



The potato psyllid, *Bactericera cockerelli* (Sulc) (Hemiptera: Triozidae): life history, relationship to plant diseases, and management strategies

Casey D. Butler and John T. Trumble

Department of Entomology, University of California, Riverside, 900 University Ave., Riverside, CA 92521, USA e-mails: casey.butler@email.ucr.edu; john.trumble@ucr.edu Received on December 5, 2011. Accepted on December 29, 2011

Summary

The potato/tomato psyllid, *Bactericera cockerelli* (Sulc) (Hemiptera: Triozidae) has been a major pest of solanaceous crops for decades. This pest can cause damage to crop plants by direct feeding and, as has been recently discovered, by transmitting the bacterial pathogen *Candidatus* Liberibacter psyllaurous (a.k.a. *Ca.* L. solanacearum). Many studies have been conducted to determine the relationship of this pest to plant injury and to develop management strategies to alleviate the damage caused by this pest in a wide variety of solanaceous plants. Studies in the past decade have documented substantial genetic variability in this invasive species, enhanced our rapidly-evolving understanding of the interactions between the insect and the pathogen it carries, and improved our appreciation of the invasive potential of the pest. This review seeks to provide a comprehensive update to *B. cockerelli* life history, relationship to plant diseases, and the current state of management strategies against *B. cockerelli*.

Keywords

Potato psyllid; Psyllidae; 'zebra chip'; 'psyllid yellows'; management

Introduction

When Karel Sulc first described *Bactericera cockerelli* (Sulc) (Hemiptera: Triozidae) in 1909 from individuals collected on peppers (*Capsicum* sp.) in Boulder, CO, USA, he inferred that due to the large number of nymphs observed on plants, this insect may become a destructive pest (Sulc, 1909). In 1915, *B. cockerelli* was recognized as a plant pest for the first time by damaging the ornamental False Jerusalem Cherry (*Solanum capsicastrum*) in San Francisco and Sacramento, CA, USA, to the point where control measures were necessary (Compere, 1915). In 1927, the full potential of how destructive *B. cockerelli* could be was realized when many state-wide outbreaks of 'psyllid yellows' (PY) occurred on potatoes (*Solanum tuberosum* L.) starting in Utah and then

spread to many other Rocky Mountain states (Richards et al., 1927; Richards, 1928). This new disease was ascribed to the feeding behavior of *B. cockerelli* (most scientists speculated that the psyllid was releasing a toxin) and caused the heaviest yield losses yet recorded for potatoes in the USA, often leading to the complete destruction of the crop in psyllid-infested areas (Linford, 1928). A more devastating outbreak of *B. cockerelli* and PY than the 1927 epidemic occurred in 1938 (Anonymous, 1929; Jensen, 1939; Morris, 1939). In the years after the 1938 outbreak, *B. cockerelli* was managed almost exclusively by insecticides (Pletsch, 1947; Wallis, 1955; Cranshaw, 1994).

In 1994, a new potato defect was discovered in Mexico and later named 'zebra chip' (ZC) (Munyaneza et al., 2007a). This disease was later found to be transmitted by *B. cockerelli* (Munyaneza et al., 2007a, 2007b) and caused by the bacterium *Candidatus* Liberibacter psyllaurous (a.k.a. *Ca.* L. solanacearum) (Hansen et al., 2008; Liefting et al., 2009). ZC became a serious problem for the potato industry as it was more insidious than PY; even late season infection with ZC renders tubers unmarketable and thus causes significant losses at harvest, often after the full costs of crop production. Thus, *B. cockerelli* regained prominence as a key, serious pest of solanaceous crops such as potato, tomato (*Solanum lycopersicum* L.), peppers, and eggplant (*Solanum melongena* L.) in North and Central America (Cranshaw, 1994; Crosslin et al., 2010). In recent years, *B. cockerelli* has also invaded New Zealand as pest of solanaceous greenhouse crops, and outdoor potatoes and tomatoes (Gill, 2006; Davidson et al., 2008). Currently *B. cockerelli* is causing substantial economic losses across a wide geographic range.

Taxonomy and distribution

Bactericera cockerelli has two common names: the potato psyllid and the tomato psyllid (ESA, 2011). *Bactericera cockerelli* was originally described as *Trioza cockerelli* by Sulc (1909). In 1910, Crawford erected a new psyllid genus *Paratrioza*, and in 1911 *Trioza cockerelli* was assigned to *Paratrioza*. In 1997, when the genus *Paratrioza* was synonymized with the genus *Bactericera* as defined by combinations of adult, nymphal and egg characters, *B. cockerelli* also changed families from Psyllidae to Triozidae (Burckhardt and Lauterer 1997, Hodkinson 2009). Morphological descriptions of *B. cockerelli* can be found in Crawford (1911, 1914), Essig (1917), Ferris (1925), and Tuthill (1945). Tuthill (1945) and Burckhardt and Lauterer (1997) list the synonyms for *B. cockerelli* as well.

Bactericera cockerelli is endemic to North America with the distribution of this insect in the USA including Arizona, California, Colorado, Idaho, Kansas, Minnesota, Montana, Nebraska, Nevada, New Mexico, North and South Dakota, Oklahoma, Oregon, Texas, Utah, Washington, and Wyoming (Pletsch, 1947; Cranshaw, 1994; Munyaneza et al., 2009, 2010). Additionally, *B. cockerelli* can be found in the Canadian Provinces of Alberta, British Columbia, Ontario, and Saskatchewan (Pletsch, 1947; Wallis, 1955; Ferguson et al., 2002), as well as Mexico, and in several countries in Central America at least as far south as Guatemala and Honduras (Tuthill, 1945; Pletsch, 1947; Jackson et al., 2009; Crosslin et al., 2010). In the early-2000s, *B. cock-erelli* invaded New Zealand and has spread throughout this country (Gill, 2006; Davidson et al., 2008; Teulon et al., 2009).

Life history

Bactericera cockerelli is a polyphagous insect with a wide host range exceeding 20 plant families and is able to oviposit and complete development on more than 40 host species (Knowlton and Thomas, 1934; Wallis, 1951). The relative importance of host plants for *B. cockerelli* relates to the abundance, preference and proximity to agricultural areas (Wallis, 1955). In the North Platte Valley of Wyoming and Nebraska, an important non-economic host is matrimony-vine (*Lycium barbarum* L.) (Wallis, 1946, 1955). In a scientific note by Knowlton (1933), adult *B. cockerelli* were reported to be able to survive for a considerable length of time (i.e., 17-96 days) on various plant species in which nymphs were not able to successfully complete development. This host feeding may contribute to the successful survival of adult psyllids during the winter months. In general, *Bactericera cockerelli* can survive well on, and appears to prefer, plant species in the family Solanaceae (Wallis, 1955).

