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Assessing Potato Psyllid Haplotypes in Potato Crops in the Pacific Northwestern United States

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Abstract The potato psyllid, *Bactericera cockerelli* (Šulc), is a vector of the bacterium '*Candidatus* Liberibacter solanacearum' (Lso) that has been linked to the economically devastating zebra chip disease of potato. To date, four haplotypes of the potato psyllid have been identified and include Central, Western, Northwestern, and Southwestern haplotypes. Zebra chip was reported in potato crops in the Pacific Northwestern United States for the first time in 2011, and the Lso-infected psyllids collected from zebra chip-affected fields were identified as the Western haplotype. Additional studies have reported a mix of the Western and Northwestern psyllid haplotypes in the Pacific Northwest. The present study further examined psyllid population dynamics over the duration of the 2012 potato season in the Pacific Northwest by haplotype analysis of 864 potato psyllids collected from potato fields in Washington, Oregon, and Idaho. In the Yakima Valley of Washington and the lower Columbia Basin of Washington and Oregon, the Northwestern haplotype was predominant (78 %), and was detected earlier in the season than the Western haplotype. Interestingly, in south-central Idaho, all four psyllid haplotypes were identified, but the predominant haplotype was the Western haplotype (77 %). Here, Northwestern psyllids were detected early in the season from June to mid-August, whereas Central psyllids were detected in late July and thereafter. These results suggest that haplotype composition of psyllid populations in potato fields throughout the 2012 growing season in south-central Idaho differed greatly from those in Washington and Oregon. Additionally, all psyllids were analyzed for the presence of Lso, and no Lso-positive psyllids were found in Washington and Oregon, whereas Lso-positive psyllids were found in south-central Idaho. These Lso-positive psyllids consisted of the Western, Northwestern, and Central haplotypes.

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Resumen El psílido de la papa, *Bactericera cockerelli* (Šulc), es un vector de la bacteria '*Candidatus* Liberibacter solanacearum' (Lso) que se ha asociado con la enfermedad económicamente devastadora del rayado del tubérculo (zebra chip) de la papa. A la fecha se han identificado cuatro haplotipos del psílido de la papa, que incluye a los de la parte Central, Oeste, Noroccidental y Suroccidental. La zebra chip se reportó en cultivos de papa en el Pacífico Noroccidental de los EUA por primera vez en 2011, y los psílidos infectados con Lso de campos afectados por zebra chip se identificaron como el haplotipo del Oeste. Estudios adicionales han reportado una mezcla de haplotipos del psílido del Oeste y Noroccidental en el Pacífico Noroccidental. El presente estudio examinó aún más la dinámica poblacional del psílido durante la duración del ciclo de cultivo de 2012 de la papa en el Pacífico Noroccidental mediante el análisis de los haplotipos de 864 psílidos colectados de campos de papa en

Washington, Oregon y Idaho. El haplotipo Noroccidental fue predominante (78 %) en el Valle de Yakima de Washington y en la ribera baja del Columbia de Washington y Oregon, y se detectó más temprano durante el ciclo que el haplotipo del Oeste. Llama la atención que en el centro sur de Idaho se identificaron los cuatro haplotipos del psílido, pero el predominante fue el del Oeste (77 %). Aquí, los psílidos del Noroccidente se detectaron temprano en el ciclo, de junio a mediados de agosto, mientras que los psílidos Centrales se detectaron desde finales de julio en adelante. Estos resultados sugieren que la composición de haplotipos de las poblaciones del psílido en los campos de papa a lo largo del ciclo de cultivo de 2012 en el centro sur de Idaho fue diferente en gran medida a la de Washington y Oregon. Además, todos los psílidos se analizaron para la presencia de Lso, y no se encontraron positivos en Washington y Oregon, mientras que los Lso-positivos se encontraron en el centro sur de Idaho. Estos psílidos Lso-positivos consistieron de los haplotipos del Oeste, Noroccidental y Central.

