American Journal of Potato Research (2020) 97:278–288
https://doi.org/10.1007/s12230-020-09772-6

Effects of Potato Psyllid Vector Density and Time of Infection on Zebra Chip Disease Development after Harvest and during Storage

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Published online: 1 April 2020

Abstract

"*Candidatus* Liberibacter solanacearum" (Lso) (="*Candidatus* Liberibacter psyllarous") is an uncultured, phloem-limited bacterium that is associated with zebra chip disease (ZC) in potato (*Solanum tuberosum* L.) and transmitted by the potato psyllid (*Bactericera cockerelli* (Šulc)). Vector density and timing of infection have been shown to affect ZC prevalence at harvest; however, little work has been done on disease development during storage. Here we confirm with field-cage trials that ZC prevalence at harvest was greater with increased time between inoculation and vine kill. Moreover, we show that with Pacific Northwest growing conditions, ZC can develop over time during storage. Plants inoculated 2 to 3 weeks before vine kill showed little or no ZC symptoms in tubers at harvest, but higher prevalence of symptoms after 3 months in storage. For plants inoculated at 4 to 5 weeks before vine kill, tubers exhibited notable symptoms at harvest, but still showed evidence of symptom development after storage. Plants inoculated within 1 week before vine kill exhibited little or no risk of ZC in tubers at harvest or after storage. Higher vector density tended to contribute to ZC prevalence, but was far less important than timing of infection. These results underscore the potential danger of underestimating ZC prevalence at harvest for tubers being stored long term, and suggest that plants at risk of Lso infection should be protected from potato psyllids until at least 2 weeks before vine kill.

Resumen

"*Candidatus* Liberibacter solanacearum" (Lso) (="*Candidatus* Liberibacter psyllarous") es una bacteria obligada limitada al floema, asociada con la enfermedad de la papa rayada (zebra chip, ZP) en papa (*Solanum tuberosum* L.), que se transmite por el psílido de la papa (*Bactericera cockerelli* (Sulc)). Se ha demostrado que la densidad del vector y el tiempo de la infección afectan la prevalencia de la ZC a la cosecha, no obstante, se ha hecho poco trabajo en el desarrollo de la enfermedad durante el almacenamiento. Aquí confirmamos, con ensayos de jaulas de campo, que la prevalencia de ZC en la cosecha era mayor con aumento del tiempo entre la inoculación y la quema del follaje. Aún más, demostramos que con las condiciones de crecimiento del Pacífico Noroccidental, ZC se puede desarrollar a lo largo del tiempo durante el almacenamiento. Las plantas inoculadas 2 a 3 semanas antes de la quema del follaje mostraron pocos o ningún síntoma de ZC en los tubérculos a la cosecha, pero con una mayor prevalencia de síntomas después de tres meses en el almacén. Para las plantas inoculadas 4 a 5 semanas antes de destruir el follaje, los tubérculos exhibieron síntomas notables a la cosecha, pero aún mostraron evidencia de desarrollo de síntomas después del almacenaje. Las plantas inoculadas dentro de una semana previa a la destrucción del follaje exhibieron algo o ningún riesgo de ZC en tubérculos en la cosecha o después del almacenamiento. Una densidad mayor de vectores tuvo la tendencia de contribuir a la prevalencia de ZC, pero fue mucho menos importante que el tiempo de infección. Estos resultados destacan el daño potencial de desestimar la prevalencia de ZC a la cosecha para tubérculos que serán almacenados por largo tiempo, y sugieren que las plantas en riesgo de infección por Lso deberían protegerse de los psílidos de la papa hasta por lo menos dos semanas antes de la quema de follaje.

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Keywords *Bactericera cockerelli* · Russet Burbank · Tomato potato psyllid

Introduction

The Pacific Northwest (PNW) states of Idaho, Washington, and Oregon account for nearly 60% of potato (*Solanum tuberosum* L.) production in the United States (USDA-NASS Statistics 2017). During recent years, the PNW has seen substantive increases in production costs (Greenway and Rondon 2018; Patterson 2012, 2014) in relation to management of zebra chip disease (ZC), an emerging disease of potato. ZC is associated with the bacterium "*Candidatus* Liberibacter solanacearum" (Lso) (="*Candidatus* Liberibacter psyllarous") (Hansen et al. 2008; Liefting et al. 2008; Sengoda et al. 2010), a phloem-limited organism that remains uncultured. ZC infection in potato results in tubers exhibiting striped necrotic patterns that are more pronounced when tubers are fried, which makes chips and fries unmarketable (Munyaneza et al. 2007a, 2008). First identified in potato in the PNW at the end of the 2011 season (Crosslin et al. 2012a, 2012b; Hamm et al. 2011; Nolte et al. 2011), ZC continues to be a management concern in the region.

Lso is transmitted by the potato psyllid, *Bactericera cockerelli* (Šulc) (Hemiptera: Triozidae) (Hansen et al. 2008; Liefting et al. 2008; Munyaneza et al. 2007a, 2007b; Sengoda et al. 2010). Monitoring efforts in Idaho (Wenninger et al. 2017), Washington (Munyaneza et al. 2009), and Oregon (Rondon 2012) show that potato psyllids occur at relatively low levels during much of the year, but may increase considerably toward the end of the potato growing season. This increase mainly occurs as much of the crop is being vine killed or otherwise close to being harvested. At this time, growers may be less inclined to apply insecticides due to limited yield effects from managing direct foliar pests. Moreover, late-season insecticide options are limited by pre-harvest interval restrictions. It is important to know to what extent late-season infection with Lso contributes to ZC development since this information will better inform management strategies. This is especially critical in the PNW, where most potatoes are stored for later use in processed potato products (Holland and Beleicks 2006; Taylor et al. 2007).