However, despite these observations by Knowlton (1933), most researchers hypothesize that adult migrations provide the primary mechanism by which *B. cockerelli* arrives in agricultural crops. Glick (1939) collected *B. cockerelli* by airplane in Mexico at altitudes up to 1200 m suggesting that this species can migrate via air currents. Evidence of this is also noted by Papp and Johnson (1979) as *B. cockerelli* have been found on the alpine snowfields in the Sierra Nevada Mountains in California.

Romney (1939) found spring breeding populations of B. cockerelli on Lycium andersonii Gray and Lycium macrodon Gray in southern Arizona, and on Lycium spp. in southern Texas. Breeding on these plants occurs from January to May with peak populations building in April and early May after several generations have been produced (Romney, 1939). By the middle of June, adults move out of these habitats, and are not seen again until a large influx of adults move back to these habitats in late October to early November (Romney, 1939). Observations by Romney (1939) and using information regarding the migration patterns of other insect species such as the beet leafhopper, Circulifer tenellus (Baker) and the psyllid Heteropsylla mexicana (Crawford) suggests that *B. cockerelli* from breeding populations in southern Arizona migrate north and west of the Continental Divide, while B. cockerelli populations in southern Texas migrate north and east of the Continental Divide. However, populations of B. cockerelli can occur much further south on the east coast area of Mexico (Pletsch, 1947). Thus, the possibility exists that primary overwintering sites may be in both the USA and Mexico. Wallis (1946) found that B. cockerelli does not overwinter in Wyoming and Nebraska, and the arrival of psyllids observed during the early potato crop in May and June provides circumstantial evidence of B. cockerelli migration. Recent genetic data based on inter simple sequence repeat (ISSR) markers by Liu et al. (2006) support that B. cockerelli populations were of two groups, one from western

North America and the other from central USA and eastern Mexico. Liu et al. (2006) also found that there was genetic transfer between these populations. To date, the northernmost overwintering site known is in coastal Ventura County, California (Trumble, unpublished).

There is often great variation from year to year regarding the numbers of *B. cockerelli* found on economic and non-economic host plants (Wallis, 1946). Bactericera cockerelli is considered to be a 'temperature-zone' species (Knowlton, 1933; List, 1939), meaning this species life history characteristics are severely impacted by extremely hot or cold conditions. In the laboratory, the optimum range for *B. cockerelli* development is rather narrow (Wallis, 1946). Individuals reared at 26.7°C exhibit the best survival, development, and oviposition, with reductions in these life history characteristics at 32.2°C (List, 1939). Temperatures at 38.8°C for one or two hours are lethal to eggs and nymphs, and adult stop laying eggs (List, 1939); however, the data provided by List (1939) were not statistically analyzed. Romney (1939) believes the combination of high temperatures and/or the decline in the quality of host plants contribute to B. cockerelli leaving spring breeding sites. The temperature results agree with observation in agricultural fields (Wallis, 1946). Further research suggests that factors playing a role in *B. cockerelli* numbers in the field are related to temperature, size of the spring migration, and the size of crop plants. Larger plant canopies may shade B. cockerelli from the hot summer temperatures above 32.2°C as the temperature within the plant canopy is several degrees cooler, which can allow optimal development of populations (Wallis, 1946).

Essig (1917) described the life cycle of *B. cockerelli* in California. In California, *B. cockerelli* now appears to consistently overwinter (Liu et al., 2006). Essig (1917) found that winters were passed on evergreen host plants or sheltered places. Adults begin to lay eggs and could be found in southern California on wild host species in April (Essig, 1917; Jensen, 1954). Generations can vary from three or more in California with all life stages found from May until the end of November (Essig, 1917). Jensen (1954) provides further evidence of *B. cockerelli* populations increasing on wild host species in southern California and then moving northward in the spring, as well as the return of *B. cockerelli* to *Lycium* spp. host plants in November.

Description of life stages

Egg. Bactericera cockerelli eggs are yellow, oblong in shape and attached to the leaves of the host plant with short stalks (Pletsch, 1947) (Figure 1A). The average length and width of a *B. cockerelli* egg is 0.3 mm and 0.1 mm, respectively, with the length of the stalk being 0.2 mm (Compere, 1916; Lehman, 1930; Pletsch, 1947). Eggs that are not fertilized do not hatch (Lehman, 1930). Eggs are deposited on the upper and lower surfaces of leaves, and most abundantly on the young apical leaves (Knowlton and Janes, 1930), but this varies with the host crop (Butler and Trumble, 2011a; Butler personal observation). Eggs can take from 3-15 days to hatch, and exhibit a 1:1 sex ratio of females to males (Pack, 1930; Knowlton and Janes, 1930).

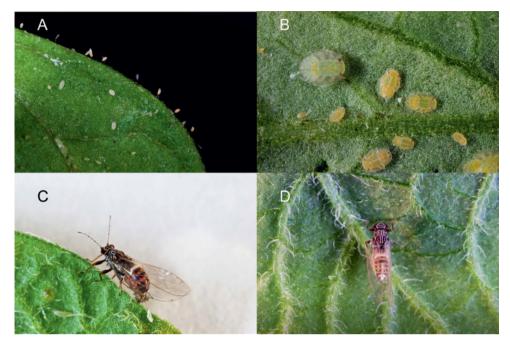


Figure 1. Life stages of the potato psyllid. (A) eggs; (B) nymphs; (C) red color morph of adult; (D) brown color morph. Picture credit: Michael Lewis.

