



Psyllids as major vectors of plant pathogens

Aranzazu Moreno¹, Marcelo P. Miranda², and Alberto Fereres^{1,*}

¹ Instituto de Ciencias Agrarias, Consejo Superior de Investigaciones Científicas, ICA-CSIC, 28006 Madrid, Spain

² Fund for Citrus Protection (Fundecitrus), Av. Adhemar Pereira de Barros, 201, Araraquara, SP, 14807-040, Brazil

* Corresponding author: a.fereres@csic.es

With 5 figures and 1 table

Abstract: Most psyllid species, also known as jumping plant lice, are well known agricultural pests, in part because many of them are vectors of devastating plant pathogens. This is the case for the best-known psyllid-transmitted disease, Huanglongbing (HLB), which is vectored by two psyllid species: *Diaphorina citri* and *Trioza erytreae*. In this review, the morphology and biology, and transmission characteristics of the main psyllid vector species transmitting emerging plant pathogens are described. Additionally, new findings on the transmission ability of CaLsol by *Bactericera nigricornis* are reported. Finally, the various management practices that can be used for the control of these plant pathogen-carrying vectors, such as optical and physical barriers, trap or border crops, biocontrol agents, and systemic insecticides are illustrated and critically discussed.

Keywords: CaLas, CaLafr, CaLsol, Phytoplasma, Management

1 Introduction: the economic impact of psyllids as vectors of plant diseases

Psyllids comprise about 3,800 species that belong to the superfamily Psylloidea, Suborder Sternorrhyncha, Order Hemiptera (Ouvrard et al. 2017). Their common name is jumping plant lice and they are subdivided into 11 families, although 3 of them are extinct: Aphalaridae, Calophyidae, Carsidaridae, Homotomidae, Liadopsyllidae, Liviidae, Malmopsyllidae, Neopsylloididae, Phacopteronidae, Psyllidae and Triozidae (Ouvrard 2017). Most of the species that are pests in agriculture belong to the following families: Psyllidae, Triozidae, Homotomidae and Liviidae. Only less than 1% of the total known psyllid species (>25) are regarded as serious pests in agriculture and forestry (Burckhardt 1994; Munyaneza 2010), similarly aphids, where only 100 species (about 2% of all known species) are considered economically important pests (Dixon 1998).

At the species level, psyllids exhibit very narrow host-plant ranges, particularly at the nymphal stage, are associated almost exclusively with dicotyledonous plants, with the exception of a few species that develop on monocotyledonous angiosperms and four that develop on conifers (Burckhardt 2005). Psyllids have a worldwide distribution, but are most diverse in tropical and subtropical areas. They share similar morphological characteristics with aphids, a taxonomically related group and also serious pests of a wide

range of crops. However, psyllids, as opposed to aphids, are able to jump and lack siphunculi. Psyllids reproduce sexually and only a few cases of facultative parthenogenesis are known (Hodkinson 1984). A very important feature that psyllids share with aphids is that they are phloem-feeders, although their feeding strategy differs from that of aphids as they do not make brief intracellular stylet punctures in superficial leaf tissues prior to the intercellular penetration into phloem sieve elements (Bonani et al. 2010; Pearson et al. 2014; Antolinez et al. 2017a). This is probably one of the reasons why they do not transmit plant viruses but are efficient vectors of phloem-limited bacteria and phytoplasmas.

Among the species considered as agricultural pests, only few are known vectors of plant pathogens (Burckhardt 1994). Their economic importance has risen in the past 20 years probably due to globalization (increasing trade of plant material over the world) and also due to global warming that facilitates the expansion and adaptation of psyllid pests into new habitats and geographical regions (Fereres 2015).

Psyllids are vectors of economically important phytoplasma diseases of fruit trees such as pear decline (PD), apple proliferation, and European stone fruit yellows (Bertaccini et al. 2019). All these diseases are transmitted by a single genus: *Cacopsylla* spp., and are mainly restricted to the Palearctic regions. *Cacopsylla melanoneura* (Foerster 1848; Hemiptera: Psyllidae) and *C. picta* (Foerster 1848; Hemiptera: Psyllidae) are well-known vectors of apple

proliferation phytoplasma (*Candidatus* Phytoplasma mali; Tedeschi & Alma 2004; Bertaccini et al. 2019). This serious disease is spread across Europe and infects apples. Other economically important diseases in fruit trees are PD transmitted by *C. pyricola* (Foerster 1848; Hemiptera: Psyllidae) in the UK (Davies et al. 1992) and by *C. pyri* (Linné, 1961; Hemiptera: Psyllidae) in France (Lemoine 1991) and Italy (Carraro et al. 1998a). Additionally, European stone fruit yellows phytoplasma is transmitted by *C. pruni* (Scopoli 1763; Hemiptera: Psyllidae) (Carraro et al. 1998b).

Nevertheless, psyllids have become extremely important pests in agriculture in the last decades because several species are vectors of the phloem-limited bacteria of the genus *Candidatus* Liberibacter spp. (Table 1). They transmit emerging diseases that cause very severe damage in cash-crops such as citrus or potatoes (Munyanza 2010). Perhaps, the best-known psyllid-transmitted disease is Huanglongbing (HLB), which is the main yield-limiting factor for citrus production worldwide (Bové 2006). The unculturable phloem-limited bacteria causing HLB is transmitted by two species of psyllids, *Diaphorina citri* (Kuwayama 1908; Hemiptera: Psyllidae) and *Trioza erytreae* (Del Guercio 1918; Hemiptera: Triozidae) (Burckhardt et al. 2021). Other complex of emerging bacterial diseases that cause severe losses in horticultural crops are the ones caused by *Ca. Liberibacter solanacearum* (CaLsol). The main psyllid species that transmits CaLsol

to potato and tomato crops in America and New Zealand is *Bactericera cockerelli* (Šulc, 1909; Hemiptera: Triozidae) (Munyanza 2010). In Europe, CaLsol causes severe disease of carrots among other Apiaceae that is transmitted by *B. trigonica* (Hodkinson 1981; Hemiptera: Triozidae) and *T. apicalis* (Foerster 1848; Hemiptera: Triozidae) (Munyanza et al. 2010a; Antolinez et al. 2017b).

Here we collate morphology, biology and transmission characteristics on the main psyllids to enable quick identification and prevention of disease spread. Furthermore, we report new findings on the transmission ability of CaLsol by *B. nigricornis* (Foerster 1848; Hemiptera: Triozidae) to carrot and potato plants.

2 Description, biology, and transmission characteristics of the psyllid vectors of *Candidatus* Liberibacter asiaticus/americanus/africanus, *Diaphorina citri* and *Trioza erytreae*

Three bacterial species are known to cause Huanglongbing (HLB) or greening disease: “*Ca. L. asiaticus*” (CLas), “*Ca. L. africanus*” (CLaf), and “*Ca. L. americanus*” (CLam) (Jagoueix et al. 1996; Teixeira et al. 2005). HLB is the most

Table 1. List of the main vector species and carriers of *Candidatus* Liberibacter spp. (modified after Ouvrard (2017)).

Psyllid species	Host plants
<i>Diaphorina citri</i> (Kuwayama 1908)	CITRUS
<i>Trioza erytreae</i> (Del Guercio 1918)	
<i>Cacopsylla citrisuga</i> (Yang & Li 1984)	
<i>Diaphorina communis</i> (Mathur 1975)	SOLANACEAE
<i>Bactericera cockerelli</i> (Šulc 1909)	
<i>Bactericera trigonica</i> (Hodkinson 1981)	
<i>Trioza apicalis</i> (Foerster 1848)	APIACEAE
<i>Trioza anthrisci</i> (Burckhardt 1986)	
<i>Bactericera nigricornis</i> (Foerster 1848)	POLYPHAGOUS
<i>Arytainilla spartiophila</i> (Foerster 1848)	CYTISUS SCOPARIUS
<i>Bactericera tremblayi</i> (Wagner 1961)	LEEK AND OTHER LILIACEAE
<i>Cacopsylla ambigua</i> (Foerster 1848)	SALIX SP.
<i>Cacopsylla nigrita</i> (Zetterstedt 1828)	
<i>Cacopsylla pyri</i> (Linné 1758)	
<i>Cacopsylla pyricola</i> (Foerster 1848)	ROSACEAE
<i>Cacopsylla pyrisuga</i> (Foerster 1848)	
<i>Cacopsylla breviantennata</i> (Flor 1861)	
<i>Cacopsylla affinis</i> (Löw 1880)	
<i>Cacopsylla melanoneura</i> (Foerster 1848)	
<i>Cacopsylla peregrina</i> (Foerster 1848)	

destructive citrus disease worldwide, due to the severity of symptoms, potential for disease progression, and susceptibility of all commercial citrus varieties (Bové 2006). In addition to a reduced fruit quantity and quality (Baldwin et al. 2010), HLB causes indirect losses due to the high costs involved in disease management (Bové 2006; Gottwald 2010). Successful management of HLB depends on the knowledge of the relationships between the pathogen, the insect vectors, host plants, and the environment (Bové 2006). These bacteria are phloem-restricted and their natural spread depends on two psyllid species, *D. citri* and *T. erytreae*, which are the only known vector species transmitting the three bacteria species causing HLB.

2.1 *Diaphorina citri*

2.1.1 Description

As other psyllid species, *D. citri* has three developmental stages (egg, nymph, and adult). The females oviposit exclusively on flush shoots (tender tissue) of the host plants, mainly in the terminal part of the shoots (folded leaves) (Tsai & Liu 2000; Cifuentes-Arenas et al. 2018). Eggs are oval with light yellow color when freshly laid on the plant, and turn into bright orange with two distinct red eye spots at maturity. The average size is 0.31 mm length and 0.14 mm width (Tsai & Liu 2000).

The nymphal stage is composed of five instars. The nymphs are dorsoventrally compressed and vary in color from yellow to dark orange-yellowish brown at maturity. According to Tsai and Liu (2000), the average first-instar nymphs are 0.30 mm long and 0.17 mm wide. These nymphs, in general, feed on the locations close to where the eggs were laid. Second-instar nymphs are 0.45 mm long and 0.25 mm wide. From this instar, it is possible to see rudimentary wing pads on the dorsum of thorax. Third-instar nymphs are 0.74 mm long and 0.43 mm wide on average, and the

wing pads are developed. From this stage on, the nymphs are more mobile. Fourth-instar nymphs are 1.01 mm long and 0.70 mm wide on average, with well-developed wing pads. The average fifth-instar nymphs were 1.60 mm long and 1.02 mm wide, with well-developed wing pads (Tsai & Liu 2000).

Diaphorina citri adults are white yellowish when newly emerged and become brownish after a few hours (Fig. 1A). The presence of mottled brown forewings is one of the key features for identification of this insect. Adults may have three different abdominal colors (gray to brown, blue to green, and orange to yellow; Wenninger & Hall 2008). The biological significance of abdominal polyphenism is not completely revealed, but it is possible that abdomen color may be related to the presence of eggs in the female abdomen, mate preference, flight capacity, and susceptibility to insecticides (Wenninger & Hall 2008; Tiwari et al. 2013; Martini et al. 2014; Stockton et al. 2017). The mean size of females is 3.3 mm long and 1.0 mm wide, and males are 2.7 mm long and 0.8 mm wide (Tsai & Liu 2000).

2.1.2 Biology

Diaphorina citri has a wide host plant range within the family Rutaceae subfamily Aurantioideae. However, there are significant differences in the oviposition and development of *D. citri* on Rutaceae/Aurantioideae plant species and/or their hybrids (Westbrook et al. 2011; Richardson & Hall 2013; Borgoni et al. 2014; Sétamou et al. 2016a). The *D. citri* female can lay up to 858 eggs per lifetime (Tsai & Liu 2000). In the citrus orchards of São Paulo state, Brazil, it was observed that the *D. citri* female lays an average of 8.3 eggs per flush shoot (Paiva & Parra 2012). Eggs hatch within 2.6 to 9.7 d, the duration of the nymphal stage varies from 9.4 to 39.6 d, and the biological cycle (egg to adult) varies from 12.1 to 49.3 d at temperatures from 15 to 32 °C (Nava et al. 2007). Egg viability ranges from 81.6 to 96.2 % at 15–32 °C

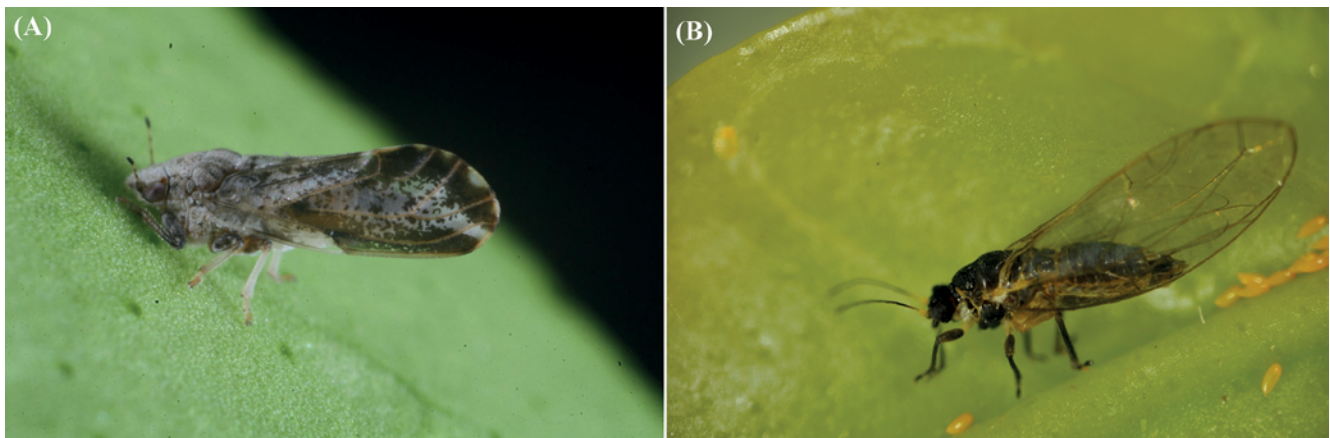


Fig. 1. Psyllid vectors of *Candidatus Liberibacter asiaticus/americanus/africanus*: (A) Adult of *Diaphorina citri* and (B) Adult and eggs of *Trioza erytreae*.

(Liu & Tsai 2000; Nava et al. 2007); nymph viability ranges from 70 to 77.5 % at 18–30 °C; however, it is dramatically reduced (only 7 %) at a constant temperature of 32 °C (Nava et al. 2007). At 15 to 33 °C, female longevity varies from 88.3 to 28.7 d and is 38 % higher than male longevity (Liu & Tsai 2000; Nava et al. 2007). Overall, the optimum temperature range for population growth of *D. citri* is between 25 °C and 28 °C (Liu & Tsai 2000). This psyllid is well-adapted to humid and warm weather, but it may survive in cold, including freezing temperatures (Hall et al. 2011). In part, this fact explains why *D. citri* is currently present in most continents, with the exception of Europe (CABI 2020). Recently, it has been introduced in several African countries, including West (Oke et al. 2020) and East Africa (Shimwela et al. 2016).

