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REVIEW

Friend or foe? Relationship between '*Candidatus* Liberibacter asiaticus' and *Diaphorina citri*

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Abstract
Interactions between insects and plant pathogens have been more enthusiastically studied in the recent decade, especially those relationships which takes the insects as vectors. The spectrum of these interactions ranges from mutualistic to pathogenic. The length of the co-evolutionary process will determine whether a microorganism shares a friend or a foe relationship with its host, and a friendship connection is frequently observed if the coexistence is longer. This review updates knowledge about the morphological, physiological and genetic mechanisms that drive the interaction between '*Candidatus* Liberibacter asiaticus' (Las) and its vector, the Asian citrus psyllid, *Diaphorina citri*. Las is the predominant causal agent of citrus huanglongbing (HLB) disease, the major constrain to citrus production worldwide. This bacterium is transmitted by *D. citri*, in a propagative-circulative manner during its feeding from plant host. Understanding of the interactions among vector, plant pathogen and host plant are important for the management of this vector-borne disease complex.

Keywords Huanglongbing · '*Candidatus* Liberibacter asiaticus' · Asian citrus psyllid · Vector-borne pathogens · Bacteria-vector interactions · Multitrophic interaction

Introduction

In recent decades, vector-borne bacteria have devastated citrus production. Among them, huanglongbing (HLB), also known as citrus greening, induces several symptoms including blotchy mottling leaves, yellow shoots, leaves showing zinc deficiency and vein corking, twig dieback, stunted growth, suppression of new root growth, small, green, and lopsided fruits, with aborted seeds (Bove et al. 2006; Wang et al. 2017). These symptoms have been related with the disruption of phloem function by callose deposition and accumulation of phloem proteins in the sieve tubes (Albrecht and Bowman 2008; Boava et al. 2017; Granato et al. 2019).

HLB is associated with three species of phloem limited, Gram-negative, fastidious alpha-proteobacteria: '*Candidatus* Liberibacter asiaticus' (Las), '*Candidatus* L. americanus' (Lam) and '*Candidatus* L. africanus' (Laf) (Jagoueix et al. 1997; Garnier et al. 2000; Teixeira et al. 2005). Las and Lam are transmitted between citrus trees by *Diaphorina citri* Kuwayama (Hemiptera: Liviidae), and Laf by African citrus trizoid *Trioza erytreae* Del Guercio (Hemiptera: Triozidae) (Bove 2006; Perilla-Henao and Casteel 2016). Las epidemics have led to serious economic losses in citrus industries in North and South America (Coletta-Filho et al. 2004). Las genome is rather small, approximately 1.23 Mb containing about 2,394 genes, lacking key enzymes-coding genes involved in oxidative phosphorylation and synthesis of some amino acids (Duan et al. 2009). This suggests that Las has a limited capacity for aerobic respiration, probably because it resides in phloem sieve cells of infected citrus plants or into *D. citri* (Duan et al. 2009). Furthermore, Las needs to utilize a range of

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amino acids from citrus as well as from *D. citri* as a source of energy (Hijaz and Killiny 2014).

The propagative-circulative nature of *D. citri*-Las interaction has been confirmed by many researchers (Inoue et al. 2009; Pelz-Stelinski et al. 2010; Mann et al. 2011; Ammar et al. 2016; Canale et al. 2017; Ammar et al. 2018). Acquisition occurs by intake of Las during *D. citri* phloem sap ingestion, Las reaches the hemocoel through the gut barrier (Ghanim et al. 2016) and spreads across *D. citri* organs and tissues (Ammar et al. 2011). Microscopy analysis showed Las colonizing a diverse of *D. citri* tissues, such as midgut, fat body, muscle, salivary glands, filter chamber and reproductive organs (Ammar et al. 2011, 2016; Hall et al. 2012). Besides, Las accumulates and propagates in *D. citri* endoplasmic reticulum associated vacuoles (Ghanim et al. 2017; Ammar et al. 2019). Finally, Las is inoculated into the plant phloem together with salivary secretions during *D. citri* feeding (Wu et al. 2016) and high titer of Las in the salivary glands of *D. citri* is required for proper inoculation (Inoue et al. 2009; Ammar et al. 2011).

Although the genetic mechanism of Las-*D.citri* interaction is still unclear, it is assumed that Las promotes strong transcriptomic and metabolic reprogramming of *D. citri* cells and these changes are more evident in adults than in immature stages (Mann et al. 2018). It is evident that Las possibly manipulates the vector *D. citri* to enhance its spread and transmission as was shown in other insect-borne plant pathogens (Pradit et al. 2019). This manipulation can be direct, within the vector after acquisition, or indirect mediated by the plant (Gross 2016; Eigenbrode et al. 2018). Manipulation includes changes in the vector behavior and performance and they can be dynamic with plant stage or disease progression. The evolutionary association time between plant pathogens and their vectors can provide insights into the interactions, whether beneficial or deleterious. Positive effects of plant pathogens on their vector's fitness are suggestive of an evolutionarily old relationship between the pathogen with its insect host while negative effects may indicate an evolutionarily young relationship (Purcell 1982; Pelz-Stelinski and Killiny 2016).

During the last decade, research on *D. citri*, Las and HLB has tried to find novel control strategies of this citrus disease that has inflicted economic damages. Recent research highlighted the role of symbiotic microorganisms in the coevolution of hosts and their parasites (Dheilly et al. 2015), which stresses its potential importance in biological control programs. Here we review the literature on the *D. citri*-Las interaction and its effects on fitness and behavior, immune system, metabolism, morphology and *D. citri* symbiotic microorganisms with the aim of increasing our understanding and suggesting future integrated management techniques based on the multitrophic interaction.