Nymph. Development in the Hemiptera is of the hemimetabolous type, in which the adult stage is preceded by stages that are similar in appearance, but without wings. *Bactericera cockerelli* has five instars, and completion of development can vary from 12-44 days with an average of 15.4 days (Knowlton and Janes, 1930; Pack, 1930; Yang and Liu, 2009). The first four instars require an average of 2.4-2.8 days to complete development, but the fifth instar averages 4.9 days to complete (Knowlton and Janes, 1930). The range of the size of each instar can be found in Pletsch (1947). The nymphal stage is often where the greatest natural mortality occurs (Abdullah, 2008). Host plant and geographic origin can have an impact on nymphal growth and development of *B. cockerelli* (Liu and Trumble, 2007; Yang and Liu, 2009). First instar nymphs are pale yellow with an orange-colored head and abdomen, and as development occurs the color changes to a pale yellowish-green or can still remain yellowish-orange (Essig, 1917) (Figure 1B). Nymphs prefer the abaxial leaf surface and seldom move (Lehman, 1930).

Adult. After the last nymphal molt, adults are initially pale green or light amber, but soon become darker with considerable variation in the degree and intensity of colors (Essig, 1917; Lehman, 1930; Knowlton and Janes, 1930) (Figure 1C and D). The length of the adult body can vary from 1.3-1.9 mm (Essig, 1917; Lehman, 1930; Liu and Trumble, 2007). The adult life span can range from 16-97 days, however like all insects; developmental rates vary with temperature (Knowlton and Janes, 1930;

Lehman, 1930; Davis, 1937; List, 1939; Yang and Liu, 2009; Yang et al., 2010). The following conditions can also impact adult life history characteristics: 1) host plant, 2) geographic origin of populations, 3) sex and, 4) whether the measurement were conducted under field or laboratory conditions (Liu and Trumble, 2007; Yang and Liu, 2009; Yang et al., 2010).

Odorant sex attraction has been studied by Guedot et al. (2010) and they found that females and males of *B. cockerelli* emit odors that attract males; this was the first study to document male-male attraction within the Psylloidea. Adult females can lay eggs three days after emergence with a preoviposition period that can vary from 3-25 days (Knowlton and Janes, 1930; Abdullah, 2008). The ovipositon period lasts an average of 21.5-27.8 days (Knowlton and Janes, 1930; Davis, 1937), and ovipositing females can usually deposit 5-50 eggs during 24 hours. After a single mating, which lasts on average 6 minutes, *B. cockerelli* females produce fertile eggs for up to 27.8 days (Knowlton and Janes, 1930). Adult females can lay on average up to 330 eggs over her lifetime (Knowlton and Janes, 1930).

Adult *B. cockerelli* feed primarily of the underside of leaves of host plants (Eyer and Crawford, 1933). However, some individuals have been observed to feed on the upper surface of leaves as well as stems and petioles (Knowlton and Janes, 1931; Eyer and Crawford, 1933; personal observation). Based on the histology of feeding punctures of *B. cockerelli*, this insect, like aphids, are phloem-feeders (Eyer and Crawford, 1933). When *B. cockerelli* probes a plant, penetration through the leaf epidermis and into the leaf is intercellular through the spongy mesophyll until the stylets reach the phloem parenchyma cells, which is the region of the leaf where the most extensive feeding occurs (Eyer and Crawford, 1933). Penetration of the xylem occurs only occasionally (Eyer and Crawford, 1933; Butler, 2011).

Endosymbionts

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Mutualistic associations between psyllids and intracellular bacteria or endosymbionts are common (Baumann, 2005). Endosymbionts are localized intracellularly in specialized host cells called bacteriocytes or mycetocytes that may constitute a larger structure called a bacteriome or mycetome (Buchner, 1965; Nachappa et al., 2011). The mycetome of *B. cockerelli* was described by Rowe and Knowlton (1935). Psyllid endosymbionts fall within two categories: primary (P) (obligatory and those that aid in psyllid nutrition) and secondary (S) (facultative and those with functions less clear than P endosymbionts, and those that vary among populations) (Hodkinson, 2009). Within the mycetomes of *B. cockerelli* can be found the P endosymbionts *Candidatus* Carsonella ruddii and two strains of *Wolbachia* (Liu et al., 2006; Nachappa et al., 2011); and the S endosymbiont *Candidatus* Liberibacter psyllaurous (Hansen et al., 2008) (to be discussed later).

Psyllid yellows

In 1927, a destructive outbreak of a potato disease severely affected the potato crops in Colorado, Idaho, Montana, Utah and Wyoming with some fields exhibiting 100%

infection of plants (Richards et al., 1927; Richards, 1928). The early potato crop and home garden plots were described as 'complete failures' due to the affected plants producing few if any marketable tubers, and the late planted potato crops were not free from the disease either (Richards et al., 1927). Ensuing research found feeding by the nymphs of *B. cockerelli* associated with the diseased plants and suggested the name for this new disease as 'psyllid yellows' (PY) (Richards, 1928). Economic estimates in Utah alone in 1927 suggest that 25-30% of the total potato crop valued at ca. \$750,000 was lost due to PY. In the growing season after 1927, additional outbreaks of PY were noted in various section of the USA with varying degrees of severity (Richards, 1929; Richards et al., 1933). However, in 1938, one of the worst outbreaks of PY occurred in Colorado, Montana, Nebraska, and Wyoming as well as several reports of infection in California (Anonymous, 1929; Jensen, 1939; Morris, 1939). Even with insecticide applications, end of the year losses attributed to PY for potatoes ranged from 25-75% in the states affected (Anonymous, 1939). In western Nebraska alone, a 25% yield loss of potatoes equaled 27,200 metric tons (Hill, 1947). Other infestations that occurred after 1939 appeared to have been managed by new insecticides that were developed, including DDT, and the elimination of alternative breeding hosts such as matrimonyvine (Hill, 1947; Pletsch, 1947; Wallis, 1955; Cranshaw, 1994).

PY disease is systemic, and the entire plant becomes infected (Carter, 1939). Plant symptoms of PY include a reduction in growth, erectness of new foliage, chlorosis or reddening/purpling of leaves, basal cupping of leaves, shortened and thickened internodes, enlarged nodes, aerial tubers, premature senescence and plant death (Pletsch, 1947; Cranshaw, 1994). The marginal yellowing and upward rolling or cupping of younger leaves is a diagnostic character of PY (Richards et al., 1933). Histology of the diseased plants by Eyer and Crawford (1933) and Eyer and Miller (1938) found large deposits of starch granules in the cortex and pith of the stems and petioles as well as phloem necrosis in stems, stolons, and roots. Other reports found decreased nitrates/ nitrogen, chlorophyll, and carotene contents, and decreased starch contents in tubers of PY diseased plants (Eyer, 1937; Schaal, 1938; Carter, 1973).