Keywords Potato diseases · Psyllid haplotypes · Liberibacter

Introduction

Approximately 55 % of United States potatoes are grown in the Pacific Northwestern states of Washington, Oregon, and Idaho (National Agricultural Statistics Services 2012). In such a large potato production region, many pests and pathogens are present that can be devastating to potato crops. Among these pests, the potato psyllid, *Bactericera cockerelli* (Šulc), came to the forefront during the 2011 potato season. The potato psyllid is a vector of the bacterium '*Candidatus* Liberibacter solanacearum' (Lso), which is associated with zebra chip (ZC) disease of potato (Liefting et al. 2008; Munyaneza 2012). The pathogen causes potato plant stunting, purpling of the leaves, leaf scorch, rapid plant decline, and striped patterns of necrosis in the tubers which make them unmarketable (Munyaneza et al. 2007; Munyaneza 2010; Crosslin et al. 2010; Munyaneza 2012). In 2011, during the ZC outbreak in the Pacific Northwest, potato psyllids from fields in Washington, Oregon, and Idaho, showed a 5–10 % infection rate with Lso, and ZC was reported for the first time in this region (Crosslin et al. 2012a, b). In 2012, ZC was again found in the Pacific Northwest, but the distribution of Lso-infected samples was different from the 2011 season, and concentrated almost exclusively in Idaho (Wenninger et al., unpublished data).

Throughout the United States, four haplotypes of the potato psyllid have been identified, which predominate in specific geographical regions: Central, Western, Northwestern, and Southwestern (Liu et al. 2006; Swisher et al. 2012, 2013a, c, 2014). Haplotyping analyses identified the Northwestern haplotype in Washington state as early as 1998, whereas the Western haplotype was identified as early as 2008 (Swisher et al. 2013a). In 2011, psyllids collected from Lso-infected ZC fields in the Columbia Basin of Washington and Oregon were identified as the Western haplotype with an Lso infection rate of 5–10 %, while psyllids collected nearby in healthy fields in the Yakima Valley were predominantly the Northwestern haplotype and did not carry Lso (Swisher et al. 2012, Crosslin, unpublished data). Taken together, these analyses indicate that the Western haplotype was present in the Pacific Northwest prior to its Lso-infection in 2011. While the important question regarding origin of the Lso in these psyllids remains unanswered, it is possible that environmental factors, grower practices, or greenhouse nursery practices changed prior to the 2011 season, thereby enabling the Lso-infected psyllids to become present in the region.

Following the identification of Lso-infected potato psyllids in the Pacific Northwest, and the finding of two different psyllid haplotypes in this region, questions emerged concerning population dynamics of potato psyllids. While it was long believed that the potato psyllid could not survive the harsh winters of the Pacific Northwest and therefore migrated into the region each season, psyllids were recently found overwintering on the wild host plant *Solanum dulcamara* L. (Murphy et al. 2013; Swisher et al. 2013c). Interestingly, samples of these overwintering psyllids were predominantly of the Northwestern haplotype (97 %), whereas psyllids of the Western haplotype were found at low levels (3 %) and no psyllids of the Central or Southwestern haplotype were detected. Since the Northwestern psyllids have not been identified outside of Washington, Oregon, and Idaho, their ability to overwinter in this region suggests they may be native to the area. As its name suggests, in addition to Washington, Oregon, and Idaho, the Western haplotype has also been identified in Baja Mexico, Southern California, and New Mexico (Liu et al. 2006; Swisher et al. 2012). Due to the large geographical expanse that the Western psyllid covers, it is possible that the Western psyllid migrates into the Pacific Northwest during the spring and summer months from Southern California. Alternatively, it is possible that an additional overwintering host of the Western psyllid has yet to be determined in the Pacific Northwest that could allow the Western psyllid to permanently maintain local populations.

