the same column which share a letter are not significantly different ($P > 0.05$)

Bibliography

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

Abe, J. and Y. Kamimura (Mar. 2015). "Sperm economy between female mating frequency and male ejaculate allocation." *The American Naturalist* 185.3, pp. 406–416. DOI: 10.1086/679586.

Aguilar, E., V. G. Sengoda, B. Bextine, K. F. McCue, and J. E. Munyaneza (Oct. 2013). "First report of "*Candidatus* Liberibacter solanacearum" on tobacco in Honduras." *Plant Disease* 97.10, pp. 1376–1376. DOI: 10.1094/pdis-04-13-0453-pdn.

Alvarado, V. Y., D. Odokonyero, O. Duncan, T. E. Mirkov, and H. B. Scholthof (May 2012). "Molecular and physiological properties associated with zebra complex disease in potatoes and Its relation with *Candidatus* Liberibacter contents in psyllid vectors." *PLoS ONE* 7.5, e37345. DOI: 10.1371/journal.pone.0037345.

Anderson, J. A. D., G. P. Walker, P. A. Alspach, M. Jeram, and P. J. Wright (Oct. 2012). "Assessment of susceptibility to zebra chip and *Bactericera cockerelli* of selected potato cultivars under different insecticide regimes in New Zealand." *Am. J. Potato Res.* 90.1, pp. 58–65. DOI: 10.1007/s12230-012-9276-x.

Arnqvist, G. (Nov. 2013). *Sexual Conflict*. Princeton University Press. 352 pp.

Bates, D., M. Mächler, B. Bolker, and S. Walker (2015). "Fitting linear mixed-effects models using lme4." *Journal of statistical software* 67.1. DOI: 10.18637/jss.v067.i01.

Buchman, J. L., T. W. Fisher, V. G. Sengoda, and J. E. Munyaneza (Mar. 2012). "Zebra chip progression: from inoculation of potato plants with Liberibacter to development of disease symptoms in tubers." *Am. J. Potato Res.* 89.2, pp. 159–168. DOI: 10.1007/s12230-012-9238-3.

Buchman, J. L., V. G. Sengoda, and J. E. Munyaneza (Oct. 2011). "Vector transmission efficiency of Liberibacter by *Bactericera cockerelli* (Hemiptera: Triozidae) in zebra chip potato disease: effects of psyllid life stage and inoculation access period." *J. Econ. Entomol.* 104.5, pp. 1486–1495. DOI: 10.1603/ec11123.

Butler, C. D., B. Gonzalez, K. L. Manjunath, R. F. Lee, R. G. Novy, J. C. Miller, and J. T. Trumble (Sept. 2011). "Behavioral responses of adult potato psyllid, *Bactericera cockerelli* (Hemiptera: Triozidae), to potato germplasm and transmission of *Candidatus* Liberibacter psyllaurous." *Crop Prot.* 30.9, pp. 1233–1238. DOI: 10.1016/j.cropro.2011.05.006.

Butler, C. D. and J. T. Trumble (Jan. 2012). "The potato psyllid, *Bactericera cockerelli* (Šulc) (Hemiptera: Triozidae): life history, relationship to plant diseases, and management strategies." *Terrestrial arthropod reviews* 5.2, pp. 87–111. DOI: 10.1163/187498312x634266.

Butler, C. D., G. P. Walker, and J. T. Trumble (Jan. 2012). "Feeding disruption of potato psyllid, *Bactericera cockerelli*, by imidacloprid as measured by electrical penetration graphs." *Entomol. Exp. Appl.* 142.3, pp. 247–257. DOI: 10.1111/j.1570-7458.2012.01219.x.

Cao, H., H. Liu, Z. Zhang, and T. Liu (Feb. 2016). "The green peach aphid *Myzus persicae* perform better on pre-infested chinese cabbage *Brassica pekinensis* by enhancing host plant nutritional quality." *Sci. Rep.* 6.1. DOI: 10.1038/srep21954.

Casteel, C. L., L. L. Walling, and T. D. Paine (Oct. 2006). "Behavior and biology of the tomato psyllid, *Bactericerca cockerelli*, in response to the Mi-1.2 gene." *Entomol. Exp. Appl.* 121.1, pp. 67–72. DOI: 10.1111/j.1570-8703.2006.00458.x.