2.1.3 Transmission

Diaphorina citri transmits *Ca. Liberibacter africanus* (CLaf), *Ca. L. asiaticus* (CLas), and *Ca. L. americanus* (CLam) (McClean & Oberholzer 1965; Capoor et al. 1967; Yamamoto et al. 2006). However, most studies related to transmission of *Ca. Liberibacter* spp. by *D. citri* were performed with CLas. This bacterium has a persistent propagative relationship with *D. citri* (Inoue et al. 2009; Ammar et al. 2011; Orlovskis et al. 2015). Regarding transmission characteristics of CLas, there is a wide variation in the literature on the data on the period and efficiency of acquisition, inoculation, latency, and persistence. This may, in part, be explained by the dependency of early studies on visual assessment of symptom development. Therefore, only the studies that have used molecular techniques, polymerase chain reaction (PCR) or real-time PCR, to detect CLas in the psyllid and plant have been considered here. CLas acquisition by *D. citri* adults may occur during a short exposure (60 min) to infected plants (Bonani et al. 2010); however, acquisition rate increases after longer access periods (Pelz-Stelinski et al. 2010; Wu et al. 2016). Moreover, *D. citri* nymphs acquire CLas more efficiently than during the adult stage (Inoue et al. 2009; Pelz-Stelinski et al. 2010). Furthermore, nymphs ingest phloem sap for longer periods of time than adults, which may explain why they can transmit CLas more efficiently than adults (George et al. 2018). Similarly, although CLas inoculation by *D. citri* may occur within a short period (≈ 1.5 h) of exposure of healthy plants to bacteriliferous psyllids (Wu et al. 2016), the inoculation rate increases exponentially when *D. citri* feeds for a longer period (Raiol-Junior et al. 2017). The mean latent period of CLas in *D. citri* is 16 d (Canale et al. 2017), and the bacteria may persist in the psyllid body for 8–12 weeks (Hung et al. 2004; Canale et al. 2017). The process of transmission may be influenced by the citrus vegetative stage; acquisition and inoculation rates are higher when *D. citri* adults feed on flush shoots compared with mature leaves (Hall et al. 2016; Sétamou et al., 2016b). Also, environmental temperature may influence the acquisition process. For instance, Lopes et al. (2013) observed that

warmer temperature regimes (24–38 °C) reduced CLas titers in flush shoots and the percentages of CLas-positive psyllids when compared to that of plants maintained in cooler regimes (14–28 °C). Then, in favorable conditions (psyllids reared on infected plants, inoculation on flush shoot, and temperature around 25 °C) the CLas transmission rate per psyllid may reach 41 % (Carmo-Sousa et al. 2020). At low rates, CLas may also be transmitted from parent to offspring (2–6 %) (Pelz-Stelinski et al. 2010) and during copulation (≈ 4 %) (Mann et al. 2011).

2.2 *Trioza erytreae*

2.2.1 Description

Trioza genus comprises 439 species, but only *T. erytreae* can feed on Rutaceae plants. It is widely distributed across the African continent, but is also present in Europe (Spain and Portugal) and Saudi Arabia (EPPO 2020a).

Eggs have an average length of 0.28 mm and are oval, smooth and pear-shaped, with a sharp point anteriorly and are laid on the margins of young leaves (only when plants are sprouting). Each egg has a short stalk, which is inserted into the leaf tissue. Newly oviposited eggs are lemon yellow, and as the embryo develops, the egg turns dark yellow (Fig. 1B). Shortly before eclosion, two red nymphal eye spots become visible towards the anterior end of the egg (Moran & Blowers 1967).

Nymphs are almost sedentary, although they can move around when disturbed. They are dorsoventrally compressed and form a characteristic concave open gall on the abaxial side of the leaf after a few days of feeding. They vary in color from yellow, olive-green to dark grey, and have a marginal fringe of white, waxy filaments. There are five nymphal instars. On molting to the fourth instar, two pale brown spots appear on the abdomen. The average lengths of the first to fifth instar are 0.345 mm, 0.50 mm, 0.72 mm, 1.025 mm, and 1.52 mm, respectively (Moran & Blowers 1967).

Adults are winged, pale green, initially, and later turn brown (Fig. 1B). Males are smaller than females and can be distinguished by the shape of the abdomen, which ends in a sharp point in females and bluntly in males. The external genitalia also differ in structure. The average lengths of adult males is 2.17 mm and that of females is 2.24 mm (Moran & Blowers 1967). The process of sclerotization of the body is completed in about 5 d, while 10 days after adult emergence the Malpighian tubes become visible through the dorsal abdomen. When feeding adults raise the abdomen at an angle of about 35° to the feeding surface (Cocuzza et al. 2017).

2.2.2 Biology

The life cycle of *T. erytreae* has not been characterized in detail. Several studies have been conducted in South Africa with varying temperatures but the results are variable, sometimes contradictory, and the duration of each life stage (egg,

nymph and adult) is unclear. Unfortunately, reliable basal and upper developmental temperatures from which phenological models could be developed using minimum and maximum temperature thresholds have not been determined.

Nymphal development depends mainly on temperature and may take from 17 to 43 d at 25 °C and 14 °C, respectively (Catling 1973). The lower temperature threshold for development is about 10 °C (Catling 1973), whereas a temperature of 32 °C, with low relative humidity, is particularly deleterious for all instars (Moran & Blowers 1967). The first instar lasts the longest, probably because of the long time needed for the crawlers to settle and establish themselves. Nymphal development is prolonged on poorly nourished citrus leaves. In the field, young growth in poor condition also causes high rates of mortality and produces flattened nymphs of reduced size (Catling 1971). Almost immediately after the wings have expanded, the adult usually commences feeding close to the nymphs. The oviposition period starts three to seven d following adult emergence and lasts from 23 to 71 d (Catling 1973). Moran (1968) claimed that young leaves of lemon, *Citrus limon* (L.) Burro. f., were significantly more attractive as feeding sites for adults of the citrus psylla compared with four indigenous host plants. *Trioza erytreae* is a highly fecund species and produces as many as 1,300 eggs per female after continuous mating (Catling 1973). It has no diapause and can have as much as 6–8 generations per year under favorable conditions (Catling 1972). Adults overwinter on semi-dormant trees and may live for 2–3 months feeding on mature leaves. Preliminary results indicate that most flight activity takes place shortly before sunset and ceases at dusk. These studies have found that *T. erytreae* adults can fly for at least 1.5 km, with absence of flushes as main driver of adults dispersal (Van den Berg & Deacon 1988).

2.2.3 Transmission

McClellan & Oberholzer (1965) were the first reporting the citrus psylla as vector of greening or HLB diseases (CLaf). Generally, it has been found that only adult psyllids can acquire and transmit the causal agent (Moll & Martin 1973). However, McClellan (1974) stated that the nymphal stage may become infected by feeding on diseased tissue. Adults are the only stage that moves from plant to plant, so nymphs do not contribute to the spread of the disease. *Trioza erytreae* is the major vector of CLaf, which is widely present in Africa but is less destructive and less adapted to high temperatures than the Asian variant (CLas) (Bové 2006).

When acquired by *T. erytreae*, CLaf reaches the gut and then replicates in the internal organs, including the salivary glands (Moll & Martin 1973). The bacterium can be acquired after 1–2 h of feeding on diseased sweet orange seedlings and can be transmitted after 3–4 d. Transmission to healthy plants occurs in about 24 h when the psyllid has fed for at least 8–24 h, with an efficiency rate of 12 % that progressively increased to 32 % by day 7 (Van Vuuren et al. 1986;

Van den Berg et al. 1992). Adults can remain infective for all their lives and the transovarial transmission of the pathogen may occur (van den Berg et al. 1992). *Trioza erytreae* can also transmit CLas, the causal agent of the Asian HLB (Massoné et al. 1976). Although none of the forms of citrus HLB have been found yet in Europe (Lopez et al. 2015), the vector *T. erytreae* is already present in the coastal regions of Portugal, from Porto to Setubal, and of Spain, all over the Cantabric coast, from Galicia to the Vasque Country (EPPO 2020b).

2.3 Description, biology, and transmission characteristics of the psyllid vectors of *Candidatus Liberibacter solanacearum* (CaLsol), *Bactericera cockerelli*, *B. nigricornis*, *Trioza apicalis*, *B. trigonica*, *B. tremblayi* and *T. erytreae*

Candidatus Liberibacter solanacearum is an intracellular phloem-limited bacterium that infects and replicates in the sieve elements of plants as well as in different organs and tissues of its psyllid vectors (Brown 2016; Haapalainen 2014; Perilla-Henao & Casteel 2016). Psyllid feeding behavior plays a key role in the horizontal transmission of CaLsol (Antolínez et al. 2017a). The CaLsol transmission is a complex and slow process that includes various steps (acquisition, latency period, and inoculation). The process is known as circulative-propagative as it requires the pathogen to circulate through the gut to reach the psyllid hemolymph and then reach the salivary glands. It is propagative because it multiplies in different organs of the psyllid vector (Fisher et al. 2014; Cicero et al. 2016a; 2016b). There are several vector species that transmit CaLsol, with *B. cockerelli*, *B. trigonica*, and *T. apicalis* the best known (EPPO 2020c). Other species, such as *B. tremblayi* (Wagner 1961; Hemiptera: Triozidae) tested positive for the bacteria as they can acquire and carry the pathogen, but are unable to transmit CaLsol from plant to plant (Antolínez et al. 2017b). Other potential vector species (*T. anthrisci* (Burckhardt 1986; Hemiptera: Triozidae) and *T. urticae* (Linné 1758; Hemiptera: Triozidae)) have been detected recently in Europe, but their role as vectors of CaLsol is unclear (Haapalainen et al. 2018b; Sumner-Kalkun et al. 2020). Recently, we identified at ICA-CSIC (Madrid) a new vector species, *B. nigricornis*, which is able to transmit CaLsol to carrot and potato plants (experiments are described in the following sections).

2.4 Psyllid vector species in Solanaceae (Zebra chip disease)

The main vector species of CaLsol in potato and other solanaceous crops is *B. cockerelli*, a species that is found in Central and North America, and New Zealand, but is absent in Europe (Pletsch 1947; Wallis 1955; Rubio-Covarrubias et al. 2006; Teulon et al. 2009). However, *B. nigricornis* has been found colonizing potatoes in Spain and Iran and could

potentially transmit CaLsol to potatoes (Fathi et al. 2011; Antolínez et al. 2019).

2.5 *Bactericera cockerelli*

Bactericera cockerelli (potato/tomato psyllid) was originally described as *T. cockerelli* by Šulc (1909) and belongs to the family Triozidae (Burckhardt & Ouvrard, 2012). The eggs of *B. cockerelli* are deposited singly principally on the lower surface of leaves and usually near the leaf edge. They are dark yellow or orange just before hatching (3–7 d after oviposition) but initially are light yellow (Knowlton & Janes 1931; Abdullah 2008). Nymphs of *B. cockerelli* are dorso-ventrally planed and mobile. After egg hatching, the nymphs are orange, but they become green as they mature. Nymphal size is variable and instars can be distinguished by their morphological structures because the wing pads become more pronounced with each subsequent molt. Development of the nymphs is dependent on the temperature and the host plant, and can last from 12 to 24 d (Knowlton & Janes 1931; Abdullah 2008; Yang & Liu 2009). Adults are active in contrast to the largely sedentary nymphal stages. The morphometry of adult individuals of *B. cockerelli* is variable, depending on the host, sex of the insect, and the interactions

between these factors (Vargas-Madriz et al. 2013) (Fig. 2A). *Bactericera cockerelli* adults are small, measuring about 2.5–2.75 mm long, with females having a greater body size than the males (Burckhardt & Lauterer 1997).

The potato psyllid is believed to be a native of southwestern USA and northern Mexico. Its current geographic distribution is limited to western USA, Canada, Mexico, Central America, and New Zealand (Pletsch 1947; Wallis 1955; Rubio-Covarrubias et al. 2006; Teulon et al. 2009) but, to date, it has not been found in Europe. *Bactericera cockerelli* is known to develop on Solanaceae, Convolvulaceae and Menthaceae and it has also been shown to complete its life cycle on a number of non-crop species (Vereijssen et al. 2018). The survival of *B. cockerelli* on this vast range of non-crop host plants sustains the populations when crop plants are unavailable (Vereijssen et al. 2018). A complete list of plant species on which adult psyllids could feed, but which could not sustain nymphal development, was included by Knowlton & Thomas (1934).

The life cycle of *B. cockerelli* is highly dependent on temperature and can be completed in 21 to 35 d, with an optimum at 27 °C; however, oviposition, hatching, and survival are inhibited at temperatures higher than 35 °C (List 1939;

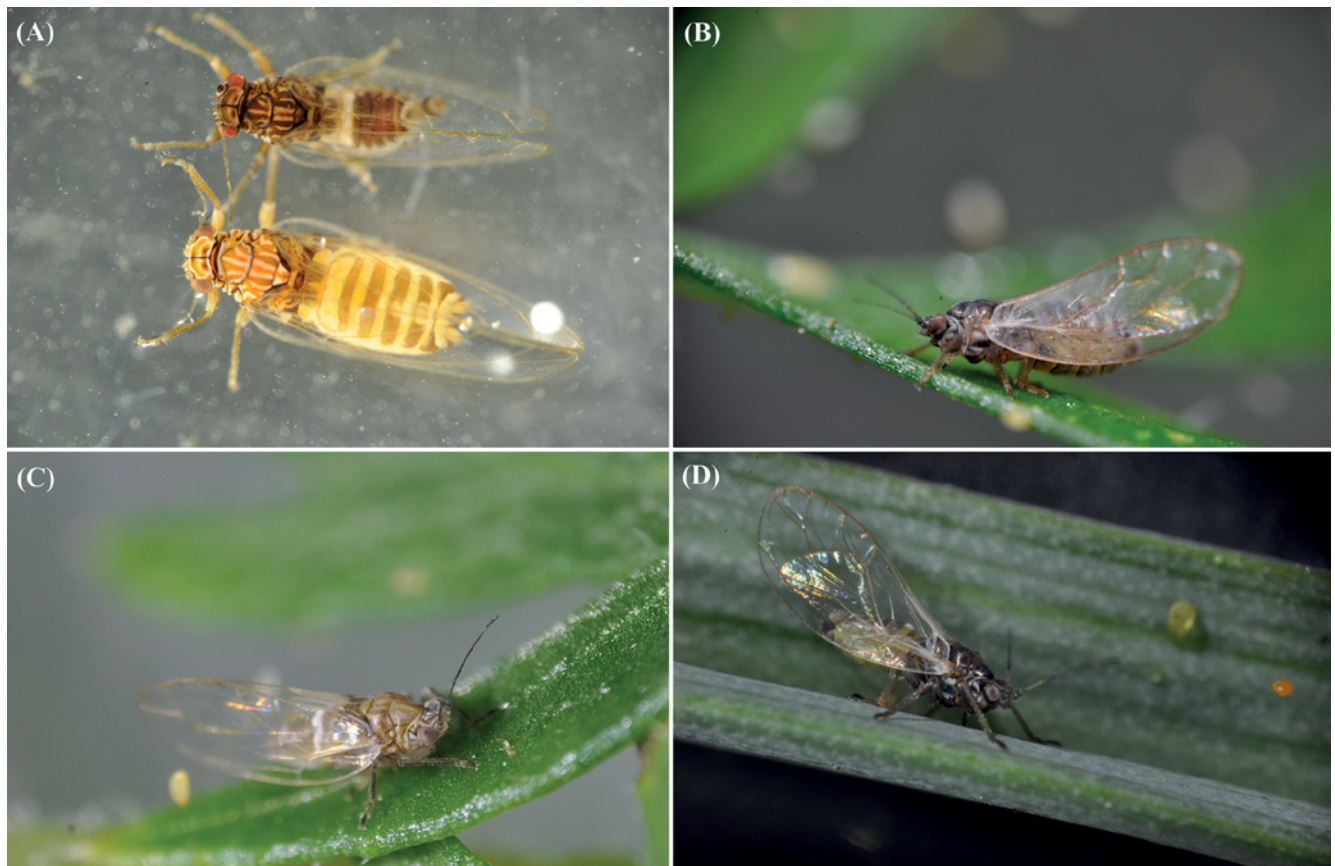


Fig. 2. Psyllid vectors of *Candidatus Liberibacter solanacearum* (CaLsol): (A) Adults of *Bactericera cockerelli*, (B) Adult of *B. trigonica*, (C) Adult of *B. nigricornis*, and (D) Adult of *B. tremblayi*.

Abdullah 2008; Yang & Liu 2009; Yang et al. 2010; Butler & Trumble 2012). Interestingly, both adults and nymphs are cold tolerant (Henne et al. 2010).

