

# *Bactericera cockerelli* (Hemiptera: Triozidae) and *Candidatus Liberibacter solanacearum* in Potatoes in New Zealand: Biology, Transmission, and Implications for Management

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## Abstract

*Bactericera (Paratrioza) cockerelli* (Šulc) (Hemiptera: Triozidae) is a native American psyllid species that was first reported in New Zealand in 2006. In 2008, the insect was associated with a new-to-science pathogen, *Candidatus Liberibacter solanacearum* (syn. 'Ca. L. psyllauros') (Rhizobiales: Rhizobiaceae). This pathogen is the putative causal agent of zebra chip disease of potato tubers, which makes them unsuitable for processing, causes disease in seed tubers, and is perceived to affect the taste of fresh market potatoes, as well as their internal appearance. The insect/pathogen complex is also an important economic pest of other solanaceous crops, including tomato, capsicum, tamarillo, and eggplant. Here, we review the literature on the phloem-limited pathogen and focus on the integrated management of its insect vector in New Zealand. Comparisons with other regions of the world are made where appropriate. We review the current understanding and paradigms of insect-mediated transmission of plant pathogens, an increasingly important area as more *Liberibacter* species are discovered world-wide. Knowledge gaps are identified and recommendations made for future research aimed at defining the fundamental biological parameters underpinning the epidemiology and pathology of the disease caused by *Ca. L. solanacearum* in potato.

**Key words:** pest management, vector-borne pathogens-plant, potato, Psyllidae

## The Plant Pathogen: *Candidatus Liberibacter*

The taxon *Liberibacter* was first used by Garnier et al. (2000) to describe a bacterium-like organism (BLO) found in *Calodendrum capense* (L. fil.) Thunb., an ornamental rutaceous tree in South Africa. *Liberibacter* is an orthographic correction of the original 'Liberobacter' originally proposed by Jagoueix et al. (1994) for an unculturable phloem-limited BLO associated with the citrus disease Huanglongbing. This disease, also known as citrus greening, had been present since the late 19th century in southern China (Bové 2006). The first molecular description and taxonomic placement, based on part of the 16S rRNA gene, placed this BLO as a new member of the  $\alpha$ -proteobacterium subdivision of the class Proteobacterium (Jagoueix et al. 1994). In the same year, Murray and Schleifer (1994) proposed the category *Candidatus* for unculturable bacteria that could only be identified by a limited number of

characteristics. A year later, this proposal was implemented with the category *Candidatus* used to describe the provisional status of incompletely described prokaryotes (Murray and Stackebrandt 1995). Both *Candidatus Liberobacter asiaticus* and *Ca. Liberobacter africanus*, the only species nominated at that time, were considered to be suitable sequence-based taxa for designation as *Candidatus* (Murray and Stackebrandt 1995). Currently seven *Ca. Liberibacter* species and one *Liberibacter* species (*Liberibacter crescens*) (Rhizobiales: Rhizobiaceae) are known. All *Ca. Liberibacter* species are associated with psyllid (Superfamily Psylloidea) insect vectors and some are known to be plant pathogenic on crop plant species (Table 1). For a more detailed list of all *Ca. Liberibacter* species refer to Wang et al. (2017). In New Zealand, *Ca. L. europaeus*, which has been associated with *Arytainilla spartiophila* Förster (Hemiptera: Psyllidae), has been found to cause symptoms in the invasive leguminous exotic

shrub *Cytisus scoparius* (L.) Link. Two recent additions to the list of *Ca. Liberibacter* are *Ca. L. brunswickensis*, which has been found in *Acizzia solanicola* Kent & Taylor (Hemiptera: Triozidae) in Australia (Morris et al. 2017) and *Ca. L. ctenarytainae* from the New Zealand native fuchsia psyllid *Ctenarytainia fuchsiae* Maskell (Hemiptera: Aphalaridae) (Thompson et al. 2017). This is the first finding of a *Liberibacter* species associated with a psyllid species in the Aphalaridae; all other associations have been with psyllids in the Triozidae or Psyllidae. Both new *Liberibacter* species have not been associated with plant disease.

### Candidatus *Liberibacter solanacearum*

*Candidatus Liberibacter solanacearum* was first proposed as the name for the putative causal agent of zebra chip in potato (*Solanum tuberosum* L.) by Liefing et al. (2009a, 2009b) following the initial note in 2008 of the first report of a *Liberibacter*, based on molecular sequence, in potato (Liefing et al. 2008b). *Ca. L. psyllauros* was discovered independently around the same time in the psyllid *Bactericera cockerelli* (Šulc) (Hemiptera: Triozidae) and tomato in the United States (Hansen et al. 2008) and is generally regarded as a synonym of *Ca. L. solanacearum*.

Classification systems have been proposed to describe the genetic variability within *Ca. L. solanacearum*. Currently there are five clades of *Ca. L. solanacearum* (A to E) based on single nucleotide polymorphisms (SNPs) in the ribosomal ribonucleic acid (rRNA) operon (Nelson et al. 2011, Nelson et al. 2013, Teresani et al. 2014) (Table 2). These descriptors, referred to as haplotypes, are consistent with biological differences (psyllid vector and plant host) and geographic distribution between these *Ca. L. solanacearum* clades despite these SNPs not being consistently present in all three copies of the rRNA operon.

*Ca. L. solanacearum* has also been reported from a number of non-solanaceous plant host species (Table 3). In Europe (Finland, France, Norway, Sweden, Spain [mainland and Canary Islands], Germany, Greece, and Austria) and Morocco, it has been found in carrot (*Daucus carota* L.) plants (Munyanze et al. 2010a, Munyanze et al. 2011, Alfaro-Fernández et al. 2012a, Alfaro-Fernández et al.

2012b, Munyanze et al. 2012b, Loiseau et al. 2014, Tahzima et al. 2014, EPPO 2015, Munyanze et al. 2015, Hajri et al. 2017, Holeva et al. 2017) and to a lesser extent in celery (*Apium graveolens* L.) plants in Spain (Teresani et al. 2014), Austria (EPPO 2015) and France (Hajri et al. 2017), in parsnip (*Pastinaca sativa* L.) and parsley (*Petroselinum crispum* (Mill.) Fuss) plants in Spain (Alfaro-Fernández et al. 2017) and France (Hajri et al. 2017), and in fennel (*Foeniculum vulgare* Mill.) and chervil (*Anthriscus cerefolium* (L.) Hoffm.) plants in France (Hajri et al. 2017). Additionally, it was found in commercially available packages of parsley seed in the United Kingdom and Australia (Monger and Jeffries 2016, Nursery & Garden Industry Australia 2017). Interestingly, Monger and Jeffries (2018) detected *Ca. L. solanacearum* haplotypes C, D, and E in historical commercial seed from different species of the family Apiaceae from different countries and in wild carrot from Lebanon, the earliest infected seed lot dating from 1973. As the authors indicate, the bacterium 'is not an emerging pathogen in European Apiaceae crops but rather one that has gone unnoticed and undetermined for a long time; only reaching economic levels when vector populations increase under favorable environmental conditions to cause epidemics as have occurred in Finland and Spain'. The data on detection of *Ca. L. solanacearum* in seed lots lack detail about where the bacterium was found in the seed—as a contaminant in, or on, the outside of the seed coat or within the embryo. This knowledge would provide more insight into the possibility and rate of seed transmission of *Ca. L. solanacearum*. However, the data by Monger and Jeffries (2018) show that haplotype C, D, and E of the pathogen were present long before they became an economic problem. These findings pose questions around, why only recently, these have become a problem, or has it been indeed just an increase in vector abundance that has led to the disease reaching economic levels in some years as Monger and Jeffries (2018) propose. Further, is the same true for haplotypes A and B found only in Solanaceae? The finding of haplotype E in potato in Spain has yet to be reconciled with the current haplotype descriptions (Cambra et al. 2014). Additional questions regarding how the five different *Ca. L. solanacearum*-haplotypes developed and how their relationship with the

**Table 1.** Hemipteran insect vectors and plant host taxonomy for *Candidatus Liberibacter* species that are pathogenic to agricultural plants

Bacterium	Insect vector (family)	Plant host family	Reference of association bacterium with vector
<i>Ca. L. asiaticus</i>	<i>Diaphorina citri</i> (Psyllidae)	Rutaceae (various spp)	Capoor et al. (1967)
	<i>Trioza erytreae</i> (Trioizidae)	Rutaceae (various spp)	McClellan and Oberholzer (1965)
	<i>Cacopsylla citrisuga</i> (Psyllidae)	Rutaceae (lemon)	Cen et al. (2012)
<i>Ca. L. americanus</i>	<i>Diaphorina citri</i> (Psyllidae)	Rutaceae (various spp)	Teixeira et al. (2005)
<i>Ca. L. africanus</i>	<i>Trioza erytreae</i> (Trioizidae)	Rutaceae	McClellan and Oberholzer (1965)
<i>Ca. L. caribbeanus</i>	<i>Diaphorina citri</i> (Psyllidae)	Rutaceae ( <i>Citrus</i> spp, <i>Murraya paniculata</i> )	Keremane et al. (2015)
<i>Ca. L. solanacearum</i>	<i>B. cockerelli</i> (Trioizidae)	Solanaceae (various spp)	Liefing et al. (2009a)
	<i>Trioza apicalis</i> (Trioizidae)	Apiaceae (carrot)	Munyanze et al. (2010b)
	<i>Bactericera trigonica</i> (Trioizidae)	Apiaceae (carrot, celery)	Alfaro-Fernández et al. (2012a)

