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REVIEW

Bactericera cockerelli (Sulc), a potential threat to China's potato industry

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Abstract

The potato psyllid *Bactericera cockerelli* (Hemiptera: Triozidae) has recently emerged as a serious pest of potatoes and other solanaceous crops. It causes direct feeding damage and also vectors *Candidatus* Liberibacter solanaceaerum (Lso), a pathogen that causes zebra chip disease in potatoes and which potentially costs growers millions of dollars each year. Such producers rely on frequent sprays of pesticides for psyllid control but the results are unsatisfactory and there are negative side effects. The psyllid has spread beyond its native range in southwest US and northern Mexico to Canada, El Salvador, Honduras, Guatemala and Nicaragua *via* medium to long range dispersal flights perhaps aided by wind currents, and through anthropogenic means. It was accidentally introduced into New Zealand in 2006 and most recently Australia, most likely through the importation of infested plant material. This review summarizes information from studies on the biology, impact and management of *B. cockerelli*, and highlights the imminent risk of this insect and its associated pathogen invading China, the world's largest producer of fresh potatoes. Development of risk maps leading to increased surveillance, could prevent or delay an incursion and facilitate early detection or eradication should this occur. Long-term management with Lso-tolerant potato cultivars and psyllid control using the parasitic wasp *Tamarixia triozae* and other natural enemies should be pursued, rather than depending on synthetic pesticides.

Keywords: *Bactericera cockerelli*, tomato-potato psyllid, invasive pest, *Candidatus* Liberibacter solanaceaerum, biological control, *Tamarixia triozae*

1. Introduction

The potato, *Solanum tuberosum* L. (Solanaceae) is of global importance, consumed by approximately one billion people worldwide and surpassed in that respect only by wheat and rice (CIP 2018). It is grown in 100 countries across every continent apart from Antarctica, and total production exceeds 300 million metric tonnes per annum (FAO 2018). However, as with many other crops, sustainable production of potato

is threatened by the rapid expansion of pathogens and pests into new areas due to rising volumes of international travel and trade as a consequence of globalization (Early *et al.* 2016). *Bactericera cockerelli* (Sulc) (Hemiptera: Triozidae), commonly known as the tomato-potato psyllid (TPP), is an insect pest of potatoes and other solanaceous crops, which spread from North America to New Zealand, probably through international trade and travel (Teulon *et al.* 2009; Thomas *et al.* 2011) and subsequently from New Zealand to Australia through a similar route (Walker P W *et al.* 2015). This insect causes severe economic losses in potatoes and other Solanaceae through its phloem feeding, which causes direct damage, and also vectors a bacterial pathogen *Candidatus* Liberibacter solanaceaerum (Lso) that causes significant reductions in crop yield and quality, and in extreme cases, loss of entire crops (Liefting *et al.* 2009a; Munyaneza 2012, 2015). Consequently, *B. cockerelli* is currently viewed as one of the most destructive pests of potato and a significant threat to the global potato industry (Munyaneza 2015).

In this article, we review historical and recently published research on aspects of the biology, ecology, economic significance, and management of *B. cockerelli*. We highlight the possibility that this pest, which was introduced into New Zealand and Australia as a result of international trade, could enter China *via* the same processes and conclude by recommending strategies for China to prevent an incursion by the pest, and for a comprehensive response should an invasion occur. This review will be particularly valuable to growers, bio-protection agencies and researchers in potato-producing countries where the psyllid is not yet present and where knowledge of the pest and its management is generally lacking or limited.

2. Identification and life cycle

Bactericera cockerelli life stages include adults, nymphs and eggs. The eggs are tiny (0.3 mm long and 0.1 mm wide), yellow and oval-shaped, with stalks for attachment to plant parts. They are usually found on the undersides, margins, or top of leaves, and occasionally, on petioles and stems. (Lehman 1930; Knowlton and Janes 1931; Abdullah 2008). The nymphs are dorsoventrally flattened and have a scale-like appearance with a short fringe of filaments along the lateral edge. Young nymphs have an orange-coloured head and abdomen, while older ones have visible wing pads and are at first pale yellow but turn green by the fifth instar (Wallis 1955). Nymphs are mostly sessile, but can walk when disturbed (Lehman 1930). Adult *B. cockerelli* measure between 2.5–2.75 mm long, are pale green when newly eclosed, turn amber or brown within 2–3 days and eventually, grey to black (Linford 1928; Knowlton and Janes

1931). In contrast to nymphs, adults have powerful hind legs and jump readily when disturbed (Knowlton and Janes 1931). Adults of the insect have a pair of clear membranous hindwings that extend beyond the abdomen and are held roof-like over the body at rest. This can cause them to be mistaken for tiny cicadas (Hemiptera: Cicadidae), but white markings on the head and thorax, a broad white band on the dorsum of the first abdominal segment, and an inverted white "V" on the last segment make the potato psyllid easily distinguishable (Pletsch 1947).