Several studies have examined the effects of timing of infection on Lso and/or ZC symptom development in potato tubers at harvest. Potato plants that are infected earlier during the season show greater incidence and severity of ZC (Gao et al. 2016; Rashed et al. 2013, 2014, 2015). ZC symptoms have been shown to develop in tubers that were inoculated as late as two weeks (Rashed et al. 2014) before harvest or even when infection occurred within two days before vine kill and tubers were harvested one month later (Rush et al. 2014, 2015). In another study, tubers from plants infected 4 days before harvest showed increased Lso incidence after cold storage and simulated retail storage, though ZC symptoms developed only for plants infected 10 or 14 days before harvest (Rashed et al. 2018). Similarly, plants infected 1 week before harvest, showed higher Lso development when held at room temperature for longer periods following cold storage (Rashed et al. 2015). All of these studies were conducted under Texas growing conditions—often with tubers harvested while potato vines were still green—using either a fresh market variety (Rashed et al. 2018) or chipping varieties not typically grown in the PNW. Growers in the PNW often apply an herbicide or desiccant to kill potato vines before harvest, and potato vines usually are undergoing natural senescence by the time the vines are "killed." Thus, late-season potatoes under PNW growing conditions are in a different physiological state relative to potatoes that are "green harvested" as in these Texas studies. Therefore, the effects of timing of infection on ZC development both at harvest and after storage remain to be investigated for production conditions and market classes that are typical of a majority of the potatoes grown in the United States.

In the current study, we sought to clarify how potato psyllid density and timing of infection affected ZC development both at harvest and after storage. We performed two field studies, each over two years, in which individually caged potato plants were inoculated with Lso-positive potato psyllids at different timings in relation to vine kill, and tubers were rated for ZC symptoms and fry quality both shortly after harvest and after ca. three months in storage. The results presented here clarify how late-season infection with Lso under PNW growing conditions affects disease development both at harvest and during storage, and informs the development of integrated pest management systems for potato psyllids and ZC.

Materials and Methods

2014 To 2015 Field Studies

Studies were conducted at the University of Idaho Kimberly Research & Extension Center, near Kimberly, Idaho. 'Russet Burbank' seed pieces were planted by hand ca. 30 cm deep on 24 April 2014 and 21 April 2015. During 2014, eight total replicates of each treatment were established; during 2015, ten replicates were planted. Individual plants were caged ca. one month after planting, just as some plants were beginning to emerge. The "hoop house"' style cages were constructed using fiberglass poles and mesh insect netting. The frame for each cage was made by curving a fiberglass pole into a parabolic

shape and inserting the two ends of the pole into the soil with the ends 0.9 m apart; a second pole was positioned in the same manner parallel to and 0.9 m from the first pole. In this way a 1-m tall frame was made with a "footprint" of 0.9 × 0.9 m. Over this frame, we draped a piece of mesh netting (0.4 × 0.45 mm hole size) and buried the edges of the netting in the soil around the perimeter of the frame. Field plots were maintained using standard agronomic practices with respect to fertilizer, irrigation, herbicide, and fungicide application; however, herbicide management of weeds around cages was supplemented with hand weeding. No insecticides other than those described below were applied to the plots.

Plants were inoculated using potato psyllids from Lso-positive colonies that were maintained in a greenhouse. The greenhouse was maintained between 25 to 31 °C, an average of ca. 30% RH, and with a photoperiod of 16:8 (light:dark). Natural lighting was supplemented with artificial lights to extend the photoperiod as necessary. Psyllids were held in cages with both Russet Burbank potato and 'Yellow Pear' tomato (*Solanum lycopersicum*). Plants were grown in pots of ca. 8.5 cm length × 8.5 cm width × 9.5 cm height, with a soil mixture of 4:4:4:1 peat moss: compost: coconut coir: perlite. Plants were fertilized once weekly with ca. 17 g of 24:8:16 N:P:K fertilizer per gallon of water (MiracleGro® All Purpose Plant Food, Scotts Company, Marysville, OH). Plants were replaced as needed. The presence of Lso in potato psyllids was determined by Polymerase Chain Reaction (PCR) using methods described by Wenninger et al. (2017). The Lso status of the colonies was regularly tested and typically ranged from 80 to 100%. The Central psyllid haplotype and Lso B haplotype were confirmed prior to inoculations also as described previously. Briefly, psyllid haplotype was determined by partial sequencing of the mitochondrial CO1 gene (Swisher et al. 2012) and Lso haplotype was determined using the CAPS marker designed in the 16S–23S interspace region of the bacterium genome (Dahan et al. 2017).

Inoculations using 2 or 5 psyllids per plant were conducted 7 weeks, 3 weeks, 1 week, or 2 days before vine kill. Plants were inoculated with psyllids by opening a glass vial near the soil surface at the base of a green stem, allowing the psyllids to walk out of the vial and onto the plant. One set of plots served as a check and was not inoculated with psyllids. The plots that were inoculated 7 weeks and 3 weeks before vine kill were sprayed with abamectin (21.5 g ai per hectare in 64 l of water per hectare) one week and two weeks following inoculations using a CO_2-powered backpack sprayer. This was done to kill psyllids and prevent population development that could considerably increase inoculum levels relative to treatments with later inoculation timings.

