

Distribution, biology, ecology and control of the psyllid *Diaphorina citri* Kuwayama, a major pest of citrus: A status report for China

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Abstract

The Asiatic citrus psyllid *Diaphorina citri* Kuwayama (Hemiptera: Psyllidae) is a major pest of citrus in China. Its status derives, not from the damage it causes, but from its role as the only known vector in China of huanglongbing, a phloemlimited bacterial disease of international importance. The disease can devastate orchards within a few years of planting. It also poses a major threat to endangered indigenous citrus germplasm in Asia and Australasia. The distribution, biology, ecology and control of the psyllid in China are reviewed in these contexts. Constraints and challenges related to control of the vector in China are discussed.

Keywords: Diaphorina citri, huanglongbing, distribution, biology, ecology, control

1. Introduction

Asiatic citrus psyllid (Diaphorina citri Kuwayama [Hemiptera: Psyllidae]) was recognised as a major pest of citrus in subtropical and tropical Asia, initially in India and then elsewhere in the region (Husain and Nath 1927; Pruthi and Mani 1945; Ebeling 1950). The available evidence suggests that it is indigenous to the Indian subcontinent (Hollis 1987) and has spread from this region to other citrus-producing regions of Asia and also to Réunion, Mauritius, New Guinea (Waterhouse 1998), and South America (Halbert and Nunez 2004). Most recently, it has reached the southeastern citrus-producing regions of the USA (Halbert and Manjunath 2004). Adults and nymphs suck sap from the phloem of tender shoots and buds, whilst adults also feed on the phloem of mature leaves. Severe infestations in orchards and gardens lead to withering, distortion, and loss of immature leaves and irregular-shaped canopies. Growth of sooty mould fungi (possibly several species: see Reynolds 1999) on honeydew excreted by nymphs leads to blemishing of foliage and fruit, and can reduce photosynthesis (Wang et al. 2001). However, the status of the psyllid as a pest in orchards is due to it being the vector of huanglongbing (Tirtawidjaja et al. 1965; Teaching & Research Group of Phytopathology of Guangdong Agricultural and Forest College 1977; Xu et al. 1988), a devastating disease caused by the phloem-limited

gram-negative bacterium Candidatus Liberibacter asiaticus Jagoueix, Bové & Garnier (α-Proteobacteria) (Jagoueix et al. 1994; Garnier et al. 2000). 'Huanglongbing' is the official name of the disease (van Vuuren 1996) although it has a number of common names and is most widely known as citrus greening (da Graca 1991; Halbert and Manjunath 2004) and in Indonesia as citrus vein-phloem degeneration (Tirtawidjaja et al. 1965). The devastating nature of the disease is well described by Aubert (1990) and Ke (1991). Aubert (1990) reported that 20% of trees in a poorly managed orchard in Shantou in Guangdong were lost to huanglongbing within four years of planting. The disease spread so rapidly that the orchard lost its commercial value within 7 to 8 years of planting. Ke (1991) reported that it destroyed dozens of millions of citrus trees in China between 1920 and 1970. Of increasing importance is the potential threat of the disease to rare germplasm, particularly Citrus spp. (sensu stricto), all of which are native to the Indian subcontinent, southeast Asia and Australasia (see Mabberley 1997, 1998, 2001, 2002, 2004; Ramón-Laca 2003).

In this paper, we review the biology, ecology and control of *D. citri* in China. We summarise valuable but poorly accessible information of growing importance to a now almost worldwide crisis facing both commercial citrus production and the preservation of rare germplasm. Effective containment and

Correspondence: Y. Yang, Guangdong Entomological Institute, 105 Xingang Road West, Guangzhou 510260, Guangdong, People's Republic of China. Tel: 86 0 13729806164 or 86 20 84197197. E-mail: reiiyyp@yahoo.com management of the disease in China, one of the world's largest citrus producers, can only be achieved through use of disease-free trees, suppression of D. citri populations to minimum levels, quarantine, eradication of the disease and its vector where practicable (Chen and Liao 1982; Wang et al. 2002), education of farmers, and prohibition of unacceptable propagation practices such as marcotting (air-layering: vegetative propagation achieved by encouraging roots to form on a branch while it is still attached to the selected parent tree). Control of the vector is costly and difficult; tolerant citrus species and cultivars have not been identified (He 2000), and the search for such germplasm for use as scions and rootstocks is hampered by inadequate knowledge about the origins of the disease, the vector, and their hosts. These are issues of increasing importance in southeast Asia and more broadly, given detection of disease in Brazil in 2004 and Florida in 2005 and the distribution of D. citri in the USA and South America (Halbert and Manjunath 2004; Halbert and Nunez 2004).