Pathogen-vector interactions

Fitness and behavior

Plant pathogens can modify the fitness of their vectors by inducing changes in the fecundity, fertility, development rate, survival, life table and population growth (Belliure et al. 2005; Guo et al. 2010; Nachappa et al. 2014; Eigenbrode et al. 2018).

It has been shown that Las affects *D. citri* fertility. The Las-positive *D. citri* females lay more eggs than Las-negative *D. citri* females (Pelz-Stelinski and Killiny 2016) (Fig. 1A). However, the mean percentages of fertile eggs produced by Las-positive and Las-negative *D. citri* females have no difference (Pelz-Stelinski and Killiny 2016). Also, the development time of *D. citri* may be affected due to Las infection. The development time of eggs laid by Las-positive *D. citri* females and the development time of Las-positive nymphs are significantly faster than Las-negative *D. citri* eggs and Las-negative nymphs, respectively. Likewise, there is a decrease of almost one-day in the development time, from the egg until adult, between Las-positive *D. citri* (16.62 days) and Las-negative *D. citri* (17.50 days) (Ren et al. 2016). This indicates that Las infection has a positive effect on the *D. citri* development, and Las-positive *D. citri* reaches the adult stage earlier than Las-negative *D. citri.*

D. citri survival is also affected by Las infection. Pelz-Stelinski and Killiny (2016) reported that the survival of Las-positive is lower than Las-negative *D. citri* adults under greenhouse conditions (photoperiod of 14 h light:10 h dark, 25–28 ^{o}C, and 60–80% relative humidity). Despite the studies show decreasing or no effect in *D. citri* longevity, the net reproductive rate reveals that the infection of Las benefits *D. citri* by increasing its population. More female adults are produced per day by Las-positive than Las-negative *D. citri*, suggesting a positive effect of Las on fecundity of *D. citri* (Pelz-Stelinski and Killiny 2016; Ren et al. 2016). In conjunction with an increased fecundity and population growth rates of Las-positive *D. citri*, reports about a possibility of transovarial Las-transmission (Pelz-Stelinski et al. 2010) propose a long evolutionary relationship between Las and *D. citri* (Pelz-Stelinski and Killiny 2016).

The dispersal and flight capacity of *D. citri* also may be manipulated directly by Las infection. For instance, the frequencies of short-distance and long-distance dispersal flights in Las-positive *D. citri* are higher than Las-negative *D. citri*. Moreover, *D. citri* that acquire Las initiates the flight sooner than Las-negative *D. citri* (Martini et al. 2015). The pathogen-induced increases in flight initiation and a short-distance dispersal by the vector probably favor multiple inoculations of the plant host at different locations, whereas an increase in long-distance dispersal may benefit the spread of the pathogen to distant areas (Martini et al. 2015; Stelinski 2019). Las does not affect the duration and speed of the long flights of *D. citri*.

