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MINI REVIEW

Asian citrus psyllid, *Diaphorina citri*, vector of citrus huanglongbing disease

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Abstract

The Asian citrus psyllid (ACP), *Diaphorina citri* Kuwayama (Hemiptera: Psyllidae), is an important pest of citrus because it transmits phloem-limited bacteria [*Candidatus* Liberibacter spp., notably *Ca.* L. asiaticus (LAS)] associated with huanglongbing (HLB; citrus greening disease), currently considered the world's most serious disease of citrus. Asian citrus psyllid transmits LAS in a persistent manner and, although the rate of LAS transmission by ACP individuals usually is low, HLB can spread rapidly in a citrus grove and the geographic range of the disease is expanding, threatening citrus industries in new areas. Intensive chemical control of ACP is the primary management strategy currently advocated for HLB, but this strategy is costly, unsustainable, and generally ineffective. The scientific community is searching aggressively for solutions to HLB on many fronts, but it could still be years before solutions are found and implemented. Plant resistance to LAS is one area of research being pursued, whereby traits that confer resistance are identified and incorporated into citrus germplasm through conventional or transgenic methods. It remains to be seen if a solution to HLB can be found that specifically targets ACP, but research on ACP has been stepped up in a number of areas, notably on ACP–LAS–plant interactions, on host plant resistance to ACP, and on molecular methods of silencing ACP genes to induce mortality or to block its ability to transmit HLB-causing bacteria. Advancements in these and other research areas may depend greatly on a better understanding of basic ACP biology and vector–pathogen–host plant interactions at the molecular, cellular, and community levels. Here, we present an updated review of ACP and HLB with an emphasis on the problem in Florida.

Introduction

The Asian citrus psyllid (ACP), *Diaphorina citri* Kuwayama (Hemiptera: Psyllidae), is an important pest of citrus because it transmits phloem-limited bacteria (*Candidatus* Liberibacter spp.) strongly implicated in huanglongbing (HLB; citrus greening disease), which is the world's most serious disease of citrus (McClean & Schwartz, 1970; Bové, 2006). Husain & Nath (1927) presented an early, detailed review of ACP in India, which touched on systematics, distribution, food plants, biology and ecology, behavior, damage, and control. Asian citrus psyllid and HLB have since spread to citrus-growing regions nearly worldwide (Halbert & Manjunath, 2004; Halbert & Núñez, 2004; Pluke et al., 2008), increasing research efforts on ACP and HLB over the past 85 years and expanding our knowledge of the insect, the disease, and their interactions. More recent reviews of ACP or HLB were compiled by Halbert & Manjunath (2004), Bové (2006), Hall (2008a,b, 2010), and Gottwald (2010).

Asian citrus psyllid invaded many countries in Central and North America starting in the 1990s and HLB subsequently has been detected in the USA, eastern and western Mexico, Belize, Puerto Rico, and Cuba. Following the discovery of HLB in Florida during 2005, a three-component management program against HLB was advocated initially

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and implemented by some citrus growers: intensive chemical control of ACP, aggressive removal of HLB-infected trees, and planting disease-free nursery stock (Su et al., 1986; Gottwald, 2007; Hall & Gottwald, 2011). Florida imposed strict nursery compliance agreements to help ensure disease-free nursery stock, but this reduced the number of qualified sources for young trees and inflated prices. Hundreds of thousands of trees in Florida that probably were infected before the management program was implemented were removed from groves. The extent to which the three-tiered management program negates incidence and spread of the disease may depend largely on levels of inoculum within and around a grove. Within less than 7 years of the discovery of HLB in Florida, most growers found the three-tiered program too expensive, were reluctant to remove infected trees that were productive, and consequently abandoned efforts to remove trees (Spann et al., 2011) unless they were non-productive. Regional increases in inoculum loads therefore have occurred across Florida. More recently, a number of growers have implemented increased tree nutritional programs hoping to sustain the productivity of infected trees (Hall & Gottwald, 2011; Spann et al., 2011). Empirical observations suggest that some nutritional programs in combination with insecticide sprays against ACP may help sustain the productivity of infected trees at least in some situations, but as of yet there have been no published research reports supporting these observations. In fact, the only published report we are aware of indicates that none of several nutritional programs had any value for sustaining the productivity of infected trees (Gottwald et al., 2012).

Solutions to HLB are needed desperately and must be implemented soon to ensure the sustainability of commercial citrus. Novel tactics are needed for areas such as Florida where the HLB problem is severe, as little or no progress has been made using more conventional strategies, such as classical biological control by insect predators and parasitoids. Plant resistance to the HLB bacterium is one area of research being pursued vigorously by plant breeders and pathologists, whereby traits that confer resistance are being identified and incorporated into citrus germplasm through conventional or transgenic methods. The United States Department of Agriculture – Agricultural Research Service (USDA-ARS) in Fort Pierce, FL, USA, is generating thousands of citrus plants transformed to express different antimicrobial peptides known to have activity against plant pathogens in hopes of an HLB solution, and a high throughput screening program is in place for faster evaluations. Curative therapies for HLB-infected trees are being investigated, including infusion of antibiotics into trees and heat treatments. As an alternative or complement to an HLB solution based on disruption of the pathogen–host plant relationship, research has been expanded that targets ACP–pathogen or ACP–host plant interactions. This review presents an updated summary of information on ACP with an emphasis on experiences in Florida citrus.

Geographical distribution and invasion history

The geographical origin of ACP is thought to be southwestern Asia (Halbert & Manjunath, 2004; Beattie et al., 2009). According to Beattie et al. (2009), all evidence concerning the origin of ACP supports that it evolved in India. Asian citrus psyllid occurs in China (incl. Hong Kong), India, Myanmar, Taiwan, Philippine Islands, Malaysia, Indonesia, Sri Lanka, Pakistan, Thailand, Nepal, Ryukyu Islands (Japan), Afghanistan, Saudi Arabia, Réunion, and Mauritius (Mead, 1977; Halbert & Manjunath, 2004). Asian citrus psyllid has been in South America since the 1940s, invading Brazil and subsequently Argentina and Venezuela, and it invaded the West Indies (Guadeloupe), Abaco Island, Grand Bahama Island, Cayman Islands, and Florida, USA, in the 1990s (Tsai & Liu, 2000; Halbert & Núñez, 2004). During 2001, ACP was found in the Dominican Republic, Cuba (Halbert & Núñez, 2004), Puerto Rico (Pluke et al., 2008), and Texas, USA (French et al., 2001). Asian citrus psyllid has been reported more recently in many new areas in the Americas, including Mexico, Costa Rico, Belize, Honduras, and the states of Alabama, Arizona, California, Georgia, Louisiana, Mississippi, and South Carolina in the USA [see Halbert et al. (2010) for a recent summary].

