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Behavioral responses of adult potato psyllid, *Bactericera cockerelli* (Hemiptera: Triozidae), to potato germplasm and transmission of Candidatus *Liberibacter psyllaurous*

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ABSTRACT

The potato psyllid, *Bactericera cockerelli* (Sulc) (Hemiptera: Triozidae), is a major pest of potatoes that can cause yield loss by direct feeding on crop plants and by transmitting a bacterial pathogen, Candidatus *Liberibacter psyllaurous* (a.k.a. Candidatus *Liberibacter solanacearum*) associated with zebra chip disease of the crop. In recent years, there have been no studies regarding resistance of potato to the potato psyllid or the bacterial pathogen that the psyllid transmits. Thus, the objectives of this study were to determine the effects of potato germplasm on adult potato psyllid behavior and transmission of Ca. *L. psyllaurous*. A total of twenty-two potato (*Solanum tuberosum L.*) breeding clones and varieties were examined. Plant genotype significantly affected the occurrence and duration of psyllid probing, the duration of psyllid cleaning, resting and the amount of time psyllids spent off the potato leaflet as well as transmission of Ca. *L. psyllaurous*. For the potato genotypes in which there were significant decreases in transmission compared to controls, there was often an unclear relationship between the occurrences and duration of behaviors and subsequent bacterial transmission. We discuss the implications of our results for an integrated pest management program for the potato psyllid and Ca. *L. psyllaurous* control on potatoes.

1. Introduction

The potato psyllid, *Bactericera cockerelli* (Sulc) (Hemiptera: Triozidae), is a serious pest of solanaceous crops in Central and North America (Cranshaw, 1994; Jackson et al., 2009). Direct feeding of this insect can cause significant decreases in yield and quality of crop plants (Richards and Blood, 1933; Munyaneza et al., 2008). Additionally, the potato psyllid is an important vector for the transmission of Candidatus *Liberibacter psyllaurous* (a.k.a. Candidatus *Liberibacter solanacearum*). This bacterium is associated with zebra chip (ZC) disease in potatoes (Hansen et al., 2008; Crosslin et al., 2010). The disease results in lower yields and decreased crop quality, and is characterized by a distinctive pattern of necrosis that is evident when infected tubers are fried (Munyaneza et al., 2007a; Hansen et al., 2008; Crosslin et al., 2010). Current pest management practices rely on use of insecticides to control the potato psyllid to reduce ZC incidence and increase yields (Liu and Trumble, 2004, 2005; Goolsby et al., 2007; Vega-Gutierrez et al., 2008; Gharalari et al., 2009).

Host plant resistance can be an integral component of an integrated approach for the management of arthropod pests (Pedigo and Rice, 2006). The use of resistant varieties has been investigated as a management option against the potato psyllid in tomatoes (Liu and Trumble, 2004, 2005, 2006; Casteel et al., 2006, 2007). Some resistance by the *Mi-1.2* gene has been documented in tomatoes showing antixenosis (decreased host selection by the potato psyllid on plants with the resistant genotype) and antibiosis (significant decreases in survival of potato psyllid reared on the resistant genotype) (Casteel et al., 2006). In addition, antixenosis (reported as decreased feeding and oviposition) and antibiosis (described as increased developmental time and decreases in survival) were observed for a wild-type accession tomato (PI 134417) when compared to the tomato varieties '7718 VFN', 'Yellow Pear', 'QualiT 21' and 'Shady Lady' (Liu and Trumble, 2004, 2005,

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2006). Throughout the years, potato resistance research has focused on wild tuber-bearing South American *Solanum* species by primarily examining antixenosis and antibiosis to a variety of insect potato pests, and this tactic is still being investigated (Smith, 2005; Strand, 2006). However, research determining the use of resistant potato varieties to the potato psyllid has not been reported in over 20 years (Cranshaw, 1989). To date, no formal studies regarding resistance of potato varieties to the potato psyllid and ZC have been reported. There is some evidence of varieties in the field showing significant differences in the percentage of raw as well as fried tubers exhibiting ZC symptoms (Munyaneza et al., 2007a,b; Goolsby et al., 2007). Potential mechanisms of resistance related to potato varieties still remain to be examined.