Casteel, C. L., L. L. Walling, and T. D. Paine (Apr. 2007). "Effect of Mi-1.2 gene in natal host plants on behavior and biology of the tomato psyllid *Bactericerca cockerelli* (Sulc) (Hemiptera: Psyllidae)." *Journal of Entomological Science* 42.2, pp. 155–162. DOI: 10.18474/0749-8004-42.2.155.

Chávez, E. C., O. H. Bautista, J. L. Flores, L. A. Uribe, and Y. M. O. Fuentes (Sept. 2015). "Insecticide-resistance ratios of three populations of *Bactericera cockerelli*

(Hemiptera: Psylloidea: Triozidae) in regions of Northern Mexico." *Florida Entomologist* 98.3, pp. 950–953. DOI: 10.1653/024.098.0322.

Cicero, J. M., T. W. Fisher, and J. K. Brown (Feb. 2016). "Localization of '*Candidatus* Liberibacter solanacearum' and evidence for surface appendages in the potato psyllid vector." *Phytopathology* 106.2, pp. 142–154. DOI: 10.1094/phyto-04-15-0088-r.

Cooper, W. R. and J. B. Bamberg (Apr. 2014). "Variation in *Bactericera cockerelli* (Hemiptera: Triozidae) oviposition, survival, and development on *Solanum bulbocastanum* germplasm." *Am. J. Potato Res.* 91.5, pp. 532–537. DOI: 10.1007/s12230-014-9384-x.

Crosslin, J. M., H. Lin, and J. E. Munyaneza (June 2011). "Detection of '*Candidatus* Liberibacter solanacearum' in the potato psyllid, *Bactericera cockerelli* (Sulc), by conventional and real-time PCR." *Southwestern Entomologist* 36.2, pp. 125–135. DOI: 10.3958/059.036.0202.

Crosslin, J. M., N. Olsen, and P. Nolte (Mar. 2012). "First report of zebra chip disease and *Candidatus* Liberibacter solanacearum on potatoes in Idaho." *Plant Dis.* 96.3, pp. 453–453. DOI: 10.1094/pdis-10-11-0853.

Dahan, J., E. J. Wenninger, B. Thompson, S. Eid, N. Olsen, and A. V. Karasev (May 2017). "Relative abundance of potato psyllid haplotypes in southern Idaho potato fields during 2012 to 2015, and incidence of '*Candidatus* Liberibacter solanacearum' causing zebra chip disease." *Plant Dis.* 101.5, pp. 822–829. DOI: 10.1094/pdis-05-16-0668-re.

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

Davis, T. S., D. R. Horton, J. E. Munyaneza, and P. J. Landolt (Nov. 2012). "Experimental infection of plants with an herbivore-associated bacterial endosymbiont influences herbivore host selection behavior." *PLoS ONE* 7.11, e49330. DOI: 10.1371/journal.pone.0049330.

Delignette-Muller, M. L. and C. Dutang (2015). "fitdistrplus: an R package for fitting distributions." *Journal of Statistical Software* 64.4. DOI: 10.18637/jss.v064.i04.

Diaz-Montano, J., J. C. Reese, W. T. Schapaugh, and L. R. Campbell (Oct. 2006). "Characterization of antibiosis and antixenosis to the soybean aphid (Hemiptera: Aphididae) in several soybean genotypes." *J. Econ. Entomol.* 99.5, pp. 1884–1889. DOI: 10.1093/jee/99.5.1884.

Diaz-Montano, J., B. G. Vindiola, N. Drew, R. G. Novy, J. C. Miller, and J. T. Trumble (Dec. 2013). "Resistance of selected potato genotypes to the potato psyllid (Hemiptera: Triozidae)." *Am. J. Potato Res.* 91.4, pp. 363–367. DOI: 10.1007/s12230-013-9356-6.

