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REVIEW

A perspective of citrus Huanglongbing in the context of the Mediterranean Basin

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Abstract

Huanglongbing (HLB) is one of the most catastrophic citrus diseases. HLB pathogens *Candidatus* Liberibacter asiaticus (Las), *Ca*. L. africanus (Laf), and *Ca*. L. americanus (Lam) and their insect vectors Asian citrus psyllids (ACP, *Diaphorina citri*) and African citrus psyllids (AfCP, *Trioza erytreae*) are invading citrus producing regions where HLB was absent previously, including the Mediterranean basin. Importantly, the Mediterranean region is one of the two major citrus producing areas without HLB. Here, I provide a short perspective regarding a) information related to the distribution of the HLB pathogens and psyllid vectors in this region and neighboring countries, b) predicted distribution of the HLB for this region, c) the possible evolution of Liberibacters and how they could have established their relationship with different hosts, and d) approaches to fend off HLB. Specifically, I emphasized the following measurements: quarantine measures against AfCP, ACP, Las, Laf, and Lam, early detection and diagnosis of HLB and removal of inoculum, surveillance of AfCP and ACP and eradication of citrus psyllids once identified.

Keywords Citrus · HLB · Huanglongbing · Liberibacter · Phloem · Psyllids

Citrus Huanglongbing (HLB), also known as citrus greening, is the most devastating disease in many citrus producing areas worldwide. HLB is caused by *Candidatus* Liberibacter asiaticus (Las), *Ca*. L. africanus (Laf), and *Ca*. L. americanus (Lam) that are yet to be cultured (Merfa et al. 2019). Among them, Las is the most widely distributed and has been reported in Asia, North America, South America, and Africa, Laf is only present in Africa, and Lam, originally identified in Brazil, is diminishing and being taken over by Las. Las and Lam are naturally transmitted by Asian citrus psyllids (ACP, *Diaphorina citri*) and Laf by African citrus psyllids (AfCP, *Trioza erytreae*). The HLB pathogens and insect vectors have been spreading to new territories including Brazil (Coletta-Filho et al. 2004; Texeira et al. 2005), multiple states of the United States (Kumagai et al. 2013); Belize (Manjunath et al. 2010); countries in the Caribbean including Cuba (Martinez et al. 2009) and the Dominican Republic (Matos et al. 2009); Bhutan (Doe et al. 2003); and Ethiopia (Saponari et al. 2010). Currently, the Mediterranean Basin and Australia are the two major citrus producing regions that are free of HLB. Despite the challenges to study the Liberibacters, a lot of exciting progress has been made in understanding the citrus HLB pathosystem that have been reviewed extensively (Bové 2006; Gottwald 2010; Wang and Trivedi 2013; Wang et al. 2017; Bendix and Lewis 2018; Blaustein et al. 2018; Coyle et al. 2018; Munir et al. 2018; Zheng et al. 2018; Kruse et al. 2019). Here, I will therefore focus on some areas that have not been reviewed intensively in the past and tailor it to the Mediterranean citrus producing region for the readership of the journal, and summarize some perspectives regarding how this region can fend off the invasion by HLB.

HLB at the doorstep of the Mediterranean Basin

Las and ACP were reported in the neighboring countries of the Mediterranean Basin: Iran (Faghih et al. 2009) and Saudi Arabia (Bové 2006). Las and ACP were also reported in several African countries that are not adjacent to the Mediterranean Basin: Tanzania (Shimwela et al. 2016) and

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Uganda (Kalyebi et al. 2015). However, the identification of Las in those two countries have been challenged by Roberts and colleagues as probable misidentifications that were reclassified as *Ca.* L. africanus subsp. clausenae (Roberts et al. 2017). Only Las but not ACP was reported in Ethiopia (Saponari et al. 2010). Only ACP but not Las is present in the United Arab Emirates and Oman. Both Laf and AfCP are present in Saudi Arabia, Yemen, Burundi, Cameroon, Central African Republic, Comoros, Ethiopia, Kenya, Madagascar, Malawi, Mauritius, Réunion, Rwanda, Saint Helena, Somalia, South Africa, Swaziland, Tanzania, Uganda, and Zimbabwe. In addition, AfCP has been reported in Spain and Portugal even though HLB pathogens have not been found in either place (Cocuzza et al. 2017). AfCP has been shown experimentally to transmit Las (Massonié et al. 1976) and carry Las in field populations of AfCP in Ethiopia (Ajene et al. 2019). On the other hand, ACP is also known to transmit either Las or Laf under experimental conditions (Lallemand et al. 1986). Thus, HLB and its vectors present an immediate threat to the citrus industry of the Mediterranean Basin, echoing the concerns by many esteemed European colleagues (Aubert 2011; Bové 2014; Duran-Vila et al. 2014; Janse 2012; Siverio et al. 2017).