Within 48 hours of emergence, *B. cockerelli* adults are reproductively mature (Guédot *et al.* 2012), but there is usually a pre-mating period of about four days, and females exhibit a three to 10-day pre-oviposition period (Abdullah 2008). Oviposition reaches a peak between days 15–18 but can last up to 53 days (Abdullah 2008). An individual female can lay 300–500 eggs over its lifespan (Knowlton and Janes 1931; Pletsch 1947; Abdullah 2008). Eggs hatch into first instar nymphs after 3–8 days and the duration of nymphal development involving four moults, varies from 12–44 days with a mean of 15.4 days depending on temperature and host plant (Lehman 1930; Knowlton and Janes 1931; Abdullah 2008; Yang and Liu 2009). The life cycle from egg to adult is strongly influenced by temperature; optima for reproduction and development are between 24–27°C, while temperatures above 31°C are harmful and result in the insect's death (Tran *et al.* 2012; Lewis *et al.* 2015). Below 7°C, development ceases, although nymphs of the Central Haplotype in the US survived a temperature of –15°C for up to 24 hours (Henne *et al.* 2010a). Development rates and survival of *B. cockerelli* are also impacted by their host plants and under similar experimental conditions, the life cycle required a mean of 18, 20 and 21 days on tomato, potato and capsicums respectively (Liu and Trumble 2007; Yang and Liu 2009).

3. Distribution, dispersal and population genetics

Bactericera cockerelli is native to the Rocky Mountain region of the United States of America (USA) and northern Mexico, and was first recorded on pepper plants (*Capsicum* spp.) in Boulder, Colorado and described in 1909 by Karel Sulc (Butler and Trumble 2012c). Within the US, the insect occurs in the south, central and north-western states of Arizona, California, Colorado, Idaho, Kansas, Minnesota, Nebraska, Nevada, New Mexico, North Dakota, Oklahoma, South Dakota, Texas, Utah, Washington and Wyoming (Munyaneza 2010). Migrating populations extend the psyllid's range to Alberta, British Columbia, Ontario, and Saskatchewan in Canada, while established native populations are present in Mexico, El Salvador, Guatemala,

Honduras and Nicaragua in Central America (EPPO 2013). *Bactericera cockerelli* was reported for the first time in New Zealand in tomato glasshouses around Auckland in 2006 (Gill 2006) and an investigation into its entry pathway concluded that the insect was introduced accidentally on infested plant material imported illegally from the USA (Thomas *et al.* 2011). The insect spread quickly across New Zealand aided by the unwitting distribution of infested seedlings, and is now a major pest of potatoes, tomatoes, capsicums and tamarillos in that country (Teulon *et al.* 2009). Australia implemented strict monitoring and biosecurity measures to prevent incursion by the pest (Walker P W *et al.* 2015), but despite those precautions, *B. cockerelli* was detected in Perth, Western Australia in February 2017 (DPIRD 2018). It has however, not been found in eastern Australia (Reynolds O. 2018, personal communication).

The means by which *B. cockerelli* disperses over long distances has remained contentious, and reports of seasonal dispersal by the psyllid over a few kilometres, are limited (e.g., Nelson *et al.* 2014). Adults are known to readily disperse within crops by jumping and flying (Henne *et al.* 2010b) and dispersal over distances of 100 to 250 m (perhaps aided by wind) have been observed (Cameron *et al.* 2013). It was once thought that expansion of the psyllid's range in the US was due to seasonal migrations from south to north, however, supporting experimental evidence for such behaviour is lacking (Horton *et al.* 2015). Instead, overwintering behaviour of the psyllid, which has recently been confirmed, may partly explain seasonal increases in psyllid numbers in potato crops in more northerly areas of the US (Nelson *et al.* 2014). So, while short to medium range dispersal flights may account for how *B. cockerelli* infests crops from overwintering sites and spreads within and between regions, long range dispersal of this pest between regions and countries may be solely through anthropogenic means, especially the accidental trade of infested plants.

