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Biology, Ecology, and Management of the Potato Psyllid, *Bactericera cockerelli* (Hemiptera: Triozidae), and Zebra Chip Disease in Potato

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Keywords

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Abstract

The potato psyllid, *Bactericera cockerelli* (Šulc) (Hemiptera: Triozidae), transmits the pathogen "*Candidatus* liberibacter solanacearum" (Lso), the putative causal agent of zebra chip disease (ZC). ZC is a disease of potato that reduces yield and quality and has disrupted integrated pest management programs in parts of the Americas and New Zealand. Advances in our understanding of the ecological factors that influence ZC epidemiology have been accelerated by the relatively recent identification of Lso and motivated by the steady increase in ZC distribution and the potential for devastating economic losses on a global scale. Management of ZC remains heavily reliant upon insecticides, which is not sustainable from the standpoint of insecticide resistance, nontarget effects on natural enemies, and regulations that may limit such tools. This review synthesizes the literature on potato psyllids and ZC, outlining recent progress, identifying knowledge gaps, and proposing avenues for further research on this important pathosystem of potatoes.

INTRODUCTION

The potato psyllid, *Bactericera cockerelli* (Šulc) (Hemiptera: Triozidae), has been among the most damaging potato pests in North America for over 100 years. In the species description, Šulc (113) observed large numbers of nymphs on pepper plants and stated that "we may infer that the insect can become very destructive" (p. 108). This presaged the frequent outbreaks of this pest that would soon plague potato growers in the western United States and later across the globe. Although psyllid yellows was the primary concern associated with potato psyllids in the early 1900s (93), potato production currently is threatened more by zebra chip disease (ZC) (146). ZC is associated with "*Candidatus* Liberibacter solanacearum" (Lso) (also known as "*Candidatus* Liberibacter psyllaurous"), which is transmitted by potato psyllids (79). ZC is an emerging disease that reduces yield and quality, increases production costs, and complicates integrated pest management for potato wherever the pathogen and psyllid vector occur. Previous reviews have covered potato psyllids and ZC (10, 79), ZC in New Zealand (135), and comprehensive overviews of all psyllid pests of potatoes (146). These reviews should be consulted for earlier work on potato psyllids and ZC. This review summarizes recent insights into potato psyllid biology and ecology, then focuses on advances in understanding and managing the ZC pathosystem, synthesizing progress, and identifying knowledge gaps to set future research directions.

GEOGRAPHIC DISTRIBUTION OF POTATO PSYLLID

Native to western North America, the potato psyllid is present throughout the central to western United States; most Canadian provinces bordering the United States; Mexico; and the Central American countries of Guatemala, Honduras, El Salvador, and Nicaragua (146; **https://gd.eppo.int**) (**Figure 1**). Climate models indicate that nearly 80% of global potato-growing land is suitable for potato psyllids, including more than 96% of such land in South America, Eurasia, and Australia (142). Several introductions have been reported: in New Zealand in the early 2000s; Australia in 2014 to 2017; Ecuador in 2017; and, most recently, Columbia and Peru (14, 146; **https://gd.eppo.int**) (**Figure 1**). Potato psyllids are established in all potato-growing regions of New Zealand, as well as in Western Australia and the Australian territory of Norfolk Island (135, 146) (**Figure 1**).

BIOLOGY AND ECOLOGY OF POTATO PSYLLID

Host Range

Potato psyllids have been observed on many plant species across numerous families; however, reproduction and development occur primarily on plants within the Solanaceae (23, 93, 140). Solanaceous crop hosts include potato (*Solanum tuberosum*), tomato (*Solanum lycopersicum*), pepper (capsicum; *Capsicum* spp.), and eggplant (aubergine; *Solanum melongena*). Noncrop solanaceous hosts reported from North America and New Zealand include various nightshade species (*Solanum* spp.), groundcherry (*Physallis* spp.), matrimony vine (boxthorn; *Lycium* spp.), and several other weeds and ornamentals (23, 36). Potato psyllids also feed and reproduce on plants in the Convolvulaceae, including sweet potato (*Ipomoea batatas*) and field bindweed (*Convolvulus arvensis*) (23, 132). Adults may use a wide diversity of other plant species as transient hosts or shelter hosts that do not support the complete development of immature stages (93, 140).

