Variation in *Bactericera cockerelli* (Hemiptera: Triozidae) Oviposition, Survival, and Development on *Solanum bulbocastanum* Germplasm

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Abstract The potato psyllid, *Bactericera cockerelli*, is a key pest of potato and important vector of the pathogen that causes zebra chip disease. Control of zebra chip relies entirely on the use of insecticides to reduce populations of this vector. The development of potato varieties resistant to *B. cockerelli* would contribute to cost-effective control of this insect. Wild potato germplasm are key sources for desirable traits including pest resistance to develop new potato cultivars. Our objective was to screen *Solanum bulbocastanum* germplasm for resistance to *B. cockerelli*. The combined use of choice and no-choice assays demonstrated considerable variability among *S. bulbocastanum* populations in their susceptibility to psyllids. At least six *S. bulbocastanum* populations exhibited resistance to *B. cockerelli*: PI 243512, PI 243513, PI 255518, PI 275194, PI 275197, and PI 283096. The documentation of the variability among *S. bulbocastanum* germplasm populations in their susceptibility to *B. cockerelli* can aid the development of potato cultivars that are naturally resistant to the potato psyllid.

Resumen El psílido de la papa, *Bactericera cockerelli*, es una plaga clave de la papa y un vector importante del patógeno que causa la enfermedad del tubérculo rayado o "zebra chip". El control de esta enfermedad se confía completamente en el uso de insecticidas para reducir las poblaciones de este vector. El desarrollo de variedades de papa resistentes a *Bactericera cockerelli* contribuirá al control costeable de este insecto. El germoplasma silvestre de papa es una fuente clave para características deseables incluyendo resistencia a plagas para el desarrollo de nuevas variedades. Nuestro objetivo fue evaluar germoplasma de *Solanum bulbocastanum* para resistencia a *B. cockerelli*. El uso combinado de ensayos de selección y no selección demostró variabilidad considerable entre poblaciones de *S. bulbocastanum* en su susceptibilidad a los psílidos. Por lo menos seis poblaciones de *S. bulbocastanum* exhibieron resistencia a *B. cockerelli*: PI 243512, PI 243513, PI 255518, PI 275194, PI 275197, y PI 283096. La documentación de la variabilidad entre las poblaciones del germoplasma de *S. bulbocastanum* respecto a su susceptibilidad a *B. cockerelli* puede ayudar en el desarrollo de variedades de papa que son resistentes de forma natural al psílido de la papa.

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Introduction

The potato psyllid, *Bactericera cockerelli* (Šulc) (Hemiptera: Triozidae) is a key pest of Solanaceous crops (Solanales: Solanaceae) (Wallis 1955; Teulon et al. 2009; Munyaneza 2012). Feeding by this insect causes plant decline, decreased yields, and foliar symptoms known as 'psyllid yellows' (Richards 1933; Munyaneza 2012). Although *B. cockerelli* has long been considered a pest of Solanaceous crops, the pest-status of this insect recently increased after it was identified as the vector of a newly recognized bacterial plant pathogen, "*Candidatus* Liberibacter solanacearum" (aka "*Ca.* Liberibacter psyllaurous") (Munyaneza et al. 2007; Liefting et al. 2008, 2009; Secor et al. 2009; Teulon et al. 2009; Munyaneza 2012). Crop damage by "*Ca.* Liberibacter solanacearum" was first reported in the southern United States and northern Mexico in the mid-1990's, but the

pathogen has since spread to other potato growing regions of the western United States, Mexico, Central American, and New Zealand (Munyaneza 2012). This pathogen causes plant mortality and decreased yields in all Solanaceous crops, and is the causal agent of zebra chip disease of potato (Munyaneza 2012). Zebra chip disease is characterized by the development of striped patterns in tubers that render the potatoes unmarketable leading to millions of dollars in losses to potato growers in the United States (Munyaneza 2012).