**Table 2.** Descriptors, distribution, and plant hosts of *Ca. L. solanacearum* clades

Clade	SSR lineage type	MLST	Haplotype	Region	Insect host	Host plant family
1	2	1	ST2	Americas, New Zealand	<i>B. cockerelli</i>	Solanaceae
2	1	2	ST1	Americas	<i>B. cockerelli</i>	Solanaceae
3			C	Scandinavia	<i>Trioza apicalis</i>	Apiaceae
4			D	Europe, Morocco	Unknown	Apiaceae
5			E	Europe, Morocco	<i>Bactericera trigonica</i>	Apiaceae

**Table 3.** Non-solanaceous plant host species and known psyllid vectors for clades of *Ca. L. solanacearum*

Country	<i>Ca. L. solanacearum</i> haplotype	Plant host/Psyllid vector	Associated psyllid vector in the study	Initial reference/Source
Austria	Unknown	<i>Daucus carota</i> subsp. <i>sativus</i>	N/A	EPP0 (2015)
	Unknown	<i>Apium graveolens</i>	N/A	EPP0 (2015)
Finland	C	<i>Daucus carota</i> cv. Maestro, Nanda, Nipomo, Nerac, and Fontana	<i>Trioza apicalis</i>	Munyaneza et al. (2010a), Nelson et al. (2013)
France	C, D, E	<i>Daucus carota</i>	N/A	Loiseau et al. (2014), Hajri et al. (2017)
	E	<i>Petroselinum crispum</i>	N/A	Hajri et al. (2017)
	E	<i>Apium graveolens</i>	N/A	Hajri et al. (2017)
	E	<i>Anthriscus cerefolium</i>	N/A	Hajri et al. (2017)
	E	<i>Foeniculum vulgare</i>	N/A	Hajri et al. (2017)
	E	<i>Pastinaca sativa</i>	N/A	Hajri et al. (2017)
Germany	C	<i>Daucus carota</i> cv. Nerac	<i>Trioza apicalis</i>	Munyaneza et al. (2015)
Greece	D	<i>Daucus carota</i> cv. Dordogne and Newhall	N/A	Holeva et al. (2017)
Morocco	D, E	<i>Daucus carota</i> cv. Mascot	N/A	Tahzima et al. (2014)
Norway	C	<i>Daucus carota</i>	<i>Trioza apicalis</i>	Munyaneza et al. (2011), Nelson et al. (2013)
Spain (mainland)	D, E	<i>Daucus carota</i>	N/A	Alfaro-Fernández et al. (2012b), Nelson et al. (2013), Alfaro-Fernández et al. (2017)
	D, E	<i>Daucus carota</i> cv. Bangor	N/A	Teresani et al. (2014), Alfaro-Fernández et al. (2017)
	D, E	<i>Pastinaca sativa</i>	N/A	Alfaro-Fernández et al. (2017)
	D, E	<i>Petroselinum crispum</i>	N/A	Alfaro-Fernández et al. (2017)
	D, E	<i>Apium graveolens</i>	N/A	Alfaro-Fernández et al. (2017)
Spain (Canary Islands)	D, E	<i>Daucus carota</i>	<i>Bactericera trigonica</i>	Alfaro-Fernández et al. (2012a), Nelson et al. (2013), Alfaro-Fernández et al. (2017)
	D	<i>Apium graveolens</i> cv. Loretta, Imperial, and Monterrey	N/A	Teresani et al. (2014), Alfaro-Fernández et al. (2017)
	E	<i>Petroselinum crispum</i>	N/A	Alfaro-Fernández et al. (2017)
Sweden	C	<i>Daucus carota</i> cv. Nevis and Florida	<i>Trioza apicalis</i>	Munyaneza et al. (2012b), Nelson et al. (2013)

This table does not include results from the historic commercial seed lots and wild carrots of [Monger and Jeffries \(2018\)](#).

different psyllid species developed should be further investigated in light of recent research findings.

Indeed, *Ca. L. solanacearum* has also been reported from a number of psyllid species in addition to *B. cockerelli* ([Teresani et al. 2015](#), [Borges et al. 2017](#)), although the ability of some of these psyllid species to vector *Ca. L. solanacearum* to host plant species still needs to be assessed. More recently, *Ca. L. solanacearum* has been found in the psyllid *Trioza anthrisci* Burckhardt (Hemiptera: Triozidae) in the United Kingdom, it is however, unknown whether the insect is a vector for *Ca. L. solanacearum* and as to date no feeding host plants of *T. anthrisci* have been found positive for this pathogen ([Sjölund et al. 2017](#)).

A real threat to plant health and biosecurity is when unknowingly, infected, asymptomatic plant material is imported. Although the bacterium itself is limited to its plant host, the presence of possible psyllid vectors in the new environment other than the ones currently known could have major effects for agricultural or horticulture sectors.

### Symptoms of *Ca. L. solanacearum* in Plants

*Ca. L. solanacearum* can be introduced into the phloem of a plant by feeding of psyllids (see the vector section, below). In addition to horizontal (insect-mediated) transmission, the pathogen can also be transmitted vertically via infected plant material (e.g., grafting, or infected seed tubers) ([Table 4](#)).

In potato, disease symptoms of *Ca. L. solanacearum* on stems and leaves include upward rolling of leaves ([Fig. 1A](#)), yellow to purple discoloration, bushy new growth at the top and swollen nodes ([Fig. 1B](#)), axillary bud proliferation ([Fig. 1C](#)), aerial tubers ([Fig. 1D](#)) and leaf chlorosis. Freshly-cut infected tubers show a browning of vascular tissues and streaks in the medullary ray tissues ([Fig. 2](#)), most likely associated with increases in phenolic and polyphenol oxidase levels ([Wallis et al. 2012](#)). The commercially unacceptable variable patterns of light and dark stripes, streaks, and blotches ([Fig. 3](#)) observed in fried slices from infected tubers are likely caused by an increase in reducing sugars (i.e., fructose and glucose) and amino acids ([Wallis et al. 2012](#), [Rashed et al. 2013](#)), and are referred to as zebra chip disease. This term was first used by [Secor and Rivera-Varas \(2004\)](#) for an unknown disease in U.S. potatoes. Later, [Abad et al. \(2009\)](#) suggested that *Ca. L. solanacearum* may be involved in causing zebra chip disease. There is evidence that potato cultivars respond differently to infection with this bacterium, especially when the pathogen is tuber-borne (mother tuber infection) (A. R. Pitman, personal communication) and transmission in the plant is initially vertical, very likely because of genetic differences of ancestral lines. Additionally, differences in tuber disease expression between New Zealand and the United States have been observed. In the United States, *Ca. L. solanacearum* haplotype A and B are present, whereas in New Zealand only haplotype A is present ([Thompson et al. 2015](#)). Furthermore, the within and between variation in the haplotype





**Fig. 1.** Symptoms of *Ca. L. solanacearum* in potato in New Zealand. (A) Upward rolling of leaves with a yellow to purple discoloration of leaf edges. (B) Bushy new growth because of shortening of the nodes. (C) Axillary bud proliferation. (D) Development of aerial tubers which are still visible after desiccation.



**Fig. 2.** Raw potato tuber symptoms as a result of an infection with *Ca. L. solanacearum* in New Zealand, where the vascular bundle is more pronounced and brown streaks are visible. Copyright: The New Zealand Institute for Plant and Food Research Limited. All rights reserved.

genomes, may partly explain the difference in disease symptoms between the two countries (Thompson et al. 2015) in addition to variations in bacterial titer, cultivar, agronomy and environment. Vertical transmission of *Ca. L. solanacearum* (from mother tuber to daughter plant and tubers) has been shown at very low percentages in potato in the absence of the insect vector *B. cockerelli* (Pitman et al. 2011). In New Zealand, the following characteristics have been observed with respect to mother tubers infected with *Ca. L. solanacearum*: 1) do not germinate, 2) germinate but grow many spindly plants, 3) germinate and grow a diseased plant (and subsequently infected daughter tubers) or 4) germinate and grow a non-diseased plant (Pitman et al. 2011). Tuber transmission is an issue for breeders, the seed potato industry and the subsequent buyers of seed. In the field, the symptomatic plants grown from infected mother tubers, although mostly stunted and delayed in emergence, could provide a source of *Ca. L. solanacearum* for *B. cockerelli*. Another source of *Ca. L. solanacearum* for *B. cockerelli* in the environment is through volunteer potatoes, which grow in subsequent crops.

In tomato, disease symptoms include chlorotic apical growth (Fig. 4B), curling or cupping of leaves (Fig. 4A), misshapen fruit in some cultivars and overall stunting resulting in yield loss



**Fig. 3.** After frying individual crisps of potato tubers infected with *Ca. L. solanacearum* in New Zealand, the streaky and blotchy patterns of the raw tubers become even more pronounced and is referred to as zebra chip disease. Copyright: The New Zealand Institute for Plant and Food Research Limited. All rights reserved.