Currently, there is no published information available to aid producers in choosing potato varieties that might reduce damage caused by the potato psyllid. Antixenosis and especially antibiosis are favored resistance modalities for limiting spread of arthropod-transmitted plant pathogens (Hesler and Tharp, 2005). Also, there is no published information on the potential of any commercial potato varieties or wild potato species to resist the key pathogen, Ca. *L. psyllaurous*. Thus, the objectives of this study were to determine the effects of potato germplasm on adult potato psyllid behavioral responses and determine if specific breeding clones or varieties can prevent or decrease transmission of Ca. *L. psyllaurous*. The use of pesticides can be reduced by knowing which potato varieties can tolerate or even resist insect pests (Smith, 2005), potentially reducing the need for pesticide applications and lower production costs. Plant resistance also has many advantages and can serve as a component tactic that may be integrated with other combinations of pest control. Understanding the effects of potato germplasm on adult psyllid behaviors could lead to more effective selection for psyllid resistance, and facilitate the identification and development of resistant potato varieties, thereby providing new opportunities for pest management. Limiting infestations and feeding-related activity can be a key component in preventing yield loss and ZC transmission with its associated detrimental effect on potato processing quality.

2. Materials and methods

2.1. Insects

B. cockerelli were originally obtained from field collections in Texas, USA. The colony was maintained at ambient conditions of 21–26 °C and 40–60% RH at the University of California, Riverside, Insectary and Quarantine facility. Host plants were tomatoes (*Solanum lycopersicum L.* cv. 'Yellow Pear'). A host plant other than potato was chosen as the rearing host to avoid insects developing a preference for their natal host plant (Tavormina, 1982). Post-teneral adult females were selected for all behavioral tests.

2.2. Potato breeding clones and varieties

A total of twenty-two potato (*Solanum tuberosum L.*) breeding clones and varieties were examined for effects on adult potato psyllid behaviors. These breeding clones or varieties were either from Texas or Idaho, USA. The eight advanced breeding clones, which had been field-screened by the Texas Potato Breeding and Variety Development Program and found to exhibit some level of tolerance to the ZC complex, were 'BTX1749-1W/Y', 'NDTX731-1R', 'TX05249-10W', 'ATX85404-8W', 'ATTX98500-3PW/Y', 'BTX1544-2W/Y', 'AOTX95295-1W ' and 'NY138'. The check-varieties 'Russet Norkotah' and 'Atlantic' were included because of their widely accepted susceptibility to ZC; 'King Harry', a variety known for its high pubescence levels, was also included.

Entries from the Aberdeen, ID, USA, potato breeding program consisted of a *S. tuberosum* subsp. tuberosum haploid- species hybrid [US-W730 × *Solanum berthaultii* (PI 265857)] designated as '463-4' that was used in somatic hybridizations with the potato species *Solanum etuberosum* as described by Novy and Helgeson (1994). Four generations of backcross progeny derived from somatic hybrids were also included: 'P2-3' and 'P2-4' (BC_1), 'Etb 5-31-3', 'Etb 6-21-3', and 'Etb 6-21-5' (BC_2), 'A00ETB12-2' and 'A00ETB12-3' (BC_3), and 'A05379-69' and 'A05379-211' (BC_4). In addition, 'GemStar Russet', a potato variety with putative resistance to psyllids and their associated feeding damage (Creighton Miller, personal communication), was also included in the study.

Potato breeding clones and varieties used in all tests were grown in 4.9-L pots with UC mix (Matkin and Chandler, 1957) and fertilized three times per week with the label rate of Miracle Gro® nutrient solution (Scotts Company, Marysville, OH, USA). Plants were used for tests once they reached the 'vegetative growth' stage (Growth Stage II), which is marked by the plant producing 8-12 leaves (Strand, 2006). Plant leaves used as substrates for the behavioral assays were standardized by selecting the uppermost, fully-expanded leaf.

