Biology and Management of Asian Citrus Psyllid, Vector of the Huanglongbing Pathogens

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Abstract

The Asian citrus psyllid, *Diaphorina citri* Kuwayama (Hemiptera: Psyllidae), is the most important pest of citrus worldwide because it serves as a vector of "*Candidatus* Liberibacter" species (*Alphaproteobacteria*) that cause huanglongbing (citrus greening disease). All commercially cultivated citrus is susceptible and varieties tolerant to disease expression are not yet available. Onset of disease occurs following a long latent period after inoculation, and thus the pathogen can spread widely prior to detection. Detection of the pathogen in Brazil in 2004 and Florida in 2005 catalyzed a significant increase in research on *D. citri* biology. Chemical control is the primary management strategy currently employed, but recently documented decreases in susceptibility of *D. citri* to several insecticides illustrate the need for more sustainable tools. Herein, we discuss recent advances in the understanding of *D. citri* biology and behavior, pathogen transmission biology, biological control, and chemical control with respect to "*Candidatus* Liberibacter asiaticus." Our goal is to point toward integrated and biologically relevant management of this pathosystem.

INTRODUCTION

Protandry: condition in which an animal begins life as a male and becomes a female

Protogyny: condition in which an animal begins life as a female and becomes a male

Immunomarking: technique in which animals are marked in the field with benign proteins to allow tracking of their movement by identification with enzyme-linked immunosorbent assay

The Asian citrus psyllid, *Diaphorina citri* Kuwayama (Hemiptera: Psyllidae), is the most serious pest of citrus worldwide, due primarily to its role as a vector of "*Candidatus* Liberibacter asiaticus" (Las), the bacterium that causes the highly destructive Asian huanglongbing (HLB) (citrus greening) of citrus (17). *D. citri* can also transmit "*Candidatus* Liberibacter americanus," which is known only from Brazil and currently at low incidence (17) and "*Candidatus* Liberibacter africanus" (72), which is not known to occur in the Americas. HLB-infected trees develop symptoms that include chlorotic leaves; twig dieback; fruit drop; misshapen, small fruit; lower internal fruit quality; and eventual tree death (17, 39). There is currently no cure for the disease.

D. citri was first described in Taiwan in 1907 (71), and the infectious nature of HLB was demonstrated in south China (76), although Beattie et al. (9) have argued for Indian origins of both. *D. citri* and HLB are currently found throughout much of Asia. The psyllid was found in Brazil in the 1940s (75), expanded its range to Florida in the late 1990s (41), and now infests most of the citrus-producing states of the United States, as well as Mexico, Belize, Costa Rica, and much of the Caribbean and South America (31, 45, 62, 79). The asiatic form of HLB was first found in the Western Hemisphere in Brazil in 2004 (138, 139), in Florida in 2005 (42), and has since been found in Belize, Mexico, Texas, and California. In most of these areas, it spread rapidly in residential and commercial plantings through natural and human-assisted transport of infected psyllids and infected plant material (43, 44). The recent rapid spread of the disease in the Americas has stimulated extensive research to understand Asian citrus psyllid biology, ecology, and management tactics.

Worldwide, control of *D. citri* to reduce its role as a vector has been one of three critical components of HLB management, in addition to planting pathogen-free nursery stock and removing inoculum by destroying infected trees. Due to the difficulty in detecting early infections of Las in trees and the rapid spread of HLB, factors that have hindered rogueing efforts, management programs in the Americas have concentrated on vector control (10, 111). Halbert & Manjunath (43) produced a literature review and an HLB risk assessment for Florida when *D. citri* first arrived in that region and two additional reviews (17, 27) focused on HLB. The current review provides subsequent developments in knowledge of the biology, ecology, and management of *D. citri* with respect to "*Ca.* Liberibacter asiaticus."

BIOLOGY AND ECOLOGY OF *DIAPHORINA CITRI*

Life Cycle and Reproduction

The life cycle of *D. citri* was previously reviewed in detail by Halbert & Manjunath (43). *D. citri* females are prolific and can develop rapidly, laying up to 800 eggs per lifetime, which are deposited only on young tissue, particularly newly expanded leaf growth 1 to 5 days after budbreak, known as feather flush. Eggs hatch within 2 to 4 days; five instars are completed within 11 to 15 days; and a total life cycle typically ranges between 15 and 47 days depending on temperature (77). Male and female *D. citri* emerge simultaneously with no protandry or protogyny (157). Copulation duration ranges between approximately 20 and 100 min and occurs exclusively on new leaf flush and during photophase (157). The female *D. citri* requires multiple matings throughout her lifetime to maintain maximum reproductive output; however, maximum oviposition can be constrained by the presence of multiple males, possibly due to harassment or an excess of acquired male accessory gland products (158). Females begin to lay eggs 1 day after mating (157).