Analysis of mitochondrial cytochrome oxidase I (COI) gene sequences and inter sequence repeat (ISSR) markers of *B. cockerelli* populations across the USA, initially revealed three geographically separated and genetically distinct haplotypes designated as Central (Texas, Nebraska), Northwestern (Washington and Idaho) and Western (South California and Baja, Mexico) (Liu *et al.* 2006; Swisher *et al.* 2012). A fourth, the Southwestern haplotype, was later identified among psyllids from potato fields in Colorado and New Mexico (Swisher *et al.* 2014a), but additional studies revealed both regional separation and co-occurrence of psyllid haplotypes (Swisher *et al.* 2014b). *Bactericera cockerelli* samples from Mexico, El Salvador, Honduras, and Nicaragua similarly analysed were identified as the Central haplotype (Swisher *et al.*

2013). Mitochondrial CO1 gene sequences of five psyllid specimens collected in New Zealand were compared to data available in GenBank and closely matched the Western haplotype (L. Kumarasinghe, Ministry of Agriculture and Forestry, unpublished data cited by Thomas *et al.* 2011).

Examination of the almost complete mitochondrial genome rather than single genes of *B. cockerelli*, revealed a close relationship between the Southwestern and Central haplotypes. The Western one was divergent from the Central and Southwestern clades and found to be the probable precursor of the Northwestern haplotype (Montiel *et al.* 2016). Differences in fitness traits, and reproductive incompatibility have been observed among the recognised *B. cockerelli* haplotypes. The Northwestern one, for example, is more cold-tolerant than the Central and Western ones and is unable to produce viable eggs when mated with either of these (Swisher *et al.* 2013). Haplotypes also exhibit differences in their invasiveness, resistance to pesticides, and performance on different host plants (Liu and Trumble 2007; Swisher *et al.* 2013; Mustafa *et al.* 2015). These differences may have implications for damage potential and management of the pest.

4. Host plants

The potato psyllid is extremely polyphagous and has been observed feeding on plants from at least 20 different families (Knowlton and Thomas 1934; Butler and Trumble 2012c). It can be considered to be a "tourist" (Southwood *et al.* 1982) on plants that may provide it food and shelter but on which it does not reproduce. Martin (2008) asserts that "true hosts" of the psyllid are those on which it can complete its life cycle. These belong mainly to the Solanaceae and include cultivated plants such as potato, peppers (*Capsicum annum* L.), tomato (*Solanum lycopersicum* L.), and non-crop hosts such as bittersweet nightshade (*S. dulcamara* L.) and matrimony-vine (*Lycium barbarum* L.) (Wallis 1951; Wallis 1955; Butler and Trumble 2012c). Non-crop hosts of *B. cockerelli* can enable its survival during winter or when crop hosts are not available, and may facilitate the insect's establishment in newly invaded areas. In the Pacific Northwest of the US, the psyllid overwinters on *S. dulcarama* and disperses into potato fields during summer (Jensen *et al.* 2012; Murphy *et al.* 2013; Horton *et al.* 2015). Adults and nymphs of the psyllid are present on African boxthorn *Lycium ferocissimum* L. during winter in New Zealand, from which adults invade potato crops in summer (Dohmen-Vereijssen *et al.* 2013). The Jerusalem cherry (*Solanum pseudocapsicum* L.), poroporo (*S. aviculare* Forster) and Jimsonweed (*Datura stramonium* L.) are other non-crop hosts of the psyllid in New Zealand (Martin 2008), which may serve as reservoirs for the pest and its associated

pathogen (Barnes et al. 2015).

The psyllid can also complete development on a few species in the Convolvulaceae (bindweeds) (Puketapu and Roskruge 2011). However, this group of plants are not favoured hosts and Kaur et al. (2018) suggested a possible explanation. They found that 11 of 14 species of Convolvulaceae in the study contained a fungal symbiont (Periglandula spp.) that produced two classes of ergot alkaloids (clavines and amides of lysergic acid) lethal to the psyllid. Bactericera cockerelli was rapidly killed on five of the 11 symbiont-harboring species, which contained high amounts of the alkaloids, but completed development on the species that lacked the symbiont and in which ergot alkaloids were not detected (Kaur et al. 2018).

5. Crop damage and economic impact

By feeding on the phloem of its host plants, B. cockerelli induces a condition known as psyllid yellows, characterised by foliar symptoms that include leaf curling, chlorosis, stunting, and in extreme cases, plant death (Richards and Blood 1933). Wallis (1995) speculated that these symptoms were due to a toxin secreted in the saliva of the insect's nymphs but this remains unconfirmed. In 1927, widespread outbreaks of psyllid yellows occurred on potatoes in Utah and other states in the Rocky Mountain region, causing total destruction of potato crops in some areas, and the heaviest potato yield losses recorded up till that time in the USA (Linford 1928). More devastating outbreaks of psyllid yellows occurred about a decade later and ushered in an era of intensive insecticide use for potato psyllid control (Pletsch 1947; Wallis 1955).