2.3. Behavioral bioassays

All assays were based on the protocols of Liu and Trumble (2004). Assays were monitored in arenas made by layering the following components: A Plexiglass rectangle (9 by 11.5 cm) serving as the base, a 9-cm-diameter Whatman® filter paper on the Plexiglass, the test leaflet (psyllid was placed on abaxial surface), foam (0.5 × 8 × 9 cm) with a 2.5 cm^2 hole, and an additional 12.5-cm-diameter glass plate that covered the arena. The leaflet was not detached from the plant in order to avoid potential chemical changes associated with leaf excision. An adult female was placed into the arena and allowed to adjust for 5 min before initiating behavioral recording. An observation period lasted 15 min. Preliminary studies (Liu and Trumble, unpublished data) indicated that the 15 min observation period was sufficient for the psyllids to exhibit most of the behaviors recorded. The observations were recorded using the Noldus Observer program (Noldus, Wageningen, The Netherlands).

Specific behaviors recorded included cleaning (using legs to cleanse or wipe antennae, appendages or abdomen), probing (stylet penetration into leaflet observed on electrical penetration graphs, Butler et al. unpublished), jumping (leaping from one point to another on the leaflet), off-leaflet (exiting or abandoning the leaf surface), tasting (tapping the mouthparts on the leaf surface sporadically), resting (no activity on the leaflet and mouthparts not in contact with the leaflet), and walking (walking on the leaf surface). Jumping occurred so rapidly that accurately recording duration time was not possible, so only numbers of occurrences were recorded. The behavioral observations were replicated 20 times with different psyllids and leaves for each of the plant entries.

2.4. Transmission assays

Ten psyllids (subsequently determined to be infected, see below) were caged on a 7 × 7.5 cm cage on the terminal leaflet of one of the fully-expanded potato leaves for a 24-h inoculation access period for each of the plant genotypes. After 24 h, the psyllids were removed from the leaflet, placed in 100% ethanol and stored at −20 °C until real-time PCR analysis. Munyaneza (2010) noted that it takes as few as one infective psyllid per potato plant in three weeks or less for ZC symptoms to develop after exposure to infective psyllids. Thus, the plants were held for 2 wk after potato psyllid exposure to allow disease development. The potato leaves

fed upon by the psyllid was then removed from the plant and placed in a Ziploc® bag and stored at −80 °C until real-time PCR analysis was conducted.

2.5. Real-time PCR analysis

Potato psyllids were tested in aliquots of three adults per extraction using a procedure described earlier (Manjunath et al., 2008; Butler et al., 2011) for the presence of Ca. *L. psyllaurous*. A minimum of two extractions was conducted from each sample. Briefly, psyllids were transferred to a Whatman filter paper #1, air-dried for about 10 min and further processed using Fast DNA spin kit (MP Biomedicals Ltd., Solon, OH, USA). Final elution of DNA was done in a volume of 100 μl of elution buffer per extraction. Two negative extractions were used for each batch of 24 extractions to monitor possible cross contaminations between samples. A Taqman-based real-time PCR assay was employed in detection of LPS by using a protocol modified from Li et al. (2006) and Manjunath et al. (2008). DNA concentrations were estimated using a NanoDrop spectrophotometer (Thermo Fisher Scientific, Wilmington, DE, USA). The forward primer HLBf was replaced by LPSf (5′-TCGAGCGCTTATTTTTAATAGG-3′) and used along with HLBp and HLBr. Samples with a cycle threshold (ct) value of 35 and above indicated absence of LPS.

DNA extraction from frozen potato leaf samples was conducted using Qiagen MagAttract 96 DNA Plant Core kit (Qiagen Inc., Valencia, CA, USA) according to the manufacturer. 100 mg of midrib samples were cut into small pieces using a sterile razor blade and placed in appropriate well in a 96 deepwell plate sealed using TPE capcluster mat (USA Scientific Co., Ocala, FL, USA). Duplicate extractions were conducted for each sample. Extractions conducted with water served as negative extraction controls. After loading all the samples, the cluster caps were removed and the plate was sealed with Airpore Tape sheet (Qiagen) and freeze dried overnight. Next day, about 20 zironium beads (2.5 mm; Glen Mills, Clifton, NJ, USA) were added into each well, sealed using cluster caps as above, and the tissue was homogenized in a beadbeater (Biospec Inc. Bartlesville, OK, USA) for 5 min. Homogenization was conducted again in the presence of 300 μl of RLT buffer. The homogenized sample was processed further according to the manufacturer. The final elution of DNA was done in a volume of 100 μl per extraction. Real-time PCR assay was conducted essentially as described by Li et al. (2006) except for the forward primer (LPSf) as described above. The primer-probe set for mitochondrial cytochrome oxidase gene (COX) served as internal control for detection of potato DNA. The results of the PCR tests for LPS were analyzed as described above.