Phylogeographic and genetic studies of ACP populations in the Americas indicated that two founding events of ACP probably occurred, one in South America and one in North America (De León et al., 2011). Phylogenetic analyses among worldwide collections of ACP suggested that there are two major haplotype groups of ACP with preliminary geographic bias between southwestern and southeastern Asia (Boykin et al., 2012). The recent invasion of ACP into the USA and Mexico originated from only the southwestern group, but both the southwestern and southeastern groups invaded separate locations in Brazil. A haplotype unique to the Caribbean (Puerto Rico and Guadeloupe) was found, indicating that a distinction exists between tested populations in the USA and the Caribbean. Additional investigations into the phylogenetic relationships among worldwide populations of ACP might be worthwhile, as research by Boykin et al. (2012) did not distinguish mitochondrial DNA from nuclear DNA, polymerase chain reaction (PCR) products were directly sequenced rather than cloned prior to sequencing, and relatively few ACP from the Old World were sampled.

Asian citrus psyllid description, life cycle, and biology

Adult ACP are small (2.7-3.3 mm long) with mottled brown wings (Figure 1A). Adults have three relatively distinct abdominal colors (gray/brown, blue/green, and orange/yellow), the significance of which remains unknown (Wenninger & Hall, 2008a). The sex ratio in a population is approximately equal (Aubert & Quilici, 1988). Adults rest or feed on citrus leaves or young shoots with their bodies held ca. at a 45° angle from the plant surface (Figure 1A).

Adult males and females locate mates, in-part, by using substrate-borne vibrational sounds (Wenninger et al., 2009a). Behavioral evidence indicates that females emit a sex pheromone, but none has been identified (Wenninger et al., 2008). Males and females mate multiple times with different partners (Wenninger & Hall, 2008b). Mating, oviposition, and other movement are restricted to daylight hours (Wenninger & Hall, 2007). Females can lay eggs throughout their lives if young leaves are present. Adult females typically lay 500–800 eggs over a period of 2 months, with a maximum of 1 900 (Husain & Nath, 1927; Tsai & Liu, 2000; Nava et al., 2007). The lower and upper temperature thresholds for oviposition are 16.0 and 41.6 °C, respectively, and most eggs are oviposited at 29.6 °C (Hall et al., 2011). Humidity also influences oviposition: ACP produces fewer eggs when relative humidity drops below 40% (Skelley & Hoy, 2004).

Eggs are oval, light yellow when freshly deposited, and bright orange with two distinct red eye spots at maturity (Figure 1B). Eggs are anchored to new flush with a tapered stalk (pedicel) at the posterior/lower end (Figure 1C); ACP egg stalks were reported to be 0.038-mm long (Husain & Nath, 1927). Many eggs may be found on a single flush shoot (Figure 1B). Asian citrus psyllid has five instars (Figure 1D). Early instars are docile and move only when disturbed or overcrowded (Tsai & Liu, 2000), whereas older nymphs and adults are more mobile.

Developmental times of eggs and nymphs vary with temperature: mean development from egg to adult ranges from 14.1 days at 28 °C to 49.3 days at 15 °C (Liu & Tsai, 2000; Fung & Chen, 2006). New adults reach reproductive maturity within 2–3 days and oviposition begins 1–2 days after mating (Wenninger & Hall, 2007). The optimal temperature range for ACP development is 24–28 °C and the population generation time at 25 °C is 20–22 days (Liu & Tsai, 2000; Fung & Chen, 2006). Nava et al. (2007) reported that adult males live an average of 21–25 days and females live an average of 31–32 days at 24 °C. Liu & Tsai (2000) report maximum adult longevity as 117 days at 15 °C to 51 days at 30 °C, but we found that virgin females lived up to 188 days (on average 90 days) at 27 °C on a favorable host plant (Richardson & Hall, 2012). A number of factors may influence survival, including relative humidity, host plant, and reproductive status (McFarland & Hoy, 2001; Nava et al., 2007).

Skelley & Hoy (2004) presented methods of rearing ACP on orange jasmine [*Murraya exotica* L. = *Murraya paniculata* auct. non.; USDA-ARS-NGRP, 2012]. USDA-ARS has reared ACP on orange jasmine and also on *Citrus macrophylla* Wester (Hall & Richardson, 2012). Based on ACP colonization of different genotypes under field conditions (Westbrook et al., 2011), several other plant species may be good hosts for rearing ACP, including *Citrus reticulata* Blanco, *Bergera koenigii* L., *Citrus maxima* (Burm.) Merr., *Citrus medica* L., *Citrus taiwanica* Tanaka & Y. Shimada, and *Citrus aurantiifolia* (Christm.) Swingle. Little progress has been made on an artificial diet for ACP, although adult ACP can survive relatively long feeding on a sucrose solution through a membrane (Hall et al., 2010a). Asian citrus psyllid females feeding on artificial diet through a membrane rarely laid eggs, possibly because the feeding chambers studied, and in particular the membrane, may have been inadequate with respect to encouraging oviposition and accommodating insertion of the egg stalks (Hall et al., 2010a). Information on stylet length of nymphs (Ammar & Hall, 2012) could be valuable in determining how thin the feeding membrane would need to be for early instars.

Adults feed on young stems and on leaves of all stages of development. Nymphs feed on young leaves and stems, continuously secreting copious amounts of tube-like material from the anus covered by waxy white material reportedly secreted by the circumanal glands (Figure 1E; Tsai & Liu, 2000). Adult females also produce a white excretory substance, but males produce clear sticky droplets (Hall et al., 2010a). Asian citrus psyllid has piercing-sucking mouthparts and insert their stylets into citrus plants to feed on phloem tissue (Bonani et al., 2010), leaving their salivary sheaths/stylet tracks behind (Figure 1F,G). USDA-ARS has identified the constituents of the sheaths and is pursuing methods of blocking their formation as a possible ACP management tactic (Shatters, 2011).

Flight activity

Asian citrus psyllid apparently cannot fly very far or sustain a long flight because it has weak muscles relative to the size of its wings (Husain & Nath, 1927; Sakamaki, 2005). The longest flight duration by ACP in a flight mill was 47 min for females and 49 min for males; the longest flight distance was 978 m for females and 1 241 m for males (Arakawa & Mivamolo, 2007). Extrapolating data from Arakawa & Mivamolo (2007), flight speed averaged