(Liefting et al. 2009b), as well as premature plant death (Fig. 4C) and post-harvest cleaning of fruit (Fig. 4D). However, unlike the situation with potatoes, infected field tomatoes (Fig. 4E) can still be used for processing. *Capsicum* spp., which seem to be less affected by infestation of *B. cockerelli* and infection by *Ca. L. solanacearum* than potato and tomato, exhibit chlorotic or pale green apical growth and leaf cupping (Fig. 5A), sharp tapering of the leaf apex, shortened internodes, and an overall stunting (Munyanzeza et al. 2009). Similar to tomatoes, fruit is affected by psyllid excretions used as a substrate by sooty molds (Fig. 5B) and presence of psyllid life stages on the calyx (Fig. 5C) and, requiring post-harvest cleaning.

In carrot, disease symptoms, previously thought to have been induced by the psyllid *Trioza apicalis* Forster (Hemiptera Triozidae) feeding but now attributed to *Ca. L. solanacearum*, include leaf curling, yellowish, bronze, and purplish discoloration of leaves (Nissinen et al. 2007, Munyanzeza et al. 2010b, Alfaro-Fernández et al. 2012a, Alfaro-Fernández et al. 2012b). Below ground, stunting of the shoots and roots and proliferation of secondary roots can be observed (Fig. 6A) (Munyanzeza et al. 2010b, Alfaro-Fernández et al. 2012a, Alfaro-Fernández et al. 2012b). In Israel, *Bactericera trigonica* Hodkinson transmits *Ca. L. solanacearum* to carrot (Fig. 6B).

*Ca. L. solanacearum* is also found in the crop hosts cape gooseberry (*Physalis peruviana* L.) and tamarillo (*Solanum betaceum* Cav.) (Liefting et al. 2008a) and leads to tree death in the latter species (Fig. 7A–F) (Watson 2009). Additionally, some non-crop host plant species have been shown to support *Ca. L. solanacearum* and in most cases do not show symptoms. In the United States, bitter-sweet nightshade (*Solanum dulcamara* L.) and silverleaf nightshade (*Solanum elaeagnifolium* Cav.) (Murphy et al. 2014, Thinakaran et al. 2015b) and in New Zealand, Jerusalem cherry (*Solanum pseudocapsicum* L.) and Jimsonweed (*Datura stramonium* L.) (Vereijssen et al. 2015) tested positive for *Ca. L. solanacearum* and consequently act as reservoirs for the pathogen outside the cropping season.

## The Insect Vector

The Hemiptera are an agriculturally important order of insects because of the large number of direct and indirect pest species.

There are four suborders: Heteroptera (the true bugs); Coleorrhyncha (moss bugs); Auchenorrhyncha (cicadas, leafhoppers, treehoppers, planthoppers, and froghoppers); and Sternorrhyncha (aphids, whiteflies, scale insects, mealybugs, and psyllids). Psyllids, or jumping plant-lice, are small, often host-specific, phloem-feeding insects (Burckhardt et al. 2014). The classification was recently revised and the superfamily, Psylloidea, now consists of 11 families of almost 4,000 described species worldwide (Burckhardt and Ouvrard 2012, for up to date information, also see Ouvrard 2017).

Psyllids occur in all biogeographical habitats from the sea to alpine level. Many tropical and southern temperate species are polyvoltine while northern temperate species tend to be univoltine or bivoltine (Burckhardt 1994). In the United States, the seasonal absence of *B. cockerelli* in an area or the seasonal influx of high numbers of *B. cockerelli* (e.g., List 1939, Romney 1939, Pletsch 1947) or genetic variation (Liu et al. 2006), have been associated with (mass) migration of the insect. In 2014, the migration theory was questioned by Nelson et al. (2014), as observations of overwintering *B. cockerelli* in the northern regions of the insect's native zone in the United States and 'identification of geographically-defined and genetically distinct populations' of *B. cockerelli*, 'suggest a static regional status of at least some populations'. Seasonal migration of *B. cockerelli* has not been observed in New Zealand, where potato crops along the length of the country are infested around the same time of the year and *B. cockerelli* life stages have been observed on non-crop host plants year round, even in areas with frost and snow (J. Vereijssen, unpublished data). Additionally, a 7-m high-suction trap for capturing aphids only very sporadically, approximately once a year, captured one *B. cockerelli*.

*B. cockerelli* (Fig. 8A and B) overwinter as eggs, young nymphs, or adults. The life cycle typically comprises an egg stage, five nymphal stages, and a sexually reproducing adult stage (Hodkinson 2009). Females produce several hundred individually laid oblong-shaped eggs with a basal pedicel, which is inserted in the plant tissue (Hodkinson 1974). Psyllid nymphs are dorso-ventrally flattened insects and mobile in all instars (Ossiannilsson 1992). The different instars can be distinguished by their increasing size and the differentiation of morphological structures. Later instars possess wing buds,





**Fig. 4.** Tomato plants have similar foliar symptoms to potatoes in New Zealand. (A) Leaf curling. (B) Purpling and yellowing discoloration along the edges of the leaves. (C) Premature plant death caused by a severe infestation by *B. cockerelli* and *Ca. L. solanacearum*. (D) Field tomatoes affected by *B. cockerelli* and *Ca. L. solanacearum*. (E) A major concern for tomato growers is the fruit being covered by *B. cockerelli* excretions (psyllid sugars) and the resulting black mold, which requires extra post-harvest cleaning of the fruit for fresh market. Photo B and D by Natasha Agnew, Plant & Food Research.

and the last instar stage usually has a tarsal segment separated from the tibiotarsus. All nymphal stages feed in the phloem and thus produce liquid excreta (commonly referred to as psyllid sugars) which favors fungal infestation and may cause damage to the plant. The fact that all stages feed on the same plant and in the same organ (phloem) makes them effective vectors of plant pathogenic bacteria.

### Psyllid Species Associated With *Ca. L. solanacearum*

Since *Liberibacter* cannot be cultured on artificial medium, Koch's Postulates (Koch 1880) cannot be fulfilled. All vector species are therefore putative from a plant pathology perspective; from an entomological perspective and for the sake of brevity and simplicity of language, we will refer to them as vectors. *B. cockerelli* (Fig. 8A and B) is a native American psyllid species that was first reported in New Zealand in 2006 (Gill 2006). Soon after its introduction to New Zealand, symptomatic tomato and then capsicum plants

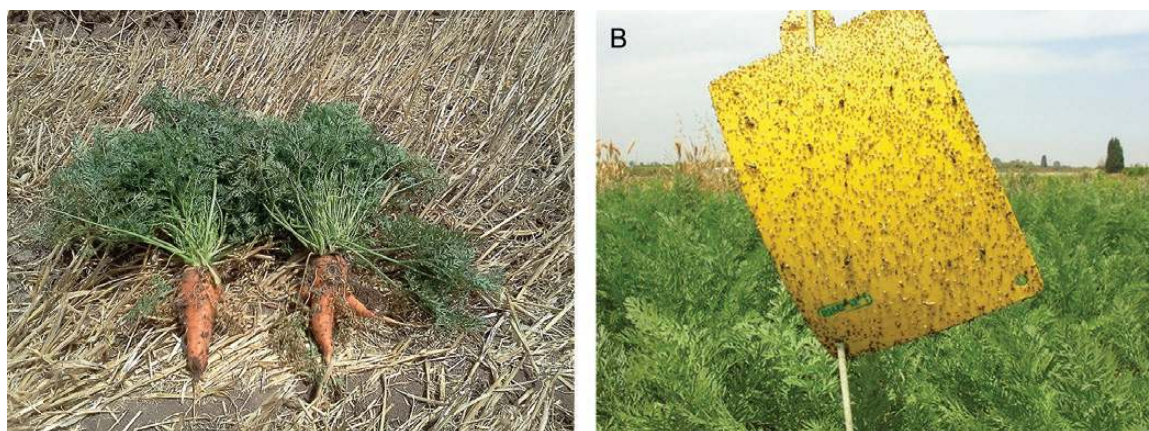
were observed (Liefjting 2009) and 3 mo later diseased potato plants (Liefjting et al. 2008b). Around the same time, *B. cockerelli* was associated with zebra chip disease in potato (Munyanze et al. 2007) and later with *Ca. L. solanacearum* (Secor et al. 2009). In 2013, *B. cockerelli* and the pathogen it vectors were also found on Norfolk Island (AGDA 2015, Thomas et al. 2017), and in February 2017, *B. cockerelli* but not *Ca. L. solanacearum* was found in Perth and surroundings on mainland Australia (DAFWA 2017).

*B. cockerelli* has been shown to complete its life cycle on a number of non-crop species in New Zealand, many of which are Solanaceae as are the affected crop plants. Examples of solanaceous hosts for *B. cockerelli* in New Zealand include: African boxthorn (*Lycium ferocissimum* Miers) (Fig. 9A–C), Chinese boxthorn (*L. barbarum* L.), Poroporo (*Solanum aviculare* G. Forster), Jimsonweed (*D. stramonium* L.), Apple of Peru (*Nicandra physalodes* (L.) Gaertner) (Fig. 10), and Jerusalem cherry (*S. pseudocapsicum* L.) (Martin 2008, Barnes et al. 2015, J. Vereijssen, unpublished data). A species of the genus Convolvulaceae, field bindweed (*Convolvulus*





**Fig. 5.** Foliar symptoms in greenhouse capsicum plants in New Zealand. (A) Leaf curling and chlorosis. (B) Heavily infested capsicum plant covered with excretions (psyllid sugars) by *B. cockerelli* and the resulting black mold. (C) Nymphal stages of *B. cockerelli* on the calyx of the capsicum fruit, therefore, as with tomato fruit, extra post-harvest cleaning of the fruit for fresh market is required.



