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Seasonal Population Dynamics of the Potato Psyllid (Hemiptera: Triozidae) and Its Associated Pathogen "*Candidatus* Liberibacter solanacearum" in Potatoes in the Southern Great Plains of North America

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Seasonal Population Dynamics of the Potato Psyllid (Hemiptera: Triozidae) and Its Associated Pathogen "*Candidatus* Liberibacter solanacearum" in Potatoes in the Southern Great Plains of North America

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ABSTRACT The potato psyllid, *Bactericera cockerelli* (Sulc) (Hemiptera: Triozidae), and its associated pathogen "*Candidatus* Liberibacter solanacearum" (*Ca.* L. solanacearum), the putative causal agent of zebra chip (ZC) disease in potatoes (*Solanum tuberosum* L.), were sampled in commercial potato fields and untreated control plots for 3 yr in multiple locations in Texas, Kansas, Nebraska, and Colorado. Populations of the potato psyllid varied across years and across potato growing regions. However, the percentage of potato psyllids infected with *Ca.* L. solanacearum although variable across years, was consistently highest in the Lower Rio Grande Valley of Texas (LRGV), the reported overwintering location for this pest. The numbers of *Ca.* L. solanacearum–infected psyllids collected on field traps and large nymphs counted on leaf samples were both positively correlated with the final percentage of ZC in tubers. In the LRGV, where vector and disease pressure is the highest, population levels of immature life stages of the psyllid and percentage of ZC differed greatly between commercial and untreated fields. These results show that the pest management program that was used can be effective at controlling development of the psyllid and ultimately reducing the incidence of ZC.

KEY WORDS *Bactericera cockerelli*, zebra chip, Liberibacter, insect vector, areawide pest management

Zebra Chip (ZC) disease of potatoes (*Solanum tuberosum* L.) was first noted in Mexico in the 1990s (Cadena-Hinojosa and Guzman-Plazola 2003, Rubio-Covarrubias et al. 2006, Munyaneza et al. 2009) and in the Lower Rio Grande Valley of Texas in 2000 (Secor et al. 2006; Gudmestad and Secor 2007; Goolsby et al. 2007a,b); Munyaneza et al. 2007a,b). The disease spread to potato production areas of the southwestern United States, including Texas, Kansas, Nebraska, New Mexico, California, and Colorado (Crosslin and Bester 2009, Wen et al. 2009). Recently, the disease has been documented in the Pacific Northwest, including Idaho, Oregon, and Washington (Crosslin et al. 2011, 2012a,b; Rondon and Hamm 2011). The disease also is present in New Zealand and Central America (Crosslin et al. 2010, Munyaneza 2010). The causal agent of the disease was shown to be graft transmissible (Crosslin and Munyaneza 2009, Secor et al. 2009) and was later identified as "*Candidatus* Liberibacter solanacearum" (syn. *Ca.* L.=psyllaurous) (Hansen et al. 2008; Liefting et al. 2009; Lin et al. 2009, 2011), an agent that is related to other alpha-protobacteria, most notably citrus greening, Huanaglongbing (HLB), "*Candidatus* Liberibacter asiaticus" (Gottwald 2010). In potatoes, ZC disease causes lower yields, discolored chips and French fries, and storage losses, and it limits exports. Economic losses in effected areas have been high (Rosson et al. 2006), leading to intensive pest management programs to minimize the impact of the disease (Goolsby et al. 2007a,b; Berry et al. 2009; Gharalari et al. 2009; Butler et al. 2011).

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The potato psyllid, *Bactericera cockerelli* (Sulc) (Hemiptera: Triozidae) harbors *Ca.* L. solanacearum *Ca.* L. solanacearum and vectors(?) to potatoes and other plants (Munyaneza et al. 2007a,b, 2010; Gao et al. 2009; Munyaneza 2010) through its feeding activity (Buchman et al. 2011). The potato psyllid is indigenous to the southwestern United States and Northern Mexico and is known to exploit the "climatic trumpet" of the Great Plains of North America to migrate long distances to locate its solanaceous hosts, including the native wolfberry (*Lycium* spp.) and nightshades (*Solanum* spp.) (Romney 1939, Wallis 1955, Drees and Jackman 1999, Liu and Trumble 2004, Goolsby et al. 2007a). Distinct populations of *B. cockerelli* have been characterized using molecular markers that separate populations of the psyllid from California and Great Plains of North America (Liu et al. 2006) and the Lower Rio Grande Valley (LRGV) of Texas from Mexico and Guatemala (Jackson et al. 2009). These differences reflect stable breeding populations in each region, although there is evidence of gene flow between them (Jackson et al. 2009). Each population may have a unique life history and exposure to wild and cultivated solanaceous hosts that influences their acquisition and transmission of *Ca.* L. solanacearum. In addition, laboratory studies have shown that low and high temperatures can slow or inhibit the development of *Ca.* L. solanacearum in the infected tubers (Munyaneza et al. 2011b). Therefore, under field conditions, abiotic factors such as temperature, humidity, and rainfall may influence the acquisition, transmission, and seasonal association of *Ca.* L. solanacearum with *B. cockerelli.*