Bactericera cockerelli increased in significance following its association with a disease of potatoes known as zebra chip (Goolsby et al. 2007b; Munyaneza et al. 2007) first recorded in potato fields near Saltillo, Mexico in 1994 (Secor et al. 2009). The disease reached the south of Texas in 2000, and by 2006, it had spread all over that state (Munyaneza et al. 2007). It has since been reported in all potato growing areas of the US, Mexico, Guatemala, Honduras and Nicaragua (Crosslin and Bester 2009; Crosslin et al. 2012; Munyaneza 2012; Crosslin 2014), New Zealand (Liefting et al. 2009a) and the Norfolk Islands, an external territory of Australia (Thomas et al. 2018). The disease is unreported from Western Australia where the psyllid was most recently detected; perhaps because the invading population of psyllids did not carry the pathogen that causes the condition.

Zebra chip disease is caused by a non-culturable, Gram-negative, phloem-limited bacterium identified as Lso in New Zealand (Liefting et al. 2008; Liefting et al. 2009) and C. Liberibacter psyllaurosus in the US (Hansen et al. 2008).

It is closely related to the liberibacters associated with Huanglongbing or citrus greening disease of citrus in Asia, Africa, and the Americas, which is spread primarily by other psyllid vectors (Bové 2006; Grafton-Cardwell et al. 2013). Five Lso haplotypes (A, B, C, D and E) differentiated by single-nucleotide polymorphisms (SNPs) and insertion-deletions (indels) in the ribosomal RNA (rRNA) region have been identified (Nelson et al. 2011; Nelson et al. 2013; Teresani et al. 2014). However, only haplotypes A and B are transmitted by B. cockerelli to solanaceous plants (Nelson et al. 2011). Field observations in Texas indicated that Lso haplotype B produced more severe symptoms than does haplotype A (Wen et al. 2013), and this has been confirmed experimentally (Grimm et al. 2018). Lso haplotypes C–E cause disease in other crops and have been detected in carrot plants in Finland, vectored by the psyllid Trioza apicalis Förster, and in the same crop in Sweden and Norway (Munyaneza et al. 2010, 2011, 2012). Some or all of these haplotypes have been reported in carrots and the psyllid Bactericera trigonica Hodkinson on the Canary Islands (Alfaro-Fernández et al. 2012b) and carrots on mainland Spain (Alfaro-Fernández et al. 2012a). The occurrence of Lso in non-solanaceous plants and in other psyllid species indicates that this bacterium may have a wider range of host plants and insect vectors than is currently known. Nevertheless, B. cockerelli is the primary vector of Lso in potatoes and other Solanaceae and its efficiency is such that a single adult psyllid can transmit the bacterium by feeding on uninfected plants for six hours (Buchman et al. 2011). Adults also transmit the bacterium transovarially to their offspring (Hansen et al. 2008) and this facilitates the spread of the disease to new areas when such offspring disperse (Crosslin et al. 2010). Lso can also be transmitted through the grafting of infected scions to potatoes and tomatoes (Crosslin and Munyaneza 2009; Secor et al. 2009), and from seed potatoes to daughter plants and tubers (Pitman et al. 2011). This is problematic for potato breeders, the seed potato industry, and subsequent buyers of seed, as plants grown from infected tubers could provide a reservoir of the pathogen for uninfected B. cockerelli (Buchman et al. 2011; Pitman et al. 2011).

The above-ground symptoms of potato zebra chip disease are similar to those of psyllid yellows, but include the proliferation of axillary buds, shortened internodes, swollen nodes, aerial tubers and rapid plant death (Munyaneza et al. 2007; Secor 2009; Munyaneza 2012). Fresh cut tubers from plants affected by zebra chip also show a brown discoloration, which develops into dark blotches, stripes, or streaks when such tubers are processed into chips or French fries and makes them unattractive to consumers (Munyaneza 2012). Thus, reduction in crop yield and quality due to psyllid yellows and zebra chip

disease are the main economic impacts of *B. cockerelli* on potatoes, with additional costs incurred for psyllid control (Munyaneza 2015). Besides, zebra chip-infected tubers are more expensive to process and are usually rejected by processors (Munyaneza 2012). Individual farms in Texas have recorded financial losses in excess of US$ 2 million annually due to zebra chip disease, and in 2006, it was estimated that over 35–40% of the potato acreage in Texas was vulnerable to zebra chip disease with potential losses of about US$ 33.4 million per annum (CNAS 2009). The requirement of testing export produce for Lso, and limited access to foreign markets due to stricter quarantine requirements constitute added incidental costs (Crosslin *et al.* 2010). The New Zealand tomato industry suffered such losses with respect to tomato and potato exports to Australia after the initial discovery of *B. cockerelli* and Lso in New Zealand (Walker P W *et al.* 2015).