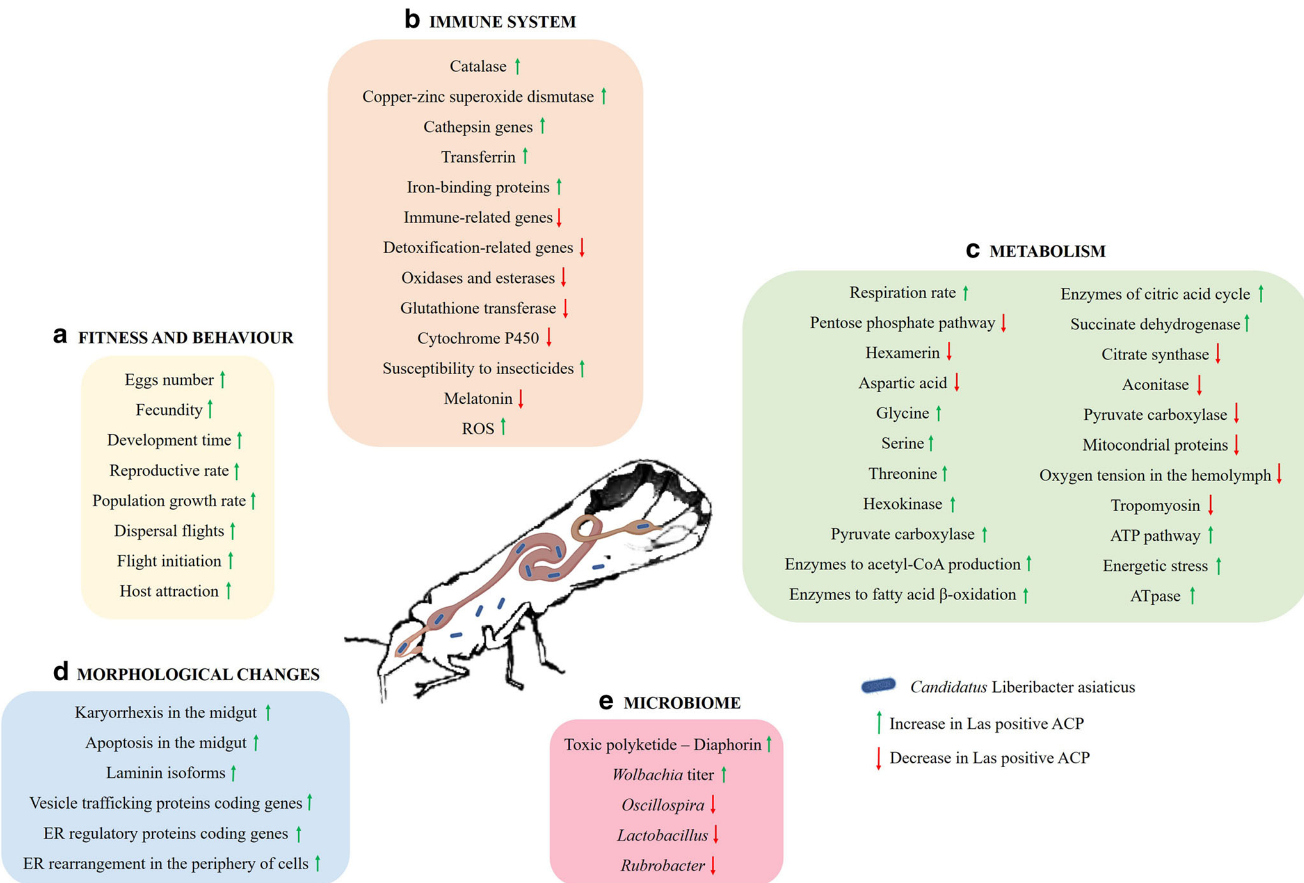

Fig. 1 '*Candidatus* Liberibacter asiaticus' manipulating Asian citrus psyllid (ACP) life-history traits during their interaction. The increase and decrease are related to Las-infected ACP in compare to Las-negative ACP. (A) Fitness and behavior; (B) Immune system; (C) Metabolism; (D) Morphological changes; (E) Microbiome

The increase of dispersal and flight initiation was explained by Killiny et al. (2017), who showed a significant reduction in total non-probing time, salivation time, and time from the last wave (E2 - phloem ingestion) of Electrical Penetration Graph (EPG) to the end of recording, indicating that Las-positive *D. citri* adults were at a higher hunger level and tended to forage more often.

Some studies have shown that *D. citri* adult males are more attracted to the odors of Las-positive *D. citri* female adults (Wenninger et al. 2008; Gharaei et al. 2014; Zanardi et al. 2018) and attractiveness of female Las-positive *D. citri* to male increases proportionally as the Las titers rise in female *D. citri* body. Thus, Las may have a positive effect in manipulating the movement of *D. citri* during selection of the mate for copulation, which is a possible evolutionary mechanism to promote the spread of the pathogen (Martini et al. 2015).

Immune system and metabolism

D. citri possesses a limited immune system, lacking a complete immune deficiency (Imd) pathway and most of the antimicrobial peptides (Arp et al. 2016), which reduces the ability of this insect to fight against Las infection (Arp et al. 2017). The incomplete immune system is also observed in other insect vectors and it has been suggested that this may be a result of coevolution between these insects and their endosymbiont bacteria (Arp et al. 2016, 2017).

Proteomic analysis showed that despite an incomplete immune system, *D. citri* responds to Las infection by activating several defense proteins such as catalase and copper-zinc superoxide dismutase (Gill et al. 2017) (Fig. 1B). Moreover, cathepsin genes are up-regulated in response to Las (Ramsey et al. 2017; Yu et al. 2019). Cathepsins are multifunctional proteins involved in apoptosis, immune response and development (Sun et al. 2017). Transferrin and other iron-binding proteins-coding genes are also up-regulated in response to Las (Ramsey et al. 2017; Kruse et al. 2017). These proteins limit Las access to iron, and regulate Las multiplication within the *D. citri* (Kruse et al. 2017). Higher levels of transferrin proteins were found in adult *D. citri* proteome in comparison with *D. citri* nymphs (Ramsey et al. 2017). These results indicate that these proteins may be related to a specific stage of *D. citri* development, explaining the difference of Las susceptibility between *D. citri* adults and nymphs (Fisher et al. 2014; Ramsey et al. 2017; Kruse et al. 2017).

In addition, two phagocytosis-inducing genes, GTP-binding Di-Ras and vacuolar protein sorting 16B (Vps16B) were up-regulated in Las-positive *D. citri* adults compared to Las-positive *D. citri* nymphs, suggesting that Las may enhance the activity of these genes to promote epithelial cell death and/or apoptosis and increase cellular vacuolation, promoting Las dissemination during the *D. citri* life stage which presents well developed immune system (Fisher et al. 2014; Kruse et al. 2017). Hemocyanin proteins-coding genes are also up-regulated in Las-positive *D. citri* (Ramsey et al. 2017; Kruse et al. 2018). *D. citri* hemocyanin 1 interacts physically with a protein of Las involved with the coenzyme A (CoA) biosynthesis, suggesting that this protein may participate in *D. citri* immune system (Ramsey et al. 2017).

Many *D. citri* genes are also down-regulated in response to Las (Fisher et al. 2014; Vyas et al. 2015; Kruse et al. 2017). For instance, detoxification-related genes are strongly suppressed in Las-positive *D. citri* (Tiwari et al. 2011b; Kruse et al. 2017). Several studies have demonstrated that Las promotes a reduction of general oxidases and esterases genes, such as glutathione transferase and cytochrome P450, which regulate the insecticide metabolism. Because of that, these genes are the main active site of most commercial insecticides (Tiwari et al. 2011a, b, c).

Furthermore, Nehela and Killiny (2018) have shown that Las infection affects negatively the melatonin (antioxidant) content in *D. citri*. The reduction of melatonin biosynthesis promoted by Las may contribute to the elevation of oxidative stress by the accumulation of both reactive oxygen species (ROS) and reactive nitrogen species (RNS). Another hypothesis is that Las utilizes tryptophan, the precursor of melatonin, in its metabolism.).