Host Plants

Previous reviews and summaries of *D. citri* biology indicate a broad host range within the rutaceous subfamily Aurantioideae (43, 167). Oviposition and development on commonly grown citrus cultivars and related orange jasmine, *Murraya paniculata* (L.), are similar and increases are influenced mainly by flush production (97, 150). At least 10 genera, in addition to *Citrus*, are known host plants (5). More recently, investigations have focused on identification of citrus and citrus-related genotypes that display resistance to colonization and/or subsequent development by *D. citri*. 'Jatti khatti' (*Citrus jambhiri* Lushington) and 'Kagzi lime' [*Citrus aurantifolia* (Christm.) Swingle] are reported as poor hosts compared with sweet orange [*Citrus sinensis* (L.) Osbeck] (98). Also, oviposition, development, and survival of *D. citri* are significantly lower on 'Sunki' mandarin [*Citrus sunki* (Hayata) Tanaka] (97) and 'Cleopatra' mandarin (*Citrus reshni* Hort. ex Tan.) (149) than on known suitable host plants. In addition, *D. citri* avoids colonizing trifoliate orange, *Poncirus trifoliata* (L.), and will not colonize the citrus-related genotype, white sapote (*Casimiroa edulis* Llave et Lex) (163). Given that trifoliate orange readily hybridizes with other *Citrus* spp., it may be a promising candidate for citrus breeding efforts aimed at developing cultivars that express partial resistance to *D. citri* (163).

Temperature Limits

Optimal nymphal development and egg laying occur between 25°C and 28°C (77) and between 28°C and 29.6°C, respectively (55, 77). Fung & Chen (32) reported that female *D. citri* did not lay eggs at 16°C; however, this research conflicts with Liu & Tsai (77), who reported that female *D. citri* laid eggs at 15°C, albeit at a reduced (25%) rate compared with the optimal temperature. The upper and lower thresholds for oviposition were estimated to be 16°C and 41.6°C, respectively (55). The minimum temperature thresholds for development have been estimated at approximately 10°C (77) and 11°C to 13°C (32). A majority of *D. citri* survive several hours of exposure at −6°C and large percentages of eggs hatch following exposure to −8°C (55). It also appears that *D. citri* becomes acclimated to the cold during winter (55). Acclimatization to heat has also been suggested by Hall et al. (55), as *D. citri* has been reported to survive at 45°C in Saudi Arabia (see 55 and references therein). However, the thermal requirements of *D. citri* are identical for populations from diverse regions characterized by both cooler and warmer annual temperatures (96). Despite adaptation to temperatures characterizing tropical and subtropical climates, *D. citri* can survive temperature extremes, including freezes in citrus that have been defined as severe (<−6.5°C) (55).

Dispersal

Epidemiological investigations of HLB progression through citrus groves over time have inferred that *D. citri* routinely disperses distances of 25 to 50 m (39). Based on movement of disease between islands, the greatest distance over which dispersal has been recorded is 470 km and is thought to be mediated by lower jet streams (126). An immunomarking technique was adapted for tracking the movement of *D. citri* in Florida by marking psyllids in situ and then tracking their undisturbed movement behavior over time (11). *D. citri* was capable of moving 100 m within 3 days, with abandoned citrus groves serving as a source of infestation for nearby managed citrus (11). Subsequent investigations showed that *D. citri* was capable of dispersing 400 m within 4 days and that 2–14% of the psyllids moving from abandoned into managed groves carried the Las pathogen (143). More recently, Lewis-Rosenblum (74) determined a dispersal distance of at least 2 km within 12 days using the immunomarking technique. This distance is similar to the maximal distance of dispersal (1.5 km) reported for the African citrus psyllid, *Trioza erytreae* (Del Guercio), using mark-release-recapture (152). Also using mark-release-recapture, Kobori et al. (70) recorded

5- to 12-m dispersal distances of laboratory-reared psyllids and suggested that *D. citri* moves infrequently for the initial few days following colonization of a host plant. No distinct seasonal movement of *D. citri* has been observed to date; however, peak movement appears to occur following the spring flush of citrus foliage (48, 74). Commercial citrus can be infested by immigrating psyllids throughout the entire year on the east central coast of Florida where capture of adults on traps was not correlated with wind speed, sunlight, or temperature (48). The flight capabilities of *D. citri* have also been measured in detail with a laboratory flight mill (3). *D. citri* adults are capable of approximately 50 min of continuous flight and up to 1,241 m of continuous flight (3). Yet, curiously, Arakawa & Miyamoto (3) concluded that the flight capability of *D. citri* "is not so high" and that their dispersal likely consists of short flights. The laboratory flight mill data are consistent with the long-range flight capability suggested by tracking psyllid movement with immunomarking in the field.