2. Hosts plants and spread of D. citri in China

2.1. Host plants

According to He (2000), hosts of D. citri in China include up to 27 species within seven genera of Rutaceae: Atalantia, Citrus, Fortunella and Poncirus within the tribe Aurantieae (Citreae), Murraya and Clausena within the tribe Clauseneae, and Euodia (misspelt as Evodia) within the tribe Zanthoxyleae. The tribes Aurantieae and Clauseneae fall within the subfamily Aurantioideae, while the Zanthoxyleae is a tribe within the Rutoideae. However, recent research has questioned the taxonomic status of some of these species and placement of genera within tribes. The taxonomy of host species has serious implications for our understanding of host-plant relationships. Without this basic knowledge, development of management plans for the disease, preservation of germplasm, and selection of tolerant scions and rootstocks will be greatly hindered. Most notably, Mabberley (2004) considers sweet and sour oranges (C. \times aurantium), lemon (C. \times limon), lime $(C. \times aurantiifolia)$ and grapefruit $(C. \times aurantium)$ to be hybrids. He has also reunited Fortunella (kumquat), trifoliate orange rootstock Poncirus trifoliata (L.) Raf., and Australasian Microcitrus and Eremocitrus with Citrus (Mabberley 1997, 1998, 2002, 2004). Murraya (sensu stricto) has recently been transferred from the Clauseneae to the Autantieae and curry bush is once again Bergera koenigii L. not M. koenigii (L.) (Samuel et al. 2001). Euodia rutaecarpa (A. Juss.) Benth, the single species of Euodia cited by He (2000), is now Tetradium ruticarpum (A. Juss.) T. Hartley.

In Zhejiang, the preferred hosts are commercial citrus, followed by Murraya paniculata (L.) Jack

(mock or jasmine orange) and trifoliate orange, then other hosts; among commercial citrus, citron (*C. medica* L.) is the most seriously damaged, followed by sweet orange, and then mandarins (*C. reticulata* Blanco) (Xie et al. 1989a). In Guangdong and Fujian, the preferred host is jasmine orange (Xu C et al. 1994; Waterhouse 1998). Xu et al. (1988) cited wampee (*Clausena lansium* (Lour.) Skeels) and Chinese box orange (*Severinia buxifolia* (Poir.) Ten. (=*Atalantia buxifolia* (Poir.) D. Oliver) as hosts on which the psyllid can survive and reproduce easily.

2.2. Distribution of D. citri in China

In China, *D. citri* is now distributed within 10 provinces, one autonomous region and two Special Administrative Regions. These comprise, in decreasing order of economic impact of the disease, Guangdong, the Guangxi Zhuang Autonomous Region, Taiwan (Husain and Nath 1927; Huang 1953; Catling 1970; Lin et al. 1973; He 2000), Fujian, Zhejiang, Jiangxi, Hunan, Guizhou, Yunnan, Sichuan, Hainan (Hoffmann 1936), and the Macao (Huang 1953) and Hongkong (So 1967; Catling 1970) Special Administrative Regions.

The highest infestations of the psyllid, and therefore the highest incidence of the disease, occur in Guangxi, Guangdong, Fujian, and Taiwan in the southeast sector of the county, with the boundary separating high from low incidence running from 29°N in Zhejiang to 25°N in Yunnan in a sea-facing convex arc running slightly inland from the mountain ranges that separates inland Sichuan, Guizhou, Hunan and Jiangxi from coastal Guangxi, Guangdong, Fujian and Zhejiang. However, the records extend further northwards, particularly along river valleys, to between 24° and 28°N in inland Sichuan, Guizhou, Hunan and Jiangxi and 29°N in coastal Zhejiang. Records are summarised in Table I.

The northernmost distribution of D. citri varies annually. In Zhejiang, populations are governed by migration of adult psyllids and the severities of winters (Xie et al. 1988a). Li et al. (1992) found that survival and northerly distributions of populations in southern Hunan required: (i) narrow divergence between mean daily and minimum temperatures in January in the year under consideration and that of long-term (24 years) data for the same variables; (ii) large populations of D. citri in the neighbouring regions of Guangxi, Guangdong and Jiangxi; and (iii) overwintering populations in relatively warm basin-shaped valleys. Likewise, variability of distributions of the psyllid in the vicinity of Guilin of northern Guangxi may be also governed by climate (Qiu and Huang 1996). Relatively warm conditions, particularly consecutively warm winters (Zhou et al. 1992; Liao 1999), have led to northerly expansion of boundaries in Guangxi (Zhou et al.

Table I. Distribution and occurrence of D. citri in China.