2.6. Statistical analysis

The experiment was conducted as a randomized block design with two blocks. Blocks were the origin of the potatoes (i.e., Idaho or Texas). The 'Idaho' block consisted of 20 replicates of the 12 potato entries, and the 'Texas' block consisted of 20 replicates of the ten potato entries. Treatment differences in the number of occurrences and duration of behaviors were analyzed using analysis of variance (ANOVA) in a general linear models procedure of SAS version 9.2 (PROC GLM; SAS Institute, 2008). The numbers of occurrences of probing were reciprocal transformed to homogenize variances. The durations of probing were square root transformed, and the durations of times spent off the potato leaflet were reciprocal square root transformed. When treatment effect was significant ($P < 0.05$) a least significant difference (LSD) test was used to discriminate significant differences among treatment means. The number of potato plants infected with Ca. *L. psyllaurous* from a given potato genotype were compared against their respective positive controls (i.e., Idaho block: 'Atlantic' and Texas block: 'Russet Norkotah') with Mann–Whitney *U*-tests (PROC NPAR1WAY; SAS Institute, 2008).

3. Results

3.1. Occurrences of psyllid behaviors

The number of occurrences of each behavior was recorded for each of the potato lines (Table 1). There were significant differences between the potato genotypes for the number of occurrences of probing ($F = 1.86$; df = 21, 431; $P = 0.0125$). Psyllids probed less on the potato breeding clones 'P2-4' and 'TX05249-10W', and these

Table 1
Number of occurrences of selected behaviors of the potato psyllid in response to potato breeding clone or variety.