Vibrational communication: a mode of communication that takes place by striking and thus vibrating the substrate upon which the animals occur

Plant volatiles: chemicals released by plants that have a specific chemistry that allows for volatilization

Acquisition: period during which a pathogen is acquired by a vector

Latency: a specific duration following acquisition and prior to inoculation required for successful transmission of a pathogen by a vector

Inoculation: period during which a pathogen is transmitted to a host by a vector

Host- and Mate-Finding Behavior

D. citri is attracted to yellow and yellowish-green colors that mimic reflectance spectra of host plants (54, 162). *D. citri* is attracted both to natural host plant odors (162) prevalent in the headspace collections of citrus and to a synthetic terpene mixture modeled on the principal volatiles collected from *M. paniculata* (101). In the presence of attractive visual cues, behavioral response to host plant odors increases (162). Tender tissue is required for egg laying, with young shoots and leaves preferred, which typically harbor the highest densities of each life stage (168). There is also evidence of a volatile sex attractant and, surprisingly, males are more attracted to mated females than to virgins (160). *D. citri* occurs in distinct color morphs, and when crushed, greenish females are attractive to males, whereas crushed, brownish females are not (161). A cuticular hydrocarbon attractive to males, which may partially explain the odor-based sex attraction, has recently been identified (84). In addition to visual and olfactory cues, short-range mate-finding behavior subsequent to adult rendezvous on host plant flush is mediated by substrate-borne vibrational communication between the sexes (159). Las infection of citrus induces the release of a specific volatile olfactory signal (methyl salicylate) that renders infected plants more attractive to *D. citri* than noninfected plants; nevertheless, host selection behavior of psyllids is identical whether or not they are carriers of the pathogen (80). However, trees infected with the pathogen are less suitable hosts for *D. citri* compared with uninfected counterparts (22, 80); therefore, psyllids tend to leave infected plants after acquiring the pathogen and move to nearby healthy plants, which appears to be a mechanism that escalates pathogen spread (80).

To date, practical exploitation of *D. citri* host-finding behavior has mainly composed of using yellow sticky traps for monitoring the activity of adults (48, 50, 130). Identification of potential pheromones or attractive host plant volatiles (80, 84, 101) may improve the practical use of sticky traps for monitoring *D. citri* by increasing their attractiveness and/or facilitating development of attract-and-kill technologies.

TRANSMISSION OF "*CANDIDATUS* LIBERIBACTER" SPP. BY *DIAPHORINA CITRI*

Acquisition, Latency Period, Inoculation, and Transmission Efficiency

Transmission of Las by *D. citri* is a process composed of an acquisition access period (AAP) during which the feeding nymphs or adults acquire the pathogen, a period of latency required for the bacteria to enter the salivary gland that may also include bacterial multiplication (68), and an inoculation access period (IAP) during which the psyllid introduces bacteria into the plant. Early, nonmolecular investigations reported AAPs ranging from 15 min to 24 h and IAPs ranging from 15 min to 7 h (18, 20, 122). In these studies, latency periods between 1 and 25 days were inferred on the basis of visual symptom development (122, 166). Early studies reported predominantly low rates of transmission efficiency: 1.3% (61) and 12.2% (165), with one exception reporting 80% efficiency (166).

More recent investigations that used either conventional polymerase chain reaction (PCR) or real-time PCR (qPCR) to detect Las reported 13% to almost 90% acquisition efficiencies for adult *D. citri* following feeding on Las-infected plants; however, the AAP for this may be highly variable (63, 68, 102). Acquisition of Las by *D. citri* increases proportionally to the duration of confinement on Las-infected plants (102). Furthermore, acquisition of Las is approximately 20% greater when it occurs during nymphal development than during the adult stage only (102). A transmission efficiency of 67% has been quantified by conventional PCR for adults that emerged from nymphs reared on Las-infected plants (68). Even though a single infected *D. citri* adult is capable of infecting a plant (e.g., 102, 166), rates of inoculation increase proportionally to the number of infected *D. citri* that is allowed an IAP (102). Uneven distribution or differential titer of the bacteria within different plants, depending on age and variety tested, may also influence results, as in the case of "*Ca.* Liberibacter americanus" (140).