6. Management of *B. cockerelli* and zebra chip disease

With no available treatments for Lso, management of *B. cockerelli* populations is the most widely used strategy for minimizing its costs and this is currently dominated by frequent applications of broad-spectrum chemical insecticides (Butler and Trumble 2012c; Guenthner *et al.* 2012). Potato growers in New Zealand have been known to use 15 foliar insecticide applications each season to protect their crops from zebra chip (Walker G P *et al.* 2015), and in Mexico, the number of sprays may be as high as 30 per season (Rubio-Covarrubias *et al.* 2006). Such intensive use of pesticides has negative effects on the environment, food safety and human health (Dich *et al.* 1997; Geiger *et al.* 2010) and often selects for resistance in pests. This has been reported in *B. cockerelli* populations in some areas of Mexico (Cerna *et al.* 2013).

To delay the emergence of this problem in Texas, Goolsby *et al.* (2007a) designed a reduced spray protocol involving application of imidacloprid (a systemic neonicotinoid insecticide) at planting followed by foliar applications of a range of insecticides with different active ingredients and modes of action at approximately 7-day intervals. This reduced the number of sprays to 8 or 9 per season and kept the incidence of zebra chip below economic thresholds (Goolsby *et al.* 2007a). Walker G P *et al.* (2015) also showed, from trials in the Pukekohe region of New Zealand, that a reduced spray programme of sequential applications of abamectin, spirotetramat and spimetoran (guided by an action threshold of 3 adult psyllids/sticky trap/week) reduced the incidence of zebra chip in harvested potato tubers to commercially acceptable levels of about one percent (Walker P W *et al.* 2015). The action threshold was based on earlier

work that involved three years of monitoring untreated early potato crops in the same region, in which no significant zebra chip damage was recorded when trap catches did not exceed 3 TPP adults per trap per week (Walker *et al.* 2012).

But after six years of implementing the protocol of Goolsby *et al.* (2007a) in south Texas, populations of *B. cockerelli* from that area were found to be less susceptible to imidacloprid (Prager *et al.* 2013). Szczepaniec *et al.* (2019) have also reported resistance to imidacloprid and another insecticide, thiamexotam in populations of the pest from Colorado and New Mexico where similar protocols have been used (Szczepaniec *et al.* 2019). While there are no published reports of *B. cockerelli* resistance to insecticides in New Zealand, the above reports from the US indicate that this is likely to occur eventually, and that chemical sprays may not be the long-term solution to *B. cockerelli*.

Biological control using natural enemies of the psyllid is viewed as an attractive alternative to pesticides. Based on surveys in potato, bell pepper and tomato fields in Southern California, Butler and Trumble (2012a) found that natural enemies of the psyllid included several species of spiders, hemipteran bugs, ladybird beetles and two parasitoid wasps- *Tamarixia triozae* (Burks) (Hymenoptera: Eulophidae) and *Metaphycus psyllidis* Compere (Hymenoptera: Encryrtidae). *T. triozae* was present in most of the sampled fields, and although its parasitism rate was estimated to be <20%, the wasp was considered as having the potential to control the psyllid in non-crop habitats or on crops that were not repeatedly treated with pesticides (Butler and Trumble 2012a). The minute pirate bug *Orius tristicolor* (White) (Hemiptera: Anthocoridae), western big-eyed bug *Geocoris pallens* Stål (Hemiptera: Geocoridae), and convergent lady beetle *Hippodamia convergens* Guérin-Méneville (Coleoptera: Coccinellidae) were identified as important natural enemies of the pest in the surveyed fields and recommended for further investigation and inclusion as biocontrol agents (BCAs) in integrated pest management (IPM) of the psyllid (Butler and Trumble 2012a).