**Fig. 6.** Carrot plants affected by *Ca. L. solanacearum*, which is transmitted by the psyllid *Bactericera trigonica* in Israel. (A) The roots of a carrot plant infected with *Ca. L. solanacearum* show a proliferation of secondary roots compared to an uninfected plant. (B) Numerous *B. trigonica* trapped on a yellow sticky trap after a week in a carrot field.

*arvensis* L.), was also identified as a host plant for *B. cockerelli* (Barnes et al. 2015, J. Vereijssen, unpublished data). In North America, *B. cockerelli* is known to develop on Solanaceae, Convolvulaceae and one record on Menthaceae (Knowlton and Thomas 1934, Jensen et al. 2012, Murphy et al. 2013, Thinakaran et al. 2015a, Thinakaran et al. 2017). Knowlton and Thomas (1934) included a list of over 30 plant species on which adult psyllids would feed, but which could not sustain nymphal development. This large range of non-crop host-plants may sustain populations when crop plants are unavailable.

### Acquisition, Latent Period, and Inoculation of *Ca. L. solanacearum* in Crop Host Plants

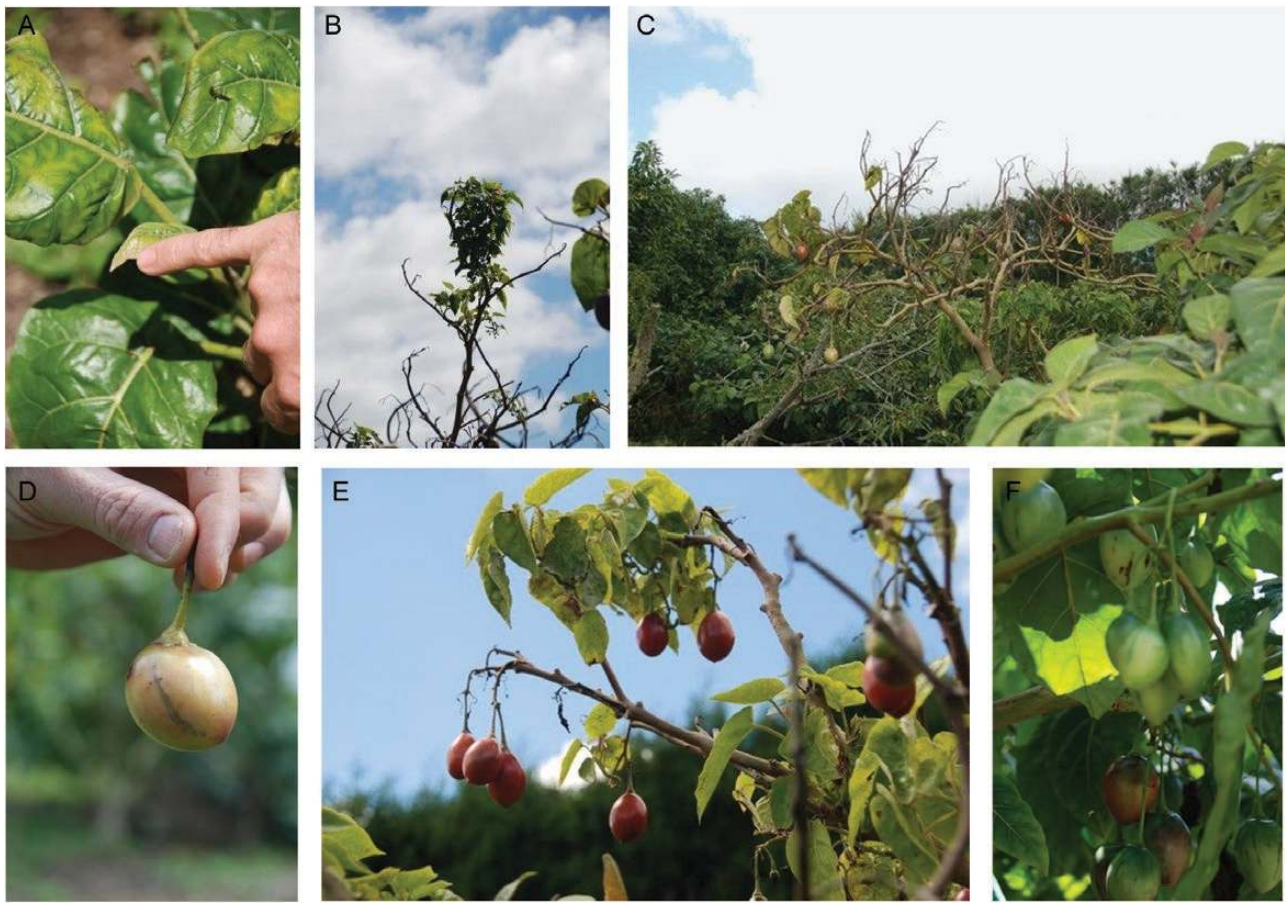
*B. cockerelli* has been found feeding on leaves, petioles and stems of tomato, capsicum and potato plants. Infection of host plants by *Ca. L. solanacearum* is systemic: the bacterium can be found in

above- and below-ground tissue of potato plants, but distribution is uneven (Wen et al. 2009, Levy et al. 2011, Pitman et al. 2011, Beard et al. 2012). Bacterial *in planta* distribution will be further influenced by growth stage of the plant (e.g., pre- or post-tuber setting) and net mass transport direction of the phloem sap. Rashed et al. (2012) did not find significant differences in titer between above-ground potato tissues, but this may have been due to the small sample size in their study.

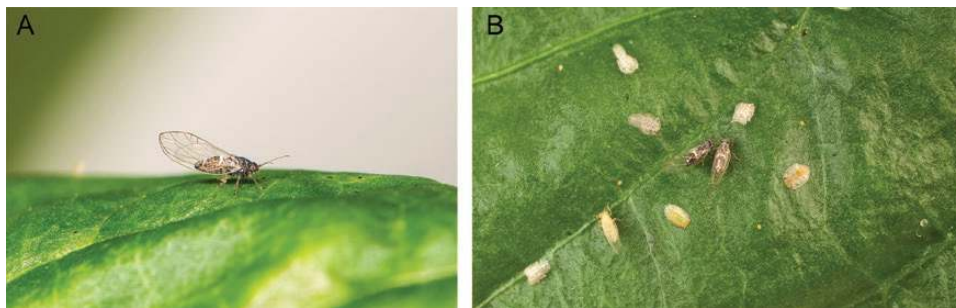
### Latent Period in *B. cockerelli*

The length of time from *Ca. L. solanacearum* acquisition by the psyllid until the time it can be vectored to a new host plant is unclear. A latent period may be essential for the bacterium to translocate from the alimentary canal to the salivary gland of the psyllid before inoculation of a plant by the insect can occur (Cooper et al. 2014). *Ca. L. solanacearum*-free psyllids, presumably all adults, that





**Fig. 7.** Tamarillo trees affected by *B. cockerelli* and *Ca. L. solanacearum* in New Zealand. (A) Leaf pinking. (B) Leaf clustering. (C) A heavily infected tree near death. (D) Off-center, deformed, fruit. (E) Skinny fruit. (F) Healthy fruit in the bottom cluster and infected fruit in the top cluster.



**Fig. 8.** The psyllid *B. cockerelli* is the vector of *Ca. L. solanacearum*. (A) Adult *B. cockerelli*. (B) Late instars of *B. cockerelli* and young (green colored) and mature (dark brown/black) adults, the small yellow dots are eggs. Copyright: The New Zealand Institute for Plant and Food Research Limited. All rights reserved.

acquired *Ca. L. solanacearum* through feeding on infected plants, were then capable of transmitting the pathogen after a 2-wk incubation period, when titers in the insect peaked (Sengoda et al. 2014). A complicating factor is that in their studies they used sweet potato (*Ipomoea batatas* (L.) Lam.) (Convolvulaceae) as a non-host for *Ca. L. solanacearum* to maintain psyllids between experiments; however, Torres et al. (2015) showed that the pathogen can be present in *I. batatas*, which brings into question the experimental protocol and the results of Sengoda et al. (2014). Further, the latent period seems to be variable, depending on the titer of *Ca. L. solanacearum* in the host plant (Sengoda et al. 2013).

### Acquisition Success

Acquisition success (measured as percentage of *B. cockerelli* positive for *Ca. L. solanacearum* after feeding on an infected plant) is influenced by the feeding site on the plant, probably due to the uneven pathogen distribution. The highest acquisition rate of the bacterium was achieved when adult *B. cockerelli* had access to the whole potato plant, followed by stem petiole or leaf tissue only (Rashed et al. 2012). Rashed et al. (2012) also showed that the resulting positive *B. cockerelli* tended to have highest bacterium titers when fed on the whole plant or stem tissue, and that plants with multiple *B. cockerelli* had higher bacterial titer at the point of inoculation





**Fig. 9.** African boxthorn (*Lyrium ferocissimum*) was used in New Zealand as a hedging plant and occurs in many coastal areas. (A) A hedge of mixed pine and African boxthorn adjacent to a potato field. (B) A *B. cockerelli* adult and eggs on African boxthorn. (C) Nymphs of *B. cockerelli* and psyllid sugars on African boxthorn.