Haplotypes

To date, four genetically distinct haplotypes of potato psyllids have been described based on high-resolution melting analysis of the mitochondrial *CO1* gene and named after their apparent

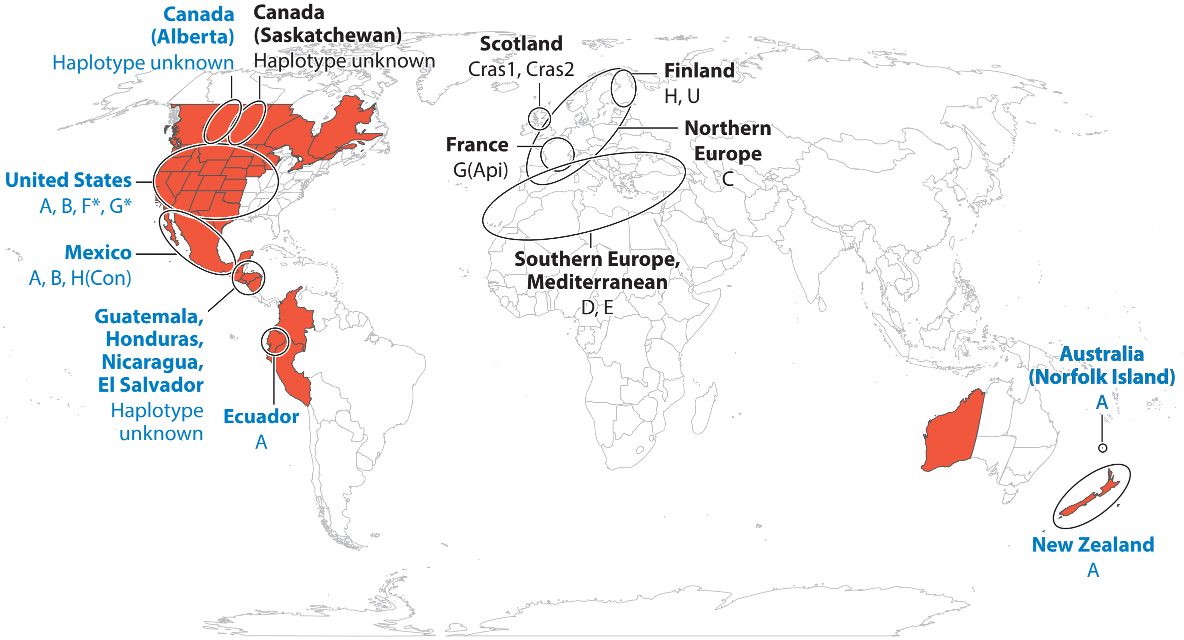

Figure 1

Map showing distributions of potato psyllids by country or state (*red*), approximate distributions of the different haplotypes of "*Candidatus* Liberibacter solanacearum" (Lso), and whether zebra chip disease has been confirmed (*blue text*) or not (*black text*). *Haplotypes F and G were identified, respectively, from one potato tuber sample and an herbarium sample of *Solanum umbelliferum* (19, 54–56, 73, 79, 110, 114, 121, 141, 146; **https://gd.eppo.int**).

geographic associations in North America: Western, Northwestern, Central, and Southwestern (116, 117). Haplotype occurrence and prevalence have been reported extensively in the United States (31, 32, 115–120, 144, 148).

Some differences in biology among haplotypes have been observed, particularly concerning host plant associations, life history traits, and cold tolerance (31–33, 83, 119, 129, 144, 146). Breeding incompatibility has been observed between certain haplotypes (83). However, differences in the transmission efficiency of Lso have not been observed (122). Despite these among-haplotype differences, haplotype characterizations are less accurate predictors of population structure relative to using a broader range of molecular markers such as genome-wide single nucleotide polymorphisms (SNPs) (43, 65).

Life Cycle and Reproductive Biology

Considerable variation exists in findings published on the life history of potato psyllids, attributed primarily to differences in biotic and abiotic environmental conditions associated with each study. Adult longevity in the lab may average approximately 15 days, with some individuals living well over 100 days (83, 93). Females generally live longer than males, and longevity varies on different host plants (83).

