

Zebra Chip Disease of Potato: Biology, Epidemiology, and Management

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Published online: 30 August 2012
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Abstract Zebra chip (ZC), a new and economically important disease of potato (*Solanum tuberosum* L.), has been documented to occur in commercial potato fields in the United States, Mexico, Central America, and New Zealand. This disease has caused millions of dollars in losses to the potato industry. Whole crops might be rejected because of ZC, often leading to abandonment of entire fields. Plant growth and yield are severely affected by the disease. Additionally, chips or fries processed from ZC-infected tubers exhibit dark stripes that become markedly more visible with frying, and hence are commercially unacceptable. The disease causes serious losses to the fresh market, tablestock and export potato industry as well. ZC-infected tubers usually do not sprout and if they do, produce hair sprouts or weak plants. Finally, there are indications that ZC symptoms might develop in tubers during storage. ZC has been associated with a previously undescribed species of liberibacter, tentatively named “*Candidatus Liberibacter solanacearum*”, also known as “*Ca. L. psyllaerous*”. The bacterium is transmitted to potato by the potato psyllid, *Bactericera cockerelli* (Šulc). All commercial potato cultivars appear to be susceptible to ZC, and management tactics targeted against the potato psyllid are currently the only means to effectively manage the disease. Furthermore, there are concerns about quarantine and trade issues in psyllid-affected regions because some countries may require that shipments of potatoes from certain growing regions be tested for the disease before the shipments are allowed entry. ZC history, geographic distribution, biology, epidemiology, and management are discussed herein.

Resumen Se ha documentado que Zebra chip (ZC), una enfermedad nueva y económicamente importante de la papa (*Solanum tuberosum* L.), se presenta en los campos comerciales de papa en los Estados Unidos, México, América Central y Nueva Zelanda. Esta enfermedad ha causado millones de dólares en pérdidas a la industria de la papa. Se pudieran rechazar cultivos completos debido a ZC, que conducen a menudo al abandono total de los campos. Se afecta severamente el crecimiento y el rendimiento de la planta por la enfermedad. Además, las hojuelas o papas fritas procesadas de tubérculos infectados con ZC exhiben líneas oscuras que se vuelven marcadamente más visibles con el freído, y por lo tanto son inaceptables comercialmente. La enfermedad causa pérdidas serias al mercado fresco, al doméstico y a la industria de la exportación también. Los tubérculos infectados con ZC generalmente no brotan, y si lo hacen, producen brotes ahilados y plantas débiles. Finalmente, hay indicaciones de que los síntomas de ZC pueden desarrollarse en los tubérculos durante el almacenamiento. Se ha asociado a la ZC con una especie previamente descrita de *Liberibacter*, tentativamente llamada “*Candidatus Liberibacter solanacearum*”, también conocida como “*Ca. L. psyllaerous*”. La bacteria se transmite a la papa por el psílido *Bactericera cockerelli* (Šulc). Todas las variedades comerciales de papa parecen ser susceptibles a ZC, y las tácticas de manejo dirigidas contra el psílido de la papa son a la fecha los únicos medios para manejar la enfermedad efectivamente. Aún mas, hay preocupación acerca de cuarentena y temas de comercio en regiones afectadas por el psílido, debido a que algunos países pudieran requerir que los embarques de papas de ciertas regiones de cultivo fueran analizados para la enfermedad antes de permitir la entrada de los envíos. De aquí que se discute la historia de ZC, la distribución geográfica, biología, epidemiología y el manejo.

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Keywords Potato psyllid · *Bactericera cockerelli* · Liberibacter · Potato · Zebra chip · Disease biology · Disease management

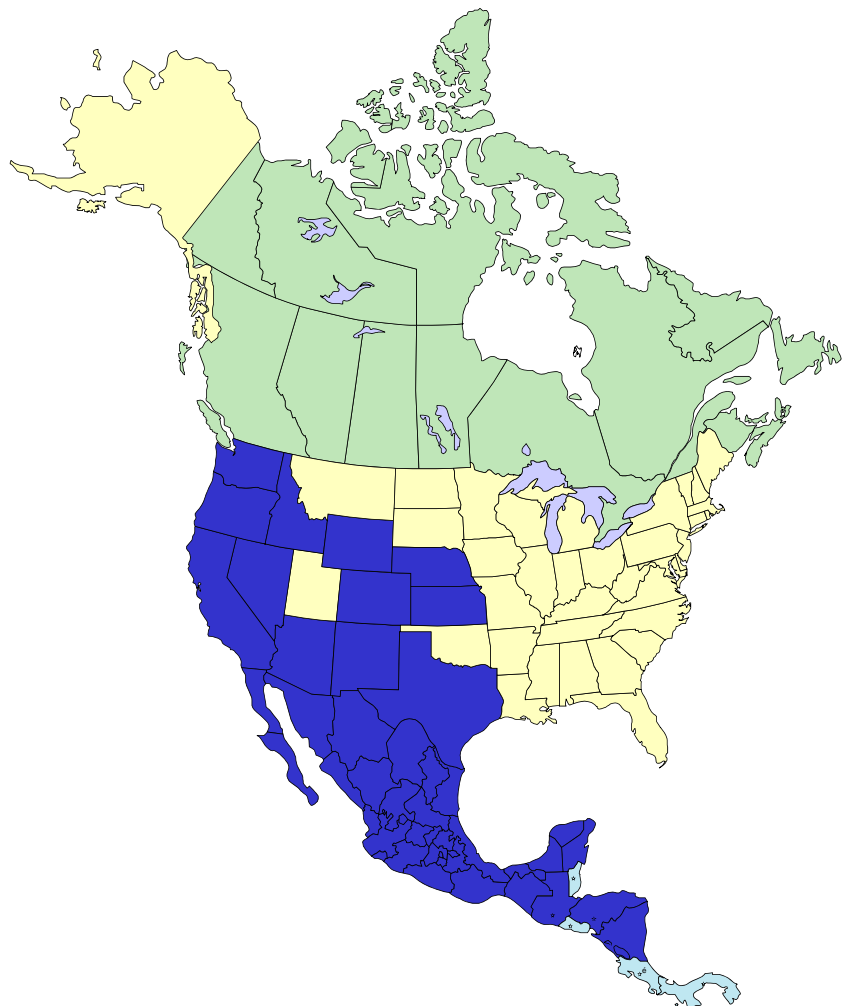
Introduction

Zebra chip (ZC), a new and economically important disease of potato (*Solanum tuberosum* L.), has so far been documented to occur in commercial potato fields in the United States, Mexico, Central America, and New Zealand (Secor and Rivera-Varas 2004; Munyaneza et al. 2007a; Liefting et al. 2008a; Secor et al. 2009; Crosslin et al. 2010; Espinoza 2010; Galviz et al. 2010; Munyaneza 2010; Rubio-Covarrubias et al. 2011a, b) (Fig. 1). ZC was first reported in 1994 in potatoes growing near Saltillo, Mexico (Secor and Rivera-Varas 2004; Munyaneza et al. 2007a, b; Crosslin et al. 2010; Secor et al. 2009). Initial records of the disease in the United States are from 2000 in potato fields in southern Texas (Munyaneza et al. 2007a, b; Secor et al. 2009). Infected fields of potatoes have since been documented

in several other states, including Nebraska, Colorado, Kansas, Wyoming, New Mexico, Arizona, Nevada, and California (Munyaneza et al. 2007a, b; Secor et al. 2009; Crosslin et al. 2010; Munyaneza 2010), and most recently in Idaho, Oregon, and Washington (Hamm et al. 2011; Nolte et al. 2011; Crosslin et al. 2012a,b). In Central America, ZC has been reported from Guatemala and Honduras (Secor and Rivera-Varas 2004; Munyaneza et al. 2007a, b; Espinoza 2010; Rehman et al. 2010), and most recently from Nicaragua (Nicaragua-MAGFOR 2012). The disease is widespread in New Zealand (Teulon et al. 2009), where it was initially documented in 2008 (Liefting et al. 2008a). ZC is characterized by a severe dark and light striped symptom pattern in raw and fried chips and fries processed from infected tubers, affecting their taste and making them commercially unacceptable. Consumption of products processed from ZC-infected tubers is not known to pose any human health issues.

ZC was of sporadic importance until 2004, when it began to cause millions of dollars in losses to potato growers in the Americas, often leading to the abandonment of entire fields (Secor and Rivera-Varas 2004; CNAS 2006; Gudmestad and

Fig. 1 Map (dark blue) showing geographic distribution of zebra chip disease in North and Central America



Secor 2007; Munyaneza et al. 2007a, b; 2009b; Crosslin et al. 2010; Galviz et al. 2010; Espinoza 2010; Munyaneza 2010; Rehman et al. 2010; Rubio-Covarrubias et al. 2011a, b). The disease has also devastated the potato industry in New Zealand (Liefting et al. 2008a; Teulon et al. 2009; Ogden 2011). ZC has been linked to a previously undescribed species of the bacterium liberibacter, tentatively named “*Candidatus Liberibacter solanacearum*”, also known as “*Ca. Liberibacter psyllauros*” (Hansen et al. 2008; Liefting et al. 2008a; 2009a,c). The bacterium is transmitted to potato by the potato/tomato psyllid, *Bactericera cockerelli* (Šulc) (Munyaneza et al. 2007a, b; Hansen et al. 2008; Secor et al. 2009; Buchman et al. 2011b; Butler and Trumble 2012a).