A 3-yr multistate field survey program was initiated to learn more about the seasonal phenology and variability of the psyllid and its associated pathogen. Field data were needed from both commercial fields and untreated controls to document the intensity and variability of the disease pressure for each potato growing region. The ultimate goal was to use these data to develop an effective pest management program, so that insecticide inputs could be optimized, thus improving profitability and sustainability of potato production regions impacted by ZC.

Materials and Methods

Study Sites. Surveys were conducted during the 2009–2011 growing seasons. Commercial potato fields with a history of ZC occurrence were selected for the study. The fields were located near McAllen and Weslaco (LRGV), TX; Pearsall and Uvalde (TX Wintergarden), TX; Olton, Springlake, Halfway, and Dalhart (TX High Plains), TX; Garden City (Kansas), KS; Minden, Bridgeport, Alliance, Imperial and Scottsbluff, NE; and Wray and Alamosa, CO (Fig. 1). In each region, an untreated ≈0.33-acre control plot was planted to assess the impact of the potato psyllid and the *Ca.* L. solanacearum pathogen without pest management inputs, except at the TX Wintergarden sites and all sites in Nebraska in 2009. Most fields in the study were planted with chipping potato varieties Atlantic or Frito Lay (FL) 1867, but FL1879, FL1833, Megachip, Russet Norkotah, Rio Grande, and Durango also were planted. All of the seed potatoes were obtained from Colorado and Nebraska. Although there are some minor varietal differences in tolerance to potato psyllids, all varieties were known to be susceptible to *Ca.* L. solanacearum and expression of ZC (Goolsby et al. 2007a, Munyaneza et al. 2011a). The commercial fields were planted after the earliest frost-free date starting in Dec/Jan in McAllen and progressing to May in Dalhart, TX. The commercial potatoes were planted with an in-furrow application of a neonicotinoid such as imidacloprid, Admire Pro (Bayer Crop Science, Leverkusen, North Rhine-Westphalia, Germany) insecticide followed by consecutive applications each of spirotetramat, Movento (Bayer Crop Science), abamectin, Agrimek (Syngenta, Basil, Switzerland), dinotefuran, Oberon (Bayer Crop Science, City, NC), and/or pymetrozine, Fulfill (Syngenta) and generally applied at weekly intervals until 14 d preharvest interval. Aboveground emergence of plants from tubers occurred 30–45 d after planting with first foliar insecticide application beginning at 45–55 d. This pest management strategy became the "best management practice" used by potato growers in the survey and sampling program. A complete listing of locations, planting dates, varieties, and pest management applications can be found at http://agrilife.org/zebrachip/resources/potato-psyllid-survey-report-archive/.

Potato Psyllid Sampling. Unbaited yellow sticky traps (Trécé, Inc., Adair, OK) placed 1 m above ground on a wooden stake were used to trap adult psyllids. The preseason sampling for adult psyllids began at planting of tubers ≈4 wk before emergence of potato leaves and continued for 2 wk until plants were ≈10 cm in height. In the preseason survey, 100 traps placed 20 m apart in a straight or meandering transect were used in one location in each growing region to assess the percentage of psyllids positive for *Ca.* L. solanacearum. Once the potato leaves emerged from the tubers, the preseason transect was discontinued and the in-season survey were initiated in each of the selected commercial fields and untreated control plot for each region. Each in-season transect had five traps placed broadside toward the edge of the field at intervals of 20 m from the closest accessible field margin toward the center of the irrigation pivot. In addition, leaf samples were collected weekly until harvest from each field to determine density of immature potato psyllids and impact of the pest management program. Ten of the oldest fully expanded leaves were sampled each week from 10 fixed locations around the perimeter of the field. Leaves and traps were collected from each field and sent by overnight courier to the USDA–ARS laboratory in Weslaco, TX, for processing. Counts were conducted with a MZ 7.5 dissecting stereomicroscope (Leica, Wetzlar, Germany) at ≈35×. Psyllids on the leaves were classified as eggs, small nymphs (first and second instars), or large nymphs (third and fourth instars). Adults on the sticky traps (in both pre and in-season transects) were counted, removed, and