As Las is an obligatory intracellular parasite lacking several biosynthetic pathways, metabolic enzymes and secretion systems (Duan et al. 2009; Jain et al. 2017; Coyle et al. 2018), possibly it obtains essential compounds from its hosts. Las infection alters the rate of glycolysis, tricarboxylic acid (TCA) cycle metabolites, respiration rates and ATP content of *D. citri* (Jain et al. 2017). Several enzymes from the respiratory electron transport chain, which are absent in Las genome, are found in smaller quantities in Las-positive *D. citri* (Lu and Killiny 2017) (Fig. 1C). Expression of enzymes-coding genes involved in purine, carbon, pyrimidine, glycerophospholipid, and choline metabolic pathways were altered by Las in *D. citri* (Vyas et al. 2015).

Las-positive *D. citri* adults have less hexamerin, an amino acid-storage protein, which suggests that Las may manipulate free amino acid viability (Kruse et al. 2017). Moreover, the concentrations of L-proline, the main energy source of insects (Teulier et al. 2016), and L-aspartic acid were lower in Las-positive *D. citri* compared with the uninfected control (Killiny et al. 2017; Killiny and Jones 2018). The decrease in both amino acid concentrations may result from their oxidation to supplement the TCA cycle intermediates, which have higher demand under the energetic stress caused by Las infection. It may also result from the increase in its consumption by Las, once Las is unable to synthesize proline and L-aspartic acid (Duan et al. 2009; Wang and Trivedi 2013). This suggestion is supported by the respiration rate increase in Las-positive *D. citri*. On the other hand, the content of glycine and L-serine is increased in Las-positive *D. citri* compared with Las-negative *D. citri* (Killiny et al. 2017). Glycine and serine can be converted to 3-phosphoglycerate and incorporated through the glycolysis pathway. The increase of these amino acids could indicate the induction of glycolysis pathway on Las-positive *D. citri*. The increase in glycolysis rate is supported by increase in the gene expression of enzymes implicated in glycolysis such as hexokinase and pyruvate carboxylase (Killiny et al. 2017). Interestingly, unlike Las-positive adults, Las-positive *D. citri* nymphs have a reduction of glycine content, suggesting that Las should use this amino acid during nymphal stages (Killiny and Jones 2018).

Transcriptomic, proteomic and metabolomic studies suggest that not only glycolysis but also the TCA cycle is changed by Las in both nymphal and adult life stages (Killiny et al. 2017; Killiny and Jones 2018). The activation of TCA cycle in Las-positive *D. citri* indicated that it is under nutrient and energy stress. The enzymes that catalyze the first and the second step in fatty acid β-oxidation and the production of acetyl-CoA, as well as enzymes involved in the citric acid cycle, were induced in Las-positive *D. citri* adult. Citric acid was induced in both Las-positive *D. citri* nymphs and adults (Killiny et al. 2017; Killiny and Jones 2018). Succinate dehydrogenase and succinate semialdehyde dehydrogenase enzymes were also enhanced in Las-positive *D. citri* (Killiny et al. 2017). On the other hand, the level of malate and succinate in Las-positive *D. citri* were lower than the uninfected control. Since Las lacks isocitrate lyase, malate synthase (Duan et al. 2009), and glyoxylate bypass (Wang and Trivedi 2013; Jain et al. 2017), it is believed that Las is dependent on exogenous fumarate, malate, succinate, and aspartate as carbon substrates (Wang and Trivedi 2013; Killiny et al. 2017). Thus, it is possible that Las uptake TCA intermediaries from *D. citri*.

Despite the metabolism changes in full-body of Las-positive *D. citri*, differences in hemolymph are minimal between Las-positive and Las-negative *D. citri*. Proteome of the insect gut demonstrated that citrate synthase, aconitase, and pyruvate carboxylase, as well as several other mitochondrial proteins, were reduced in response to Las infection, indicating depression of mitochondrial function in this organ (Kruse et al. 2017, 2018). Likewise, a recent study indicated that the average oxygen tension in the hemolymph of Las-positive *D. citri* was significantly lower than that of Las-negative

D. citri, suggesting that this may be a result of the oxygen consumption by Las or due to the elevated *D. citri* respiration rate (Molki et al. 2019).

Expression of tropomyosin, an actin-binding protein, is decreased in response to Las infection (Lu and Killiny 2017; Lu et al. 2019). *D. citri* tropomyosin interacts with energy metabolism enzymes such as V-type proton ATPase subunit β-like (VAT) and citrate synthase. Knockdown of *D. citri* tropomyosin gene caused a reduction of VAT mRNA levels, indicating that *D. citri* tropomyosin could be related to ATP accumulation observed in Las-positive *D. citri* (Lu et al. 2019). Thus, Las may induce the ATP pathway in *D. citri* to fulfill its energy needs. This increase in energetic stress could be explained by the repression of ATPase/GTPase activities by Las, which contributes to ATP accumulation (Vahling et al. 2010). Las has a functional ATP/ADP translocase gene in its genome, which could be used by this bacterium to obtain ATP from *D. citri* (Duan et al. 2009; Jain et al. 2017).

Morphological changes

Recent works have identified various morphological changes in Las-positive *D. citri*, both at the cellular and organ levels, which may be involved in *D. citri* response to Las (Fig. 1D). A significant increase in karyorrhexis in the midgut tissue of the *D. citri* raised on Las-positive citrus in comparison with *D. citri* raised on healthy citrus was observed (Mann et al. 2018). Karyorrhexis is the degradation and rupture of the cell nucleus and breakup and distribution of the chromatin in the cytoplasm. The nuclei can appear folded or shaped like a half-moon. It is one of the processes that take place during apoptosis. Apoptosis has also been reported in the salivary glands of the brown planthopper *Nilaparvata lugens* as a response to infection by *Rice ragged stunt virus* (RRSV) (Huang et al. 2015) and West Nile virus (WNV) has been shown to induce apoptosis in the midgut and salivary glands of its mosquito vector *Culex pipiens* (Vaidyanathan and Scott 2006).