CaLsol is especially important in potato (*Solanum tuberosum* L.) in which it causes a disease called “Zebra chip” (ZC) in the USA, Mexico, Honduras, Guatemala, and New Zealand (Abad et al. 2009, Nelson et al. 2011, Munyaneza 2012). *Bactericera cockerelli* was associated with zebra chip disease in potato in 2007 (Munyaneza et al. 2007) and later with CaLsol in 2009 (Secor et al. 2009). The zebra chip disease is caused by the haplotypes A and B, whereas the rest of the haplotypes (C, D, E, and H) of the bacterium cause diseases in Apiaceae. Recently, haplotypes G and F have been found in Solanaceae in the USA (Mauck et al. 2019; Swisher Grimm & Garczynski 2019).

The zebra chip disease in potato is characterized by collapsed stolons, aerial tubers, upward rolling of leaflets, purple or yellow discoloration, leaf scorch and early senescence; also, dark and striped pattern is clearly visible in infected raw tubers and in fried chips (Munyaneza 2012). CaLsol is transmitted by psyllids in a circulative-propagative manner but also by transovarial (vertical) transmission (Hansen et al. 2008; Cicero et al. 2016a). In fact, the vertical transmission rates of CaLsol in *B. cockerelli* might be up to 87 % (Casteel et al. 2012). When this vertical transmission occurs, nymphs resulting from infected eggs and newly emerged adults can efficiently transmit CaLsol to susceptible plants. This increases the vector propensity and makes CaLsol difficult to control in field conditions (Vereijssen et al. 2018).

The circulative-propagative transmission requires pathogens to circulate in the psyllid hemolymph as well as to multiply in different organs. The CaLsol transmission starts when the psyllid vector acquires the bacterium from the phloem-sieve elements of an infected plant during feeding (Mustafa et al. 2015; Sandanayaka et al. 2014). The acquisition of the bacterium is dependent on the bacterium titer in the plant (Rashed et al. 2012). The minimum acquisition access period for an adult *B. cockerelli* to acquire the bacterium is about 36 min, with only 7 min of phloem ingestion (Sandanayaka et al. 2014). The same work showed that durations of phloem activities are not related to the inoculation and acquisition of the bacterium by *B. cockerelli*. Once CaLsol reaches the psyllid digestive tract, the bacteria must pass through the midgut epithelium to reach the haemocoel and circulate in the hemolymph (Fisher et al. 2014; Cicero et al. 2016a; 2016b). From the hemolymph, CaLsol spreads to different tissues and organs where it accumulates and replicates to finally reach the salivary glands (Cicero et al. 2016b). Then, CaLsol colonizes the salivary glands and is persistently transmitted with the saliva while the insect is feeding on the phloem of a susceptible host. The period of time from acquisition to inoculation represents the latency period and seems to be variable, depending on the titer of CaLsol in the host plant (Sengoda et al. 2013; 2014). An

exhaustive revision on CaLsol transmission by *B. cockerelli* has been recently published by Vereijssen et al. (2018).

2.6 *Bactericera nigricornis* as a new vector of *Candidatus Liberibacter solanacearum* in potatoes

To date, *B. cockerelli* has been the only zebra chip disease vector identified, upon the first report by Munyaneza et al. (2007) as the main CaLsol vector in potato in the USA. No evidence of its presence has been found in Europe to date (EPPO 2020d; Ouvrard 2020). Moreover, although CaLsol is mainly associated with Apiaceae crops in Europe, it has also been found in field-grown potato crops in Finland (haplotype C; Haapalainen et al. 2018) and Spain (haplotype E; Palomo et al. 2014).

Bactericera nigricornis is a polyphagous species that can feed and reproduce in both Solanaceae and Apiaceae among other families. This species has been found on both carrot (*Daucus carota* L.) and potato crops in Europe (see section on CaLsol vectors in Apiaceae for a complete description of the species). Thus, *B. nigricornis* could potentially transmit CaLsol from carrot to potato crops and viceversa. Although eggs and immatures *B. nigricornis* are rarely observed during visual inspections in the field, the reproduction and presence of this psyllid species on potato crops has been confirmed (Hodkinson et al. 1981; Antolínez et al. 2019) and has been reported to cause severe yield losses in Iran (Fathi et al. 2011).

Although CaLsol-positive adults of *B. nigricornis* have been found in potato crops in Spain, the role of this species in transmitting the bacterium to potato was never demonstrated (Teresani et al. 2015). Accordingly, a study of the possible role of *B. nigricornis* as a vector of CaLsol on potato was strongly needed because of the important economic losses in the carrot and potato industry associated with pathogen spread (Liefsting et al. 2009; Munyaneza 2010; Munyaneza et al. 2010a; 2012; 2015; Alfaro-Fernández et al. 2012a; 2012b; Bertolini et al. 2015; Munyaneza 2015).

For this reason, we conducted a series of transmission experiments under controlled conditions at ICA-CSIC (Madrid, Spain) to evaluate the transmission rate of CaLsol (haplotype E) by *B. nigricornis* in carrot and potato plants. *Bactericera nigricornis* CaLsol-free and CaLso-infected colonies were established at the ICA-CSIC and used for the assays. First, a *B. nigricornis* CaLsol-free colony was established by collecting insects from a population in a potato field in Valladolid, Spain, in 2016. Psyllids were maintained on potato plants under greenhouse conditions (16:8 h (L:D) photoperiod and 26:18 °C (L:D)) for several generations and the colony was periodically tested by PCR (Bertolini et al. 2015) to confirm the absence of CaLsol-infected individuals. Then, *B. nigricornis* CaLsol-infected colonies were generated and maintained on infected carrot (cv. Bangor) plants under greenhouse conditions for several generations, with

the infection status of the psyllid colonies was periodically tested by PCR to confirm the presence of CaLsol. After five generations, most of the individuals (98%) were shown by real-time PCR to be CaLsol-positive. Bacteria-free potted potato plants (cv. Red Pontiac) were used as recipient plants.

To assess the transmission rate of CaLsol from infected carrot to potato plants and the settling preference of *B. nigricornis* on host plants, different experiments under non-choice and dual-choice conditions were performed. For non-choice assays, two $1 \times 1 \times 1$ m cages covered with an aphid-proof mesh net were used. Each cage contained one treatment: (T1) 36 potato plants and (T2) 36 carrot plants. Potted plants were disposed in six rows and six columns with 12.5 cm between plants. Two hundred CaLsol-infected adults of *B. nigricornis* were collected from the colony with a vacuum aspirator and released on a flight platform placed 0.5 m above the plants inside each cage. The flight platform was similar to that described by Fereres et al. (1999). Adults were released at solar noon and all cages were rotated 180° daily to avoid orientation bias. After 72 h of inoculation access period (IAP), mean of eggs per plant, percentage of adults settled per cage, and the percentage of plants infested per cage were calculated. Then plants were treated with 1 g L^{-1} of Confidor® (Bayer, MO, USA) and kept under greenhouse conditions for 8 weeks to be tested for CaLsol by visual inspection of symptoms and by real-time PCR (Bertolini et al. 2015).

A procedure similar to the one described for non-choice assays was used for dual-choice assays. The assay included one treatment with 18 potato plants and 18 carrot plants disposed alternatively in the same cage in six rows and six columns with 12.5 cm between plants as described by Antolínez et al. (2017b). Both non-choice and dual-choice assays were replicated four times and conducted in a glasshouse under greenhouse conditions. All data collected were analyzed using BM SPSS v23 statistics software package. Shapiro-Wilk W-test was used to test the normality of the variables. Mean of eggs per plant was transformed by $\ln(x + 1)$ to achieve normality. Afterwards, mean of eggs, percentage of adults settled per cage, percentage of plants infested and percentage of CaLsol-infected plants for each treatment were compared using a Student's t-test.

Bactericera nigricornis ovipositional preference was similar for carrot and potato plants in both non-choice and dual-choice assays (mean number of eggs per plant: non-choice: 4.55 ± 0.7 on potato and 7.88 ± 1.28 in carrot, $t = 0.660$, $p = 0.534$; dual-choice: 9.29 ± 1.72 in potato and 6.99 ± 1.57 in carrot, $t = 0.519$, $p = 0.623$). No differences in the percentage of infested plants were observed (non-choice: 63.19 ± 7.12 on potato and 68.75 ± 8.28 in carrot, $t = -0.509$, $p = 0.629$; dual-choice: 79.17 ± 3.49 in potato and 77.78 ± 6.8 in carrot, $t = 0.862$, $p = 0.182$). Although no settling preferences were found between carrot and potato plants in the non-choice assays (percentage of settled psyllids: 29.12 ± 4.03 in potato and 24.5 ± 4.36 in carrot, $t = 0.778$, $p = 0.466$),

the percentage of adults settled was significantly higher on potato compared with that on carrot plants in the dual-choice assays (percentage of settled psyllid: 20 ± 1.27 in potato and 14.25 ± 1.2 in carrot, $t = 3.286$, $p = 0.017$) (Fig. 3 and Fig. 4).

Visual symptoms of infection developed 4–5 weeks after the exposure of the plants to the CaLsol-positive adults (Fig. 5). Aerial tubers and leaf yellowing of apical leaves were the main symptoms observed in potato plants as opposed to the typical yellow and purple discoloration of carrot leaves. The transmission rate of CaLsol by *B. nigricornis*, under both non-choice and dual-choice conditions was higher in carrot than in potato (non-choice: 11.11 ± 5.89 % in potato and 59.03 ± 7.11 % in carrot, $t = 5.186$, $p = 0.002$; dual-choice: 12.5 ± 5.26 in potato and 62.5 ± 9.18 in carrot, $t = -4.728$, $p = 0.003$; Fig. 3 and Fig. 4). Results showed that *B. nigricornis* was able to transmit CaLsol from carrot to potato plants, although the percentage of CaLsol-infected plants was significantly reduced on potato compared to carrot plants.

Here, it is important to highlight that, while in this study CaLsol symptoms typically associated with CaLsol haplotypes A and B were clear in infected potatoes (Fig. 5), no symptoms were observed in potato plants infected with haplotype C (Haapalainen et al. 2018). Differences observed in symptom expression by different CaLsol haplotypes could be related to distinct CaLsol titres in the infected plants, potato cultivars used as recipient plant or haplotype-host interactions. In fact, haplotype C titres in asymptomatic potato were comparable to those obtained from symptomatic plants infected with haplotypes A and B, suggesting that the downward movement of haplotype C in potato phloem is slower than that of the American haplotypes A and B (Haapalainen et al. 2018). Moreover, in the same work, attempts to transmit CaLsol (haplotype C) to potato by *T. apicalis* were not successful, result that could be easily explained because potato is not a host plant for *T. apicalis*. By contrast, *B. nigricornis* is known to be able to properly feed from the phloem and colonize potato crops (Fathi et al. 2011; Antolínez et al. 2019), which facilitates the transmission of phloem-restricted pathogens. Further studies are needed to answer all these questions concerning the CaLsol haplotypes-psyllid species-host plant interactions and the CaLsol epidemiology.

The vector propensity of *B. nigricornis* from potato-to-potato plants was also assessed in an additional study. Potato (cv. Gazel) plants that were infected by CaLsol in the previous experiment were used as source plants. A CaLsol-free *B. nigricornis* colony maintained on potato plants under greenhouse conditions was used for the study. After 18 d of AAP and latency period on CaLsol-infected potato plants, psyllids were transferred in groups of 10 individuals to healthy potato plants, each contained in a transparent, cylindrical, plastic cage. The psyllids had access to the entire plant for an inoculation access period (IAP) of 72 h. Later, the psyllids were removed and the receptor plants

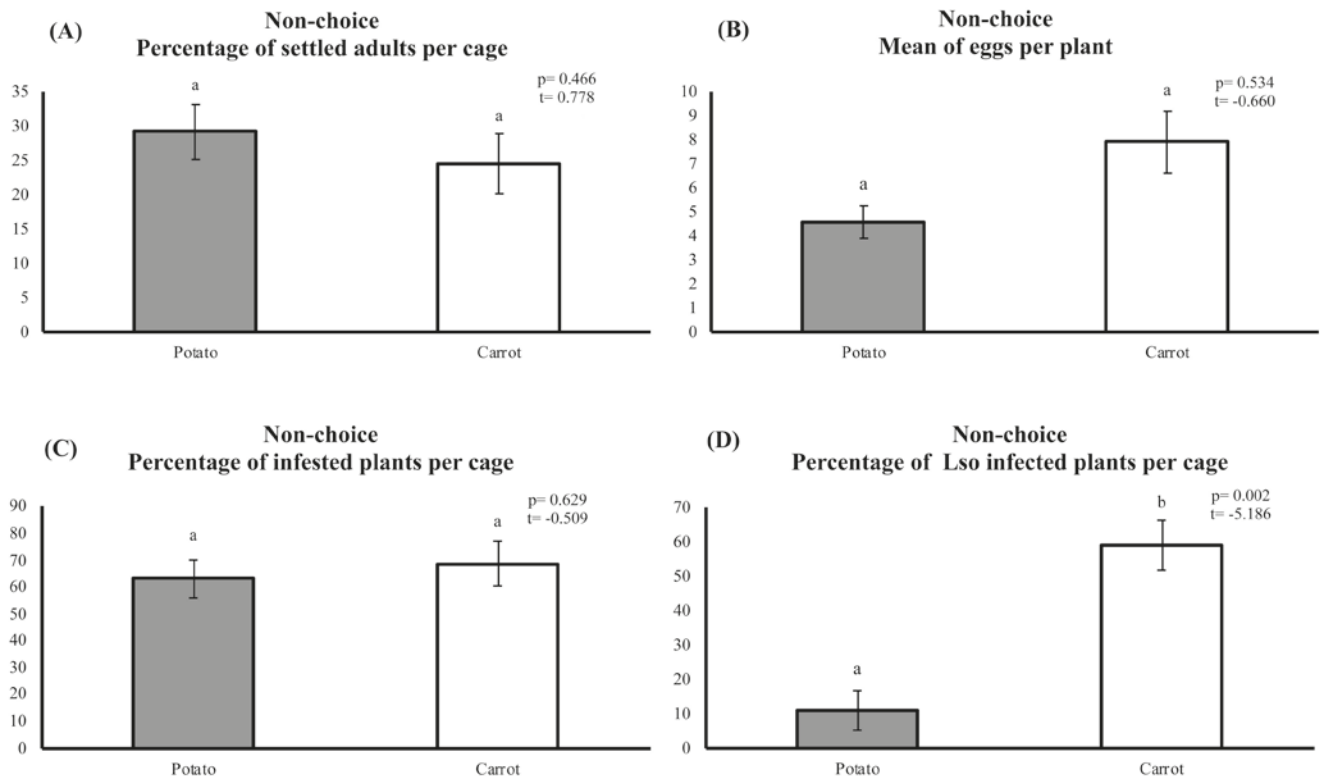


Fig. 3. *Candidatus Liberibacter solanacearum* (CaLsol) transmission and ovipositional and settling preferences of *Bactericera nigricornis* on potato and carrot plants in non-choice assays: **(A)** Percentage of settled adults per cage; **(B)** mean of eggs per plant; **(C)** percentage of infested plants per cage and **(D)** percentage of CaLsol infected plants per cage. Different letter represents significant differences between treatments according to Student t-test analysis.

were sprayed with 1 g L⁻¹ of Confidor ® (Bayer, MO, USA) on days 0 and 10 and were maintained under greenhouse conditions for 8 weeks to test for CaLsol by visual inspection of symptoms and by real-time PCR (Bertolini et al. 2015). Three different assays were performed, with 12, 6 and 24 receptor plants, respectively.

According to the symptoms and PCR results, *B. nigricornis* was able to acquire and inoculate the bacterium from potato to potato, although the transmission rate was very low at 7.1 % with 10 insects per test plant, which results in a 1 % of transmission rate by a single insect (transmission rate by a single insect estimated by Gibbs and Gower formula, 1960). These results showed that despite the ability of *B. nigricornis* to transmit CaLsol to potato crops, its efficiency as a vector of CaLsol is very low. This low transmission efficiency could be related with the low susceptibility of potato plants to CaLsol E haplotype. Further research is needed to conclude if the bacterium transmission by this psyllid species is a real threat to potato crops in Europe. Nevertheless, monitoring its populations is highly recommended as a preventive measure to avoid potential outbreaks in those areas where *B. nigricornis* is present.