**Fig. 10.** Life stages of *B. cockerelli* have also been found on Apple of Peru (*Nicandra physalodes*) in New Zealand.

than plants with only one psyllid (Table 4). The minimum time for an adult *B. cockerelli* to acquire *Ca. L. solanacearum* from a host plant (minimum acquisition access period) was about 36 min, with only 7 min of phloem ingestion (Sandanyaka et al. 2014).

#### Titer of *Ca. L. solanacearum* in *B. cockerelli*

Casteel et al. (2012) showed that the bacterial titer increased with increasing developmental stage of the *B. cockerelli*. Titer of *Ca. L. solanacearum* increased over time in psyllids with increasing acquisition access periods and also depended on host plant, where titers were higher when the pathogen was acquired from tomato instead of potato (Sengoda et al. 2013).

#### Inoculation Success

Inoculation success is measured as the percentage of plants positive for *Ca. L. solanacearum* after feeding of infected *B. cockerelli* on that plant. One adult *B. cockerelli* was capable of inoculating a single potato plant within 6 h (Buchman et al. 2011). However, this was the shortest inoculation access period (IAP) they tested for an individual *B. cockerelli*, so the minimum and average inoculation times are currently unknown (Table 4). Butler et al. (2011) showed that 10 *Ca. L. solanacearum*-positive *B. cockerelli* could inoculate a potato leaf within 24 h. However, 2 wk after inoculation, only 56% of the potato leaves tested positive for the bacterium using quantitative polymerase chain reaction (qPCR). More recently, Mustafa et al. (2015) using electrical penetration graph (EPG) technology, showed that the probability of transmitting *Ca. L. solanacearum* increased with feeding time; but even after long feeding periods, some psyllids still did not transmit the bacterium. Sandanyaka et al (2014) showed in inoculation assays using EPG that the durations of salivation into the phloem sieve elements and phloem ingestion recorded from *B. cockerelli* on *Ca. L. solanacearum*-positive and -negative tomato plants were not significantly different. Similarly for *Ca. L. solanacearum*-positive and negative adults, there was no statistical difference between durations of EPG parameters measured (Sandanyaka et al. 2014).

Inoculation success can be mediated by the temperature at which pathogen transmission occurs in at least four ways, by affecting: 1) pathogen multiplication in source hosts, 2) pathogen multiplication within vectors (i.e., vector latent period), 3) the establishment of infection in the host (i.e., minimum infective dose), or 4) vector behavior (e.g., feeding rate, probing behavior, or movement) (Daugherty et al. 2009). In *B. cockerelli*, potato plants inoculated

by *Ca. L. solanacearum*-positive adults developed foliar symptoms and leaves tested positive for the bacterium using PCR at all tested daily temperature regimes (12 to 17°C, 25 to 30°C, and 33 to 37°C) (Munyaneza et al. 2012a). However, one hundred percent inoculation success was achieved at the 12 to 17°C and 25 to 30°C regimes and only 30% at the 33 to 37°C regime (Munyaneza et al. 2012a), indicating inoculation success of potato plants with *Ca. L. solanacearum* is temperature dependent. Temperatures as low as 17°C have been reported to slow growth of the bacterium, as have temperatures over 32°C (in: Lin and Gudmestad 2013), whereas 7.1°C was indicated as the overall lower development threshold for *B. cockerelli* (Tran et al. 2012). However, this development temperature threshold is different for the different psyllid life stages (Pletsch 1947, Henne et al. 2010, Tran et al. 2012, Whipple et al. 2012, Lewis et al. 2015), and psyllid life stages were present throughout winter in Canterbury, New Zealand (J. Vereijssen, unpublished data).

### From Inoculation to Disease Symptoms

*B. cockerelli* adults and nymphs can both transmit *Ca. L. solanacearum* to a plant. Once a plant has been inoculated with the pathogen, it takes time for the foliar and/or tuber disease symptoms to develop. For this section, it must be noted that most acquisition and inoculation studies are conducted using laboratory-reared *Ca. L. solanacearum*-positive adults, where (close to) 100% of the adults were positive for the bacterium. This may not reflect what is happening in field populations, e.g., adults taken from a natural psyllid population showed 'decreased ability' to inoculate a potato plant with *Ca. L. solanacearum* compared with adults from colonies (Munyaneza et al. 2008). The New Zealand experience is that within a field population of psyllids, not all adults carry the bacterium (I. A. W. Scott, personal communication), and that titers in infected adults can vary greatly (A. R. Pitman, personal communication). Nevertheless, the majority of populations tested continue to show very low levels of incidence and titer over the season. It is unclear whether this is an artifact of an insecticide sprayed landscape, where even competitive fitness might come into play. However, given these factors, it is likely that transmission rates are also highly variable under field conditions.

Exposure of a single potato plant, at tuber-initiation stage, to 20 *B. cockerelli* adults for a period of 1 h resulted in zebra chip disease symptoms in the tubers 75–90 d after inoculation in a laboratory experiment (Buchman et al. 2011). Buchman and colleagues (2011) also found that nymphs alone were less effective at inducing zebra chip disease in potato tubers than adults alone.

Disease symptoms following inoculation with *Ca. L. solanacearum* start to become visible in potato foliage and tubers 3–5 wk after inoculation (J. Vereijssen, unpublished data). Alvarado et al. (2012) concluded from their experiments that bacterial titer in the *B. cockerelli* population directly affected the rate of disease development in potato plants, in contrast to Rashed et al. (2012) who found that neither the titer of *Ca. L. solanacearum* at point of inoculation, nor the number of adult *B. cockerelli* per plant, had a significant effect on the rapidity of disease development measured by symptom expression. However, onset of disease symptoms was generally earlier when four adult *B. cockerelli* had access to a plant instead of one.

Determining the titer and distribution of *Ca. L. solanacearum* in a plant during the latency period is an area that needs further research to understand the epidemiology of this disease.

### Location of *Ca. L. solanacearum* in *B. cockerelli*

When a psyllid begins feeding on a plant, it constantly probes the plant tissue to determine if it has reached the phloem cells.

To accomplish this, a small amount of saliva is constantly ejected and then imbibed until the phloem is attained. As the psyllid feeds on the phloem of an infected plant, the bacteria are acquired along with the plant sap; however, the movement of the bacteria within the insect has not been fully elucidated. The results by Sengoda et al. (2014) suggest that acquisition and transmission of *Ca. L. solanacearum* by psyllids follows a pattern consistent with a propagative, circulative, and persistent mode of transmission.

Using fluorescence in situ hybridization, Cooper et al. (2014) used 7-d-old mature adults and fifth instar *B. cockerelli* from *Ca. L. solanacearum*-infected potato plants and non-infected tomato plants. The bacterium was observed in the alimentary canal, hemolymph, salivary glands and the bacteriomes of nymph and adult psyllids; there was no difference in infection rates between adult males and females. For both stages, bacterial fluorescence was more intense in the alimentary canal than in other organs. Infection of the salivary glands differed between nymphs and adults; 40% of the adults show positive fluorescence for *Ca. L. solanacearum* whereas only 10% of the nymphs fluoresced. Additionally, the bacterium was detected in the psyllids' excrement.

When studying the bacterium in *Ca. L. solanacearum*-positive *B. cockerelli* on tomato plants, Cicero et al. (2016) found there were two morpho-types of the bacterium present in the psyllid: 1) A rod-shaped type of variable length with a rough, granular cytosol which formed a biofilm with presence in the gut, salivary glands and oral region tissues and 2) one which possessed pili- and flagella-like appendages, found in midgut tissue. The *Ca. L. solanacearum* genome contains genes for producing both morpho-types (Lin et al. 2011). Pili are involved in adhesion leading to colonization and biofilm formation (Kline et al. 2010), whereas the flagella are generally used for motility (Thormann and Paulick 2010) but it is unknown whether both structures are found in the insect, as found by Cicero et al. (2016), and plant host.

### Effect of *Ca. L. solanacearum* on *B. cockerelli*

All the studies noted below used colony-reared *B. cockerelli* and thus it is difficult to tease out the host plant effect from that of *Ca. L. solanacearum*. Overall, the bacterium seems to have a detrimental effect not only on the host plant but also on the insect vector in regards to important life history parameters. Nachappa et al. (2014) showed in their study that higher titers of *Ca. L. solanacearum* in the psyllid have a more pronounced effect on the biological parameters assayed. In initial studies using laboratory colonies of *B. cockerelli*, *Ca. L. solanacearum* was shown to negatively affect 7-d fecundity and nymphal survival percentages of *B. cockerelli* (Nachappa et al. 2012). Unfortunately, the authors did not specify the titers of the bacterium in these laboratory reared *B. cockerelli* that were kept on tomato. In a later study, Nachappa et al. (2014) did measure these titers in the insects from their 2012 studies. For negative versus positive *B. cockerelli*, infection levels of *Ca. L. solanacearum* in founders or mothers was negatively correlated with 7-d fecundity, nymph survival percentage, and number of first filial generation ( $F_1$ ) progeny including eggs, nymphs and adults. Overall, females experienced decreasing levels in fecundity with increasing titer. These researchers concluded from both sets of experiments that the negative effect of the pathogen was directly on the psyllid and not mediated through the plant. Alvarado et al. (2012) observed a slight delay in development in infected laboratory-based populations of *B. cockerelli* compared with insects in bacterium-free colonies. In New Zealand, *Ca. L. solanacearum*-positive colonies of *B. cockerelli* have been kept on tomato plants at two locations for 9 yr and fecund offspring are still



being produced, despite a sub-sample of adults, tested on a monthly basis, all containing very high titer of the bacterium. However, we cannot deduce the effect of the pathogen as the negative colonies are maintained on a different host plant. In view of the information above, we propose that *Ca. L. solanacearum* is a plant pathogen that can have a negative effect on psyllid fecundity under certain conditions.