The purpose of this study was to understand the population dynamics of the potato psyllids collected in or near potato fields over the duration of the 2012 potato growing season in the Yakima Valley of Washington, the lower Columbia Basin of Washington and Oregon, and south-central Idaho. The 2012 season was especially interesting because Lso-infected psyllids were present in Idaho throughout the entire season, but no infected psyllids were found in the Yakima Valley of

Washington or lower Columbia Basin of Washington and Oregon. Potato psyllids collected throughout the 2012 potato growing season were analyzed for psyllid haplotype by high resolution melting (HRM) analysis of a portion of the mitochondrial cytochrome *c* oxidase subunit I (CO1) gene. HRM of the CO1 gene has been used previously to consistently identify the four known potato psyllid haplotypes, and has been supported by DNA sequencing analyses (Swisher et al. 2012, 2013a, b, c, 2014; Chapman et al. 2012). Psyllids collected over the course of the potato growing season also were tested for the presence of Lso to determine if the incidence of the bacterium was associated with specific psyllid populations. Haplotyping analyses were conducted to determine which Lso haplotype was present in the Lso-positive psyllids. These studies provide insight into how disease incidence (Lso-infection) is associated with particular psyllid haplotypes throughout the 2012 potato growing season.

Materials and Methods

Origin of Psyllids Potato psyllids were collected from commercial or research potato fields located near Moxee, Prosser, and Paterson (all Washington), near Hermiston, Oregon, and in south-central Idaho. For these distinct locations, the data include psyllids collected from different fields that were pooled together to represent the specific location. Psyllids from near Moxee and Prosser, Washington, and near Hermiston, Oregon, were collected on a weekly or near-weekly basis from potato plants using a gas-powered leaf vacuum device (see Rondon et al. 2012 for description). Psyllids from Paterson, Washington were collected on a weekly basis from yellow sticky cards placed along the edge, but within the potato fields. In south-central Idaho, yellow sticky cards were deployed within six commercial potato fields in Twin Falls, Jerome, Gooding, and Minidoka counties, and in one field at the University of Idaho Kimberly Research and Extension Center. Each sticky trap was attached to a wood lath stake using a binder clip, with the trap positioned just above the potato canopy. Traps were placed within 9 m from the edge of potato fields and replaced at weekly intervals. A maximum of 24 individual psyllids were analyzed per collection date for each collection site.

Nucleic Acid Extractions DNA extractions of the potato psyllids collected near Moxee, Prosser, and Paterson, Washington, as well as near Hermiston, Oregon, were done using the cetyl trimethyl ammonium bromide extraction method described in Crosslin et al. (2011). A Dellaporta DNA extraction method was used to isolate total nucleic acids of potato psyllids collected in south-central Idaho (Hu et al. 2009). All DNA extracts were analyzed for psyllid haplotype by HRM and for the presence of Lso by conventional PCR, as described below.

High Resolution Melting Analysis Haplotyping analyses of the individual potato psyllids were conducted using the LightCycler 480 and LightCycler 480 Gene Scanning Software (Roche Applied Science, Indianapolis, Indiana) as previously described (Swisher et al. 2013c, 2014). For all psyllids collected in Washington and Oregon, a 326-bp partial CO1 amplicon was generated using primers CO1 meltF and CO1 353R (Swisher et al. 2013c). This amplicon clearly distinguishes the Northwestern and the Western psyllid haplotypes from Central and Southwestern haplotypes, however, the Central and Southwestern haplotypes are indistinguishable from each other. For psyllids collected in Idaho the 326-bp CO1 amplicon was used, along with a 67- and/or a 94-bp amplicon (Swisher et al. 2014). The 67-bp partial CO1 amplicon is generated using the CO1 meltF and CO1 meltR primers, and the 94-bp CO1 amplicon is generated using the CO1 F3 and CO1 meltR primers (Swisher et al. 2014). The 326-bp amplicon was used to haplotype 92 of the 144 psyllids collected in south-central Idaho. The 67- and/or 94-bp amplicons were used to haplotype 47 of the 144 psyllids collected in Idaho, many of which gave weak amplification with the 326-bp amplicon. For all HRM analyses, individual psyllid samples from previously published analyses for each of the four known psyllid haplotypes were used as controls (Swisher et al. 2012, 2014).

DNA Sequencing Analysis Psyllids that showed weak amplification during HRM analysis were haplotyped by DNA sequence analysis (5 psyllids collected in south-central Idaho). Conventional PCR as described in Crosslin et al. (2011) was used to generate the 326-bp partial CO1 amplicon. Purified PCR products (Wizard PCR Clean Up Kit; Promega, Madison, Wisconsin) were then directly sequenced using primers CO1 meltF and CO1 353R to determine psyllid haplotypes.