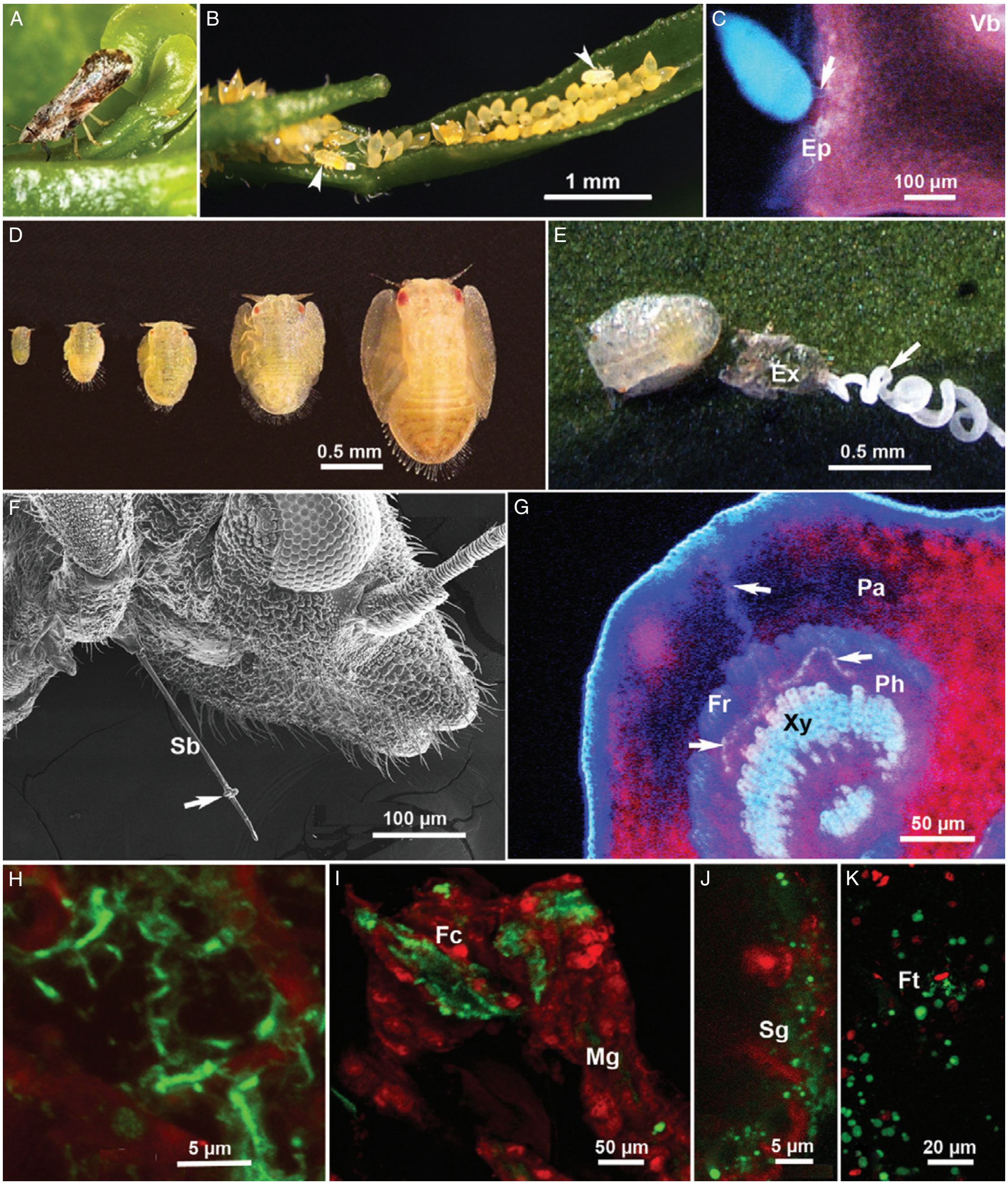

Figure 1 (A) Adult Asian citrus psyllid (ACP). (B) ACP eggs and newly hatched nymphs (arrowheads) on a folded young citrus leaf. (C) Epifluorescence micrograph of a section in a young petiole, showing the egg stalk (arrow) embedded in the epidermal layers (Ep), far from the vascular bundle (Vb). (D) ACP instars 1–5 from left to right, respectively. (E) A newly molted nymph that crawled out of its exuvia (Ex) leaving long, white, tube-like excretion material attached to it (arrow). (F) Scanning electron micrograph of an adult ACP head showing the extended stylet bundle (Sb) with part of the salivary flange around the stylets (arrow). (G) Epifluorescence micrograph of a section in a citrus leaf midrib showing ACP salivary sheath (arrows) into the phloem (Ph); Xy, xylem. (H–K) Confocal laser scanning micrographs showing *Candidatus* Liberibacter asiaticus bacteria (green obtained with fluorescence in situ hybridization) in the phloem of infected citrus leaf (H), and in various tissues of infected ACP (I–K), including the filter chamber (Fc), midgut (Mg), salivary gland cells (Sg), and fat tissue (Ft). Panels H–K are modified from Ammar et al. (2011b).

1.4 km h^{-1} (0.9 mph) in the absence of wind and a single flight averaged 25.4 min. Adult ACP is active during daylight, but flight activity is pronounced during sunny afternoon hours (Sétamou et al., 2011). Asian citrus psyllid flies from citrus to distances of 30–100 m during almost every month in Florida, but flight activity regularly peaks in spring (Hall & Hentz, 2011). Asian citrus psyllid also regularly flies 60–100 m between pairs of managed and unmanaged groves, with net movement toward managed groves (Boina et al., 2009).

Long-distance dispersion by ACP probably consists of repeated short-distance flights (Arakawa & Mivamolo, 2007). Long-distance movement by ACP between and within Japanese islands such as Yoron and Kyushu was theorized as possible, but wind-dependent (Sakamaki, 2005). Asian citrus psyllid theoretically could be transported 0.5–1 km by wind drifts, depending on wind speed and duration of sustained flight (Aubert & Hua, 1990). Circumstantial evidence indicates that ACP moved at least 51 km northwest across an area of the Florida Everglades lacking known host plants (Halbert et al., 2008). This was the shortest distance across the Florida Everglades between urban coastal southeast Florida, where HLB was first found to be well established in September 2005, and several large commercial groves in Hendry County on the western boundary of the Everglades. The eastern edges of these groves had many symptomatic trees by October 2005. Prevailing wind direction during the 5 years prior to the discovery of the disease in Hendry County was from the southeast, supporting the hypothesis that wind played a role in dispersing ACP across the Everglades (Hall, 2010). Some other hemipterans, such as aphids, can be carried with wind, and thus can transmit plant pathogens over much longer distances than they can fly by themselves (Zeyen & Berger, 1990).

Seasonal population dynamics

Seasonal population fluctuations of ACP are correlated closely with the growth of new, young flush on citrus trees because eggs are laid exclusively on young flush and nymphs develop exclusively on young plant parts. Large infestations of ACP commonly occur during late spring through mid-summer in North America, but outbreaks can occur any time of year if environmental conditions are favorable and young flush is available (Hall et al., 2008a). Nine generations of ACP were recorded over a 1-year period in India on citrus and it was speculated that two more generations could have developed if more flush had been present during late summer and early fall (Husain & Nath, 1927).

Adult ACP, but not eggs, become cold acclimated during the winter through exposure to lower temperatures. However, all three life stages can survive short periods of cold: relatively many adults and nymphs survive after being exposed for several hours to temperatures as low as −6 °C and relatively many eggs hatch after being exposed for several hours to temperatures as low as −8 °C (Hall et al., 2011). Mild to moderate freeze events usually are non-lethal to adult ACP even if they are not cold acclimated (Hall et al., 2011), but a freeze that kills flush would be expected to result in mass mortality of young ACP.

Detection and monitoring

Growers, researchers, and regulatory personnel often need methods for detecting ACP and monitoring ACP populations. Visual searches by trained personnel may be the fastest way to detect an infestation of ACP, and eggs and nymphs are best quantified using visual searches per unit of time or per plant sample (flush shoots) (e.g., Sétamou et al., 2008). Eggs and nymphs are aggregated among sampling units, whereas adults may be dispersed more randomly (Dharajothi et al., 1989). The minimum number of flush shoots per tree needed to estimate ACP densities varies from four for adults to eight for eggs (Sétamou et al., 2008). A sampling plan consisting of 10 trees and eight flush shoots per tree would provide acceptable density estimates of the three life stages of ACP (Sétamou et al., 2008). Sampling for immature stages, especially eggs, has been considered critical with respect to most pest management decisions (Dharajothi et al., 1989). However, the life stage to sample to make ACP management decisions may depend on management strategies. In Florida, growers have tended to base control decisions on numbers of adults.