Province	Geographical Location	Distribution of D. citri
Guangdong	20°13′ ~ 25°31′ N; 109°39′ ~ 117°19′ E	Whole province (Chen and Liao 1982; Liao 1999)
Guangxi	$20^{\circ}54' \sim 26^{\circ}23' \text{ N}; 104^{\circ}08' \sim 112^{\circ}04' \text{ E}$	Whole province (Chen and Liao 1982; Zhou et al. 1989; Liao 1999)
Taiwan	$21^{\circ}53' \sim 25^{\circ}18' \text{ N}; 120^{\circ}01' \sim 121^{\circ}59' \text{ E}$	Whole province (Lin et al. 1973; Chen and Liao 1982; Liao 1999)
Fujian	$23^{\circ}30' \sim 28^{\circ}22' \text{ N}: 115^{\circ}50' \sim 120^{\circ}40' \text{ E}$	Whole province (Chen and Liao 1982; Liao 1999)
Zhejiang	$27^{\circ}01' \sim 31^{\circ}10' \text{ N}; 118^{\circ}01' \sim 123^{\circ}08' \text{ E}$	Southern part northwards to Tiantai (29°08' N 121°01' E) and Xianju (27°30' N 120°33' E) (Wang et al. 2003)
Jiangxi	24°29' ~ 30°04' N; 113°34' ~ 118°28' E	Southern part and parts of central Jiangxi (Zhu 1993)
Hunan	$24^{\circ}39' \sim 30^{\circ}28' \text{ N}; 108^{\circ}47' \sim 114^{\circ}45' \text{ E}$	Regions between 24°39' N (Jianghua) and 26°50' N (Anren) (Li et al. 1992)
Guizhou	$24^{\circ}37' \sim 29^{\circ}13' \text{ N}; \ 103^{\circ}36' \sim 109^{\circ}35' \text{ E}$	Regions of river valley in the south with distributions extending northwards along the river to Ceheng (24°58′ N 105°49′ E), Guanling (25°56′ N 105°37′ E) and Zhenning (26°04′ N 105°46′ E) when hosts are abundant (Wang 2002)
Sichuan	$26^{\circ}03' \sim 34^{\circ}19' \text{ N}; 97^{\circ}21' \sim 110^{\circ}21' \text{ E}$	Southwestern regions such as Panzhihua (26°6′ ~ 26°39′ N; 101°33′ ~ 101°35′ E) and Xichang (27°32′ ~ 28°10′ N; 101°46′ ~ 102°25′ E) (Peng et al. 1996)
Yunnan	$21^{\circ}08' \sim 29^{\circ}15' \text{ N}; 97^{\circ}31' \sim 106^{\circ}11' \text{ E}$	Parts of Yunnan including Binchuan (25°45′ N 100°30′ E), Baoshan (24°08′ ~ 25°51′ N; 98°25′ ~ 100°02′ E) and Huaning (23°59′ ~ 24°34′ N; 102°49′ ~ 103°09′ E) (Xu et al. 1994; Li and Qiu 2000)

1989; Sun 1999), Fujian (Fan et al. 2003), Zhejiang (Wang et al. 2001, 2002) and Guizhou (Wang 2002), and movement of populations to higher altitudes within all regions. In suitably warm winters, host plants produce flush growth suitable for the development and continuity of psyllid populations and an increase in the number of annual generations (Zhou et al. 1989; Liao 1999; Sun 1999; Wang et al. 2001). Expansion of commercial citrus production and propagation of alternative hosts has also enhanced spread of populations to higher latitudes and altitudes (Zhou et al. 1992; Fan et al. 2003), and winds from the South China Sea assisted northward expansion of D. citri populations in Guilin in Guangxi by 0.5° latitude in 1982 and 1987 (Qiu and Huang 1996). Strong southerly winds also influence populations in the neighbouring regions of northern Guangxi and southern Hunan from June to August each year (Zhou et al. 1989).

2.3. Geographical factors influencing distribution

The influence of altitude varies within regions. In Guizhou, the psyllid usually occurs in southern areas at altitudes less than 600 m above sea level (asl) (Xu S et al. 1994). Near Panzhihua, in subtropical southern Sichuan, it normally occurs at altitudes between 600 m and 1200 m (Peng et al. 1996). In Hunan, however, it is absent in some regions ranging from 500 m to 900 m asl, while in others at 618 m, large populations can be found (Li et al. 1992). In Zhejiang, the psyllid does not occur in some regions at altitudes above 500 m, but in other regions it can be found at 600 m asl (Zhu 1993) or even at 840 m (Xie et al. 1988a). Topography, particularly high mountains, can have a major influence, as high mountains restrict spread of populations. In Guizhou, they serve as natural barriers to migration and as a consequence, populations are limited to certain areas (Ma and Wang 2001; Wang 2002). Likewise, in northern Fujian mountains impose similar restrictions on populations (Fan et al. 2003).

