# Ecology of Citrus Aphids and Their Importance to Virus Transmission

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#### Abstract

World aphid species attacking citrus are reviewed. The 4 aphids, *Toxoptera citricidus, T. aurantii, Aphis gossypii* and *A. spiraecola* are the major species whereas other 11 species are less important. Their occurrence varies with the countries or districts. Aphid life cycle in general and that of the major 4 species are described. Ecology of and factors affecting the occurrence of 3 important citrus aphids in Japan are described and relations between aphid populations and some factors controlling aphid populations are outlined. Transmission of citrus tristeza virus (CTV) is reviewed and transmission rate of *T. citricidus* and *A. gossypii* is compared in relation to different strains of CTV or of aphids. All of 4 world important species can transmit CTV. Especially, *T. citricidus* and *A. gossypii* are efficient vectors of CTV in different areas of the world.

# Discipline: Insect pest

Additional key words: Aphis gossypii, Aphis spiraecola, CTV, Toxoptera citricidus, Toxoptera aurantii

# World aphid species attacking citrus

Several aphid species attack citrus in the world<sup>2,4,13,22,35,37)</sup>. All belong to the family Aphididae. Four important species include *Toxoptera citricidus, Toxoptera aurantii, Aphis gossypii* and *Aphis spiraecola* (Table 1). The species composition and seasonal occurrence differ in each area or country. *T. citricidus* is not distributed in the Mediterranean region and North America. Other major 3 species show a worldwide distribution. *A. spiraecola* invaded the Mediterranean region in the 1960s and became a serious citrus pest there<sup>35)</sup>. In Japan, *T. aurantii* is not a major species but is abundant on tea<sup>20)</sup>. Other 11 species also

attack citrus but they occur occasionally and their populations are small.

# General biology of aphids

Fig. 1 depicts the aphid life-cycle. Aphid propagates parthenogenetically and parthenogenesis is linked to viviparity. Sexual and parthenogenetic reproduction alternates in the life cycle, which is referred to as cyclical parthenogenesis. Usually, sexual forms appear in fall and oviposit overwintering eggs on the primary host. This phenomenon is referred to as holocyclic life-cycle. Eggs hatch in spring and hatched larvae develop to parthenogenetic reproducing mothers (fundatrix). Several aphid species or some strains of a species reproduce

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Species	Distribution		
Major species			
Toxoptera citricidus	Asia, South Africa, Central and South America,		
	Australia, New Zealand		
Toxoptera aurantii	Worldwide		
Aphis gossypii	Worldwide		
Aphis spiraecola $(=A. \ citricola)$	Worldwide		
Minor species			
Aphis craccivora	Worldwide		
Aphis fabae	Almost worldwide		
Aphis nerii	The Old and New World tropics		
Aulacorthum magnoliae	Japan, Korea, India		
Aulacorthum solani	Worldwide		
Brachyunguis harmalae	Israel, Sudan		
Brachycaudus helichrysi	Worldwide		
Myzus persicae	Worldwide		
Macrosiphum euphorbiae	Worldwide		
Toxoptera odinae	South and East Asia, South Africa		
Ureleucon jaceae	Europe, the Middle East and Central Asia		

Table 1. Aphid species attacking citrus in the world



Fig. 1. Outline of aphid life-cycle

parthenogenetically all the year round (anholocyclic life-cycle). Host alternation is another characteristic of aphids. Aphids migrate among host plants of different families. Overwintering eggs are deposited on one host (primary host), and parthenogenetic reproducing generation occurs on another host (secondary host). Usually, the primary host is the overwintering host and the secondary host is the summer host. The term heteroecious is used for the host alternating life-cycle. Some aphid species do not change hosts and live on a plant or a group of kin plants. This life-cycle is designated as autoecious or monoecious. The aphid life cycle is generally defined by two criteria, the appearance of sexual forms and host alternation. Some aphid species, including A. gossypii, A. spiraecola and T. citricidus, have both holocyclic and anholocyclic strains.

Aphids exhibit many morphs differing in morphological and physiological characteristics<sup>10)</sup>. Winged and wingless forms appear. Winged parthenogenetic females (vivipara or virginopara), disperse and look for new host plants while wingless parthenogenetic females (apterous vivipara) can quickly reproduce on host plants. In the host alternating species, the winged female migrates between primary and secondary hosts. The fundatrix or its daughter produces winged females that fly to the secondary host. Some morphs appear in a particular season. The gynopara appears in fall and produces sexually reproducing female (ovipara), that produces overwintering eggs. The male also appears in fall and mates with the ovipara. The fundatrix appears in spring. In some species, the parthenogenetic female produces both ovipara and male. Aphid life cycles are complicated due to the pattern and polymorphism.