2.7 *Trioza apicalis*, *Bactericera trigonica*, and other vectors of *Candidatus Liberibacter solanacearum* in Apiaceae

Candidatus Liberibacter solanacearum also affects plants from the family Apiaceae such as celery (*Apium graveolens* L.) and carrot in Europe, Africa and the Middle East (Munyanza et al. 2010a; 2015; Alfaro-Fernández et al. 2012a; 2012b; Loiseau et al. 2014; Tahzima et al. 2014; Teresani et al. 2014). Symptoms of CaLsol in carrot and celery include abnormal proliferation of shoots, stem curling, as well as purple or yellow discoloration and root size reduction. In recent years, CaLsol has caused severe economic losses to the fresh carrot market in Norway, Finland, Germany and Spain (Munyanza et al. 2010a; Teresani et al. 2014; Bertolini et al. 2015).

Four different haplotypes of CaLsol (C, D, E, and H) have been found to infect Apiaceous crops in Europe. Haplotype C is transmitted by *T. apicalis* and it has been generally found infecting carrot crops in North Europe (Burckhardt 1985; Nelson et al. 2011; Munyanza et al. 2015). Haplotypes D and E are transmitted by *B. trigonica* and affects Apiaceae in Mediterranean regions (Nelson et al. 2013; Teresani et al.

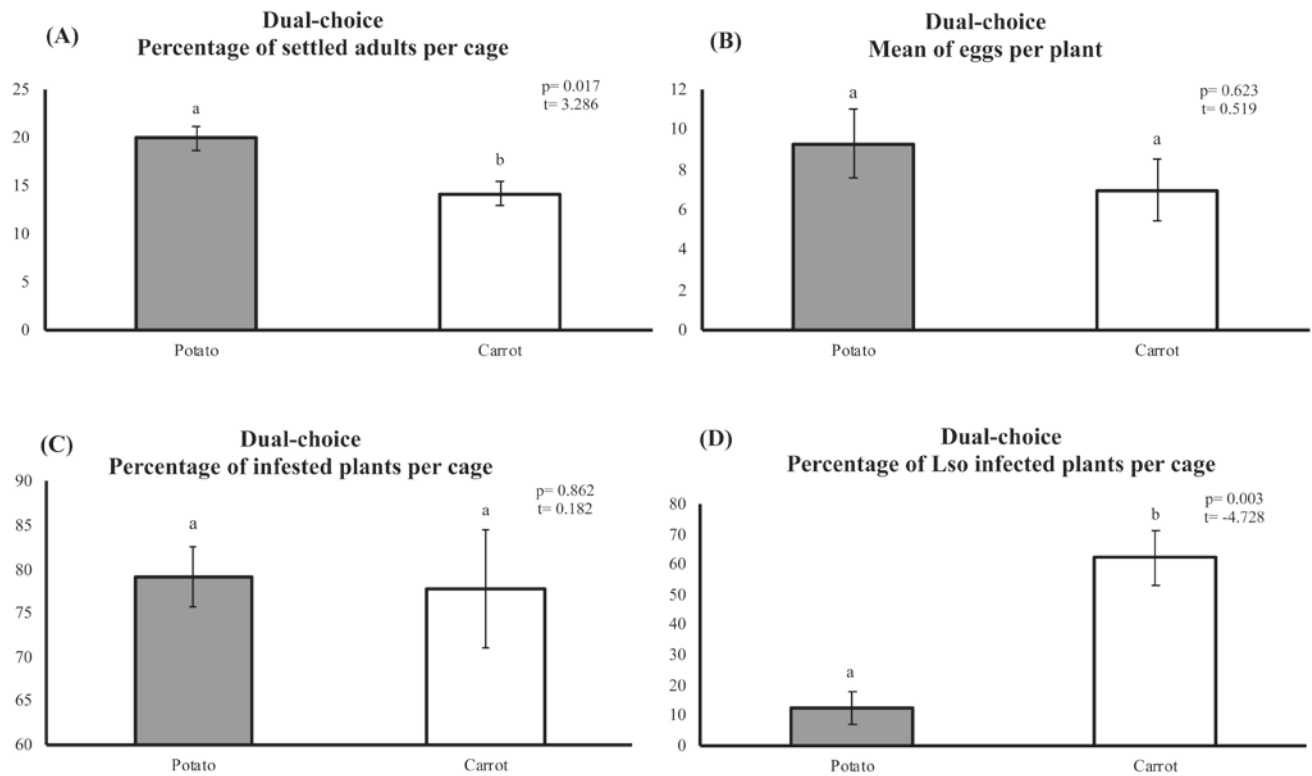


Fig. 4. *Candidatus* Liberibacter solanacearum (CaLsol) transmission and ovipositional and settling preferences of *Bactericera nigricornis* on potato and carrot plants in dual-choice assays: **(A)** Percentage of settled adults per cage; **(B)** mean of eggs per plant; **(C)** percentage of infested plants per cage and **(D)** percentage of CaLsol infected plants per cage. Different letter represents significant differences between treatments according to Student t-test analysis.

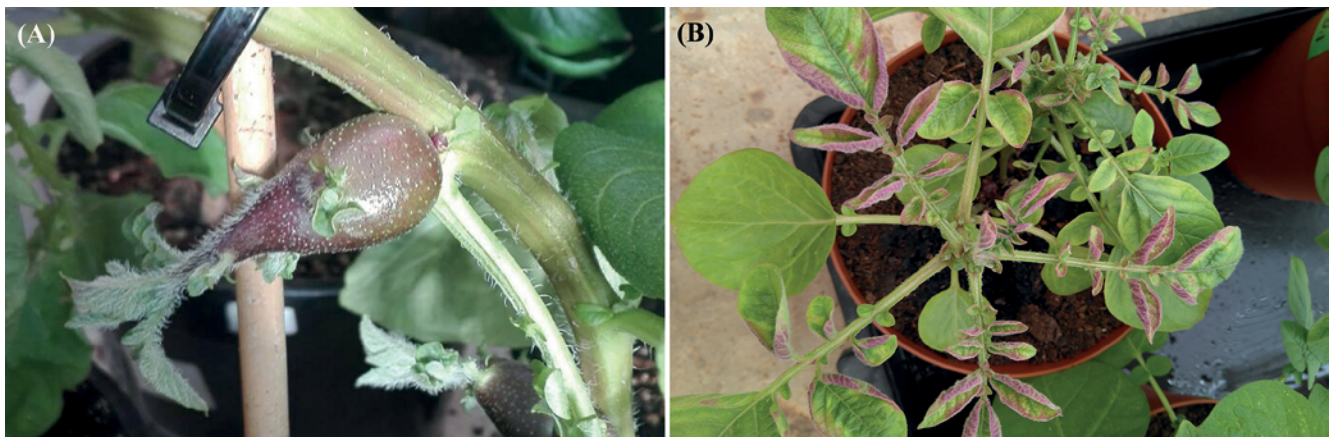


Fig. 5. *Candidatus* Liberibacter solanacearum (CaLsol) symptoms in potato plants: **(A)** Aerial tuber and **(B)** CaLsol symptomatic leaves.

2014; Alfaro-Fernández et al. 2017). Finally, haplotype H is the most recently discovered haplotype in Finland, in symptomatic cultivated carrots and parsnips (*Pastinaca sativa* L.; Haapalainen et al. 2020). The vector (s) species transmitting haplotype H is still unknown, although based on the other CaLsol species, it is likely that the vector of haplotype H also belongs to the family Psyllidae. Moreover, three other haplotypes have been found infecting non-cultivated hosts or in several psyllid vectors. Haplotype U has been described in symptomatic *Urtica dioica* L. and in *Trioza urticae* (Linné 1758; Triozidae) in Finland and Scotland (Haapalainen et al. 2018b; Sumner-Kalkun et al. 2020). Recently, two novel haplotypes were found in *Craspedolepta nebulosa* (Zetterstedt 1828, Aphalaridae) and *Craspedolepta subpunctata* (Foerster 1848, Aphalaridae) and named Cras1 and Cras2 (Sumner-Kalkun et al. 2020).

In summary, the main psyllid vector species transmitting CaLsol in Apiaceae in Europe are *T. apicalis* and *B. trigonica* (EPPO 2020c). Moreover, the transmission ability of CaLsol in Apiaceae by other psyllid species, such as *T. erytreae* and *B. tremblayi* has been also reported recently (Antolínez et al. 2017b; Quintana-Gonzalez de Chavez et al. 2020). For this reason, the description, biology and transmission ability of these psyllid species have been included in the present review. In addition, unpublished information on the transmission ability of CaLsol by *B. nigricornis* to carrot plants is also described.

2.7.1 *Trioza apicalis*

Trioza apicalis, commonly known as the carrot sucker psyllid, was described by Förster in 1948 (syn. *Trioza viridula* Zett.) (Láska 2011). A taxonomic revision of the *T. apicalis* group, together with an identification key of the eight recognized species were published by Burckhardt (1985). More recently, Láska (2011) summarized the main aspects of the biology and morphology of this psyllid species. The eggs of *T. apicalis* do not have a peduncle and are white after being laid. Thereafter, they turn weakly yellowish with an asymmetric shape length 0.357 mm and width 0.180 mm (Ozols 1925). As for other psyllid species, the embryonic development is dependent on the temperature, ranging from 5 d at 23 °C (Bey 1931) to 14 d at 16.8 °C (Láska 1974). The eggs hatch into nymphs that live rather sedentarily on the underside of the plant leaves. The size of the instars of *T. apicalis* and their duration under constant laboratory conditions of 21 °C were estimated by Láska (1974) and Rigg (1977), respectively. According to these works, size of the immature stages of *T. apicalis* varies from 0.35–0.43 mm in length and 0.17–0.21 in width for the first instar to 1.75–2.15 mm in length and 0.89–1.07 in width for the fifth instar; the total larval development lasts 42.6 d at 21 °C. In the same work, Láska (1974) showed that the larval development time was shorter (40 d) at lower temperatures but that only a few individuals completed development when the study at 16.3 °C.

The total development time (including eggs) for *T. apicalis* has been estimated under controlled conditions by several authors with variable results (Rygg 1977). Under field conditions with mean temperatures of 17 °C, the total development time for *T. apicalis* took a median of 54 d (Láska 1974). After hatching, *T. apicalis* adults have a light green head with antennae with a cream coloring base and dark apical segments. The legs are yellowish with a greenish tinge. Morphology of 1-year-old overwintered adults is variable with predominance of bluish-green specimens with light brown heads, often with an orange spot (Láska 1974). *Trioza apicalis* has only one generation per year (Kristoffersen & Anderbrant 2007).

Trioza apicalis is a frequently occurring pest in the carrot fields in northern Europe. These psyllids overwinter on coniferous trees and, in the summer, they move to the carrot seedlings to feed and reproduce (Nissinen et al. 2020a). Although carrot has been reported as the main summer host of *T. apicalis*, other species among the Apiaceae serve as alternative hosts: parsley (*Petroselinum crispum* (Miller) Fuss), coriander (*Coriandrum sativum* L.), or fennel (*Foeniculum vulgare* Miller) (Valterová et al. 1997; EPPO 2020e). Migration between winter and summer host is affected by both the photoperiod and changes in the concentration of secondary metabolites in the winter host (Valterová et al. 1997; Nissinen et al. 2007).

Trioza apicalis is the vector of the CaLsol haplotype C in northern Europe (Nissinen et al. 2014). The first report of the association between *T. apicalis* and CaLsol was published in 2010 (Munyanze et al. 2010b). In addition to leaf curling, *T. apicalis* feeding damage includes yellowish, discoloration of leaves, stunting of the shoots and roots, and proliferation of secondary roots (Nissinen et al. 2007). Damage to carrots are mainly associated with adults, with females causing more severe symptoms than males, although nymphs can also cause damage to the crop (Markkula et al. 1976; Nissinen et al. 2014).

2.7.2 *Bactericera trigonica*

This psyllid species, together with *B. nigricornis* and *B. tremblayi*, belong to a taxonomic group called the *B. nigricornis* Förster group (Ouvrard & Burckhardt 2012) (Fig. 2B). This group is composed of multivoltines species characterized by the posterior extension of the male proctiger, the short female terminalia, the absence of surface spinules in the forewing, the small genal cones and the narrow third antennal segment (Klimaszewski 1975). The three species were often confused in the literature because they are very close in their morphology with considerable variation within species, thus the species complex was revised and described by Hodkinson (1981). Within species, males and females can be clearly distinguished by their genitalia that is also the morphological character used to distinguish between males of the three species. More specifically, the length of the api-

cal segment of the aedeagus and the shape of its apex are useful to distinguish between males of the different species. Regarding their reproduction, in the sexual phase, after mating and egg maturation, females oviposit in the edges or in the underside of the host plant leaves. Similarly to the three species belonging to the *B. nigricornis* group, the eggs possess a characteristic basal pedicel that is inserted into the host plant tissue through which is believed an interchange of water with the plant occurs to avoid desiccation of the egg (Othmen et al. 2019). After hatching, the nymphal or immature stages are dorsoventrally compressed (first instars are more elongated than the last stages that are discoid) and orange or light brown in color (Ouvrard & Burckhardt 2012). *Bactericera trigonica* has two or three generations per year (Hodkinson 1981; 2009).

Bactericera trigonica has been found in different countries in the Mediterranean region feeding mainly on plants of the family Apiaceae, especially on carrot and celery crops (Hodkinson 1981; Burckhardt & Freuler 2000). Nevertheless, low numbers of adults have also been collected from potato fields (Teresani et al. 2015; Antolínez et al. 2019).

Regarding CaLsol transmission, *B. trigonica* has been demonstrated as a highly efficient vector in Apiaceae with differences in the transmission rates achieved by males and females (transmission rate: 81.66 ± 7.26 for males and 80.00 ± 12.58 for females). Females of *B. trigonica* significantly reached the phloem more times and tended to salivate longer than males, thereby affecting the CaLsol titer transmitted. Thus, females of *B. trigonica* with high CaLsol titers inoculate higher titers than males. These gender-related differences may affect field transmission of CaLsol depending on the natural populations of *B. trigonica* (Antolínez et al. 2017a).

2.7.3 *Bactericera nigricornis*

Bactericera nigricornis belong to the *B. nigricornis* group (Fig. 2C). It has been reported as a polyphagous species able to feed on wild species belonging to the families Amaranthaceae, Boraginaceae, Brassicaceae, Apiaceae, Liliaceae, Papaveraceae, and Solanaceae (Hodkinson et al. 1981; Teresani et al. 2015; Othmen et al. 2019; Antolínez et al. 2019). The level of polyphagy in this group is exceptional among Psylloidea, which are usually host-specific (Hodkinson 1974). *Bactericera nigricornis* is present in many countries (Ouvrard et al. 2020) but little is known about its biology and dispersal ability, although it has been reported overwintering on conifers (Cermák et al. 2008). Further research on the life cycle of this species in Apiaceae crops is needed to identify its overwintering hosts and migration habits from wild host species under Mediterranean conditions.

Regarding the capability of *B. nigricornis* to transmit CaLsol, previous field work has shown that *B. nigricornis* can become naturally infected with CaLsol haplotype E

(Teresani et al. 2014; 2015), so further research to assess the vector efficiency of this psyllid species was needed. Thus, we conducted a study at ICA-CSIC (Madrid, Spain) to test the ability of *B. nigricornis* as a vector of CaLsol (haplotype E) in carrot crops. Adult *B. nigricornis* individuals were tested for the transmission of CaLsol using carrots as source and receptor plants. The same transmission protocol described above to assess the vector propensity of *B. nigricornis* in potato was used. After 18 d of AAP and latency period on CaLsol-infected carrots plants, psyllids were transferred in groups of 10 individuals (per plant) to carrot receptor plants and confined for a 72 h of IAP. Then, receptor plants were treated with 1 g L⁻¹ of Confidor® (Bayer, MO, USA) and kept under greenhouse conditions until CaLsol detection (Bertolini et al. 2015). Results showed that *B. nigricornis* is able to acquire and transmit the bacterium from carrot to carrot with a very high transmission rate (100%; N = 10). Thus, our study shows that *B. nigricornis* could be a relevant vector of CaLsol in Apiaceae crops because of its high ability to colonize carrot crops and its high vector propensity.

