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REVIEW

Reciprocal effects of huanglongbing infection and nutritional status of citrus trees: a review

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Abstract
In the past 15 years, the global citrus industry has experienced significant losses in the fruit production, largely due to the huanglongbing (HLB). This bacterial disease impairs water and nutrient uptake by roots causing nutritional disorders and, reciprocally, metabolic imbalances associated to oxidative stress and carbohydrate distribution in trees. The sustainability of optimum yield and fruit quality of citrus are achieved by growing canopy and rootstock varieties with superior horticultural characteristics in well-established orchards, which relies on efficient irrigation and/or fertilization, as well crop protection. Then, attention to enhanced nutrient supply increased significantly in commercial groves. In order to better understand the pathological processes, this review discusses recent scientific advances and major findings in most citrus-producing regions of the world, critically analyzing nutrient management practices as a component of an intricate strategy to maintain tree health, fruit yield, and quality. Moreover, we consider the role of balanced and constant nutrition of citrus trees to sustain citrus production under endemic HLB or non-HLB conditions.

Keywords Mineral nutrients · Nutrient management · Fertilizer use · Citrus greening · *Candidatus* Liberibacter · Sustainability

Introduction

The citrus industry contributes with most fruits produced in the world (FAOSTAT 2016). Such outstanding rank is achieved with optimum yield and fruit quality in commercial citrus groves established with canopy and rootstock varieties with superior horticultural characteristics, managed with efficient irrigation and/or fertilization, as well crop protection.

Nonetheless, citrus orchards worldwide have been mostly affected by huanglongbing (HLB), a disease caused *Candidatus* Liberibacter spp. that affects fruit yield and ultimately leads to tree losses (da Graça 1991; Bové 2006; Baldwin et al. 2010, 2018; Bassanezi et al. 2011; Dala Paula et al. 2019), challenging growers to adopt advanced practices to manage tree health (Belasque Jr et al. 2010; Gottwald 2010). However, the increase in the use of agricultural inputs threatens the sustainability of the industry (Irey et al. 2008; Gottwald and Graham 2014; Fundecitrus 2017; Singerman 2019).

Presently, no resistant citrus cultivars have been identified (Halbert and Manjunath 2004; Gottwald 2010; Stover and McCollum 2011; Albrecht and Bowman 2012). The quick spread of HLB, the long latency period of the infection, and the high efficiency of transmission by vectors make eradication and control of the disease difficult (Gottwald 2010). Thus, studies focusing on plant-vector-pathogen-environmental interactions have been conducted (National Academies of Sciences, Engineering, and Medicine 2018), which includes the selection of citrus varieties less susceptible to HLB (Folimonova et al. 2009; Stover et al. 2010; Westbrook et al. 2011; Albrecht and Bowman 2011, 2012; Albrecht et al. 2012; Richardson et al. 2013; Boava et al. 2015), genome and genetic transformation of citrus trees, gene editing, vector control, RNA interference (Febres et al. 2009; Stansly et al. 2013; Fan et al. 2012; Martinelli et al. 2012; Stansly and Kostyk 2013; Martinelli et al. 2013; Aritua et al. 2013; Mafra et al. 2013; Zheng and Zhao 2013; Hao et al. 2016;

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Baldwin et al. 2017; Zanardi et al. 2018), and microbiome (Trivedi et al. 2016; Fujiwara et al. 2018).

In addition, the efficacy of short-term management strategies based on planting bacteria-free trees, removal of infected trees, and monitoring and suppressing disease vector have been conducted in the field (Bové 2006; Belasque Jr et al. 2010) based on the development of citrus health management areas (CHMAs), such as those conducted in Brazil (FUNDECITRUS 2019b) depend on the participation of citrus growers, not easily achieved in other areas such as in USA (Graham and Gottwald 2020).

Noteworthy, commercial groves have relied on the use of enhanced foliar and soil nutrient supply (Spann et al. 2010; Ahmad et al. 2011; Timmer et al. 2011; Gottwald et al. 2012; Stansly et al. 2013; Shen et al. 2013; Zhao et al. 2013; Morgan et al. 2016; Zhang et al. 2016; Vashisth and Grosser 2018; Zambon et al. 2019; Mendis et al. 2019; Hamido et al. 2019; Milani et al. 2019; Silva et al. 2020) among other HLB management practices. These include the use of plant growth promoters (Albrigo and Stover 2015; Canales et al. 2016), soil conditioners (Xu et al. 2013), and chelates (Mendis et al. 2019) that have been also been considered in scientific reports as potential alternatives for orchard management.