Clone/Variety	Tasting[a]		Probing		Cleaning		Jumping[b]		Resting		Walking		Off-leaflet	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
'P2-4'	0.9a	0.3	1.0a	0.2	0.1a	0.1	0.1	0.1	1.2a	0.4	1.4a	0.4	0.5a	0.1
'TX05249-10W'	0.3a	0.2	1.3a	0.2	0.2a	0.1	0.0	0.0	0.9a	0.3	1.2a	0.4	0.4a	0.2
'463-4'	1.1a	0.3	1.1ab	0.2	0.1a	0.1	0.6	0.3	1.3a	0.3	2.8a	0.6	1.2a	0.2
'Etb 6-21-3'	0.3a	0.1	1.3ab	0.2	0.9a	0.2	0.2	0.2	1.4a	0.3	1.3a	0.3	0.3a	0.2
'GemStar Russet'	0.6a	0.3	1.3abc	0.2	0.3a	0.2	0.3	0.2	1.3a	0.4	1.8a	0.7	0.3a	0.2
'King Harry'	0.4a	0.2	1.4abcd	0.3	0.5a	0.2	0.0	0.0	0.9a	0.2	1.1a	0.3	0.3a	0.1
'Etb 6-21-5'	0.5a	0.2	1.5abcd	0.2	0.6a	0.2	0.0	0.0	1.3a	0.3	1.6a	0.5	0.3a	0.3
'A05379-211'	0.4a	0.1	1.5abcde	0.3	0.5a	0.2	0.2	0.2	1.2a	0.3	1.7a	0.4	0.7a	0.2
'ATX85404-8W'	0.3a	0.1	1.6abcde	0.3	0.5a	0.2	0.1	0.1	0.8a	0.3	1.2a	0.3	0.3a	0.2
'AOTX95295-1W'	0.5a	0.2	1.7abcde	0.4	0.4a	0.2	0.6	0.5	1.8a	0.6	2.3a	0.7	0.4a	0.2
'P2-3'	0.6a	0.3	1.8abcde	0.3	0.4a	0.2	0.0	0.0	0.5a	0.2	1.0a	0.3	0.1a	0.1
'A00ETB12-2'	0.9a	0.3	1.9abcde	0.4	0.9a	0.4	1.0	0.5	0.5a	0.3	2.2a	0.9	1.0a	0.5
'ATTX98500-3PW/Y'	0.3a	0.1	1.9abcde	0.4	0.9a	0.3	0.2	0.1	1.2a	0.4	1.1a	0.4	0.3a	0.1
'BTX1749-1W/Y'	1.0a	0.3	1.9abcde	0.4	0.2a	0.1	0.0	0.0	0.7a	0.3	1.8a	0.6	0.6a	0.3
'Russet Norkotah'	0.6a	0.2	1.8bcde	0.3	0.6a	0.3	0.2	0.2	1.0a	0.2	1.4a	0.5	0.3a	0.2
'A00ETB12-3''	0.7a	0.2	1.9cde	0.3	0.2a	0.1	0.1	0.1	1.0a	0.2	1.9a	0.4	0.5a	0.2
'NDTX731-1R'	0.7a	0.2	2.0cde	0.3	0.8a	0.4	0.0	0.0	1.4a	0.4	1.9a	0.5	0.3a	0.1
'Etb 5-31-3''	1.1a	0.3	2.1de	0.3	0.3a	0.1	0.2	0.1	1.6a	0.5	3.2a	0.7	0.8a	0.3
'A05379-69'	0.6a	0.2	2.3de	0.3	0.9a	0.3	0.3	0.3	1.2a	0.4	1.9a	0.7	0.6a	0.3
'NY138'	1.1a	0.3	2.1e	0.4	0.3a	0.1	0.0	0.0	0.9a	0.2	1.9a	0.4	0.4a	0.1
'Atlantic'	0.9a	0.3	2.4e	0.4	0.6a	0.2	0.2	0.1	1.3a	0.5	2.4a	0.6	0.3a	0.1
'BTX1544-2W/Y'	1.1a	0.5	2.7e	0.5	0.6a	0.2	0.3	0.1	1.2a	0.4	2.8a	0.8	0.6a	0.2

[a] Means within a column followed by different letters are significantly different using the LSD test.
[b] No statistics were analyzed for this behavior due to the presence of zeroes that violate the assumptions of ANOVA.

values were significantly lower than the values on the potato varieties and breeding clones 'Russet Norkotah', 'A00ETB12-3', 'NDTX731-1R', 'Etb 5-31-3', 'A05379-69', 'NY138', 'Atlantic', and 'BTX1544-2W/Y' (Table 1). The number of occurrences of tasting, cleaning, resting, walking, and number of occurrences off the potato leaflet were not significantly different between the potato germplasm tested.

3.2. Duration of psyllid behaviors

Potato germplasm had a significant effect on the probing duration of psyllids ($F = 1.96$; df = 21, 431; $P = 0.0074$). Psyllids spent significantly less time probing on '463-4' compared to 'Etb 5-31-3', 'ATX85404-8W', 'King Harry', 'ATTX98500-3PW/Y', 'BTX1544-2W/Y', 'A00ETB12-3', 'P2-4', 'A00ETB12-2', 'A05379-69', 'Etb 6-21-3', 'P2-3', 'Etb 6-21-5', and 'Russet Norkotah' (Table 2). The next lowest duration of probing by psyllids was on the potato breeding clone 'NY138' which was significantly lower than 'A00ETB12-3', 'P2-4', 'A00ETB12-2', 'A05379-69', 'Etb 6-21-3', 'P2-3', 'Etb 6-21-5', and 'Russet Norkotah' (Table 2). Psyllids spent the most time cleaning on 'AOTX95295-1W' and 'King Harry' compared to 'A05379-211', 'P2-4', 'A00ETB12-3', 'NDTX731-1R', 'P2-3', 'Etb 6-21-5', 'GemStar Russet', 'BTX1544-2W/Y', 'Atlantic', 'Etb 5-31-3', 'TX05249-10W', '463-4', and 'NY138' ($F = 1.89$; df = 21, 431; $P = 0.0104$) (Table 2). Psyllids spent the most time resting on the varieties 'BTX1749-1W/Y' and 'TX05249-10W' compared to 'Russet Norkotah', 'A05379-69', 'P2-3', 'P2-4', and 'A00ETB12-2' ($F = 1.81$; df = 21, 431; $P = 0.0164$) (Table 2). Psyllids spent the most time off the potato variety '463-4' compared to all other breeding clones or varieties except for 'A05379-211' and 'NY138' ($F = 2.00$; df = 21, 431; $P = 0.0057$) (Table 2). No significant differences among clones were noted for the duration of tasting and walking behaviors.