Disease Description and Identification

ZC is characterized by symptoms that develop in potato tubers, which consist of collapsed stolons, browning of vascular tissue, concomitant with necrotic flecking of internal tissues and streaking of the medullary ray tissues, all of which can affect the entire tuber (Fig. 2). Upon frying, these symptoms become more pronounced and chips or fries processed from infected tubers show very dark blotches, stripes, or streaks, rendering them commercially unacceptable (Munyaneza et al. 2007a,b; 2008; Secor et al. 2009; Crosslin et al. 2010; Miles et al. 2010; Buchman et al. 2011a,b; 2012) (Fig. 3). Foliar symptoms associated with ZC closely resemble those caused by psyllid yellows disease (Wallis 1955; Arslan et al. 1985; Sengoda et al. 2010) and purple top (Crosslin et al. 2005; Munyaneza et al. 2006; Ember et al. 2011), and include upward rolling of the top leaves developing into a basal cupping of the leaflets, accompanied with yellowish or purplish discoloration, proliferation of axillary buds, shortened internodes, swollen nodes, aerial tubers, leaf chlorosis and scorching, and rapid plant death (Munyaneza et al. 2007a,b; Secor et al. 2009; Crosslin et al. 2010) (Fig. 4). The characteristic marking symptoms in potato tubers have led to the disease being named “zebra chip”

(Munyaneza et al. 2007a,b; Secor et al. 2009; Crosslin et al. 2010; Munyaneza 2010).

Disease Causal Agent: “*Candidatus Liberibacter solanacearum*”

The putative causal agent of ZC was unknown until 2008, when studies conducted in the United States and New Zealand showed that ZC is associated with a previously undescribed species of the bacterium liberibacter, tentatively named “*Candidatus Liberibacter solanacearum*” (referred to as “Lso” hereafter), also known as “*Ca. Liberibacter psyllauros*” (Hansen et al. 2008; Liefting et al. 2008a; 2009a, c; Butler and Trumble 2012a). Subsequently, a series of studies confirmed presence of this bacterium in ZC-infected potatoes from several geographic locations (Abad et al. 2009; Crosslin and Bester 2009; Crosslin and Munyaneza 2009; Lin et al. 2009; Munyaneza et al. 2009b; Secor et al. 2009; Sengoda et al. 2010; Crosslin et al. 2010; Rehman et al. 2010; Crosslin et al. 2012a,b). A comprehensive review of the history and association of this bacterium with ZC and other diseases of solanaceous crops was provided by Crosslin et al. (2010) and Munyaneza (2010). This bacterium is closely related to the liberibacters associated with Huanglongbing or citrus greening, the most destructive disease of citrus, which occurs in Asia, Africa, and the Americas (Bové 2006; Hansen et al. 2008; Liefting et al. 2009a, c; Lin et al. 2009; Wen et al. 2009; Lin et al. 2011a, b). The liberibacters are phloem-limited, Gram-negative, unculturable bacteria that belong to the *Alphaproteobacteria* group (Jagoueix et al. 1994; Bové 2006). These plant pathogens are spread from infected to healthy plants primarily by psyllid vectors (Bové 2006).

Hosts and Geographic Distribution

Lso has been reported from the western and central United States (Texas, Nebraska, Colorado, Kansas,

Fig. 2 Fresh potato tubers with zebra chip disease symptoms



Fig. 3 Fried potato chips (a) and fries (b) processed from zebra chip disease-infected tubers



Wyoming, New Mexico, Arizona, Nevada, California, Idaho, Oregon, and Washington) (Hansen et al. 2008; Abad et al. 2009; Crosslin and Bester 2009; Crosslin and Munyaneza 2009; Lin et al. 2009; McKenzie and Shatters 2009; Secor et al. 2009; Brown et al. 2010; Crosslin et al. 2010; French-Monar et al. 2010; Munyaneza 2010; Crosslin et al. 2012a,b), Mexico (Munyaneza et al. 2009b,c,d), Central America (Guatemala, Honduras, and Nicaragua) (Rehman et al. 2010; Nicaragua-MAGFOR 2012), and New Zealand (Liefting 2008a; 2009a,c). This species of liberibacter has also been documented on carrot (*Daucus carota* L.) in Northern Europe (Finland, Norway, and Sweden) (Munyaneza et al. 2010c,d; 2011c; 2012b,c) and the Mediterranean Region (Spain and the Canary Islands) (Alfaro-Fernández et al. 2012a,b). Furthermore, Lso has recently been reported on celery (*Apium graveolens*) crops in Spain (EPPO 2012).

Lso is known to primarily infect solanaceous crops, including potato, tomato (*Solanum lycopersicon*), pepper (*Capsicum annuum*), eggplant (*Solanum melongena*), tomatillo (*Physalis* spp.), tamarillo (*Solanum betaceum*), and several weeds in the family Solanaceae (Hansen et al. 2008; Liefting et al. 2008a,b; 2009a,c; Abad et al. 2009; Crosslin and Munyaneza 2009; Lin et al. 2009; Munyaneza et al. 2009b,c,d; Secor et al. 2009; Wen et al. 2009; Brown et al. 2010; Crosslin et al. 2010; Munyaneza 2010; Rehman et

al. 2010; Sengoda et al. 2010). The pathogen is transmitted to solanaceous species by *B. cockerelli*. As noted above, Lso has very recently been detected for the first time in carrot plants in Finland, where it is vectored to carrot by the psyllid *Trioza apicalis* Förster (Munyaneza et al. 2010c, d; 2011c); this constitutes the first report of Lso in a non-solanaceous species. Subsequently, the bacterium was also detected in carrots and *T. apicalis* in Sweden and Norway (Munyaneza et al. 2012b, c). Most recently, Lso has been reported in carrot and celery crops and the psyllid *Bactericera trigonica* in the Canary Islands and mainland Spain (Alfaro-Fernández et al. 2012a, b; EPPO 2012). Damage to carrots by Lso-infected psyllids in Europe can cause up to 100 % crop loss (Munyaneza et al. 2010b, c; 2012b, c; Alfaro-Fernández et al. 2012a, b; Nissinen et al. 2012). In addition, there are reports of Lso having been detected in unidentified species of psyllids in the genera *Acizzia* and *Trioza* collected from *Acacia* and *Pittosporum* species, as well as foliage samples from these plant species in New Zealand (Scott et al. 2009). Furthermore, Lso was detected in one specimen of the psyllid *Trioza chenopodii* collected from Russia; however, further testing of other specimens failed to confirm presence of the bacterium (Kölber et al. 2010). These recent findings on the association of Lso with non-solanaceous species suggest that this liberibacter species is likely to have more host plants and insect vectors than currently known.

Fig. 4 Potato plants infected with zebra chip disease and exhibiting symptoms of stunting, leaf chlorosis, yellowish and purplish discoloration, upward rolling of leaves, shortened internodes, and proliferation of axillary buds



Biology

Scanning electron microscopy images of Lso in sieves of infected plants showed that this bacterium has a rod-shaped morphology (Liefing et al. 2009a; Secor et al. 2009). The bacterium is about 0.2 μm wide and 4 μm long (Liefing et al. 2009a). Similarly to other liberibacters, Lso is spread from plants to plants by grafting (Crosslin and Munyaneza 2009; Secor et al. 2009) and psyllid vectors (Munyaneza et al. 2007a,b; Hansen et al. 2008; Secor et al. 2009; Munyaneza et al. 2010c,d; Buchman et al. 2011b; Alfaro-Fernández et al. 2012b). The pathogen has been shown to be transmitted to *B. cockerelli* both vertically (transovarially) and horizontally (from feeding on infected plant hosts) (Hansen et al. 2008; Munyaneza and Sengoda, unpublished data). Vertical transmission may contribute to the spread of ZC between geographic regions by dispersing psyllids, and also helps maintain the bacterium in geographic regions during the insect's overwintering period (Crosslin et al. 2010). No information is currently available on vertical transmission of Lso for *T. apicalis* and *B. trionica*. It appears that Lso is not transmitted through true seed from infected solanaceous plants (Munyaneza, unpublished data; Liefing, personal communication).