Dwelle, R. B., J. M. Alvarez, P. Bain, C. R. Baird, E. J. Bechinski, W. H. Bohl, D. L. Corsini, C. V. Eberlein, L. L. Ewing, B. F. Finnigan, B. D. Geary, J. F. Guenthner, S. L. Hafez, P. J. S. Hutchinson, W. B. Jones, B. A. King, G. E. Kleinkopf, J. S. Miller, P. Nolte, R. Novy, N. Olsen, S. Palanisamy, P. E. Patterson, L. E. Sandvol, R. L. Stoltz, D. T. Westermann, and J. C. Whitmore (2003). "Potato production systems." In: The University of Idaho agricultural communications. Chap. 2, pp. 12–14. ISBN: 1-58803-001-6.

Echegaray, E. R. and S. I. Rondon (May 2017). "Incidence of *Bactericera cockerelli* (Hemiptera: Triozidae) under different pesticide regimes in the lower Columbia Basin." *J. Econ. Entomol.* 110.4, pp. 1639–1647. DOI: 10.1093/jee/tox135.

Eigenbrode, S. D., N. A. Bosque-Pérez, and T. S. Davis (Jan. 2018). "Insect-borne plant pathogens and their vectors: ecology, evolution, and complex interactions." *Annu. Rev. Entomol.* 63.1, pp. 169–191. DOI: 10.1146/annurev-ento-020117-043119.

Eyer, J. R. and R. F. Crawford (Aug. 1933). "Observations on the feeding habits of the potato psyllid (*Paratrioza cockerelli* Sulc.) and the pathological history of the "psyllid yellows" which it produces." *J. Econ. Entomol.* 26.4, pp. 846–850. DOI: 10.1093/jee/26.4.846.

Frias, A. A. T., F. Ibanez, A. Mendoza, W. M. de Carvalho Nunes, and C. Tamborindeguy (June 2018). "Effects of "*Candidatus* Liberibacter solanacearum" (haplotype b) on *Bactericera cockerelli* fitness and vitellogenesis." *Insect Science*. DOI: 10.1111/1744-7917.12599.

Gharalari, A. H., C. Nansen, D. S. Lawson, J. Gilley, J. E. Munyaneza, and K. Vaughn (June 2009). "Knockdown mortality, repellency, and residual effects of insecticides for control of adult *Bactericera cockerelli* (Hemiptera: Psyllidae)." *J. Econ. Entomol.* 102.3, pp. 1032–1038. DOI: 10.1603/029.102.0322.

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

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

Greenway, G. (July 2014). "Economic impact of zebra chip control costs on grower returns in seven US states." *Am. J. Potato Res.* 91.6, pp. 714–719. DOI: 10.1007/s12230-014-9404-x.

Greenway, G. A. and S. Rondon (Jan. 2018). "Economic impacts of zebra chip in Idaho, Oregon, and Washington." *Am. J. Potato Res.* DOI: 10.1007/s12230-018-9636-2.

Guenthner, J., J. Goolsby, and G. Greenway (Sept. 2012). "Use and cost of insecticides to control potato psyllids and zebra chip on potatoes." *Southwestern Entomologist* 37.3, pp. 263–270. DOI: 10.3958/059.037.0302.

Hänninen, L. and M. Pastell (May 2009). "CowLog: Open-source software for coding behaviors from digital video." *Behav. Res. Methods* 41.2, pp. 472–476. DOI: 10.3758/brm.41.2.472.

Hansen, A. K., J. T. Trumble, R. Stouthamer, and T. D. Paine (Aug. 2008). "A new huanglongbing species, "*Candidatus* Liberibacter psyllaurous," found to infect tomato

and potato, is vectored by the psyllid (Bactericera cockerelli) (Sulc)." *Appl. Environ. Microbiol.* 74.18, pp. 5862–5865. DOI: 10.1128/aem.01268-08.