MacDonald *et al.* (2016) conducted choice and no-choice laboratory assays using the predators *Micromus tasmaniae* Walker (Neuroptera: Hemerobiidae) and small hoverfly *Melanostoma fasciatum* Macquart (Diptera: Syrphidae) which are native to New Zealand, and three exotic ones: Pacific damsel bug *Nabis kingbergii* Reuter (Hemiptera: Nabidae); 11-spotted ladybird *Coccinella undecimpunctata* L. (Coleoptera: Coccinellidae) and large spotted ladybird *Harmonia conformis* (Boisduval) (Coleoptera: Coccinellidae) that are found in unsprayed potato crops. All five predators attacked all life stages of *B. cockerelli* and were considered to be beneficial for its control although the native predators were considered to be more effective (MacDonald *et al.* 2016). The

southern ladybird *Cleobora mellyi* Mulsant (Coleoptera: Coccinelidae) which was introduced into New Zealand in 1977 to control the Eucalyptus tortoise beetle *Paropsis charybdis* (Coleoptera: Chrysomelidae) (Martin 2016) was tested against *B. cockerelli* in no-choice laboratory assays and adults and 4th instar larvae of the ladybird consumed 100 nymphs of the psyllid on potato leaf discs in 24 hours (O'Connell *et al.* 2012). This ladybird also showed good control of the pest for up to six weeks on potato when provided access to buckwheat flowers in a glasshouse cage experiment (Pugh *et al.* 2015). However, these results have not been repeated in the field.

In surveys of potato fields in Oaxaca Mexico that had not been sprayed extensively with pesticides, *T. triozae* was abundant with very high parasitism rates ~80% on *B. cockerelli* (Bravo and Lopez 2007); cited by Rojas *et al.* (2015). This finding may have sparked renewed interest in the parasitoid, as evidenced by studies on its biology (Rojas *et al.* 2015; Vega-Chavez *et al.* 2016); sensitivity to pesticides commonly used for psyllid control (Martinez *et al.* 2015; Morales *et al.* 2018); functional response and prey stage preference (Yang *et al.* 2015), and its effectiveness for biological control of the psyllid in combination with other natural enemies under glasshouse conditions (Ramírez-Ahuja *et al.* 2017; Calvo *et al.* 2018). Combination of *T. triozae* with the zoophytophagous bug *Dicyphus hesperus* (Knight) (Heteroptera: Miridae) provided additive reduction of *B. cockerelli* on tomatoes and yielded better control of the pest compared to when both natural enemy species were applied separately (Ramirez-Ahuja *et al.* 2017). In 2017, *T. triozae* was approved for importation and mass release in New Zealand mainly to suppress *B. cockerelli* populations on non-crop hosts and secondarily for trials in tomato glasshouses. Preliminary trials indicate that use of the wasp in combination with the generalist predatory mite *Amblydromalus limonicus* (Garman and McGregor) (Acari: Phytoseiidae) may have potential for *B. cockerelli* control on tomatoes (Olaniyan *et al.*, unpublished data).

Successful application of *T. triozae* and complementary natural enemies for biological control of *B. cockerelli* in commercial glasshouses may be possible, but would require selective use or discontinuation of pesticides (Rojas *et al.* 2015). In field potatoes where climate cannot be controlled and pest pressure may be continuous throughout the season, inundative releases of natural enemies for biological control would be more expensive and likely to be unsustainable. On the other hand, it is thought that releasing *T. triozae* and other natural enemies on non-crop host plants of TPP could reduce populations of the psyllid available to infest crops (Davidson M. 2019, personal communication). However, whether or not this approach proves effective, remains to be determined. Biological control of *B. cockerelli*

in field potatoes has not been adequately explored but the understanding that this approach will not prevent the transmission of Lso may be an impediment to its adoption in both protected and field crops.

Cultural and physical control practices that prevent or reduce infestation of crops by *B. cockerelli* and limit the rate of increase of infesting psyllid populations and spread of zebra chip within crops are also important. These could include the removal of zebra chip infected plants and all non-crop host plants of the psyllid from the vicinity of potato fields (Butler and Trumble 2012c). A binomial sequential sampling plan that enables detection of low-level infestations of the psyllid in potato fields so that the insect's spread and damage within the crop can be limited has been developed (Butler and Trumble 2012b). Trials conducted in Canterbury, New Zealand, showed that a finely woven nylon mesh laid over potatoes at planting could provide effective physical control of *B. cockerelli* in field potatoes (Merfield *et al.* 2015). Very few psyllids were found under the mesh and plants in mesh-covered plots produced higher yields with a greater proportion of large tubers, and even showed reduction in early blight infestation compared to uncovered plots treated with or without the pesticide and fungicide regimens commonly employed in the area (Merfield *et al.* 2015). However, the green peach aphid *Myzus persicae* Sulzer (Hemiptera: Aphididae), was able to breach the mesh and multiply rapidly, probably because the mesh excluded its natural enemies. It was suggested that introducing natural enemies of the aphid under the mesh at the time of planting along with insect prey that are not potato pests on banker plants may solve this problem without the need for pesticides (Merfield *et al.* 2015).