Analysis of Lso Infection All psyllids were tested for the presence of the Lso bacterium as described in Crosslin et al. (2011). Briefly, conventional PCR was done using the primer pairs, OA2 and OI2c and/or OMB-F and OMB-R to detect the Lso. A water-only check and/or a previously determined Lso-free psyllid were used as negative controls in all analyses. Additionally, a previously determined Lso-infected psyllid was used as a positive control in all analyses. A 1.0–1.5 % agarose gel stained with ethidium bromide was used to visualize all PCR reactions, and the presence of the predicted 1168-bp (OA2/OI2c) or 605-bp (OMB-F/OMB-R) DNA bands signified a psyllid was infected with Lso. Haplotyping of Lso was

done using conventional PCR with primers Lso-SSR-1 F and Lso-SSR-1R, as described in Wen et al. (2013).

Results

High Resolution Melting Analysis

A total of 720 individual psyllids were analyzed by HRM from collections made between June and November, 2012, in Washington and Oregon (Fig. 1). Psyllids from Moxee, Washington, between July and October were predominantly (85 %) of the Northwestern haplotype. The Northwestern psyllids were the only haplotype identified at the beginning of the growing season (July 2012), but an increase in the Western population (27 %) was seen toward the end of the growing season in late September and early October (September 24, 2012 to October 8, 2012). Psyllids collected in Prosser, Washington, between June and November, 2012, were also predominantly (98 %) of the Northwestern haplotype. Western psyllids were found in July, August, and October, but did not show an increase as the season progressed.

Psyllids from collections made in Paterson, Washington, comprised both the Northwestern (60 %) and Western (40 %) haplotypes (Fig. 1). The Northwestern haplotype was first detected in mid-July, whereas the Western haplotype was not collected until the end of July. Significant numbers of both haplotypes were present throughout the remainder of the growing season. Similar to what was found in the Paterson collections, the collections made in Hermiston, Oregon, showed a mix of the Northwestern (59 %) and Western (41 %) haplotypes. Again, the Northwestern psyllids were collected earlier in the season, but the Western haplotype appeared shortly thereafter and increased in relative frequency throughout the remainder of the growing season (compare 13 % on July 23, 2012, 35 % on August 20, 2012, and 75 % on September 24, 2012).

All four psyllid haplotypes were identified in Idaho from 144 psyllids collected between June and September, 2012 (Fig. 1). The predominant haplotype in south-central Idaho was the Western haplotype (77 %), which was present in all weekly collections. Psyllids of the Northwestern haplotype were present in June, July and early August, but were not found after mid-August. Interestingly, psyllids of the Central haplotype were found in late July, August, and early September. A single Southwestern psyllid was identified in mid-July. Out of the 144 psyllids tested by HRM from collections made in south-central Idaho, haplotypes for 5 psyllids could not be confidently determined by HRM analysis. The haplotypes of these samples were therefore determined by DNA-sequencing analysis of the 326-bp partial CO1 amplicon; 2 of these psyllids were identified as the Northwestern haplotype, and 3 were identified as the Western haplotype.

Analysis of Lso Infection

Psyllids from collections in Washington, Oregon, and Idaho, were additionally tested for the presence of the Lso bacterium. No Lso was detected in the psyllids collected from Washington or Oregon locations. In contrast, 80 of the 144 psyllids tested from Idaho collections were positive for Lso. The presence of Lso-positive psyllids in south-central Idaho made it possible to compare psyllid haplotypes from Lso-positive and Lso-negative psyllids (Fig. 2). In this region, Lso was detected in Western, Central, and Northwestern psyllid haplotypes. The single Southwestern psyllid found in mid-July tested negative for Lso. Interestingly, in total, 56 % of the Western psyllids, and 73 % of the Central psyllids were positive for Lso, but only 29 % of the Northwestern psyllids were Lso-positive.