Females have been reported to reach reproductive maturity on the day of adult eclosion and males one day after eclosion (79), although earlier reports suggested a longer premating period (93). Oviposition begins within 1–5 days after mating, with older females beginning oviposition sooner after mating than younger females (79). Fecundity varies considerably, ranging from approximately 200 to over 1,000 eggs (e.g., 83, 93). This variation reflects differences in the host plants (23, 83, 84, 93), haplotypes (83, 95), and experimental conditions used. At least some of the variability among these studies might be attributed to changes in psyllid biology related to host switching (68, 95). Fecundity, longevity, and intrinsic rate of increase in potato psyllids were found to be greater under laboratory conditions than under field conditions in a study in south Texas (152), underscoring the need to exercise caution before extrapolating laboratory studies to the field. Additional studies will be needed to better understand life history traits under different field conditions in various localities.

Eggs hatch after 4–6 days at approximately 27°C, with each of the five nymphal instars developing over approximately 2–6 days; potato psyllids tend to develop faster on tomatoes and potatoes than on eggplants and peppers (146, 152). Potato psyllids may complete one generation in under three weeks in the lab or slightly longer under field conditions (152). Development time from egg to adult may be similar or considerably longer on various weed hosts, depending upon their apparent suitability as host plants (23). The sex ratio of newly eclosed adults has been reported to be approximately 1:1 (93, 146).

Evidence of olfactory communication has been demonstrated in the potato psyllid, with males attracted and females repelled by odors from both sexes and a refractory period of diminished attraction after mating (50). Vibrational cues are also involved in communication between the sexes, and the potential for reducing mating by disrupting vibrational communication has been demonstrated in the laboratory (8). The development of applied tools that exploit these behaviors warrants further investigation, though the combination of sensory modalities used in communication between the sexes likely will complicate such efforts.

Endosymbionts

Associations of the primary endosymbiont "*Candidatus* Carsonella ruddii" and the facultative endosymbiont *Wolbachia* with potato psyllids have long been recognized (79). Recently, the presence of other bacterial endosymbionts, including *Liberibacter*, *Sodalis*, and *Rickettsia*, was confirmed in potato psyllids (24). "*Candidatus* Carsonella" and *Sodalis* may benefit potato psyllids by synthesizing essential amino acids lacking in the phloem (24), and the greater abundance of Carsonella in females is consistent with higher demand for amino acids to support reproduction (28). Conversely, *Liberibacter* is known to have adverse effects on the metabolic processes of potato psyllids (4, 85). *Wolbachia* is found in the Central and Western psyllid haplotypes, which might explain the nonviability of eggs produced when females of the Northwestern haplotype mate with males of either of these haplotypes (28, 83); however, this possible explanation requires further study to validate it. Endosymbionts and their interactions with the potato psyllid can be manipulated to reduce the reproductive fitness of the vector (e.g., *Wolbachia*), increase vector susceptibility to natural enemies (e.g., *Rickettsia*), or reduce transmission efficiency (in *Liberibacter*). Further investigations are encouraged into the interactions among potato psyllids and their endosymbionts both to improve our understanding of psyllid biology and to develop control methods (see the section titled Emerging Technologies).

Phenology

The optimum temperature for survival and development of potato psyllids has been estimated to be between approximately 24°C and 27°C but varies depending on factors such as psyllid life stage and host plant (67, 93, 133). The lower developmental threshold has been estimated to range from approximately 4°C to 8°C (67, 133). As temperatures exceed 30°C, oviposition, egg hatching, and survival decrease substantively, with some variation among studies existing in the intensity of effects (67, 93, 133).

Nymphs may be more cold tolerant than adults, but both life stages may survive at least short exposures to temperatures as low as –20°C, and Lso infection may enhance cold tolerance (146). More work is needed to clarify the cold tolerances of potato psyllids, including studies of the interactions among psyllids, Lso, and host plants, but potato psyllids appear to survive at temperatures lower than previously thought (93, 140).

The seasonal phenology of the potato psyllid in potato has been investigated primarily within its native geographic range in the central and western United States (18, 37, 79, 143, 144, 146). Phenology patterns have been similar across most potato-growing regions in the United States, with potato psyllids often found in potatoes at or shortly after emergence and populations peaking shortly before harvest. Similar patterns have been reported in New Zealand (135).

Inverse-distance-weighted interpolation models have been developed to predict the risk of psyllid incidence across landscapes (18). Psyllid abundance appears to be higher in landscapes with high connectivity, low crop diversity, and large natural areas, as well as in areas or years with higher levels of winter moisture (52). These models could be enhanced with a better understanding of factors that contribute to high Lso incidence in psyllids and incorporation of this aspect of ZC risk into prediction tools.