Presence and relative abundance of adult ACP can be ascertained with stem-tap samples, yellow sticky traps, vacuum samples per unit of time, suction traps, sweep net samples, visual searches per unit of time, and samples of flush shoots or pairs of mature leaves (Aubert & Quilici, 1988; Sétamou et al., 2008; Hall & Hentz, 2010; Thomas, 2012). The choice of a sampling method in-part depends on the age of plants being sampled as well as the reason for sampling. For example, sweep sampling could damage newly planted citrus or spread citrus canker disease, so other sampling methods would be preferred, such as sticky traps or visual inspection of plant samples. When flush is not present, infestations of ACP adults on mature leaves can be quantified to follow population levels and for estimates of absolute population densities (Hall et al., 2008a; Hall, 2009). USDA-ARS presented a preliminary sample-size recommendation of 200 pairs of mature leaves (five pairs of leaves per tree on 40 trees) for determining the average number of adult ACP per pair of mature leaves, a sample size that provided adequate precision of commercial estimates at means of 0.1 or more adults per sample (Hall, 2010). In Florida citrus, stem-tap sampling has become one of the most popular monitoring methods for adult ACP (Stanlsy et al., 2010a), and formal procedures for tap sampling have been developed for making density estimates with a known level of precision (Hall & Hentz, 2010; Stanlsy et al., 2010a). The Citrus Health Management Area program in Florida includes a large-scale ACP monitoring effort based on tap samples for adults (Rogers et al., 2012a).

Yellow sticky card traps are used widely to monitor adult ACP and they catch more ACP than blue sticky traps (Aubert & Quilici, 1988; Aubert & Hua, 1990; Hall et al., 2007, 2008a; Flores et al., 2009). Yellow and green traps are more attractive to ACP than orange or red, but having some red and orange in the color spectrum of a trap enhances the capture rate (Hall et al., 2010b). The number of adult ACP captured on traps generally increases as trap reflectance increases in the yellow, orange, and red wavelength regions, but decreases as reflectance increases in the blue wavelength region (Hall et al., 2010b). Hall et al. (2010b) found no evidence that any of six traps varying in yellow and green intensity would be best at detecting psyllids when adult populations are low. Irrespective of the exact yellow/green color of a trap, whether larger traps might be more effective for catching adult ACP than smaller traps remains to be investigated.

Stem-tap sampling requires less time than sticky trap sampling, requires only one visit to a site, and is cheaper (Hall & Hentz, 2010). A drawback to stem-tap sampling, however, is that it can be difficult to count adult ACP before some escape. Stem-tap samples and sticky traps are effective for detecting adult ACP in trees when moderate adult densities (>1 adult per sample) are present, but sticky traps are more effective when the density of ACP is lower (Hall et al., 2007; Hall, 2009). Sticky traps can be used in short trees (<1-m high), whereas tap sampling cannot. Sticky traps also serve as a record of what has been collected, are useful for training individuals to identify ACP, and are less likely to be influenced by variation among individuals collecting samples than stem-tap sampling. Comparisons of sticky trap counts of adult ACP within or among blocks of trees should be made with caution because sticky traps can be inconsistent indicators of ACP densities due to the influence of sunlight and temperature on flight activity by adults (Hall, 2009).

Asian citrus psyllid detection and monitoring activities could be greatly enhanced if a chemical attractant for the psyllid was available. Asian citrus psyllid relies at least on olfaction and vision to locate citrus hosts (Wenninger et al., 2009b; Sétamou et al., 2011), and they may find mates through olfaction, visual cues, and substrate vibrational communication (Wenninger et al., 2008, 2009a). Chemical ecologists have been searching not only for ACP attractants but also for repellents and confusants. Volatiles that elicit ACP antennal responses can be identified using coupled gas chromatography/electroantennogram preparations, but this research has been challenging due to the small size of the ACP antenna. Olfactometers, wind tunnels, and other methods such as ring and leaf assays (Patt et al., 2011) can be used to study behavioral responses to volatiles. Asian citrus psyllid behavior is stimulated by mixtures of synthetic versions of host plant volatiles from orange jasmine, *C. aurantiifolia* (Christm.) Swingle, and *Citrus sinensis* (L.) Osbeck, and odor composition and concentration have a strong effect on ACP response (Patt & Sétamou, 2010; Patt et al., 2011). The search for ACP attractants continues and is supported by the fact that female pear psylla [*Cacopsylla pyricola* (Förster)] was shown to produce a sex pheromone that attracts conspecific males (Guédot et al., 2009). Continued research in the area of ACP chemical ecology should be beneficial as it relates to ACP flight, host finding, feeding, mate finding, oviposition, and other biological parameters. Other possible physical attractants or stimuli such as light, sound, and electromagnetic fields also should be investigated.

Vector–pathogen interactions

Huanglongbing, associated with three phloem-limited *Ca.* Liberibacter species in various regions of the world, often spreads quickly in a citrus planting and eventually kills citrus trees, particularly young ones (Xu et al., 1988; Gottwald, 2010). For example, 50–70% of the citrus trees in Guangdong and Fujian provinces of China became infected before they reached fruit bearing age during 1981–1983 (Xu et al., 1988). Whereas *Ca.* Liberibacter africanus and *Ca.* Liberibacter americanus can cause HLB, and another psyllid, *Trioza erytreae* (del Guercio), can transmit HLB pathogens, most cases of HLB worldwide currently are related to *Ca.* Liberibacter asiaticus (LAS) transmitted by ACP (Hall & Gottwald, 2011). The Asian form of HLB is considered to be more severe than the African form (Gottwald, 2007). Asian citrus psyllid nymphs have the highest rates of acquisition of the pathogen, can acquire the pathogen during the later instars of development, and can transmit the pathogen as nymphs or adults (Inoue et al., 2009; Pelz-Stelinski et al., 2010). Fourth and fifth instars of ACP can transmit the pathogen, but first to third instars reportedly do not (Xu et al., 1988).

Adult ACP are more highly attracted to LAS-infected trees before feeding on them, but they are more attracted to uninfected trees after feeding on infected ones, which may promote the spread of the pathogen (Mann et al., 2012). Uninfected adult ACP feeding on a diseased tree can acquire the pathogen within 0.5–5 h (Xu et al., 1988), but only 40% of adults feeding on diseased citrus tested positive for the pathogen after 35 days using PCR tests

(Pelz-Stelinski et al., 2010). Cen et al. (2012) reported that the severity of HLB symptoms associated with a diseased tree negatively influenced phloem feeding activity by adult ACP, which could contribute to differences in acquisition rates of LAS. Asian citrus psyllids that acquired LAS only during the adult stage were poor vectors of the pathogen, unlike adults that acquired the pathogen as nymphs (Inoue et al., 2009; Pelz-Stelinski et al., 2010). A latent period of 1–25 days may be required before an adult ACP can transmit the pathogen after acquisition from diseased citrus (Xu et al., 1988), but adults developing from nymphs that acquire the pathogen can transmit as soon as they eclose (Xu et al., 1988). Adult ACP can remain inoculative (infective) with LAS bacterium throughout their life after acquiring the pathogen as nymphs (Xu et al., 1988; Hung et al., 2004). Interestingly, LAS-infected ACP develop faster and have higher fecundity (Pelz-Stelinski, 2011).