Three geographic haplotypes of Lso have been described (Nelson et al. 2011). Two haplotypes (A and B) are associated with diseases caused by this bacterium in potatoes and other solanaceous plants, whereas the third (C) is associated with diseased carrots and the psyllid *T. apicalis*. The haplotypes were described by single nucleotide polymorphisms (SNPs) on the 16 s rRNA, 16 s/23 s ISR and 50s rplJ and rplL ribosomal protein genes (Nelson et al. 2011). These SNPs are inherited as a package across the three genes. Haplotype "A" has been found primarily from Honduras and Guatemala through western Mexico to Arizona and California, and in New Zealand. Haplotype "B" is currently known from eastern Mexico and northwards through Texas to south central Washington. These two haplotypes show some range overlap in Texas, Kansas and Nebraska. Haplotype "C" has been found in Finland (Nelson et al. 2011) and recently in Sweden and Norway (Munyaneza and Nelson, unpublished data). A new and fourth Lso haplotype referred to as "D" was very recently described from infected carrots and the psyllid *B. trionica* in Spain and the Canary Islands (Munyaneza and Nelson, unpublished data). The four haplotypes are not yet known to elicit biological differences in the plant or insect hosts. These apparently stable haplotypes suggest separate long-lasting populations of the bacterium. Furthermore, a study on the genetic diversity of Lso strains using simple sequence repeat (SSR) markers identified two major lineages of this bacterium in the United States and only one lineage in Mexico (Lin et al. 2012).

Little is known on the effects of environmental conditions on development of Lso in plant and insect hosts.

Temperature has been shown to have a significant effect on the development of this bacterium in potato plants (Munyaneza et al. 2012a). Compared to liberibacters associated with citrus greening disease, Lso appears to be heat-sensitive, and seems not to tolerate temperatures above 32 °C (Munyaneza et al. 2012a). Additionally, temperatures at or below 17 °C may significantly slow, but not prevent, Lso development in potato (Munyaneza et al. 2012a). The optimum development of Lso and ZC symptoms in potato plants was observed at a daily temperature regime of 27–32 °C. At the higher daily temperature regimes of 32–35 and 35–40 °C, no Lso was detected in potato plants inoculated with the bacterium using insects and no ZC symptom development occurred (Munyaneza et al. 2012a). The vector of the pathogen in the Americas and New Zealand, *B. cockerelli*, appears to have similar temperature preferences (Pletsch 1947; Abdullah 2008; Yang et al. 2010a). Studies have also shown that Lso within the adult potato psyllid is sensitive to high and low temperatures, with the highest bacterial titers occurring at approximately 28 °C (Rush et al. 2010). This temperature is very similar to the preferred optimum temperature (27 °C) for potato psyllid reproduction and liberibacter development in the plant (Munyaneza 2010; Munyaneza et al. 2012a). It has also been determined that Lso titer does not differ between males and females, exists at very low titer in fifth-instar nymphs, and increases with age of the adult psyllid (Rush et al. 2010). Furthermore, it has been shown that Lso has a negative effect on population growth rate of *B. cockerelli*, at least when the psyllid is reared on tomato (Nachappa et al. 2012).

Diagnosis and Detection

The characteristic plant symptoms of Lso infection in both potatoes and other solanaceous species resemble those caused by phytoplasmas: plant stunting, erectness of new foliage, chlorosis and purpling of foliage with basal cupping of leaves, upward rolling of leaves throughout the plant, shortened and thickened terminal internodes resulting in plant rosetting, enlarged nodes, axillary branches, leaf scorching, disruption of fruit set, and production of numerous, small, misshaped, and poor quality fruits (Liefing et al. 2008b; Liefing et al. 2009a; McKenzie and Shatters 2009; Munyaneza et al. 2009c,d; Secor et al. 2009; Brown et al. 2010; French-Monar et al. 2010; Crosslin et al. 2010). Symptoms in carrots infected with Lso include leaf curling, yellowish, bronze and purplish discoloration of leaves, stunting of the carrot shoots and roots, and proliferation of secondary roots (Munyaneza et al. 2010c,d; 2012b,c; Alfaro-Fernández et al. 2012a,b). Symptoms in carrots collectively resemble those caused by leafhopper-transmitted

phytoplasmas and *Spiroplasma citri* (Font et al. 1999; Lee et al. 2006; Cebrián et al. 2010; Munyaneza et al. 2011c).

The genome of Lso isolated from zebra chip-infected potatoes has recently been sequenced and published (Lin et al. 2011b). Detection methods for Lso have been developed and include both conventional and quantitative real-time polymerase chain reaction (PCR) (Hansen et al. 2008; Crosslin and Munyaneza 2009; Li et al. 2009; Liefting et al. 2008a, 2009a; Lin et al. 2009; Wen et al. 2009; Munyaneza et al. 2010d; Crosslin et al. 2011b; Lin et al. 2011a; Pitman et al. 2011; Ravindran et al. 2011a, b; Wen et al. 2011). Detection of the bacterium in psyllids by PCR is relatively straightforward (Munyaneza et al. 2010d; Crosslin et al. 2011b). Uneven distribution and variation in Lso titer in different parts of infected potato plants have been observed, making detection by PCR sometimes inconsistent (Crosslin and Munyaneza 2009; Li et al. 2009; Buchman et al. 2011a; Levy et al. 2011). Development of better and more accurate detection methods by PCR is currently underway. Mixed infections of Lso and phytoplasmas have been reported in potato (Liefting et al. 2009b; Munyaneza unpublished data) and carrot (Munyaneza et al. 2011c), while mixed infections of Lso, phytoplasmas, and *S. citri* have been detected in carrots in the Mediterranean region (Alfaro-Fernández et al. 2012a).

Insect Vector: *Bactericera cockerelli*

The potato/tomato psyllid, *Bactericera* (= *Paratrioza*) *cockerelli* (Šulc) (Hemiptera: Triozidae) was linked to ZC for the first time in 2007 by Munyaneza et al. (2007a, b), preceding the identification of Lso as the putative causal agent of the disease (Hansen et al. 2008; Liefting et al. 2008a; Butler and Trumble 2012a). The psyllid feeds upon the phloem using piercing-sucking mouthparts. The potato psyllid is known as a serious and economically important pest of potatoes, tomatoes, and other solanaceous crops in the western United States, southern Canada, Mexico, Central America and New Zealand.

Identification and Description

A detailed diagnostic description of *B. cockerelli* and other potato psyllids around the world was recently provided by Halbert and Munyaneza (2012). Cicero et al. (2009) gave a detailed description of the digestive system of this psyllid in relation to potential location and movement of Lso in the insect body. Adult potato psyllids (Fig. 5) are small, measuring about 2.5 mm long, and resemble tiny cicadas, largely because they hold their wings roof-like (Wallis 1955). Body color ranges from pale green at emergence to dark green or brown within 2–3 days, and eventually becomes gray or black thereafter. Prominent white or yellow lines are

found on the head and thorax, and dorsal whitish bands are located on the first and terminal abdominal segments. These white markings are distinguishing characteristics of the psyllid, particularly the broad, transverse white band on the first abdominal segment and the inverted V-shaped white mark on the last abdominal segment (Pletsch 1947; Wallis 1955). Adults are active in contrast to the largely sedentary nymphal stages. The adult psyllids are good fliers and may jump readily when disturbed. Adult longevity ranges from 20 to 62 days, and females usually live two to three times longer than males, depending on host plant (Pletsch 1947; Abernathy 1991; Abdullah 2008; Yang and Liu 2009; Yang et al. 2010a). The oviposition period may extend to almost 50 days, with an average fecundity of 300–500 eggs per female over her lifetime (Knowlton and Janes 1931; Pletsch 1947; Abdullah 2008; Yang and Liu 2009; Yang et al. 2010a).

The light to dark yellow or orange eggs of *B. cockerelli* (Fig. 6) are deposited singly, principally on the lower surface of leaves and near the leaf edge. Often, females will lay numerous eggs on a single leaf (Pletsch 1947; Wallis 1955; Halbert and Munyaneza 2012). The eggs are mounted on short stalks and hatch 3–7 days after oviposition (Pletsch 1947; Wallis 1955; Capinera 2001; Abdullah 2008; Yang et al. 2010a; Butler and Trumble 2012a; Halbert and Munyaneza 2012). The orange or yellowish-green nymphs (Fig. 7) are flat with a scale insect-like appearance (Halbert and Munyaneza 2012; Butler and Trumble 2012a). There are five nymphal instars, of similar appearance other than size (Rowe and Knowlton 1935; Pletsch 1947; Wallis 1955). The eyes are reddish and quite prominent. A short fringe of wax filaments is present along the lateral margins of the body. During the third instar, the wing pads, light in color, are evident and become more pronounced with each subsequent molt. Potato psyllid nymphs may be confused with the nymphs of whiteflies, although only the former move when disturbed. Because nymphs prefer sheltered and shaded locations, they are mostly found on the lower surfaces of leaves and usually remain sedentary during their development. Total nymphal development time depends on temperature and host plant and has been reported to have a range of 12 to 24 days (Knowlton and Janes 1931; Abdullah 2008; Yang and Liu 2009; Yang et al. 2010a). Both nymphs and adults produce large quantities of whitish excrement particles.