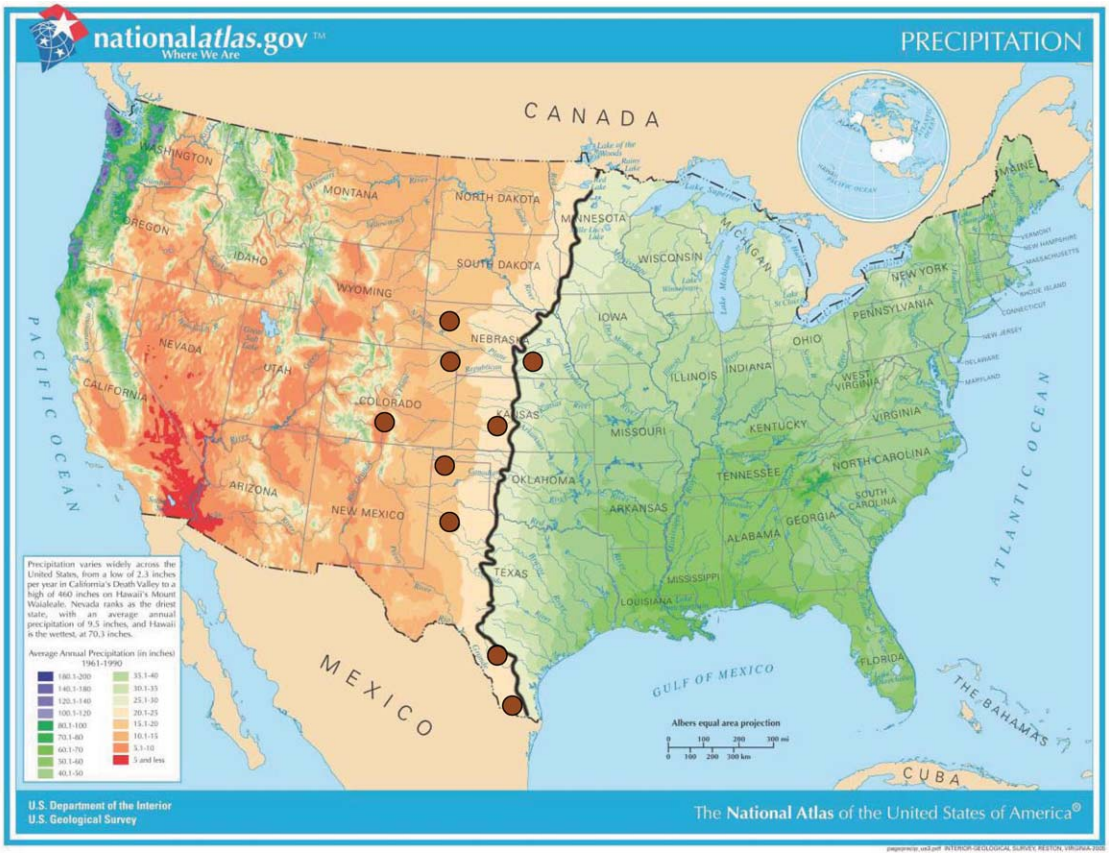

Fig. 1. Map of United States, with sampling locations shown with brown dots. Black line indicates the 22-inch rainfall line.

placed in empty vials for shipment to the USDA–ARS laboratory in Prosser, WA for *Ca.* L. solanacearum testing by polymerase chain reaction (PCR) assay. At harvest a sample of 100 tubers were collected from each field and sent to Weslaco to score the percentage showing ZC symptoms. Tubers were cut at the stem end and scored positive for ZC if they showed the typical starburst necrosis.