Candidatus Liberibacter asiaticus may be transmitted at low rates from infected females transovarially to their progeny (Pelz-Stelinski et al., 2010) and from infected males to uninfected females during mating (Mann et al., 2011a). These studies used PCR to detect LAS in the offspring and mates, but it remains to be validated that infected offspring and mates can transmit the pathogen. van den Berg et al. (1992) postulated that females of the African citrus psyllid could transmit HLB pathogens transovarially and/or during oviposition or that eggs imbibed the pathogen from infected plants. However, we consider the latter hypothesis unlikely for ACP because cross-sections of leaf petioles and shoots on which eggs were laid showed that egg stalks are embedded only in epidermal cell layers (Figure 1C), well short of the vascular bundle or phloem tissue that the pathogen needs to come into contact with to infect a plant (Bonani et al., 2010). Transovarial transmission would explain the results of experiments performed by van den Berg et al. (1992; Halbert & Manjunath, 2004).

For a persistent pathogen to be transmitted by an insect, the pathogen must be ingested, passed through the alimentary canal wall, moved through hemolymph or other tissues to the salivary glands, and passed with salivary secretions into the host plant during feeding (Ammar, 1994; Hogenhout et al., 2008). Using PCR and fluorescent in situ hybridization, LAS was found in the phloem of citrus plants (Figure 1H) as well as in most of ACP's organs and tissues (Figure 1I–K) including the salivary glands, hemolymph, filter chamber, midgut, fat and muscle tissues, and ovaries (Ammar et al., 2011a,b). This systemic infection of LAS in ACP organs and tissues seems to be similar to that of propagative plant pathogens that are known to multiply in their hemipteran vectors (Hogenhout et al., 2008; Ammar et al., 2009). Inoue et al. (2009) and Pelz-Stelinski et al. (2010) reported that LAS multiplies in ACP when acquired by nymphs but not when acquired by adults. They suggested that multiplication of the bacterium within ACP is essential for effective transmission. Polymerase chain reaction tests on various organs of adult ACP suggested that LAS either accumulates or replicates in the alimentary canal and salivary glands (Ammar et al., 2011a). However, among LAS-infected adult ACP, the proportion of infected (LAS-positive) salivary glands is significantly lower than that of the alimentary canal or other organs, suggesting that a salivary gland infection barrier (to LAS) may exist (Ammar et al., 2011a, b). This also is supported by the fact that LAS transmission to plants by individual psyllids is normally much lower than the proportion of LAS-infected ACP. For example, Pelz-Stelinski et al. (2010) reported that 40–60% of ACP that fed on LAS-infected plants became PCR-positive, but successful LAS inoculation to citrus plants by individual ACP ranged from 4 to 10%. Ammar et al. (2011c) reported similar results using a detached/excised leaf assay method. Barriers within the ACP body preventing the movement of LAS to and from the salivary glands could play an important role in reducing transmission rates of the pathogen, but many other factors alone or in combination could influence transmission rates including plant defenses, environmental conditions, and genetic differences among ACP in their ability to acquire and transmit LAS. Further research on transmission barriers, and receptors associated with them (Hogenhout et al., 2008; Ammar et al., 2009), may help in devising novel control methods aimed at blocking LAS transmission by ACP, and such research could be more fruitful if investigations such as those by Ammar et al. (2011c) were expanded to include nymphs. Further elucidation of barriers to acquisition, transmission, systemic infection of plants, and disease development could provide information necessary to devise strategies to protect plants.

Transmission rates reported in early studies of HLB may be unreliable because they were dependent on the development of disease symptoms in host plants rather than presence or absence of the pathogens, determined by PCR testing. Transmission efficiency of LAS by individual infected adults is reported to range from 2 to 10% in Florida (Pelz-Stelinski et al., 2010; Ammar et al., 2011c), but up to 80% in China (Xu et al., 1988). Differences in transmission efficiency of HLB by ACP may occur among geographic areas. However, the study in China (Xu et al., 1988) used a small number of seedlings (5–10 per test) and only symptoms were used to score infected plants rather than PCR or other more reliable tests. The lag in time between transmission of the pathogen by ACP and onset of visual symptoms can be quite variable depending on the time of the year when transmission occurs, environmental conditions, tree age, species/cultivar, and horticultural health (Gottwald, 2007). Manjunath et al. (2008) and Halbert et al. (2012) showed that LAS-positive nymphs can be found on some plants 9 months or more prior to development of symptoms.

Control of Asian citrus psyllid and huanglongbing

Intensive chemical control programs against ACP have been deemed necessary to combat HLB by growers in many areas such as Brazil and Florida. Applying insecticides at critical flushing periods and during winter can greatly reduce populations of ACP. Informal surveys indicate that intensive chemical programs and aggressive removal of infected trees reduce the rate of newly infected trees in Brazil. Insecticide schedules for ACP in Florida citrus have been recommended (Rogers, 2008; Stanlsy et al., 2010b, 2012), and insecticides such as imidacloprid, fenpropathrin, chlorpyrifos, and dimethoate are considered effective and registered for citrus in Florida (Rogers et al., 2012b). However, empirical observations indicate that even intensive insecticide programs against ACP are generally ineffective for preventing the introduction and spread of HLB, especially in new citrus plantings. These observations have been substantiated by research in many geographical areas (Gottwald, 2007) including Florida (DG Hall, unpubl.), Brazil (Berhamin-Filho et al., 2009), and Vietnam (Ichinose et al., 2010). Meanwhile, populations of ACP in Florida are becoming less susceptible to some insecticides (Tiwari et al., 2011).

Natural enemies

Asian citrus psyllid is subjected to various levels of control by natural enemies throughout its geographic distribution. Asian citrus psyllid nymphs commonly are attacked by generalist predators worldwide including ladybeetles (Coleoptera: Coccinellidae), syrphid flies (Diptera: Syrphidae), lacewings (Neuroptera: Chrysopidae, Hemerobiidae), and spiders (Araneae) (Aubert, 1987; Michaud, 2001, 2002, 2004; González et al., 2003). Little is known regarding the extent to which these predators reduce infestations of ACP, but some are considered important biological control agents. For example, coccinellid predators (such as *Harmonia axyridis* Pallas, *Olla v-nigrum* Mulsant, *Exochomus children* Mulsant, *Cycloneda sanguinea* L., and *Curinus coeruleus* Mulsant) may be the most important biological control agents of ACP in Florida (Michaud, 2001, 2002, 2004; Michaud & Olsen, 2004). Spiders have been noted as ACP predators in Florida (Michaud, 2002), and in Saudi Arabia they have accounted for 34% of the total predators of ACP (Al-Ghamdi, 2000). Several other predators in Saudi Arabia are important, including the histerid beetle *Saprinus chalcites* Illiger and the carabid *Egapola crenulata* Dejean (Al-Ghamdi, 2000).