Along with karyorrhexis, an increased incidence of apoptosis has also been observed in *D. citri* midgut tissues (Ghanim et al. 2016). The increase in apoptosis and karyorrhexis has only been found in *D. citri* adults that were exposed to Las. Exposed *D. citri* nymphs do not exhibit these effects of Las infection. It is hypothesized that these nymphs have an attenuated immune response that provides a window for Las establishment. Researchers speculate that the nymph immune response is dampened to help in the establishment of bacterial endosymbiont titers. The first line of defense for *D. citri* after feeding on the phloem sap of the Las-positive citrus tree is the gut tissue. Apoptosis of infected cells would be one way for the insect to clear itself of a bacterial infection, however the Las is able to manipulate the hosts' cells in other ways to ensure its survival (Mann et al. 2018).

Las interact with intercellular matrix and membrane proteins to promote the adhesion and invasion to *D. citri* membranes and other surfaces (Vyas et al. 2015). For example, mucin 5AC, a gel-forming protein that act limiting/enhancing microbe infections (Nakjang et al. 2012), is increased in *D. citri* nymphs compared to adults, indicating that this protein may contribute to a gut environment more supportive for Las acquisition (Ramsey et al. 2017). Laminin isoforms genes are up-regulated in Las-positive *D. citri* nymphs compared to Las-negative *D. citri*. This protein is important for membrane formation during insect development, indicating that Las infection may disrupt membrane formation (Vyas et al. 2015). Moreover, cytoskeleton-related proteins, such as vinculin and talin, had down-regulated genes in Las-positive nymphs, suggesting that Las manipulate cytoskeleton networks to get access to intracellular and intercellular spaces (Ghanim et al. 2016).

Las resides and multiplies inside structures in the midgut tissue of *D. citri*, Liberibacter containing vacuoles (LCV). These vacuoles are comprised of two layers of rough endoplasmic reticulum (RER) filled with the Las. A side by side examination of Las-negative *D. citri* gut cells with Las-positive *D. citri* gut cells shows the Las-negative cells have a normal endoplasmic reticulum (ER) structure, while the Las-positive *D. citri* gut cells exhibited the LCV along with ER rearrangement in the periphery of cells (Ghanim et al. 2017). ER of Las-positive *D. citri* had a 'whorl' structure and this formation is similar to the midgut cells of *Aedes aegypti* mosquitoes which develop ER whorls upon blood digestion (Zhou et al. 2011). In *D. citri*, it was also found that the size of the vacuoles and the quantity of Las varied from cell to cell. This led the researchers to speculate that Las uses the vacuoles to multiply inside *D. citri* gut tissue (Ghanim et al. 2017).

As shown for other bacteria such as *Salmonella enterica* (Diacovich et al. 2017), *Legionella pneumophila* (Isberg et al. 2009), *Shigella flexneri* (Killackey et al. 2016) and *Brucella* spp. (Celli 2015), these vacuoles could be a means of protecting these procariotes during apoptosis and help it spread to other tissues once apoptosis is complete. A normal cell response to ER misfolding or disruptions is to send out ER-associated degradation (ERAD) and unfolded protein response (UPR) to restore ER homeostasis (Ghosh et al. 2019). If these cellular responses to ER disruption do not repair this organelle, apoptosis will occur.

These physical changes to the hosts' cells are not the only mechanism that Las uses to survive. The up-regulation of genes that are advantageous to the bacteria survival is common among intracellular organisms. In Las-positive *D. citri*, genes that code for vesicle trafficking proteins and ER regulatory proteins are significantly upregulated during an infection (Kruse et al. 2017). Thus, vesicle trafficking is a means for material transportation intercellularly and extracellularly, and the ER regulatory proteins mentioned before are a response to ER stress and protein misfolding.

Another morphological characteristic of *D. citri* is the three distinct phenotypes in abdominal color which can be blue, yellow or gray-brown (Wenninger et al. 2009b; Tiwari et al. 2012). Abdominal color morphology is not caused by Las but has been shown to play a role in Las infection. The blue coloration in *D. citri* abdomens has been attributed to the unusually high concentration of hemocyanin in the hemolymph (Ramsey et al. 2017) and blue *D. citri* has a significantly lower Las titer than the non-blue morphologies. Thus, the authors hypothesized that the reduction of hemocyanin expression would reduce the *D. citri* immune response and an increase in the titer of Las would be observed. However, Las titers decreased slightly in response to hemocyanin silencing (Hosseinzadeh et al. 2019).

The changes in cellular morphology that have been observed in *D. citri* midgut tissues may help to keep acquisition and transmission rates of Las low in adult psyllids even though they do not possess an Imd pathway to clear Gram-negative bacterial infections (Arp et al. 2017). It is in the *D. citri* nymph stages that the greatest acquisition and transmission rates of Las occurs (Ammar et al. 2016; George et al. 2018). *D. citri* nymphs may offer no resistance to infection by Las which, after acquisition, can successfully proliferate during *D. citri* life span (Mann et al. 2018).

Microbiome

Insect symbionts are involved in many aspects of their host life including physiology, biology, evolution, nutrition, and host life traits (Bourtzis and Miller 2008; Engel and Moran 2013; Minard et al. 2013; Ben-Yosef et al. 2014). The microbial communities that inhabit within insects vary among insect instars and host-plant species (Medina et al. 2011; Priya et al. 2012; Gauthier et al. 2015) and can be changed through time, developmental stage and insect age (Augustinos et al. 2019). The microbiota complements the host insect metabolism by producing metabolites that the insect is unable to produce (Cardoza et al. 2006; Adams et al. 2009), and by triggering an immune response that enables the insect host to overcome plant defenses and protect from invasion of pathogens (Oliver et al. 2003; Dillon and Dillon 2004; Engel and Moran 2013).