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

Hodkinson, I. D., C. V. Achterberg, M. Ahola, M. Barták, V. Behan-Pelletier, J. M. Bird, K. Bøg, F. Brodo, P. N. Buhl, C. Dahl, R. H. L. Disney, K. Dittmar, A. Fjellberg, Ø. Gammelmo, M. Forshage, R. Gerecke, C. A. Gertsson, M. M. L. Haastriter, J. P. Haenni, O. E. Heie, J. M. Heraty, C. Hodgson, D. Horsfield, J. T. Huber, M. Jaschoff, F. Jensen, K. A. Johanson, R. Jussila, O. Karsholt, E. Krzeminska, V. I. Lantsov, P. Láska, C. Lindegaard, L. Lyneborg, O. Makarova, Y. M. Marusik, W. N. Mathis, L. Mazánek, V. Michelsen, T. Munk, W. L. Murphy, S. A. Nielsen, T. R. Nielsen, J. S. Noyes, P. Oosterbroek, A. L. Ozerov, T. Pape, J. D. Pinto, M. Pollet, E. Rindal, J. Rohácek, T. J. Simonsen, V. S. Smith, G. Söli, J. Starý, R. Z. Strassen, B. W. Svensson, L. Vilhelmsen, P. Vilkamaa, M. Wilson, and T. Zatwarnicki (2015). "Psyllidae (jumping plant-lice, psyllids)." In: *The Greenland entomofauna: an identification manual of insects, spiders and their allies (Fauna Entomologica Scandinavica)*. Brill Academic Pub. Chap. 10, p. 113. ISBN: 978-9004256408.

Kaloshian, I. (Dec. 2004). "Gene-for-gene disease resistance: bridging insect pest and pathogen defense." *J. Chem. Ecol.* 30.12, pp. 2419–2438. DOI: 10.1007/s10886-004-7943-1.

Kennedy, G. G., F. Gould, O. M. B. Deponti, and R. E. Stinner (Apr. 1987). "Ecological, agricultural, genetic, and commercial considerations in the deployment of insect-resistant germplasm." *Environ. Entomol.* 16.2, pp. 327–338. DOI: 10.1093/ee/16.2.327.

Klingler, J., R. Creasy, L. Gao, R. M. Nair, A. S. Calix, H. S. Jacob, O. R. Edwards, and K. B. Singh (Apr. 2005). "Aphid resistance in *Medicago truncatula* involves

antixenosis and phloem-specific, inducible antibiosis, and maps to a single locus flanked by NBS-LRR resistance gene analogs." *Plant Physiol.* 137.4, pp. 1445–1455. DOI: 10.1104/pp.104.051243.

Knowlton, G. F. and M. J. Janes (June 1931). "Studies on the biology of *Paratrioza cockerelli* (Sulc)." *Ann. Entomol. Soc. Am.* 24.2, pp. 283–292. DOI: 10.1093/aesa/24.2.283.

Knowlton, G. F. and W. L. Thomas (Apr. 1934). "Host plants of the potato psyllid." *J. Econ. Entomol.* 27.2, pp. 547–549. DOI: 10.1093/jee/27.2.547.

Kogan, M. (Nov. 1988). "Integrated pest management theory and practice." *Entomol. Exp. Appl.* 49.1-2, pp. 59–70. DOI: 10.1111/j.1570-7458.1988.tb02477.x.

Levy, J., A. Ravindran, D. Gross, C. Tamborindeguy, and E. Pierson (Nov. 2011). "Translocation of '*Candidatus* Liberibacter solanacearum', the zebra chip pathogen, in potato and tomato." *Phytopathology* 101.11, pp. 1285–1291. DOI: 10.1094/phyto-04-11-0121.

Li, W., J. A. Abad, R. D. French-Monar, R. J., A. Wen, N. C. Gudmestad, G. A. Secor, I. M. Lee, Y. Duan, and L. Levy (July 2009). "Multiplex real-time PCR for detection, identification and quantification of '*Candidatus* Liberibacter solanacearum' in potato plants with zebra chip." *J. Microbiol. Methods* 78.1, pp. 59–65. DOI: 10.1016/j.mimet.2009.04.009.

Li, W., J. S. Hartung, and L. Levy (July 2006). "Quantitative real-time PCR for detection and identification of *Candidatus* Liberibacter species associated with citrus huanglongbing." *J. Microbiol. Methods* 66.1, pp. 104–115. DOI: 10.1016/j.mimet.2005.10.018.

Liefting, L. W., L. I. Ward, J. B. Shiller, and G. R. G. Clover (Nov. 2008). "A new '*Candidatus* Liberibacter' species in *Solanum betaceum* (tamarillo) and *Physalis peruviana* (cape gooseberry) in New Zealand." *Plant Dis.* 92.11, pp. 1588–1588. DOI: 10.1094/pdis-92-11-1588b.