2.4. Environmental factors influencing distribution

Ambient temperatures are the most important environmental factor limiting the distribution of D. citri. Xu (1985) stated that potential distribution areas were in accordance with the places in which the lowest temperature was within the tolerance of overwintering adults psyllids. Winters with low temperatures and intense temperature fluctuations are one cause of high mortality of overwintering populations (Xie et al. 1989a; Huang et al. 1992). In northern Guangxi, populations during 1980-1987 varied from year to year, which was possibly due to low temperatures in winter (Zhao 1987). Survival in Taizhou in Zhejiang has been positively correlated with temperatures in January and also to the lowest temperatures recorded annually (Wang et al. 2003). In Guangdong, frosts can significantly reduce overwintering populations (Liao 1999). Yang (1989) concluded that high temperatures and high humidity had significant negative impacts on D. citri populations in contrast to the negative impacts of high temperatures and low humidity on the African citrus psylla Trioza erytreae (del Guercio) (Hempitera: Triozidae).

According to Xie et al. (1988a) average temperatures of the coldest month, minimum temperature, and the duration of cold weather are critical factors restricting distributions. Zhu (1993) proposed that 6.4° C, the minimum monthly mean temperature over 20 consecutive years, should be used as the limiting factor instead of mean daily temperature exceeding 10°C and the minimum temperature over years. He considered both of the latter criteria to be inappropriate, despite slight influences on distributions. Division of regions into zones has also been proposed. On the basis of key indices, such as freezing injury to citrus and minimum temperatures, Xie et al. (1988a) divided Zhejiang into four zones: suitable for distribution, borderline, potential, and unlikely. Zhu (1993) used isotherms based on the index of minimum monthly mean temperatures to divide Jiangxi into three zones: most suitable, slightly suitable and potentially spreading, with the temperature index mentioned above of $>7.5^{\circ}$ C, $6.4^{\circ} - 7.4^{\circ}$ C and $5.4^{\circ} - 6.3^{\circ}$ C respectively.

3. Biology and Ecology of D. citri in China

3.1. Annual generations

Several generations may occur annually with the number greatest in regions with the most favourable conditions (Table II), particularly those suitable for overwintering of adults and nymphs and for production of flush growth for oviposition. Overlapping of generations may occur, particularly in warmer regions (Lin et al. 1973; Chen and Liao 1982; Huang et al. 1999) and on some hosts more than others. In Fujian there are 3-4 more generations on jasmine orange than on commercial citrus species and hybrids, and populations on this host are also larger than those on citrus because it tends to produce new growth continuously under the prevailing conditions (Xu C et al. 1994). Generally, there are three population peaks annually in citrus orchards and these coincide with the spring, summer and autumn flush cycles. Damage caused by the psyllid is usually most severe on autumn flush and least severe on summer flush. In some instances this order of severity varies due to variation in flush phenology, the abundance of flush growth, host type and age, and management practices. In orchards at Yangcun (23°25′ N, 114°30′ E) in eastern Guangdong populations may also peak in winter (Chen and Liao 1982); in southern Hunan, peaks occur on summer and autumn flushes (Huang et al. 1992). In Huaning county (24°11' N, 102°55' E) in Yunnan most damage occurs on commercial citrus in spring and summer

(Luo et al. 1997). In most regions in Guangxi, there are five population peaks for all life stages, and these occur from April–December each year (Sun 1999); and in southern Zhejiang, egg peaks occur on summer and autumn flushes (Xie et al. 1989b).

3.2. Overwintering activity of D. citri in China

Increasingly warmer winters in recent years/decades has led to the psyllid overwintering in regions where has not been known to do so previously, and its geographical distribution has spread northwards and inland, such as in northern Guangxi (Zhou et al. 1992; Sun 1999). One factor appears to be mean daily temperature in January each year as Quan et al. (1998) found that overwintering could occur when the mean exceeds 6.3°C. Such occurrences lead to infestations on spring growth flush, a situation that has critical implications for transmission and spread of huanglongbing (Liao 1999). Local weather conditions and host phenology determine the life-stages that active during winter. In Taiwan, all life-stages are active as immature flush growth is present and winter temperatures favour development and movement (Lin et al. 1973). In Guangzhou, all stages can survive winter when immature flush growth is present, but only adults are present when flush growth is rare or absent, and their movement is restricted (Liu and Liu 1989). In Zhejiang, when winter temperatures are too low for the immature stages to develop and survive, adults are the only stage likely to survive, but their movement is very restricted (Xie et al. 1989a). In Hunan, where winter temperatures vary greatly from year to year, only adults can survive in normal years whereas, in years when winter temperatures are too low for development and survival, no stage can survive (Huang et al. 1992). Information is summarised in Table II.