PY diseased potatoes and tomatoes exhibit significant decreases in yields. Tubers from potato plants infected with PY are tiny, misshapen, flabby, and have a rough skin (Lindford, 1928; Cranshaw, 1994). These tubers often have associated with them various defects such as early sprouting, weak sprouts, and significantly smaller plants (Metzger, 1936; Cranshaw, 1994). In tomatoes, foliar symptoms are similar to those of potatoes and fruit set, size, texture and yield can be significantly decreased due to PY (Cranshaw, 1994), with losses reaching 80% (Liu and Trumble, 2007).

In general, the nymphal stages of *B. cockerelli* are the life stage that produce the PY disease, and it appears they are inherently toxigenic (Cranshaw, 1994). Through repeated tests, Richards (1931) and Richards et al. (1933), found that densities as high as 1,000 *B. cockerelli* adults per potato plant, failed to produce PY symptoms. However, Daniels (1954) found that adults were able to produce disease symptoms on tomato seedlings. Richards (1931) found that fewer than 15 nymphs did not induce uniform disease symptoms in potatoes, but with higher infestations, symptoms appear in 4-6 days. Potato plants may resume a healthy, normal appearance if nymphs are removed 5-10 days after the appearance of first symptoms, but this does not always

happen (Richards, 1931; Arslan et al., 1985). For tomatoes, relationships regarding the number of nymphs per plant and the resulting damage threshold can vary among cultivars; however symptoms of PY will appear when at least 8 nymphs feed on 2 week old tomato plants (Liu and Trumble, 2006). Additional studies by Liu et al. (2006) found that the tested tomato cultivars also exhibit differing recovery potentials, and as a conservative measure recommend treating tomato cultivars when the number of psyllids approach 10 nymphs per plant for a period of 5 days.

Through grafting experiments on potatoes, PY has proven capable of being transmitted to healthy plants; however, succeeding grafts result in a gradual recovery of plants (Daniels, 1954; Cranshaw, 1994), which suggest that a pathogenic microorganism is not involved with PY and supports the 'toxin' hypothesis. The identification of this 'toxin' still remains unknown (Abernathy, 1991).

Zebra chip disease

'Zebra chip' (ZC) disease was first documented in potato fields near Saltillo, Mexico, in 1994 (Munyaneza et al., 2007a). ZC-affected potatoes exhibit the following aboveground symptoms: stunting, chlorosis, swollen internodes of the upper growth, proliferation of axillary buds, aerial tubers, browning of the vascular system, leaf scorching, and early plant death (Munyaneza et al., 2007b) (Figure 2 A-B). Symptoms of the infected tubers are shown through the entire tuber from the stem end to the bud end and include enlarged lenticels of the underground stem, collapsed stolons, brown lesions of the vascular ring, necrotic flecking of internal tissues, and occasionally streaking of the medullary ray tissues (Munyaneza et al., 2007a). Chips that are processed from infected tubers exhibit severe dark brown streaking, thus the name 'zebra chip', which causes the rejection of fresh and processing potatoes for market (Munyaneza et al., 2007a) (Figure 2C). The color changes are most evident following frying, but can often be detected in fresh tubers. Additionally, ZC-infected tubers sprout significantly less than ZC-free tubers or do not sprout at all; if they do sprout, hair sprouts or weak plants are produced that have significantly decreased survival (Henne et al., 2010; Munyaneza et al., 2007a). Furthermore, the physiological effects of ZC infection on the potato tuber include significantly increased levels of tyrosine, phenolic compounds, salicyclic acid and ion leakage as well as altered mineral content in ZC-affected tubers compared to ZC-free tubers (Navarre et al., 2009; Miles et al. 2009, 2010).

In the USA, ZC was first identified in commercial fields in Pearsall and the lower Rio Grande Valley in Texas in 2000 and since that time ZC has been recorded in Arizona, California, Colorado, Kansas, Nebraska, Nevada, and New Mexico (Secor and Rivera-Varas, 2004; Munyaneza et al., 2007a). In the 2004-2006 potato growing seasons, economic losses due to ZC to both potato producers and processors in numerous locations in the USA and Mexico often led to the abandonment of fields resulting in losses exceeding millions of dollars (Munyaneza et al., 2007a). In Texas alone, ZC has been responsible for a reduction in potato hectarage by > 20%, and is estimated to be responsible for a loss of \$25 million during the 2004-2006 outbreaks (CNAS, 2006;

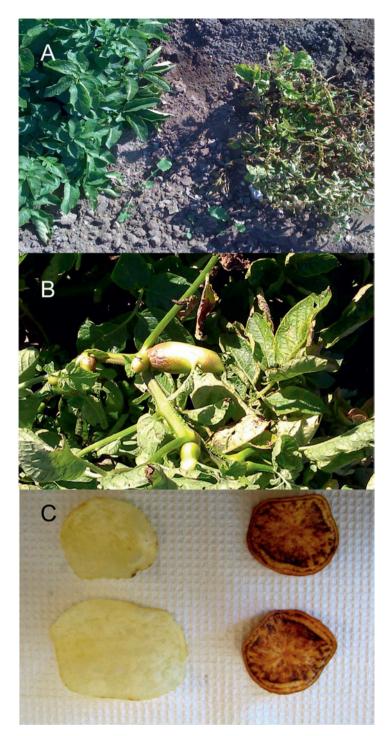


Figure 2. Damage associated with *Candidatus* Liberibacter psyllaurous in potatoes. (A) a healthy plant (left) and an infected plant exhibiting stunting and leaf scorching; (B) aerial tuber; (C) potato chips from a healthy tuber (left) and from an infected tuber (right). Picture Credit: Gregory Kund.

Wen et al., 2009). ZC disease has also been documented in potato fields in Guatemala and Honduras with field incidences as high as 80% and total losses because of unmarketable tubers (Secor and Rivera-Varas, 2004; Crosslin et al., 2010).