Management programs for "Ca. Liberibacter solanacearum" rely solely on the use of insecticides to target the insect vector, potato psyllid (Butler and Trumble 2012). Management of this pathogen and vector is difficult even with the use of insecticides, and current research efforts seek to provide new management strategies (Munyaneza 2012). The development of potato varieties which exhibit resistance to the pathogen, vector, or both would provide cost-effective tools to reduce the risk of zebra chip disease. Efforts are reportedly underway to identify potato varieties with resistance or tolerance to "Ca. Liberibacter solanacearum," (Munyaneza 2012), and two studies have identified variation in host suitability to B. cockerelli among breeding clones (Butler et al. 2011; Diaz-Montano et al. 2013).

Wild potato germplasm provide sources of resistance to diseases and insects in the development of new crop cultivars (Plaisted and Hoopes 1989; Spooner and Bamberg 1994; Jansky 2000). Previous reports indicated that certain populations of wild potato germplasm exhibit resistance to aphids (Hemiptera: Aphididae), which have phloem-feeding strategies and behaviors similar to those of psyllids (Graham et al. 1959; Flanders et al. 1992, 1997; Park et al. 2005; van der Vossen et al. 2005; Le Roux et al. 2007; Pelletier et al. 2010; Davis et al. 2012). However, wild potatoes have not yet been screened for resistance to potato psyllids. The objective of our study was to compare the susceptibility to B. cockerelli among germplasm populations of the wild potato species, S. bulbocastanum Dun. We chose to screen S. bulbocastanum because the native range this potato species overlaps with that of B. cockerelli, increasing the probability that psyllid resistance has evolved in populations of S. bulbocastanum (Flanders et al. 1997; Walters 2011).

Materials and Methods

Plants and Insects

S. bulbocastanum germplasm (all 53 populations available in 2012) were obtained from the US Potato Genebank in Sturgeon Bay, WI. Full details on these populations are available at http://www.ars-grin.gov/npgs/acc/acc_queries.html under the specific Genebank sample code for each accession (Table 1). Experimental plants were grown from seed in either 450-cm^3 plastic pots for the choice screening assays, or in 900-cm^3 plastic pots for the no-choice performance assays. For both sets of experiments, plants were grown in soil consisting of a 1:2:2 ratio of pumice, sand, and peat mixed with Osmocoat slow-release fertilizer (Scotts Miracle-Gro Company, Marysville, OH). The plants were maintained in a greenhouse with supplemental lighting to provide a 16:8 (L:D) h photoperiod, and were fertilized once every 2 weeks with Miracle-Gro (Scotts Miracle-Gro Company). S. bulbocastanum plants of similar size were selected for assays about 3.5 months after sowing seeds. Four-week old 'Russet Burbank' potatoes grown from virus-free tubers were included in the performance assays as a general comparison between psyllid performance on S. bulbocastanum and S. tuberosum.

Potato psyllids were obtained from a laboratory colony maintained on 'Ranger Russett' potato and 'Moneymaker' tomato at 25 °C with a 16:8 (L:D) h photoperiod and ≈50 % relative humidity. The colony was originally established from psyllids (western haplotype) collected from fields of potato near Prosser, WA in the spring of 2012. Subsets of colony insects were routinely screened for the presence of "Ca. Liberibacter solanacearum" using PCR to ensure that the colony was maintained pathogen-free.

Choice Pre-Screening Assays

Table 1 provides a complete list of germplasm included in our pre-screening assays. Three populations were not included in our assays due to low numbers of usable plants at the start of the experiments. Fifty plants, one from each germplasm population, were placed into each of two dome cages. Each cage was infested with 100 adult potato psyllids, which were evenly distributed throughout the cages. Twenty-one days after releasing adults, the numbers of eggs, early instars (first through third instars), and late instars (fourth and fifth instars) present on each plant were counted. The 21-day duration was chosen because the eggs oviposited on the day of adult releases should reach the fifth instar by this time, but not yet molt to adult (Tran et al. 2012). The experiment was repeated three times with different cohorts of plants and insects for a total of 6 cages. The large number of plant populations included in the assays prevented meaningful statistical comparisons in susceptibility to psyllids among germplasm populations. Instead, plant susceptibility to B. cockerelli was ranked based on the mean numbers of eggs, early instars, and late instars observed on the plants at the end of the experiment. The lower and upper quartiles associated with the mean numbers of each insect age class, regardless of germplasm population, were calculated using SAS 9.3 (SAS Institute 2012). The least susceptible populations were identified as those with mean numbers of eggs, early instars, and late instars each below the lower quartile of their respective insect age class. The most susceptible populations were identified as those with