Perspective distribution of HLB in the Mediterranean Basin

Las prefers temperatures >30 °C whereas Laf thrives at temperatures less than 30 °C (Jagoueix et al. 1994). Las appears to have a wider tolerance to temperature (10.1 to 38 °C) than its psyllid vector (12.85 to 37 °C) (Gutierrez and Ponti 2013). AfCP is sensitive to hot and dry conditions and favors cool and moist areas. Gutierrez and Ponti (2013) predicated the prospective distribution of Las and ACP and suggested that North Africa, southern Spain and the Middle East are most suitable for Las, whereas the rest of southern Europe has intermediate favorability for Las. Furthermore, the authors suggested that ACP is more restricted in term of its prospective distribution. Overall, the authors suggested that both Las and ACP have the capacity to invade all of the citrus growing regions of the Mediterranean Basin. Another predication suggested large areas of Africa are suitable for ACP and Las, the Mediterranean area is moderately suitable for ACP but less suitable for Las, except for that in southern Portugal and Spain (Narouei-Khandan et al. 2016). However, one of the models predicated that Mediterranean countries in North Africa and southern Europe are highly suitable for Las (Narouei-Khandan et al. 2016). Risk analysis for Laf and AfCP has not been reported previously. However, AfCP has already been reported in northwestern Iberian Peninsula of Spain and Portugal (Cocuzza et al. 2017) even though neither Laf nor Las is currently present in the Mediterranean region. AfCP has also shown capacity to adapt and establish in new citrus-producing regions of the world with different environmental conditions by spreading and invading over 30 countries in Africa, Europe and Asia (https://www.cabi.org/isc/datasheet/54914, accessed on March 5, 2020).

Potential evolutionary pathways of Liberibacters

Understanding the evolution of Liberibacters might help prevent or prepare for the emergence of new diseases resulting from Liberibacters infecting new hosts. So far, seven *Ca.* Liberibacter species have been reported including HLB causal agents Las, Laf, and Lam, *Ca.* L. solanacearum (Lso, syn. *Ca.* L. psyllaurous) causing diseases on many solanaceous plants and on carrot, celery, parsley, and parsnip, *Ca.* L. europaeus (Leu) infecting scotch broom (Thompson et al. 2013), *L. crescens* (Lcr), and *Ca.* L. brunswickensis (Lbr) (Hansen et al. 2008; Jagoueix et al. 1994, 1997; Leonard et al. 2012; Liefting et al. 2008; Morris et al. 2017; Raddadi et al. 2011; Texeira et al. 2005; Thompson et al. 2013). One potential explanation of the evolutionary pathway of Liberibacters is “plant-first model”. *Ca.* Liberibacter spp. belong to alpha-proteobacteria and are phylogenetically related to Rhizobium and Sinorhizobium that are capable of endocytosis, a phenomenon through which bacteria can get inside the cytoplasm (Verma 1992). Even though endocytosis is very common for bacteria infecting mammals, only few plant associated bacteria are capable of entering the cytoplasm of plant cells. It was suggested that ancestors of Liberibacters first established their presence inside the phloem of legume ancestors via endocytosis (Wang 2019) (Fig. 1). Liberibacters inside the phloem further established their association with phloem-sucking psyllid ancestors. Subsequent host jumps of psyllids led to divergence of different *Ca.* Liberibacter species. Interestingly, both Laf and Lam might have gone through a host jump to cause HLB on citrus (Wang et al. 2017). It was suggested that multiple Laf subspecies *Ca.* L. africanus subsp. capensis, *Ca.* L. africanus subsp. clausenae, *Ca.* L. africanus subsp. vepridis, *Ca.* L. africanus subsp. zanthoxyli, and *Ca. L. africanus* subsp. tecleae were present in indigenous rutaceous species in Africa such as *Calodendrum capense*, *Clausena anisate*, *Vepris lanceolate*, or *Zanthoxylum capense* (Garnier et al. 2000; Roberts et al. 2015; Roberts and Pietersen 2017) before the introduction of citrus, suggesting HLB-causing Laf has evolved from the ancestor of Laf subspecies via host jump (Phahladira et al. 2012; Roberts et al. 2015). Another possibility for Liberibacter origin is described in the “insect-first model” that suggests Liberibacters have been initially insect commensals that have evolved to be associated with the phloem tissues following repeated inoculations by insects (Bové and Garnier2002; Nadarasah and Stavrinides 2011).