Annual infestations of potato psyllids in potatoes near the Rocky Mountains historically had been thought to result from long-distance migration (61, 87). However, overwintering has also been confirmed in this region on bittersweet nightshade (*Solanum dulcamara*) (81, 144) and matrimony vine (*Lycium* spp.) (129). Seasonal phenologies across Idaho are consistent with the idea that many psyllids infesting potato fields come from local overwintering sources (143). Nevertheless, the overwintering hosts studied to date cannot fully account for potato psyllid infestations on crops in this region (143, 146). Successful overwintering may occur on various transient or shelter hosts (93), and, indeed, autumn-dispersing psyllids feed on a diversity of such plants (26). Further clarification of the importance of other overwintering hosts, including shelter hosts, is needed.

Potato psyllid phenology has been studied less extensively in areas other than the northwestern United States. In New Zealand, seasonal migration has not been observed, and all life stages may be found on noncrop hosts year round, even in areas with frost and snow (135). In regions that do not feature major seasonal changes during the winter and in which suitable host plants are consistently available (e.g., parts of Mexico and Central America), potato psyllids might be able to reproduce and develop year round, but data are needed to test this hypothesis. This hypothesis would be consistent with observations in New Zealand and with evidence from the northwestern United States, where potato psyllids overwinter in a temperature-controlled quiescence rather than in a true diapause (62).

PSYLLID YELLOWS

Psyllid yellows, a condition associated with potato psyllid feeding on potatoes, was widely considered to be the most destructive of all potato disorders in the western United States in the first half of the twentieth century (10, 93, 146). However, as chemical control options developed, the outbreaks faded, as did research into the etiology of psyllid yellows (10, 146). Considerable knowledge gaps remain, including the identification of the suspected salivary toxin or a possible yet-to-be-identified pathogen (146). However, recent decades have shifted attention squarely to ZC.

ZEBRA CHIP DISEASE

Symptoms

ZC was first reported in potato fields near Saltillo, Mexico, in 1994 (79). Aboveground symptoms are like those of psyllid yellows and include chlorosis and purpling of foliage, twisted stems, swollen nodes, aerial tubers, vascular discoloration, and scorching and wilting of leaves. Belowground symptoms include collapsed stolons and enlarged lenticels on tubers. However, the main tuber symptom is brown discoloration of the vascular ring and medullary rays; these are initially expressed at the stolon attachment end but eventually extend through the tuber. Striped necrotic patterns run through the length of tubers, a diagnostic symptom that separates ZC from other potato diseases and led to the name "zebra chip." Tuber symptoms are more pronounced in fried potato products, making them unmarketable due to a burnt appearance and unpleasant taste (79).

Liberibacter, the Putative Causal Agent of Zebra Chip Disease

The bacterium associated with ZC was first detected in 2008 (10, 79). The synonyms "*Candidatus* Liberibacter psyllaurous" and "*Candidatus* Liberibacter solanacearum" are both used in the literature. "*Candidatus* Liberibacter" species are Gram-negative α-proteobacteria, and to date, pathogenic liberibacters have not been cultured in vitro (74). Potato psyllids were implicated in the transmission of the putative causal agent of ZC as early as 2006–2007 and confirmed as the vector of Lso shortly thereafter (10, 79).

Lso Haplotypes

To date, 13 different haplotypes of Lso have been described by SNPs on the 16s rRNA, 16s/23s ISR and 50s rplJ, and rplL ribosomal protein genes: A, B, C, D, E, F, G, G(Api), H, H(Con), U, Cras1, and Cras2. Haplotypes A and B are confirmed to be associated with the potato psyllid and ZC in potato (79). Haplotypes F and G were identified, respectively, from one potato tuber sample from Oregon (121) and an herbarium sample of *Solanum umbelliferum* (73), so transmission details are unknown. Haplotype B has been shown to cause more severe ZC symptoms in solanaceous hosts than haplotype A (57, 58, 122). Numerous weeds, primarily in the Solanaceae, have been found to harbor Lso and/or to be infected with Lso by potato psyllids, though the haplotype has not been identified in all studies (19, 23, 80, 105, 130, 132, 135).