Asian citrus psyllid is attacked by two primary parasitoid species native to Asia: *Tamarixia radiata* (Waterston) (Figure 2A) and *Diaphorencyrtus aligarhensis* (Shafee, Alam & Agarwal). Viraktamath & Bhumannavar (2002) list several other parasites of ACP: *Psyllaephagus diaphorinae* Lin & Tao may be a primary parasite; *Syrphophagus taiwanus* Hayat & Lin, *Syrphophagus diaphorinae* Myartseva & Tryapitsyn, and *Marietta* spec. nr. *exitiosa* Compere are probably hyperparasites; and *Diaphorencyrtus diaphorinae* Lin & Tao is listed as a hyperparasite, but may be a primary parasitoid. *Tamarixia radiata* and *D. aligarhensis* have been introduced in several countries invaded by ACP, such as Mauritius, Réunion Island, and the USA (Hoy & Nguyen, 2001). Higher percentages of ACP nymphs were parasitized by *T. radiata* than by *D. aligarhensis* in Réunion (Aubert, 1987). *Tamarixia radiata* also was released in Taiwan and Guadeloupe and inadvertently introduced in other areas, such as Puerto Rico, Venezuela, Brazil, and China (Étienne et al., 2001; French et al., 2001; Torres et al., 2006; Pluke et al., 2008). *Tamarixia radiata* in India and other areas in Asia are attacked by a complex of hyperparasitoids (Aubert, 1987). Care must be taken to avoid importing hyperparasitoids along with primary parasitoids of ACP.

Tamarixia radiata is a solitary ectoparasitoid that specializes on ACP and is native to India (Chien, 1995; as cited by Skelley & Hoy, 2004). Female *T. radiata* attack third through fifth instars of ACP (Figure 2B; McFarland & Hoy, 2001; Skelley & Hoy, 2004). Females lay one egg (sometimes two) on the ventral surface of an ACP nymph, attaching it externally to the cuticle (Figure 2C). Developing parasitoid larvae feed externally (Figure 2D, E), eventually transforming the host into a mummy sealed to plant tissue. Pupation occurs beneath the mummy and, when new adults emerge, they exit through a hole they make at the thoracic or head region of the mummy (Figure 2F). Although more than one egg may sometimes be laid beneath a nymph, only one parasitoid usually reaches the adult stage. At 25 °C, fifth instars parasitized by *T. radiata* are mummified within about 7 days, and new adult parasitoids emerge ca. 6 days later (Skelley & Hoy, 2004). In addition to killing ACP nymphs through parasitism, adult *T. radiata* feed on early instars of ACP. A single *T. radiata* adult can kill up to 500 nymphs though predation and parasitism, with the majority of mortality due to predation (Chien, 1995; as cited by Skelley & Hoy, 2004).

Figure 2 (A) Adult parasitic wasp *Tamarixia radiata*. (B) Female *T. radiata* laying an egg beneath an Asian citrus psyllid (ACP) nymph. (C) *Tamarixia radiata* eggs (arrows) laid on the ventral side of ACP nymphs near their hind coxae. (D,E) *Tamarixia radiata* larvae (earlier and later instars, respectively) feeding on the ventral side of ACP nymphs. (F,G) Exit holes (arrows) of the parasitic wasps *T. radiata* (F) and *Diaphorencyrtus aligarhensis* (G) in mummies of ACP nymps.

Tamarixia radiata significantly reduced populations of ACP in Réunion Island, greatly mitigating HLB (Étienne & Aubert, 1980). The parasitoid was reported to provide good levels of biological control of ACP in India (Husain & Nath, 1927), Taiwan (Chien & Chu, 1996 as cited by Skelley & Hoy, 2004), Guadeloupe (Étienne et al., 2001), and Puerto Rico (Pluke et al., 2008), although it remains unclear to what extent ACP population levels were reduced at these locations and, at least in Taiwan where hyperparasites may have interfered (Chiu et al., 1988), population reduction provided by *T. radiata* was insufficient to manage HLB. In contrast to *T. radiata* mitigating HLB in Réunion Island and providing large percentages of biological control of ACP in some locations, *T. radiata* generally has provided little biological control of ACP in Florida (Tsai et al., 2002; Michaud, 2004; Hall et al., 2008a; Qureshi et al., 2008). Field data reported by Michaud (2004) indicate that parasitism by *T. radiata* contributed to only 0.2–1.3% mortality of psyllid nymphs in central Florida. *Tamarixia radiata* might be a less effective biological control agent of ACP in Florida than in some other geographical areas because of environmental differences, interguild competition with other beneficial organisms, or, based on Barr et al. (2009), genetic differences. Populations of *T. radiata* from Taiwan and Vietnam were originally released in Florida, but other haplotypes of the parasitoid might be more effective in Florida. New haplotypes from south China, north Vietnam, and Pakistan are being released in Florida citrus and urban areas in hopes of boosting levels of parasitism to reduce the general ACP population equilibrium level and provide some relief from HLB. In the meantime, growers should be aware that chemicals used in citrus such as insecticides, miticides, chemicals for plant diseases, spray oils, and nutritional sprays may negatively influence the effectiveness of *T. radiata*. The following chemicals were highly toxic to adult *T. radiata* based on the toxicity of direct sprays and potentially long residual life on leaves: carbaryl, chlorpyrifos, and fenpropathrin (Hall & Nguyen, 2010). Pesticides that may be more compatible with biological control by *T. radiata* are aluminum tris, copper hydroxide, diflubenzuron, and kaolin clay (Hall & Nguyen, 2010).

Diaphorencyrtus aligarhensis is a solitary endoparasitoid that specializes on ACP and is native to India (Yang et al., 2006). Female *D. aligarhensis* consume nymphal ACP and parasitize second through fourth instars (Skelley & Hoy, 2004; Rohrig et al., 2011). A single female *D. aligarhensis* may kill up to 280 ACP nymphs through predation and parasitism, with the majority of mortality due to predation (Chien, 1995; as cited by Skelley & Hoy, 2004). Development from oviposition to eclosion of adult *D. aligarhensis* takes ca. 12–18 days, during which time the host is mummified (Skelley & Hoy, 2004; Rohrig et al., 2011). New adult *D. aligarhensis* emerge through an exit hole in the abdominal region of mummified ACP (Figure 2G). *Diaphorencyrtus aligarhensis* became established in Réunion Island and Taiwan after releases (Chien, 1995; as cited by Skelley & Hoy, 2004), but efforts to establish the parasitoid in Florida during 1998 and 1999 failed (Michaud, 2002). Individuals of *D. aligarhensis* released in Florida were from a population in Taiwan and were infected with the intracellular endosymbiont *Wolbachia* (Jeyaprakash & Hoy, 2000). Possibly due to this endosymbiont, the population consisted only of females (Skelley & Hoy, 2004). A population of *D. aligarhensis* from Vietnam including both males and females was released in Florida during 2007–2009, but did not establish (Rohrig et al., 2012). Factors preventing establishment probably include intensive use of pesticides against ACP in citrus, low and variable populations of immature psyllids, competition with *T. radiata*, and predation of parasitized hosts by generalist predators (Rohrig et al., 2012).