2.7.4 *Bactericera tremblayi*

Bactericera tremblayi is another psyllid species whose ability to transmit CaLsol to Apiaceae has been recently screened (Antolínez et al. 2017b). Even if *B. tremblayi* is morphologically similar to *B. trigonica* and *B. nigricornis* (Fig. 2D), it is morphologically closer to the latter (Hodkinson 1981).

To assess the potential role of *B. tremblayi* as a vector of CaLsol, Antolínez et al. (2017b) carried out several assays to assess the probing behavior of *B. tremblayi* using the electrical penetration graph (EPG) technique and its settling preference on different Apiaceae crops (leek (*Allium ampeloprasum* L.) and carrot), as well as its vector propensity. In this study, *B. tremblayi* preferred to settle, oviposit, and feed on leek but also settled and fed from the phloem of carrot plants. This result was unexpected because previous attempts to rear *B. tremblayi* on carrots were unsuccessful (Hodkinson 2009). Regarding its role as a vector of CaLsol in Apiaceae, the work of Antolínez et al. (2017b) also showed that *B. tremblayi* is able to ingest from the phloem of carrot plants and consequently can acquire the bacterium but failed to transmit it from carrot-to-carrot plants.

To date, *B. tremblayi* has been found in very low populations in carrot fields (Teresani et al. 2015; Antolínez et al. 2019). However, it has been reported as a serious direct pest in onion (*Allium cepa* L.) and leek crops in Spain, France, Bosnia-Herzegovina, Bulgaria, Greece, Turkey, Serbia and Iran (Ouvrard & Burckhardt 2012), suggesting that this psyllid may constitute a potential threat to carrot crops because leek and onion fields are commonly grown in the vicinity of carrot crops. Moreover, individuals of this psyllid species have also tested positive for CaLsol using real-time PCR (Teresani et al. 2015). However, it is important to note here that the presence of a pathogen in a given vector spe-

cies does not mean that the species is capable of transmitting that pathogen. The case of *B. tremblayi* and CaLsol is a good example of an insect species that can acquire the pathogen from an infected plant but fails to transmit it to a healthy plant, and thus cannot be considered a vector.

2.7.5 *Trioza erytreae*

The ability of *T. erytreae*, a species that sporadically can visit carrot, to transmit CaLsol to carrot was studied by Quintana-Gonzalez de Chavez et al. (2020). *Trioza erytreae* is able to transmit CaLsol from carrot to carrot plants when forced to feed on them. However, when CaLsol transmission was tested under multiple choice conditions, thus mimicking field conditions, *T. erytreae* failed to transmit the bacterium to carrots probably because this plant is a non-host for this psyllid species. Thus, *T. erytreae* should not be considered a vector of CaLsol in Apiaceae.

2.8 Other psyllids species as vectors of phytoplasma diseases

Phytoplasmas are transmitted in a persistent propagative manner by phloem-sucking insects, with psyllids, along with phloem-feeding Auchenorrhyncha, being their main vectors (Jarausch et al. 2019). In addition to horizontal transmission, psyllids can also vertically transmit phytoplasmas to their progeny (Mittelberger et al. 2017).

The most important psyllid species that act as vectors of Phytoplasma diseases are exclusively under the genus *Cacopsylla*. These psyllids are vectors of three important diseases that affect apple, pear, and stone fruits: apple proliferation, PD, and European stone fruit yellows disease, respectively. *Cacopsylla melanoneura* and *C. picta* are the species that are involved in the transmission of *Ca. P. mali*, the etiological agent of apple proliferation disease, which is a major threat in several apple-growing regions of the world (Bertaccini et al. 2014).

Most of these psyllid species are univoltine. *Cacopsylla picta* is present only in Europe and is monophagous on apple, it has one generation per year, and overwinters as adult on conifers. *Cacopsylla picta* is considered the main vector of ‘*Ca. P. mali*’ and transmits the disease polycyclically whenever psyllids are present on apple trees.

Cacopsylla melanoneura has a holo-Palaearctic distribution and is oligophagous on Rosaceae plants such as *Crataegus* spp., *Malus domestica* (Borkh.), *Mespilus germanica* (L.), and *Pyrus communis* (L.) (Ouvrard 2017). This species transmits ‘*Ca. P. mali*’ and can be an important vector species when *C. picta* is absent. This species also spends the winter on conifers and colonizes apple at the beginning of spring.

Cacopsylla pyri, *C. pyricola*, and *C. pyrisuga* (Foerster 1848; Hemiptera: Psyllidae) are the vectors of *Ca. P. pyri*, the causal agent PD, initially considered a virus (Jensen et al. 1964). *Cacopsylla pyri* is reported from Europe, the

Caucasus region, Central Asia, the Russian Far East, and China; *C. pyricola* naturally occurs in the western Palearctic region and has been introduced into the USA and Canada in the early nineteenth century (Ouvrard 2017). The two species of pear psyllids are oligophagous on *Pyrus* species.

Cacopsylla pruni, the vector of *Ca. P. prunorum*, is an oligophagous species that feeds on different species of the genus *Prunus* sp. and causes the disease known as European stone fruit yellows. A recent review provides a complete description of the morphology, life cycle and transmission ability of all these psyllid species (Jarausch et al. 2019).

3 Management strategies

The main damage caused by psyllids is due to their ability to transmit plant pathogenic bacteria and phytoplasmas. The management options include cultural, biological, chemical, and host-plant-resistance strategies. In this section we will focus on the control options interfering with the psyllid vectors alone and without describing other options to manage the plant pathogens they transmit.

Transmission of phloem-limited pathogens by psyllids is a relatively fast process. Psyllids take an average of 2.5–3 h to reach the phloem (Bonani et al. 2010; Antolínez et al. 2017a), but in some cases they may reach the phloem in only 6 min, as observed for *D. citri* (Miranda et al. unpublished data). Thus, control strategies require preventive measures that interfere either with the activity of the vector (by reducing the number of vectors landing and settling on the crop) or their propensity to transmit the pathogen. Therefore, psyllids should be controlled at the source (infected crops) and at the sink (susceptible crop where vectors land), as demonstrated in the management of aphids that transmit viruses in a persistent manner (Feres et al. 2017).

Insecticides proved to be a useful tools for reducing the spread of HLB in Brazil by reducing the numbers of *D. citri* present in citrus orchards (Bassanezi et al. 2020). In addition, some insecticides may interfere with the feeding and settling behavior of *D. citri* on citrus plants (Miranda et al. 2016). In fact, systemic insecticides such as thiamethoxam and imidacloprid disrupted the feeding behaviour of *D. citri* by reducing the proportion of psyllids that exhibit sustained phloem ingestion, consequently lowering the transmission rate of CLAs (Carmo-Sousa et al. 2020).

Biological control can also be a complementary strategy to reduce vector numbers and delay psyllid build-up at the source (infected crops). For example, the parasitoid *Tamarixia dryi* (Waterson 1922) (Hymenoptera: Eulophidae) was shown to be an effective biocontrol agent of *T. erytreae* (Etienne & Aubert 1980). In Brazil, *T. radiata* (Waterson 1922) is released in external sources of inoculum (abandoned orchards and backyards) to reduce the migration of *D. citri* from these areas to commercial citrus orchards (Miranda and Ayres 2020).

However, insecticides or biocontrol alone may not prevent the transmission and spread of bacterial diseases vectored by psyllids. Preventive strategies based on habitat manipulation can interfere with landing, settlement, and movement of psyllids and should be considered a part of integrated pest management programs. In this sense, barrier or trap crops can be effective measures to reduce primary spread of infective psyllids reaching the crop. For example, *Murraya paniculata* (L.) treated with thiamethoxam was very attractive as a trap crop and acted as a sink for *D. citri*. The trap crop reduced both the number of psyllids captured in yellow sticky traps and the psyllids settled on citrus trees compared to fallow mowed grass fields by 40 % and 83 %, respectively. The trap crop also reduced HLB incidence by 43 % (Tomaseto et al. 2019). In addition, physical or optical barriers can be effective tactics to reduce psyllid landing and reduce the primary spread of the disease incidence at the sink. Another promising alternative for *D. citri* management strategy is the preventive applications of processed kaolin in citrus orchards (Miranda et al. 2018). Nets and other physical barriers proved to be effective measures to control *B. cockerelli* and the transmission of CaLsol to potatoes in New Zealand (Merfield et al. 2015). Similar results were obtained in Finland where insect nets as well as processed kaolin sprayed on carrot plants were an effective strategy to control *T. apicalis*, the major vector of CaLsol in northern Europe (Nissinen et al. 2020b). A metalized mulch covering the soil of a young citrus orchard was able to slow the spread of *D. citri* and reduce HLB pressure (Croxtan & Stansly 2014). UV-absorbing plastics were able to reduce the movement and spread of *D. citri* in enclosed environments (Miranda et al. 2015). In summary, a combination of optical and physical barriers, trap or border crops, biocontrol agents, and systemic insecticides could represent an effective and sustainable management strategy for psyllid populations and psyllid-transmitted bacterial diseases.

Acknowledgments: We would like to acknowledge our laboratory colleagues María Plaza, Sandra Pla, and Irene Ontiveros (ICA-CSIC Madrid) for their help with the CaLso transmission experiments. Furthermore, we would like to acknowledge all the advice given by the Dr. Jose Luis Palomo from the Centro Regional de Diagnóstico, Junta de Castilla y León, Salamanca (Spain) with the CaLso transmission assays. The European Union Horizon 2020 research and innovation programme under grant agreement No. 635646, POnTE (Pest Organisms Threatening Europe), No. 817526, PRE-HLB (Preventing HLB epidemics for ensuring citrus survival in Europe) and the National Institute for Agronomic Research (INIA) (E-RTA2014-00008-C04-04) provided financial support for the CaLso transmission experiments described in this work.

References

- Abad, J. A., Bandla, M., French-Monar, R. D., Liefting, L. W., & Clover, G. R. G. (2009). First report of the detection of ‘*Candidatus Liberibacter*’ species in Zebra Chip disease-infected potato plants in the United States. *Plant Disease*, 93(1), 108–109. <https://doi.org/10.1094/PDIS-93-1-0108C>
- Abdullah, N. M. (2008). Life history of the potato psyllid *Bactericera cockerelli* (Homoptera: Psyllidae) in controlled environment agriculture in Arizona. *African Journal of Agricultural Research*, 3(1), 5A6795F34070. <https://doi.org/10.5897/AJAR.9000464>
- Alfaro-Fernández, A., Cebrián, M. C., Villaescusa, F. J., de Mendoza, A. H., Ferrándiz, J. C., Sanjuán, S., & Font, M. I. (2012a). First Report of “*Candidatus Liberibacter solanacearum*” in Carrot in Mainland Spain. *Plant Disease*, 96(4), 582–582. <https://doi.org/10.1094/PDIS-11-11-0918-PDN>
- Alfaro-Fernández, A., Hernández-Llopis, D., & Font, M. I. (2017). Haplotypes of ‘*Candidatus Liberibacter solanacearum*’ identified in Umbelliferous crops in Spain. *European Journal of Plant Pathology*, 149(1), 127–131. <https://doi.org/10.1007/s10658-017-1172-2>
- Alfaro-Fernández, A., Siverio, F., Cebrián, M. C., Villaescusa, F. J., & Font, M. I. (2012b). “*Candidatus Liberibacter solanacearum*” Associated with *Bactericera trigonica*-affected carrots in the Canary Islands. *Plant Disease*, 96(4), 581–581. <https://doi.org/10.1094/PDIS-10-11-0878-PDN>
- Ammar, E. D., Shatters, R. G., Jr., Lynch, C., & Hall, D. G. (2011). Detection and relative titer of *Candidatus Liberibacter asiaticus* in the salivary glands and alimentary canal of *Diaphorina citri* (Hemiptera: Psyllidae) vector of citrus Huanglongbing disease. *Annals of the Entomological Society of America*, 104(3), 526–533. <https://doi.org/10.1603/AN10134>
- Antolínez, C. A., Fereres, A., & Moreno, A. (2017a). Sex-specific probing behaviour of the carrot psyllid *Bactericera trigonica* and its implication in the transmission of “*Candidatus Liberibacter solanacearum*”. *European Journal of Plant Pathology*, 147(3), 627–637. <https://doi.org/10.1007/s10658-016-1031-6>
- Antolínez, C. A., Fereres, A., & Moreno, A. (2017b). Risk assessment of “*Candidatus Liberibacter solanacearum*” transmission by the psyllids *Bactericera trigonica* and *B. tremblayi* from Apiaceae crops to potato. *Scientific Reports*, 7(1), 45534. <https://doi.org/10.1038/srep45534>
- Antolínez, C. A., Moreno, A., Ontiveros, I., Pla, S., Plaza, M., Sanjuán, S., ... Fereres, A. (2019). Seasonal abundance of psyllid species on carrots and potato crops in Spain. *Insects*, 10(9), 287. <https://doi.org/10.3390/insects10090287>
- Baldwin, E., Plotto, A., Manthey, J., McCollum, G., Bai, J., Irey, M., ... Luzio, G. (2010). Effect of *Liberibacter* infection (Huanglongbing disease) of citrus on orange fruit physiology and fruit/fruit juice quality: Chemical and physical analyses. *Journal of Agricultural and Food Chemistry*, 58(2), 1247–1262. <https://doi.org/10.1021/jf9031958>
- Bassanezi, R. B., Lopes, S. A., de Miranda, M. P., Wulff, N. A., Volpe, H. X. L., & Ayres, A. J. (2020). Overview of citrus Huanglongbing spread and management strategies in Brazil. *Tropical Plant Pathology*, 45(3), 251–264. <https://doi.org/10.1007/s40858-020-00343-y>