Studies have identified different endosymbionts in distinct *D. citri* populations (Subandiyah et al. 2000; Meyer and Hoy 2007; Marutani-Hert et al. 2011). *D. citri* harbors two intracellular endosymbiotic microorganisms within its bacteriome, which is a specialized symbiotic organ. Fluorescence *in situ* Hybridization (FISH) targeting 16 s rRNA confirmed the location of '*Candidatus* Profftella armatura' and '*Candidatus* Carsonella ruddii' in *D. citri* (Nakabachi et al. 2013a). *Profftella* has a conserved gene which produces toxic polyketide, Diaphorin, which plays a defensive role against invaders (Nakabachi et al. 2013b). Diaphorin has been shown to increase significantly in Las-positive *D. citri* in comparison to Las-negative insects (Fig. 1E). It is assumed that changes in polyketide synthesis may be associated to *Profftella*'s response to the pathogen directly or may be a response to the cellular changes caused by the pathogen (Ramsey et al. 2015).

Profftella and *Carsonella* can move from bacteriome to the ovary during transovarial transmission (Dan et al. 2017). Presence of these two endosymbionts in the ovary, hemolymph and within the host cell increases their chance to interact with *Liberibacter* spp. *Liberibacter* exhibits a propagative and circulative manner within the psyllid vector and can enter the bacteriome of *D. citri* and has a chance of horizontal gene transfer with endosymbionts. From that, there is evidence that *Profftella* transfer *lyse-E* type gene to the *Liberibacter* family horizontally, and this gene can facilitate resistance to toxic compounds, and balance the intracellular concentration of metabolites (Nakabachi et al. 2013a).

From all endosymbionts detected in *D. citri* population, most studies were focused on *Wolbachia*. This bacterium has been reported with some variation in all *D. citri* populations from all over the world (Guidolin and Cônsoli 2013). This variation can be related to temperature, host gender, *D. citri* age, *Wolbachia* strain, and host genetics (Hoffmann et al. 2014). *Wolbachia* has been localized in bacteriocytes, somatic and reproductive tissue, and it is maternally inherited symbiont (Fagen et al. 2012; Saha et al. 2012). *Wolbachia* is distributed in the midgut, filter chamber, Malpighian tubules. Las is also localized within these organs, but these microbes have not shown a high degree of co-localization (Kruse et al. 2017).

Studies of the correlation between *D. citri* microbial communities and Las has shown a negative correlation between Las titer and syncytium endosymbiont, but a positive relationship with *Wolbachia* (Fagen et al. 2012; Saha et al. 2012). In another report, *Wolbachia* levels were reported to be higher in Las-positive than in Las-negative *D. citri*. However, the occasional absence of *Wolbachia* in Las-positive *D. citri* suggests that *Wolbachia* is not an important factor in acquiring Las (Chu et al. 2016). Recently, Song et al. (2019) showed differences in the relative abundance of bacterial communities between Las-negative *D. citri* and Las-positive *D. citri*. For example, the relative abundance of most dominant bacteria decreased, such as *Oscillospira*, *Lactobacillus* and *Rubrobacter*, whereas the relative abundance of *Wolbachia* increased (Fig. 1E).

Multitrophic interactions: plant x pathogen x vector

The transmission of plant pathogens goes beyond a physical association with their vector and involves active modulation of plant processes by the bacteria to promote insect herbivore attraction, colonization and pathogen transmission (Orlovskis et al. 2015; Nehela et al. 2018). Phytophagous insects have a close relationship with their hosts, which use them mainly as a food source, oviposition sites and shelter. The host selection process involves several factors ranging from host location (guided by visual and olfactory cues emitted by plants) to nutritional adequacy (Ballhorn et al. 2008; Sule et al. 2012; Simon et al. 2015). *D. citri* has a range of hosts with more than 50 Rutaceae species, which presents fitness and preference differenced depending on the host (Halbert and Manjunath 2004; Teck et al. 2011; Alves et al. 2014, 2018).

The host-choice behavior by *D. citri* is complex and involves several factors, such as the host plant (e.g. phenological or nutritional plant stage), the sex and physiological stage of this insect (Wenninger et al. 2009a). Other psyllids species can be attracted by the color and mainly by the volatile organic compounds (VOC) released by a host plant (Horton and Landolt 2007; Guédot et al. 2009). Several VOC functions are assigned, whether ranging from protecting plants from insect and pathogen attack or attracting pollinators and beneficial insects such as parasitoids and predators. VOC profiles can be changed after biotic or abiotic stress (Baldwin 2010).

Insect vector feeding and pathogen infection may induce drastic changes in plant physiology (Blanc and Michalakis 2016).Vector-borne pathogens may change not only the host-plant phenotypic (morphological and physiological) characteristics, but can also modify the behavior and fitness of their insect vector (Mauck et al. 2010, 2016; Pelz-Stelinski and Killiny 2016; Maluta et al. 2017; Tamborindeguy et al. 2017). Changes in the performance of the insect vector (fitness and behavior) in infected host plants is mediated as a function of a series of plant responses upon infection, which include expression of different defensive genes, production of primary and secondary metabolites, nutritional quality and changes on the volatile profile (Mauck et al. 2016).