### Vertical Transmission of *Ca. L. solanacearum*

Vertical or transovarial transmission in insects is defined as the transfer of pathogens to succeeding generations through invasion of the ovary and infection of the eggs. The first report of transovarial transmission of *Ca. L. solanacearum* in *B. cockerelli* was by Hansen et al. (2008). Later, Casteel et al. (2012) found that transovarial transmission of the bacterium for all six tested isofemale lines ranged from about 47–88%. However, in both studies, the females' oviposition sites were not separated from their feeding sites; infected females feeding on a host plant could have led to infection of the eggs with the bacterium even when eggs were transferred to uninfected plant material, as demonstrated by Van den Berg et al. (1992) for the psyllid *Trioza erytreae* (Del Guercio). The results reported by Hansen et al. (2008) and Casteel et al. (2012) need careful consideration as it has long been known that the egg stalk or 'pedicel' of psyllid species is inserted into plant tissue and serves as both an anchor for the egg and conduit for water uptake from the plant (White 1968). Thus the option for *Ca. L. solanacearum* to infect an uninfected *B. cockerelli* egg via transport with solutes in the pedicel needs to be further investigated.

### Host Plant Choice

Numerous insect vectors, including aphids, thrips, whiteflies, and leafhoppers that transmit plant viruses or pathogenic bacteria and fungi, are more attracted to plants infected with a pathogen (Mauck et al. 2010, Casteel et al. 2012, Mauck et al. 2012, McMenemy et al. 2012). The pathogen may change the plant to be visually more attractive (Fereses et al. 1999, Marucci et al. 2005) or to emit volatiles to attract uninfected potential vector species (Mayer et al. 2008, Orlovskis et al. 2015).

Potato (Davis et al. 2012) and tomato (Mas et al. 2014) plants infected with *Ca. L. solanacearum* have an altered volatile emission. Davis et al. (2012) found that *B. cockerelli* first landed and fed on the bacterium-infected plant and then moved to a non-infected plant. Davis et al. (2012) found no evidence that plants infected with the pathogen diminished *B. cockerelli* population growth or egg production, but flowering by potato plants (both *Ca. L. solanacearum*-positive and negative plants) was correlated with a decrease in adult psyllid performance. Mas et al. (2014) found that the infection status of the psyllids affected plant choice; *Ca. L. solanacearum*-positive *B. cockerelli* preferentially landed more on tomato plants without the bacterium and vice versa. The induced behavioral change in *B. cockerelli* promotes *Ca. L. solanacearum* acquisition and transmission.

### Psyllid and Pathogen Management

Understanding the insect (vector)-pathogen transmission mechanism is a key component of any insect management strategy to limit or manage horizontal, or vector-mediated, transmission of a pathogen into a crop (e.g., Fry 1983, Weintraub 2012). Management often requires a multipronged approach in which several pathways (vector

and plant host; pathogen and plant host) are interrupted (e.g., Hilje et al. 2001, Almeida et al. 2005, Jones et al. 2010). Currently for the *B. cockerelli*/*Ca. L. solanacearum* system, this understanding is limited, in part by the contradictory and conflicting experimental data and conclusions between countries, and in part because of different diagnostic assays and the different concepts and definitions of 'transmission' being applied.

### Distribution of *B. cockerelli* in Crops and Pathogen Reservoir Plants

Scientists in New Zealand (Walker et al. 2013) and the United States (Anonymous 2009, Butler and Trumble 2010) reported that at the beginning of the season, *B. cockerelli* were more abundant on plants at field edges and from there were readily able to colonize the nearby field. However, in two other studies in the South Island of New Zealand (Horne et al. 2012; J. Vereijssen, unpublished data) these results were not substantiated. In these trials, transects of yellow sticky traps from the edge to the middle of potato fields, established shortly after potato emergence, did not always first trap *B. cockerelli* at the field margin before in the middle of the crop. The less apparent edge effect in some New Zealand potato crops compared with those in their U.S. equivalents may be due to differences in monitoring (trapping vs. scouting), field size or crop margin management. Crop paddocks in New Zealand commonly have grassy or weedy margins and verges (Fig. 11), and sometimes dense shelterbelts consisting of mixed trees and shrubs. The benefits of these unmanaged field margins regarding the provision of habitat for beneficial insect species (predators and/or parasitoids) is widely published (Landis et al. 2000, Bokenstrand et al. 2004). Therefore, the presence of natural enemies of *B. cockerelli* at New Zealand potato crop margins could be responsible for the less apparent edge effect. In contrast, the ground bordering arable crops in the United States is often herbicide-treated bare earth (Stachler 2012), a much less hospitable environment for beneficial insects, suggesting the crop may provide the first landing place for *B. cockerelli*. However, in both New Zealand and the United States, foliar symptoms as a result of infection with *Ca. L. solanacearum* in both United States and New Zealand potato fields have been found to mostly be more intense along the edges of a potato field than infield (Workneh et al. 2012; J. Vereijssen, unpublished data).



Fig. 11. Potato crops in New Zealand are generally surrounded by weeds, many of them nightshades in this picture.

Within the potato field, symptomatic foliage loci did not develop in a spatially random pattern, but in clusters, with symptomatic plants situated in close proximity to each other (Henne et al. 2012). Analysis of these United States data from contiguous 10 × 10 m quadrats suggested primarily secondary spread of the pathogen from an initial point of infection (Henne et al. 2012). This matches observations in New Zealand potato crops, where on a few individual potato plants an adult could be found first, and subsequently that plant would have several eggs and nymphs on it. It appears that a few adult females can land in a crop and start aggregated clusters of populations. Indeed, field studies in New Zealand have putatively show that *B. cockerelli* does not migrate *en masse* from one host plant to the other in spring or autumn, but spreads more by individual psyllids landing ‘by accident’ on a crop host plant from a non-crop host plant (J. Vereijssen, unpublished data). If this is the mechanism of insect dispersal, then in some cases control of weeds that are *B. cockerelli* host plants might contribute to management of *B. cockerelli* and *Ca. L. solanacearum*. As noted in the section ‘Symptoms of *Ca. L. solanacearum* in Plants’ non-crop hosts have been shown to harbor the bacterium. Weed control could thus decrease pathogen reservoirs, decrease overwintering places for the vector, and perhaps also decrease vector populations and prevent vector movement.

## Designing Management Strategies

Various management strategies can be used, encompassing the principal components of integrated pest management; cultural, biological, and chemical control. A cultural method that underpins effective strategies is through the use of clean, certified pathogen-free or pathogen-resistant seed or plant material. Additionally, planting in an area free of diseased plants, including non-crop alternative hosts, as part of an appropriate crop rotation schedule can also contribute to effective management. Cultural methods to prevent pathogen acquisition or inoculation by the vector, such as physical barriers discussed below, can also contribute to managing disease epidemiology.

Biological control by natural enemies in a crop can contribute to natural pest suppression. Natural enemies of *B. cockerelli* have been found in sprayed and unsprayed potato crops in New Zealand and have been attributed to contribute to limiting psyllid populations below damaging levels in early summer in some regions (MacDonald et al. 2010). However, such natural pest suppression can be disrupted by the use of chemical insecticides, and is unlikely to have been exploited to its full potential for reasons outlined below.

The final option, if all previous strategies fall short and psyllid numbers reach unacceptable levels, is chemical control (i.e., insecticide applications). Unfortunately, this is often the first control option that growers use (Perring et al. 1999) and can lead to environmental consequences and, in a worst-case scenario, to insecticide resistance, not only in *B. cockerelli* but also in other (pest) insects in a crop. There are alternatives to conventional synthetic insecticides and these include those described as biorational insecticides. However, uptake of such alternatives is slow, as discussed below.

### Cultural Strategies—Physical Barriers

In New Zealand, there are limited management options for organic potato growers. Consequently, studies have been undertaken to evaluate the use of a mesh cover as a mechanical barrier for *B. cockerelli* (Merfield et al. 2015a, Merfield et al. 2015b). The authors found that mesh covers reduced numbers of *B. cockerelli* nymphs and adults, increased tuber size, increased overall yield, enhanced storage

potential compared with uncovered plots, and slightly reduced number of potato early blight spores. In more recent research with mesh, Merfield (2017a) confirmed findings by Vereijssen (unpublished data) that showed severe aphid infestations under the mesh covers, resulting in premature senescence of the crop. One solution to managing aphid infestations under mesh may be to not dig in the mesh at all sides, thus allowing predators under the mesh during the growing season; an observation recorded when mesh was used on a commercial organic potato crop (N. M. Agnew, personal communication). Using mesh with a smaller pore size to prevent aphid nymphs crawling through the pores gave contradicting results in two consecutive years and needs more research (Merfield 2017b).