The significant number of reports focused on understanding the nutritional status of HLB-affected trees raises the question: why have nutrients played such an important role on HLB management in commercial citrus orchards? Historically, because when the disease was described, visual symptoms observed in HLB-affected trees were associated to small and chlorotic leaves, twig dieback, and deformed fruits that dropped off trees prematurely, which were similar to the effects of mineral nutrient deficiencies (da Graça 1991). In fact, HLB infection affects particularly nutrient uptake, associated with root loss or root growth impairment that lead to changes in plant ionome (Koen and Langenegger 1970; Jagoueix et al. 1994; Pustika et al. 2008; Spann and Schumann 2009; Etxeberria et al. 2009; Nwugo et al. 2013; Johnson et al. 2014; Medina et al. 2014; Saccini et al. 2014; Kumar et al. 2018). Moreover, increased tree life span, optimized shoot to root growth, and improved fruit yield were reported in Florida in response to fertilizer applications (Spann et al. 2010), which could be associated to the activation of specific defense mechanisms (systemic acquired resistance, SAR) (Dordas 2008; Shen et al. 2013).

Although plant disease resistance and tolerance are genetically controlled (Agrios 2005), they are modified by environmental conditions and especially by mineral nutrient disorders (Krauss 1999; Marschner 2012).

There is some understanding about the positive effects of improved and balanced mineral nutrition in hindering plant disease progress and severity, by altering tissue structure and integrity, plant metabolism, carbon allocation, and consequently fruit yield and quality of crops. However, comprehensive knowledge on the interaction of plant nutrition and systemic vascular diseases, like HLB, is still not conclusive (Mattos Jr et al. 2010; Spann et al. 2010; Gottwald 2010; Gottwald et al. 2012). Thus, it is necessary to better and reciprocally characterize processes between nutritional status and HLB infection in citrus trees, in order to establish rational orchard management strategies that minimize losses of both fruit yield and quality caused by the disease.

HLB affects fruit quality and yield of citrus trees

HLB symptomatic fruits are small, asymmetric, and have a bitter taste (McClean and Schwarz 1970) due to increased concentrations of limonin and nomilin, which negatively impact sensory attributes of juice (Bové 2006; Baldwin et al. 2010, 2018; Dala Paula et al. 2019). Such fruits frequently fall prematurely, while those that remain on trees exhibit brownish and black aborted seeds, as well as abnormal peel color so that they turn from green to yellow/orange in the peduncular end while the style end remains green (Dala Paula et al. 2019).

Although the detrimental flavor attributes of symptomatic fruits would be largely diluted in commercial juice blends, from fruits of several varieties, locations, and seasons, those symptomatic fruits are likely rejected by industry since weight and juice content are reduced (McCollum and Baldwin 2017; Baldwin et al. 2018; Dala Paula et al. 2019). Furthermore, a positive relationship between number of fruits and yield per tree has been described, suggesting that yield reductions are primarily caused by either the lack of fruit set or the early fruit drop on affected branches (Bassanezi et al. 2011). Thus, depending on the disease severity, a 30–100% yield reduction can be observed in HLB-affected plants (McClean and Schwarz 1970; da Graça 1991; Bové 2006; Batool et al. 2007; Bassanezi et al. 2011; Liao and Burns 2012; Dala Paula et al. 2019; Tang et al. 2019).

Anatomical and physiological disfunctions in HLB-affected trees

Damages to fruit quality and yield are likely associated to the several anatomical and physiological disfunctions observed in trees resulting from the HLB. Such anatomical disorders were first described in the 1960s associated to necrotic phloem and abnormal cambial activity (Tirtawidjaja et al. 1965; Schneider 1968; Tanaka and Doi 1974).

The formation of cytoplasmic membranes from plasmalemma invaginations, mitochondrial collapse, and aberration of the chloroplast thylakoids were also reported (Wu and Faan 1988). Such disfunctions were then associated to the accumulation of starch in the sieve elements and, therefore, plunging of sieve pores (da Graça 1991; Etxeberria et al. 2009; Aritua et al. 2013; Cimò et al. 2013).