Table 1 Mean ± S.E. numbers of eggs, early instars (first through third), and late instars (fourth and fifth) of potato psyllid on *S. bulbocastanum* germplasm 21 days after releasing 100 adults into cages containing one plant from each population

S. bulbocastanum Accession Number	Eggs	Early instars	Late instars
Lower quartile [a]			
PI 243510	14.8±8.27	7.8±5.20	0.5±0.50
PI 243512	33.8±14.08	42.5±14.76	5.3±2.70
PI 255518	9.0±3.16	5.2±2.48	0
PI 275194	23.2±14.73	21.7±15.15	2.2±1.45
PI 275197	2.7±2.67	7.0±6.51	0
PI 283096	30.7±15.91	24.8±17.77	4.3±3.59
Mid quartiles [b]			
PI 243345	73.5±30.12	56.0±22.25	5.8±2.73
PI 243504	88.6±23.53	132.2±45.80	14.4±6.89
PI 243505	24.8±9.46	66.3±31.93	6.2±3.18
PI 243506	36.5±14.13	106.3±35.56	10.3±4.12
PI 243507	34.7±15.70	72.5±24.95	12.0±4.59
PI 243508	139.3±63.16	145.0±72.05	16.8±10.54
PI 243511	60.8±38.06	40.2±24.88	6.0±4.42
PI 253210	38.7±23.13	59.3±47.39	15.0±15.00
PI 243513	37.6±12.50	30.4±12.37	1.2±0.80
PI 255518	201±106.50	166±154.00	48±43.50
PI 310960	11.0±2.08	82.7±25.85	13.7±8.09
PI 595471	63.3±16.98	120.5±46.33	13.2±5.78
PI 590930	42.5±13.61	102.3±58.32	7.5±4.16
PI 595473	76.7±28.78	117.3±51.77	8.0±4.43
PI 275184	90.4±21.37	170.0±66.52	50.4±38.03
PI 275185	90.0±26.14	77.0±19.40	18.5±9.26
PI 275187	100.2±32.84	63.8±24.33	14.3±7.13
PI 275188	50.0±24.66	79.7±66.84	16.2±15.77
PI 275189	67.0±31.22	111.5±40.84	30.7±24.10
PI 275191	29.3±10.27	55.3±30.50	14.2±12.45
PI 275192	45.8±23.60	99.4±58.10	3.8±3.56
PI 275193	46.3±27.45	73.8±38.45	13.3±6.66
PI 275195	60.5±34.50	74.5±37.50	5.0±5.00
PI 275196	74.2±25.51	116.2±40.48	15.4±9.36
PI 275198	50.0±27.54	34.0±16.92	0
PI 275199	10.7±5.61	20.0±20.00	6.3±6.33
PI 275200	92.5±51.45	145.3±73.50	27.3±18.94
PI 347758	63.5±30.50	93.0±25.00	14.5±8.50
PI 498011	118.2±23.86	132.3±68.07	25.0±12.38
PI 498223	124.2±52.62	139.2±40.73	17.0±12.81
PI 498224	116.8±102.88	77.3±52.61	10.0±6.84
PI 498225	39.4±21.77	50.4±21.91	16.4±12.97
PI 545751	47.0±23.79	64.2±17.59	0.5±0.34
PI 545752	41.2±13.42	51.4±28.44	5.4±2.16
PI 558377	58.2±20.68	71.7±24.62	4.2±1.78
PI 558379	89.8±23.80	111.8±46.34	25.8±12.34
PI 604051	115.0±67.54	130.5±57.27	11.5±6.21
PI 604065	85.5±18.12	135.5±58.79	2.3±1.05