Munvaneza et al. (2007a) were the first to elucidate the association between B. cockerelli feeding and ZC expression on potato. In a greenhouse and a Washington field study by Munyaneza et al. (2007a), potato plants not exposed to B. cockerelli did not exhibit ZC symptoms, but potato plants exposed to B. cockerelli exhibited symptoms three weeks after the initial *B. cockerelli* release. Furthermore, psyllid exposed plants exhibited initial plant symptoms which included upward rolling of the leaves and yellowish-reddish discolorations with later symptoms of plants and tubers that exhibited typical ZC symptoms (Munyaneza et al., 2007a). Comparable results were documented by Munyaneza et al. (2007b) in Texas too, whereby potato plants not exposed to *B. cockerelli* did not show ZC symptoms and plants exposed to psyllids showed ZC symptoms. In these field locations, the most predominant insect collected where ZC was prevalent was B. cockerelli (Munyaneza et al., 2007a; Goolsby et al., 2007a). Later research found that *B. cockerelli* populations from different geographic localities varied in their ability to infect potato with ZC (Munyaneza et al., 2008). Additionally, B. cockerelli reared upon the agricultural host plants of potato, tomato, bell pepper and eggplant can infect potato with ZC, although B. cockerelli reared on bell pepper and eggplant can cause relatively more severe ZC infections compared to psyllids reared on tomato and potato (Gao et al., 2009).

Hansen et al. (2008) were the first to identify a new bacterial species of Candidatus Liberibacter that was vectored by B. cockerelli. The bacterium was first sequenced 3 January 2008 at UCR's IIGB Bioinformatics Facility based on the 16S-ISR-partial 23S rRNA sequences found in *B. cockerelli* and infected plants (Hansen et al., 2008). These sequences were later deposited in GenBank 18 June 2008. The bacterium was named Candidatus Liberibacter psyllaurous and is an unculturable Gram-negative α -proteobacterium that is associated with the phloem tissue of plants (Hansen et al., 2008; Lin et al., 2009). Results indicated that Ca. L. psyllaurous infection can occur throughout B. cockerelli life stages but can vary with eggs exhibiting a 15-47 percent infection frequency, which suggests transovarial transmission of Ca. L. psyllaurous (Hansen et al., 2008). For B. cockerelli reared on potato, Ca. L. psyllaurous infection from the first instar to adults appeared to be fixed at 100%, while B. cockerelli reared on tomato exhibited 100% infection of Ca. L. psyllaurous at the third instar (Hansen et al., 2008). This research also revealed transmission of Ca. L. psyllaurous by B. cockerelli after one week of exposure to a potato or tomato plant and subsequently displayed of symptoms, which were consistent with Munyaneza et al. (2007a) description of ZC (Hansen et al., 2008). Later research by Munyaneza (2010) has reported that as few as one B. cockerelli can transmit Ca. L. psyllaurous within two hours of colonizing the plant. The exact mechanism of transmission is unknown, but we suspect the bacteria are injected during salivation into the phloem.

In January 2008, related research was conducted in New Zealand regarding the etiology of a new disease of greenhouse grown tomatoes and peppers (Crosslin et al., 2010). In April 2008, Liefting et al. (2009) discovered a bacterium-like organism in the phloem of symptomatic plants. In May 2008, various polymerase chain reaction (PCR) primers were used to amplify putative prokaryotic DNA extracted from healthy and symptomatic tomato and pepper; the result was the detection of what the authors named *Ca.* L. solanacearum (Liefting et al., 2008). Recent research has suggested haplotypes of *Ca.* L. solanacearum exist as described by single-nucleotide polymorphisms and *rplJ* and *rplL* ribosomal protein genes and the publication of the complete genome sequence of *Ca.* L. solanacearum is currently available (Nelson et al., 2010; Lin et al., 2010).

Since publication of the primers by Hansen et al. (2008) and Liefting et al. (2009), multiple laboratories in the USA, Mexico, and New Zealand have documented Ca. L. psyllaurous and Ca. L. solanacearum infection in solanaceous agricultural crops and additional solanaceous hosts such as L. barbarum, tamarillo (Solanum betaceum), cape gooseberry (Physalis peruviana), silverleaf nightshade (Solanum elaeagnifolium), and black nightshade (Solanum ptychanthum) (Abad et al., 2009; Brown et al., 2010; Crosslin and Bester, 2009; French-Monar, 2010; Li et al., 2009; Liefting et al., 2008a,b; McKenzie and Shatters, 2009; Munyaneza et al., 2009a,b,c; Rehman et al., 2010; Wen et al., 2009). Sequence analysis of the 16S and 23S rRNA suggests that Ca. L. psyllaurous and Ca. L. solanacearum are the same bacterium as a number of BLAST analyses of consensus sequences often show 99-100% identity of Ca. L. solanacearum with Ca. L. psyllaurous (Crosslin and Bester, 2009; French-Monar, 2010; Munyaneza et al., 2009a,b,c; Secor et al., 2009; Wen et al., 2009; Crosslin et al., 2010). Both names are in current use, and the final 'official' naming of the bacterium will not occur until all of Koch's postulates can be fulfilled when the bacterium can be cultured in the laboratory.

Management strategies

Detection and monitoring

Surveys for the purpose of population detection and monitoring of *B. cockerelli* have been conducted by various authors in cultivated and non-cultivated host plants (Pletsch, 1947; Wallis, 1955; Cranshaw, 1994; Al-Jabr, 1999, 2007; Goolsby et al., 2007a,b). These methods have involved suction traps, vacuum sampling of plants, sweep net sampling, examination of plant material, and colored sticky traps. Suction traps and vacuum samplers were found to be ineffective at detecting and sampling *B. cockerelli*, respectively (Cranshaw, 1994; Goolsby et al., 2007). The use of sweep nets to obtain a relative estimate of *B. cockerelli* has been used extensively (Pletsch, 1947 and reference therein). Pletsch (1947) used these data to calculate a "psyllid index" based on the number of *B. cockerelli* captured per 100 sweeps, and found the index correlated with the amount of PY observed in agricultural fields (Cranshaw, 1994). Information from the sweep net sampling of *B. cockerelli* have revealed patterns regarding the infestation and disease spread within agricultural fields. Within agricultural fields, *B. cockerelli* were first detected on the edges and as the number of psyllids build in the field they progress toward the center (Jensen, 1939; Wallis, 1955; Cranshaw, 1994).

Examinations of leaf samples have often been described as 'tedious and time consuming' for *B. cockerelli*, but have provided detailed information regarding the population density of this pest (Pletsch, 1947; Goolsby et al., 2007). These data have also revealed that relative to other parts of potato plants, *B. cockerelli* prefer to inhabit leaves on the abaxial surface (Knowlton and Janes, 1931; List, 1939; Pletsch, 1947). Despite this information, a sampling plan for *B. cockerelli* has yet to be developed in agricultural fields. However, only recently has a statistically verifiable sampling plan been developed for an agricultural crop (Butler and Trumble, 2011a).