The influence of the pathogen on the host plant may vary depending on the species of plants and pathogens involved (Tamborindeguy et al. 2017). One of the most studied changes is the manipulation in the host-choice behavior of the vector insect (Mauck et al. 2010, 2016; Mann et al. 2012; Martini et al. 2015). For insect-borne pathogens, plant-emitted VOCs may be interesting features to manipulate, as sucking insects such as psyllids use odors as the main foraging clues in the search for potential plant host. Furthermore, plant infection by the pathogen alters the sensory cues (color and odor) used by herbivores in their favor and is considered an adaptive pathogen strategy with significant implications for its transmission and dissemination to new sites and hosts (Mauck et al. 2016).

D. citri adult have a strong preference for infected plants, however, over a period of several days, the *D. citri* disperses from infected to healthy plants. The initial attraction of *D. citri* to Las-positive plants was attributed to the changes in the VOC profile released by plants (Nehela et al. 2018). When quantified, significantly more methyl salicylate (MeSA) was released by Las-positive than Las-negative plants. In addition to VOCs, nutritional differences between hosts have been noticed. Las-positive plants showed lower levels of some nutrients such as nitrogen, phosphorus, sulfur, zinc, and iron than healthy plants (Mann et al. 2012; Patt et al. 2018). These results clearly indicate that the modifications mediated by pathogen-induced emission of the volatile compound attracts the *D. citri* at first. However, after some time, *D. citri* is able to realize that it is a sub-optimal nutritional host, migrating posteriorly, to a potentially suitable host (healthy plant).

A recent study showed that the attraction of *D. citri* to Las-positive citrus plants may be influenced the disease stage of the citrus plant. Recently Las-positive plants (< 6 months) presented a VOC profile with high concentrations of MeSA and β - caryophyllene, while plants with advanced disease progression (> 1 year) had low concentrations of MeSA and limonene, so that *D. citri* showed preference on landing on recently Las-positive plants (Martini et al. 2018). This difference in host choice behavior as a function of plant condition may be directly related to the poor nutritional quality of plants in which disease progression is advanced.

In a study carried out by Wu et al. (2015), a higher attractiveness of *D. citri* by Las-positive plants in different plant phenological stages was observed. Both shoots and mature leaves of Las-positive plants were initially more attractive to *D. citri* than Las-negative plants. In addition to the volatiles profile, the authors attribute coloration of the Las-positive plants as attractive for the *D. citri*. Zhao et al. (2013), indicated that the levels of sucrose, fructose, and glucose were significantly higher on the surfaces of Las-positive shoots than on the surfaces of healthy shoots. Thus, as previously reported by Mann et al. (2012), after feeding for some time on Las-positive plants, *D. citri* subsequently move to healthy plants probably because of either poor nutrition on the Las-positive hosts. In systems where an initial attraction to Las-positive plants is observed followed by dispersal toward uninfected counterparts and consequently aiding in the spread of the pathogen to new hosts are described as the "deceptive host phenotype hypothesis" (Mauck et al. 2010) and appear to be a common feature in psyllids (Davis et al. 2012;).

Another aspect that should be taken into consideration when studying a multitrophic interaction system is regarding the movement of the bacteriliferous vector insect (which is carrying the pathogen), which may later be responsible for the spread of the pathogen in disease-free areas. A study carried out by Martini et al. 2015, showed that when *D.citri* was reared on Las-positive plants, the short dispersal distance of *D. citri* male was higher compared to *D. citri* reared on Las-negative plants. In addition, *D. citri* that had a higher Las titer had a greater propensity for long-haul flights. In conclusion, the study showed that Las infection increases the probability of *D. citri* dispersal.

Host mediation by the pathogen can also affect the biological parameters of the vector insects. The fact that Las-positive plants are nutritionally poor (sub-optimal condition) can affect, besides the behavior, also the fitness of *D. citri* (Teck et al. 2011; Alves et al. 2014, 2018). Cen et al. (2012), using EPG technique, observed that there was an increase in the duration of the pathway phase and a decrease in the phloem phase on *D. citri* feeding in plants with advanced symptoms when compared to healthy plants. Furthermore, as symptom severity increased in the plant, longer *D. citri* spent salivating and the time spent in phloem was reduced, indicating that it was harder to *D. citri* to explore the host aiming feeding, probably due to the poor nutritional quality of Las-positive plants (Bonani et al. 2009).

In addition to the complexity of the plant – pathogen – *D. citri* interaction, we can also consider a fourth organism in this system, the ectoparasitoid *Tamarixia radiata* (Hymenoptera: Eulophidae). This wasp is considered the main parasitoid of *D. citri* nymphs and has been used as an important component in the HLB management (Chen and Stansly 2014; Parra et al. 2016). *T. radiata* uses the odor emitted by both host plants and *D. citri* nymphs to guide themselves in the environment (Alves et al. 2016; Liu et al. 2019). As well as the *D. citri*, the parasitoid is also more attracted to VOCs emitted by Las-positive plants (mainly MeSA) when compared to healthy plant odor (Martini et al. 2014), indicating that Las-mediated host interactions can be even more complex and should always be considered in a multitrophic approach.