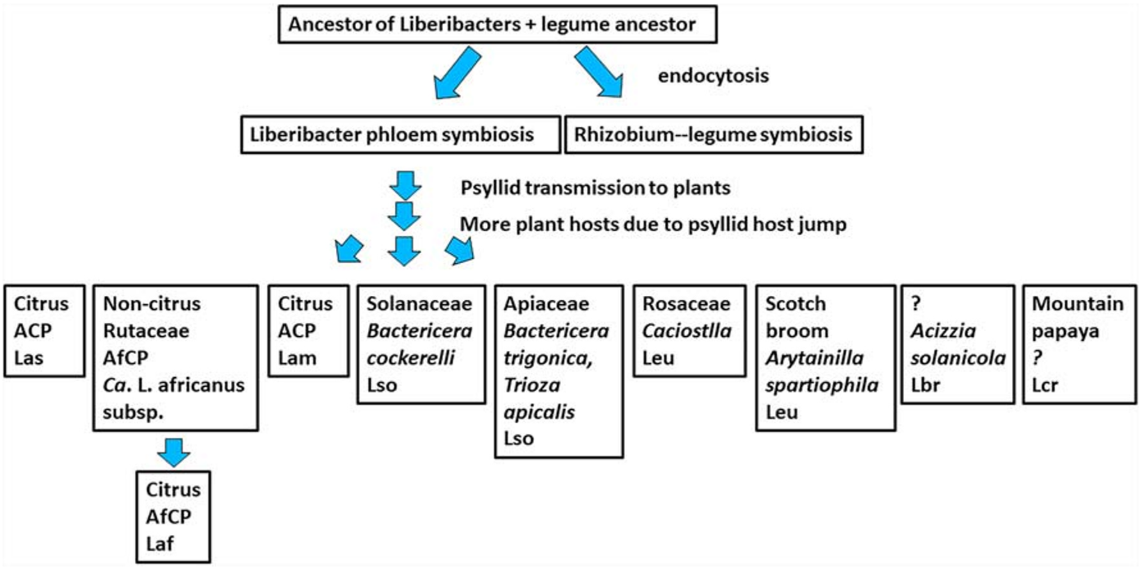

Fig. 1 Evolution of *Candidatus* Liberibacter. The ancestor of Liberibacters is capable of endocytosis. The ancestor of Liberibacters and the ancestor of legume have evolved two different symbiosis relationships, with one represented by the Rhizobium-legume symbiosis, and the phloem symbiosis represented by *Candidatus* Liberibacter. The relationship between psyllid ancestor and legume ancestor allows the transmission of Liberibacter. Psyllid host jump further expands host range of Liberibacters. Las: *Candidatus* Liberibacter asiaticus; *Ca.* L. africanus includes: *Ca.* L. africanus, *Ca.* L. africanus subsp. capensis, *Ca.* L. africanus subsp. clausenae, *Ca.* L. africanus subsp. vepridis, *Ca.* L. africanus subsp. zanthoxyli, *Ca.* L. africanus subsp. tecleae; Lam: *Ca.* L. americanus; Leu: *Ca.* L. europaeus; Lso: *Ca.* L. solanacearum; Lbr: *Ca.* L. brunswickensis; Lcr: *L. crescens*; ACP: Asian citrus psyllid; AfCP: African citrus psyllid

Fending-off HLB

As clearly pointed out by Bové (2006), the best strategy against HLB is to prevent the introduction, and establishment rather than to cure the HLB disease. To fend off HLB in the Mediterranean region and other HLB-free citrus production regions, the following measures are emphasized: a) quarantine measures against AfCP, ACP, Las, Laf, and Lam, b) early detection and diagnosis of HLB and its vectors, c) removal of inoculum, surveillance of AfCP and ACP and eradication of citrus psyllids once identified. The recommendations mentioned here are by no means comprehensive. The readers are referred to many excellent recommendations that have been reviewed before (Bové 2006; Cocuzza et al. 2017; Duran-Vila et al. 2014).

Quarantine

Human-mediated spread is an important trajectory for many agricultural pests (Shigesada and Kawasaki 1997). Introduction of HLB to new territories mediated by human activities has been reported in many cases. For example, all the HLB-positive trees in California identified in the early stage of introduction are in the residential locations, suggesting human-mediated introduction. In addition, human activities such as movement of fruit and/or plant material are suggested to be necessary for long distance dispersion of *D. citri* (Halbert et al. 2010). Due to the relative isolation of the citrus production areas in the Mediterranean Basin from other citrus production areas in the world, quarantine measures for citrus materials (e.g., budwood, grafted trees, seedlings) as well as ornamental rutaceous species (e.g., Murraya) have been suggested and implemented to prevent the introduction of HLB pathogens and psyllid vectors (Duran-Vila et al. 2014). However, hurricanes or storms have been suggested to play important roles in long distance dispersal of Asian citrus psyllids (Gottwald 2010; Wang et al. 2017), suggesting other approaches beyond quarantine are required to prevent HLB/psyllid from infecting and/or spreading in the Mediterranean Basin.