***Ca.* L. solanacearum Screening.** Adult psyllids were analyzed for the presence of *Ca.* L. solanacearum using the methods developed by Crosslin et al. (2011). Each psyllid was analyzed individually and processed within 1 wk of field collection. In brief, psyllids were removed from sticky traps and placed into polystyrene vials and shipped to the Prosser laboratory for analysis. Psyllids were removed from the vials with sterile pipet tips and placed into microcentrifuge tubes with 600 μl of CTAB buffer (Zhang et al. 1998). Samples were heated for 15 min at 65°C. Psyllids were then ground with a sterile micropestle and incubated an additional 15 min at 65°C. Samples were left at room temperature for 5 min, and then 300 μl of chloroform was added and the sample was vortexed for 10 s. The emulsion was broken by centrifugation at 15,000 *g* for 3 min, and 500 μl of the upper aqueous phase was removed to a new microcentrifuge tube to which was added 500 μl of isopropanol and 5 μg of glycogen (Invitrogen, Carlsbad, CA). Samples were placed on ice for 15 min and centrifuged for 10 min at 15,000 *g*. Nucleic acid pellets were resuspended in 50 μl of sterile distilled water. Two microliters were used for PCR analysis in 50-μl reactions by using primers OA2 (5′-GCGCTTATTTTTAATAGGAGCGGCA-3′) and OI2c (5′-GCCTCGCGACTTCGCAACCCAT-3′) as described in Crosslin et al. (2011). Ten microliters of the PCR products was analyzed by agarose gel electrophoresis. Presence of the predicted 1,168-bp amplicon indicated that a sample was positive for *Ca.* Liberibacter solanacearum. All other non *B. cockerelli* psyllids on the traps were tested for presence of *Ca.* L. solanacearum by PCR as described.

Data Analysis. Inherent problems always exist with these types of field studies where many potential sources of error often exist across large geographical distances and field seasons. Therefore, a simple but appropriate method of analyzing these data was conducted. Fields surveyed in the study were categorized into growing regions: LRGV, TX Wintergarden, TX High Plains, TX Panhandle, Kansas, Nebraska, and Colorado. These categorizes were selected to provide as much balance of the data as possible. The total numbers of adults captured on traps in the preseason surveys were used to assess the density of migrating psyllids in each region across years. In the preseason

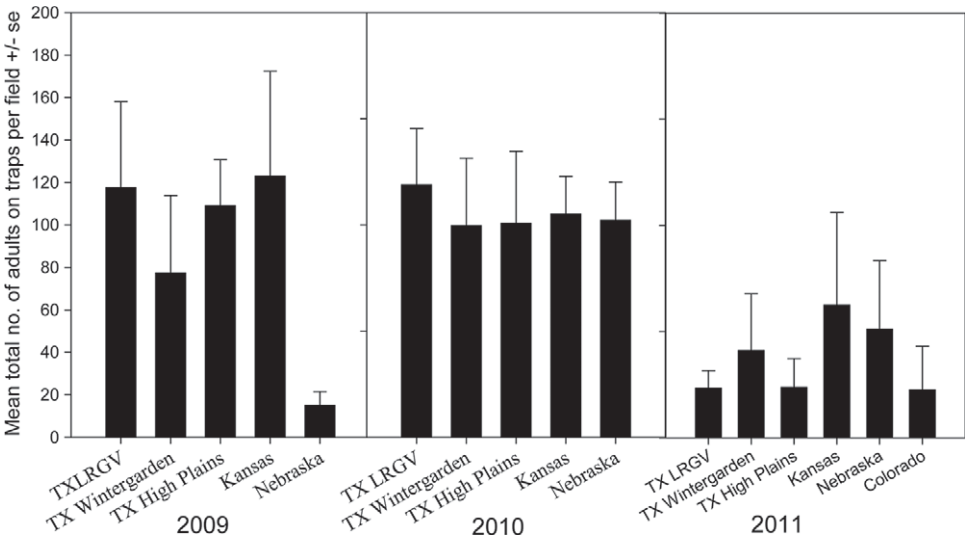

Fig. 2. Total number of adult potato psyllids captured on traps in preseason transects for each growing region.

surveys, total number of adults in traps for each field was averaged to calculate the seasonal mean for each region. The in-season surveys were used to compare the densities of psyllids in commercial fields between regions and across years. To determine the percentage of *Ca.* L. solanacearum infected adults per region, the total number of infected adults caught on the traps for each region was divided by the total number of adults captured in both the pre and in-season surveys. The mean densities and standard error of each psyllid life stage for each field and year were calculated using the univariate procedure in SAS 9.1 (SAS Institute, Cary, NC) and were correlated with the final ZC incidence in the tubers (JMP 9.0.2, SAS Institute). To evaluate the impact of the pest management program, the mean numbers of total nymphs, infected psyllids, and final percentage of ZC in the tubers were compared between the untreated controls and commercial fields in the LRGV. Data from 2009 to 2010 seasons in the LRGV were used because this region consistently had the highest vector and disease pressure.