3.3. Transmission assay

The mean percentage and number of psyllids and potato plants that were infected with Ca. *L. psyllaurous* are shown in Table 3. All of the psyllids tested were infected with Ca. *L. psyllaurous*. There were significant decreases in the number of potato plants that were infected with Ca. *L. psyllaurous* based on plant genotype compared to 'Atlantic' ('A00ETB12-3': $z = -2.15$, $P = 0.0318$; 'Etb 6-21-3': $z = -2.15$, $P = 0.0318$; 'P2-4': $z = -2.15$, $P = 0.0318$) and 'Russet Norkotah' ('BTX1544-2W/Y': $z = -2.15$, $P = 0.0318$; 'TX05249-10W': $z = -2.15$, $P = 0.0318$). Each of the breeding clones 'A00ETB12-3', 'Etb 6-21-3', 'P2-4', 'BTX1544-2W/Y', and 'TX05249-10W', reduced infection 63% from their respective controls.

4. Discussion

Potato breeding clones and varieties evaluated affected the occurrences and durations of probing, durations of cleaning, resting, the amount of time spent off the potato leaflet as well as transmission of Ca. *L. psyllaurous*. The occurrences of probing by psyllids on 'P2-4' and 'TX05249-10W' were reduced significantly relative to their respective controls and may help explain why there was a significant decrease in transmission of Ca. *L psyllaurous*. However, the duration of probing by psyllids on 'P2-4' and 'TX05249-10W' relative to variety controls were significantly different only for 'TX05249-10W' relative to 'Russet Norkotah'. The probing durations were lowest for psyllids on '463-4' and 'NY138' and time spent off the potato leaflets was greatest for psyllids on '463-4' and 'NY138' as well. Also psyllid probing durations on '463-4' and 'NY138' were reduced by 48–62% compared to 'Russet Norkotah'. Additionally, the amount of time spent off the potato leaflet was 72% greater for '463-4' compared to 'Atlantic' and 94% greater for 'NY138' compared to 'Russet Norkotah', thus indicating some repellency. The repellency observed in '463-4', is likely contributed by its *S. berthaultii* parent, which was derived from an accession (PI 265857) noted for having A and B glandular trichomes, as well as resistances to a myriad of pests, including Colorado potato beetle, fleabeetle, leafhopper, mites, and tarnished plant bug (United States National Plant Germplasm System, Germplasm Resources Information Network [GRIN]). However, this deterrence to probing and repellency was not enough to significantly lower transmission of Ca. *L. psyllaurous* as compared to controls. The amount of time psyllids spent resting was significantly longer on 'BTX1749-1W/Y' and 'TX05249-10W' compared to 'Russet Norkotah' by nearly 65%, but the combination of the

Table 2
Duration (in seconds) of selected behaviors of the potato psyllid in response to potato breeding clone or variety.