Overwintering adults, especially females, have a much longer lifespan than females in other generations. They can live for 8-9 months. Their tendency

Province Annual number of generations Overwintering stage(s) Guangdong 8-11 (Huang 1990) All stages (Liu and Lin 1989) 7-8 in Guilin $(24^{\circ}15' \sim 26^{\circ}23' \text{ N}; 109^{\circ}36' - 111^{\circ}29' \text{ E})$ Guangxi Mainly adults, sometimes nymphs and eggs (Sun 1999) (Quan et al. 1998) Taiwan 8-9 in the north; more than 10 in the central and southern All stages are active (Lin et al. 1973) regions (Lin et al. 1973) Fujian 6-8 on citrus, and 9-11 on Murraya paniculata Nymphs (occasionally) and adults (Xu C et al. 1994) (Xu C et al. 1994; Yan et al. 1996) Zhejiang 6-7 in Pingyang (27.68° N; 120.55° E), 3-7 in Taizhou Adults only (Xie et al. 1989a) (Wang et al. 2001) Jiangxi Up to 7 in the south region with a partial eighth generation in Adults only (Yan et al. 1996) some years; fewer generations centrally (Yan et al. 1996) Hunan 6 in Yizhang (25.41° N; 113.96° E) (Li et al. 1992) Adults; but in some years when it is too cold, no stage can survive (Huang et al. 1992) Guizhou 8 in Luodian (25.43° N; 106.74° E) (Ma and Wang 2001) In normal years, all stages; mostly adults or adults only in colder years (Ma and Wang 2001)

Table II. Annual generations and overwintering activity of D. citri in China.

to congregate on the abaxial surfaces of leaves is also more obvious than in other generations. There is no complete diapause or dormancy, and although development and mating proceed at relatively low rates, females can still lay eggs, and can continue to do so in the following spring when hosts start to produce new growth (Xie et al. 1989b). When Xie et al. (1988a,c) determined cold tolerance of the psyllid in laboratory studies they noted that overwintering adults, both males and females, that possessed a strong ability for cold tolerance were able to withstand low-temperatures of about $-18^{\circ}C$ for 10 minutes, and -4° to $-12^{\circ}C$ for 4 h. However, despite their strong cold tolerance, overwintering adults cannot survive in some high latitude regions. For example, in Zhejiang, the survival rate of overwintering adults is low due to the influence of low temperatures (Wang et al. 2001, 2003); in Sichuan, when the lowest monthly-mean-temperature is below 8°C, adults cannot survive (Peng et al. 1996). Laboratory studies indicated that the survival rate of overwintering adults is lower when males and females are reared separately than when they are reared together (Quan et al. 1998).

3.3. Oogenesis and oviposition

Maximum fecundity of a female is near 1900 eggs, averaging 630-1230 (Huang 1990). Yang and Huang (1991) excluded influences such as rainfall and the density of young twigs, and constructed oviposition index submodels of *D. citri* females in spring, summer and autumn flushing cycles, respectively. There is a close correlation between realised fecundity and longevity. Results of laboratory studies reported by Ma and Wang (2001) indicate that females that lay their quota of eggs soon after eclosion have shorter lifespans than females that lay eggs over longer periods.

Yang (1989) studied the effects of light, temperature and humidity on the development, reproduction and survival of D. citri. He found that light intensity and duration significantly affect the pre-oviposition period and realised fecundity of D. citri females: when light intensity was below 11000 lx and light duration was below 18 h per day, the number of eggs laid increased and the pre-oviposition period and mortality of females decreased with increases in light intensity and photoperiod. He attributed these effects to the influence of light on adult feeding and therefore on ovarian development. He found no apparent effects of temperature or humidity on the percentage of eggs hatching, while nymphal mortality was high at higher temperatures with higher humidity and low at moderate temperatures $(20-30^{\circ}C)$ with lower humidity (43-75%).