Plants were mechanically vine killed using pruning shears on 4 September 2014 and 2 September 2015. All tubers under each plant were harvested by hand two weeks after vine kill and transferred to a storage facility in which they were cured for up to two weeks at 12.8 °C with 95% RH. At that point (26 September 2014 and 9 October 2015), half of the replicates were evaluated for ZC symptoms and fry color (see *Tuber evaluation*, below). For the remaining replicates, the storage temperature was decreased by 0.3 °C per day until reaching a final holding temperature of 7.2 °C, at which point the tubers were stored for an additional 67 (2014) or 65 (2015) days before evaluation. Thus, the second evaluation occurred after a total of ca. 90 days in storage.

2016 To 2017 Field Studies

Studies were conducted as described above under *2014 to 2015 field studies* except that different inoculation treatments were used. In addition, this set of studies featured ten replicates per treatment in each of the two years. Plots were planted on 29 April 2016 and 2 May 2017. All inoculations featured four psyllids per plant and were conducted 5, 4, 3, 2, or 1 week(s) before vine kill. One set of plots served as a check and was not inoculated with psyllids. During 2016, early senescence of all potatoes eliminated the 5-week treatment. The plots that were inoculated 5, 4, or 3 weeks before vine kill were sprayed with abamectin one week and two weeks following inoculations; the 2-week treatment was sprayed one week following inoculation.

Plants were mechanically vine killed on 2 September 2016 and 6 September 2017. Tubers were harvested by hand 13 (2016) or 23 (2017) days after vine kill and transferred to a storage facility as described above under *2014 to 2015 field studies*. On 5 October 2016 and 6 October 2017, half of the replicates were evaluated for ZC symptoms and fry color (see *Tuber evaluation*, below). The remaining replicates were held in storage, as described above under *2014 to 2015 field studies* for a total of 88 (2016) or 80 (2017) days before evaluation.

Tuber Evaluation

Each individual tuber, separately for each plant, was cut using a Keen Kut Shoe Stringer French fry cutter (Shaver Specialty, Torrance, CA) and a fry plank (3.0 cm × 0.8 cm) was removed for ZC symptom rating and fry quality evaluations. All raw tubers harvested from each plant were evaluated. The plank that was used for evaluation included all or most of the stolon, where ZC symptoms should be most evident (Rashed et al. 2013; Navarre et al. 2009). Each plank was given a categorical ZC symptom rating of A (no symptoms), B (some visual discoloration near the stem end), or C (obvious ZC symptoms with discoloration throughout the tuber). Because roughly 95% of tubers across the four years of studies fell into either the A or C categories, we excluded B ratings from analyses and used the proportion of tubers from each plant with a rating

of C (severe ZC) as the response variable. The remaining tissue from each tuber—separately for each of the three rating categories—was subsampled at the stem end and a composite sample of ca. 25 g was tested for Lso by real time PCR in order to confirm ZC symptom ratings.

The 25 g tuber sample was macerated in a masticating juicer (Omega J8006; Omega Juicers, Harrisburg, PA) and the juice added to 10 mL CTAB tissue extraction buffer (5% CTAB with NaCl and Tris HCl). The sample was vortexed to mix thoroughly, passed through mesh to filter out large particles and 1 mL of the solution was added to a 2 mL microcentrifuge tube. DNA from the sample was then purified for real time PCR using a Kingfisher mL magnetic particle processor (Thermo Scientific, Vantaa, Finland) and the Promega Wizard Magnetic DNA Purification System for Food Kit (Promega, Madison, WI). PCR was carried out on a BioRad CFX Connect (Bio-Rad Laboratories, Hercules, CA) using 2 μL of DNA to 18 μL of master mix. The master mix consisted of 1 μL forward primer, 1 μL reverse primer, 10 mL Taqman Environmental Master Mix, 0.5 mL probe and 5.5 mL PCR-grade water for each reaction. For analysis and quantification of results, the Ct values of the standards were used to form a standard curve, ensuring that the r-squared values were always 0.91 or higher. Values (Ct) for the samples were then compared to the standard curve to determine relative quantities of Lso DNA in the samples.

Tuber planks were fried in canola oil at 191 °C for 3.5 min. From each plot, we fried up to ten planks from each of the three ZC rating categories. Fried planks were again rated for visual ZC symptoms as well as for fry quality. Within 3 min of frying, fry color was determined using a Photovolt Reflection Meter (model 577, Photovolt Instruments Inc., Minneapolis, MN). A green filter was used and calibrated using a black-cavity standard as 0.0% reflectance and a white plaque (Cat. No. 26–570-08) as 99.9% reflectance. Measurements were taken on the bud and stem ends of each plank, and mean fry color reflectance was taken as an average between these two measurements. A relationship between USDA fry color and reflectance as measured by our instrument and methodology was previously established. Briefly, a USDA 1 fry color rating was equal to a 43.0 or greater reflectance rating, a USDA 2 rating was between 43.0 to 35.3 reflectance reading, a USDA 3 rating was between 35.3 to 25.8 reflectance reading, and a USDA 4 rating was less than 25.8 reflectance rating (Kincaid et al. 1993).