Finally, there is increasing evidence that potato breeding lines and varieties exhibit varying levels of tolerance to Lso infections (Lévy *et al.* 2015; Rubio-Covarrubias *et al.* 2017; Anderson *et al.* 2018), and improvement of such lines through traditional breeding approaches or genetic engineering may offer an additional tool for managing zebra chip disease. Long-term sustainable management of zebra chip disease of potato will no doubt require an integrated pest management (IPM) approach using some or all of the methods that have been discussed above.

7. Preventing and preparing for *B. cockerelli* incursion and establishment in China

China currently leads global potato production with approximately 100 million metric tonnes per annum and has sustained this level for the past three years (FAO 2018). Because of the crop's importance as a source of food and livelihood in China, increasing or at least maintaining this

production rate and diversifying the processing of potatoes is considered an economic priority (Zhang *et al.* 2017). Such efforts would however be jeopardized if TPP and Lso were to enter China; most likely *via* accidental importation of infested plant material from Australia and Zealand or even from Mexico and the USA. The vulnerability of China to invasion by alien pests as a consequence of booming international trade has been previously highlighted (Ding *et al.* 2008). In total, 560 invasive alien species have been documented in China; 125 of these are insects, and 27 of these records were made between 2000 and 2008 (Wan and Yang 2016). The entry of TPP into New Zealand and Australia despite routine and strict biosecurity measures underlines the risk to China, however, China can be better prepared by learning from the experiences of both countries.

Bactericera cockerelli likely entered New Zealand in the summer of 2005 (December 2005-February 2006). This at a time when there was little awareness of the pest, and none, about its association with Lso and the huge economic impact this could have (Gill 2006). Thus, although the psyllid was discovered in March 2006, official confirmation of its identity was only done in June, almost three months later (Teulon *et al.* 2009). By the time a delimiting survey was conducted by staff of the Ministry of Agriculture and Forestry Biosecurity New Zealand (MAFBNZ), the pest was widespread in tomato and capsicum glasshouses and field potatoes across Auckland and Taupo in the North Island. This led to the conclusion that the pest was well established and its eradication was not feasible (Gill 2006). There was also no attempt to establish a quarantine area or restrict the sale and distribution of host crops of the pest and this contributed to the rapid spread of the psyllid to the South Island (Teulon *et al.* 2009). The biosecurity response following the discovery of TPP in New Zealand may thus be described as weak, and contrasts with the Australian response.

Once Australia was notified of the presence of *B. cockerelli* and Lso in New Zealand, Biosecurity Australia immediately undertook a pest risk analysis to identify potential entry pathways for the pathogen and its vector and listed them as quarantine organisms (Biosecurity Australia 2009). Accidental or intentional importation of fresh fruit, potato tubers and nursery stock, or hitch-hiker transportation of psyllids on plant or non-plant materials were identified as the most likely entry routes (Biosecurity Australia 2009; PHA 2010) and importation of TPP host crops from New Zealand was suspended until December 2008 when procedures had been put in place to ensure that imports could be certified as TPP and Lso-free (Teulon *et al.* 2009). These actions probably helped to keep the psyllid out of mainland Australia for close to 11 years. Monitoring of the psyllid using yellow sticky traps in potato growing areas on the east coast of

Australia, which was considered to be most at risk of being invaded by the psyllid *via* New Zealand, was initiated in 2011 with funding from potato industry partners (Walker P W *et al.* 2015). Furthermore, a contingency plan was developed to assist with preparedness for an incursion of the psyllid and its associated pathogen into Australia. The plan contained detailed information on TPP and Lso and their potential impact on the solanaceous industry and was made available to growers and members of the public to create awareness and increase the chances of early detection in the event of an incursion (PHA 2010).

However, in February 2017 when a TPP incursion into Australia was discovered, it was not in Eastern Australia, but in Perth, Western Australia (WA) (DPIRD 2018). Immediately following the discovery, delimiting surveys conducted by the WA Department of Primary Industries and Regional Development (DPIRD) showed that the psyllid was widespread at home and commercial gardens around the Perth metropolitan area, and it was decided that eradication not feasible (DPIRD 2018). Nevertheless, a quarantine area was quickly established and new domestic quarantine rules regulating the movement of risk plants and plant material produced in WA were enacted, including rules for interstate certification of produce from the region (DAFWA 2018). These steps were taken to prevent spread of the psyllid beyond the region, and appeared to have been successful as *B. cockerelli* has not been found in any other Australian state (DPIRD 2018). About 9 000 psyllid samples collected from all over Perth have been tested for Lso and the pathogen has not been detected (DPIRD 2018). There is an ongoing national TPP surveillance program coordinated by the Tasmanian Institute of Agriculture, which involves the placement of many traps in eastern Australia to enable early detection in case the pest should spread. Laboratory and glasshouse trials are also being conducted to develop both pesticide and natural enemy-based management strategies for the psyllid in Australia (DPIRD 2018).