Liefting, L. W., B. S. Weir, S. R. Pennycook, and G. R. G. Clover (July 2009). "'*Candidatus* Liberibacter solanacearum', associated with plants in the family

Solanaceae." *Int. J. Syst. Evol. Microbiol.* 59.9, pp. 2274–2276. DOI: 10.1099/ijs.0.007377-0.

Lin, H., H. Doddapaneni, J. E. Munyaneza, E. L. Civerolo, V. G. Sengoda, J. L. Buchman, and D. C. Stenger (2009). "Molecular characterization and phylogenetic analysis of 16S rRNA from a new "*Candidatus* Liberibacter" strain associated with zebra chip disease of potato (*Solanum tuberosum* L.) and the potato psyllid (*Bactericera cockerelli* Sulc)." *Journal of plant pathology* 91.1, pp. 215–219.

Liu, D. and J. T. Trumble (June 2004). "Tomato psyllid behavioral responses to tomato plant lines and interactions of plant lines with insecticides." *J. Econ. Entomol.* 97.3, pp. 1078–1085. DOI: 10.1093/jee/97.3.1078.

Marchini, D., G. D. Bene, R. Viscuso, and R. Dallai (Oct. 2011). "Sperm storage by spermatodoses in the spermatheca of *Trioza alacris* (Flor, 1861) Hemiptera, Psylloidea, Triozidae: a structural and ultrastructural study." *J. Morphol.* 273.2, pp. 195–210. DOI: 10.1002/jmor.11017.

Martin, N. A. (2008). "Host plants of the potato/tomato psyllid: a cautionary tale." *The Weta* 35.1, pp. 12–16.

Marzachi, C., F. Beratti, and D. Bosco (Aug. 1998). "Direct PCR detection of phytoplasmas in experimentally infected insects." *Ann. Appl. Biol.* 133.1, pp. 45–54. DOI: 10.1111/j.1744-7348.1998.tb05801.x.

Mas, F., J. Vereijssen, and D. M. Suckling (Nov. 2014). "Influence of the pathogen *Candidatus* Liberibacter solanacearum on tomato host plant volatiles and psyllid vector settlement." *J. Chem. Ecol.* 40.11-12, pp. 1197–1202. DOI: 10.1007/s10886-014-0518-x.

Mayer, C. J., A. Vilcinskas, and J. Gross (July 2008). "Phytopathogen lures its insect vector by altering host plant odor." *J. Chem. Ecol.* 34.8, pp. 1045–1049. DOI: 10.1007/s10886-008-9516-1.

Munyaneza, J. E. (Aug. 2012). "Zebra chip disease of potato: biology, epidemiology, and management." *Am. J. Potato Res.* 89.5, pp. 329–350. DOI: 10.1007/s12230-012-9262-3.

Munyaneza, J. E., J. L. Buchman, V. G. Sengoda, T. W. Fisher, and C. C. Pearson (Sept. 2011). "Susceptibility of selected potato varieties to zebra chip potato disease." *Am. J. Potato Res.* 88.5, pp. 435–440. DOI: 10.1007/s12230-011-9209-0.

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

Munyaneza, J. E., J. M. Crosslin, and J. E. Upton (June 2007). "Association of *Bactericera cockerelli* (Homoptera: Psyllidae) with 'zebra chip,' a new potato disease in Southwestern United States and Mexico." *J. Econ. Entomol.* 100.3, pp. 656–663. DOI: 10.1603/0022-0493(2007)100[656:aobchp]2.0.co;2.

Munyaneza, J. E., V. G. Sengoda, J. M. Crosslin, G. D. la Rosa-Lozano, and A. Sanchez (May 2009). "First report of '*Candidatus* Liberibacter psyllaurous' in potato tubers with zebra chip disease in Mexico." *Plant Dis.* 93.5, pp. 552–552. DOI: 10.1094/pdis-93-5-0552a.

Murphy, A. F., S. I. Rondon, and A. S. Jensen (Dec. 2012). "First report of potato psyllids, *Bactericera cockerelli*, overwintering in the Pacific Northwest." *Am. J. Potato Res.* 90.3, pp. 294–296. DOI: 10.1007/s12230-012-9281-0.