Phloem cells from HLB-affected trees also become obstructed with callose and P-protein plugs (Achor et al. 2010), deposited in both lateral pit fields (Koh et al. 2012) as well as in and around sieve plates (Folimonova and Achor 2010; Koh et al. 2012). Thereby, the development of HLB symptoms primarily occurs due to phloem plugging that leads to necrosis of cell wall, sieves elements, and companion cells followed by phloem collapse (Achor et al. 2010; Folimonova et al. 2010; Etxeberria et al. 2009).

Altogether, such disturbances hinder the transport of photoassimilates (nitrogenous and reduced carbon compounds) from photosynthetic source leaves to sink tissues (Etxeberria and Narciso 2012) further promoting sugar conversion into starch in the chloroplasts until this organelle structure is disrupted, resulting in chlorosis and leaf mottling (Etxeberria et al. 2009). Nonetheless, leaf mottling has not always been associated to phloem plugging (Fan et al. 2010).

In healthy plants, the photosynthates produced in the source leaves are translocated down to the stem and roots for utilization in meristematic regions (Khan 2013), so that the starch produced in chloroplasts during daytime photosynthesis is degraded during the following night, providing a continued supply of sugars to sustain plant's metabolism (Zeeman et al. 2007). Given the imbalances in carbohydrate partitioning in HLB-affected plants (Fan et al. 2010) due to the previous described anatomical disorders (Achor et al. 2010; Folimonova et al. 2010; Etxeberria et al. 2009), the complex process associated to starch synthesis/breakdown is somehow disrupted (Lu et al. 2005; Gibon et al. 2004, 2009; Etxeberria et al. 2009).

In addition, important enzymes associated to starch degradation into maltose, such as beta-amylases and isoamylases, could either have their synthesis reduced or inactivated due to oxidation of cell compartments, increasing starch accumulation in HLB-affected trees (Smith 2012; Stettler et al. 2009; Mikkelsen et al. 2005). Low maltose levels, as well as reduced expression of genes associated to sugar transport, are present in infected plants (Fan et al. 2010). Starch degradation/biosynthesis metabolism is complex and has not been fully elucidated so far. It may be possible that other enzymes known to play key roles in starch breakdown metabolism, such as glucan water dikinases (Smith 2012), could also be involved in the accumulation of starch under HLB. The effects of HLB on starch metabolism require further studies in order to be better understood.

Thereby, key components of plants' carbon balance, such as photosynthesis, are impaired in HLB-affected plants (Fan et al. 2010; Martinelli et al. 2012), as significant down-accumulation of ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO), RuBisCOactivase, and proteins associated to the photosystem II stability have been reported in HLB-affected plants (Nwugo et al. 2013). Such damages to photosynthetic capacity can further cause the production of reactive oxygen species (ROS) (Martinelli et al. 2012) with peroxiredoxins and Cu/Zn superoxide dismutase production upregulated in HLB-affected plants, although other important components of H_2O_2 detoxification, such as peroxidase and catalase, have been reported to be downregulated (Nwugo et al. 2013).

ROS also affects intercellular transport of metabolites and proteins in plants and causes negative effects on phloem loading/unloading process (Stonebloom et al. 2012). Then, ROS production either causes phloem plugging or is a consequence of this process; this cause/effect relationship requires more comprehensive investigation. In addition, leaf respiration, a second key component in the leaf carbon balance and, therefore, plant growth, has received less attention than photosynthesis in HLB-affected plants, even though it has been reported that citrate, a sub product of the TCA cycle, is the main source of energy for the HLB-associated bacteria (Cruz-Munoz et al. 2018).

Besides, the potential correlation between respiration rates and HLB-associated bacteria development can also have important consequences for plant carbon budget since carbohydrate catabolism through respiration can release up to 80% of carbon previously assimilated by photosynthesis (Amthor 2000).

Based on the previous arguments, we can say that the negative effects of HLB on key components of plant's carbon balance associated with reduced capacity of infected plants to transport carbohydrates from carbon sources to sink tissues clearly damage plant growth, and therefore, biomass partitioning.

Leaves of HLB-affected plants present higher weight per unit area due to starch accumulation in leaves (Spann and Schumann 2009) associated with starch depletion in the roots (Etxeberria et al. 2009). Therefore, debilitation of the root system, especially feeder (fibrous) roots in HLB-affected plants, restricts the capacity of absorption, assimilation, transport, and utilization of water and nutrients (Jagoueix et al. 1994; Etxeberria et al. 2009; Medina et al. 2014; Saccini et al. 2014; Johnson et al. 2014).