Data Analysis

All data were analyzed using SAS 9.4 (SAS Institute 2002–2012, Cary, NC). For ZC incidence data from 2014 to 2015, the effect of the number of psyllids and time of inoculation on the proportion of ZC-infected tubers was analyzed using a Generalized Linear Mixed Model with a binomial distribution and a logit-link function using PROC GLIMMIX. The design was a $2 \times 4 + 1$ design, with two psyllid density treatments by four inoculation timing treatments plus a non-treated check. The proportion of infected tubers was compared among these nine treatment levels (fixed effect), with replicate and the two-way interaction between replicate and treatment included as random effects (Stroup 2014). Single and multiple degrees of freedom orthogonal contrasts were used to break down the overall treatment effect into tests for the main effects of psyllid density and inoculation timing as well as their interaction and selected comparisons with the check treatment. Separate analyses for each year were run for raw and fried tubers as well as for the two evaluation times (shortly after harvest and after ca. three months in storage). ZC incidence data from 2016 to 2017 were analyzed similarly, except that time of inoculation was the only fixed effect. The random effects were replicate and the interaction between replicate and time of inoculation.

For the 2014 to 2015 study, fry color was compared among treatments in a manner similar to that described above for ZC responses, but with the assumption of a normal distribution with fixed treatment effect and a random effect of replication. Separate analyses were conducted for fries examined shortly after harvest and those examined after ca. three months in storage. Similar analyses were performed on the 2016 to 2017 data, except that the model only included the effects of time of inoculation and replicate. For all analyses the statistical significance level was set at $\alpha = 0.05$.

Results

2014 To 2015 Field Studies

For both raw and fried tubers, both shortly after harvest and after ca. three months in storage, the number of psyllids used in inoculations did not significantly affect ZC symptom severity in either year (Table 1). However, the percentage of tubers with severe ZC symptoms tended to be higher in most cases for the 5-psyllid versus 2-psyllid treatment (Table 2). In nearly all cases, no apparent ZC symptoms were observed in the non-inoculated check plots, for fried, at-harvest samples during 2014 (Table 2). For the few samples that fried dark, PCR testing did not show Lso (data not shown).

Inoculation timing significantly affected ZC symptom severity for both raw and fried tubers, both shortly after harvest and after ca. three months in storage during both years of the study (Table 1). In nearly all cases, for both 2014 and 2015, no ZC symptoms were observed in the check, 2-day, and 1-week treatments (Table 3). Moreover, for both raw and fried at-harvest samples in both years, there was significantly greater prevalence of ZC symptoms for the 7-week treatment relative to all other timing treatments, which did not differ among each

Table 1 ANOVAs examining effects of number of psyllids, inoculation timing, and their interaction on the percentage of raw and fried potato tubers with severe ZC symptoms during 2014 to 2015 both after harvest and after ca. three months in storage

			After harvest				After storage			
			Raw		Fried		Raw		Fried	
Year	Effect	df[a]	F	*P* value	F	P value	F	P value	F	P value
2014	No. psyllids	1,24	2.23	0.148	2.65	0.116	0.95	0.338	0.70	0.410
	Inoculation time	3,24	21.2	<0.001	13.98	<0.001	9.91	<0.001	8.68	<0.001
	Psyllids × Time	3,24	2.17	0.110	1.63	0.209	1.97	0.145	2.09	0.128
2015	No. psyllids	1,32	1.27	0.268	1.08	0.307	0.15	0.699	0.00	0.983
	Inoculation time	3,32	18.8	<0.001	17.2	<0.001	21.0	<0.001	22.1	<0.001
	Psyllids × Time	3,32	0.83	0.489	0.30	0.825	1.01	0.401	1.36	0.274

Each raw tuber sample comprised all tubers from a single plant; each fried tuber sample comprised up to ten tubers from each of the three rating categories

[a] Numerator, denominator degrees of freedom

other (Table 3). During 2014, ZC symptom severity after storage was significantly higher for both the 7-week and 3-week treatments relative to the other timing treatments (Table 3). Results after storage were similar during 2015, but the 7-week treatment showed the highest percentage of ZC tubers, with the 3-week also exhibiting greater symptom severity relative to the remaining treatments (Table 3). Thus, during both 2014 and 2015, we observed evidence of an increase in ZC symptoms over time during storage, at least for the 3-week treatment. We did not observe significant interaction effects between vector density and timing of inoculation.

Fry color showed significant responses to the treatment combinations during both 2014 and 2015 after harvest and storage (Table 4). Only for 2014 samples after harvest did the number of psyllids significantly affect fry color. Darker fries were observed for the 5-psyllid treatment relative to the 2-psyllid treatment and the check, which did not differ from each other (Table 5).

Table 2 Mean (± SEM) percentage of raw and fried tubers with severe ZC symptoms from inoculations with different psyllid densities, evaluated after harvest or after storage, 2014 to 2015

		After harvest		After storage	
Year	No. psyllids	Raw	Fried	Raw	Fried
2014	0 (check)	0.0 ± 0.0	2.5 ± 2.5	0.0 ± 0.0	0.0 ± 0.0
	2	2.6 ± 2.6	7.8 ± 3.6	17.8 ± 7.4	18.2 ± 7.2
	5	23.5 ± 10.2	29.2 ± 9.9	30.8 ± 10.4	30.5 ± 10.3
2015	0 (check)	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
	2	15.3 ± 8.2	15.0 ± 8.2	25.3 ± 8.8	25.8 ± 8.8
	5	24.4 ± 9.6	24.6 ± 9.6	27.1 ± 8.5	24.3 ± 8.1