Table 1 (continued)

S. bulbocastanum Accession Number	Eggs	Early instars	Late instars
PI 604066	97.0±25.53	151.7±55.71	11.7±6.72
PI 604074	34.3±8.28	164.2±126.64	22.8±22.23
Upper quartile [c]			
PI 255516	140.8±71.84	239.2±71.29	23.2±14.49
PI 347757	134.3±40.94	246.8±38.61	43.5±18.52
PI 365379	137.5±36.89	209.7±48.46	33.0±16.94
PI 604073	94.8±46.92	197.2±56.79	17.5±5.84

Results are based on six replications

[a] Germplasm populations with mean numbers below the lower quartile for each respective insect age class (eggs=35.6, early instars=53.4, and late instars=5.4 per plant)

[b] Germplasm populations with a mean number of at least one insect age class between the lower or upper quartiles

[c] Germplasm populations with mean numbers above the upper quartile for each respective insect age class (eggs=93.7, early instars=133.9, and late instars=17.3 per plant)

mean numbers of eggs, early instars, and late instars above the upper quartile of their respective age class. Germplasm that supported numbers of at least one insect age class between the lower and upper quartiles were ranked as having intermediate susceptibility to *B. cockerelli*.

No-Choice Performance Assays

Oviposition rates and nymph survival and development were compared using no-choice performance assays among a subset of *S. bulbocastanum* populations selected based on results of the choice pre-screening assays. Three reproductively mature (>7 d old) female psyllids were confined to each of 5 seedlings per germplasm using a cage made of fine mesh. A rubber band enclosed the mesh cage around the rim of the pot, and a bamboo rod supported the weight of the cage. The adults were removed from the cages after 4 days, and the number of eggs on each plant was counted with the aid of an illuminated bench-top magnifier (2.25×). Twenty-one days after insect releases, each plant was examined for numbers of early instars (first through third), fourth instars, fifth instars, and adults, and offspring development was estimated using the weighted mean life-stage present on each plant (Pfeiffer and Burts 1983).

All statistical analyses were performed using SAS 9.3 (PROC GLIMMIX, SAS Institute 2012). In separate ANOVAs, the numbers of eggs, surviving offspring, and mean life-stage of offspring were compared among germplasm populations. The proportion of surviving

offspring was compared among germplasm using logistic regression with offspring/eggs as the dependent variable. Germplasm population was included as the fixed effect in each analysis. Because of the difficulty imposed by compound leaves, curled leaflets, and dense leaf pubescence in accurately counting eggs on 'Russet Burbank', these plants were not included in analyses of oviposition rates or proportion of surviving offspring. Data were examined for heterogeneity of variance and non-normality of errors by inspecting residual and normal quantile-quantile plots, respectively. Based on these plots, count data for analyses of numbers of eggs and surviving offspring were modeled assuming a Poison distribution. Where differences among populations were indicated, means were compared using the simulation-based multiple comparison (Edwards and Berry 1987).

Results and Discussion

Numbers of eggs, early instars (first through third) and late instars (fourth and fifth) varied among the 50 *S. bulbocastanum* germplasm populations screened in our choice assays (Table 1). The mean numbers of insects observed among germplasm populations ranged from 3 to 141 eggs per plant, 7 to 247 early instars per plant, and 0 to 50 late instars per plant. Six *S. bulbocastanum* populations supported mean numbers of eggs, early instars, and late instars that were each below the lower quartile of their respective insect age classes observed on all *S. bulbocastanum* (Table 1, lower quartile). The low numbers of eggs and nymphs observed on plants from these germplasm suggests that these plants may exhibit traits that reduce *B. cockerelli* oviposition preference or the rate of nymph development. Several germplasm populations, including PI 243513, PI 275192, PI 275198, and PI 545751, had mean numbers of eggs or early instars that were above the lower quartile for their respective age class, but supported few late instars (Table 1). Although females may readily oviposit on these plants, nymph survival or development rates may be lower relative to those on most other germplasm populations. Four populations supported mean numbers of eggs, early instars, and late instars that were each above the upper quartiles observed for their respective age classes (Table 1, upper quartile), and may represent the most psyllid-susceptible *S. bulbocastanum* populations included in our study.