Sticky card traps have been used as monitoring tools in the greenhouse and the field (Al-Jabr, 1999; Goolsby et al., 2007). Al-Jabr (1999) was the first to study the effective detection and monitoring of *B. cockerelli* in greenhouse tomato. The results of his study indicated that *B. cockerelli* were most attracted to neon-green, neon-orange, and standard yellow sticky traps that were placed above the crop canopy and in the shade (Al-Jabr, 1999). Goolsby et al. (2007a,b) used yellow sticky cards to monitor adult *B. cockerelli* in potato fields in Texas, and suggested they could be an effective tool to detect *B. cockerelli* in cultivated and non-cultivated host plants at low densities. However, an evaluation of sticky traps compared to other sampling techniques has yet to be conducted. Also, there has been no publication that has reported a predictive relationship between the numbers of adults on traps and the numbers of nymphs in the foliage. Thus, this technique probably has the most utility for determining when adults are migrating into an area.

Insecticidal control

Insecticidal control of *B. cockerelli* has been the subject of extensive research. Compounds used for *B. cockerelli* control included oils, nicotine, pyrethrum, zinc arsenite sprays and calcium cyanide dusts (Knowlton, 1931, 1933b; Pletsch, 1942, 1947). One of the first and most broadly used insecticides in the 1930's and 1940's for *B. cockerelli* control was lime-sulfur, which gave good control of this pest in tomatoes and potatoes with increases in yields for both of these crops (List, 1918, 1935, 1938; List and Daniels, 1934). Lime-sulfur was effective in killing the immature and adult stages of *B. cockerelli* as well as being repellent to the adults. However, lime-sulfur had the problem of being phytotoxic to crops (List, 1935; Pletsch, 1942). In the greenhouse, the residual toxicity of lime-sulfur lasted for up to five weeks (Tate and Hill, 1944). In 1945, DDT was used against *B. cockerelli* for the first time in Nebraska and was described as providing more effective control for a longer period of time compared to the other compounds available at the time (Hill, 1945; Pletsch, 1947).

In the 1960's, organophosphates such as phorate, parathion, disulfoton, and demeton, and the carbamate aldicarb were used for control of *B. cockerelli* (Gerhardt and Turley, 1961; Harding, 1962; Gerhardt, 1966). In the 1980's Cranshaw conducted extensive tests on insecticides for *B. cockerelli* management (Cranshaw, 1985a,b,c, 1989a,b,c, 1993). Foliar sprays of diazinon, endosulfan, permethrin, acephate and many pyrethroid insecticides were among the better compounds for *B. cockerelli* control; and the systemic soil applied applications of phorate and disulfoton still provided control of *B. cockerelli* early in the growing season (Cranshaw, 1985a,b,c, 1989a,b,c). The carbamates such as aldicarb, carbofuran, cloetiocarb, carbaryl, and the organochlorine methoxylchlor were ineffective treatments at controlling *B. cockerelli* (Cranshaw, 1985a,c). Al-Jabr (1999) found for greenhouse tomatoes neem-derived compounds, spinosad and acetamiprid were effective in killing *B. cockerelli* 24 h post-application, and other compounds such as horticultural spray oil and pymetrozine were effective in killing *B. cockerelli* 5 days post-application.

Further research on tomatoes by Liu and Trumble (2004, 2005), found complex interactions between tomato cultivars and insecticides tested for the behaviors of *B. cockerelli* and life history characteristics measured. The compounds tested included imidacloprid, kaolin particle film, pymetrozine, pyriproxyfen, and spinosad. While *B. cockerelli* on insecticide-treated plants exhibited significant decreases in the duration of probing behavior and reduced egg-adult survivorship (Liu and Trumble, 2004, 2005), non-feeding behaviors (resting, cleaning, etc.) and other life history characteristics (antixenosis, oviposition) often exhibited unexpected interactions between the insecticide and tomato cultivar. Also, Liu and Trumble (2007) found resistance to imidacloprid and spinosad in populations of *B. cockerelli* in California compared to psyllids from the central USA. Subsequent experiments using the electrical penetration graph technique determined that imidacloprid interfered with penetration behaviors and could provide substantial reductions in *Ca.* L. psyllauraous transmission for at least 4 weeks after application (Butler, 2011; Butler et al., 2012).

Since the association was made between *B. cockerelli* feeding and ZC, management practices for potatoes in the USA have relied on insecticides to control *B. cockerelli* to lower ZC incidences and increase yields. In Texas, in-furrow applications of phorate followed by several in-season applications of foliar insecticides including imidacloprid + cyfluthrin, endosulfan, and methamidophos reduced ZC incidence in tubers to 12.9-20.4% (Goolsby et al., 2007a). Insecticides also were used as a management tool to further lower ZC incidence in tubers to 0.4-2.3% in a pest management plan that included an in-furrow application of imidacloprid, and weekly applications of dinote-furan and spiromesifen used in rotation applied at weekly intervals until the two week pre-harvest interval (Goolsby et al., 2007b).

In California, existing UC Pest Management Guidelines recommend treating potato plants with imidacloprid at planting, and additional treatments with abamectin, spiromesifen, or spinosad if monitoring indicates that psyllid populations are at one to two per leaf or ten per plant during the growing season (UC IPM Online, 2008). Further research by Gharalari et al. (2009) evaluated the knockdown effect for a variety of insecticides on *B. cockerelli* adults with thiamethoxam and abamectin being the most effective. The dosage and exposure time of abamectin can also significantly increase the mortality rates of *B. cockerelli* adults; however, after 24 h under field conditions the mortality rates on abamectin-treated potato plants are not significantly different from controls (Gharalari et al., 2009). Similar work has been conducted in Mexico and New Zealand, which examined several compounds at the recommended fields and the subsequent impact on mortality of *B. cockerelli* nymphs (Vega-Gutierrez et al., 2008; Berry et al., 2009). In recent years, evaluations of selected biorational insecticides and kaolin particle film for the repellency of *B. cockerelli* have been examined in the laboratory and the field (Yang et al., 2010; Butler et al., 2011a; Peng et al., 2011). Results indicated reasonably good control (>50% for some psyllid stages) suggesting these materials are suitable for further investigation designed to incorporate them into integrated control programs.