Each raw tuber sample comprised all tubers from a single plant; each fried tuber sample comprised up to ten tubers from each of the three rating categories

Inoculation time significantly affected fry color for both years, both after harvest and storage (Table 4). For samples evaluated after harvest during both years, fry color was significantly darker for the 7-week inoculation treatment relative to all other treatments, which did not differ among each other (Table 6). Mean fry color ratings for the 7-week treatment during both years were equivalent to a USDA 4 rating. During 2014, the other treatments exhibited mean fry colors that were in the USDA 3 rating range, whereas during 2015, mean fry colors were equivalent to a USDA 1 rating. For samples evaluated after storage during 2014, fry color was significantly darker for the 7-week and 3-week treatments (which did not differ between each other), relative to the other treatments, which also did not differ among each other (Table 6). A similar pattern was observed for the 2015 data, though the 7-week treatment was significantly darker than all others, and the 3-week treatment was darker than the remaining treatments except for the check (Table 6). During 2014, the after-storage fry color within each treatment was similar to fry color after harvest. However, during 2015 the after-storage fry color within each treatment tended to be lower, with most means dropping to the USDA 3 category.

During 2014, a significant interaction effect was observed with respect to fry color (Table 4). For both after harvest and after storage samples, the 7-week inoculation treatment showed darker fry color for the 5-psyllid treatment relative to the 2-psyllid treatment (Table 7). Within the other inoculation timings, no significant differences were observed between psyllid density treatments.

2016 To 2017 Field Studies

During 2016, the percentage of tubers exhibiting severe ZC symptoms differed significantly among treatments for raw tubers after harvest and for both raw and fried tubers after storage (Table 8). ZC prevalence in raw tubers was significantly

Table 3 Mean (± SEM) percentage of raw and fried tubers with severe ZC symptoms after harvest and after ca. three months in storage from plants inoculated with psyllids at different times before vine kill, 2014 to 2015

		After harvest		After storage	
Year	Inoculation time before vine kill	Raw	Fried	Raw	Fried
2014	Check (no psyllid inoculation)	0.0 ± 0.0 b	2.5 ± 2.5 b	0.0 ± 0.0 b	0.0 ± 0.0 b
	2 days	0.0 ± 0.0 b	6.2 ± 4.1 b	0.0 ± 0.0 b	0.0 ± 0.0 b
	1 week	0.0 ± 0.0 b	1.3 ± 1.3 b	0.0 ± 0.0 b	0.0 ± 0.0 b
	3 weeks	1.4 ± 1.4 b	10.2 ± 5.9 b	36.9 ± 11.6 a	37.6 ± 11.4 a
	7 weeks	50.8 ± 16.2 a	56.2 ± 14.6 a	60.3 ± 14.6 a	59.7 ± 14.1 a
2015	Check (no psyllid inoculation)	0.0 ± 0.0 b	0.0 ± 0.0 b	0.0 ± 0.0 c	0.0 ± 0.0 c
	2 days	0.0 ± 0.0 b	0.0 ± 0.0 b	0.0 ± 0.0 c	0.0 ± 0.0 c
	1 week	0.0 ± 0.0 b	0.0 ± 0.0 b	0.0 ± 0.0 c	0.0 ± 0.0 c
	3 weeks	1.3 ± 0.86 b	1.0 ± 1.0 b	24.3 ± 8.0 b	21.9 ± 8.0 b
	7 weeks	78.2 ± 13.2 a	78.2 ± 13.2 a	80.4 ± 9.4 a	78.3 ± 9.4 a

Each raw tuber sample comprised all tubers from a single plant; each fried tuber sample comprised up to ten tubers from each of the three rating categories

Means within a year and column that share the same letter are not significantly different based on pairwise comparisons and 95% confidence levels

greater for the 4-week treatment relative to all but the 3-week treatment; the 3-week treatment did not differ from any other treatment (Table 9). Responses were similar in fried tubers, though the differences were not statistically significant. After storage, both raw and fried tubers showed significantly greater percentages of ZC-infected tubers in the 4-week treatment relative to the other treatments, which did not differ significantly among each other (Table 9).

During 2017, treatment effects after harvest were not statistically significant for raw ZC symptoms, though they were marginally significant ($P < 0.10$) for fried tubers (Table 8). For evaluations after storage, both raw and fried tubers showed significant differences in ZC symptoms among treatments (Table 8). After storage, for both raw and fried tubers, the percentage of tubers with severe ZC symptoms was significantly greater for the 5-week treatment relative to all others, which did not differ among each other (Table 9).

In all cases, for both 2016 and 2017 data, no ZC symptoms were observed in the check and 1-week treatments (Table 9). During both 2016 and 2017, ZC symptoms showed evidence of increase over time during storage. Symptoms were rarely observed in the 2-week treatment shortly after harvest; however, after-storage symptoms were observed in this treatment in both raw and fried tubers during both years (Table 9). Evidence of similar changes in ZC prevalence was observed for the 3-, 4-, and 5-week treatments after-harvest versus after-storage.