Available evidence suggests that the other Lso haplotypes are of lesser importance in the epidemiology of ZC. The risk may be mitigated by the limited effects of these haplotypes on potato and/or the lack of an efficient psyllid vector that feeds on both potato and other Lso hosts. For example, haplotypes C, D, and E infect apiaceous plants in Europe and the Mediterranean region (5, 6, 54, 55, 79, 86, 114, 146), but *Bactericera nigricornis* (Förster), a vector of haplotype E, is the only psyllid species in Europe known to reproduce on potato (6, 7). Preliminary evidence showed transmission of haplotype E by *B. nigricornis* to potato (6). However, extensive surveys in Spain suggested low ZC risk for potatoes due to scarcity of *B. nigricornis*, low Lso incidence in potential vectors (7), and lack of haplotypes A and B (110). More work is needed to clarify the risk in other parts of Europe. Another species, *Bactericera trigonica* Hodkinson, transmitted Lso haplotype E to potato at low rates and showed very limited settling, oviposition, and feeding rates on potato, suggesting limited epidemiological importance for this species as well (5). In Finland, Lso haplotype C was found in potato, but with no ZC symptoms (55).

The other recently discovered haplotypes [G(Api), H, H(Con), U, Cras1, and Cras2] might also pose little risk to potatoes given their associations with nonsolanaceous hosts and/or psyllids that do not feed on potato (19, 54–56, 114). Lso was recently detected in cottony ash psyllids [*Psyllopsis discrepans* (Flor)], but the haplotype was not reported (141). As more Lso haplotypes will almost certainly be discovered, the complex interactions among plant and psyllid hosts of these haplotypes must be further explored and considered with respect to ZC epidemiology and other diseases that may be associated with these haplotypes.

Geographic Distribution of Zebra Chip Disease

Following the first report of ZC in 1994, the disease was not reported in the United States until 2000, when it was found in commercial potato fields in Texas (10, 79). By 2004, ZC was causing considerable damage in southwest Texas, and incidence was as high as 80% in some fields in Mexico (10, 79). By 2007, ZC symptomatic potatoes had been reported from Nebraska, Colorado, Kansas, New Mexico, Arizona, Nevada, and California. During the 2011 growing season, ZC was reported in Idaho, Washington, and Oregon (79), which together make up a region that produces more than half of US potatoes. ZC has since been reported in Wyoming and Utah, as well as Alberta, Canada (146; **https://gd.eppo.int**). The Lso haplotypes A and B have been observed widely in North America, with individual samples of haplotypes F and G also found (**Figure 1**).

ZC similarly spread south through Central America. Having been previously reported from Guatemala, ZC was reported from Honduras as early as 2006, Nicaragua in 2011, and El Salvador in 2012 (79, 146). Lso haplotypes have not been reported from Central America (**Figure 1**).

At least three countries outside of the vector's apparent native range have reported introductions of both the potato psyllid and Lso on solanaceous hosts. Lso was reported in potatoes in New Zealand not long after the initial detection of the potato psyllid and was soon widely observed across the country (135). In 2013, Lso haplotype A was collected from tomato plants on Norfolk Island, Australia, and the next year, potato psyllids were collected from potato and tomato plants (146). Potato psyllids (in 2017), Lso, and ZC-infected potatoes (in 2019) were reported for the first time in South America (Ecuador) (11, 14). Only Lso haplotype A has been reported from these introductions (**Figure 1**).

To date, the Lso haplotypes typically associated with ZC symptoms (A and B) have not been found in Europe or the Mediterranean region, limiting the current risk of ZC for potato crops (see the section titled Lso Haplotypes). However, numerous other Lso haplotypes that have not been reported to cause ZC symptoms in potatoes are present in these areas (**Figure 1**).

Epidemiology

Potatoes are vegetatively propagated, which facilitates tuber transmission of many other potato pathogens. However, despite some conflicting results in previous studies, it is clear that, when Lso-infected tubers are planted, plant emergence, development, and Lso infection in daughter tubers are severely diminished (102, 123, 149). Thus, the risk of Lso spread through infected seed pieces is negligible.

The spread of Lso by potato psyllids is of primary epidemiological importance. Transovarial transmission of Lso has been reported, and both nymphs and adults can transmit the pathogen (27, 79). However, adults play a more important role in pathogen spread given their typically higher Lso titer (27, 79) and capacity for long-distance dispersal (140).