Haplotyping analyses of Lso identified 67 Lso-infected psyllids tested from Idaho as carrying Lso haplotype A (Nelson et al. 2011), also known as Type 1 (Wen et al. 2013). Among these 67 psyllids, 57 were the Western haplotype (collected during the months of June, July, August, and September), 9 were the Central haplotype (collected during the months of July, August, and September), and 1 was the Northwestern haplotype (collected in June). No Lso-infected psyllids were identified as carrying Lso haplotype B (Nelson et al. 2011), also known as Type 2 (Wen et al. 2013).

Discussion

This study identified fluctuations of potato psyllid haplotypes from potato fields in the 2012 growing season in the Yakima Valley of Washington, the lower Columbia Basin of Washington and Oregon, and in south-central Idaho. The difference in psyllid haplotype composition between south-central Idaho populations and those in Washington and Oregon was striking. Of the psyllids analyzed from collections made in Washington and Oregon, 78 % were of the Northwestern haplotype and only 22 % were of the Western haplotype. In contrast, in south-central Idaho, 77 % of the psyllids were of the Western haplotype. Interestingly, the remaining 23 % of psyllids were composed of Northwestern, Central, and Southwestern psyllids. This indicates that south-central Idaho may be a 'melting pot' for psyllid populations, at least in comparison to what is observed in the Yakima Valley and Columbia Basin.

Previous haplotyping analyses from psyllids collected on potato and *S. dulcamara* in southern Idaho have identified both the Northwestern and Western psyllids (Swisher et al.