During 2016, fry color showed significant responses to inoculation treatment after both harvest and storage (Table 10). Fries evaluated after harvest were significantly darker in the 4-week inoculation treatment relative to all other treatments, which did not differ among each other (Table 11). Mean fry color for the 4-week treatment was equivalent to a USDA 3 rating, whereas all other treatments exhibited a mean fry color that corresponded to a USDA 1 rating. Within each

Table 4 ANOVAs examining effects of number of psyllids, inoculation timing, and their interaction on fry color during 2014 to 2015 both after harvest and after ca. three months in storage

			After harvest		After storage	
Year	Effect	df[a]	F	P value	F	P value
2014	No. psyllids	1,24	4.72	0.040	1.00	0.327
	Inoculation time	3,24	64.4	<0.001	77.0	<0.001
	Psyllids × Time	3,24	3.97	0.020	3.55	0.029
2015	No. psyllids	1,32	0.94	0.340	0.71	0.406
	Inoculation time	3,32	122.8	<0.001	138.5	<0.001
	Psyllids × Time	3,32	1.45	0.248	1.22	0.317

[a] Numerator, denominator degrees of freedom

Table 5 Mean (± SEM) fry color from inoculations with different psyllid densities, evaluated after harvest or after storage, 2014 to 2015

Year	No. psyllids	After harvest	After storage
2014	0 (check)	34.9 ± 1.6 a	36.0 ± 2.5
	2	31.2 ± 1.2 a	30.7 ± 1.9
	5	26.9 ± 2.7 b	28.6 ± 2.3
2015	0 (check)	44.8 ± 1.8	32.1 ± 1.5
	2	38.6 ± 2.3	30.8 ± 1.8
	5	36.6 ± 2.8	29.6 ± 1.5

Means within a year and column followed by the same letter are not significantly different based on pairwise comparisons and 95% confidence levels

Table 6 Mean (± SEM) fry color after harvest and after ca. three months in storage from plants inoculated with psyllids at different times before vine kill, 2014 to 2015

Year	Inoculation time before vine kill	After harvest	After storage
2014	Check (no psyllid inoculation)	34.9 ± 1.6 a	36.0 ± 2.5 a
	2 days	32.5 ± 1.8 a	35.8 ± 1.3 a
	1 week	32.4 ± 1.4 a	33.9 ± 1.5 a
	3 weeks	30.1 ± 2.9 a	27.1 ± 2.4 b
	7 weeks	21.2 ± 3.7 b	21.9 ± 3.5 b
2015	Check (no psyllid inoculation)	44.8 ± 1.8 a	32.1 ± 1.5 ab
	2 days	42.0 ± 0.9 a	35.4 ± 1.2 a
	1 week	43.1 ± 1.0 a	34.4 ± 1.8 a
	3 weeks	43.9 ± 2.0 a	29.8 ± 2.0 b
	7 weeks	21.5 ± 3.5 b	21.3 ± 1.0 c

Means within a year and column that share the same letter are not significantly different based on pairwise comparisons and 95% confidence levels

treatment, fry colors after storage during 2016 tended to be darker than ratings after harvest. After storage, the 4-week and 3-week treatments did not differ, and the 1-, 2-, and 3-week treatments did not differ among each other; the check treatment did not differ among the 1-week and 2-week treatments (Table 11).

During 2017, fry color showed significant responses to inoculation treatment after storage, but not after harvest (Table 10). The mean fry color for the check, 1-week, and 2-week treatments was equivalent to a USDA 2 rating, fry color in the 3-week and 4-week treatments corresponded to a USDA 3 rating, and fries in the 5-week treatment corresponded to a USDA 4 rating (Table 11). Thus, fries tended to be darker with earlier inoculation times. Within each treatment, fries evaluated after storage exhibited mean fry colors that were strikingly similar to colors observed after harvest. The 5-week treatment was significantly darker than all other treatments (Table 11).

Table 8 ANOVAs comparing among inoculation times the percentage of raw and fried tubers with severe ZC symptoms, examined either after harvest or after three months in storage, 2016 to 2017

Year	ZC rating	Raw or fried	df[a]	F	P value
2016	After harvest	Raw	4,12	3.79	0.032
		Fried	4,12	2.56	0.093
	After storage	Raw	4,12	5.90	0.007
		Fried	4,12	6.41	0.005
2017	After harvest	Raw	5,15	2.06	0.128
		Fried	5,15	2.38	0.089
	After storage	Raw	5,15	4.63	0.009
		Fried	5,15	4.73	0.009

Each raw tuber sample comprised all tubers from a single plant; each fried tuber sample comprised up to ten tubers from each of the three rating categories

[a] Numerator, denominator degrees of freedom

The 2-, 3-, and 4- week treatments did not differ among each other, nor did the check, 1-, or 2-week treatments (Table 11).

Discussion

Management of ZC in potato is focused on control of the psyllid vector of Lso using insecticides (Echegaray and Rondon 2017; Goolsby et al. 2007). Development of an insecticide program to manage potato psyllids depends both on seasonal phenology of psyllids in the potato crop as well has how ZC development relates to timing of infection. Early infection of potato with the ZC pathogen has been shown to contribute to greater incidence and severity of the disease (Gao et al. 2016; Rashed et al. 2014), underscoring the importance of early season management when psyllids carrying Lso are present. However, in the PNW, potato psyllid

Table 7 Mean fry color for each treatment combination for fries evaluated after harvest or after ca. three months in storage, 2014 to 2015