Cultural control

Cultural control refers to the purposeful manipulation of a cropping environment to reduce rates of pest increase and damage (Pedigo and Rice, 2006). For *B. cockerelli* management, this area of research has occasionally been investigated. These areas of research and observations have included the timing of crop planting, fertilization, trap crops, destruction of breeding sites, colored pesticide sprays, and mulches.

One of the first observations regarding timing of planting and damage by *B. cocker-elli* was provided by Eyer and Enzie (1939). These authors observed that late-planted tomatoes and potatoes in New Mexico did not develop PY as severely as those planted earlier. Similar observations were noted by Starr (1939) and Hartman (1947) who noted that fields planted in Wyoming in early June appeared to be damaged less than fields planted before that time (Starr 1939, Hartman 1947). Wallis (1948) found that *B. cockerelli* populations were significantly higher in early plantings of potatoes in Wyoming and Nebraska compared to middle and late season plantings. Additional studies using current cultivars and modern production practices are clearly justified.

Ever and Enzie (1939) also pointed out the possible value of fertilizers to correct the lack of chlorophyll and nitrates/nitrogen on B. cockerelli plant afflicted with PY, although no research studies regarding this have been formally conducted. In Colorado, pepper plants were recommended as an alternate trap crop for *B. cockerelli* to attract this pest from potatoes (Cranshaw, 1994). Starting in the 1930's, local practices recommended the removal of potential spring and early summer breeding places through the elimination of early potato plantings, non-economic solanaceous host plants such as *L. barbarum*, and volunteer potatoes in cull dumps to curtail *B. cockerelli* population buildups (Knowlton, 1934; Hill, 1947; Cranshaw, 1994). A single study regarding colored sprays has been investigated as a method to impact the number of B. cockerelli colonizing agricultural fields (Cranshaw and Liewehr, 1990). The study used the following compounds, which were sprayed on potatoes: yellow-colored maneb, white-colored cholorathalonil, and a white-colored inorganic insecticide sodium fluoaluminate; however results showed no significant differences in the captures of B. cockerelli in fields (Cranshaw and Liewehr, 1990). Colored mulches have offered promise as a cultural control method for B. cockerelli management in home garden tomato plants in Colorado as aluminum and white plastic mulches can be used to significantly decrease the population density of *B. cockerelli* on tomato (Demirel and Cranshaw, 2006).

Host plant resistance

Similar to cultural control, studies regarding host plant resistance have seldom been investigated as a management technique for B. cockerelli. Host plant resistance refers to genetic resistance of plants to insects as categorized as antixenosis (inability of a plant to serve as a host for an arthropod), antibiosis (negative effects of a resistant plant that affect the biology an arthropod attempting to use that plant as a host) and tolerance (possessing the ability to withstand or recover from damage caused by arthropod populations equal to those on susceptible genotypes) (Smith, 2005). One of the first studies regarding host plant resistance involved examining potato varieties for tolerance to PY (Babb and Kraus, 1937). Results from the study by Babb and Kraus (1937) indicated that none of the thirty-nine varieties tested were immune to PY, and due to a lack of statistical analyses there was difficulty determining if the varieties were significantly more or less tolerant compared to each other. In field studies, Linford (1928) and Starr (1939) found that none of the commercial potato varieties tested exhibited enough resistance to *B. cockerelli* to provide a substantial benefit. Cranshaw (1989) found that for various varieties of potato, tomato, and pepper tested in Colorado fields that some varieties had increased numbers of *B. cockerelli*, but there was often an unclear relationship between the varieties preferred by *B. cockerelli* and the damage to the crop, suggesting that different varieties may need different thresholds.

The use of resistant varieties has been investigated as a management option against *B. cockerelli* in tomatoes (Liu and Trumble, 2004, 2005, 2006; Casteel et al., 2006, 2007). Some resistance by the *Mi-1.2* gene has been documented in tomatoes showing antixenosis (decreased host selection by *B. cockerelli* on plants with the resistant genotype) and antibiosis (significant decreases in survival of *B. cockerelli* reared on the resistant genotype) (Casteel et al., 2006). In addition, antixenosis (reported as decreased feeding and oviposition) and antibiosis (described as increased developmental time and decreases in survival) were observed for a wild-type accession tomato (PI 134417) when compared to the tomato varieties '7718 VFN', 'Yellow Pear', 'QualiT 21', and 'Shady Lady' (Liu and Trumble, 2004, 2005, 2006). Butler et al. (2011b) documented changes in stylet penetration behaviors that reduced transmission in putatively resistant varieties from breeders in Texas and Idaho. However, reports of how effective these might be when incorporated into an IPM program are not yet available.

Biological control

In North America, a number of natural enemies attack *B. cockerelli*. Generalist predators that attack *B. cockerelli* include chrysopid larvae (*Chrysoperla* spp.), various coccinellids (i.e., *Hippodamia convergens* Guerin-Meneville, *Hippodamia quinquesignata* (Kirby), *Hippodamia tredecimpunctata* (L.), and *Hippodamia americana* Crotch), syrphid fly larvae, and Hemiptera such as *Geocoris decoratus* Uhler, *Orius tristicolor* (White), *Anthocoris tomentosus* Pericart, *Deraeocoris brevis* (Uhler) and *Nabis ferus* (L.) (Knowlton 1933a,b, 1933c, 1934a,b; Knowlton and Allen, 1936; Romney, 1939; Pletsch, 1947). However, most of the observations of predators attacking *B. cockerelli* have been performed under artificial laboratory conditions, with the exception of chrysopid larvae observed attacking *B. cockerelli* nymphs in Utah potato fields (Knowlton, 1933a) and the field observations by Butler (2011). Field observations by Romney (1939) indicated that coccinellids and chrysopids reduced the number of eggs and nymphs of *B. cockerelli* on *Lycium* spp. to varying degrees from year to year. Recent research by Butler (2011) found through two years of field studies (2009-2010) at four different sites and laboratory feeding tests, identified *O. tristicolor, Geocoris pallens* Stal (Hemiptera: Geocoridae), and *H. convergens* as key natural enemies of *B. cockerelli* in southern California potatoes, tomatoes, and bell peppers. The number of these natural enemies exhibited either significant positive or negative relationships with the number of *B. cockerelli* population dynamics using exclusion cage experiments in the potato crop and in American nightshade, *Solanum americanum* Miller, found the number of *B. cockerelli* surviving was significantly greater in the closed cage treatments (approximately 65% greater), thus confirming the impact natural enemies can have on *B. cockerelli*.