Females only oviposit on immature flush growth produced by hosts, the eggs being deposited in crevices of buds, on young leaves and twigs, and in leaf axils (Huang et al. 1999). Development of nymphs, especially females, relies heavily on sucking phloem sap from nutrient-laden buds (Wu 1980). However, breeding activity is largely suspended when citrus trees are dormant (Waterhouse 1998). Initiation of oogenesis and subsequent maturation of eggs within ovaries are closely related to the presence of buds (Dai et al. 1982; Huang 1990; Huang et al. 1999). Eggs only hatch in bud-seams where the humidity is high enough during flushing cycles (Huang et al. 1999). Most eggs are laid within the first 12 days of new growth commencing (Lin et al. 1973). In laboratory studies reported by Chen and Liao (1982) oviposition peaked when flushes on citrus seedlings were 5-50 mm long. In the field, oviposition peaks when they are 5 mm long (Sun 1999), and eggs are almost absent on flush longer than 50 mm (Lin et al. 1973). Egg density is the highest on the first leaf and lowest on the fourth, fifth and subsequent leaves (Xu C et al. 1994). In regions where weather conditions are suitable, e.g. Guangzhou in Guangdong, the only factor restricting adults from laying eggs is the presence or absence of sequential flush growth on hosts (Liu and Liu 1989). Adults normally lay eggs at ambient temperatures above 20° C, but not below $14-15^{\circ}$ C (Wu 1980). Adults that overwinter after laying eggs in autumn resume doing so in spring as new flush growth appears (Xie et al. 1989b).

3.4. Spatial patterns, and daily and seasonal activity

Adults are mainly confined to warmer sites in the tree canopy, particularly protruding foliage facing south. They also prefer to settle on young flush leaves and twigs, and when flush is present, most adults and nymphs are found on the penultimate leaf, then in declining numbers (Xu S et al. 1994). On jasmine orange, Tsai et al. (1984) found that the highest incidence of adults was on leaf midveins (43%), followed by petioles (31%), leafblades (24%) and stems (<3%). Adults are inactive below 8°C (Wu 1980; Xie et al. 1989b). At around 11°C they become active, and noticeably so at $13^{\circ} - 15^{\circ}$ C. In winter they move slowly and congregate on adaxial surfaces of leaves (Wu 1980). Movement is quite vigorous above 22°C and adults jump energetically at ambient temperatures between $24^{\circ} - 29^{\circ}C$ (Xie et al. 1989b). In warm direct sunlight adults move around on leaf surfaces; in shade they hide on abaxial surfaces (Wu 1980). Diurnal activity of adults differs on fine, cloudy, and on days with heavy rain (Ke 1991) and is influenced by season (Chen and Liao 1982). Adults are poor flyers and seldom disperse actively: dispersal is assisted by wind (Ke 1991). Distribution patterns of eggs and nymphs follow an aggregated distribution, the former is related to adult behaviour and the latter is related to environmental factors (Huang and Huang 1986). Nymphs are essentially sedentary (Wu 1980) but newly-eclosed first instar nymphs assemble on neighbouring buds, immature leaves and twigs, and will move downwards during development but not settle on mature leaves (Huang et al. 1999). Young nymphs tend to aggregate closely then disperse more widely on immature leaves as they develop to the fifth and last nymphal instar.

3.5. Natural enemies of D. citri

Natural enemies comprise entomopathogens, predators and two primary parasitoids. They cannot prevent transmission of huanglongbing but can maintain populations of the psyllid below levels that cause significant direct damage to its hosts (Liu 1989a, 1989b; Huang et al. 1999). Liu (1989b) reported average parasitism of D. citri by one of its two primary parasitoids, the ectoparasitic Tamarixia radiata Waterston (Hymenoptera: Eulophidae) (cited as 'Tetrastichus sp.'), to be 36% on summer flush and 46% on autumn flush in a mature orange orchard in Guangzhou in 1986. It has been recorded in Fujian, Jiangxi, Taiwan, and other regions of south China (Tang 1988; Huang et al. 1999) and probably occurs wherever permanent populations of its host exist: it was introduced to Taiwan from Réunion Island in 1983 (Chien 1988; Tang 1988; Huang et al. 1999). Tang (1988) also considered that T. radiata might be indigenous to mainland China as it was not introduced. The other primary parasitoid, the endoparasitic Diaphorencyrtus aligarhensis (Shafee, Alam & Agarwal) (Hymenoptera: Encyrtidae) has been recorded in Guangdong and Taiwan. Huang et al. (1999) recorded 30-50% parasitism of nymphs by T. radiata and D. aligarhensis (cited as Psyllaephagus sp.), and both primary parasitoids have reduced D. citri populations in Taiwan (Chien and Chu 1996). Another 17 parasitoid species (including six aphelinids, eight encyrtids, one eulophid, one pteromalid and one signiphorid) have been reported, but all of these are hyperparasitoids. Some of attack both primary parasitoids and others only one (Institute of Plant Protection, Chinese Academy of Agricultural Sciences 1996; Waterhouse 1998). Predators include ladybirds (Coleoptera: Coccinellidae), green lacewings (Neuroptera: Chrysopidae), praying mantids (Mantodea: Mantidae), ants (Hymenoptera: Formicidae), spiders and mites (Acari), all of which are polyphagous. The coccinellids include Chilomenes quadriplagiata Swartz, Cheilomenes (= Menochilus) sexmaculata (Fabricius), Coelophora biplagiata (Mulsant), Harmonia axyridis (Pallas), Harmonia octomaculata (Fabricius), Lemnia (= Phrynocaria) circumusta (Mulsant) (Wei et al. 1995) and Propylea japonica (Thunberg), and the chrysopids Chrysopa boninensis Okamoto and Chrysopa septempunctata Wesmael. The whirligig mite Anystis baccarum (Linnaeus) (Acari: Anystidae) also preys on D. citri (Wu 1994). Four entomopathogens have been recorded in association with the psyllid in China. These are: Acrostalagmus aphidum Oudem,