		2014		2015	
No. psyllids	Inoculation timing	After harvest	After storage	After harvest	After storage
–	Check	34.9 ± 1.6 a	36.0 ± 2.5 a	44.8 ± 1.8	32.1 ± 1.5
2	2 days	31.3 ± 2.2 ab	35.4 ± 2.3 a	42.8 ± 1.2	36.6 ± 2.1
5	2 days	33.6 ± 3.1 ab	36.3 ± 1.4 a	41.2 ± 1.3	34.3 ± 1.4
2	1 week	30.0 ± 1.9 ab	33.4 ± 3.2 ab	43.1 ± 1.2	34.3 ± 2.8
5	1 week	34.8 ± 1.1 a	34.4 ± 0.9 a	43.0 ± 1.8	34.5 ± 2.5
2	3 weeks	33.9 ± 1.5 ab	25.1 ± 4.1 b	42.4 ± 1.6	32.4 ± 3.1
5	3 weeks	26.3 ± 5.3 b	29.1 ± 2.6 ab	45.3 ± 3.7	27.1 ± 2.2
2	7 weeks	29.4 ± 3.9 ab	28.9 ± 4.6 ab	26.1 ± 6.5	20.1 ± 1.4
5	7 weeks	13.1 ± 1.7 c	14.9 ± 2.0 c	16.9 ± 1.8	22.5 ± 1.3

Means within a column followed by the same letter are not significantly different based on pairwise comparisons and 95% confidence levels

Table 9 Mean (± SEM) percentage of tubers with severe ZC symptoms for different timings of psyllid inoculations before harvest, 2016 to 2017

		After harvest		After storage	
Year	Inoculation timing[a]	Raw	Fried	Raw	Fried
2016	Check	0.0 ± 0.0 b	0.0 ± 0.0	0.0 ± 0.0 b	0.0 ± 0.0 b
	1 Week	0.0 ± 0.0 b	0.0 ± 0.0	0.0 ± 0.0 b	0.0 ± 0.0 b
	2 Weeks	0.0 ± 0.0 b	0.0 ± 0.0	2.1 ± 2.1 b	2.3 ± 2.3 b
	3 Weeks	7.3 ± 3.5 ab	16.1 ± 11.2	14.0 ± 9.3 b	17.0 ± 8.8 b
	4 Weeks	25.2 ± 13.7 a	28.8 ± 11.0	48.9 ± 11.2 a	51.9 ± 9.1 a
2017	Check	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0 b	0.0 ± 0.0 b
	1 Week	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0 b	0.0 ± 0.0 b
	2 Weeks	0.0 ± 0.0	2.5 ± 2.5	11.4 ± 8.6 b	10.6 ± 7.9 b
	3 Weeks	4.6 ± 4.6	4.6 ± 4.6	25.7 ± 14.9 b	24.9 ± 14.4 b
	4 Weeks	8.3 ± 8.3	8.3 ± 8.3	30.6 ± 18.5 b	30.6 ± 18.5 b
	5 Weeks	38.5 ± 21.5	39.1 ± 21.2	94.1 ± 3.4 a	94.1 ± 3.4 a

Each raw tuber sample comprised all tubers from a single plant; each fried tuber sample comprised up to ten tubers from each of the three rating categories

Means with the same letter within a year and column are not significantly different based on pairwise comparisons and 95% confidence levels

[a] Early senescence during 2016 eliminated the 5-week inoculation treatment

abundance typically is very low early during the season, increasing considerably around the time of harvest (Munyaneza et al. 2009; Rondon 2012; Wenninger et al. 2017). Similar phenologies have been reported in Texas (Goolsby et al. 2007; Workneh et al. 2014) and New Zealand (Cameron et al. 2009). The degree to which such late-season spikes in psyllid abundance warrant control depends upon how ZC development is influenced, not only at harvest, but also during storage (Rush et al. 2015).

Here, we show that ZC development exhibits a strong relationship with timing of Lso infection. Consistent with previous studies using other varieties and growing conditions (Gao et al. 2009, 2016; Rashed et al. 2013, 2014, 2015), ZC prevalence generally was greater with increased time between inoculation and harvest. Moreover, we show that under PNW growing conditions, ZC can develop over time during storage. Plants that were inoculated with Lso-positive potato psyllids at 2 to 3 weeks before vine kill showed little or sometimes even no symptoms at harvest, consistent with Buchman et al. (2012) who showed that plants infected less than 3 weeks before harvest usually produce tubers without ZC symptoms. However, we observed notable prevalence of ZC symptoms in these tubers after time in storage. This underscores the potential danger of underestimating ZC prevalence of a field being placed into storage for later marketing. Even plants inoculated at 4 or 5 weeks before vine kill (which showed considerable prevalence of ZC symptoms at harvest), exhibited evidence of higher prevalence of ZC after time in storage. Only for plants inoculated at 7 weeks before vine kill was there no evidence of increased disease during storage. Given that it is impossible to know the extent and timing of infection in commercial fields, for any field exhibiting a mild level of ZC incidence at harvest it may be advisable for such fields to be processed as soon as possible to guard against potential progression of symptoms during storage that could more severely affect processing quality later.