Unfortunately, biological control by predators and parasitoids usually is not compatible with chemical control nor considered an acceptable management option once a grove is infected by HLB (Halbert & Manjunath, 2004; Yang et al., 2006). Therefore, it is unlikely that traditional biological control by itself will provide a solution to HLB, at least in Florida under current circumstances. Environmental conditions in other citrus areas in the USA, such as California or Texas, might be more favorable for classical biological control of ACP. However, HLB remains a serious problem in most areas where the parasitoid is established including Taiwan, Indonesia, the Philippines, and even in India where *T. radiata* is native.

Entomopathogens

Several species of entomopathogenic fungi have been reported to infect ACP worldwide and may be useful as biopesticides, including *Isaria fumosorosea* Wize (= *Paecilomyces fumosoroseus*) (Samson, 1974; Subandiyah et al., 2000), *Hirsutella citriformis* Speare (Rivero-Aragon & Grillo-Ravelo, 2000; Subandiyah et al., 2000; Étienne et al., 2001), *Lecanicillium* (= *Verticillium*) *lecanii* Zimm. (Xie et al., 1988; Rivero-Aragon & Grillo-Ravelo, 2000; Yang et al., 2006), *Beauveria bassiana* (Bals.) Vuill. (Rivero-Aragon & Grillo-Ravelo, 2000; Yang et al., 2006), *Cladosporium* spec. nr. *oxysporum* Berk. & MA Curtis (Aubert, 1987), *Acrostalagmus aphidum* Oudem, *Paecilomyces javanicus* (Friederichs & Bally) AHS Brown & G Smith (Yang et al., 2006), and *Capnodium citri* Berk. & Desm. (Aubert, 1987).

Cladosporium spec. nr. *oxysporum* and *C. citri* are important mortality factors for ACP in Réunion Island, where mortality of nymphs can exceed 60% (Aubert, 1987). An isolate of *I. fumosorosea* caused 95% mortality in spray applications to ACP in laboratory bioassays and 70% mortality when ACP were exposed to cards that had been sprayed with a liquid blastospore suspension (Moran et al., 2011). Therefore, devices that auto-disseminate fungi may be useful for controlling ACP, especially in areas where insecticides are not applied such as ornamental plantings and public areas as well as citrus grown for the organic market.

Hall et al. (2012) reported that *H. citriformis* killed the most adult ACP in Florida during fall and winter months, with mummified psyllids sometimes exceeding 75% of the total number of adults observed on mature leaves. However, it is probable that the actual percentage of adults killed by *H. citriformis* was as low as 3–4% based on numbers of adults on young leaves being 6 times higher than on mature leaves. A laboratory investigation into the toxicity to *H. citriformis* of six chemicals commonly used in citrus indicated that copper hydroxide, petroleum oil, and elemental sulfur at maximum label rates each significantly reduced the infectivity of a laboratory culture of *H. citriformis*, whereas copper sulfate pentahydrate, aluminum tris, and alpha-keto/humic acids did not. Therefore, citrus growers interested in capitalizing on *H. citriformis* as a control agent of *D. citri* should avoid applying high rates of copper hydroxide, oil, and sulfur.

Although *I. fumosorosea* and *H. citriformis* both occur naturally in Florida citrus, there has been little evidence that natural populations of these pathogens would ever contribute much to an HLB solution in Florida. Augmentative sprays of these pathogens at certain times of the year could be explored as a potential component of an integrated management program for ACP and HLB. A commercial formulation of a strain of *I. fumosorosea* is already registered for citrus (PFR-97 Microbial Insecticide, Certis, USA, Columbia, MD, USA). No commercial formulations of *H. citriformis* are available but the fungus can be cultured in vitro (Hall et al., 2011), a first step in developing a formulation for testing against ACP.

Host plants and resistance

Asian citrus psyllid has a wide host range, but the vast majority of host plant species falls within the family Rutaceae, subfamily Aurantioideae (citrus subfamily) (Halbert & Manjunath, 2004). Asian citrus psyllid reproduces mainly on a narrow range of host plants within the family Rutaceae; however, some non-preferred plants outside of this family may be acceptable alternatives, including *Ficus carica* L. (Moraceae) (Thomas & De León, 2011). Although most species in the genus *Citrus* are regarded as common hosts of ACP, some species within the genus may differentially influence the development, longevity, and reproduction of ACP (Tsai & Liu, 2000; Fung & Chen, 2006; Nava et al., 2007; Tsagkarakis & Rogers, 2010). Among species in other genera within the Rutaceae, some are good/preferred host plants [e.g., *M. exotica*, *Microcitrus* spp., and *B. koenigii*], and some are potentially poor hosts [e.g., *Atalantia* spec., *Eremocitrus glauca* (Lindley) Swingle, *Fortunella* spp., and *Merrillia caloxylon* (Ridley) Swingle]. Reducing or eliminating alternative host plants of ACP in the vicinity of citrus, such as *M. exotica*, a common ornamental hedge plant in Florida, may help reduce area-wide populations of ACP. Fortunately, whereas *M. exotica* is a suitable host for ACP, it appears to be a poor reservoir of HLB: only very low titers of LAS were found by PCR in this plant species as well as in ACP collected from *M. exotica* in east-central Florida (Walter et al., 2012). However, nursery trade in *M. exotica* is implicated in the dissemination of LAS-positive psyllids from the Miami area (Halbert et al., 2012).

Halbert & Manjunath (2004) surveyed citrus species and relatives for ACP in Winter Haven, Florida. Two species of *Zanthoxylum* (subfamily Toddalioideae), *Zanthoxylum clavahercules* L. and *Zanthoxylum fagara* (L.) Sarg., hosted zero and few ACP, respectively. Another apparent non-host in the subfamily Toddalioideae is white sapote, *Casimiroa edulis* Llave & Lex. (Halbert & Manjunath, 2004; Westbrook et al., 2011). Very low abundances of ACP also were found on two genotypes of *Poncirus trifoliata* L. in a field survey (Westbrook et al., 2011). Nearly all genotypes of *P. trifoliata*, and many genotypes of ×*Citroncirus* spp. (hybrids of *P. trifoliata* and another parent species), were found to be resistant to ACP in no-choice tests (Richardson & Hall, 2012). *Poncirus trifoliata* is a trifoliate species that is graft compatible with *Citrus*, is used as rootstock in many citrus-growing regions (Ziegler & Wolfe, 1981; Krueger & Navarro, 2007), is an important parent in intergeneric hybrids with *Citrus* (Krueger & Navarro, 2007), and may have some resistance to another important pest of citrus, the citrus leafminer, *Phyllocnistis citrella* Stainton (Richardson et al., 2011). Therefore, *P. trifoliata* may be useful in breeding programs as a potential source of genes that confer resistance to multiple species of insects and may ultimately lower the incidence of HLB. Research is ongoing to explore the possibility of managing ACP and HLB via resistant host plants. Citrus germplasm with even moderately increased resistance to the pathogen (achieved through traditional breeding, genetic transformation, or by other means) in combination with traditional control tactics for ACP might be effective enough against the disease to sustain commercial citrus.