After acquisition through feeding, Lso multiplies (111) and circulates through the psyllid's body, reaching the salivary glands in approximately two weeks (112). Following this two-week latent period, the insect is infective for the remainder of its life. Lso is inoculated into a new host plant within an hour of feeding, during the salivation stage, and inoculation success increases with feeding duration (79, 111) and vector density (100).

The onset of ZC symptoms in the field typically occurs after three to four weeks in foliage but within two weeks in tubers (101). Higher vector density may shorten ZC incubation time (100) but has little effect on symptom severity or disease progression (44, 145).

Relative to Lso haplotype A, Lso haplotype B exhibits faster replication in the psyllid gut, a shorter latent period, a higher transmission rate, and higher virulence, causing more severe symptoms and tuber yield reduction (57, 58, 122, 128). These differences between haplotypes could explain the greater prevalence of haplotype B in some areas (31, 32).

The heterogeneous distributions of Lso within the host plant and psyllids on their hosts (10, 20, 79, 136) may influence psyllid exposure to the pathogen. Although limiting psyllid access to specific plant tissues did not elucidate such relationships (100, 135), unrestricted access to the plant resulted in greater acquisition (100).

At the field scale, ZC prevalence is often initially higher on the edges, likely related to the early season buildup of vector populations in natural vegetation (25, 135, 146) and in volunteer potatoes from the previous year's crop (140). Many noncrop solanaceous hosts can serve as reservoirs of potato psyllids and/or Lso in host plants or the psyllids themselves (25, 33, 80, 104, 106, 130, 135, 144). Within fields, the pattern of Lso distribution is influenced by the spatiotemporal movement of infective potato psyllids, typically exhibiting a nonrandom pattern (59). As psyllids reproduce and disperse over the season, ZC appears in the inner parts of the field (79, 146).

Dispersal of potato psyllids and Lso may be affected by pathogen manipulation of the vector. Lso-negative psyllids preferentially settle on Lso-infected plants, and after Lso acquisition, potato psyllids preferentially colonize healthy plants (34, 71). Lso-positive psyllids reach the sieve elements more quickly and exhibit increased salivation, probing, and phloem ingestion (134). These behavioral shifts should accelerate pathogen spread, suppressing overall yield and reducing economic return from repeated insecticide sprays (41).

Lso is also pathogenic to psyllids, negatively affecting reproduction and survival (4, 85, 131). The evolutionary development of this seemingly antagonistic relationship has yet to be clarified but might contribute to cyclical population dynamics in psyllids among years (143). Negative effects of Lso on psyllid biology are influenced by the host plant (85, 131), emphasizing the importance of considering the host plant when studying vector–pathogen interactions.

Lso can be transmitted between *Bactericera maculipennis* (Crawford) and potato psyllids when they are feeding on the same Convolvulaceae host plant (132). This and similar cross-transmission between potato psyllids and other psyllid species via shared hosts (e.g., *B. nigricornis* that feeds on potatoes and carrots; 6) needs further investigation with respect to ZC epidemiology.

Economics

Factors contributing to economic losses from ZC include lower yield and lower quality resulting in reduced or lost market value, as well as increased input costs associated with insecticide applications (48, 49, 51). Losses from ZC were initially sporadic but, by the mid-2000s, reached tens of millions of dollars in the United States, Mexico, and Central America (146). Insecticide applications targeting potato psyllids were estimated to exceed US$700 per hectare in the southcentral United States (51) and US$11 million across the northwest United States (49). Detailed examinations of the economic effects of ZC in other countries are lacking, but these effects likely have been substantial, especially in New Zealand.

MANAGEMENT

Monitoring

Monitoring potato psyllids is key to informing decisions on insecticide application, the primary means of managing potato psyllids and ZC. Yellow sticky traps are the most widely used monitoring tool for adults, having been found to be more efficient than other methods (143, 144, 153). Vacuum and beat sheet sampling may be preferred when sampling adults on alternative host plants, where active dispersal may be less likely (129, 144). Direct inspection of leaf samples is the standard approach for monitoring immature stages of potato psyllids (39, 143, 146). Nymphs may be more abundant in the top or middle of the potato plant canopy (136, 146). Correlations between psyllid densities and ZC incidence have generally not been clear (39, 147), likely due to the high temporal and spatial variability in Lso incidence among psyllids (31–33, 143, 144). Action thresholds have been proposed in New Zealand (137), and binomial sequential sampling plans have been proposed in California (10), but these remain to be more rigorously tested in other regions. Any threshold should consider both psyllid numbers and incidence of Lso, which would require a rapid diagnostic assay. Monitoring protocols should consider the aggregated distribution of psyllids and ZC infection within fields, including likely greater densities on field edges (10, 59, 140). In addition, refinement of phenology models will aid in developing risk prediction tools (18, 52).