The response of Australia to the threat of incursion by the psyllid and that post-incursion, were better than the New Zealand response of 2006. This is no doubt related to the fact that the link between TPP, Lso and zebra chip became well known two years after the psyllid invaded New Zealand. Australia recognized the risks, identified pathways of entry and took immediate action to prevent an incursion. However, limiting the pre-incursion surveillance to Eastern Australia based on the assumption that TPP could disperse from New Zealand to that region of Australia *via* wind currents (Walker P W *et al.* 2015), may have prevented early detection of the incursion in Perth, and ruled out any chance of eradicating the pest. Still, having a contingency plan that provided for a post incursion response has enabled restriction of the psyllid to WA. Extensive collaboration and consultation

with New Zealand researchers and biosecurity experts who had gained considerable knowledge on the biology and management of TPP and Lso, were vital to the swift and effective post-incursion response of Australia (Dohmen-Vereijssen 2019, personal communication).

In light of the above, the steps below are recommended to enable China prevent, or prepare to effectively manage an incursion into its borders of the tomato potato psyllid:

7.1. Increased surveillance and public awareness

The Administration of Quality Supervision, Inspection and Quarantine (AQSIQ), which is the agency responsible for protecting China from biological invasions (http://english.aqsiq.gov.cn/) should list *B. cockerelli* and Lso as quarantine organisms and raise its current level of vigilance. Awareness should be created by providing information on the psyllid to biosecurity agencies, growers and industry stakeholders.

7.2. Pest risk analysis

Pest risk analysis should be conducted to identify potential entry pathways for TPP and Lso separately or together, into China and the risks quantified. Estimating this risk would involve among other steps, analysis of the kinds of goods (especially Solanaceae) imported into China from psyllid-infested countries. Accuracy of the estimate could be improved by using indices such as climatic factors and the presence and distribution of potential host plants of the psyllid to develop risk maps for the psyllid. Pest risk maps help to predict where invasive alien species might arrive, establish, spread, or cause harmful impacts and inform strategic management decisions, such as potential restrictions on international trade, increased surveillance at ports of entry, the design of pest surveys and domestic quarantine (Venette *et al.* 2010) and would be useful for developing a TPP monitoring programme in China.

7.3. Preparation of a contingency plan with a strong research component

Recognizing that the above precautions may not prevent an incursion or even guarantee early detection if it occurs, a TPP and Lso-specific contingency and management plan outlining the steps to be taken in the event of an incursion should be developed. In addition to providing clear guidelines for delimiting surveys, establishment of quarantine areas and restrictions on movement on TPP host plants, the contingency plan should include research on management options. Indeed, China could initiate pre-emptive research on the psyllid and its management through collaborations with researchers and experts

based in New Zealand and Australia. The Bio-Protection Research Centre (BPRC) at Lincoln University, New Zealand in partnership with industry stakeholders, is currently researching *T. triozae* and culturing this parasitoid in large numbers. Approximately 8 000 wasps have been provided to commercial tomato growers in New Zealand to date, and the culturing and experimental expertise developed could be used to train Chinese scientists and practitioners. China could also establish cultures of *T. triozae* and TPP under strict quarantine to conduct further experiments. Potential biological control agents of the psyllid in China, and other management options should also be investigated.

8. Conclusion

This article reviewed some aspects of the biology and severe economic impacts of *B. cockerelli* as the vector of the bacterial pathogen, *Candidatus* Liberibacter solanaceaerum, which causes zebra chip disease in potatoes and psyllid yellows in other solanaceaous crops. It shows that despite some progress, effective and sustainable protocols for managing the psyllid and the pathogen it transmits are currently lacking and as such, the pest continues to have significant economic impacts in widely-spread countries where it is present. *Bactericera cockerelli* remains a threat to China, which is the world's leading producer of potatoes and has a high rate of exotic pest incursion and establishment due to huge volumes of international trade. It is recommended that China develops a comprehensive strategy to prevent and manage an incursion of *B. cockerelli* by drawing on the experiences and expertise developed in New Zealand and Australia.

Acknowledgements

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