Geographical Distribution

The potato psyllid is native to North America and occurs mainly in the Rocky Mountain region of the United States and Canada, from Colorado, New Mexico, Arizona, and Nevada, north to Utah, Wyoming, Idaho, Montana, Alberta and Saskatchewan (Pletsch 1947; Wallis 1955; Cranshaw 1993; Ferguson and Shipp 2002). This insect pest is

Fig. 5 Adult potato psyllids with characteristic whitish bands on the abdomen and white or yellow lines on the head and thorax



common in southern and western Texas and has also been documented in Oklahoma, Kansas, Nebraska, South Dakota, North Dakota, Minnesota and as far west as California and British Columbia. Interestingly, the psyllid has not been documented east the Mississippi River (Richards and Blood 1933; Pletsch 1947; Wallis 1955; Cranshaw 1993; Capinera 2001; Butler and Trumble 2012a). Contrary to reports in the older literature (Pletsch 1947; Wallis 1955; Cranshaw 1993, 2001), the potato psyllid does indeed occur in Washington and Oregon, where it usually colonizes potato fields in late June and early July (Munyanza et al. 2009a; Munyanza 2010; Crosslin et al. 2012a). There are also indications that the psyllid may overwinter in the Pacific Northwest (Jensen 2012). The potato psyllid also occurs in Mexico and Central America, including Guatemala and Honduras (Pletsch 1947; Wallis 1955; Rubio-Covarrubias et al. 2006; Trumble 2008, 2009; Crosslin et al. 2010; Espinoza 2010; Munyanza 2010; Rehman et al. 2010; Rubio-Covarrubias et al. 2011a), and most recently was reported from Nicaragua (Nicaragua-MAGFOR 2012). The psyllid was accidentally introduced into New Zealand, apparently sometime in the early 2000s (Gill 2006; Liefting et al. 2009a; Teulon et al. 2009; Thomas et al. 2011), and is now established on both North and South Island where it causes extensive damage to the potato, tomato, pepper, and tamarillo crops (Teulon et al. 2009). It is not clear how the insect arrived in New Zealand;

however, it has been suggested that the psyllid was introduced into the country from the western United States, probably through smuggled primary host plant material (Thomas et al. 2011).

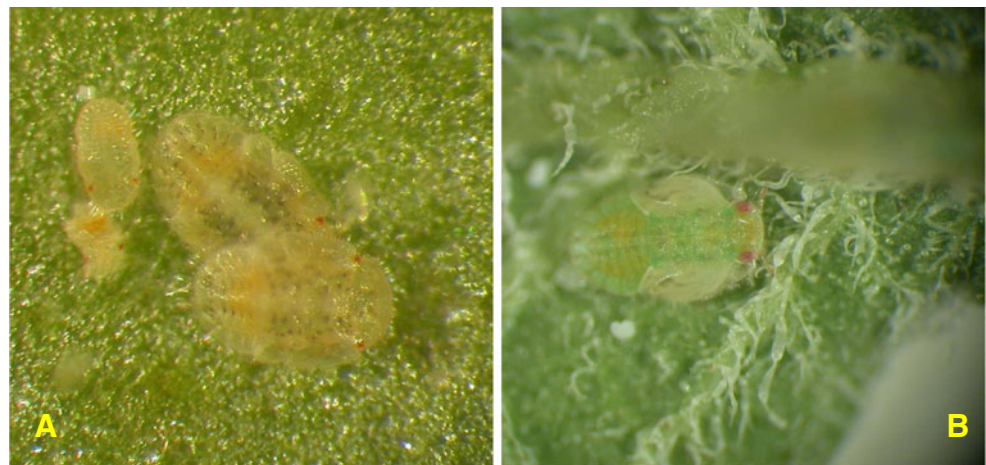
Biology

Bactericera cockerelli is found primarily on plants within the family Solanaceae, but also attacks, reproduces, and develops on a variety of cultivated and weedy plant species (Essig 1917; Knowlton and Thomas 1934; Pletsch 1947; Jensen 1954; Wallis 1955; Butler and Trumble 2012a), including crop plants such as potato, tomato, pepper, and eggplant, and non-crop species such as nightshade (*Solanum* spp.), groundcherry (*Physalis* spp.), and matrimony vine (*Lycium* spp.). Adults have been collected from plants in numerous plant families, including the Pinaceae, Salicaceae, Polygonaceae, Chenopodiaceae, Brassicaceae, Asteraceae, Fabaceae, Malvaceae, Amaranthaceae, Lamiaceae, Poaceae, Menthaceae, and Convolvulaceae, but this is not an indication of the true host range of this psyllid (Pletsch 1947; Wallis 1955; Cranshaw 1993), as these plants rarely if ever support reproduction and growth. Besides solanaceous species, *B. cockerelli* has been shown to reproduce and develop on some species in the family Convolvulaceae, including field bindweed (*Convolvulus* spp.) and sweet potato (*Ipomoea*

Fig. 6 Eggs of potato psyllid



Fig. 7 Nymphs of potato psyllid: second to fourth instars (**a**) and fifth instar with evident wing pads (**b**)



batatas) (Knowlton and Thomas 1934; List 1939; Wallis 1955; Puketapu and Roskrige 2011; Munyaneza, unpublished data). Interestingly, numerous attempts to inoculate field bindweed and sweet potato with Lso-infected psyllids were unsuccessful, suggesting that members of Convolvulaceae are not suitable hosts to Lso, although they can support reproduction and development of its insect vector (Munyaneza, unpublished data).

Weather is an important element governing the biology of *B. cockerelli* and its damage potential. The potato psyllid seems to be adapted for warm but not hot temperatures. Cool weather during migrations, or at least the absence of elevated temperatures, has been associated with outbreaks of this insect (Pletsch 1947; Wallis 1955; Capinera 2001; Cranshaw 2001). Optimum psyllid development occurs at approximately 27 °C, whereas oviposition, hatching, and survival are reduced at 32 °C and cease at 35 °C (List 1939; Pletsch 1947; Wallis 1955; Cranshaw 2001; Abdullah 2008; Yang and Liu 2009; Yang et al. 2010a; Butler and Trumble 2012a). A single generation may be completed in three to five weeks, depending on temperature. The number of generations varies considerably among regions, usually ranging from three to seven. However, once psyllids colonize an area, prolonged oviposition causes the generations to overlap, making it difficult to distinguish between generations (Pletsch 1947; Wallis 1955; Munyaneza et al. 2009a). Both adults and nymphs are very cold tolerant, with nymphs surviving temporary exposure to temperatures of -15 °C and 50 % of adults surviving exposure to -10 °C for over 24 h (Henne et al. 2010a).

In North America, driven primarily by wind and hot temperatures in late spring, *B. cockerelli* annually migrates from its overwintering and breeding areas in southern and western Texas, southern New Mexico, Arizona, California, and northern Mexico (Pletsch 1947; Wallis 1955). The migration occurs especially through the midwestern states and Canadian provinces along the Rocky Mountains (Romney 1939; Pletsch 1947; Jensen 1954; Wallis 1955). In these regions, damaging

outbreaks of potato psyllid in potatoes and tomatoes occurred at regular intervals beginning in the late 1800s and extending into the 1940s (List 1939; Wallis 1946; Pletsch 1947). In more recent years, psyllid outbreaks have also occurred in regions outside of the midwestern United States, including in southern California, Baja California, Oregon, Washington, Idaho, and Central America (Trumble 2008, 2009; Munyaneza et al. 2009a; Wen et al. 2009; Crosslin et al. 2010; Munyaneza 2010; Espinoza 2010; Butler and Trumble 2012a; Crosslin et al. 2012a,b; Nicaragua-MAGFOR 2012).

Outbreaks in Baja California and coastal California led to the discovery that potato psyllid in those regions is genetically distinct from psyllids that overwinter in southern Texas and eastern Mexico, suggesting the existence of two different potato psyllid biotypes referred to elsewhere as “western and central” biotypes (Liu et al. 2006; Jackson et al. 2009). The western biotype differs from southern Texas populations in several life history traits (Liu and Trumble 2007) and possibly overwinters in geographic areas different from regions used by psyllids of the midwestern United States (Trumble 2008). Following the 2011 reports of ZC in Idaho, Oregon, and Washington (Hamm et al. 2011; Nolte et al. 2011; Crosslin et al. 2012a, b), a genetic study by Swisher et al. (2012) using high resolution melting analysis of the mitochondrial Cytochrome C Oxidase subunit I-like gene of *B. cockerelli* led to the identification of a third biotype (referred to as “northwestern haplotype”), so far known only from the Pacific Northwest. This northwestern potato psyllid biotype is genetically different from the central and western biotypes (Swisher et al. 2012). Interestingly, ZC has yet to be shown that it is associated with this northwestern psyllid biotype (Swisher et al. 2012).

Information about migration of *B. cockerelli* within Mexico and Central America is lacking. In the southwestern United States, potato psyllids reappear in overwintering areas between October and November, presumably dispersing southward from northern locations (Capinera 2001); however, their origin has not been determined. In countries and regions

where there are no significant seasonal changes during the winter, temperatures are relatively cool, and where suitable host plants are available (e.g., Mexico, Central America), the potato psyllid is able to reproduce and develop all year round (Espinoza 2010; Rubio-Covarrubias et al. 2011b).

In an effort to identify and develop a sex pheromone and other attractants that can be used to develop improved integrated pest management programs for *B. cockerelli*, reproductive biology and the role of chemical signals in sex attraction in the potato psyllid were studied by Guédot et al. (2010, 2012). It was determined for the first time that the potato psyllid possesses a female-produced pheromone that attracts males (Guédot et al. 2010). Guédot et al. (2012) also showed that adult potato psyllids reach reproductive maturity within 48 h post-eclosion, with females being mature on the day of eclosion and males at one day post-eclosion. In addition, oviposition generally began two days after mating but was delayed when females mated within two days post-eclosion.