The debilitation of feeder roots in HLB-affected trees is the primary cause of plant water deficit (Hamido et al. 2017), likely associated with thicker xylem cell walls, which reduces the lumen of xylem vessels and restricts water and nutrient uptake (Spann and Schumann 2009; Kumar et al. 2018). As expected, a general decrease in nutrient concentrations due to HLB, particularly those of Fe, Zn, Cu, Ca, and Mg, have been reported (Spann and Schumann 2009; Nwugo et al. 2013).

Decreases in nutrient concentrations can reduce the production of proteins associated with oxidative stress defense, energy production/regulation, and protein synthesis/transport, especially due to Fe deficiency (Nwugo et al. 2013). Furthermore, reduction in nutrient content can ultimately cause the cannibalization of key proteins, such as RuBisCO, in order to release nutrients, which would further damage important physiological processes such as photosynthesis (Huber and Haneklaus 2007).

Balanced nutrient management enhances fruit yield in HLB-affected trees

Mineral nutrient supply plays important roles in plant health either by reducing the susceptibility of plant tissue to insect attack and pathogen infection or by changing the chemical composition of the soil-plant system, which can impair the survival and activity of those individuals (Dordas 2008; Walters and Bingham 2007; Spann and Schumann 2009; Fones et al. 2010; Yuan et al. 2010; Carvalhais et al. 2013; Shen et al. 2013; Musetti et al. 2013; Zhao et al. 2013; Kadyampakeni et al. 2016; Zambon et al. 2019).

On the other hand, uptake and use of nutrients by plants are affected by other phytosanitary problems, which changes concentration and accumulation of nutrients in plant tissues (Walters and Bingham 2007; Spann and Schumann 2009; Marschner 2012; Nwugo et al. 2013; Oliver et al. 2014).

Use of either liquid forms of fertilizer *via* fertigation or controlled release form of fertilizer has been shown to mitigate the devastating impacts of HLB by increasing nutrient uptake in Florida where sandy soils tend to exacerbate the nutrient leaching problem (Kadyampakeni et al. 2014a, 2014b, 2016; Vashisth and Grosser 2018; Vashisth and Livingston 2019; Kadyampakeni 2020).

Despite practical evidence, information about the use of enhanced nutrient supply and management in commercial citrus orchards affected by HLB is still limited and does not yet fully support decision making for widespread use as a management tool that effectively contributes to disease control and management. Nevertheless, different approaches under different soil and plant growing conditions have been proposed and are addressed in the following sections of this review.

Visual symptoms of HLB and nutritional disorders

Visual symptoms in leaves at early infection stage of HLB resemble those induced by Zn, Fe, and Mg deficiencies (da Graça 1991; Li et al. 2006; Martinelli et al. 2012; Tian et al. 2014). More severe symptoms as enlarged, swollen, and corky leaf veins resemble B deficiency (Spann and Schumann 2009). Moreover, some of those symptoms are related to starch accumulation in leaves (Etxeberria et al. 2009; Cimò et al. 2013), which is also a general response of plants to Ca, Mg. and Zn deficiencies (Marschner 2012; Cakmak and Kirkby 2008).

As a consequence of starch accumulation, leaf thickness and weight per unit area increase, even though total area of fully expanded leaves does not change (Silva et al. 2020). Therefore, the interpretation of leaf chemical analysis is influenced when nutrient concentrations are expressed either in a dry mass (g kg^{-1}) or in a leaf area (g m^{-2}) basis (Spann and Schumann 2009).

Following these observations, studies conducted so far have focused on understanding reciprocal effect between nutrient content and HLB symptom expression (Razi et al. 2011; Zhao et al. 2013; Nwugo et al. 2013; Gottwald et al. 2012), and also, extending this idea in order to use of hyperspectral remote sensing techniques to identify diseases that causes chlorosis and starch accumulation such as HLB (Stuckens 2010).

Based on the relationships here described, research and extension service in Florida have recently proposed a program to improve the overall health and productivity of citrus groves affected by HLB by fine tuning production horticultural practices, in particular, by adjusting fertilization programs assisted by soil and leaf analysis tools (Schumann et al. 2019).