Mustafa, T., D. R. Horton, W. R. Cooper, K. D. Swisher, R. S. Zack, H. R. Pappu, and J. E. Munyaneza (Sept. 2015). "Use of electrical penetration graph technology to examine transmission of '*Candidatus* Liberibacter solanacearum' to potato by three haplotypes of potato psyllid (*Bactericera cockerelli*; (Hemiptera: Triozidae)." *PLoS ONE* 10.9, e0138946. DOI: 10.1371/journal.pone.0138946.

Nachappa, P., J. Levy, and C. Tamborindeguy (Sept. 2012). "Transcriptome analyses of *Bactericera cockerelli* adults in response to "*Candidatus* Liberibacter solanacearum" infection." *Molecular genetics and genomics* 287.10, pp. 803–817. DOI: 10.1007/s00438-012-0713-9.

Nachappa, P., A. A. Shapiro, and C. Tamborindeguy (Jan. 2012). "Effect of '*Candidatus* Liberibacter solanacearum' on fitness of its insect vector, *Bactericera*

cockerelli (Hemiptera: Triozidae), on tomato." *Phytopathology* 102.1, pp. 41–46. DOI: 10.1094/phyto-03-11-0084.

Nachappa, P. J. Levy, E. Pierson, and C. Tamborindeguy (Jan. 2014). "Correlation between "*Candidatus* Liberibacter solanacearum" infection levels and fecundity in its psyllid vector." *J. Invertebr. Pathol.* 115, pp. 55–61. DOI: 10.1016/j.jip.2013.10.008.

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

Navarre, D. A., R. Shakya, J. Holden, and J. M. Crosslin (Jan. 2009). "LC-MS Analysis of phenolic compounds in tubers showing zebra chip symptoms." *Am. J. Potato Res.* 86.2, pp. 88–95. DOI: 10.1007/s12230-008-9060-0.

Patt, J. M., W. G. Meikle, A. Mafra-Neto, M. Sétamou, R. Mangan, C. Yang, N. Malik, and J. J. Adamczyk (Dec. 2011). "Multimodal cues drive host-plant assessment in asian citrus psyllid (*Diaphorina citri*)." *Environ. Entomol.* 40.6, pp. 1494–1502. DOI: 10.1603/en11149.

Pfeiffer, D. G. and E. C. Burts (June 1983). "Effect of tree fertilization on numbers and development of pear psylla (Homoptera: Psyllidae) and on fruit damage." *Environ. Entomol.* 12.3, pp. 895–901. DOI: 10.1093/ee/12.3.895.

Pfeiffer, D. G. and E. C. Burts (Dec. 1984). "Effect of tree fertilization on protein and free amino acid content and feeding rate of pear psylla (Homoptera: Psyllidae)." *Environ. Entomol.* 13.6, pp. 1487–1490. DOI: 10.1093/ee/13.6.1487.

Prager, S. M., I. Esquivel, and J. T. Trumble (Apr. 2014). "Factors influencing host plant choice and larval performance in *Bactericera cockerelli*." *PLoS ONE* 9.4, e94047. DOI: 10.1371/journal.pone.0094047.

Prager, S. M., O. M. Lewis, J. Michels, and C. Nansen (Apr. 2014). "The influence of maturity and variety of potato plants on oviposition and probing of *Bactericera cockerelli* (Hemiptera: Triozidae)." *Environ. Entomol.* 43.2, pp. 402–409. DOI: 10.1603/en13278.

Prager, S. M., B. Vindiola, G. S. Kund, F. J. Byrne, and J. T. Trumble (Dec. 2013). "Considerations for the use of neonicotinoid pesticides in management of *Bactericera cockerelli* (Šulk) (Hemiptera: Triozidae)." *Crop Prot.* 54, pp. 84–91. DOI: 10.1016/j.cropro.2013.08.001.

Prager, S. M., C. M. Wallis, M. Jones, R. Novy, and J. T. Trumble (Nov. 2017). "Examining the potential role of foliar chemistry in imparting potato germplasm tolerance to potato psyllid, green peach aphid, and zebra chip disease." *J. Econ. Entomol.* 111.1, pp. 327–336. DOI: 10.1093/jee/tox255.