- Bertaccini, A., Duduk, B., Paltrinieri, S., & Contaldo, N. (2014). Phytoplasmas and phytoplasma diseases: A severe threat to agriculture. *American Journal of Plant Sciences*, 5(12), 1763–1788. <https://doi.org/10.4236/ajps.2014.512191>
- Bertaccini, A., Oshima, K., Kube, M., & Rao, G. P. (2019). *Phytoplasmas: Plant Pathogenic Bacteria-III*. Springer; <https://doi.org/10.1007/978-981-13-2832-9#toc>
- Bertolini, E., Teresani, G. R., Loiseau, M., Tanaka, F. A. O., Barbé, S., Martínez, C., ... Cambra, M. (2015). Transmission of “*Candidatus Liberibacter solanacearum*” in carrot seeds. *Plant Pathology*, 64(2), 276–285. <https://doi.org/10.1111/ppa.12245>
- Bey, N. S. (1931). Untersuchungen über Möhrenblattsauger. *Zeitschrift für Angewandte Entomologie*, 18(1), 175–188. <https://doi.org/10.1111/j.1439-0418.1931.tb00199.x>
- Bonani, J. P., Fereres, A., Garzo, E., Miranda, M. P., Appezzato-Da-Gloria, B., & Lopes, J. R. S. (2010). Characterization of electrical penetration graphs of the Asian citrus psyllid, *Diaphorina citri*, in sweet orange seedlings. *Entomologia Experimentalis et Applicata*, 134(1), 35–49. <https://doi.org/10.1111/j.1570-7458.2009.00937.x>
- Borgoni, P. C., Vendramim, J. D., Lourencão, A. L., & Machado, M. A. (2014). Resistance of citrus and related genera to *Diaphorina citri* Kuwayama (Hemiptera: Liviidae). *Neotropical Entomology*, 43(5), 465–469. <https://doi.org/10.1007/s13744-014-0230-0>
- Bové, J. M. (2006). Huanglongbing: A destructive, newly-emerging, century-old disease of citrus. *Journal of Plant Pathology*, 88(1), 7–37. <https://doi.org/10.4454/jpp.v88i1.828>
- Brown, J. K. (2016). *Vector-Mediated Transmission of Plant Pathogens*. APS Press; <https://doi.org/10.1094/9780890545355>
- Burckhardt, D. (1985). Taxonomy and host plant relationships of the *Trioza apicalis* Förster complex (Hemiptera, Homoptera: Triozidae). *Insect Systematics & Evolution*, 16(4), 415–432. <https://doi.org/10.1163/187631285X00379>
- Burckhardt, D. (1994). Psyllid pests of temperate and subtropical crop and ornamental plants (Hemiptera, Psylloidea): A review. *Trends in Agricultural Sciences. Entomology*, 2, 173–186.
- Burckhardt, D. (2005). *Ehrendorferiana*, a new genus of Neotropical jumping plant lice (Insecta: Hemiptera: Psylloidea) associated with conifers (Cupressaceae). *Organisms, Diversity & Evolution*, 5(4), 317–319. <https://doi.org/10.1016/j.ode.2005.08.001>
- Burckhardt, D., & Lauterer, P. (1997). A taxonomic reassessment of the trioizid genus *Bactericera* (Hemiptera: Psylloidea). *Journal of Natural History*, 31(1), 99–153. <https://doi.org/10.1080/00222939700770081>
- Burckhardt, D., & Freuler, J. (2000). Jumping plant-lice (Hemiptera, Psylloidea) from Sticky traps in carrot fields in valais Switzerland. *Bulletin de la Société Entomologique Suisse*, 73, 191–209. <https://doi.org/10.5169/seals-402777>
- Burckhardt, D., & Ouvrard, D. (2012). A revised classification of the jumping plant-lice (Hemiptera: Psylloidea). *Zootaxa*, 3509(1), 1–34. <https://doi.org/10.11646/zootaxa.3509.1.1>
- Burckhardt, D., Ouvrard, D., & Percy, D. M. (2021). An updated classification of the jumping plant-lice (Hemiptera: Psylloidea) integrating molecular and morphological evidence. *European Journal of Taxonomy*, 736, 137–182. <https://doi.org/10.5852/ejt.2021.736.1257>
- Butler, C. D., & Trumble, J. T. (2012). Identification and impact of natural enemies of *Bactericera cockerelli* (Hemiptera: Triozidae) in Southern California. *Journal of Economic Entomology*, 105(5), 1509–1519. <https://doi.org/10.1603/EC12051>
- CABI (2020). *Diaphorina citri* (Asian citrus psyllid). *Invasive Species Compendium*. <https://www.cabi.org/isc/datasheet/18615#toPictures> 2020.
- Canale, M. C., Tomaseto, A. F., Haddad, M. L., Coletta-Filho, H. D., & Lopes, J. R. S. (2017). Latency and persistence of “*Candidatus Liberibacter asiaticus*” in its psyllid vector, *Diaphorina citri* (Hemiptera: Liviidae). *Phytopathology*, 107(3), 264–272. <https://doi.org/10.1094/PHYTO-02-16-0088-R>
- Capoor, S. P., Rao, D. G., & Viswanath, S. M. (1967). *Diaphorina citri*, a vector of the greening disease of citrus in India. *Indian Journal of Agricultural Sciences*, 37, 572–576.
- Carmo-Sousa, M., Garcia, R. B., Wulff, N. A., Fereres, A., & Miranda, M. P. (2020). Drench application of systemic insecticides disrupts probing behavior of *Diaphorina citri* (Hemiptera: Liviidae) and inoculation of *Candidatus Liberibacter asiaticus*. *Insects*, 11(5), 314. <https://doi.org/10.3390/insects11050314>
- Carraro, L., Loi, N., Ermacora, P., Gregoris, A., & Osler, R. (1998a). Transmission of pear decline by using naturally infected *Cacopsylla pyri* L. *Acta Horticulturae*, (472): 665–668. <https://doi.org/10.17660/ActaHortic.1998.472.89>
- Carraro, L., Osler, R., Loi, N., Ermacora, P., & Refatti, E. (1998b). Transmission of European stone fruit yellows phytoplasmas by *Cacopsylla pruni*. *Journal of Plant Pathology*, 80, 233–239. <https://doi.org/10.4454/jpp.v80i3.823>
- Casteel, C. L., Hansen, A. K., Walling, L. L., & Paine, T. D. (2012). Manipulation of plant defense responses by the tomato psyllid (*Bactericera cockerelli*) and its associated endosymbiont *Candidatus Liberibacter Psyllaurous*. *PLoS One*, 7(4), e35191. <https://doi.org/10.1371/journal.pone.0035191>
- Catling, H. D. (1971). The bionomics of the South African citrus psylla, *Trioza erytrae* (Del Guercio) (Homoptera: Psyllidae) 3. The influence of host plant quality. *Journal of the Entomological Society of Southern Africa*, 34, 381–391.
- Catling, H. D. (1972). The bionomics of the South African citrus psylla, *Trioza erytrae* (Del Guercio) (Homoptera: Psyllidae). 6. Final population studies and a discussion of population dynamics. *Journal of the Entomological Society of Southern Africa*, 35, 235–251.
- Catling, H. D. (1973). Notes on the biology of the South African citrus psylla, *Trioza erytrae* (Del Guercio) (Homoptera: Psyllidae). *Journal of the Entomological Society of Southern Africa*, 36(2), 299–306.
- Cermák, V., & Lauterer, P. (2008). Overwintering of psyllids in South Moravia (Czech Republic) with respect to the vectors of the apple proliferation cluster phytoplasmas. *Bulletin of Insectology*, 61, 147–148.
- Cicero, J. M., Fisher, T. W., & Brown, J. K. (2016a). Localization of “*Candidatus Liberibacter solanacearum*” and evidence for surface appendages in the potato psyllid vector. *Phytopathology*, 106(2), 142–154. <https://doi.org/10.1094/PHYTO-04-15-0088-R>
- Cicero, J. M., Fisher, T. W., Qureshi, J. A., Stanly, P. A., & Brown, J. K. (2016b). Colonization and intrusive invasion of potato psyllid by “*Candidatus Liberibacter solanacearum*”. *Phytopathology*, 107(1), 36–49. <https://doi.org/10.1094/PHYTO-03-16-0149-R>
- Cifuentes-Arenas, J. C., Goes, A., de Miranda, M. P., Beattie, G. A. C., & Lopes, S. A. (2018). Citrus flush shoot ontogeny modulates biotic potential of *Diaphorina citri*. *PLoS One*, 13(1), e0190563. <https://doi.org/10.1371/journal.pone.0190563>
- Cocuzza, G. E. M., Urbaneja, A., Hernández-Suárez, E., Siverio, F., Silvestro, S. D., Tena, A., & Carmelo, R. (2017). A review on *Trioza erytrae* (African citrus psyllid), now in mainland

- Europe, and its potential risk as vector of huanglongbing (HLB) in citrus. *Journal of Pest Science*, 90(1), 1–17. <https://doi.org/10.1007/s10340-016-0804-1>
- Croxton, S. D., & Stansly, P. A. (2014). Metalized polyethylene mulch to repel Asian citrus psyllid, slow spread of huanglongbing and improve growth of new citrus plantings. *Pest Management Science*, 70(2), 318–323. <https://doi.org/10.1002/ps.3566>
- Davies, D. L., Guise, C. M., Clark, M. F., & Adams, A. N. (1992). Parry's disease is similar to pears decline and is associated with mycoplasma-like organisms transmitted by *Cacopsylla pyricola*. *Plant Pathology*, 41(2), 195–203. <https://doi.org/10.1111/j.1365-3059.1992.tb02338.x>
- Dixon, A. F. G. (1998). *Aphid Ecology: and optimization approach* (2nd ed.). Chapman and Hall.
- EPPO. (2020a). Distribution of *Trioza erytreae*. EPPO Global Database. <https://gd.eppo.int/taxon/TRIZER>
- EPPO. (2020b). Update of the situation of *Trioza erytreae* in Spain. *EPPO Reporting Service* no. 08, num. article 2020/164. <https://gd.eppo.int/reporting/article-6842>
- EPPO. (2020c). *Candidatus Liberibacter solanacearum*. *OEPP. Bulletin OEPP. EPPO Bulletin. European and Mediterranean Plant Protection Organisation*, 50(1), 49–68. <https://doi.org/10.1111/epb.12611>
- EPPO. (2020d). *Bactericera cockerelli* and '*Candidatus Liberibacter solanacearum*'. *Bulletin OEPP. Bulletin OEPP. EPPO Bulletin. European and Mediterranean Plant Protection Organisation*, 47(3), 513–523.
- EPPO. (2020e). *Trioza apicalis*. <https://gd.eppo.int/taxon/TRIZAP>
- Etienne, J. & Aubert, B. (1980). Biological control of psyllid vectors of greening disease on reunion island. International Organization of Citrus Virologists Conference Proceedings (pp. 118–121).
- Fathi, S. A. A. (2011). Population density and life-history parameters of the psyllid *Bactericera nigricornis* (Forster) on four commercial cultivars of potato. *Crop Protection (Guildford, Surrey)*, 30(7), 844–848. <https://doi.org/10.1016/j.cropro.2011.03.003>
- Fereres, A. (2015). Insect vectors as drivers of plant virus emergence. *Current Opinion in Virology*, 10, 42–46. <https://doi.org/10.1016/j.coviro.2014.12.008>
- Fereres, A., Kampmeier, G. E., & Irwin, M. E. (1999). Aphid attraction and preference for soybean and pepper plants infected with Potyviridae. *Annals of the Entomological Society of America*, 92(4), 542–548. <https://doi.org/10.1093/aesa/92.4.542>
- Fereres, A., Irwin, M. E., & Kampmeier, G. E. (2017). Aphid Movement: Process and Consequences. In H. van Emden & R. Harrington (Eds.), *Aphids as Crop Pests* (2nd ed., pp. 196–224). Oxfordshire: CABI. <https://doi.org/10.1079/9781780647098.0196>
- Fisher, T. W., Vyas, M., He, R., Nelson, W., Cicero, J. M., Willer, M., ... Brown, J. K. (2014). Comparison of potato and Asian citrus psyllid adult and nymph transcriptomes identified vector transcripts with potential involvement in circulative, propagative *Liberibacter* transmission. *Pathogens (Basel, Switzerland)*, 3(4), 875–907. <https://doi.org/10.3390/pathogens3040875>
- George, J., Ammar, E. D., Hall, D. G., Shatters, R. G., Jr., & Lapointe, S. L. (2018). Prolonged phloem ingestion by *Diaphorina citri* nymphs compared to adults is correlated with increased acquisition of citrus greening pathogen. *Scientific Reports*, 8(1), 10352. <https://doi.org/10.1038/s41598-018-28442-6>
- Gibbs, A. J., & Gower, J. C. (1960). The use of a multiple-transfer method in plant virus transmission studies: Some statistical points arising in the analysis of results. *Annals of Applied Biology*, 48(1), 75–83. <https://doi.org/10.1111/j.1744-7348.1960.tb03506.x>
- Gottwald, T. R. (2010). Current epidemiological understanding of citrus Huanglongbing. *Annual Review of Phytopathology*, 48(1), 119–139. <https://doi.org/10.1146/annurev-phyto-073009-114418>
- Haapalainen, M. (2014). Biology and epidemics of *Candidatus Liberibacter* species, psyllid-transmitted plant-pathogenic bacteria. *Annals of Applied Biology*, 165(2), 172–198. <https://doi.org/10.1111/aab.12149>
- Haapalainen, M., Latvala, S., Rastas, M., Wang, J., Hannukkala, A., Pirhonen, M., & Nissinen, A. I. (2018). Carrot pathogen '*Candidatus Liberibacter solanacearum*' haplotype C detected in symptomless potato plants in Finland. *Potato Research*, 61(1), 31–50. <https://doi.org/10.1007/s11540-017-9350-3>
- Haapalainen, M., Wang, J., Latvala, S., Lehtonen, M., Pirhonen, M., & Nissinen, A. (2018b). Genetic variation of '*Candidatus Liberibacter solanacearum*' Haplotype C and identification of a novel haplotype from *Trioza urticae* and stinging nettle. *Phytopathology*, 108(8), 925–934. <https://doi.org/10.1094/PHTO-12-17-0410-R>
- Haapalainen, M., Latvala, S., Wickström, A., Wang, J., Pirhonen, M., & Nissinen, A. I. (2020). A novel haplotype of '*Candidatus Liberibacter solanacearum*' found in Apiaceae and Polygonaceae family plants. *European Journal of Plant Pathology*, 156(2), 413–423. <https://doi.org/10.1007/s10658-019-01890-0>
- Hall, D. G., Albrecht, U., & Bowman, K. D. (2016). Transmission rates of '*Ca. Liberibacter asiaticus*' by Asian citrus psyllid are enhanced by the presence and developmental stage of citrus flush. *Journal of Economic Entomology*, 109(2), 558–563. <https://doi.org/10.1093/jee/tow009>
- Hall, D. G., Wenninger, E. J., & Hentz, M. G. (2011). Temperature studies with the Asian citrus psyllid, *Diaphorina citri*: Cold hardiness and temperature thresholds for oviposition. *Journal of Insect Science*, 11(83), 1–15. <https://doi.org/10.1673/031.011.8301>
- Hansen, A., Trumble, J., Stouthamer, R., & Paine, T. (2008). A new Huanglongbing species, '*Candidatus Liberibacter psyllauros*,' found to infect tomato and potato, is vectored by the psyllid *Bactericera cockerelli* (Sulc). *Applied and Environmental Microbiology*, 74(18), 5862–5865. <https://doi.org/10.1128/AEM.01268-08>
- Henne, D. C., Paetzold, L., Workneh, F., & Rush, C. M. (2010). Evaluation of potato psyllid cold tolerance, overwintering survival, sticky trap sampling, and effects of *Liberibacter* on potato psyllid alternative host plants. In F. Workneh, & C. M. Rush (Eds.), *Proceedings of the 10th Annual 2010 Zebra Chip Reporting Session*, Dallas (pp 149–153).
- Hodkinson, I. D. (1974). The biology of the Psylloidea (Homoptera): A review. *Bulletin of Entomological Research*, 64(2), 325–338. <https://doi.org/10.1017/S0007485300031217>
- Hodkinson, I. D. (1981). Status and taxonomy of the *Trioza* (*Bactericera*) *nigricornis* Förster complex (Homoptera: Triozidae). *Bulletin of Entomological Research*, 71(4), 671–679. <https://doi.org/10.1017/S0007485300010208>
- Hodkinson, I. D. (1984). The biology and ecology of the gall-forming Psylloidea (Homoptera). In T. N. Ananthakrishnan (Ed.), *Biology of gall insects* (pp. 59–77). Hodder Arnold H&S.
- Hodkinson, I. D. (2009). Life cycle variation and adaptation in jumping plant lice (Insecta: Hemiptera: Psylloidea): a global synthesis. *Journal of Natural History*, 43(1–2), 65–179. <https://doi.org/10.1080/00222930802354167>