Plant predisposition/susceptibility to HLB and nutritional status

Mechanisms regulating nutrient-induced changes on HLB development and severity are complex and depend on multiple direct and indirect factors associated to the pathogen (Dordas 2008), plant growth and development (Stamp 2003; Matyssek et al. 2005; Underwood 2012), and plant resistance mechanisms (Oostendorp et al. 2001; Lecourieux et al. 2006). Thereby, nutrients are involved in the interactions between plant hosts and microorganisms (Fones et al. 2010; Yuan et al. 2010; Carvalhais et al. 2013; Musetti et al. 2013; Zhao et al. 2013) and likely microorganisms and vectors (Silva et al. 2020).

Considering the common HLB effects on citrus production as a result of the impaired absorption of water and nutrients by roots, physiological disfunctions, and imbalanced plant nutritional status (McClean and Schwarz 1970; da Graça 1991; Jagoueix et al. 1994; Bové 2006; Batool et al. 2007; Etxeberria et al. 2009; Fan et al. 2010; Bassanezi et al. 2011; Martinelli et al. 2012; Liao and Burns 2012; Dala Paula et al. 2019; Johnson et al. 2014), growers have adopted several approaches to overcome disease effects, such the use of enhanced fertilization practices in orchards (Vashisth and Vincent 2018), based on information that losses of feeder root mass density are already substantial in HLB pre-symptomatic trees, being in a range of 30% (Graham and Johnson 2013; Milani et al. 2019).

Given the importance of Ca for the cell wall structure and function of plant membranes (Marschner 2012; Dordas 2008;

Petená et al. 2016), it is likely that the decreases in Ca contents of infected trees restrict water and nutrient uptake by reducing the area available of conducting vessels to mass flow. Moreover, under Ca deficiency, the low stability of cell membranes favors the leakage of low molecular weight compounds, such as sugars and amino acids, from the cytoplasm to the apoplast (Dordas 2008), aggravating distribution of carbohydrates from shoots to roots. Calcium uptake is limited to maintenance of electrochemical equilibrium in plants (Hinsinger et al. 2003), which is of greatest importance in citrus given its high demand for this nutrient (Mattos Jr et al. 2003). Thus, in order to improve Ca uptake by trees in fertilization programs focused on HLB management, it will be likely important to consider an optimum NO_3^-:NH_4^+ and NO_3^-:Ca^{2+} absorption ratios (Quaggio et al. 2014, 2019). Interestingly, Mg-deficient source leaves accumulate sucrose, suggesting specific inhibition of phloem loading of sucrose, probably as the result of low activity of the proton pumping ATPase at the sieve tube membranes, a motive force energizing the sucrose symporters (Cowan 2002; Cakmak and Kirkby 2008). Such deficiency also causes photooxidative damage catalyzed by ROS and leads to unbalanced partitioning of photosynthetic carbon to the roots, which increases shoot to root dry weight ratios (Cakmak and Kirkby 2008).

Nonetheless, it is still unclear the contribution of both Ca and Mg to the transport of carbohydrates in HLB-affected plants. However, photosynthetic capacity of young infected trees grown in containers and supplied with increased doses of Ca presented increased starch transport from shoots to roots. Accordingly, infected trees supplied with either high rates of Ca or Ca + Mg presented higher electron transport rates (ETR) than control plants supplied with reduced concentrations of these nutrients (Milani et al. 2019). Thus, could enhanced Ca and Mg specially fertilizations alleviate HLB negative effects on photosynthetic capacity and starch metabolism in citrus trees?

Increased levels of ROS are harmful to cells because they cause the oxidation of lipids, proteins, DNA, and other components important for the plant metabolism (Puig et al. 2007; Andrade et al. 2010; Hippler et al. 2018). Since metal micronutrients (Fe, Cu, Mn, and Zn) are co-factors of superoxide dismutase (SOD) enzymes, involved in membrane protection against oxidative damages through the detoxification of superoxide radicals (Gupta et al. 1993; Cakmak 2000; Alscher et al. 2002; Hippler et al. 2018), nutrient supply *via* foliar sprays or soil came to attention as another tool to protect HLB-affected trees in the field.