Identification of symbionts associated with *B. cockerelli* is currently being investigated. “*Candidatus Carsonella ruddii*”, the obligate and primary endosymbiont of psyllids has been confirmed in the potato psyllid (Nachappa et al. 2011; Hail et al. 2012). Beside Lso, several other secondary endosymbionts associated with the potato psyllid have recently been reported and include the bacteria *Wolbachia*, *Acinetobacter*, *Methylobium*, *Rhizobium*, *Gordonia*, *Mycobacterium*, and *Xanthomonas* (Nachappa et al. 2011; Hail et al. 2012; Butler and Trumble 2012a). Currently, little information is available on the interactions and symbiont relationship between these microorganisms and the potato psyllid.

Pest Significance of *Bactericera cockerelli* and *Candidatus Liberibacter solanacearum*

The potato psyllid is one of the most destructive potato pests in the western hemisphere (Cranshaw 1993; Butler and Trumble 2012a). It was recognized by the early 1900s that *B. cockerelli* had the potential to be an explosive and injurious insect (Šulc 1909; Compere 1915, 1916; Essig 1917). By the 1920s and 1930s, *B. cockerelli* had become a serious and destructive pest of potatoes in many parts of the southwestern United States, giving rise to the description of a new disease that became known as ‘psyllid yellows’ (Richards 1928, 1931, 1933; Binkley 1929; Richards and Blood 1933; List and Daniels 1934). Historically, the extensive damage to solanaceous crops observed during the potato psyllid outbreaks in the early 1900s is thought to have been due to *B. cockerelli*’s association with the psyllid yellows disease, presumably caused by a toxin that is transmitted during the insect’s feeding activities, especially by nymphs

(Eyer and Crawford 1933; Eyer 1937). However, this toxin has yet to be demonstrated and identified.

Above-ground plant symptoms of psyllid yellows are similar to those of ZC and potato purple top disease and include arrested growth, erectness of new foliage, chlorosis and purpling of new foliage with basal cupping of leaves, upward rolling of leaves, shortened and thickened terminal internodes resulting in rosetting, enlarged nodes, axillary branches, and aerial potato tubers (List 1939; Pletsch 1947; Daniels 1954; Wallis 1955; Arslan et al. 1985; Cranshaw 1993; Butler and Trumble 2012a). Below-ground symptoms include setting of excessive numbers of tiny misshaped potato tubers, production of chain tubers, and early breaking of tuber dormancy (Richards and Blood 1933; Eyer 1937; List 1939; Pletsch 1947; Wallis 1955; Arslan et al. 1985; Cranshaw 1993). However, unlike in ZC-infected plants, tubers affected by psyllid yellows do not develop any necrotic symptoms, whether raw or processed into fried chips or fries. A detailed review of phenotypic and etiological differences between psyllid yellows and ZC diseases of potato is provided by Sengoda et al. (2010). In areas where outbreaks of psyllid yellows have occurred, the disease was often present in 100 % of plants in affected fields, with yield losses exceeding 50 % in some areas (Pletsch 1947; Cranshaw 1993).

In recent years, potato, tomato, and pepper growers in a number of geographic areas of the world have suffered extensive economic losses associated with outbreaks of potato psyllids (Trumble 2008, 2009; Munyaneza et al. 2007a,b; 2008; 2009b,c,d; Liefing et al. 2008a,b; 2009a; Secor et al. 2009; Crosslin et al. 2010; Munyaneza 2010; Rehman et al. 2010; Butler and Trumble 2012a; Crosslin et al. 2012a,b; Halbert and Munyaneza 2012; Nicaragua-MAGFOR 2012). The severe damage to these solanaceous crops is mainly due to the recent association of the potato psyllid with Lso. In the United States, ZC has moved steadily northward following its initial appearance in northern Mexico in 1994, arriving as far north as potato fields in Wyoming by 2007. Despite annual psyllid infestations in the Pacific Northwest, ZC was not previously thought to have expanded beyond its 2007 range into the Pacific Northwest region of the United States. That changed dramatically in September 2011, when ZC was widely reported in potato fields in Washington, Idaho, and Oregon (the three states responsible for over 50 % of the total United States potato production), leading to losses in the millions of dollars (Hamm et al. 2011; Nolte et al. 2011; Crosslin et al. 2012a,b; Rondon et al. 2012). This event not only marks a troubling expansion of ZC, it also poses a major threat to a significant acreage of the United States potato production. The source of Lso-infected psyllids responsible for the ZC outbreak in the Pacific Northwest in 2011 is not known but recent studies on genetic analysis of psyllid populations collected in the region in 2011 (Swisher et al. 2012),

coupled with air parcel trajectory analysis (Workneh et al. 2011) suggest that the psyllids in the infested regions of the Pacific Northwest were primarily or exclusively of the western biotype, most likely originating from the southern California area and/or northwest Mexico, and not from the south central United States.

In a number of potato growing regions where the potato psyllid occurs, entire fields have been abandoned because of ZC (Secor and Rivera-Varas 2004; Munyaneza et al. 2007a; Crosslin et al. 2010; Munyaneza 2010) (Fig. 8). Studies conducted under controlled field cage conditions in Texas and Washington by Munyaneza et al. (2008, 2011d) reported yield losses due to psyllids and ZC damage ranging from 43 to 93 % in several commercial potato varieties. The potato industry in Texas estimates that ZC could affect over 35 % of the potato acreage in the state, with potential losses annually to growers exceeding US\$25 million dollars (CNAS 2006; Rosson 2009). Control costs for the potato psyllid have dramatically increased. For example, costs to control the psyllid averaged US\$300 (ranging from US\$170 to \$590) per acre in the southwestern and central United States from 2009 to 2011 (Guenthner and Greenway 2010; Guenthner et al. 2011). During this period, estimates of yield loss due to ZC and psyllids in the region ranged from 0.5 to 75 % (Guenthner and Greenway 2010; Guenthner et al. 2011). In addition, potato processing quality was affected severely. Since arriving in New Zealand in 2006, the potato psyllid and Lso have cost the potato industry at least US\$96 million, with US\$22.5 million in the 2010–2011 growing season alone (Ogden 2011). ZC has caused devastating epidemics in potato growing area of northern Mexico, where up to 60 % of potato crops have been affected (Galviz et al.

2010; Rubio-Covarrubias et al. 2011a,b). Insecticide applications targeting potato psyllid have increased about 300 % in some areas of Mexico (Rubio-Covarrubias et al. 2011b). The potato psyllid was first detected in Honduras in 2002 and has since spread to the entire potato growing region of the country, causing significant losses and an increase in insecticide use (Espinoza 2010). In 2012, severe ZC outbreaks were reported for the first time from Nicaragua (Nicaragua-MAGFOR 2012), causing significant potato crop losses and prompting extensive use of insecticides.

Finally, quarantine issues have begun to emerge in potato psyllid-affected regions because some countries now require that shipments of solanaceous crops from certain growing regions must be free of the psyllid and be tested for Lso before the shipments are allowed entry into the countries (Crosslin et al. 2010). In 2012, Costa Rica temporarily banned all imports of potato upon the discovery of the potato psyllid and ZC in neighboring Nicaragua (Costa Rica-MAG 2012).

Zebra Chip Transmission, Biology, and Epidemiology

Little is known about vector-pathogen-plant interactions in the ZC/potato psyllid complex, especially mechanisms by which the potato psyllid acquires and transmits Lso to potato and other host plants, and how transmission leads to development of ZC. This basic knowledge about these interactions is essential for devising effective management strategies. Specifically, information is needed on how psyllids acquire and transmit Lso, latency period of Lso, densities and

Fig. 8 A potato field severely infected with zebra chip disease in the Columbia Basin of Washington in September of 2011



feeding durations needed to transmit Lso, and physiology of the bacterium in the plant.

To increase the understanding of pathogen transmission by the potato psyllid, biology and feeding behavior of this insect vector were studied by Pearson et al. (2010). Using Electrical Penetration Graph (EPG) technology, Pearson et al. (2010) analyzed stylet penetration behavior of the potato psyllid while feeding on potato (cv. Atlantic, a chipping variety highly susceptible to ZC). Feeding patterns referred to as ‘waveforms’ were identified and then defined using light microscopy of salivary sheath termini in plant tissue after probes were artificially terminated. Four main probing activities were identified and characterized, including stylet pathway activities representing the secretion of the salivary sheath while probing in the vicinity of epidermal and parenchyma cells (C), ingestion from xylem tissue (G), salivation prior to phloem ingestion (E1), and phloem ingestion (E2). It is thought that during the duration of waveform E2 the pathogen is most likely acquired from an infected host plant, whereas the pathogen is most likely inoculated into the host plant via egestion occurring when the vector is salivating during the phase corresponding to waveform E1 (Pearson et al. 2010). Furthermore, these waveforms are useful in screening plants for host plant resistance to either direct feeding or Lso transmission by psyllids and to assess effectiveness and mode of action of insecticides used to control the potato psyllid (Butler et al. 2012).