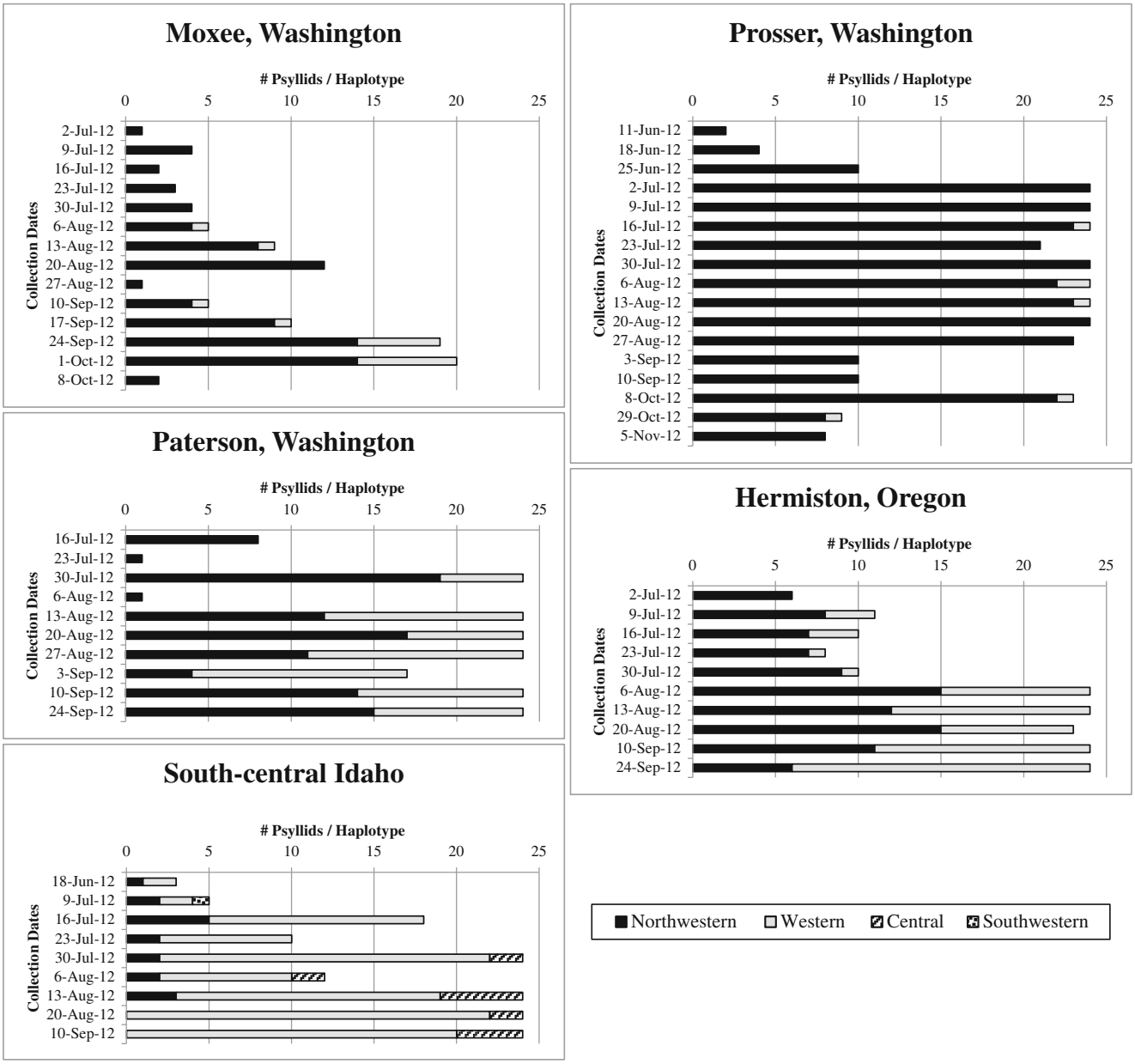

Fig. 1 Summary of HRM results from potato psyllids collected in potato fields in the Pacific Northwest during the 2012 potato growing season. The haplotype of 720 individual potato psyllids collected in the Yakima Valley of Washington (Moxee and Prosser), and the lower Columbia Basin of Washington and Oregon (Paterson and Hermiston), as well as 144 individual potato psyllids collected in south-central Idaho, were determined by HRM analysis of a portion of the mitochondrial CO1 gene

2012, 2013c). Although limited in sample number, these early studies showed that the Western haplotype was predominant on potatoes during the potato season, whereas the Northwestern haplotype was the only population identified overwintering on *S. dulcamara* in Idaho. This present study utilized a much higher sample size and again identified the Western psyllid as the predominant population in south-central Idaho during the potato growing season. It also identified a notable presence of the Central psyllid haplotype in south-central Idaho. To our knowledge, this is the first report of the Central psyllid haplotype in Idaho. However, due to a low number of samples from south-central Idaho in the years prior to the 2012 potato season, it is possible that the Central population has been present in this region before.

An interesting fluctuation of the Northwestern psyllid haplotype and the Central psyllid haplotype in south-central Idaho during 2012 was also noted. The Northwestern psyllids were identified in collections made in June, July, and early August, but were not found in samples after mid-August. In contrast, the Central psyllids were first identified in late July and persisted throughout August and into September. Separating the psyllid haplotypes into groups of Lso-positive or Lso-