Results and Discussion

Populations of adult potato psyllids in the preseason transects were variable among regions across years (Fig. 2). The in-season surveys showed the same variability. (Fig. 3). The percentage of *B. cockerelli* in-

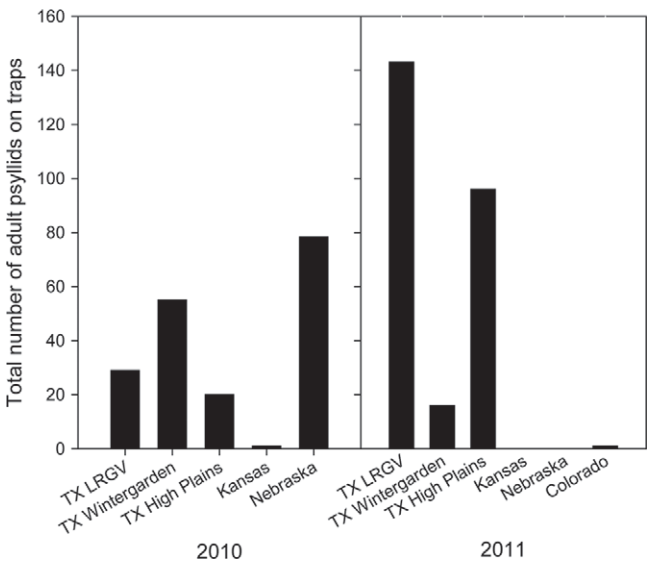

Fig. 3. Mean total number of adult potato psyllids per field captured per on traps in during in-season survey in each growing region by year.

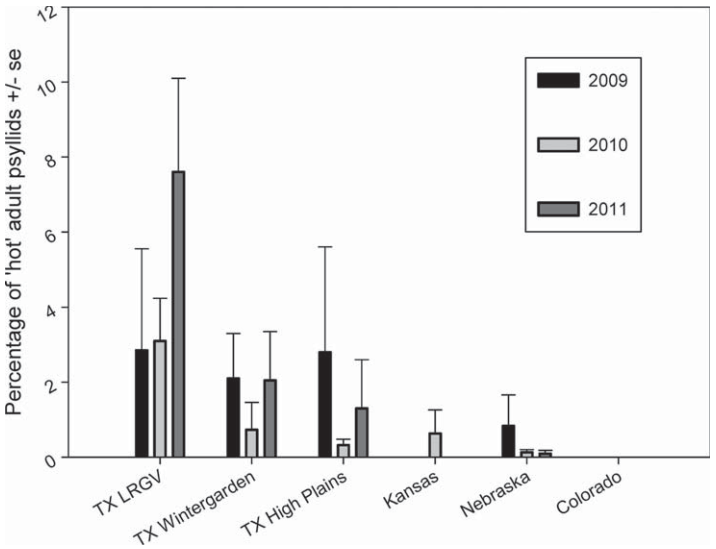

Fig. 4. Percentage of *Ca.* L. solanacearum–infected adult psyllids collected in traps by region.

fected with *Ca.* L. solanacearum also was variable across years but was consistently highest in the LRGV (Fig. 4). The percentage of infected psyllids also showed a strong south to north pattern across the seasonal planting cline. This result is reflected in percentage of ZC in tubers that was variable across years but highest in the LRGV and at very low incidence in the Kansas, Nebraska, and Colorado (Table 1). In the correlation analysis (Fig. 5), the average numbers of total large nymphs and infected adult psyllids per field were both positively correlated with ZC incidence in the tubers at harvest (Figs. 6 and 7).

In the evaluation of the impact of the pest management program in the LRGV, the total numbers of infected psyllids were similar between commercial and untreated controls However, the average numbers of large nymphs and incidence of ZC was very significantly different between untreated controls and commercial fields (Fig. 8).