Our observation that plants inoculated 2 or 7 days before vine kill had little or no risk of ZC after harvest or storage is more or less consistent with a study conducted by Rashed et al. (2018), showing higher ZC symptoms following storage of tubers from plants inoculated 10 or 14 days before harvest, but not for plants inoculated 4 days before harvest. Interestingly, Rush et al. (2014) observed ZC symptoms when plants were inoculated as late as two days before vine kill; however, these tubers were left in the ground for one month

Table 10 ANOVAs examining effects of inoculation timing on fry color during 2016 to 2017 both after harvest and after ca. three months in storage

			After harvest		After storage	
Year	Effect	df[a]	F	P value	F	P value
2016	Inoculation time before vine kill	4,12	5.01	0.013	4.93	0.014
2017	Inoculation time before vine kill	5,15	1.94	0.148	18.62	<0.001

[a] Numerator, denominator degrees of freedom

Table 11 Mean fry color for each treatment for fries tested after harvest or after three months in storage, 2016 to 2017

	2016		2017	
Inoculation timing	After harvest	After storage	After harvest	After storage
Check	45.3 ± 2.8 a	43.5 ± 1.9 a	38.4 ± 1.9	40.6 ± 0.7 a
1 week	44.7 ± 2.2 a	38.8 ± 1.2 ab	38.1 ± 1.0	40.7 ± 1.1 a
2 weeks	47.5 ± 1.8 a	37.5 ± 2.0 ab	37.5 ± 2.1	37.8 ± 2.1 ab
3 weeks	44.5 ± 2.8 a	33.1 ± 3.9 bc	33.1 ± 5.2	32.9 ± 2.7 b
4 weeks	36.6 ± 3.1 b	29.8 ± 2.1 c	33.7 ± 1.4	32.9 ± 2.3 b
5 weeks[a]	–	–	24.5 ± 5.9	19.1 ± 1.1 c

Means within a column followed by the same letter are not significantly different based on pairwise comparisons and 95% confidence levels

[a] Early senescence during 2016 eliminated the 5-week inoculation treatment

before harvest. Warm soil temperatures might contribute to movement of Lso and disease progression more so than would be expected under PNW conditions in which tubers typically remain in the ground for only 2 to 3 weeks following vine kill and soil temperatures are lower than in Texas. Moreover, unlike in the Texas studies, plants in our study were undergoing natural senescence with few green stems present at the time of the latest inoculations. Lso movement in potato appears to reflect passive movement in the phloem (Cooper et al. 2015; Levy et al. 2011). Thus, it is plausible that Lso might move more readily through the phloem to the tubers when plants are more actively growing, as in the case of the Texas studies. These observations also suggest that symptom development is temperature driven; thus, symptoms might be mitigated somewhat by limiting exposure of late-infected tubers to warm temperatures. However, Wallis et al. (2017) reported that ZC and Lso progression were higher for tubers stored at cooler temperatures.

Lso infection in potato has been shown to increase levels of reducing sugars (Gao et al. 2009) and phenolic compounds (Navarre et al. 2009; Wallis et al. 2012), with the latter effect being responsible for enzymatic browning observed in infected tubers. It is not surprising that our fry color results were more or less consistent with the ZC responses to treatments observed. Fry color was darker or tended to be darker with earlier inoculation times, consistent with increased ZC prevalence. Although it may be possible for tubers to exhibit reduced quality even with no detectable ZC symptoms (Rashed et al. 2013, 2014), we did not observe evidence of this phenomenon in the current study. Moreover, symptom expression across all studies presented here was remarkably similar between raw and fried tubers. ZC symptoms may become more pronounced (Buchman et al. 2011) or sometimes only become visible (Munyaneza et al. 2007a) after frying tubers, with certain varieties being more prone to exhibiting this trait (Munyaneza et al. 2008). However, we rarely observed such effects in the present study with Russet Burbank.

The percentage of tubers that we observed with severe ZC symptoms tended to be higher when 5 versus 2 psyllids were used for inoculations. Gao et al. (2016) and Rashed et al. (2016) showed positive correlations between psyllid density and ZC incidence or severity, but using much higher and broader ranges of psyllid densities for inoculations. However, Buchman et al. (2011) showed that a single potato psyllid was as effective as multiple psyllids at infecting a potato plant, given a long enough inoculation access period. Thus, it appears that timing of infection has a far greater potential effect on ZC prevalence than does psyllid density, which is noteworthy in light of the relatively low psyllid densities typical of potato fields in the PNW (Wenninger et al. 2017).

Potato growers have more limited insecticide options late in the season due to pre-harvest intervals, and are unlikely to see economic returns from managing direct foliar pests very close to harvest. However, the results from the current study suggest that, for situations in which ZC threatens a potato crop, growers should maintain control measures against potato psyllids until at least two weeks before vine kill. Further, when late-season infection occurs in a given field, if possible it is advisable to process tubers from that field soon after harvest, rather than storing the crop. The current study only investigated ZC symptoms after a storage period of three months. We do not have details on the timing of this development, including how quickly the disease develops or whether it might continue to develop beyond three months in storage. Moreover, although no current commercial potato variety is known to exhibit resistance to ZC, it remains to be investigated whether other varieties exhibit similar responses to those that we observed for Russet Burbank regarding ZC development during storage. For breeding programs focused on ZC resistance, tolerance to development of symptoms during storage would be a useful attribute to consider for processing cultivars grown in the PNW.

Acknowledgments We thank William Price for assistance with statistical analysis. We are grateful for the technical support provided by Lucy Standley, Amy Lockner, Lynn Woodell, Anastasia Stanzak, Jessica Vogt, Cheryn Clayton, Vince Adamson, Wyatt Shewmaker, Michaella Owens, Jeremy Kestle, Tucker Daley, Austin Fife, Kortni Cox, Aaron Vogt, Carlie Wilkinson, Jesica Lowe, Kyanne Frandsen, Chelsea Stevens, Ethan Whitten, Kevin Robison, Trent Taysom, Alicia Hodnik, and Brandon Thompson. Funding was provided by grants from the Northwest Potato Research Consortium. All experiments performed in this research comply with the laws of the United States of America.

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