The primary way that potato psyllids acquire and spread Lso is by feeding on infected plants. Results of preliminary studies indicate that the Lso latent period (time that elapses from initial Lso acquisition to the ability to transmit the pathogen) in the psyllid is about two weeks after an acquisition period of 8–24 h on Lso-infected potato plants (Munyanza and Sengoda, unpublished data). This latent period has been observed to be shorter when psyllids have fed on Lso-infected tomato plants, apparently due to much higher Lso titer in tomato than potato (Munyanza and Sengoda, unpublished data). The bacterium is also transmitted transovarially in the psyllid at a relatively high rate (Hansen et al. 2008; Munyanza, unpublished data). In addition, Lso can be transmitted to potato through grafting (Crosslin and Munyanza 2009; Secor et al. 2009), although it has been shown that Lso is transmitted to potato leading to ZC development more rapidly by psyllid activities than by grafting (Sengoda et al. 2010; Buchman et al. 2011a,b; 2012).

Buchman et al. (2011b) demonstrated that adult potato psyllids were highly efficient vectors of Lso, and that nymphs were less efficient than adults. The authors also showed that exposure of a healthy potato plant to 20 Lso-infected adult potato psyllids for a period as short as one hour resulted in ZC symptom development, whereas a single adult potato psyllid was capable of inoculating Lso to

potato within a period as short as six hours and leading to development of ZC (Buchman et al. 2011b). Moreover, results of their study showed that feeding period had little influence on overall ZC disease incidence, severity, and resulting yield loss. Furthermore, Buchman et al. (2011a) discovered that a single Lso-infective adult psyllid was as damaging as 25 infective psyllids per plant.

Buchman et al. (2012) determined how rapidly ZC symptoms develop in potato tubers following plant exposure to Lso-infected potato psyllids under field conditions, and assessed how the disease affects the yield and tuber processing quality. ZC symptoms developed in potato tubers about three weeks following exposure of plants to psyllids. Interestingly, the symptoms developed in tubers before they were observed in the above-ground parts of plants. It was also shown that tuber development ceased upon the onset of ZC symptoms, resulting in substantial yield loss (Buchman et al. 2012). It is important to note that if the plants are infected prior to the tuber initiation stage, the plants die quickly and also fail to produce tubers. In addition, Buchman et al. (2012) reported that levels of tuber solids decreased as soon as initial disease symptoms were observed, whereas reducing sugar levels in tubers increased dramatically, significantly lowering potato processing quality. Similar observations were made by Levy et al. (2011) while examining patterns of Lso translocation through phloem in potato and tomato plants under greenhouse conditions. Levy et al. (2011) found that Lso was detectable in tomato and potato plants two to three weeks after plant exposure to Lso-infected potato psyllids, most frequently in the upper- and middle-tier leaves. They also reported that Lso was detected in potato leaves of a second and non-inoculated stem when the stems remained joined via the mother tuber.

Lso has been shown to severely disrupt carbohydrate flow in potato plants, leading to ZC symptoms in the tubers. Buchman et al. (2011a, 2012) showed that ZC infection resulted in overall high glucose and sucrose levels compared with uninfected tubers. Similar conclusions regarding production of high levels of both sugars in ZC-infected tubers were reached earlier by Gao et al. (2009). It has been suggested that the necrotic flecking and streaking of the medullary ray tissue symptoms in ZC-infected tubers is related to darkening of the resulting processed chips or fries due to elevated sugar levels which caramelize when tuber slices are fried (“Maillard Reaction”). Miles et al. (2010) has shown that cell death is also associated with ZC symptoms in both raw and fried potato tubers. Navarre et al. (2009) reported high levels of aromatic amino acids and phenolic compounds in extracts from ZC-symptomatic potato tubers. During Navarre et al. (2009) study, tyrosine concentrations increased over 8-fold in ZC-symptomatic tubers, suggesting that the dramatic increase in this amino acid may significantly contribute to the browning observed in ZC-infected

tubers. Salicylic acid, a key regulator of plant defenses, was also shown to be present at very high concentrations in ZC-infected tubers, which is consistent with what would be expected from tubers mounting a defense response to a pathogen (Navarre et al. 2009). On the other hand, Wallis and Chen (2011) determined that ZC-infected tubers possessed significant high levels of peroxidase, polyphenol oxidase, chitinase, and β -1,3-glucanase. The observed increases in phenolics, amino acids, and defense-associated enzymes were significantly correlated with ZC symptom severity, but uncorrelated with Lso titers. Wallis and Chen (2011) confirmed the hypothesis of Navarre et al. (2009) that increased phenolic and polyphenol oxidase levels in ZC-infected potatoes result in increased browning of freshly cut tubers, whereas increased amino acid levels result in increased browning when ZC-tuber slices are fried. Similarly, Nissinen et al. (2012) reported significant increases in concentrations of phenolic compounds and some amino acids in roots of carrot plants attacked by Lso-infected *T. apicalis*. Furthermore, Miles et al. (2009) showed that there were significant differences in mineral content between ZC-infected and ZC-free potato tubers.

Alvarado et al. (2012) found that ZC-infected potato stems appear to be programmed to exhibit tuber-like physiological properties. It was determined that compared to healthy plants, stems of ZC-infected plants accumulate starch and proteins, including gene expression regulatory factors (e.g., cyclophilin) and tuber storage proteins (e.g., patatins). This abnormal starch and protein accumulation in stems may explain formation of aerial tubers and fleshy and succulent stems by ZC-infected plants, instead of the characteristic hollow and brittle stems of healthy plants. Furthermore, Alvarado et al. (2012) discovered that the total phenolic content in ZC-affected stems was elevated two-fold, and levels of polyphenol oxidase enzyme were also high, both serving to explain the rapid brown discoloration of air-exposed damaged tissue observed in ZC-infected potato plants and tubers.

It has been suggested that Lso manipulates plant signaling and defensive responses to benefit itself and the potato psyllid, its insect vector, on their host plants. Using tomato as a model, Casteel et al. (2012) showed that feeding by different life stages of the potato psyllid infected with Lso induced tomato genes regulated by jasmonic acid and salicylic acid, including Allene oxidase synthase, Proteinase inhibitor 2, Phenylalanine ammonia-lyase 5, and Pathogenesis-related protein 1. Gene induction was significantly more pronounced in life stages with lower Lso titer (younger nymphs) than those with higher Lso titer (older nymphs and adults). Interestingly, inoculation of Lso without insect hosts through grafting suppressed accumulation of these defense transcripts. Collectively, the results of Casteel et al. (2012) study demonstrated that the potato psyllid may influence plant defense responses by its

vectoring of Lso during feeding and that the bacterium then causes a substantial reduction of jasmonic acid/ethylene- and salicylic acid-regulated plant defense transcripts.

Although the impact of ZC has been substantially documented for processing and table potatoes, little is known on ZC-tuber transmission and the impact of this disease and its insect vector on quality of potato seed. ZC-infected potato tubers potentially being a source of the disease spread is a major concern and could be a threat to national and international trade of fresh and seed potatoes. In a study conducted in the United States, Henne et al. (2010c) showed that about 44 % of ZC-infected tubers remained viable under greenhouse conditions, but produced hair sprouts and weak plants that died prematurely; a low percentage of plants from ZC-infected tubers tested positive for Lso. Henne et al. (2010c) concluded that in areas where ZC is currently established, plants produced by ZC-infected seed tubers do not contribute significantly to ZC incidence and spread within potato fields. Studies conducted in New Zealand by Pitman et al. (2011) and Berry et al. (2011) reported a rate of potato plant emergence from tubers testing positive for Lso by PCR, but not exhibiting typical ZC symptoms, as high as 90 %. This potato plant emergence resulted in production of marketable tubers, although plant growth and potato yield were significantly reduced. Production of ZC-infected daughter tubers during Pitman et al. (2011) and Berry et al. (2011) studies was however very negligible.

As a follow up to ZC transmission through potato tubers, Munyaneza et al. (2011b) examined the impact of Lso-free and Lso-infected psyllids on plant emergence, viability, yield, and ZC incidence in nine commercial potato varieties important to the United States under controlled field cage conditions, over two years and in Washington and Texas, two different and distant locations. Potato plants were continuously exposed to either Lso-free or Lso-infected psyllids under controlled field cage conditions and, at harvest, the tubers were collected and planted in field cages the following season. Plant emergence for tubers produced by psyllid-free plants (controls) and those continually exposed to Lso-free psyllids (i.e., psyllid yellows) was 100 % two to three weeks after planting and all the plants produced ZC-free tubers. No difference in yield was observed between plants from psyllid yellows-affected tubers and those produced by psyllid-free plants. In contrast, plant emergence for ZC-infected tubers from plants that were previously exposed to Lso-infected psyllids ranged from 0–22.2 % and occurred between five and 11 weeks after planting. Although these emerging ZC-infected tubers initially produced hair sprouts which later turned into weak plants, none of the plants tested positive for Lso by conventional PCR or produced tubers with ZC symptoms, whether fresh or fried. Results of these studies support findings by Henne et al. (2010c) and indicate that ZC-infected tubers seriously affect potato seed

quality as the tubers do not sprout and if they do, produce hair sprouts and weak plants. However, Munyaneza et al. (2011b) concluded that the risk of spreading ZC through ZC-infected tubers was extremely low and not significant since the number of ZC-infected tubers giving rise to infected was negligible and these plants are short-lived.