Putten, W. H. V. der, L. E. M. Vet, J. A. Harvey, and F. L. Wäckers (Oct. 2001). "Linking above - and belowground multitrophic interactions of plants, herbivores, pathogens, and their antagonists." *Trends in Ecology & Evolution* 16.10, pp. 547–554. DOI: 10.1016/s0169-5347(01)02265-0.

Qazi, M. C. B. and L. Hogdal (Sept. 2010). "Hold on: females modulate sperm depletion from storage sites in the fly *Drosophila melanogaster*." *Journal of Insect Physiology* 56.9, pp. 1332–1340. DOI: 10.1016/j.jinsphys.2010.04.014.

R Core Team (2013). *R: a language and environment for statistical computing*. ISBN 3-900051-07-0. R foundation for statistical computing. Vienna, Austria. URL: http://www.R-project.org/.

Rashed, A., T. D. Nash, L. Paetzold, F. Workneh, and C. M. Rush (Nov. 2012). "Transmission efficiency of '*Candidatus* Liberibacter solanacearum' and potato zebra chip disease progress in relation to pathogen titer, vector numbers, and feeding sites." *Phytopathology* 102.11, pp. 1079–1085. DOI: 10.1094/phyto-04-12-0094-r.

Rashidi, M., R. G. Novy, C. M. Wallis, and A. Rashed (Aug. 2017). "Characterization of host plant resistance to zebra chip disease from species-derived potato genotypes and the identification of new sources of zebra chip resistance." *PLoS ONE* 12.8, e0183283. DOI: 10.1371/journal.pone.0183283.

Rehman, M., J. C. Melgar, C. J. M. Rivera, A. M. Idris, and J. K. Brown (Mar. 2010). "First report of "*Candidatus* liberibacter psyllaurous" or "*Ca.* liberibacter solanacearum" associated with severe foliar chlorosis, curling, and necrosis and tuber

discoloration of potato plants in Honduras." *Plant Dis.* 94.3, pp. 376–376. DOI: 10.1094/pdis-94-3-0376c.

Richards, B. L. (1928). "A new and destructive disease of the potato in Utah and its relation to the potato psylla." *Phytopathology* 18.1.

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

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

Rubio-Covarrubias, O. A., M. A. Cadena-Hinojosa, S. M. Prager, C. M. Wallis, and J. T. Trumble (Feb. 2017). "Characterization of the tolerance against zebra chip disease in tubers of advanced potato lines from Mexico." *Am. J. Potato Res.* 94.4, pp. 342–356. DOI: 10.1007/s12230-017-9570-8.

Sandanayaka, W. R. M., A. Moreno, L. K. Tooman, N. E. M. Page-Weir, and A. Fereres (Mar. 2014). "Stylet penetration activities linked to the acquisition and inoculation of *Candidatus* Liberibacter solanacearum by its vector tomato potato psyllid." *Entomol. Exp. Appl.* 151.2, pp. 170–181. DOI: 10.1111/eea.12179.

Schnakenberg, S. L., W. R. Matias, and M. L. Siegal (Nov. 2011). "Sperm-storage defects and live birth in *Drosophila* females lacking spermathecal secretory cells." *PLoS Biology* 9.11. DOI: 10.1371/journal.pbio.1001192.

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

Stroup, W. W. (2015). "Rethinking the analysis of non-normal data in plant and soil science." *Agron. J.* 107.2, p. 811. DOI: 10.2134/agronj2013.0342.

Šulc, K. (1909). "*Trioza cockerelli* n. sp., a novelty from North America, being also of economic importance." *Acta Societatis Entomologicae Bohemiae* 6, pp. 102–108.

Swisher, K. D. and J. M. Crosslin (Mar. 2014). "Restriction digestion method for haplotyping the potato psyllid, *Bactericera cockerelli*." *Southwestern Entomologist* 39.1, pp. 49–56. DOI: 10.3958/059.039.0106.