Real-time PCR: a method of polymerase chain reaction that records the cycle at which a detectible level of product (gene expression) becomes amplified; also known as quantitative PCR (qPCR)

Location of Pathogen in the Vector

The presumed causal agent of HLB was initially observed in the salivary glands, the filtration chamber of the foregut, and within cells of both the midgut and hindgut as determined by microscopy (166). More recently, qPCR, scanning electron microscopy, and fluorescence in situ hybridization techniques confirmed the presence of Las in the salivary glands, alimentary canal, filter chamber, Malpighian tubules, hemolymph, muscle and fat tissue, and ovaries of *D. citri*, indicating a systemic presence of the bacterium within psyllids following acquisition (1, 2). These results contradict the speculation of Inoue et al. (68) that Las is unable to cross the alimentary canal. In fact, the results of both Xu et al. (166) and Ammar et al. (1, 2) indicate that large numbers of bacteria presumed to be Las are found in the salivary glands following adult AAP, and suggest that the pathogen circulates to these organs within 1 to 2 days following acquisition.

Retention of Pathogen Within the Vector

Conflicting results have been reported regarding the persistence of the Las pathogen within *D. citri* following acquisition. An investigation employing qPCR reported that Las occurs in decreased levels over the lifetime of an adult *D. citri* following acquisition at the nymph stage (102). These results suggest that pathogen titer declines over time within psyllid adults if they are not continuously reacquiring the pathogen from other infected plants. Inoue et al. (68) reported similar results when *D. citri* acquired Las as adults but contradictory results when *D. citri* acquired Las as nymphs.

There is surprisingly little consistency between recent investigations employing molecular tools to detect Las with respect to retention of the pathogen following AAP. To date, retention of Las following AAP has been supported and falsified in different contemporary investigations employing similar techniques (63, 68, 102). A comparative investigation using *D. citri* from various locations, including Asia and North and South America, would help reject the hypotheses that genetic or symbiont differences account for apparent major physiological differences reported to date between *D. citri* from various locations. Using the same source of Las (or other Liberibacter species) for such a comparative investigation would also falsify the hypothesis that different strains of a Liberibacter species are contributing to these contradicting results.

Transovarial and Sexual Transmission

Evidence for a low rate (3.6%) of transovarial transmission of Las from mother *D. citri* to progeny was reported (102). Prior investigations that did not employ PCR were unable to demonstrate this phenomenon (63, 166). Transovarial transmission of related pathogens appears to be common among psyllid vector species. "*Candidatus* Liberibacter africanus" and "*Candidatus* Liberibacter psyllaurous/solanacearum" are transovarially transmitted by the African citrus psyllid, *T. erytreae* (del Guercio) (154), and the potato/tomato psyllid, *Bactericera cockerelli* (Šulc) (56), respectively. In addition to transovarial transmission, a similar, low rate (2–3%) of sexual transmission from male to female *D. citri* has been reported (81). These results indicate that Las can propagate through populations of *D. citri* horizontally in the absence of Las-infected plant inoculum sources. These alternative transmission mechanisms may facilitate persistence of Las within *D. citri* populations that occur on plants that are not hosts for the pathogen. Despite the low rates of transovarial and sexual transmission in *D. citri*, high fecundity (32) and the occurrence of extremely high population densities under certain circumstances (49) suggest that these may be important supplementary mechanisms of transmission.

Transovarial transmission: passing of pathogen during egg laying from mother to offspring

Sexual transmission: the passing of a pathogen from one gender to the other during mating

Entomopathogen: an organism causing disease in insects

Conidia: asexual spores

Mycosed cadaver: a dead organism invaded by fungi

Ectoparasitoid: a parasitoid that deposits its egg externally on the host

Endoparasitoid: a parasitoid that deposits its egg inside the host

BIOLOGICAL CONTROL

Entomopathogens

A number of fungal entomopathogens are reported to infect *D. citri*, especially under conditions of high humidity. These include *Isaria* (*Paecilomyces*) *fumosorosea* (Wize) A.H.S. Brown and G. Smith (60, 64, 91, 127, 135), *Lecanicillium lecanii* R. Zare & W Gams (164), *Beauveria bassiana* (Bals.) Vuill., and *Hirsutella citriformis* Speare (21, 90, 135).

Interest in entomopathogenic fungi as biopesticides has centered primarily on *I. fumosorosea* (7, 64), although there is yet no published account of its successful use against *D. citri* in the field. *H. citriformis* has also drawn attention with high levels of mortality reported on *D. citri* adults exposed to conidia-bearing synnemata produced in vivo and in vitro (21, 90). Incidence of *H. citriformis* on adult *D. citri* from natural field infection tends to be greatest following the rainy season in Florida (51). Mycosed cadavers are persistent in the environment for an average 68 days. However, the mucus-enveloped conidia probably do not disperse efficiently from these point sources except by contact, which perhaps explains why only infected adults are observed in the field even though nymphs are also susceptible to the fungus (90). Mixtures of conidia and mycelia of *H. citriformis* have been applied with some success against rice brown leafhopper, *Nilaparvata lugens*, by Rombach et al. (123). However, low sporulation rates, slime production by mycelia, and irregular growth limit conidia production in the laboratory. A further constraint is the inhibitory effect of commonly used pesticides, including copper hydroxide, horticultural oil, and elemental sulfur, on *H. citriformis* (51) and presumably other entomopathogenic fungi as well.