### Biological Control

Biological control can make a substantial contribution to overall management of the insect vector, but since there is often a time delay in mortality, transmission of the plant pathogen is likely to have occurred before the nymph or adult-stage vector has been killed or immobilized. The use of insecticides that are relatively innocuous to beneficial insects can assist in keeping the existing guild of natural enemies intact and enable natural enemies to contribute to the overall strategy for vector control.

There have been a number of natural enemies reported for *B. cockerelli*, but many of these reports are from greenhouse or laboratory studies where the chance of success is greater than in the field. For example, *Chrysoperla carnea* Stephens and *C. rufilabris* (Burmeister) (Neuroptera: Chrysopidae) were reported as biological control agents (BCAs) of *B. cockerelli* in greenhouse tomatoes in the United States, but one release of *C. carnea* eggs in a potato field trial did not reduce psyllid populations (Al-Jabr 1999).

The ectoparasitoid *Tamarixia triozae* (Burks) (Hymenoptera: Eulophidae) is a native parasitoid in some areas in the United States and in Mexico (Pletsch 1947, Butler and Trumble 2010) and can achieve high levels of parasitism of *B. cockerelli* nymphs in the absence of insecticides in tomato and potato (Rojas et al. 2015). The successful use of *T. triozae* in integrated pest management programs varies, depending on the insecticide and the time after application (Luna-Cruz et al. 2015, Martinez et al. 2015). Another parasitoid, *Metaphycus psyllidis* Compere (Hymenoptera: Encyrtidae), was described from *B. cockerelli* on capsicum in Southern California (Compere 1943). However, this insect, was only again noted in 2012 from capsicum in California with a very low parasitism rate (Butler and Trumble 2012). In New Zealand, *T. triozae* has been approved for release from containment (EPA 2016) and first releases were made in August 2017 in Hawke’s Bay and Canterbury (Barnes 2017).

Key natural enemies of *B. cockerelli* observed in southern California potatoes, tomatoes, and capsicum were: *Orius tristicolor* (White) (Hemiptera: Anthocoridae), *Geocoris pallens* Stål (Hemiptera: Geocoridae), and *Hippodamia convergens* Guérin-Méneville (Coleoptera: Coccinellidae) (Butler and Trumble 2012). In no-choice laboratory feeding assays, all these predators attacked all life stages of *B. cockerelli*, but that predation by coccinellids (*H. convergens*, *Coccinella septempunctata* (L.)) (Coleoptera: Coccinellidae) and *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) led to the highest mortality across all life stages of *B. cockerelli* (Butler and Trumble 2012).

New Zealand has naturally occurring native and exotic predators of *B. cockerelli*, including *Micromus tasmaniae* (Walker) (Neuroptera: Hemerobiidae), *Melanostoma fasciatum* (Macquart) (Diptera: Syrphidae), *C. undecimpunctata* and sheet web spiders (Linyphiidae) (MacDonald et al. 2010), which reside in potato crops



in varying degrees and are known to predate either on some to all *B. cockerelli* life stages in no-choice laboratory assays (MacDonald et al. 2016). In choice assays, these authors found that all predators, in all the predator life stages tested, consumed *B. cockerelli*, but that generally aphids were preferred. Field experiments showed seasonal differences in abundance of predators, with greatest abundance in spring and early summer (Walker et al. 2011a, Walker et al. 2012).

Another biological control option for *B. cockerelli* is the use of entomopathogenic fungi. Temperature and relative humidity affect germination, infection and survival of entomopathogens (Inglis et al. 2001), restricting their effectiveness and use (Magan 2001). In New Zealand, fungal isolates of *Lecanicillium muscarium* (Petch) Zare & W. Gams (Hypocreales: Cordycipitaceae) and *Isaria fumosorosea* (Wize) (Hypocreales: Clavicipitaceae), and commercially available formulations of *Beauveria bassiana* Balsamo-Crivelli (Vuillemin) (Hypocreales: Clavicipitaceae), *I. fumosorosea*, and *Metarhizium anisopliae* (Metchnikoff) Sorokin (Hypocreales: Clavicipitaceae), were successfully tested against nymphs of *B. cockerelli* in laboratory assays and adults and nymphs in greenhouse assays, outperforming a conventional spiromesifen insecticide (Mauchline and Stannard 2013). The same fungi, except *L. muscarium*, gave similar results on *B. cockerelli* nymphs and adults when tested on potato leaves under ideal conditions in the United States (Lacey et al. 2009). In potato field trials, *M. anisopliae* and *I. fumosorosea* were tested and significantly reduced *B. cockerelli* nymphs, foliar damage (psyllid yellows) and zebra chip disease symptoms (Lacey et al. 2011).

Although the above biological control options are all working individually, not all combinations of biological control were successful. For example, Tamayo-Mejía et al. (2015) found that although the parasitism rate by *T. triozae* of control and fungus-treated nymphs of *B. cockerelli* was similar, parasitoid survival was reduced after surveying or attacking fungus-infected nymphs.

### Synthetic Insecticides

For conventional growers, synthetic insecticides are the first option to manage *B. cockerelli*. The majority of synthetic insecticides, however, are not fast enough to kill the primary vectors, those that initially enter a field. Secondary vector numbers may be reduced by insecticide application and thus reduce, although not prevent, secondary pathogen transmission. In this situation the secondary vectors (offspring of the primary vectors) will colonize the natal plants and those adjacent and are less likely to move much beyond these plants (see 'Distribution of psyllids in crops and pathogen reservoir plants').

Currently, a large number of insecticides with different modes of action are applied to manage psyllids and include systemic, contact, and barrier materials. Grower surveys show that many are using a wide range of insecticides; in 2009, 16 different insecticides were used across three south central U.S. states (Guenther et al. 2012) and 11 active ingredients were registered in New Zealand in October 2014 (Potatoes New Zealand 2014).

The most commonly used systemic insecticides are neonicotinoids applied at planting for early protection, and also foliar sprays applied in mid-season. The two most common neonicotinoids are imidacloprid and thiamethoxam, applied to soil or to seed tubers. Application methods unfortunately are not clearly defined, as the amount of irrigation water used can influence efficacy of both pesticides (Byrne and Toscano 2006, Knoepp et al. 2012, Prager et al. 2013b). In western and south central United States, 40–90% of potato fields were treated with imidacloprid, whereas fewer fields were treated with thiamethoxam (Prager et al. 2013b and references therein). In New Zealand, both active ingredients are used in potato

crops as well. Reduced susceptibility to imidacloprid has been found in Californian populations of *B. cockerelli* in capsicum (Liu and Trumble 2007), as well as in Texan populations on potato (Prager et al. 2013b). In addition to killing psyllids directly, observations of altered cleaning, resting and walking behavior of psyllids fed on imidacloprid-treated plants have been observed (Butler et al. 2011). Evidence of reduced probing and feeding behaviors have been borne out by EPG studies of *B. cockerelli* (Butler et al. 2012).

A survey of 53 commercial potato fields in three states in the south central United States revealed that the most commonly used insecticides were imidacloprid and spirotetramat (Guenther et al. 2012). Although spirotetramat is a relatively new systemic tetracic acid insecticide which is applied as a foliar spray (Brück et al. 2009), it has already been successfully incorporated into management protocols. In New Zealand laboratory trials, direct sprays of spirotetramat have been shown to control *B. cockerelli* nymphs effectively within a 7-d period on capsicum leaf discs (Berry et al. 2009) and over a 6-wk period on capsicum plants (Page-Weir et al. 2011). In laboratory studies on potatoes, residues of spirotetramat also reduced egg laying by *B. cockerelli* for up to 7 days after treatment (DAT); however, it had no significant effect on adult mortality at 1, 7, or 14 DAT (Gardner-Gee et al. 2012) but a very slight reduced transmission of *Ca. L. solanacearum* was observed 1 DAT (Barnes et al. 2014). Cyantraniliprole is another relatively new systemic insecticide that affects ryanodine receptors (Selby et al. 2013), which are critical to muscle function. In laboratory trials on potatoes in New Zealand, residues of cyantraniliprole reduced egg laying of *B. cockerelli* on 1 and 14 DAT and increased adult mortality on 1 and 14 DAT (Gardner-Gee et al. 2012). No reduction in transmission of *Ca. L. solanacearum* was observed 1, 3, and 7 DAT (Barnes et al. 2014), however, this may be due to the xylem-mobile activity of cyantraniliprole (Selby et al. 2013, Barry et al. 2015). Although, chemical insecticides play a vital role in pest management of insects, they have caused land, air and water contamination, and have been responsible for insect resistance as well as adverse impacts on natural enemies and humans (Bernardes et al. 2015). New ways to manage insect pests, especially vectors of plant pathogens, need to be developed.

### Alternative Chemicals to Broad-Spectrum Insecticides

Intensive use of broad-spectrum insecticides often disrupts pest suppression by natural enemies, and can result in insecticide resistance, environmental contamination and sometimes causes secondary pest outbreaks. As a result, a need for alternative pest control tactics has developed. Although these products are referred to as benign to natural enemies, they can still affect natural enemies or BCAs and are thus relatively less innocuous (e.g., Biondi et al. 2012, Ndadikemi et al. 2016, Gardner-Gee et al. 2013).