- Hung, T. H., Hung, S. C., Chen, C. N., Hsu, M. H., & Su, H. J. (2004). Detection by PCR of *Candidatus Liberibacter asiaticus*, the bacterium causing citrus huanglongbing in vector psyllids: Application to the study of vector pathogen relationships. *Plant Pathology*, 53(1), 96–102. <https://doi.org/10.1111/j.1365-3059.2004.00948.x>
- Inoue, H., Ohnishi, J., Ito, T., Tomimura, K., Miyata, S., Iwanami, T., & Ashihara, W. (2009). Enhanced proliferation and efficient transmission of *Candidatus Liberibacter asiaticus* by adult *Diaphorina citri* after acquisition feeding in the nymphal stage. *Annals of Applied Biology*, 155(1), 29–36. <https://doi.org/10.1111/j.1744-7348.2009.00317.x>
- Jagoueix, S., Bové, J. M., & Garnier, M. (1996). PCR detection of the two “*Candidatus*” *Liberibacter* species associated with greening disease of citrus. *Molecular and Cellular Probes*, 10(1), 43–50. <https://doi.org/10.1006/mcpr.1996.0006>
- Jarausch, B., Tedeschi, R., Sauvion, N., Gross, J., & Jarausch, W. (2019). Psyllid Vectors. In A. Bertaccini, P. Weintraub, G. Rao, & N. Mori (Eds.), *Phytoplasmas: Plant Pathogenic Bacteria II* (pp. 53–78). Springer; https://doi.org/10.1007/978-981-13-2832-9_3
- Jensen, D. D., Griggs, W. H., Gonzales, C. Q., & Schneider, H. (1964). Pear decline virus transmission by pear psylla. *Phytopathology*, 54, 1346–1351.
- Klimaszewski, S. M. (1975). Psyllodea, Koliszk (Insecta: Homoptera). *Fauna Polonaise*, 3, 1–295.
- Knowlton, G. F., & Janes, M. J. (1931). Studies on the biology of *Paratrioza cockerelli* (Sulc). *Annals of the Entomological Society of America*, 24(2), 283–292. <https://doi.org/10.1093/aesa/24.2.283>
- Knowlton, G. F., & Thomas, W. L. (1934). Host plants of the potato psyllid. *Journal of Economic Entomology*, 27, 547–549. <https://doi.org/10.1093/jee/27.2.547>
- Kristoffersen, L., & Anderbrant, O. (2007). ‘Carrot psyllid (*Trioza apicalis*) winter habitats: Insights in shelter plant preference and migratory capacity’. *Journal of Applied Entomology*, 131(3), 174–178. <https://doi.org/10.1111/j.1439-0418.2007.01149.x>
- Láska, P. (1974). Studie über den Möhrenblattfloh (*Trioza apicalis* Först.) (Triozidae, Homoptera). *Acta Scientiarum Naturalium Academiae Scientiarum Bohemoslovacae*, 8, 1–44.
- Láska, P. (2011). Biology of *Trioza apicalis* – a review. *Plant Protection Science*, 47(2), 68–78. <https://doi.org/10.17221/1/2011-PPS>
- Lemoine, J. (1991). Dépérissement du poirier: Rôle de *Psylla pyri* dans sa dissémination. *Arboriculture Fruitière*, 442, 28–32.
- Liefting, L. W., Sutherland, P. W., Ward, L. I., Paice, K. L., Weir, B. S., & Clover, G. R. G. (2009). A new “*Candidatus Liberibacter*” species associated with diseases of solanaceous Crops. *Plant Disease*, 93(3), 208–214. <https://doi.org/10.1094/PDIS-93-3-0208>
- List, G. M. (1939). The potato and tomato psyllid and its control on tomatoes. *Colorado Agricultural Experimental Station Bulletin*, 454, 33.
- Liu, Y. H., & Tsai, J. H. (2000). Effects of temperature on biology and life table parameters of the Asian citrus psyllid, *Diaphorina citri* Kuwayama (Homoptera: Psyllidae). *Annals of Applied Biology*, 137(3), 201–206. <https://doi.org/10.1111/j.1744-7348.2000.tb00060.x>
- Loiseau, M., Garnier, S., Boirin, V., Merieau, M., Leguay, A., Renaudin, I., ... Gentit, P. (2014). First Report of “*Candidatus Liberibacter solanacearum*” in Carrot in France. *Plant Disease*, 98(6), 839–839. <https://doi.org/10.1094/PDIS-08-13-0900-PDN>
- Lopes, S. A., Luiz, F. Q. B. F., Martins, E. C., Fassini, C. G., Sousa, M. C., Barbosa, J. C., & Beattie, G. A. C. (2013). “*Candidatus Liberibacter asiaticus*” titers in citrus and acquisition rates by *Diaphorina citri* are decreased by higher temperature. *Plant Disease*, 97(12), 1563–1570. <https://doi.org/10.1094/PDIS-11-12-1031-RE>
- López, M. M., Marco-Noales, E., & Bertolini, E. (2015). Aumenta el riesgo de huanglongbing, causado por ‘*Candidatus Liberibacter*’ spp., que supone la mayor amenaza actual para la citricultura española. *Phytoma*, 270, 32–34.
- Mann, R. S., Pelz-Stelinski, K., Hermann, S. L., Tiwari, S., & Stelinski, L. L. (2011). Sexual transmission of a plant pathogenic bacterium, *Candidatus Liberibacter asiaticus*, between conspecific insect vectors during mating. *PLoS One*, 6(12), e29197. <https://doi.org/10.1371/journal.pone.0029197>
- Markkula, M., Laurema, S., & Tiittanen, K. (1976). Systemic damage caused by *Trioza apicalis* on carrot. *Symposia Biologica Hungarica*, 16, 153–155. https://doi.org/10.1007/978-1-4613-4274-8_24
- Martini, X., Hoyte, A., & Stelinski, L. L. (2014). Abdominal color of the Asian citrus psyllid (Hemiptera: Liviidae) is associated with flight capabilities. *Annals of the Entomological Society of America*, 107(4), 842–847. <https://doi.org/10.1603/AN14028>
- Massonie, G., Garnier, M., & Bové, J. M. (1976). Transmission of Indian citrus decline by *Trioza erytrae* (Del Guercio), the vector of South African greening. In International Organization of Citrus Virologists Conference Proceedings (1957–2010) (7, 7). <https://escholarship.org/uc/item/4dh8x79m>
- Mauck, K. E., Sun, P., Meduri, V., & Hansen, A. K. (2019). New Ca. *Liberibacter* psyllaous haplotype resurrected from a 49-year-old specimen of *Solanum umbelliferum*: A native host of the psyllid vector. *Scientific Reports*, 9(1), 9530. <https://doi.org/10.1038/s41598-019-45975-6>
- McClean, A. P. D. (1974). The efficiency of citrus psylla, *Trioza erytrae* (Del G.) as a vector of greening disease of citrus. *Phytophylactica*, 6, 45–54.
- McClean, A. P. D., & Oberholzer, P. C. J. (1965). Citrus psylla, a vector of the greening disease of sweet orange. *South African Journal of Agricultural Science*, 8, 297–298.
- Merfield, C. N., Geary, I. J., Hale, R. J., & Hodge, S. (2015). Field evaluation of the effectiveness of mesh crop covers for the protection of potatoes from tomato potato psyllid. *New Zealand Journal of Crop and Horticultural Science*, 43(2), 123–133. <https://doi.org/10.1080/01140671.2015.1015576>
- Miranda, M. P., & Ayres, A. J. (2020). Asian Citrus Psyllid management in São Paulo State, Brazil. In J. A. Qureshi & P. A. Stansly (Eds.), *Asian Citrus Psyllid: Biology, Ecology and Management of the Huanglongbing vector* (pp. 210–221). CABI. <https://doi.org/10.1079/9781786394088.0210>
- Miranda, M. P., Santos, F. L. D., Felipe, M. R., Moreno, A., & Fereres, A. (2015). Effect of UV-blocking plastic films on take-off and host plant finding ability of *Diaphorina citri* (Hemiptera: Liviidae). *Journal of Economic Entomology*, 108(1), 245–251. <https://doi.org/10.1093/jee/tou036>
- Miranda, M. P., Yamamoto, P. T., Garcia, R. B., Lopes, J. P. A., & Lopes, J. R. S. (2016). Thiamethoxam and imidacloprid drench applications on sweet orange nursery trees disrupt the feeding and settling behaviour of *Diaphorina citri* (Hemiptera: Liviidae). *Pest Management Science*, 72(9), 1785–1793. <https://doi.org/10.1002/ps.4213>

- Miranda, M. P., Zanardi, O. Z., Tomaseto, A. F., Volpe, H. X. L., Garcia, R. B., & Prado, E. (2018). Processed kaolin affects the probing and settling behavior of *Diaphorina citri* (Hemiptera: Lividae). *Pest Management Science*, 74(8), 1964–1972. <https://doi.org/10.1002/ps.4901>
- Mittelberger, C., Obkircher, L., Oettl, S., Oppedisano, T., Pedrazzoli, F., Panassiti, B., ... Janik, K. (2017). The insect vector *Cacopsylla picta* vertically transmits the bacterium ‘*Candidatus Phytoplasma mali*’ to its progeny. *Plant Pathology*, 66(6), 1015–1021. <https://doi.org/10.1111/ppa.12653>
- Moll, J. N., & Martin, M. M. (1973). Electron microscope evidence that citrus psylla (*Trioza erytreae*) is a vector of greening disease in South Africa. *Phytophylactica*, 5, 41–44.
- Moran, V. C. (1968). The development of the citrus psylla, *Trioza erytreae* (Del Guercio) (Homoptera: Psyllidae), on Citrus lemon and four indigenous host plants. *Journal of the Entomological Society of Southern Africa*, 31(2), 391–402.
- Moran, V. C., & Blowers, J. R. (1967). On the biology of the South African citrus psylla, *Trioza erytreae* (Del Guercio) (Homoptera: Psyllidae). *Journal of the Entomological Society of Southern Africa*, 30, 96–106.
- Munyanzeza, J. E. (2010). Psyllids as vectors of emerging bacterial diseases of annual crops. *The Southwestern Entomologist*, 35(3), 471–477. <https://doi.org/10.3958/059.035.0335>
- Munyanzeza, J. E. (2012). Zebra Chip Disease of potato: Biology, epidemiology, and management. *American Journal of Potato Research*, 89(5), 329–350. <https://doi.org/10.1007/s12230-012-9262-3>
- Munyanzeza, J. E. (2015). Zebra Chip Disease, *Candidatus Liberibacter*, and potato psyllid: A global threat to the potato industry. *American Journal of Potato Research*, 92(2), 230–235. <https://doi.org/10.1007/s12230-015-9448-6>
- Munyanzeza, J. E., Crosslin, J. M., & Upton, J. E. (2007). Association of *Bactericera cockerelli* (Homoptera: Psyllidae) with “zebra chip,” a new potato disease in southwestern United States and Mexico. *Journal of Economic Entomology*, 100(3), 656–663. [https://doi.org/10.1603/0022-0493\(2007\)100\[656:A0BCHP\]2.0.CO;2](https://doi.org/10.1603/0022-0493(2007)100[656:A0BCHP]2.0.CO;2)
- Munyanzeza, J. E., Fisher, T. W., Sengoda, V. G., Garczynski, S. F., Nissinen, A., & Lemmetty, A. (2010a). First Report of “*Candidatus Liberibacter solanacearum*” Associated with Psyllid-Affected Carrots in Europe. *Plant Disease*, 94(5), 639–639. <https://doi.org/10.1094/PDIS-94-5-0639A>
- Munyanzeza, J. E., Fisher, T. W., Sengoda, V. G., Garczynski, S. F., Nissinen, A., & Lemmetty, A. (2010b). Association of *Candidatus Liberibacter solanacearum* with the psyllid, *Trioza apicalis* (Hemiptera: Triozidae) in Europe. *Journal of Economic Entomology*, 103(4), 1060–1070. <https://doi.org/10.1603/EC10027>
- Munyanzeza, J. E., Swisher, K. D., Hommes, M., Willhauck, A., Buck, H., & Meadow, R. (2015). First Report of “*Candidatus Liberibacter solanacearum*” Associated with Psyllid-Infested Carrots in Germany. *Plant Disease*, 99(9), 1269. <https://doi.org/10.1094/PDIS-02-15-0206-PDN>
- Mustafa, T., Horton, D. R., Cooper, W. R., Swisher, K. D., Zack, R. S., Pappu, H. R., & Munyanzeza, J. E. (2015). Use of Electrical Penetration Graph technology to examine transmission of “*Candidatus Liberibacter solanacearum*” to potato by three haplotypes of potato psyllid (*Bactericera cockerelli*; Hemiptera: Triozidae). *PLoS One*, 10(9), e0138946. <https://doi.org/10.1371/journal.pone.0138946>
- Nava, D. E., Torres, G. M. L., Rodrigues, M. D. L., Bento, J. M. S., & Parra, J. R. P. (2007). Biology of *Diaphorina citri* (Hem., Psyllidae) on different host and at different temperatures. *Journal of Applied Entomology*, 131(9–10), 709–715. <https://doi.org/10.1111/j.1439-0418.2007.01230.x>
- Nelson, W. R., Fisher, T. W., & Munyanzeza, J. E. (2011). Haplotypes of “*Candidatus Liberibacter solanacearum*” suggest long-standing separation. *European Journal of Plant Pathology*, 130(1), 5–12. <https://doi.org/10.1007/s10658-010-9737-3>
- Nelson, W. R., Munyanzeza, J. E., McCue, K. F., & Bové, J. M. (2013). The Pangaeon origin of “*Candidatus Liberibacter*” species. *Journal of Plant Pathology*, 95, 455–461. <https://doi.org/10.4454/JPP.V95I3.001>
- Nissinen, A., Haapalainen, M., Jauhiainen, L., Lindman, M., & Pirhonen, M. (2014). Different symptoms in carrots caused by male and female carrot psyllid feeding and infection by ‘*Candidatus Liberibacter solanacearum*’. *Plant Pathology*, 63(4), 812–820. <https://doi.org/10.1111/ppa.12144>
- Nissinen, A. I., Haapalainen, M., Ojanen, H., Pirhonen, M., & Jauhiainen, L. (2020a). Spreading of *Trioza apicalis* and development of “*Candidatus Liberibacter solanacearum*” infection on carrot in the field conditions. *Annals of Applied Biology*, 178(1), 39–50. <https://doi.org/10.1111/aab.12644>
- Nissinen, A., Pihlava, J.-M., Latvala, S., & Jauhiainen, L. (2020b). Assessment of the efficiency of different control programs to reduce *Trioza apicalis* Först. (Triozidae: Hemiptera) feeding damage and the spread of “*Candidatus Liberibacter solanacearum*” on carrots (*Daucus carota* ssp. *sativus* L.). *Annals of Applied Biology*, 177(2), 166–177. <https://doi.org/10.1111/aab.12603>
- Nissinen, A., Vanhala, P., Holopainen, J. K., & Tiilikkala, K. (2007). ‘Short feeding period of carrot psyllid (*Trioza apicalis*) females at early growth stages of carrot reduces yield and causes leaf discoloration’. *Entomologia Experimentalis et Applicata*, 125(3), 277–283. <https://doi.org/10.1111/j.1570-7458.2007.00628.x>
- Oke, A. O., Oladigbolu, A. A., Kunta, M., Alabi, O. J., & Sétamou, M. (2020). First report of the occurrence of Asian citrus psyllid *Diaphorina citri* (Hemiptera: Liviidae), an invasive species in Nigeria, West Africa. *Scientific Reports*, 10(1), 9418. <https://doi.org/10.1038/s41598-020-66380-4>
- Orlovskis, Z., Canale, M. C., Thole, V., Pecher, P., Lopes, J. R. S., & Hogenhout, S. A. (2015). Insect-borne plant pathogenic bacteria: Getting a ride goes beyond physical contact. *Current Opinion in Insect Science*, 9, 16–23. <https://doi.org/10.1016/j.cois.2015.04.007>
- Othmen, S. B., Abbes, K., Imem, M. E., Ouvrard, D., Rapisarda, C., & Chermiti, B. (2019). *Bactericera trigonica* and *B. nigricornis* (Hemiptera: Psylloidea) in Tunisia as potential vectors of ‘*Candidatus Liberibacter solanacearum*’ on Apiaceae. *Oriental Insects*, 53(4), 497–509. <https://doi.org/10.1080/00305316.2018.1536003>
- Ouvrard, D. (2017). *Psyl'list* – the world psylloidea database. <http://www.hemiptera-databases.com/psyllist>
- Ouvrard, D. (2020). *The World Psylloidea Database*. <https://www.hemiptera-databases.org/psyllist/?db=psylles&lang=en&card=taxon&rank=species&id=1332>
- Ouvrard, D., & Burckhardt, D. (2012). First record of the onion psyllid *Bactericera tremblayi* (Wagner, 1961) in France (Insecta: Hemiptera: Sternorrhyncha: Psylloidea), new symptoms on leek crops and reassessment of the *B. nigricornis*-group distribution.