The variability in number of adult potato psyllids across regions and across years is typical of a native insect and the stochastic effects of abiotic and biotic mortality factors. Our study showed variability even in a highly managed cultivated cropping system. Very little is known about the ecology of the potato psyllid in North America on noncultivated hosts, such as silverleaf nightshade or wolfberry. The ecology of the psyllid and *Ca.* L. solanacearum on the wild and cultivated host reservoirs could have a large influence on the seasonal dynamics of the pest in potatoes. That the number of infected psyllids was consistently highest in LRGV could be further evidence of a wild host reservoir for the *Ca.* L. solanacearum in South Texas and northern Mexico. In addition, the diversity of solanaceous plant species in this region is high with eight herbaceous species and six woody perennials (Richardson 1995, Everitt et al. 1999, Everitt et al. 2002). Although the acreage of cultivated hosts such as tomatoes and peppers is small, these crops may serve as a seasonal refuge for the psyllid, pathogen, or both. Greenhouse tomatoes grown in the state of Tamaulipas, Mexico, adjacent to the LRGV, may serve as a minor reservoir especially considering that temperatures and humidity are regulated in these environments, which may favor the pathogen and vector. Weather may be interacting with the *Ca.* L. solanacearum in the wild host reservoirs that may be influencing the percentage of migrating adults that are positive for the pathogen. Temperature is one of the abiotic factors that is known to influence the survival of *Ca.* L. solanacearum in its host plant. Munyaneza et al. (2011b) report that temperatures <17°C and >32°C are detrimental to *Ca.* L. solanacearum. It is common for spring and summer temperatures to reach and exceed 32°C, as was the case in 2011 with the southern Great Plains experiencing extreme drought and a prolonged heat wave. Weather conditions later in the season are warmer as planting follows the seasonal cline from south to north. This may explain the result that later plantings experience a lower incidence of ZC. However, a shift to later plantings is not ideal because higher temperatures reduce the size and yield of the tubers at harvest.

The two key predictors of ZC at harvest are the number of *Ca.* L. solanacearum–infected adult psyllids

Table 1. Percentage of ZC-infected tubers in commercial fields and untreated controls by region

Region	Commercial fields			Untreated controls		
	2009	2010	2011	2009	2010	2011
Texas LRGV	1.88	0.15	0.03	57.5	36.3	14
Texas Wintergarden	5.5	0.1	4		0	
Texas High Plains	2	0.45	0.81	0.009	2.26	0.05
Kansas	0	0.1	0.05	0	0	0
Nebraska	0	0	0		0	0
Colorado			0			0

Multivariate

Correlations

	AvTotEggs	AvTotSmNy	AvTotLarNy	AvTotNym	AvTotAds	AvInfAds	ZC
AvTotEggs	1.0000	0.6932	0.5511	0.8648	0.4763	0.0707	0.0934
AvTotSmNy	0.6932	1.0000	0.7100	0.9521	0.6033	0.1657	0.1437
AvTotLarNy	0.5511	0.7100	1.0000	0.7539	0.5568	0.7458	0.7211
AvTotNym	0.8648	0.9521	0.7539	1.0000	0.6128	0.1973	0.1852
AvTotAds	0.4763	0.6033	0.5568	0.6128	1.0000	0.3056	0.2082
AvInfAds	0.0707	0.1657	0.7458	0.1973	0.3056	1.0000	0.9619
ZC	0.0934	0.1437	0.7211	0.1852	0.2082	0.9619	1.0000