Paecilomyces javanicus (Friederichs & Bally) AHS Brown & G. Smith, and *Verticillium lecanii* (Zimm.) Viegas (Anamorphic Ascomycetes), and *Beauveria bassiana* (Balsamo) Vuillemin (Anamorphic Clavicipitaceae) (Xie et al. 1988b; Ye et al. 1994). Other species of fungi recorded by these authors appear to be contaminants as they are moulds or plant pathogens.

4. Control strategies of D. citri in China

4.1. Control constraints and challenges

Biological control of D. citri by its two primary parasitoids (Chien and Chu 1996; Huang et al. 1999), polyphagous predators (Wu 1994; Wei et al. 1995) and entomopathogens (Xie et al. 1988b; Ye et al. 1994) would be possible in the absence of huanglongbing. Success would be enhanced by the impact of extreme temperatures on psyllid mortality, high humidity that favours growth of entomopathogens, and reduction of egg and nymph populations by heavy and prolonged rainfall (Wu 1980; Liu 1989b; Xie et al. 1989a; Waterhouse 1998). Populations would, ideally, tend to fluctuate within generally commercially acceptable levels and biorational pesticides, such as horticultural and agricultural mineral oils (see Rae et al. 1997, 2000; Beattie et al. 2002; Huang et al. 2005), would be suitable for use in integrated pest management (IPM) programs if populations exceeded economic thresholds. However, in the presence of the disease reliance on biological control and the influences of climate are not acceptable management options. Alternatives strategies also have serious limitations. Total reliance on chemical control is not sustainable as high pesticide use in Asia has not prevented devastation of the orchards, and use of insecticides incurs high costs and is detrimental to citrus ecosystems (Liang 1989; Huang et al. 1999; Zhao 2000; Wang et al. 2002). Integrated control based on biological control enemies, biorational chemicals, and cultural practices such as rotational high density plantings could be the most acceptable option. Loss of orchards is however inevitable. The prosperity of farmers can only be ensured through strategies that optimise profits per hectare but have negligible adverse effects on the environment and human health.

In China and elsewhere in Asia where the disease and vector occur, there is widespread, almost total reliance on synthetic pesticides, which through the 3Rs—"residues, resurgences and resistance" (Chen 1988; Tsai 1991; Zhao 2000; Wang et al. 2002) ultimately leads to ineffective control of the vector, and serious consequences for human health and the environment. Policies are required to encourage minimal use of pesticides. These can only be achieved through effective research and extension, and by discouraging or prohibiting undue promotion of pesticides and profiting from their use: see for example, Farah (1994) and Fresno (1995).

4.2. Control recommendations based on ecology

Growing public concern over pesticide use and demand for "organically grown" food require development and implementation of economically, ecologically and sociologically sound control programs with (see Chen 1985; Chen 1988; Ye 1996; Wang et al. 2002) with minimal detrimental impacts and, if possible, programs that are organically acceptable. Our recommendations for sound IPM programs for control of *D. citri* and huanglongbing in China are summarised as follows:

- citrus cultivation must be based on propagation of disease-free plants (Chen 1992);
- planting densities, and canopy dimensions and densities, must be managed to minimise light intensities that favour psyllid infestations (see Chen 1987; Yang 1989) and to allow efficient and effective application of sprays;
- windbreaks should be used to minimise movement of adult psyllids into orchards (Huang 1990; Ye 1996; Sun 1999; He 2000; Zhao 2000; Wang et al. 2002);
- alternative hosts of *D. citri*, such as *M. paniculata* and wampee (*Cl. lansium*), and huanglongbing-affected citrus trees must be removed from around and within orchards (Ke and Xu 1990; Ke 1991; Peng et al. 1996; Sun 1999; Ma and Wang 2001; Wang et al. 2001);
- ground-cover plants should be cultivated and managed to increase populations of generalist predators (e.g. lacewings and ladybirds) in orchards, and to provide sources of "green manure" (Chen 1988; Yang 1989; Huang et al. 1992; Zhang et al. 1996; Zhao 2000; Wang et al. 2002);
- pesticides should be selected on the basis of their effectiveness and potential for sustainable use through minimal impacts on orchard ecosystems and negligible risk of phytotoxicity;
- the number of chemicals used in any one spray should be minimal so as to reduce the risk of detrimental impacts on efficacy and plants;
- timing of chemical treatments should be based on monitoring of:
 - psyllid populations, to determine the presence of adults,
 - host plant phenology, to determine the onset and duration of flush cycles from the initial appearance of buds—spray application must focus on protecting buds and young flushes from feeding and oviposition by adult psyllids;
- application of sprays should be even and thorough, with sprays applied to run-off;

• use of soil drenches and tree injections should be based on tree size and phenology, and account for potential loss or diminution of active ingredient(s) through leaching, degradation or tree growth.

Psyllid populations should be monitored by means of sticky coloured traps (Xie and Xu 1988; Aubert 1990; Ke 1991; Guo and Deng 1998). Adults are attracted to yellow and red traps but attractiveness varies under different weather conditions: brownyellow traps are the most attractive on cloudy days, whereas yellow traps are preferred on fine days (Ke 1991). The colour of the traps can therefore be chosen to meet the requirements dictated by weather conditions. For example, brown-yellow traps can be used in seasons with predominantly cloudy days and yellow traps in seasons with mostly sunny days with relatively few clouds (Ke 1991).

Sprays based on tree phenology, as recommended above, will also facilitate effective control of citrus leafminer (*Phyllocnistis citrella* Stainton [Lepidoptera: Gracillariidae]) (Beattie et al. 1995; Rae et al. 1996, 1997). Use of pesticides that destabilise orchard ecosystems, such as pyrethroids and organophosphates that induce outbreaks of citrus red mite *Panonychus citri* (McGregor) (Acari: Tetranychidae) should be avoided.

Horticultural and agricultural mineral oils, which can be used to gain simultaneous control of the wide range of pests and diseases, are suitable for use in organic farming, providing emulsifiers and other additives used to formulate products that meet acceptable standards. In China they are permitted for use in Green Food programmes (e.g. Organic programmes, see Huang et al. 2005). They offer significant benefits over many other chemicals:

- they may be handled with minimum protective clothing such as overalls, goggles and simple dust masks;
- their toxicity to vertebrate animals is low—they are almost as pure as the products used for baby and hair oils, skin lotions and creams;
- they have less detrimental effects on beneficial insects and mites than most synthetic pesticides;
- they do not stimulate pest outbreaks;
- pests are not known to develop resistance; and
- oil molecules are similar to natural plant waxes, and deposits are degraded within weeks by microbes, oxidation and ultraviolet light to form simple, harmless molecules (Smith et al. 1997; Beattie et al. 2002).

To minimise the risk of phytotoxicity (see Tan et al. 2005a,b) the oils should meet international standards for use on plants (see Beattie et al. 2002) and products should only be used as recommended to avoid phytotoxicity and incompatibilities with some pesticides (Huang et al. 2005). The highest quality products are made from food-grade mineral oils.

They can be mixed with a wide range of other pesticides and can improve the efficacy of the latter (Rae 2002). Other biorational pesticides, e.g. botanical and microbial pesticides, may also be effective against *D. citri* and their potential warrants further investigation. For example, azadirachtin, a limonoid derived from *Azadirachta indica* A. Juss. (Sapindales: Meliaceae), is an efficient oviposition deterrent for *D. citri* (Wang et al. 1996; Zhang et al. 2003).

The status of M. paniculata as the favoured host of the psyllid led to it being recommended for use in IPM to lure adult psyllids from adjacent citrus trees and to signal presence of the psyllid in or near orchards, and for plant breeding to reduce the susceptibility of citrus to the disease. This wisdom, which is based on the premise that M. paniculata is not susceptible to the disease (see Guo and Deng 1998), has been questioned following recent studies (Li and Ke 2002; Siti Subandiyah, Gadjah Mada University, pers. comm. 2003) that indicates that it, or M. exotica L., is a host of disease. This has serious implications for management of the disease in China and elsewhere, as "M. paniculata" is a common ornamental plant in Fujian, Guangdong and elsewhere in southeast Asia. This conundrum is compounded by the distinct possibility that host susceptibility testing of both D. citri and huanglongbing to Murraya, Citrus and Bergera may have been based, in an unknown number of instances, on misidentified or misnamed species or cultivars.

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