Very recently, Hamm (2012) reported a significant number of ZC-infected potato volunteers being observed in Columbia Basin of Washington and Oregon corn and wheat fields, following heavy psyllid infestation and severe ZC infection in these fields in 2011 and a mild winter. Interestingly, ZC-tubers collected from the same fields generally failed to sprout or produce ZC-infected plants when planted in the greenhouse following several months in storage (Hamm, personal communication). The reasons behind this discrepancy in ZC infection between field and greenhouse conditions are not known and warrant investigation.

Contrary to reports in older literature describing psyllid yellows-affected tubers (Richards and Blood 1933; Pletsch 1947; Wallis 1955; Cranshaw 1993), tubers produced by plants with psyllid yellows symptoms (following exposure of the plants to heavy and extensive feeding by Lso-free psyllids) during Munyaneza et al. (2011b) study appeared not to affect seed germination, normal plant growth, and yield. Similar observations were made by Berry et al. (2011) who reported that exposure of growing potato plants to Lso-free psyllids at different densities and for different periods of time under controlled field conditions did not appear to have a major influence on potato yield. Collectively, these findings suggest that serious and sporadic psyllid damage outbreaks in potato fields that were reported in the past and attributed to what was believed as psyllid yellows disease were more likely associated with Lso and ZC.

Little is known on the risk of ZC developing in potato tubers while in storage. This is especially a major concern for potatoes produced in the Pacific Northwest of the United States, where majority of tubers go into storage following harvest, and where potato fields appear to be subjected to Lso infection late in the growing season because of the late psyllid migration into potato fields (Munyaneza et al. 2009a; Crosslin et al. 2012a,b). It has been determined that all plant growth stages of potato are susceptible to ZC infection (Munyaneza and Buchman, unpublished data) and that it takes about three weeks after Lso inoculation for ZC symptoms to develop in potato plants and tubers (Buchman et al. 2012). Plants exposed to Lso-infected psyllids less than three weeks before harvest usually produce tubers without ZC symptoms (Buchman et al. 2012). It is not known how extensively or how rapidly symptomless but infected tubers develop ZC symptoms in storage. However, results of preliminary trials conducted in 2010 and 2011 indicated that an average of 10–22 % and 46–66.4 %, respectively, of symptomless tubers harvested from potato (cv. Atlantic) plants

exposed to Lso-infective psyllids two to three weeks before harvest developed ZC symptoms after two and three months in storage (at 10 °C) (Munyaneza and Buchman, unpublished data). Similarly, Rashed et al. (2011) reported ZC symptom development in potato tubers of the chipping cultivar FL1867 after three months in storage (at 5 °C). The tubers were symptomless at harvest; tubers had been harvested from plants that had been exposed to Lso-infected psyllids two weeks prior to harvest. Further studies to elucidate this issue of the risk of postharvest ZC development are underway.

Disease and Vector Management

Potato Psyllid Monitoring and Sampling

Currently, all management tactics for ZC are targeted against the potato psyllid. Monitoring the potato psyllid is essential to effective management of this insect pest. Early season detection and management of this insect is crucial to minimize psyllid reproduction in the field and spread of ZC throughout fields.

Yellow sticky or water-pan traps are commonly used to monitor movement of the potato psyllid in a given region but are not recommended for estimating population density of this insect within fields (Al-Jabar and Cranshaw 2007; Goolsby et al. 2007a,b; 2012; Cameron et al. 2009; Butler and Trumble 2012a; Martini et al. 2012). Little is known on the attractiveness of different colors other than yellow to potato psyllid (Al-Jabr 1999; Al-Jabar and Cranshaw 2007; Goolsby et al. 2007a; Cameron et al. 2009). Studies by Al-Jabar and Cranshaw (2007) and Henne et al. (2010a) compared standard yellow sticky traps to those with different colors and reported that neon-green traps captured more adult potato psyllids than standard yellow traps. Efforts to identify the sex pheromone of the potato psyllid are underway (Guédot et al. 2011) and could potentially lead to an improved monitoring system for this insect pest.

Adult populations in potato fields are best sampled using sweep nets or vacuum devices, but egg and nymphal sampling requires visual examination of foliage that may necessitate the use of a field hand lens (Cranshaw 1994; Goolsby et al. 2007a, 2012; Butler and Trumble 2012a). Martini et al. (2012) recently developed a novel method referred to as “the leaf washing method or LWM” to quickly extract and count potato psyllid nymphs from leaves in commercial potato fields. The sampling method consists of immersing infested leaves in cold water to remove any dust and sand, placing the leaves in 85 °C hot water for 5 s, extracting psyllid nymphs from the heated water by passing it through a sampling unit composed of a funnel and fine mesh-organza fabric, and finally counting psyllid nymphs

adhering to the organza fabric using a microscope. With the LWM method, Martini et al. (2012) were able to quickly determine distribution of potato psyllid in different parts of the plant and showed that potato psyllid nymphs were most predominant in the middle portion of the potato canopy.

Studies of spatial and temporal distribution of the potato psyllid indicated that both psyllid populations are highest at field edges initially, but if not controlled will eventually spread throughout the crop (Henne et al. 2010b; Butler and Trumble 2012b); spatial distribution of ZC within fields appears to follow a similar pattern (Henne et al. 2012; Workneh et al. 2012). In addition, Butler and Trumble (2012b) demonstrated that psyllids were mostly distributed on the top and middle portions of the potato plant and on the underside of leaves. Butler and Trumble (2012b) also developed a binomial sequential sampling plan for the potato psyllid and determined that sample sizes ranging from 12 to 16 plants per sample were needed to reach a treatment decision based on action thresholds of 0.5, 1, and 5 psyllids per plant.

ZC incidence in a given region or field depends not only on the abundance of the potato psyllid, but also on the incidence of Lso in the psyllid populations (Goolsby et al. 2012). Therefore, applications of insecticides targeted against the potato psyllid should take into consideration the infectivity of the vector. Spatial and temporal monitoring of Lso infectivity in the potato psyllids could help predict whether populations of psyllids present in a given area pose a significant risk of producing ZC, and therefore should be targeted vigorously for control. Estimating Lso infection rate in the insects is easily accomplished by testing individuals or groups of psyllids using a PCR assay (Crosslin et al. 2011b). A potato psyllid trapping network has been established in the United States over a large geographic region (Goolsby et al. 2011, 2012); collected potato psyllids are tested weekly (Crosslin et al. 2011a) and the information is disseminated to the potato industry on a weekly basis to help potato producers make informed pest management decisions.

Chemical Control

Potato psyllid is currently controlled primarily by insecticide applications (Goolsby et al. 2007b; Vega-Gutierrez et al. 2008; Berry et al. 2009; Gharalari et al. 2009; Bynum et al. 2010; Zens et al. 2010; Butler et al. 2011a, 2012; Butler and Trumble 2012a), but even with insecticides the psyllid is difficult to manage. Good coverage, especially with contact insecticides, is important because psyllids are generally found primarily on the underside of leaves (Nansen et al. 2010; Butler and Trumble 2012b). Different life stages of the psyllid require the use of specific insecticides, as it has been shown that chemicals which control adults do not necessarily kill nymphs or eggs (Goolsby et al. 2007b; Gharalari et al. 2009; Zens et al. 2010). Therefore, caution is

necessary when selecting and applying insecticides, requiring that growers consider which life stages are present in the crop, and then timing insecticide applications accordingly. Insecticides commonly used to control the potato psyllid include acephate, metamidophos, thiacloprid, buprofezin, abamectin, cypermethrin, deltamethrin, lambda-cyhalothrin, esfenvalerate, spinosad, spirotetramat, imidacloprid, thiamethoxam, spiromesifen, dinotefuran, pyriproxyfen, and pymetrozine (Goolsby et al. 2007b; Berry et al. 2009; Gharalari et al. 2009; Bynum et al. 2010; Tucuch-Haas et al. 2010; Zens et al. 2010; Butler et al. 2011a, 2012; Butler and Trumble 2012a).

The psyllid transmits Lso to potato within a few hours of colonizing a potato plant (Buchman et al. 2011a, b; 2012), thus psyllid controls must begin immediately upon detection of the insect in fields. Until the mid-2000s, potato growers in the southwestern United States relied on pyrethroids and organophosphates to control psyllids, but these insecticides did not provide adequate control and many growers still incurred severe damage and losses due to ZC (Guenthner and Greenway 2010; Guenthner et al. 2011). Because the potato psyllid in the southwestern United States is found in fields throughout the potato growing season, many potato growers in this region now routinely apply a neonicotinoid systemic insecticide at planting, followed by applications of foliar insecticides at regular intervals (Zens et al. 2010; Guenthner et al. 2011). It has been estimated that costs associated with ZC control in Texas in 2010 and 2011 range from US\$170 to \$590 per acre for an average of six to 10 applications of insecticides (Guenthner and Greenway 2010; Guenthner et al. 2011); despite these applications, some growers have nonetheless reported losses of up to 75 %.