In fact, Zn-based products, such as Zinkcide and ZnO, were beneficial to treated trees as a bacterial agent (Mendis et al. 2019). Such results are controversial since it was previously reported that supplemental Zn increases the population of "*Candidatus* Liberibacter asiaticus" (*C*Las) in HLB-affected plants (Zhang et al. 2016). Still controversial, higher than recommended rate of Mn was also reported to suppress bacterial titers (Zambon et al. 2019); however, this latter response was not observed when Mn and B were combined at high rates, suggesting an antagonistic effect of micronutrients. For instance, high Mn concentrations reduce contents of Fe and activity of Fe-SOD in citrus (Hippler et al. 2016).

Ebel et al. (2019) demonstrated that HLB-affected trees are more sensitive to foliar applications of Cu than non-HLB trees. Overdoses of Cu applied through foliar fertilizations increase oxidative stress in citrus, which is perceived by both scion and rootstock in a complex network process (Gratão et al. 2015; Hippler et al. 2016, 2018). Moreover, excess of Cu suppresses growth of well-irrigated trees, affecting plant water relations similarly to HLB-affected trees (Hamido et al. 2019). Adjusting plant water deficit was required when trees were either affected by HLB or treated with foliar applications of Cu (Hamido et al. 2019), so that is it likely to expect a tight correlation between Cu supply and water status in HLB-affected plants?

Finally, foliar and substrate fertilizations with Cu, Mn, and Zn reduce the acquisition of *C*L as by both adults and nymphs of *D. citri*, when applied in combination (Silva et al. 2020).

Although P supply could improve growth and yield of HLB-affected plants (Pustika et al. 2008; Zhao et al. 2013), reports showed no positive effects in infected trees (Gottwald et al. 2012). In this context, it is necessary to observe that phosphate (PO_4^-) and phosphite (PO_4^-) do not present same use efficiency by plants. Phosphite is not oxidized in the assimilation process and its contribution to citrus as a nutrient does not occur (Zambrosi et al. 2012a).

Plants deficient in P exhibit several mechanisms to enhance P acquisition and utilization (Raghothama and Karthikeyan 2005), which are increased nutrient remobilization from P reserves (Zambrosi et al. 2012a) and increased activity and exudation of P-mobilizing carboxylates, as citrate, by roots (Lambers et al. 2015; Zambrosi et al. 2012b). Citrate and other TCA cycle intermediates are energy sources for *Ca.* Liberibacter crescens *in vitro* (Cruz-Munoz et al. 2018), suggesting that P-deficient trees would favor production of citrate, increasing bacteria populations in the insect vector and plant host, thereby increasing HLB symptoms in infected trees. Phosphorus deficiency in citrus trees is commonly observed in low fertility soils, in which condition tree response to P fertilization is positive and very dependent on rootstock varieties (Quaggio et al. 2004; Mattos Jr et al. 2006; Zambrosi et al. 2012a, 2012b). To the best of our knowledge, there is still no evidence of differential susceptibility of citrus to HLB associated to P nutritional status of trees grown on less efficient P rootstocks.

In addition to the direct management of nutrients *via* fertilizer applications, agricultural practices that increase chemical, physical, and biological processes of the soil (*e.g.*, use of soil organic matter, crop rotation and cover crops, intercropping and soil tillage) and, therefore, limit the imbalance of certain nutrients will improve plant growth and tolerance to abiotic and biotic stress (Dordas 2008; Huber and Graham 1999). Xu et al. (2013) used soil conditioners to improve soil quality, especially the ability to provide nutrients for plants. This practice resulted in positive effects on HLB-affected mandarins such as improved tree growth with reduced HLB symptoms, lower *C*Las titers, increased fruit yield, and improved fruit quality, likely by inducing a defense-response reaction and ameliorating physiological and biochemical process in plants (Xu et al. 2013).

On the other hand, HLB causes decreased relative abundance and/or expression activity of soil microorganisms interacting with plant roots, resulting in impaired plant-microbiome interactions (Zhang et al. 2017). In order to extend the current knowledge on agricultural practices and their contributions to overall growth and health of HLB-affected orchards, efforts will be needed to unravel the global rhizosphere microbiome, focusing on understating microbial functional traits that mediate plant-microbe and microbe-microbe interactions, nutrient acquisition, and plant growth promotion in citrus (Xu et al. 2018).

Sustainability of citrus production and nutrient management

The contribution of rational nutrient management and fertilization of citrus orchard to the increase of fruit productivity and quality is obvious. By assembling key strategies for the diagnosis of soil fertility and plant nutritional status, based on series of time and space data, it is possible to decide on better fertilizer sources, doses, and application mode and timing according to tree's demand (Mattos Jr et al. 2020).