Pairwise Correlations

Variable	by Variable	Correlation	Count	Lower 95%	Upper 95%	Signif Prob
AvTotSmNy	AvTotEggs	0.6932	20	0.3615	0.8691	0.0007*
AvTotLarNy	AvTotEggs	0.5511	20	0.1437	0.7988	0.0118*
AvTotLarNy	AvTotSmNy	0.7100	20	0.3901	0.8770	0.0005*
AvTotNym	AvTotEggs	0.8648	20	0.6842	0.9455	<.0001*
AvTotNym	AvTotSmNy	0.9521	20	0.8805	0.9812	<.0001*
AvTotNym	AvTotLarNy	0.7539	20	0.4673	0.8971	0.0001*
AvTotAds	AvTotEggs	0.4763	20	0.0428	0.7589	0.0338*
AvTotAds	AvTotSmNy	0.6033	20	0.2193	0.8254	0.0049*
AvTotAds	AvTotLarNy	0.5568	20	0.1516	0.8018	0.0108*
AvTotAds	AvTotNym	0.6128	20	0.2336	0.8302	0.0041*
AvInfAds	AvTotEggs	0.0707	20	-0.3839	0.4976	0.7672
AvInfAds	AvTotSmNy	0.1657	20	-0.2987	0.5667	0.4850
AvInfAds	AvTotLarNy	0.7458	20	0.4526	0.8934	0.0002*
AvInfAds	AvTotNym	0.1973	20	-0.2687	0.5884	0.4045
AvInfAds	AvTotAds	0.3056	20	-0.1583	0.6590	0.1900
ZC	AvTotEggs	0.0934	20	-0.3641	0.5147	0.6952
ZC	AvTotSmNy	0.1437	20	-0.3191	0.5512	0.5456
ZC	AvTotLarNy	0.7211	20	0.4092	0.8821	0.0003*
ZC	AvTotNym	0.1852	20	-0.2803	0.5802	0.4344
ZC	AvTotAds	0.2082	20	-0.2581	0.5958	0.3785
ZC	AvInfAds	0.9619	20	0.9044	0.9851	<.0001*

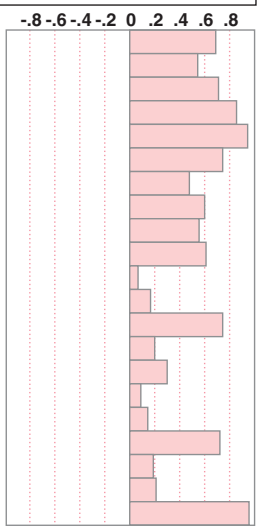

Fig. 5. Correlation of the average densities of potato psyllid immature life stages, total adults, and infected adults per field with final ZC percentage in harvested tubers. (Online figure in color.)

and the number of large nymphs. The density of infected adults increases the opportunity and probability of disease transmission. During our 3-yr study, we did not find ZC in any tubers without previously finding infected psyllids in the traps. Therefore, trapping and assessment of adults for *Ca.* L. solanacearum seems to be a key predictor of ZC risk and should be an integral part of any long-term pest management program. The density of large nymphs correlates with final ZC. Development of nymphs allows for vertical (maternal) transmission of *Ca.* L. solanacearum from

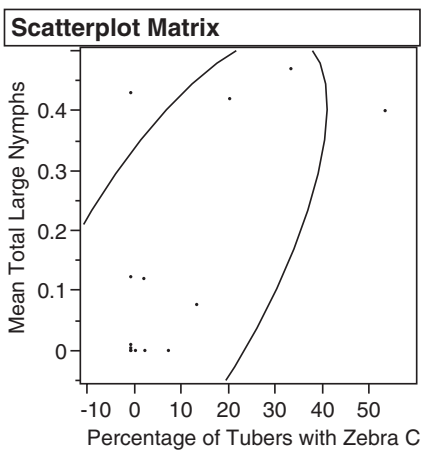

Fig. 6. Correlation of mean number of large potato psyllid nymphs (AvTotLarNy) and final percentage of zebra chip in harvested tubers (uploaded separately).

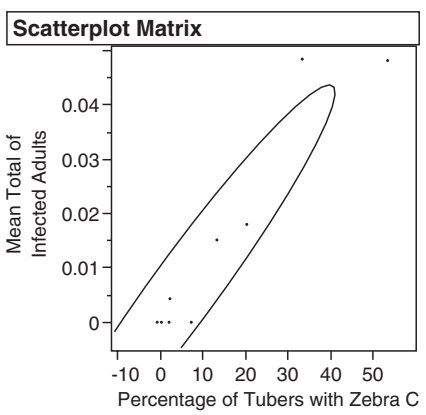

Fig. 7. Correlation of mean number of infected potato psyllid adults (AvHotads) and final percentage of zebra chip in harvested tubers (uploaded separately).