# Life-cycles of major citrus aphids

#### (1) T. citricidus

This aphid shows holocyclic and anholocyclic life-cycles. In Japan, the aphid overwinters holocyclically on citrus<sup>19)</sup> but overwintering eggs have not been found in other countries<sup>4)</sup>. Host plants are almost completely restricted to the species in the family Rutacea.

(2) T. aurantii

This species is almost completely anholocyclic. This aphid has a wide host range, and overwintering eggs have been reported in Japan. (3) A. gossypii

The taxonomic status of this species is complicated. In Europe, this aphid has been distinguished from the *Aphis frangulae* group by the absence of sexual reproduction<sup>34)</sup>. In East Asia, Japan and China, however, it has a holocyclic life-cycle in addition to an anholocyclic one<sup>12,19,38)</sup>. Primary hosts in 4 families and parthenogenetic overwintering populations have been reported in Japan. This is a highly polyphagous species and many biotypes or strains differing in host preference, life-cycle pattern and level of insecticide resistance are segregated<sup>9,11,12,30,32,33,38)</sup>.

# (4) A. spiraecola

The name of A. citricola has been used for more than 10 years after it was proposed by Eastop and Hille Ris Lambers (1976)<sup>7)</sup>. But, Eastop and Blackman reported in 1988 that A. citricola van der Goot is a synonym of A. fabae<sup>8)</sup>. Then the name of A. spiraecola has been used for the citrus-attacking green aphid. This aphid is holocyclic in North America and Japan or anholocyclic in other countries. In Japan, citrus is one of the primary hosts<sup>19)</sup> for one type and can be distinguished from another type which overwinters on Spirea<sup>15)</sup>. The former attacks mainly citrus and the latter attacks other fruit trees in Rosaceae<sup>17)</sup>. The two types can also be distinguished by the esterase banding pattern when electrophoresis is carried out<sup>18)</sup>. This aphid is polyphagous.

# Seasonal occurrence of major citrus aphids in Japan

The 3 major citrus aphids in Japan are T.

# Table 2. Citrus aphid species and their occurrence in Japan

Species	Occurrence		
Toxoptera citricidus	All seasons		
Aphis spiraecola	All seasons		
Aphis gossypii	All seasons		
Toxoptera aurantii	Spring to early summer <sup>a)</sup>		
Aulacorthum magnoliae	Spring to early summer <sup>a)</sup>		
Aphis craccivora	Spring to early summer <sup>a)</sup>		
Myzus persicae	Spring to early summer <sup>a)</sup>		
Aulacorthum solani	Spring to early summer <sup>a)</sup>		
Sinomegoura citricola	Occasional		

a): Occasional in other seasons.

citricidus, A. spiraecola and A. gossypii. T. aurantii also attacks citrus but does not cause serious damage (Table 2). These 3 aphid species continuously occur on citrus from spring to fall (Fig. 2) and overwinter on citrus as eggs. The other species occur only from spring to early summer or occasionally.

A. gossypii appears on citrus first, followed by A. spiraecola, and T. citricidus. The early appearance of A. gossypii is attributed to the fact that the aphid has a wide range of hosts other than citrus, such as vegetables and weeds, on which it overwinters parthenogenetically. The role of the citrus overwintering population



Fig. 2. Seasonal occurrence of 3 major citrus aphids in Japan<sup>20)</sup>



Fig. 3. Development processes of 3 major citrus aphids<sup>13)</sup>

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in spring infestation may be comparatively negligible, because the invasion from other hosts begins earlier than the appearance of



Fig. 4. Change of r with temperature<sup>14)</sup>



Fig. 5. Annual fluctuations of aphid populations<sup>20)</sup>



Fig. 6. Relation between aphid (A. spiraecola) population and no. of parasitized mummies Arrows indicate time sequence.

alates among populations overwintering on citrus (Fig. 3). In the case of *A. spiraecola*, the appearance of alates in populations overwintering on citrus is earlier than, or occurs at the same time as the invasion. This phenomenon suggests that the population overwintering on citrus is an important source of infestation in spring, which is supported by the fact that migrants from Spirea plants cannot reproduce well on citrus<sup>18)</sup>. In the case of *T. citricidus*, a late egg hatch, and the fact that only a few overwintering eggs are found on citrus, result in a delay in spring infestation.

The population of A. spiraecola increases from March to August and decreases after August (Fig. 2). The population of A. gossypii gives a peak in late May and decreases, and again, gives a peak in September. The population of T. citricidus gives peaks in July and August or September. Their increasing capacity may affect their pattern of occurrence. The maximum increase of the population of T. citricidus and A. spiraecola occurs at 27°C while that of A. gossypii at 22 or 23°C (Fig. 4). The population of the aphids can increase on young shoots and their numbers depend on the amount of new shoots available<sup>13)</sup>. The range of annual fluctuations is large in A. spiraecola but relatively small in T. citricidus and A. gossypii (Fig. 5). These fluctuations are associated with the amount of new shoots, climatic conditions and activity of natural enemies.