Although sources of psyllid resistance may not be limited to germplasm populations that appear resistant based on results of the choice assays, these assays were designed to identify the most psyllid-resistant populations. However, these choice assays do not provide reliable information about whether plant traits confer antixenosis or antibiosis to psyllids. Antixenosis alters the behavior of an insect and is typically expressed as an insect preferring to oviposit or feed upon a susceptible plant compared with a resistant plant. Antibiosis affects the biology of an insect and is often expressed as increased mortality of insects on resistant plants compared with susceptible plants. The efficacy of host-plant resistance used for crop protection on ecological scales may differ depending upon whether the resistance traits confer antixenosis, antibiosis, or both. It is therefore necessary to perform no-choice performance assays to identify the mechanisms of psyllid resistance in order to assess the agronomic value of the resistance traits.

Ten germplasm populations were selected for inclusion in no-choice performance assays based on results of the choice assays. These included the six germplasm that appeared resistant to *B. cockerelli* (Table 1, lower quartile), three of the most susceptible germplasm (PI 255516, PI 347757, and PI 604073), and one additional germplasm population that did not support high populations of nymphs in the choice assays (PI 243513). However, the germplasm population PI 243510 was not included in the assays due to a low number of vigorous plants at the start of the experiment. 'Russet Burbank' potato was also included in the no-choice assays as a general comparison of psyllid performance on *S. tuberosum* and *S. bulbocastanum*. Limiting the number of germplasm populations included in the performance assays allowed statistically relevant comparisons in psyllid performance among the germplasm that could not be performed if all 50 populations were included. In addition, the use of no-choice performance assays provided valuable knowledge on the basic mechanisms of potential psyllid resistance in *S. bulbocastanum*.

There were significant differences among plants for each measure of psyllid performance: number of eggs oviposited after 4 days, number of surviving offspring after 21 days, proportion of surviving offspring after 21 days, and mean life-stage of offspring after 21 days (Table 2). In general, results of the no-choice performance assays were consistent with results of the choice screening assays. The germplasm PI 604073 was more suitable to *B. cockerelli* performance compared to other *S. bulbocastanum* populations in each parameter measured. Where meaningful comparisons could be made, psyllid performance on this germplasm did not differ from that on 'Russet Burbank.' However, these comparisons should be interpreted cautiously due to the differences between *S. bulbocastanum* and 'Russet Burbank' in plant age and propagation methods. The germplasm PI 255516 was also more susceptible to *B. cockerelli* compared to most other *S. bulbocastanum* populations with regards to numbers of eggs and surviving offspring. These germplasm should be useful for use as susceptible controls in future studies to characterize psyllid resistance in *S. bulbocastanum*.

Table 2 Mean number of eggs 4 days after confining adults on *S. bulbocastanum* germplasm and 'Russet Burbank' potato, and mean number of surviving offspring per plant, proportion of surviving offspring, and weighted mean life stage of nymphs on plants 17 days after removing adults