Insecticides

ZC management is heavily reliant on insecticide applications to suppress the vector. Insecticide programs—at least in the United States and New Zealand—typically feature a neonicotinoid at-plant followed by repeated foliar sprays over the season until shortly before vine kill or harvest (38, 49, 51, 135), when potato psyllid abundance typically increases (18, 37, 143). Ideally, insecticides will kill psyllids quickly and/or reduce Lso transmission. Laboratory demonstration of reduced pathogen transmission has been rare (but see discussion of imidacloprid in 10); however, several chemistries, including abamectin, pymetrozine, cyantraniliprole, sulfoxaflor, and tolfenpyrad, alter feeding activity, which is expected to negatively affect Lso transmission (10, 40, 82, 135). Abamectin exhibits effective knockdown against psyllids, whereas other chemistries, including cyantraniliprole, imidacloprid, spinetoram, spiromesifen, and sulfoxaflor, may show stronger residual activity (10, 40, 135). To reduce ZC under high disease pressure, the specific insecticide program used might be less important than the need to continue spraying for the duration of the season (38).

Reliance on insecticides is not sustainable given that resistance to one or more chemistries—including neonicotinoids, spinosad, and abamectin—has been reported throughout North America (16, 17, 98, 124). Moreover, use of broad-spectrum insecticides is associated with higher densities of potato psyllids, likely related to the negative effects on natural enemies (96, 108). Alternatives to synthetic insecticides, including kaolin particle film, crop oils, essential oils, nanoparticles, and bactericides, have shown some efficacy against potato psyllids, Lso transmission, and/or ZC incidence, at least in the laboratory (10, 45, 53, 135, 150). However, among these, only kaolin particle film and crop oils have been evaluated in the field (10, 150); thus, more work is needed to confirm field efficacy and incorporation into integrated pest management programs with traditional insecticides.

Cultural and Physical Control

Cultural and physical options for managing potato psyllids and ZC are limited and, at present, impractical for most situations. Delayed planting may reduce psyllid densities and/or ZC incidence (140) but would be unacceptable for most growers. Elimination of spring breeding hosts has been proposed, but our incomplete understanding of these hosts and the geographic scale at which such an approach would need to be implemented limit its practicality (23, 25, 144). Mulches, UV-blocking screens, and mesh row covers have been shown to reduce potato psyllid densities in small field plots (75, 146), but efficacy against ZC remains to be demonstrated, and all of these approaches face challenges of scale.

Biological Control

Parasitoid wasps, generalist predators, and entomopathogenic fungi have been reported to attack potato psyllids, but practical recommendations for their use in field settings are lacking. *Tetrastichus* *triozae* (Burks) (Hymenoptera: Eulophidae) provided unreliable control in the United States (9, 10, 93). More potential was observed in Mexico, especially in fields with lower insecticide use (108), which is not surprising given this species' high susceptibility to insecticides (69, 78). Other factors, including hyperparasitism and a broad host range, likely limit the effects of *T. triozae* on the potato psyllid (10). Nevertheless, this parasitoid was released for biocontrol in New Zealand (135), but reports on long-term efficacy have yet to be published. Another parasitoid, *Metaphycus psyllidis* Compere (Hymenoptera: Encyrtidae), has been observed in Southern California but at even lower parasitism rates (9).

Many generalist predators, including coccinellids, chrysopids, anthocorids, geocorids, nabids, mirids, syrphids, and predatory mites, have been reported to feed on potato psyllids in the field (10, 93, 146) and in the laboratory or greenhouse (3, 12, 13, 35, 47, 64, 70, 89, 91, 92, 99, 125, 151). However, more work is needed to understand the roles of generalist predators in the field. Undoubtedly, reliance on insecticides for ZC management has limited the effectiveness of natural enemies given their high susceptibility to insecticides (2, 15, 69, 77, 78, 108). Aside from reducing insecticide applications to conserve natural enemies, we lack practical recommendations for implementing biocontrol with parasitoids and predators.