- Bulletin OEPP. EPPO Bulletin. European and Mediterranean Plant Protection Organisation, 42(3), 585–590. <https://doi.org/10.1111/epb.12005>
- Ozols, E. (1925). Zala burkanu lapu uts (*Trioza viridula* Zett.). *Lauksaimniecības Parvaldes Izdevums*. Riga. Abstract in *Review of Applied Entomology (A)*, 14, 37.
- Palomo, J., Bertolini, E., Martin-Robles, M., Teresani, G., Lopez, M. M. & Cambra, M. (2014). Detección en Patata en España de un Haplotipo de “*Candidatus Liberibacter Solanacearum*” no Descrito en Solanáceas. In *Proceedings of the XVII Congress of the Spanish Phytopathological Society*.
- Paiva, P. E. B., & Parra, J. R. P. (2012). Life table analysis of *Diaphorina citri* (Hemiptera: Psyllidae) infesting sweet orange (*Citrus sinensis*) in São Paulo. *The Florida Entomologist*, 95(2), 278–284. <https://doi.org/10.1653/024.095.0206>
- Pearson, C. C., Backus, E. A., Shugart, H. J., & Munyaneza, J. E. (2014). Characterization and correlation of EPG waveforms of *Bactericera cockerelli* (Hemiptera: Triozidae): variability in waveform appearance in relation to applied signal. *Annals of the Entomological Society of America*, 107(3), 650–666. <https://doi.org/10.1603/AN13178>
- Pelz-Stelinski, K. S., Brlansky, H. R., Ebert, T. A., & Rogers, M. E. (2010). Transmission parameters for *Candidatus Liberibacter asiaticus* by Asian citrus psyllid. *Journal of Economic Entomology*, 103(5), 1531–1541. <https://doi.org/10.1603/EC10123>
- Perilla-Henao, L. M., & Casteel, C. L. (2016). Vector-borne bacterial plant pathogens: Interactions with hemipteran insects and plants. *Frontiers in Plant Science*, 7, 1163. <https://doi.org/10.3389/fpls.2016.01163>
- Pletsch, D. J. (1947). The potato psyllid *Paratrioza cockerelli* (Sulc): its biology and control. *Montana Agricultural Experimental Station Bulletin*, 446.
- Quintana-González de Chaves, M., Teresani, G. R., Hernández-Suárez, E., Bertolini, E., Moreno, A., Fereres, A., ... Siverio, F. (2020). ‘*Candidatus Liberibacter Solanacearum*’ is unlikely to be transmitted spontaneously from infected carrot plants to citrus plants by *Trioza erytreae*. *Insects*, 11(8), 514. <https://doi.org/10.3390/insects11080514>
- Raiol-Junior, L. L., Baia, A. D. B., Luiz, F. A. Q. B., Fassini, C. G., Marques, V. V., & Lopes, S. A. (2017). Improvement in the excised citrus leaf assay to investigate inoculation of ‘*Candidatus Liberibacter asiaticus*’ by the Asian citrus psyllid *Diaphorina citri*. *Plant Disease*, 101(3), 409–413. <https://doi.org/10.1094/PDIS-08-16-1093-RE>
- Rashed, A., Nash, T. D., Paetzold, L., Workneh, F., & Rush, C. M. (2012). Transmission efficiency of “*Candidatus Liberibacter solanacearum*” and potato Zebra Chip Disease progress in relation to pathogen titer, vector numbers, and feeding sites. *Phytopathology*, 102(11), 1079–1085. <https://doi.org/10.1094/PHYTO-04-12-0094-R>
- Richardson, M. L., & Hall, D. G. (2013). Resistance of Poncirus and Citrus × Poncirus germplasm to the Asian citrus psyllid. *Crop Science*, 53(1), 183–188. <https://doi.org/10.2135/cropsci2012.02.0091>
- Rubio-Covarrubias, O. A., Almeyda-Leon, I. H., Moreno, J. I., Sanchez-Salas, J. A., Sosa, R. F., Borbon-Soto, J. T., ... Cadena-Hinajosa, M. A. (2006). Distribution of potato purple top and *Bactericera cockerelli* Sulc. in the main potato production zones in Mexico. *Agricultura Técnica en México*, 32, 201–211.
- Rygg, T. (1977). Biological investigations on the carrot psyllid *Trioza apicalis* Förster (Homoptera, Triozidae). *Meldinger fra Norges Landbruks-hogskole*, 56, 1–20.
- Sandanayaka, W. R. M., Moreno, A., Tooman, L., Page-Weir, N. E. M., & Fereres, A. (2014). Stylet penetration activities linked to the acquisition and inoculation of *Candidatus Liberibacter solanacearum* by its vector tomato potato psyllid. *Entomologia Experimentalis et Applicata*, 151(2), 170–181. <https://doi.org/10.1111/eea.12179>
- Secor, G. A., Rivera, V. V., Abad, J. A., Lee, I. M., Clover, G. R. G., Liefing, L. W., ... De Boer, S. H. (2009). Association of “*Candidatus Liberibacter solanacearum*” with Zebra Chip Disease of potato established by graft and psyllid transmission, electron microscopy, and PCR. *Plant Disease*, 93(6), 574–583. <https://doi.org/10.1094/PDIS-93-6-0574>
- Sengoda, V. G., Buchman, J. L., Henne, D. C., Pappu, H. R., & Munyaneza, J. E. (2013). “*Candidatus Liberibacter solanacearum*” titer over time in *Bactericera cockerelli* (Hemiptera: Triozidae) after acquisition from infected potato and tomato plants. *Journal of Economic Entomology*, 106(5), 1964–1972. <https://doi.org/10.1603/EC13129>
- Sengoda, V. G., Cooper, W. R., Swisher, K. D., Henne, D. C., & Munyaneza, J. E. (2014). Latent period and transmission of “*Candidatus Liberibacter solanacearum*” by the potato psyllid *Bactericera cockerelli* (Hemiptera: Triozidae). *PLoS One*, 9(3), e93475. <https://doi.org/10.1371/journal.pone.0093475>
- Sétamou, M., Alabi, O. J., Kunta, M., Jifon, J. L., & Graça, J. V. (2016b). Enhanced acquisition rates of ‘*Candidatus Liberibacter asiaticus*’ by the Asian citrus psyllid (Hemiptera: Liviidae) in the presence of vegetative flush growth in citrus. *Journal of Economic Entomology*, 109(5), 1973–1978. <https://doi.org/10.1093/jee/tow171>
- Sétamou, M., da Graça, J. V., & Sandoval, J. L., II. (2016a). Suitability of native North American Rutaceae to serve as host plants for the Asian citrus psyllid (Hemiptera: Liviidae). *Journal of Applied Entomology*, 140(9), 645–654. <https://doi.org/10.1111/jen.12300>
- Shimwela, M. M., Narouei-Khandan, H. A., Halbert, S. E., Keremane, M. L., Minsavage, G. V., Timilsina, S., ... van Bruggen, A. H. (2016). First occurrence of *Diaphorina citri* in East Africa, characterization of the Ca. *Liberibacter* species causing huanglongbing (HLB) in Tanzania, and potential further spread of D. citri and HLB in Africa and Europe. *European Journal of Plant Pathology*, 146(2), 349–368. <https://doi.org/10.1007/s10658-016-0921-y>
- Stockton, D. G., Pescitelli, L. E., Martini, X., & Stelinski, L. L. (2017). Female mate preference in an invasive phytopathogen vector: How learning may influence mate choice and fecundity in *Diaphorina citri*. *Entomologia Experimentalis et Applicata*, 164(1), 16–26. <https://doi.org/10.1111/eea.12590>
- Šulc, K. (1909). *Trioza cockerelli* n. sp., a novelty from North America, being also of economic importance. *Acta Societatis Entomologicae Bohemicae*, 6(4), 102–108.
- Sumner-Kalkun, J. C., Highet, F., Arnsdorf, Y. M., Back, E., Carnegie, M., Madden, S., ... Kenyon, D. (2020). ‘*Candidatus Liberibacter solanacearum*’ distribution and diversity in Scotland and the characterisation of novel haplotypes from *Craspedolepta* spp. (Psyllidae: Aphalaridae). *Scientific Reports*, 10(1), 16567. <https://doi.org/10.1038/s41598-020-73382-9>
- Swisher Grimm, K. D., & Garczynski, S. F. (2019). Identification of a new haplotype of ‘*Candidatus Liberibacter solanacearum*’ in

- Solanum tuberosum*. *Plant Disease*, 103(3), 468–474. <https://doi.org/10.1094/PDIS-06-18-0937-RE>
- Tahzima, R., Maes, M., Achbani, E. H., Swisher, K. D., Munyaneza, J. E., & Jonghe, K. (2014). First report of “*Candidatus Liberibacter solanacearum*” on carrot in Africa. *Plant Disease*, 98(10), 1426–1426. <https://doi.org/10.1094/PDIS-05-14-0509-PDN>
- Tedeschi, R., & Alma, A. (2004). Transmission of apple proliferation phytoplasma by *Cacopsylla melanoneura* (Homoptera: Psyllidae). *Journal of Economic Entomology*, 97(1), 8–13. <https://doi.org/10.1093/jee/97.1.8>
- Teixeira, D. C., Saillard, C., Eveillard, S., Danet, J. L., Costa, P. I., Ayres, A. J., & Bové, J. (2005). ‘*Candidatus Liberibacter americanus*’, associated with citrus huanglongbing (greening disease) in São Paulo state, Brazil. *International Journal of Systematic and Evolutionary Microbiology*, 55(5), 1857–1862. <https://doi.org/10.1099/ijs.0.63677-0>
- Teresani, G. R., Bertolini, E., Alfaro-Fernández, A., Martínez, C., Tanaka, F. A. O., Kitajima, E. W., ... Font, M. I. (2014). Association of “*Candidatus Liberibacter solanacearum*” with a vegetative disorder of celery in Spain and development of a real-time PCR method for its detection. *Phytopathology*, 104(8), 804–811. <https://doi.org/10.1094/PHTO-07-13-0182-R>
- Teresani, G., Hernández, E., Bertolini, E., Siverio, F., Marroquín, C., Molina, J., ... Cambra, M. (2015). Search for potential vectors of “*Candidatus Liberibacter solanacearum*”: Population dynamics in host crops. *Spanish Journal of Agricultural Research*, 13(1), e1002. <https://doi.org/10.5424/sjar/2015131-6551>
- Teulon, D. A. J., Workman, P. J., Thomas, K. L., & Nielsen, M. C. (2009). *Bactericera cockerelli*: Incurion, dispersal and current distribution on vegetable crops in New Zealand. *New Zealand Plant Protection*, 62, 136–144. <https://doi.org/10.30843/nzpp.2009.62.4783>
- Tiwari, S., Killiny, N., Mann, R. S., Wenninger, E. J., & Stelinski, L. L. (2013). Abdominal color of the Asian citrus psyllid, *Diaphorina citri*, is associated with susceptibility to various insecticides. *Pest Management Science*, 69(4), 535–541. <https://doi.org/10.1002/ps.3407>
- Tomaseto, A. F., Marques, R. N., Fereres, A., Zanardi, O. Z., Volpe, H. X. L., Alquézar, B., ... Miranda, M. P. (2019). Orange jasmine as a trap crop to control *Diaphorina citri*. *Scientific Reports*, 9(1), 2070. <https://doi.org/10.1038/s41598-019-38597-5>
- Tsai, J. H., & Liu, Y. H. (2000). Biology of *Diaphorina citri* (Homoptera: Psyllidae) on four host plants. *Journal of Economic Entomology*, 93(6), 1721–1725. <https://doi.org/10.1603/0022-0493.93.6.1721>
- Valterová, I., Nehlin, G., & Borg-Karlson, A. K. (1997). Host plant chemistry and preferences in egg-laying *Trioza apicalis* (Homoptera, Psyllidae). *Biochemical Systematics and Ecology*, 25(6), 477–491. [https://doi.org/10.1016/S0305-1978\(97\)00028-8](https://doi.org/10.1016/S0305-1978(97)00028-8)
- Van den Berg, M. E., & Deacon, V. E. (1988). Dispersal of the citrus psylla, *Trioza erytreae* (Hemiptera: Triozidae), in the absence of its host plants. *Phytophylactica*, 20(4), 361–368.
- Van den Berg, M. A., Van Vuuren, S. P., & Deacon, V. E. (1992). Studies on greening disease transmission by the citrus psylla, *Trioza erytreae* (Hemiptera: Triozidae). *Israel Journal of Entomology*, 25, 51–56.
- Van Vuuren, S. P., Moll, J. N., & Wagner, M. J. (1986). The dynamics of greening transmission. In *Proceedings of the Citrus and Subtropical Fruit Research Institute Symposium* (pp. 48), CSFRI Publication, Nelspruit.
- Vargas-Madriz, H., Bautista-Martínez, N., Vera-Graziano, J., García-Gutiérrez, C., & Chavarín-Palacio, C. (2013). Morphometrics of eggs, nymphs, and adults of *Bactericera cockerelli* (Hemiptera: Triozidae), grown on two varieties of tomato under greenhouse conditions. *The Florida Entomologist*, 96(1), 71–79. <https://doi.org/10.1653/024.096.0110>
- Vereijssen, J., Smith, G., & Weintraub, P. (2018). *Bactericera cockerelli* (Hemiptera: Triozidae) and *Candidatus Liberibacter solanacearum* in potatoes in New Zealand: Biology, transmission, and implications for management. *Journal of Integrated Pest Management*, 9(1), 13, 1–21. <https://doi.org/10.1093/jipm/pmy007>
- Wallis, R. L. (1955). Ecological studies on the potato psyllid as a pest of potatoes. *USDA Technical Bulletin*, 1107.
- Wenninger, E. J., & Hall, D. G. (2008). Daily and seasonal dynamics in abdomen color in *Diaphorina citri* (Hemiptera: Psyllidae). *Annals of the Entomological Society of America*, 101(3), 585–592. [https://doi.org/10.1603/0013-8746\(2008\)101\[585:DASPIA\]2.0.CO;2](https://doi.org/10.1603/0013-8746(2008)101[585:DASPIA]2.0.CO;2)
- Westbrook, C. J., Hall, D. G., Stover, E., Duan, Y. P., & Lee, R. F. (2011). Colonization of Citrus and Citrus-related germplasm by *Diaphorina citri* (Hemiptera: Psyllidae). *HortScience*, 46(7), 997–1005. Retrieved from <https://doi.org/10.21273/HORTSCI.46.7.997> <https://doi.org/10.21273/HORTSCI.46.7.997>
- Wu, T., Luo, X., Xu, C., Wu, F., Qureshi, J. A., & Cen, Y. (2016). Feeding behavior of *Diaphorina citri* and its transmission of “*Candidatus Liberibacter asiaticus*” to citrus. *Entomologia Experimentalis et Applicata*, 161(2), 104–111. <https://doi.org/10.1111/eea.12496>
- Yamamoto, P. T., Felipe, M. R., Garbim, L. F., Coelho, J. H. C., Ximenes, N. L., Martins, E. C., Leite, A. P. R., Sousa, M. C., Abrahão, D. P., & Braz, J. D. (2006). *Diaphorina citri* Kuwayama (Hemiptera: Psyllidae): vector of the bacterium *Candidatus Liberibacter americanus*. *Proceedings of the Huanglongbing-Greening International Workshop*.
- Yang, X. B., & Liu, T. X. (2009). Life History and life tables of *Bactericera cockerelli* (Homoptera: Psyllidae) on eggplant and bell pepper. *Environmental Entomology*, 38(6), 1661–1667. <https://doi.org/10.1603/022.038.0619>
- Yang, X. B., Zhang, Y. M., Hua, L., & Liu, T. X. (2010). Life history and life tables of *Bactericera cockerelli* (Hemiptera: Psyllidae) on potato under laboratory and field conditions in the Lower Rio Grande Valley of Texas. *Journal of Economic Entomology*, 103(5), 1729–1734. <https://doi.org/10.1603/EC10083>

Manuscript received: 21 January 2021

Revisions requested: 22 May 2021

Modified version received: 3 June 2021

Accepted: 1 July 2021