Many natural enemies attack citrus aphids. Some natural enemies are occasionally abundant. The parasitoid, *Lysiphlebus japonicus*, attacks the 3 major aphid species, especially *T. citricidus*. The coccinellid, *Scymnus hilalis*, also attacks these aphids, especially *A. spiraecola*, while many other species, Syrphids, Crysopids, mites are known to attack citrus aphids. Although it is assumed that natural enemies play an important role in the control of aphid populations, since these natural enemies appear after the increase of the aphid population (Fig. 6), the effect of their control occurs after citrus has been damaged.

#### Virus transmission by citrus aphids

The aphid species transmitting citrus tristeza virus (CTV) are listed in Table 3. CTV can only be transmitted by the aphids among the citrus viruses. The 4 important aphids previously described can transmit CTV1,5,23,31). Other species can transmit CTV in South Asia. Aphids transmit CTV in a semi-persistent manner except in several cases in India and the Philippines. Aphids can acquire CTV for 30 min by feeding on a virus-infected plant and transmit it for 30 min by feeding on a healthy plant. Transmissibility increases when the feeding period lasts for 24 hr and aphids lose their transmitting ability after 2-day feeding on a healthy plant<sup>31)</sup> or a synthetic diet<sup>16)</sup>. In South Asia, aphids transmit the virus non-persistently in India, Thailand and the Philippines. In this case, aphids acquire and transmit the virus by feeding for a few seconds<sup>21,27)</sup>.

Transmissibility of the virus by aphids varies with the aphid species<sup>25,29,31)</sup> and virus

Table	3.	Aphid	species	transmitting	CTV
rable	5.	Apma	species	transmitting	<b>U</b> 1

Worldwide	South Asia
Toxoptera citricidus	Aphis craccivora
Aphis gossypii	Aphis fabae
Aphis spiraecola	Aphis nerii
Toxoptera aurantii	Acythosiphon pisum
	Myzus persicae
	Uroleucon (Dactynotus) jaceae

Table 4. Transmissibility of CTV by single aphid

:	Species	Transmissibility	Reference
Τ.	citricidus	0.04	This paper
		0.02	Costa & Grant, 1951
Α.	gossypii	0.009	Raccah et al., 1980
		0.03	Roistacher et al., 1984
		0.004	Yokomi et al., 1989
Τ.	aurantii	0.33	Manjunath, 1985

strains<sup>3,36)</sup>. Transmissibility of CTV by single aphid is listed in Table 4. *T. citricidus* is the most effective vector of CTV<sup>1,5,31)</sup>. *A. gossypii* which was not an effective vector previously<sup>6,23)</sup>, has now become a serious one in the USA and Israel<sup>26,28)</sup>. *A. spiraecola* and *T. aurantii* are much less effective vectors<sup>29)</sup> except for *T. aurantii* in India<sup>21)</sup>. In *T. citricidus*, there is no difference in the virus transmissibility between alate and apterous aphids, or between adults and nymphs<sup>5,31)</sup>. Similarly adults and nymphs of *A. gossypii* can both transmit the virus equally<sup>24,28)</sup>.

Transmission curve by T. citricidus is illustrated in Fig. 7, based on experimental data using Mexican lime, and a 2-day feeding period for acquisition and inoculation. Data are fitted to the formula  $Y = 1 - \exp(-np)$ , where n is the number of aphids inoculated, and p is the average transmission rate of single aphid. In this formula, the transmissibility by single T. citricidus is estimated at 0.04 (Fig. 7). Another estimate 0.02 was calculated from the data reported by Costa and Grant (1951). For A. gossypii, the value was 0.03 according to the data reported by Roistacher et al. (1984) (Table 4) and within the range 0.01-0.11 according to other estimates<sup>36)</sup>. The differences in the virus strains and presumably the aphid



Fig. 7. CTV transmission by *T. citricidus* Circles show observed data and the regression line is Y = 1 - exp(-np), where n = number of aphids inoculated, p = transmissibility by one aphid.

strains may account for the inconsistency of the transmissibility.

T. citricidus is the most dangerous aphid in Japan as a vector of CTV due to its high transmissibility and relatively narrow host range that is exclusively restricted to citrus. In contrast to T. citricidus, A. gossypii transmits CTV at a low percentage and has many host plants so that the importance of A. gossypii as a CTV vector is negligible. A. spiraecola does not transmit CTV.

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