Parasitoids

The ectoparasitoid *Tamarixia radiata* (Waterston) (Eulophidae) and the endoparasitoid *Diaphorencyrtus aligarhensis* (Shafee, Alam and Argarwal) (Encyrtidae) are generally accepted as the only currently known primary parasitoids of *D. citri*. Both were first described from the northern Indian subcontinent (65, 132, 155). Reports of other hosts of *T. radiata* have been discounted (86), although *Diaphorina cardiae* on *Cardia ruyxa* was reported as an alternative host of *D. aligarhensis* (57). *D. aligarhensis* has been reported from Taiwan, China, Vietnam, the Philippines, Réunion Island, and Saudi Arabia (58). These last two records appear to be the result of accidental introductions.

T. radiata has been successfully introduced into Réunion Island (6); Taiwan (24); Mauritius (107); the Philippines (35); Saudi Arabia (4); East Java, Indonesia (99); Guadeloupe (30); and Florida (133), where it spread throughout the state (110). It appeared inadvertently in Brazil (36, 148), Venezuela (23), Mexico (29), Puerto Rico (105), and Texas (31). Comparison of mitochondrial cytochrome *c* oxidase subunit I sequences from field-collected populations of Puerto Rico, Guadeloupe, and Texas indicated that Florida was not a likely source of the introduction into Puerto Rico, but was a likely source of the introduction into Texas (8).

Mummies (predominantly fourth- and fifth-instar nymphs) caused by *T. radiata* are secured with silk spun around the margins by the prepupa with an emergence hole in the thorax. These mummies are easily distinguished from those caused by *D. aligarhensis*, which are secured to the leaf surface by anal secretions of the wasp larva and have the emergence hole in the abdomen (121). Although the two primary parasitoids coexist throughout much of their natural range, *T. radiata* is usually dominant. Gavarra et al. (35) reported that *D. aligarhensis* was the most important of the two species in orchards in Luzon and Mindanao, the Philippines, but only a year after introduction of *T radiata*. Husain & Nath (65) make no mention of *D. aligarhensis* occurring in Punjab, India, although their statement that the emergence hole made by *T. radiata* may occur in the thorax or the abdomen suggests that it did in fact occur there.

D. aligarhensis has yet to be successfully introduced in Florida, where multiple attempts were apparently unsuccessful (120). In contrast, *T. radiata* predominated within months of release over the already present *D. aligarhensis* (identified as *D. diaphorinae*) at most locations in Taiwan (24). Although moisture requirements for the two species are comparable (87), infection with *Wolbachia* has been cited as a possible explanation for the difficulty of establishing *D. aligarhensis* outside its range (89). More important perhaps is the competitive advantage enjoyed by the ectoparasitic *T. radiata* when both oviposit into the same host, unless the endoparasitic *D. aligarhensis* has a head start of five days or more (119). Furthermore, developmental time for *T. radiata* is approximately four days less than for *D. aligarhensis* (37, 119). An estimated value of 0.374 for the intrinsic rate of increase (r_m) for *T. radiata* is among the highest reported for any parasitoid (37). Tang & Wu (137) reported that parasitism by *T. radiata* was greater on hosts containing eggs or young larvae of *D. aligarhensis* than on unparasitized hosts, indicating a possible attraction to parasitized hosts. Female *T. radiata* are also excellent searchers, honing in on volatiles emanating from *D. citri* nymphs (82). The reported prevalence of hyperparasitism on *D. aligarhensis* may place it at an additional disadvantage. On the other hand, many species reported as hyperparasitoids of *T. radiata* (136, 167) appear to actually be from nonpsyllid hosts. Given these advantages, and the rapidity with which *T. radiata* has established and spread, it is the obvious first choice for augmentative biological control. However, a role for *D. aligarhensis* is still a viable option, especially because it appears not to interfere with *T. radiata* and therefore could only add to the mortality of *D. citri* populations.

Predators

There is general agreement that the major predators of *D. citri* are lady beetles, lacewings, syrphids, and spiders. However, the relative importance of each group is less certain due in part to the difficulty of evaluating their individual contributions to mortality. Michaud (94) reported that the coccinellids *Harmonia axyridis* (Pallas), *Olla v-nigrum* (Mulsant), and *Exochomus childreni* Mulsant were the most abundant predators visiting three sets of cohorts of *D. citri* nymphs during late summer and fall on citrus in central Florida, followed by the lady beetle *Cycloneda sanguinea* (L.) and the anyphaenid spider *Hibana velox* (Becker). However, van den Berg et al. (153) reported spiders to be the most important predators of *T. erytreae* in managed citrus orchards, followed by chrysopids, coccinellids, syrphids, hemerobiids, Hemiptera, and predatory mites.