Clone/Variety	Tasting[a]		Probing		Cleaning		Resting		Walking		Off-leaflet	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
'Russet Norkotah'	1.9a	0.5	725.6a	42.0	57.9abcd	28.0	87.6bcd	34.8	17.4a	6.9	12.8ab	10.7
'Etb 6-21-5'	3.1a	1.1	690.0ab	69.3	18.1cd	9.0	116.2abcd	51.0	16.6a	7.2	59.4ab	43.1
'P2-3'	14.6a	9.3	659.7ab	58.1	28.5cd	22.3	48.7cd	25.0	30.8a	9.3	120.4bcd	52.5
'Etb 6-21-3''	5.0a	2.3	650.9abc	71.0	50.4abcd	28.8	111.7abcd	46.5	29.9a	10.3	55.5abcd	44.8
'A05379-69'	4.0a	1.4	627.4abc	77.5	77.1abcd	40.6	50.6cd	26.0	15.3a	4.4	129.0abcd	61.5
'A00ETB12-2'	7.2a	2.6	610.5abc	80.2	71.8abcd	31.7	15.2d	10.7	39.7a	18.7	159.0abcd	67.5
'P2-4'	10. 7a	4.8	592.5abc	80.1	45.6bcd	38.1	50.0cd	34.1	35.6a	15.5	169.0abcd	73.6
'A00ETB12-3'	4.1a	1.1	559.3abc	73.5	36.1bcd	30.1	164.7abcd	62.9	24.0a	6.1	114.7abcd	58.4
'BTX1544-2W/Y'	3.0a	1.3	544.1abcd	77.1	13.6cd	12.1	224.5ab	73.3	19.0a	8.0	99.3abc	48.2
'ATTX98500-3PW/Y'	1.7a	0.3	535.1abcd	69.6	90.6abc	35.5	144.0abcd	43.2	24.4a	11.8	107.3abc	55.9
'King Harry'	5.9a	2.9	528.6abcd	72.9	131.7a	55.5	125.4abcd	46.8	23.5a	8.8	88.3ab	59.0
'ATX85404-8W'	2.4a	0.6	523.6abcd	77.1	85.0abcd	36.1	228.8ab	62.0	21.8a	7.7	41.5a	36.5
'Etb 5-31-3'	9.4a	2.6	518.5bcd	79.7	11.4cd	6.9	219.8ab	66.4	76.6a	20.9	67.0abcd	39.0
'Atlantic'	4.9a	2.3	512.1bcde	85.3	13.1cd	6.9	242.5ab	73.4	27.0a	9.5	103.7abcd	50.0
'GemStar Russet'	1.5a	0.2	509.7bcde	97.6	16.4cd	11.1	240.9ab	86.4	27.0a	10.7	107.8abcd	68.3
'TX05249-10W'	2.5a	0.9	474.2bcde	82.5	10.9cd	8.8	249.4a	76.5	19.2a	9.1	147.6abc	68.4
'NDTX731-1R'	5.4a	1.9	472.3bcde	72.2	30.7cd	22.3	225.0ab	60.6	22.4a	4.8	147.0abcd	73.0
'A05379-211'	4.1a	1.3	452.6cde	84.7	47.3bcd	27.1	141.7abcd	52.5	19.7a	5.1	237.9de	77.4
'AOTX95295-1W'	2.7a	1.0	417.2cde	75.6	132.9a	50.4	179.2abc	58.1	20.1a	5.3	150.6abcd	68.5
'BTX1749-1W/Y'	2.9a	0.8	389.0cde	58.7	115.6ab	45.0	267.9a	64.2	20.9a	6.8	106.4abcd	52.9
'NY138'	4.3a	2.3	373.5de	87.7	3.9d	2.9	236.9ab	76.4	35.0a	13.5	249.7cde	82.4
'463-4'	7.5a	3.9	276.9e	65.1	4.1d	3.0	200.2abc	62.7	42.8a	10.4	371.1e	76.5

[a] Means within a column followed by different letters are significantly different using the LSD test.

Table 3
Mean percentage and number of infected/inoculated potato psyllids and potato plants infected with Ca. *L. psyllaurous* by breeding clone or variety[a].