In the laboratory and in the field unknown species of *Chrysoperla* spp., *Chrysoperla* carnea (Stephens) and *Chrysoperla rufilabris* (Burmeister) have been further assessed as *B. cockerelli* predators (Pletsch, 1947; Al-Jabr, 1999). In laboratory experiments, *Chrysoperla* larvae can attack all life stages of *B. cockerelli* (Pletsch, 1947; Knowlton, 1933; Al-Jabr, 1999). Al-Jabr (1999) evaluated *C. carnea* and *C. rufilabris* as potential biological control agents of *B. cockerelli* and found they are capable of completing their entire life cycle on *B. cockerelli*. However, a field trial involving applications of *C. carnea* eggs to psyllid infested potatoes did not produce significant reductions in *B. cockerelli* numbers (Al-Jabr, 1999). Butler (2011) found numerous *Chrysoperla* spp. eggs in the field, but very few *Chrysoperla* spp. larvae; also the number of eggs or larvae of these predators did not correlate with the number of *B. cockerelli* that occurred on crop plants.

Natural enemies of *B. cockerelli* also include two primary parasitoids: *Metaphycus psyllidis* Compere (Hymenoptera: Encyrtidae), and *Tamarixia triozae* (Burks) (Hymenoptera: Eulophidae). Parasitism of *B. cockerelli* nymphs by *T. triozae* was noted for the first time by Romney (1939) on *Lycium* spp. in southern Arizona. *Metaphycus psyllidis* was described as a new *B. cockerelli* parasitoid species by Compere (1943). No follow-up work on *M. psyllidis* regarding its impact on *B. cockerelli* has been attempted since.

Tamarixia triozae has been found in the USA (Arizona, California, Colorado, Idaho, Kansas, Montana, New Mexico, and Washington) and recently in Mexico (Romney, 1939; Pletsch, 1947; Jensen, 1957; Lomeli-Flores and Bueno Partida, 2002). In a tomato field in Montana in 1939, 23% of the *B. cockerelli* nymphs were parasitized by *T. triozae*; although no parasitism was noted in the surrounding areas despite high *B. cockerelli* populations. Similar observations have been noted by Butler (2011) in which despite the presence of *T. triozae* in agricultural fields in southern California the percent parasitism was below 20%. Details regarding the life history of this parasitoid can be found in Pletsch (1947), and a list of additional psyllid species that *T. triozae* parasitizes can be found in Jensen (1957). In general, *T. triozae* attacks the fourth and fifth instars of *B. cockerelli* (Pletsch, 1947), and this parasitoid's dispersal can be rapid

at a distance limited to less than 1.5 m (Johnson, 1971). In the field, *T. triozae* is poorly synchronized with *B. cockerelli* populations and suffers high pupal mortality ranging from 38-100% (Johnson, 1971). In the laboratory, levels of parasitism were low averaging 13.2-26.5%, which is similar to parasitism rates found for other psyllid parasitoids (Jensen, 1957). Thus, Johnson (1971) finds control of *B. cockerelli* in agricultural settings with *T. triozae* unfeasible, but leaves the possibility of using this species as a biological control agent in the natural, overwintering areas of *B. cockerelli*. In addition, new records of *Encarsia pergandiella* Howard (Hymenoptera: Aphelinidae) and a single record tentatively identified as *Encarsia peltata* (Cockerell) (Hymenoptera: Aphelinidae) hyperparasitizing *T. triozae* have been documented on tomato and bell pepper plantings in southern California with proportions of parasitism between 5.3-6.9% (Butler and Trumble, 2011b). Despite this information, in New Zealand in 2006, *T. triozae* was imported from Mexico into quarantine for assessment as a potential biological control agent of *B. cockerelli* (Workman and Whiteman, 2009).

The entomopathogenic fungi *Beauvaria bassiana* (Balsamo) Vuillemin, *Isaria fumosorosea* (Wize), *Verticillium lecanii* (Zimmerman) and *Metarhizium anisopliae* (Metschnikoff) are known to attack *B. cockerelli* (Al-Jabr, 1999; Strand, 2006; Sanchez-Pena et al., 2007; Lacey et al., 2009, 2010). One of the first studies to document the effect of entomopathogenic fungi on *B. cockerelli* was conducted by Al-Jabr (1999). Under laboratory conditions, *B. bassiana* caused significant mortality (>82%) on *B. cockerelli* nymphs. Mixed results were obtained in the greenhouse with *B. bassiana*, *V. lecanii*, and *M. anisopliae* in terms of mortality on *B. cockerelli* nymphs on tomato (Al-Jabr, 1999). Studies by Sanchez-Pena (2007) testing *B. bassiana* and *M. anisopliae*, and Lacey et al. (2009) testing *B. bassiana*, *M. anisopliae*, and *I. fumosorosea* likewise demonstrated significant mortality on *B. cockerelli* in the laboratory compared to untreated controls. In field trials, Lacey et al. (2010) found fungal treatments of *M. anisopliae* and *I. fumosorosea* alone or in combination with insecticides caused significant reductions in *B. cockerelli* in southern Texas.

Conclusions

Much research still needs to be conducted on the basic biology and control of this pest. While a number of symbionts have been identified, the role these may play in transmission of the ZC pathogen have not been elucidated. Similarly, research is needed to determine the possible impact of the *Ca.* L. psyllaurous on the fitness of the psyllid. The effects of the ZC pathogen on use and storage of potatoes destined for fresh market use versus frying/chipping is also largely unknown. Control strategies that are currently available tend to be relatively expensive and pesticide intensive, so economic evaluation of IPM programs that incorporate biological control agents, resistant varieties, and alternative suppression strategies are critically needed. We are aware that control strategies based on controlling the bacteria within the plant or production of transgenic plants with putative resistance are in progress, but no peer-reviewed studies were available at the time this was written. We still do not fully understand how these pests are moving between countries and why the ZC pathogen is a huge problem in some locations but not in others. However, based on the intensive research efforts published in the past 10 years, and the remarkable interdiciplinary efforts of entomologists, plant pathologists, and epidemiologists, the overall outlook for management of this pest and its associated pathogen is promising.

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