A numerical response by *O. v-nigrum* was recorded following invasion of *D. citri* into Florida (92). Feeding by lacewing larvae on psyllids was rarely observed, and syrphid [*Allograpta obliqua* (Say)] predation was not observed, even though previous studies confirmed the suitability of *D. citri* nymphs as food sources for these predators (93). Pluke et al. (104) identified eight species of lady beetle that fed on *D. citri* on citrus in Puerto Rico. Qureshi & Stansly (113) found four lady beetle species in Florida—*Cycloneda sanguinea* (L.), *Curinus coeruleus* Mulsant, *O. v-nigrum*, and *H. axyridis*—commonly feeding on *D. citri* or trapped in sticky barriers on the same branch. Of these, only *O. v-nigrum* was more often encountered as larvae than as adults. Lacewings and spiders were also frequent visitors to *D. citri* colonies in the field. The introduced cockroach *Blattella asahinai* Mizukubo, known as a predator of lepidopteran eggs (103), was the most frequently observed insect caught in sticky barriers, although it was never otherwise observed in psyllid colonies by day, presumably due to its nocturnal habits. A predatory wasp has also been reported (117).

Broad-spectrum insecticides: chemicals that kill insect species indiscriminately

Impact of Biotic Mortality

T. radiata releases were credited with reducing populations of *D. citri* sufficiently in Réunion Island to mitigate the impact of HLB (6) and provided significant control of *D. citri* on the islands of Guadeloupe and Puerto Rico (30, 105). Qureshi et al. (110) found that parasitism by *T. radiata* increased over the course of the growing season to highs of over 50% in fall but averaged less than 20% over the year in Florida. In contrast, Tsai et al. (151), Michaud (94), and Qureshi & Stansly (113) reported only 1–3% parasitism from *T. radiata*, the last two studies attributing most mortality to predation. Qureshi & Stansly (113) estimated the net reproductive rate (R_0) of *D. citri* to be 5- to 27-fold greater in colonies from which predators were excluded with sleeve cages compared with unprotected colonies. Their results indicated strong though seasonally dependent biotic mortality.

CHEMICAL CONTROL

Susceptibility of *Diaphorina citri* to Insecticides

Very little information on insecticidal control against *D. citri* was reported in the literature prior to the arrival of HLB in the Americas in the mid-2000s. Recognized chemical classes for controlling this pest consisted of horticultural oils and other products derived from natural sources and/or organophosphates (69, 116). More recent studies of *D. citri*'s response to insecticides indicate sensitivity to a number of different insecticide classes, including pyrethroids, organophosphates, carbamates, neonicotinoids, some insect growth regulators (IGRs), horticultural oil, the lipid synthesis inhibitor spirotetramat, spinetoram, abamectin, and sucrose octanoate (14, 25, 26, 66, 73, 88, 109, 111, 112, 114, 115, 134, 141, 156, 167). The level of suppression and residual action against *D. citri* varies among rates and types of insecticides, insect stages, and application timing.

Efficacy of foliar applications of insecticides averaged approximately 3 weeks and ranged from 7 to 45 days. Broad-spectrum insecticides in the pyrethroid, organophosphate, and neonicotinoid classes have a greater efficacy against *D. citri* (especially adults) than do many of the other classes. Oils and IGRs are more effective against eggs and nymphs than adults (14, 26, 141). These differences influence the choice and timing of treatments. Las infection increases insecticide susceptibility in *D. citri* through decreased production of certain detoxifying enzyme groups (146) due to downregulated expression of associated *CYP*4 genes (142, 145).

Systemic soil-applied insecticides provide a longer period (months) of protection compared with foliar insecticides (weeks) (25, 66, 108, 112). However, systemic insecticides require one to three weeks for uptake into citrus trees, and the effective dose of insecticide varies depending on tree size, irrigation, soil type, and other factors (67, 131). Systemic insecticides are especially important for young trees that flush nearly continuously and thus require constant protection. The most effective methods of application are soil drenches or side dressings (108, 118), although trunk injections have also been used (128). Imidacloprid or fenobucarb used alone as a systemic for vector suppression reduced, but did not fully prevent, the spread of disease (34, 73). For *D. citri* management programs, soil-applied systemic insecticides are primarily, if not exclusively, neonicotinoids and therefore best combined with foliar insecticides employing different modes of action to reduce selection for resistance. Alternative modes of action with systemic activity are being investigated for soil application.