Kaolin, a low-abrasive, fine-grained aluminosilicate mineral, applied as a particle film, is a new version of a very old type of inorganic chemical control (Sharma et al. 2015). These clay-type materials act by masking the plant physically and changing its spectral profile (affecting feeding, egg laying, etc.), reducing virus transmission by insect vectors, and coating or being ingested by the insect, causing irritation (Sharma et al. 2015). The use of kaolin may be limited in areas or crops where the film may be washed off by frequent or heavy rainfall or overhead irrigation. Also, there are concerns that the kaolin film on the plant could disrupt the occurrence of other insects such as natural enemies (Peng et al. 2011).

Kaolin has been shown to repel adult *B. cockerelli*, reduce egg laying, and reduce nymphs on treated field-grown tomato (Peng et al. 2011)

and laboratory-grown potato plants (Prager et al. 2013a). Also, decreased tasting (tapping the mouthparts on the leaf surface sporadically), and probing/feeding were observed on potato plants in laboratory studies at different times after application (Liu and Trumble 2004, Butler et al. 2011), but there was no decrease in incidence of *Ca. L. solanacearum*-infected plants compared with a control treatment (Butler et al. 2011). In a potato field trial in New Zealand, kaolin clay was not effective in controlling populations of *B. cockerelli* or reducing zebra chip disease compared with a control treatment (Wright et al. 2013b). While kaolin does not produce effective control on its own, it may under certain circumstances be a useful alternative to more broad-spectrum insecticides within an integrated pest management strategy.

Mineral or horticultural oils applied as foliar sprays are a low-technology form of insecticide which, like kaolin, create a physical barrier on the plant and are particularly effective at interfering with aphid feeding, especially those transmitting non-persistent viruses (e.g., Simons and Zitter 1980, Boiteau et al. 2009, Boquel et al. 2013). While this has proven effective in temperate climates, mineral oil photo-degrades under ultraviolet light (Hodgkinson et al. 2002, Al-Mrabeh et al. 2010). Mineral, vegetable, and botanical oils for use against *B. cockerelli* in New Zealand were reviewed by Berry and Bourhill (2012) and their findings informed further trials. A laboratory study on potato in New Zealand showed that mineral oils were highly repellent to adult *B. cockerelli*, and a direct spray on nymphs resulted in high mortality (Jorgensen et al. 2013) and (slightly) reduced transmission of *Ca. L. solanacearum* (Barnes et al. 2014). Mortality of late-stage nymphs was also observed after a direct spray of mineral oils in a laboratory study on capsicum (Walker et al. 2010).

Another source of alternative chemicals includes plant essential oils, often extracted from aromatic herbaceous plants. These have been tested for their repellency effect on psyllids. These essential oils are attractive because they are often used in the food industry and are considered environmentally safe or 'green'. In Y-tube olfactometer studies, volatiles from peppermint (*Mentha* spp. L.), savory (*Satureja* spp. L.), clove (*Syzygium aromaticum* (L.) Merr. & L. M. Perry), thyme (*Thymus* spp. L.) and teatree (*Leptospermum* spp. J. R. Forst. & G. Forst.) oils significantly repelled adult *B. cockerelli* over a wide range of doses and remained effective for up to 20 d after application (Diaz-Montano and Trumble 2013). In no-choice laboratory trials in New Zealand, Walker et al. (2011b) showed that cedarwood, cinnamon, wintergreen, rosemary, patchouli, D-limonene and neem oils significantly deterred oviposition on capsicum leaves, and neem and patchouli also showed significant repellency to female *B. cockerelli* adults up to 48 h after applying the treatment. Wright et al. (2013a) showed garlic oil significantly reduced *B. cockerelli* nymph populations in a potato field trial in New Zealand. Ethanol extracts of dried leaves of *Ambrosia artemisiifolia* L. led to over 50% mortality in second-, third-, and fifth-stage *B. cockerelli* nymphs in lab-based experiments on tomato leaves (Granados-Echegoyen et al. 2015).

In addition to essential oils, Wright et al. (2013b) also tested dimethyl disulfide (DMDS), which is used in commercial pheromone and lure technology, but did not find it controlled populations of *B. cockerelli* or decreased zebra chip disease in a potato field trial. In contrast, applications of only DMDS (in SPLAT technology, ISCA Technologies, Riverside, CA) proved significantly effective in masking both potato and tomato leaf odors and repelling adult *B. cockerelli* in a Y-tube olfactometer assay (Diaz-Montano and Trumble 2013).

## Future Directions

*Ca. L. solanacearum* is transmitted by a mobile vector and there are numerous species of host plants to serve as reservoirs for both the

bacteria and the vector; hence, management strategies to date have not been satisfactory. Since the vector is mobile and hard to reach with sprays, changes can be made to the stationary and accessible plant hosts to synthesize various molecules to adversely affect either pathogen development in the plant or in the insect.

One such method may be the utilization of *in planta* RNA interference (RNAi), where insects can suffer high mortality when feeding on plants producing RNAi constructs targeting essential insect genes. To induce RNAi effects towards phloem feeders like psyllids, effector RNAs must be available for phloem transport, and then acquired by and induce effects on recipient insects (Wuriyangan and Falk 2013, Zotti et al. 2017). By interfering with RNA, e.g., silencing specific genes, the transmission of the bacterium can be affected, or the vector can be killed immediately (Burand and Hunter 2013, Kanakala and Ghanim 2016). Whitten et al. (2016) were successful in overcoming the problems with double-stranded (ds) RNA delivery, which had restricted reverse genetic studies and the development of RNAi-based biocides, by giving insect symbiotic bacteria the task of synthesizing constitutive dsRNA and delivering it to the insect. In *B. cockerelli*, insects feeding on plants with RNAi against the target osmoregulatory genes led to significantly increased mortality (Tzin et al. 2015). However, in New Zealand this technology is considered genetic modification which is not yet accepted in this country. Additionally, there are also still unanswered questions regarding environmental and resistance issues (Zhang et al. 2017).

Resistant or tolerant potato cultivars are a further promising future management option (Fig. 12). Although much work has already been invested in this area, no resistant or tolerant varieties are commercially available yet. However, promising results are being obtained in New Zealand (J. Anderson, personal communication), the United States (Rashidi et al. 2017), and Mexico (Rubio-Covarrubias et al. 2015, Rubio-Covarrubias et al. 2017).

There are some other areas for future management, but these are in early stages of development, e.g., using a bacteriophage against *Ca. L. solanacearum* or preventing communication between bacteria thus interrupting colonization of a plant. Also, bacterial symbionts serve numerous functions in insects from providing essential amino acids to causing sexual incompatibility, and play a pivotal role in insect-plant interactions (Frago et al. 2012, Giron et al. 2017). Since *Ca. L. solanacearum* has been observed in bacteriomes in *B. cockerelli*, there is an opportunity to manipulate this interaction and affect the health and well-being of *B. cockerelli* or their ability to transmit the bacterium.



Fig. 12. Potato plants grown from mother tubers infected with *Ca. L. solanacearum*: cultivar 'Moonlight' in the middle sided by cultivar 'Agrida'.



**Table 4.** *Ca. L. solanacearum* transmission values from the literature (empty cells indicate no information available)

Reference	Acquisition	Latency	Infectivity	Inoculation	Viruliferous progeny
Buchman et al. (2011)				One adult inoculates in 6 h (or less as this was the shortest time tested,); 20 adult inoculate within 1 h; nymphs less effective than adults	
Sandanayaka et al. (2014)	Adult: minimum acquisition access period was 36.6 min with 6.9 min phloem ingestion			Adult: minimum inoculation access period 2 h	
Sandanayaka et al. (2013)		Post-acquisition period for successful detection: 24–48 h			
Hansen et al. (2008)					Transovarial transmission of <i>Ca. L. solanacearum</i> , but did not separate female feeding from oviposition site
Rashed et al. (2012)	Influenced by feeding site on potato host			Adult: less than 24 h (this was the IAP time used and resulted in <i>Ca. L. solanacearum</i> -positive plants)	
Sengoda et al. (2014)		Potato: 2 wk after an 8- to 24-h acquisition period. This is shorter on tomato			
Author's observations			<i>Ca. L. solanacearum</i> -positive adults on cold tomato plants in the rearing stayed positive for many years	10 adult on clean potato for 24 h results in <i>Ca. L. solanacearum</i> symptoms	

## Conclusion

Understanding vector–pathogen–plant host interactions is a critical step towards effective vector management. Potatoes and outdoor tomatoes had an effective integrated pest management program in New Zealand before the arrival of the psyllid. The main aim of *B. cockerelli* / *Ca. L. solanacearum* research is to find management measures that can be integrated into that system. Components of the system could include careful timing of insecticide applications, incorporating alternative chemicals, integrating treatments with vector monitoring or sampling, establishing action thresholds (although this is difficult for vectors), determining the likelihood of infections throughout the year, and combining chemical applications with resistant or tolerant varieties. Despite both *B. cockerelli* and *Ca. L. solanacearum* being major pests in potatoes in the United States and New Zealand, there are still many fundamental biological and ecological questions that need to be answered to understand this vector–pathogen system. These relate to the role of non-crop host plants of the insect and the bacterium in movement patterns in the landscape, and to how endosymbionts affect host plant choice, infection status and other biological parameters of the vector.

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