The latter allows greater efficiency in the use of agricultural inputs in orchards, and consequently optimization of investments with environmental protection, which strategies should be revised periodically with the critical analysis of information demonstrating the accuracy of field operations and on-farm achievements, also revised in line with progress towards meeting FAO's Sustainable Development Goals (SDGs) for agricultural systems.

Despite enhanced nutritional programs varies considerably and evidences that any nutritional treatments have maintained yields of HLB-affected trees (Gottwald et al. 2012), there is an increasing interest in managing orchards in the presence of HLB through advanced production systems that supplement water and nutrients, as well related materials both to foliage and to soil (Molin et al. 2012; Campos-Herrera et al. 2013, 2014; Kadyampakeni et al. 2014c, 2016; Ferrarezi et al. 2017a, 2017b). According to current Florida sweet orange production cost analysis, fertilizers and foliar nutritional products constitute approximately 20 to 25% of the cost of total citrus production (Singerman 2019).

However, even before employing best nutrient management practices, developed based on a broad understanding of the reciprocal responses between HLB disease and the response of the infected plants, the sustainability of the citrus industry should be conducted with the maintenance of orchard quality, beginning with planting of healthy nursery trees, prevention or reduction of orchard infection, and establishment of practices to coordinately control the insect vector. That's true, since significant questions remain about the buildup and spread of inoculum in commercial orchards under a nutrient management program (Spann et al. 2010; Timmer et al. 2011).

Sustainability of citrus production under low HLB incidence

In view that HLB-resistant/tolerant canopy and rootstocks citrus varieties are not yet available to growers, as well as effective means of controlling the bacteria in the orchards, the most important strategy in citrus cultivation is to prevent the disease from spreading in the orchard. Thus, measures such as enhanced nutrient management to maintain tree health should not be a priority given the recommendations already established by the research.

This is the case of citrus in the state of São Paulo, Brazil, whose survey shows that in recent years (2015–2019; FUNDECITRUS 2019a), the occurrence of the disease has been stable, with less than 20% of infected plants in the citrus production belt.

Under low HLB occurrence, recommendations for successful disease control were prepared (FUNDECITRUS et al. 2019b), which include the following: (i) planning and selection of planting area, (ii) planting healthy nursery trees, (iii) enhance plant growth and early productivity, (iv) intensified insect vector control in the borders of orchard, (v) continuously conduct plant inspection, (vi) eradication of symptomatic trees, (vii) insect vector monitoring, (viii) and control, (ix) insect vector regional alert and management, and (x) management of external areas to reduce infected trees and bacteria inoculum.

Sustainability of citrus production under high HLB incidence

Currently, in Florida, the *C*Las infection rate ranges from 80 to 100% depending on grove; therefore, inoculum removal is not a sustainable strategy. Under such conditions, control of the vector and intensive fertilization and irrigation are the two primarily strategies adopted by Florida growers (Vashisth and Vincent 2018).

It has recently been found that the Asian citrus psyllid has developed resistance to common systemic insecticides (Langdon et al. 2018). Therefore, under such situations, it becomes nearly impossible to control infection from widespread psyllid infestation. Hence, Florida growers are actively managing good nutrition using advanced technologies for ensuring that the nutritional need of trees is properly assessed. In addition, the University of Florida has recently launched a program, “citrus nutrition box” to work with citrus growers to ensure regular/frequent leaf and soil nutrient sampling to adjust fertilizer programs on a regular basis.

Concluding remarks

Despite research development achieved over the past 15 years worldwide, HLB remains a major challenge for the citrus industry, given the significant losses it has caused to fruit production and quality. In this context, strategies for different nutritional management of HLB-affected orchards have been proposed and evaluated in order to guarantee agricultural production. These strategies are based on comprehensive understanding of the influence of mineral nutrients on tissue structure and integrity, plant metabolism and carbon allocation of plants, and their interactions with the environment.

Given this complex system, plant resilience could be expected from managing nutritional disorders and associated metabolic stresses, thereafter, reducing their predisposition to the disease progress and severity. However, measures such as enhanced macro and micronutrient supply towards tree health should take into account interactive effects of HLB on the citrus industry with a look at the sustainability of production either under endemic HLB or non-endemic HLB conditions, which are achievable with recommendations already established to growers for the overall management of orchards considering plant-vector-pathogen-environment interactions.

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