Growers in the Pacific Northwest of the United States also face a challenge because of the psyllid's mid-season (late-June to late-July) arrival into potato fields (Munyanza et al. 2009a; Rondon et al. 2012). Psyllid controls begin at plant emergence in the southwest because the psyllid is present at plant emergence. In contrast, seasonal timing of psyllid arrival into Pacific Northwest potato fields cannot be predicted year-to-year. Thus, growers in the Pacific Northwest face a great deal of uncertainty about when to begin psyllid controls in mid-season and how effective insecticides applied during that time are, although because of the shorter season fewer insecticide applications may be needed. Insecticide recommendations for the Pacific Northwest potatoes are discussed by Schreiber et al. (2012), and a model for ZC treatment decisions for Columbia was developed for the Columbia Basin of Washington and Oregon by Harris (2012). In Mexico and some Central America countries, where the psyllid is present all year round, routine weekly applications of insecticides targeted against the potato psyllid are common (Vega-Gutierrez et al. 2008; Espinoza 2010; Galviz et al. 2010; Rubio-Covarrubias et al. 2011b). For

all geographic regions, there is a concern that insecticide-heavy programs could eventually lead to resistance. Psyllids have been shown to develop insecticide resistance due to their high fecundity and short generation times (McMullen and Jong 1971).

Even a single psyllid per plant can effectively transmit Lso to potato and cause ZC. Coupled with a short inoculation access period (Buchman et al. 2011a,b; 2012), this causes a substantial challenge for growers in controlling the potato psyllid and preventing ZC transmission. Just a few infective psyllids feeding on potato for a short period can result in substantial spread of the disease within a potato field or region (Henne et al. 2012). Thus, conventional pesticides may often have only limited effectiveness at controlling ZC, as they may not kill the psyllid quickly enough to prevent Lso transmission, despite their effectiveness at reducing the overall population of psyllids. The most valuable and effective strategies to manage zebra chip would likely be those that discourage vector feeding, such as the use of plants that are resistant to psyllid feeding or that are less preferred by the psyllid.

Some conventional and biorational pesticides, including plant and mineral oils and kaolin, have been shown to reduce potato psyllid feeding and oviposition (Gharalari et al. 2009; Yang et al. 2010b; Peng et al. 2011; Butler et al. 2011a, 2012) and could be useful tools in integrated pest management programs to manage ZC and its psyllid vector. Yang et al. (2010b) showed that the biopesticides SunSpray mineral oil, BugOil (a mixture of four plant essential oils), or Requiem (a plant extract of *Chenopodium ambrosioides*) had significant repellency to adult potato psyllids (77.2–95.4 %) and strongly deterred oviposition (up to 100 %). Similarly, Diaz-Montano and Trumble (2012) have shown that volatiles from dimethyl disulfide and several plant essential oils are effective in repelling the potato psyllid and could be incorporated in IPM programs to better control ZC.

RNA interference (RNAi) technology is rapidly gaining attention as a potential strategy to manage insect pests and plant pathogens (Price and Gatehouse 2008). Efforts to investigate whether RNAi can be used to control potato psyllid are underway. With the goal of developing an RNAi-based management strategy for *B. cockerelli*, Hail et al. (2010) used pyrosequencing technology to identify target genes and synthetic dsRNA. Constructs were designed to block the activity of heat shock protein 70 and heat shock cognate 70, molecular chaperones that are intimately involved in essentially all life processes by folding and stabilizing other proteins in the potato psyllid. Hail et al. (2010) plan to target other genes and deliver RNAi to psyllids via the plant through a root soaking procedure. Wuriyangan et al. (2011) recently demonstrated the induction of specific RNAi effects in *B. cockerelli* by injection and oral acquisition of dsRNA and siRNA inducers that targeted

ubiquitously expressed and gut-abundant mRNAs, resulting in significant mortality of the psyllid. Results of this study support the possibility of potentially using RNAi-based strategies to control the potato psyllid for ZC management. Another novel strategy currently being explored to manage ZC is the use of antibiotics and metal phosphites. Results of a recent trial using foliar applications of selected antibiotics to potato plants in southern Texas by Henne et al. (2011) indicated that these products can be used to effectively remediate ZC-infected plants and/or prevent the onset of ZC symptoms.

Biological Control

Potato psyllid is attacked by a number of natural enemies, including chrysopid larvae, coccinellids, geocorids, anthorcorids, mirids, nabids, syrphid larvae, and the parasitoids *Tamarixia triozae* (Hymenoptera: Eulophidae) and *Metaphycus psyllidis* (Hymenoptera: Encyrtidae) but little is known about their effects on psyllid populations (Pletsch 1947; Wallis 1955; Cranshaw 1993; Al-Jabr 1999; Butler et al. 2010; Butler and Trumble 2012a; Liu et al. 2012). In addition, several entomopathogenic fungi, including *Beauveria bassiana*, *Metarhizium anisopliae*, and *Isaria fumosoroseae*, have been determined to be effective natural enemies of *B. cockerelli*, causing psyllid mortality up to 99 and 78 % under laboratory and field conditions, respectively (Lacey et al. 2009, 2011).

Cultural Control

Little is known about what cultural practices could help mitigate damage caused to potato crops by ZC. Studies by Munyaneza et al. (2010a) and Trevino et al. (2011) indicated that in some areas of the Lower Rio Grande Valley of southern Texas, early (December–January) planted potato crops are more susceptible to psyllid injury and ZC than crops planted mid-season or later (February–March). This trend was not observed for potato fields located north of the Lower Rio Grande Valley (Trevino et al. 2011). The reasons behind the differences in ZC incidence based on planting timing between the two regions are not known. However, it is suspected that differences in ZC incidence between the two potato growing regions of Texas may have been due to yearly and seasonal fluctuations in Lso infection rate in overwintering and migrating psyllids. The potato psyllid is believed to overwinter along the Rio Grande River between Texas and Mexico and migrates northward with increasing high temperatures (Pletsch 1947; Wallis 1955). It is possible that overwintered potato psyllids in early-planted potatoes in the Lower Rio Grande Valley of Texas were more infected with the bacterium than psyllids attacking potatoes in more northern regions (Munyaneza et al. 2010a). Further studies are

needed to elucidate the impact of planting timing on ZC incidence in potato crops.

Plant Host Resistance

Development and identification of potato varieties and/or advanced breeding lines with resistance to or tolerance of ZC, using traditional breeding methods or genetic engineering, are crucial to development of effective and sustainable management strategies for this emerging and important potato disease. Unfortunately, it has been shown that most, if not all, commercial potato varieties currently available in the United States and elsewhere are susceptible to ZC (Munyanza et al. 2011d), underscoring the urgent need to identify and/or develop potatoes that are resistant to this important disease. Efforts to develop resistant cultivars and screening trials to identify potato varieties and advanced breeding lines with resistance to ZC and the potato psyllid are currently underway (Butler et al. 2010, 2011b; Miller et al. 2010; Munyanza et al. 2010b; Novy et al. 2010; Pierson et al. 2010; Munyanza et al. 2011a; Rubio-Covarrubias et al. 2011b; Butler and Trumble 2012a). Preliminary results suggest that some advanced potato breeding lines are promising and may be resistant to or tolerant of ZC and/or the potato psyllid and warrant further evaluation (Munyanza et al. 2011a; Rubio-Covarrubias et al. 2011b). Furthermore, development of genetically modified potato material to manage the potato psyllid and ZC is being explored. Curtis et al. (2010) demonstrated that there was a delay in the onset of ZC symptoms into transgenic potato plants that were generated through *Agrobacterium*-mediated transformation carrying either plant derived antimicrobial or anti-insect genes after being exposed to Lso-infected psyllids; a reduction of the level of bacterial inoculum in plant tissues was also observed.

Conclusion

ZC is an emerging and economically important disease of potato in several parts of the world. It is imperative that management strategies be developed to effectively manage the disease. ZC is associated with Lso which is transmitted to potato by the potato psyllid. Thus, increasing the understanding of both the disease causal agent and its insect vector is essential. In this literature review paper, ZC history and geographic distribution, biology, epidemiology, and management were extensively discussed. Particularly, pertinent and available information on the disease causal bacterium and its insect vector was provided. This information will help potato producers, processors, and researchers to develop management strategies for both Lso and *B. cockerelli* in order to minimize damage caused to potato by this devastating disease.

Acknowledgments I am grateful to anonymous reviewers who made suggestions to improve an earlier version of this paper. Financial

support for this work was partially provided by Frito Lay, Inc., USDA-ARS State Partnership Potato Research Program, Texas Department of Agriculture, USDA-RAMP (Project # 2009-51101-05892) and USDA-SCRI (Project #2009-51181-20176). The use of trade, firm, or corporation names in this publication is for information and convenience of the reader. Such use does not constitute an official endorsement or approval by the United States Department of Agriculture or the Agricultural Research Service of any product or service to the exclusion of others that may be suitable. USDA is an equal opportunity provider and employer.

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