Treatments targeting overwintering *D. citri* adults have the greatest impact on populations because reproduction is severely reduced during this time (109, 115). Another advantage of these so-called dormant sprays is their minimal effect on psyllid predators due to the predators being largely absent or in protected stages when sprays are applied (115). Treatments showing a negative correlation with toxicity as a function of temperature, such as the pyrethroids, have been notably effective during this period (13). In-season, insecticide treatments are timed for periods prior to flushing to reduce or eliminate adults before reproduction and development can occur on new growth. Selective insecticides may also be directed against nymphs during flush and can provide suppression of secondary pests such as leafminers, scales, or mites but still allow natural enemies to survive. Rapid speed (8–16 km h^{-1}), low-volume (19–94 liter ha^{-1}) sprayers have been developed that can apply inexpensive and frequent applications to provide more continuous protection (15, 59, 69), especially on block borders where *D. citri* tends to congregate.

Systemic agents: those with the capability of spreading system-wide; with respect to insecticides, chemicals that move through plant xylem and/or phloem

Selective insecticides: chemicals that kill specific subsets of insects (pests) without affecting others (often beneficial insects)

Phloem salivation events: feeding behavior during which an insect introduces salivary fluids into a plant, which may lead to transmission of a plant pathogen

Antifeedants and Repellents

Antifeedants such as neonicotinoids and pymetrozine can reduce the transmission of Las by inhibiting feeding of plant sap–sucking insects (12, 16, 33). Serikawa et al. (129) and Butler et al. (19) used electrical penetration graph monitoring to observe significant decreases in the number of phloem salivation events by *D. citri* and the related potato psyllid, *B. cockerelli* (Šulc) (Hemiptera: Triozidae), on plants treated with imidacloprid. Other currently available hemipteran antifeedants, such as flonicamid (125), are being investigated and may result in additional useful tools. Sublethal effects of neonicotinoids and IGRs can reduce egg production and/or fertility and development of eggs (12, 14, 141). These insecticides could be used as a component of a much larger management program to help reduce disease spread.

Chemical repellents, including noxious plant products and horticultural oil, have been investigated with the intention of reducing oviposition by females and adult feeding (83, 85, 100, 101, 124, 169). Some of these chemicals are highly effective repellents for *D. citri* in the lab and field, but their development for practical use is still in progress. Research suggests that horticultural oils suppress or mask attractant plant volatiles, release repellent volatiles from the leaves, and/or repel adults (106). Physical repellents, such as clay particle film, have also shown utility for possibly reducing transmission-related behaviors (52).

Pesticide Resistance

Intensive chemical control of *D. citri*, with the goal of preventing single or multiple inoculations, has been heavily utilized in Brazil and Florida since 2005. In HLB-infected areas of Brazil, growers may apply as many as 6 to 15 foliar and 1 to 2 systemic insecticide treatments per year from five chemical classes in an effort to slow the spread of HLB (10). In Florida, 8 to 12 treatments per year have been commonly used. Under such intensive pressure, susceptibility of *D. citri* to neonicotinoids, organophosphates, and pyrethroids has declined (142, 144, 147). The relatively rapid development of resistance to major groups of broad-spectrum insecticides points out the need for psyllid management tactics that reduce the frequency of insecticide treatments and rotate between insecticides with different modes of action.

Pesticide Selectivity

Although broad-spectrum insecticides in the carbamate, organophosphate, neonicotinoid, and pyrethroid groups exert some of the greatest effect on *D. citri* populations, they are acutely toxic to *T. radiata* (36, 53). In these studies, insecticides found to be more compatible with *T. radiata* include diflubenzuron, horticultural oil, kaolin clay, and chenopodium oil. Spirotetramat and pyridaben were intermediate in activity. Reducing the frequency of broad-spectrum pesticide sprays and timing treatments for winter when natural enemy activity is low can help reduce their effect on many natural enemies, allowing a more integrated approach (111, 115).

IMPLICATIONS FOR MANAGEMENT OF *DIAPHORINA CITRI* AND LAS

Strategies for *D. citri* management must be viewed in light of the overarching objective of slowing the spread of HLB and managing its impact on tree health and productivity. There is general agreement that vector control and clean nursery stock are critical components of a holistic HLB management approach (10, 17, 43, 167). Management of *D. citri* is heavily reliant on insecticides to limit initial infection and reinfection of trees. Pruning affected limbs has not proved effective for "*Ca.* Liberibacter americanus," although curiously Las was not detected in regrowth of these experiments (78). Rogueing of symptomatic trees to reduce inoculum has been vigorously undertaken in Brazil (10) and Florida but remains controversial due to seemingly inexorable increases in disease incidence. This is due in part to long latency periods that make it difficult to recognize symptoms in the early stages of infection when the tree can nevertheless serve as a source of inoculum (38). Faced with the prospect of removing and replacing symptomatic trees without assurance that the attendant costs will be recovered, many growers in Florida and Brazil are currently attempting to prolong the productive life of infected trees by intensified programs of foliar nutrition to mitigate HLB symptoms, coupled with rigorous vector control to reduce reinoculation of the causal agent. There has yet to be a replicated trial establishing a positive response to nutritionals (40) and the sustainability of such programs, particularly for young trees planted in a high incidence HLB environment, is to be determined.