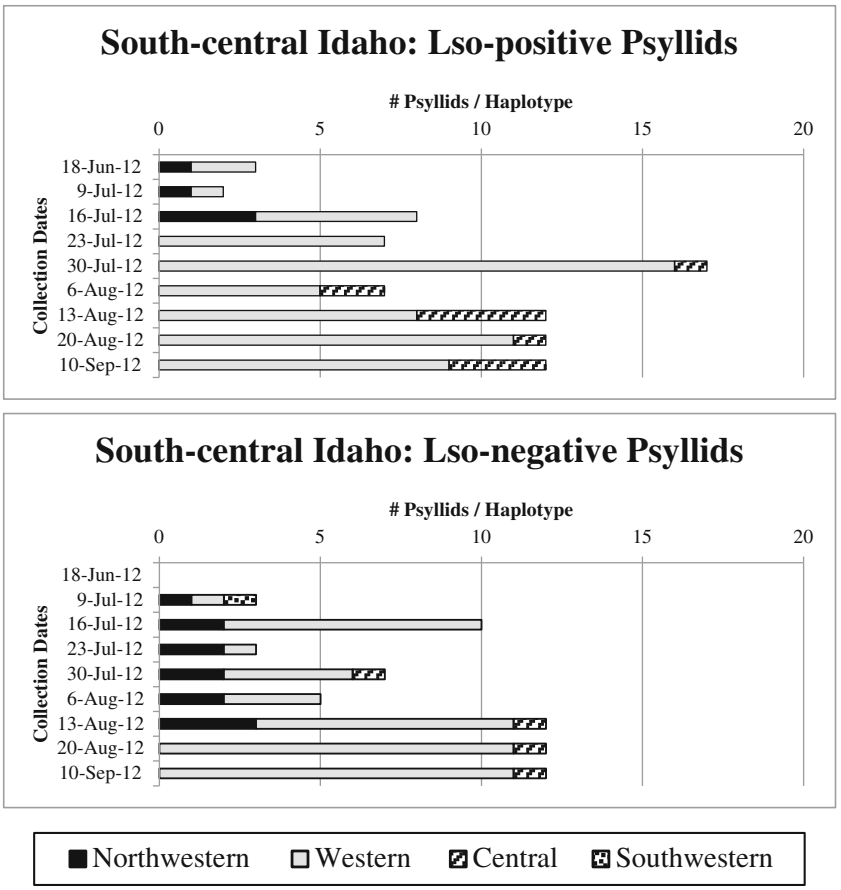

Fig. 2 Comparison of haplotypes from Lso-positive and Lso-negative psyllids collected in south-central Idaho. Psyllids were tested for the presence of the Lso bacterium and subsequently separated into Lso-positive and Lso-negative groups to compare psyllid haplotype profiles between the two groups

negative psyllids provided unexpected results. From collections made in Idaho, 64 out of 111 (58 %) of the Western psyllids and 11 out of 15 (73 %) of the Central psyllids analyzed were Lso-infected, whereas only 5 out of 17 (29 %) of the Northwestern psyllids were infected. While the sample sizes for the Central and Northwestern psyllids were low, the differences in Lso-infection rates between haplotypes, albeit preliminary, may suggest an underlying cause. Two of the possible explanations are considered here: 1) differences in Lso-acquisition rates among the Northwestern, Western, and Central psyllid populations; 2) differential population dynamics due to migration of certain haplotypes (perhaps Western and Central haplotypes) from elsewhere during the summer of 2012. In the latter explanation, the Northwestern haplotype may have been of the local, overwintering population whereas the Western and Central haplotypes may have been seasonal migrants. Studies to understand the biological difference among the psyllid haplotypes are currently underway.

In the Yakima Valley (Moxee, Prosser) of Washington, the Northwestern haplotype was observed earlier than the Western haplotype, and occurred at higher frequency than psyllids of the Western haplotype. Interestingly, in Moxee, Washington, there was a slight increase in Western psyllids as the season progressed, specifically at the end of September and beginning of October. This increase was not seen in Prosser, where only a very low number of Western psyllids were identified in July, August, and October.

The 2012 seasonal progression of psyllid haplotypes in the lower Columbia Basin of Washington and Oregon was slightly different than the population composition seen in the Yakima Valley. In both Paterson, Washington, and Hermiston, Oregon, the Northwestern haplotype was observed prior to the Western haplotype, and was the predominant psyllid haplotype identified throughout the season. However, as opposed to what was found in the Yakima Valley, there was an increase in numbers of the Western haplotype as the potato season progressed. In Hermiston, Oregon, Western haplotype psyllids were more abundant (65 %) than Northwestern psyllids during September.

The present study expands on the knowledge of potato psyllid populations in the Pacific Northwest, and indicates that psyllid populations during the 2012 potato season differed in haplotype composition among populations from south-central Idaho, the Yakima Valley of Washington, and the lower Columbia Basin of Washington and Oregon. This variation in composition between Idaho, Washington, and Oregon highlights the importance of these genotyping studies, and emphasizes the need for continued studies to better understand the seasonal psyllid dynamics and Lso incidences in

the Pacific Northwest. Additionally, results from this study reemphasize the need for analyses of biological differences between psyllid haplotypes. Because of the proximity of these two regions in the Pacific Northwest, the differences in psyllid populations between the regions were unexpected, but the differences could have an effect on the spread of ZC over time, and thereby affect grower practices in these regions.

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