Interaction-based HLB management

The epidemiology of HLB depends on *D. citri*, which is the only means of dissemination for Las. The effects of Las on *D. citri* life-history traits, such as fertility, fecundity, behavior, immune system, metabolism, morphological changes, microbiota and plant host choose may strongly influence the HLB epidemiology. Therefore, the knowledge about the Las-*D.citri* interaction is very important to improve the management of HLB. For example, long life spans of *D. citri* facilitate Las transmission, while shorter life spans decrease the HLB transmission opportunity. Furthermore, the production of more offspring in response to Las infection can positively affect the fitness dynamics of the *D. citri* population, increasing the potential for pathogen transmission (Pelz-Stelinski and Killiny 2016). Las infection of citrus trees activates the salicylic acid (SA) pathway and induces the release of MeSA, which attract more *D. citri*. However, *D. citri* disperse subsequently to Las-negative plants to make them their preferred location to settle rather than Las-positive plants (Mann et al. 2012). Las may still manipulate the movement and mate selection behavior of *D. citri* reared on Las-positive citrus plants, which is a possible evolved mechanism to promote their own spread (Martini et al. 2015). Additionally, Las-positive *D. citri* adults that developed on Las-positive plants can transmit the pathogen in 1.5 h (Wu et al. 2016). Therefore, Las infected trees may contribute more to Las spread than only serving as sources of inoculum for the vector (Pelz-Stelinski and Killiny 2016), and the recommendation for removal of HLB diseased citrus trees is essential for HLB management (Bove et al. 2006).

D. citri adults that acquire Las are considered poor vectors of the pathogen compared with those which acquire the bacteria during nymphal stages (Inoue et al. 2009; Pelz-stelinski et al. 2010; George et al. 2018). Moreover, the acquisition rates of Las are 74.3% and 51.6% for *D. citri* nymphs and adults, respectively (Canale et al. 2017). Las replicates faster and reaches higher levels in *D. citri* nymphs than in adults (Ammar et al. 2016) and the Las transmission by *D. citri* adults is 11.8% while by third-instar nymphs 43.4% (Canale et al. 2017). Additionally, the transmission of Las by a single Las-positive *D. citri* adult is highly efficient, since under field conditions, the transmission is further enhanced by repeated inoculation from the individual or multiple *D. citri*, which enhances the severity of HLB (Wu et al. 2016). However, phenotypic and molecular characterization revealed differences between *D. citri* lines, one good and another one poor vectors of the Las (Ammar et al. 2018).

Several data show Las is affecting the fitness of *D. citri*. For example, the reduction of gene expression of general oxidases and esterases in Las-positive *D. citri* promote the susceptibility to most of the commercial insecticides (Tiwari et al. 2011a, b, c). The decrease of these enzymes also causes susceptibility to entomopathogenic fungi (Hussain et al. 2018). Moreover, Las-infected plants attract the parasitoid *T. radiata*, in addition to *D. citri* (Liu et al. 2019). Therefore, integrated chemical and biological control is crucial to support HLB management (Beloti et al. 2015; Ausique et al. 2017; Ibarra-Cortés et al. 2018).

In order to reduce the environmental impact of insecticides used in agriculture, novel management strategies have been studied for the development of sustainable techniques. For instance, the study of interaction between insect vectors of crop diseases and their symbiotic microorganisms has been considered a future integrated management technique. The symbiotic bacterium *Wolbachia* in *D. citri* has been considered as a potential approach for controlling HLB through artificial manipulation of the insect by releasing a *D. citri* male population with genetically modified strain of *Wolbachia* (Ren et al. 2018). This is supported by the fact that there is an infected correlation between *Wolbachia* and Las titer in *D. citri* (Fagen et al. 2012; Saha et al. 2012). Moreover, new putative insect-specific viruses (ISVs) have been detected in *D. citri*, some of which may have the potential to be used as biocontrol agents (Nouri et al. 2016). ISVs (wild-type or engineered viruses) could be useful, for example, to negatively impact the vector competence for transmission (Goenaga et al. 2015), or to use as recombinant ISVs to induce RNAi defenses against other pathogens vectored by *D. citri* (Nouri et al. 2018), or even to target specific *D. citri* RNAs by virus-induced gene silencing (VIGS) (El-Shesheny et al. 2013; Hajeri et al. 2014; Andrade and Hunter 2017; Galdeano et al. 2017; Killiny and Kishk 2017; Kishk et al. 2017; Yu et al. 2017; Yu and Killiny 2018; Goulin et al. 2019).

In addition to the complexity of the HLB pathosystem, the knowledge about aspects of multitrophic interactions involved in this pathosystem, especially the understanding of how the pathogen can change host plant phenotype and consequently, the fitness, the attractiveness and especially the dispersion of *D. citri*, is necessary to help to understand the epidemiology of the disease, as well as support new management strategies to HLB (Mann et al. 2012; Alves et al. 2016; Beloti et al. 2018; Martini et al. 2018). These investigations can be used to determine and validate efficient management strategies as well as to predict the economic and biological longevity of a citrus orchards under management conditions.

Conclusion remarks

Insect-borne plant pathogens have an evolutionary relationship with their hosts and can manipulate either their vector or plants to increase their spread in the citrus crops. Here, we have reviewed the changes that Las infection causes in *D. citri* and host plants, which are essential to understand HLB epidemiology. The data shows the effect promoted by Las in *D. citri* fitness, such as oviposition, flight and egg development. Moreover, the reduced Las genome and high Las dependence of its host metabolite intermediaries also corroborates with the belief of a positive association between Las and *D. citri*. On the other hand, *D. citri* attempts to activate several defense lines against Las infection, such as induction of iron-related proteins, cathepsins, and hemocyanin but it does not impair the insect to become bacteriliferous.

So far, it is not clear whether the *D. citri* metabolism imbalance caused by Las is a strategy to obtain nutrients from its insect host or if this is a *D. citri* strategy to limit Las spread through its tissues, or both. Based on all the scientific material considered in this review, we conclude that the interaction between Las and its vector, *D. citri*, is yet poorly understood and many unanswered questions persist. Because of that, it is hard to determine the level of "friendship" between Las and *D. citri*. Therefore, more investigations are required to provide valuable new information about this scientifically intriguing interaction, which may support the elaboration of new approaches for controlling HLB.

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Compliance with ethical standards

Conflict of interest The authors inform consent and declare that they have no competing interests.

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