Several species of entomopathogenic fungi have been shown to be effective against potato psyllids, but primarily in the laboratory (1, 72, 79, 88, 107, 125, 126). More work is needed to confirm field efficacy and to facilitate widespread implementation of this approach across different growing areas.

Host Plant Resistance

Resistance to Lso or the potato psyllid vector has yet to be identified in or developed for commercial potato cultivars in the United States (29, 66, 79). However, potential sources of resistance have been found in several germplasms with wild *Solanum* species in their pedigree (94). In this section, we exclude screening trials that relied solely on visual symptoms to characterize resistance or tolerance and consider only a selection of recent studies that characterized symptom expression along with Lso concentrations and/or physiological shifts in plants following infection (94).

Although antibiosis resistance to potato psyllids has been documented in *Solanum verrucosum* and *Solanum bulbocastanum*, these traits have not been incorporated into cultivated potatoes (21, 22). Antixenosis resistance to ZC in some potato genotypes has been demonstrated (10). Later studies further inferred potential ZC resistance through antixenosis by quantifying differences in oviposition, feeding, and probing behavior (42, 97). The breeding clone family A07781, with *Solanum chacoense* in its ancestry (US Department of Agriculture Agricultural Research Service, Small Grains and Potato Germplasm Research, Aberdeen, ID), has emerged as a promising candidate for future incorporation into commercial cultivars (42).

Recent studies have used symptom severity, Lso titer (29, 103), and/or analytical quantification of physiological responses (109, 138, 139) to determine potato host susceptibility to ZC. Wallis et al. (138) identified 29 genotypes that expressed few or no symptoms following Lso infection. The absence of drastic shifts in amino acids, reducing sugars, and phenolics concentrations were used to explain this observed tolerance in the examined genotypes (138). Developing potato cultivars with reduced defensive and hypersensitive responses may reduce losses to ZC; however, resistance that limits the replication of the bacterium in its host is the preferred goal. Recent studies suggested that siblings from the family A07781 exhibit ZC tolerance or resistance in both the greenhouse (103) and the field (29).

Emerging Technologies

More sustainable alternatives to traditional chemical controls are needed. Progress is being made with the development of RNA interference (RNAi)-based approaches affecting potato psyllid molting, mortality, and Lso acquisition and transmission (90, 127). Although conventional RNAi technologies would not work against bacteria, a novel RNA-silencing technology called FANA has been shown to suppress liberibacter titers and disease symptoms in potatoes and citrus (63). Paratransgenic approaches that disrupt pathogen transmission through manipulation of vector microbial communities offer another avenue that is being pursued for the Asian citrus psyllid, *Diaphorina citri* Kuwayama (76), and should be evaluated in the potato psyllid. Genetically engineered potatoes could be a powerful tool to confer host plant resistance to the vector and/or pathogen, but public skepticism and marketing restrictions currently limit such applications. Recent technological advances in spectral imaging tools facilitate ZC monitoring in the field (30) or on tubers at harvest (46, 60, 154); further development of such technologies could aid in removing field inoculum and culling infected tubers after harvest. Artificial neural network classifiers can be used with spectral imaging as a tool in high-throughput potato screening, facilitating plant breeding efforts to detect sources of resistance to ZC (60).

CONCLUSIONS

A tremendous amount of research progress has been made recently on the ZC pathosystem, which is especially remarkable given that the causal agent of ZC was only identified in 2008. Despite this progress, many areas require further research to develop sustainable approaches for managing ZC. Several aspects of the epidemiology of the ZC pathosystem need to be clarified, including the role of alternative host plant reservoirs for Lso, the transmission of various Lso haplotypes to potato by other psyllid species, and potential effects of cross-transmission of the pathogen to potato psyllids from other psyllid species via shared alternative host plants. A better understanding of the sources of bacteriliferous potato psyllid infestations in potato would contribute to the improvement of models aimed at predicting regional and seasonal variation in risk to the crop. Clarification of the relationships among potato psyllid densities, Lso incidences, and ZC prevalence will be needed—along with rapid diagnostic assays for Lso—to develop economic thresholds and ensure that insecticides are applied only when justified by risk. Such decision support tools would be well complemented by new insecticide options and emerging technologies that are conducive to preserving natural enemies. More needs to be known about the role of biocontrol agents under field settings, and practicable cultural control options are almost entirely lacking. Ultimately, new potato cultivars are needed with both durable resistance to Lso and commercially acceptable agronomic traits.

DISCLOSURE STATEMENT

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