Germplasm	Eggs	Number of surviving offspring	Proportion surviving offspring	Offspring life stage
S. bulbocastanum, Resistant [a]				
PI 243512	52.6±3.36 b	14.8±1.72 c	0.26±0.026 cd	3.5±0.18 ab
PI 243513	52.8±3.25 b	20.6±2.02 bc	0.39±0.030 b	3.3±0.18 b
PI 255518	24.0±2.19 c	13.4±1.64 c	0.56±0.045 a	3.6±0.18 ab
PI 275194	53.0±3.26 b	19.6±1.97 bc	0.37±0.030 b	3.3±0.18 b
PI 275197	32.0±2.83 c	6.0±1.23 d	0.19±0.035 d	3.7±0.23 ab
PI 283096	30.6±2.47 c	6.4±1.13 d	0.21±0.033 d	3.2±0.24 b
S. bulbocastanum, Susceptible [a]				
PI 255516	92.4±4.30 a	27.8±2.36 b	0.30±0.021 c	3.3±0.18 b
PI 347757	47.2±3.07 b	14.8±1.72 c	0.31±0.031 bc	3.3±0.18 b
PI 604073	93.2±4.36 a	59.6±3.45 a	0.63±0.022 a	4.0±0.18 a
S. tuberosum				
Russet Burbank	–[b]	55.0±3.32 a	–[b]	4.4±0.18 a
	$F=53.9$; d.f.=8, 35; $P<0.001$	$F=58.8$; d.f.=9, 39; $P<0.001$	$F=24.7$; d.f.=8, 35; $P<0.001$	$F=3.9$; d.f.=9, 36; $P=0.002$

Results are based on 5 replications, and values within columns followed by the same letters are not significantly different at the $\alpha=0.05$ significant level

[a] Identified as putatively resistant or susceptible based on results of the choice assays summarized in Table 1

[b] Not included in the analyses because fewer eggs than nymphs were counted on plants

Two *S. bulbocastanum* populations, PI 283096 and PI 275197, exhibited strong resistance to *B. cockerelli* relative to other *S. bulbocastanum* populations. Both populations supported few eggs and nymphs, and a lower proportion of surviving offspring compared with other germplasm (Table 2). The reduced oviposition and survival by psyllids on these plants relative to that on other germplasm suggest that these plants exhibit both antixenosis to adults and antibiosis to nymphs. Another population, PI 255518, supported few eggs and nymphs, but the proportion of surviving offspring and the mean life-stage of offspring on these plants did not differ significantly from that on the susceptible population, PI 604073. This population may exhibit antixenosis to adults, yet lack antibiosis that reduces nymph survival and development rates. The remaining four germplasm populations (PI 243512, PI 243513, PI 275194, and PI 347757) exhibited an intermediate susceptibility relative to other populations. The high survival but young life stage of psyllids on PI 243513 and PI 275194 suggest that psyllids may develop slower on these plants compared with other germplasm. These results indicate that these six germplasm populations may provide valuable sources of resistance to *B. cockerelli*.

Plantings of potato cultivars with *B. cockerelli* resistance could provide a cost-effective control strategy for this pest and for *"Ca.* Liberibacter solanacearum." If sources of resistance to *"Ca.* Liberibacter solanacearum" are also discovered (Munyaneza 2012), then the combined use of resistance to Liberibacter and *B. cockerelli* could strengthen the long-term durability of pathogen resistance. The documentation of variation in susceptibility to *B. cockerelli* among *S. bulbocastanum* germplasm and the identification of populations exhibiting psyllid resistance should facilitate the development of new potato cultivars that are resistant to the potato psyllid. Further studies are needed to determine whether resistance traits from different populations can be combined for enhanced psyllid resistance, and to determine how much of the resistance from *S. bulbocastanum* can be transferred to the background of a marketable potato cultivar. Several R-genes that confer resistance to late blight (*Phytophthora infestans*), including *Rpi-blb2* from *S. bulbocastanum*, are expressed in interspecific hybrids involving *S. bulbocastanum* and *S. tuberosum* (Hermsen and Ramanna 1973), and in somatic hybrids of *S. bulbocastanum* PI 243510 (Table 1, lower quartile) and *S. tuberosum* (Helgeson et al. 1998; Song et al. 2003; van der Vossen et al. 2005; Park et al. 2005). These same somatic transfusions are also resistant to potato aphid and green-peach aphid (Davis et al. 2012). Therefore, future studies should also screen these somatic hybrids for psyllid resistance. It is also important to screen resistant plants against all *B. cockerelli* haplotypes identified in the United States (Swisher et al. 2012, 2013, 2014) to predict the potential durability resistance traits.

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