Surveillance of psyllids

Monitoring and surveillance of ACP and AfCP in citrus groves, on citrus and ornamental rutaceous trees elsewhere is one of the approaches that contribute to psyllid prevention. Monitoring ACP or AfCP can be conducted by visual inspection of eggs and nymphs on flush shoots (Sétamou et al. 2008), and monitoring of adult populations using sticky traps (Hall et al. 2010; Sétamou et al. 2014), stem tap sampling (Stansly et al. 2009), vacuum sampling (Thomas 2012), and/or sweep nets (Stansly et al. 2009). Among them, yellow or lime-green sticky cards are currently the most sensitive and effective method for detecting adult citrus psyllids and monitoring their populations (Hall and Hentz 2010; Monzo et al. 2015). To improve trapping efficiency, scientists have tested vibrational duetting mimics (Mankin et al. 2016), odorants released by citrus plants that attract ACP (Coutinho-Abreu et al. 2014), and sex pheromone (Zanardi et al. 2018). In addition, a strong edge effect in *D. citri* distribution in the groves has been reported by multiple groups, which will guide the efficient setup of traps to monitor ACP and AfCP (Gottwald 2010).

Eradication of ACP or AfCP

Eradication of invasive pests may provide a sensible outcome. Hundreds of successful insect eradication projects have been reported (Tobin et al. 2014; Kean et al. 2015). For example, Tobin et al. (2014) analyzed 672 arthropod eradication programs and found 395 of them were considered successful, and Kean et al. (2015) reported 508 successful eradication programs. The successful eradication operations include elimination of *Orgyia thyellina* (Lepidoptera: Lymantriidae) in New Zealand (Myers and Hosking 2002; Suckling et al. 2007); the screwworm fly [*Cochliomyia hominivorax* (Coquerel)] in the United States (Myers et al. 1998), and the Mediterranean fruit fly [*Ceratitis capitata* (Wiedemann)] in New Zealand (Holder et al. 1997). Eradication of ACP and AfCP was conducted in Australia and in the Madeira and the Canary Islands, respectively, unfortunately with opposite outcomes. ACP was reported from Australia in 1922, but it was eradicated successfully (Bellis et al. 2005). On the other hand, the eradication programs of AfCP in the Madeira and the Canary Islands, where AfCP was reported in Madeira in 1994 (Carvalho and Aguiar 1997) and the Canary Islands in 2002 (González-Hernández 2003), failed (Cocuzza et al. 2017). ACP was identified in Florida in 1998, but eradication of ACP was never conducted, leading to its establishment in Florida, and subsequent devastating effect on the citrus industry by spreading the HLB pathogen. ACP is currently under eradication in Southern California. However, it remains to be seen whether such an eradication program will be fruitful. Despite the many concerns regarding AfCP eradication, it might be the best solution to prevent more costly, and devastating challenges of the HLB introductions. Historically, HLB breakouts usually follow the introduction and establishment of citrus psyllids especially ACP although sometimes only many years later, such as in Brazil. New flush shoots are the primary resources for psyllid oviposition and immature development (Catling 1970; Hall et al. 2013), which represent an Achilles' heel of psyllids when trying to eliminate them.

Early detection and diagnosis of HLB

Immediate detection and correct diagnosis of HLB after introduction, followed by eradication measures, are critical to prevent its further spreading. Education of the stakeholders, including growers, regulatory agents, and the public, is critical for symptoms based identification. Monitoring Las and Laf in psyllids is also required. There should also be monitoring of eventual wild hosts, especially *Murraya paniculate* and related and hosts in domestic areas. A simple method has been developed to detect Las right after psyllid feeding, which allows early detection of Las before HLB symptom appearance (Pandey and Wang 2019). Importantly, canines have shown excellent sensitivity and accuracy in detecting Las directly rather than only host volatiles produced by the infection (Gottwald et al. 2020), which might help both in early detection of Las in the citrus groves and backyards as well as in quarantine measures.

Concluding remark

HLB represents a real and unprecedented threat to the Mediterranean region. To fend off HLB, it needs a coordinated effort by regulatory agencies, plant protection agencies, growers, scientists and the public in different countries of the Mediterranean region to prevent the introduction of HLB, eradicate AfCP and/or prevent its further introduction and spreading, and prevent the ACP introduction. Efforts are also needed to find long-term solution such as developing resistant citrus varieties against HLB or ACP and AfCP as rightly pointed out by Duran-Vila et al. (2014).

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