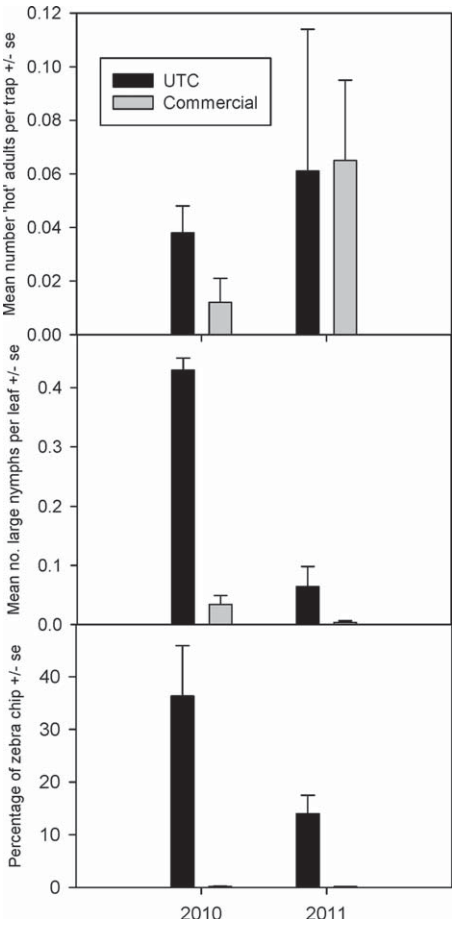

Fig. 8. In the LRGV of Texas, differences in mean numbers of infected adult psyllids and large nymphs and percentage of ZC-infected tubers are shown for the untreated control plots and in commercial fields where potato psyllids were controlled using a pest management program.

the colonizing adults into the subsequent generation (J.E.M., unpublished data). Emergence of *Ca.* L. solanacearum infected adult psyllids within the field leads to spread of the disease throughout the field (D.C.H., unpublished data). Therefore, minimizing the in-field reproduction with effective insecticides can dramatically reduce the incidence of ZC in the tubers even if significant numbers of the early colonizing adult psyllids are infected. Throughout the study many of the commercial fields in the LRGV, Pearsall and Olton experienced significant early season pressure, but the final level of ZC was low, apparently due to intensive pest management programs.

The impact of the pest management program was very apparent in the comparison of the untreated controls and commercial fields in the LRGV. Both untreated controls and commercial fields experienced consistently high levels of infected adults; yet, the percentage of ZC in the tubers in the commercial fields was low (0.1–5%). In comparison, the high level of ZC in the untreated controls showed that without control of the psyllid, the crop is not marketable. The insecticides used in the intensive management program were neonicotinoids at planting, followed by foliar applications of spirotetramat, abamectin, dinotefuran and pymetrozine all of which are systemic and slow acting with no known knockdown effect on the adults. Yet, proper timing and application of these compounds seemed to provide excellent control of ZC. This may indicate that control of in-field immature stages of the psyllid is a critical component in reducing ZC incidence. Broad-spectrum insecticides that target migrating adults do not seem to be effective, are not selective, and are probably negatively impacting populations of beneficial insect and spider predators. Finally, the length of control is not known, but it seems from laboratory and field cage experiments that late-season applications could be reduced or eliminated based on incubation period of *Ca.* L. solanacearum (Munyaneza et al. 2009, Buchman et al. 2011). Further research is required to define the period of time needed to economically and efficiently control potato psyllids to reduce the incidence of ZC in the tubers.

From this study it seems that a disease forecasting model that incorporates regional sampling of infected psyllids and key weather variables could be developed. Seasonal wind events seem to be triggers for psyllid migration south and north after the seasonal cline. Temperatures could be used to estimate the level or viability of *Ca.* L. solanacearum in the local area. For growers to fully use a disease forecasting model, monitoring of immature, trapping of adult psyllids, and assessment of the percentage of adult psyllids that are positive for *Ca.* L. solanacearum are needed. Monitoring of immature psyllids will probably require sampling of large numbers of potato leaves (100 leaves per field) and adequate magnification to check for eggs and small and large nymphs. Trapping of adults is easily accomplished with commercially available yellow sticky traps. With adequate magnification growers or consultants could identify, count, and remove potato psyllids for assessment of *Ca.* L. solanacearum. From this point, commercial diagnostic laboratories would be needed to determine the percentage infected with *Ca.* L. solanacearum.

With the available pest management tools, management of ZC in potatoes is possible. However, current best management practices require intensive control of the vector insect. Disease resistant potatoes or bactericides that target *Ca.* L. solanacearum could increase the sustainability of potato production in areas affected by ZC. This is particularly critical because ZC is spreading rapidly around the world to key potato production areas such as the U.S. Pacific Northwest in North America and New Zealand in the Southern Hemisphere.

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