Various aspects of *D. citri* biology increase the difficulty of managing the pest and disease. The psyllid is prolific, short-lived, tolerant of temperature extremes, and vagile. Acquisition of the pathogen is fairly rapid, acquisition efficiency by nymphs is high, and at molting, the pathogen is passed to highly mobile adults in which it is persistent. On the other hand, various aspects of *D. citri*, citrus, and Las biology may be exploited for improved management of both vector and disease. These include a vector host range restricted to the Aurantioideae and an even more restrictive pathogen host range, dependence by *D. citri* on young flush for egg maturation and nymphal development, a tree growth habit characterized by relatively short flushing periods interspersed with longer periods of little or no flush, and the apparent ability of infected citrus to continue to be productive under optimal growth conditions and protection from vector reinoculation. Thus, *D. citri* management programs that minimize adults moving to new flush, reduce immature population development on new flush, reduce reinoculation of the pathogen, and provide nutrients to mitigate the impact of the disease will maintain tree productivity for at least the short term.

Worldwide, unmanaged groves, urban areas, and noncitrus hosts that provide sources of *D. citri* are considered significant obstacles to disease management (10, 28). Additional challenges include young trees or alternative hosts that flush frequently and provide a constant safe haven for the immature stages as well as the demonstrated ability of *D. citri* to develop pesticide resistance. In spite of these challenges, integrated pest management programs are being developed to suppress *D. citri*. These programs utilize visual yellow sticky card and tap sampling methods to monitor *D. citri* (46, 47, 50), rotation of pesticide chemistries to manage resistance, broad-spectrum insecticides during dormant periods, and selective insecticides in season as rotational partners and to maintain natural enemy effectiveness. Coordinated area-wide *D. citri* monitoring and treatment programs, termed Citrus Health Management Areas, promise to increase the effectiveness of local control efforts and reduce impact of the disease (**http://www.FLCHMA.com**).

Research challenges for areas of recent invasion of *D. citri*, such as California and Arizona, include improved monitoring methods to detect psyllids at low levels in order to conduct more effective suppression programs. In addition, methods to detect Las-infected trees in the early stages of infection are critical in order to limit spread of the disease once it appears in these regions. In California, area-wide trapping and management of *D. citri* in both urban and commercial citrus are being undertaken in a collaborative effort by the citrus industry and the California Department of Food and Agriculture (**http://www.citrusresearch.org/cpdpc**). Educational challenges involve persuading the general public not to import citrus materials and not to transport *D. citri* to uninfested areas of the state on host plant material (**http://www.saveourcitrus.org**, **http://www.californiacitrusthreat.org**).

Living with HLB requires the use of multiple strategies and greater cooperation among growers and between the citrus industry and the urban population than the previous norm. It will be important to optimize use of insecticides and growing conditions while conserving and augmenting biological control. The development of semiochemical-based tools may improve *D. citri* detection and management and considerable investment is being made in this area. Reducing pathogen transmission by psyllids and developing HLB-tolerant or -resistant cultivars through traditional or transgenic programs are long-term goals that are being investigated intensely. Optimizing tree growth and production on less land with enhanced tree nutrition and high-density plantings may be necessary to maintain citrus production while disease resistance or transmission interruption tools are developed (95).

SUMMARY POINTS

1. The Asian citrus psyllid has successfully invaded the Americas from its Asian origins and now threatens citrus production worldwide through its role as a vector of the pathogen that causes the currently incurable HLB.
2. Biological characters such as high reproductive potential, rapid growth and development of populations, fairly wide temperature tolerance, and high transmission efficiency of nymphs that retain the pathogen as mobile adults make pest and disease management difficult.
3. Management of vector populations is improved by taking advantage of *D. citri*'s dependence on young flush for reproduction and its susceptibility to broad-spectrum insecticides applied when populations are at their weakest in the winter and just prior to periods of leaf flush.

4. Reduction of broad-spectrum insecticide use during the growing season and greater reliance on more diverse and selective chemistries as well as biological control will be essential to manage pesticide resistance and conserve a sustainable equilibrium between pests and natural enemies.
5. Vector control is a short-term solution while disease resistance or transmission interruption tools are developed.

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The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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