Experiment	Clone/Variety	Potato Psyllid		Potato[b]	
		Mean	SE	Mean	SE
Idaho					
	'A00ETB12-3'	100.0% (10/10)	0.0	30.0% (3/10) a	15.3
	'Etb 6-21-3'	100.0% (10/10)	0.0	30.0% (3/10) a	15.3
	'P2-4'	100.0% (10/10)	0.0	30.0% (3/10) a	15.3
	'GemStar Russet'	100.0% (10/10)	0.0	37.5% (3/8) b	18.3
	'Etb 5-31-3'	100.0% (10/10)	0.0	40.0% (4/10) b	18.3
	'A05379-211'	100.0% (10/10)	0.0	44.4% (4/9) b	17.6
	'463-4'	100.0% (10/10)	0.0	50.0% (5/10) b	16.7
	'Etb 6-21-5'	100.0% (10/10)	0.0	50.0% (5/10) b	16.7
	'P2-3'	100.0% (10/10)	0.0	50.0% (4/8) b	18.9
	'A05379-69'	100.0% (10/10)	0.0	70.0% (7/10) b	15.3
	'A00ETB12-2'	100.0% (10/10)	0.0	100.0% (10/10) b	0.0
	'Atlantic'	100.0% (10/10)	0.0	80.0% (8/10) b	13.3
Texas					
	'BTX1544-2W/Y'	100.0% (10/10)	0.0	30.0% (3/10) a	15.3
	'TX05249-10W'	100.0% (10/10)	0.0	30.0% (3/10) a	15.3
	'NY138'	100.0% (10/10)	0.0	40.0% (4/10) b	16.3
	'ATX85404-8W'	100.0% (10/10)	0.0	50.0% (5/10) b	16.7
	'BTX1749-1W/Y'	100.0% (10/10)	0.0	50.0% (5/10) b	16.7
	'ATTX98500-3PW/Y'	100.0% (10/10)	0.0	60.0% (6/10) b	16.3
	'King Harry'	100.0% (10/10)	0.0	60.0% (6/10) b	16.3
	'NDTX731-1R'	100.0% (10/10)	0.0	70.0% (7/10) b	15.3
	'AOTX95295-1W'	100.0% (10/10)	0.0	70.0% (7/10) b	15.3
	'Russet Norkotah'	100.0% (10/10)	0.0	80.0% (8/10) b	13.3

[a] Range of ct values: Potato psyllids [18.09–31.27], Potato [23.46–40.00].
[b] Within columns, percentages followed by different letters differ significantly (Mann–Whitney *U*-test paired comparisons with the control of their respective experiments).

behavioral and transmission assay data suggest that 'TX05249-10W' is the less susceptible genotype. In addition, 'King Harry' and 'AOTX95295-1W' increased the amount of time psyllids spent cleaning compared to 'Atlantic' by nearly 90% for both potato genotypes, however this increased duration of cleaning appeared to be not enough to significantly lower Ca. *L. psyllaurous* transmission from 'Russet Norkotah'.

Results of the transmission assays and the relationship to psyllid behaviors appear to be promising. For the potato genotypes in which there was a significant decrease in transmission compared to their controls, there was sometimes an unclear relationship between the occurrences and durations of behaviors and subsequent transmission. For 'A00ETB12-3', 'Etb 6-21-3', and 'BTX1544-2W/Y', there was no significant difference in the occurrence and duration of probing, durations of cleaning, resting and amount of time spent off the potato leaflets compared to their controls, yet transmission was significantly reduced, possibly indicative of resistance to Ca. *L. psyllaurous* rather than to its insect vector. In contrast, 'P2-4' and 'TX05249-10W' showed significant differences in the frequency, duration and reduced transmission of behaviors compared to their controls. 'P2-4' had a lower number of probing occurrences and a significantly longer resting duration compared to 'Atlantic' and 'TX05249-10W' had a lower number of probing occurrences and likewise a significantly lower duration of probing and longer resting duration compared to 'Russet Norkotah', which may help explain why transmission of Ca. *L. psyllaurous* was decreased. To better understand these variable relationships, further experiments may be needed. The use of electrical penetration graphs to further characterize the feeding behavior of potato psyllids on these potentially tolerant/resistant potato breeding clones or varieties may be needed to further elucidate the connection between potato psyllid behaviors and pathogen transmission on these plants. Also, the most promising potato breeding clones or varieties that have affected potato psyllid behaviors and lowered transmission of Ca. *L. psyllaurous* will need to be tested in the field before recommendations can be made and the most effective integration with a potato psyllid pest and Ca. *L. psyllaurous* management program can be accomplished.

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