Interplanting citrus with guava

Infestations of ACP, and consequently incidence of HLB, were reported to be controlled to a large extent in Vietnam when citrus was interplanted with guava, *Psidium guajava* L. (Beattie et al., 2006). These observations were made in high-density plantings of citrus that were intercropped with guava at a 1:1 ratio. Volatiles associated with guava may interfere with ACP's ability to locate and infest citrus (Rouseff et al., 2008; Onagbola et al., 2010; Mann et al., 2011b) or secondary compounds in guava may kill ACP. In greenhouse studies ACP was reduced on citrus caged with guava, but the level of reduction was less dramatic than anticipated (Hall et al., 2008b), and interplanting citrus and guava in the field in Florida did not reduce populations of ACP enough to mitigate incidence and spread of HLB (DG Hall, unpubl.). Furthermore, growing white and pink guava in Florida is challenging due to their sensitivity to root knot nematodes and freezes. However, interplanting citrus with guava in some geographic areas, or with other plant species in areas such as Florida, might reduce populations of ACP and this area of research deserves more attention.

Molecular research for Asian citrus psyllid/huanglongbing control

A project is ongoing by the USDA-ARS to sequence the genome of ACP. A draft sequence was completed in 2011 and an estimated 25 000 active genes will likely be identified. This sequence is already being used by the scientific community for the purpose of mining the genetic information in search of genes and metabolic pathways involved in ACP biology and the pathogenicity of *Ca.* Liberibacter spp. in ACP. The complete genome sequence of LAS has been published (Duan et al., 2009), and much progress has been made on sequencing the citrus genome (Belknap et al., 2011). Expanded investigations into vector–pathogen–plant relations at the genetic level should soon be possible.

A novel approach being investigated to control ACP is using RNA interference (RNAi) to disrupt or regulate certain genes (Marutani-Hert et al., 2010; Wuriyanghan et al., 2011). RNAi is a natural gene regulatory and immune response of eukaryotic cells and is activated by double-stranded (ds) RNA. In theory, dsRNA could be designed to target specific genes of ACP that influence mortality or the ability of ACP to acquire and transmit LAS. The dsRNA could be delivered to the insect through phloem in the host plant if the dsRNA is injected into the plant or absorbed through the roots. Artificial feeding of dsRNAs to insects, including the potato psyllid, *Bactericera cockerelli* (Sulc), has successfully resulted in RNA knockdown effects and higher mortality (Wuriyanghan et al., 2011). More knowledge about the genome of ACP is needed to facilitate identifying specific genes to target with RNAi techniques, and more research will be needed on methods of getting dsRNA to ACP. Also, molecular studies on plant resistance and pathogen–insect interactions, including transmission barriers, may provide innovative control strategies of ACP and HLB in the future.

Regulatory issues

Research on ACP and HLB has largely focused on keeping existing citrus alive and productive. However, governmental regulatory agencies have been confronted with questions pertaining to the entry, establishment, and spread of ACP and HLB that deserve attention. Controlling the movement of plants infested by ACP is the first line of defense in preventing spread of ACP and HLB to new areas. Efforts to keep ACP and HLB out of a geographical area may include quarantining nearby areas where the pests are known to be present. Information on flight activity, particularly flight distance, may be needed to establish the size of a quarantine area. Procedures also are needed for preventing or eliminating the movement of ACP on citrus products and equipment being moved out of a quarantine area. Adult ACP have been observed in truck shipments of unprocessed fruit (Halbert et al., 2010) and adults may survive on harvested fruit for 10–13 days (Hall & McCollum, 2011). The movement of citrus leaves, such as those of *C. hystrix* and *B. koenigii* which are used as spices, also are of regulatory concern because of their potential as a pathway for the spread of ACP and HLB. In fact, adult ACP have been reported to live for up to 12 days on detached leaves (Hall & McCollum, 2011). Research is needed to identify harvesting, shipping, and control procedures to eliminate live ACP from citrus products and shipping containers, but which are practical, affordable, and do not negatively affect the intended use of the citrus products. Such procedures could include cold or heat treatments (Hall et al., 2011) or possibly an application of a soft pesticide that can be washed off of plant material later, leaving no toxic residues; for example, insecticidal soap is a possibility (Hall & Richardson, 2012). Movement of ACP and HLB on nursery stock is of additional concern, as discount garden centers and retail nurseries play a significant role in the widespread distribution of psyllids and plants carrying HLB pathogens (Manjunath et al., 2008; Halbert et al., 2012).

Conclusion

Asian citrus psyllid is an important pest of citrus nearly worldwide because it vectors a serious disease of citrus, HLB. Asian citrus psyllid and HLB are difficult to manage within their current geographic range and their range is expanding, threatening citrus industries in new areas. The HLB situation in some geographic locations, including Florida, is especially severe. In such areas, novel methods are needed to control ACP and mitigate HLB that are effective, economical, environmentally safe, sustainable, and target commercial groves and public areas to reduce area-wide populations of ACP and levels of HLB pathogen inocula. To this end, there are two primary broad areas of research being pursued in search of solutions to HLB – research toward solutions based on disruption of the pathogen–host plant relationship and research toward solutions based on disruption of either the ACP–pathogen or ACP–host plant relationship. The ultimate solution to HLB will require advances in both areas. With respect to recent research advances directly related to ACP, progress has been made in some interesting research areas as follows. Asian citrus psyllid-to-ACP transmission of the HLB pathogen (to progeny or mates) has been demonstrated and, pending confirmation that these recipients of the pathogen in turn can transmit LAS, this information should be included in epidemiology models for HLB. Asian citrus psyllid infected by LAS have a shorter generation time and lay more eggs, the combined effect of which favors faster development of large populations of infected ACP. *Candidatus* Liberibacter asiaticus has been shown to be transmitted primarily by adult ACP that acquire the pathogen as nymphs feeding on infected plants; thus, guarding against infestations of nymphs is critical. *Candidatus* Liberibacter asiaticus can be found throughout the body of an adult ACP but is less common in the salivary glands, which contributes to the low transmission rates of LAS by infected ACP. Long-distance movement of ACP and LAS has been documented on wind currents across the Everglades, on fruit in trailers and on nursery stock including *M. exotica*; thus, efforts to manage ACP and HLB should include area-wide efforts.

The following areas of ACP research are challenging, but currently may hold the greatest potential for advancing management of ACP and consequently HLB in commercial citrus in Florida: (1) physical behavior stimuli, including chemical ecology, notably focused on plant volatiles that mediate ACP behavior, and responses to light and sound; (2) molecular studies in search of methods of disrupting ACP biology (e.g., feeding and digestion) and for interfering with ACP acquisition and transmission of the HLB pathogen; and (3) host plant resistance to ACP (antixenosis or antibiosis). Significant advances in one or more of these areas of research could contribute to improved integrated pest management of ACP and thus HLB.

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