Teixeira, D. d. C., C. Saillard, S. Eveillard, J. L. Danet, P. I. da Costa, A. J. Ayres, and J. Brové (Sept. 2005). "'*Candidatus* Liberibacter americanus', associated with citrus huanglongbing (greening disease) in Sao Paulo State, Brazil." *Int. J. Syst. Evol. Microbiol.* 55.5, pp. 1857–1862. DOI: 10.1099/ijs.0.63677-0.

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

Thinakaran, J., E. A. Pierson, M. Longnecker, C. Tamborindeguy, J. E. Munyaneza, C. M. Rush, and D. C. Henne (Apr. 2015). "Settling and ovipositional behavior of *Bactericera cockerelli* (Hemiptera: Triozidae) on solanaceous hosts under field and laboratory conditions." *J. Econ. Entomol.* 108.3, pp. 904–916. DOI: 10.1093/jee/tov058.

Vega-Gutiérrez, M. T., J. C. Rodríguez-Maciel, O. Díaz-Gómez, R. Bujanos-Muñiz, D. Mota-Sánchez, J. L. Martínez-Carrillo, A. Lagunes-Tejeda, and J. A. Garzón-Tiznado (2008). "Susceptibility to insecticides in two Mexican population of tomato-potato psyllid, *Bactericera cockerelli* (Sulc.) (Hemiptera: Triozidae)." *Agrociencia* 42.4, pp. 463–471.

Wallis, R. L. (Feb. 1955). *Ecological studies on the potato psyllid as a pest of potatoes*. Tech. rep. U.S. Department of Agriculture.

Wenninger, E. J., A. Carroll, J. Dahan, A. V. Karasev, M. Thornton, J. Miller, P. Nolte, N. Olsen, and W. Price (Oct. 2017). "Phenology of the potato psyllid, *Bactericera cockerelli* (Hemiptera: Triozidae), and "*Candidatus* Liberibacter solanacearum" in commercial potato fields in Idaho." *Environ. Entomol.* 46.6, pp. 1179–1188. DOI: 10.1093/ee/nvx158.

Wenninger, E. J. and D. G. Hall (Dec. 2008). "Importance of multiple mating to female reproductive output in *Diaphorina citri*." *Physiol. Entomol.* 33.4, pp. 316–321. DOI: 10.1111/j.1365-3032.2008.00633.x.

Wenninger, E. J., L. L. Stelinski, and D. G. Hall (Feb. 2009). "Roles of olfactory cues, visual cues, and mating status in orientation of *Diaphorina citri* Kuwayama (Hemiptera: Psyllidae) to four different host plants." *Environ. Entomol.* 38.1, pp. 225–234. DOI: 10.1603/022.038.0128.

Wolfner, M. F. (Nov. 2011). "Precious essences: female secretions promote sperm storage in *Drosophila*." *PLoS Biology* 9.11. DOI: 10.1371/journal.pbio.1001191.

Yang, X. B. and T. X. Liu (Dec. 2009). "Life history and life tables of *Bactericera cockerelli* (Homoptera: Psyllidae) on eggplant and bell pepper." *Environ. Entomol.* 38.6, pp. 1661–1667. DOI: 10.1603/022.038.0619.

Yang, X. B., Y. M. Zhang, D. C. Henne, and T. X. Liu (Sept. 2013). "Life tables of *Bactericera cockerelli* (Hemiptera: Triozidae) on tomato under laboratory and field conditions in southern Texas." *Florida Entomologist* 96.3, pp. 904–913. DOI: 10.1653/024.096.0326.

Yang, X. B., Y. M. Zhang, L. Hua, and T. X. Liu (Oct. 2010). "Life history and life tables of *Bactericera cockerelli* (Hemiptera: Psyllidae) on potato under laboratory and field conditions in the Lower Rio Grande Valley of Texas." *J. Econ. Entomol.* 103.5, pp. 1729–1734. DOI: 10.1603/ec10083.

Yao, J., P. Saenkham, J. Levy, F. Ibanez, C. Noroy, A. Mendoza, O. Huot, D. F. Meyer, and C. Tamborindeguy (June 2016). "Interactions "*Candidatus* Liberibacter" solanacearum - *Bactericera cockerelli*: haplotype effect on vector fitness and gene expression analyses." *Frontiers in cellular and infection microbiology* 6. DOI: 10.3389/fcimb.2016.00062.