BIOLOGY AND VIRUS TRANSMISSION OF CITRUS APHIDS

Shinkichi Komazaki
Akitsu Branch, Fruit Tree Research Station,
Ministry of Agriculture, Forestry and Fisheries,
Akitsu, Hiroshima 729-24, Japan

ABSTRACT

Aphid species of the world which attack citrus and transmit citrus tristeza virus (CTV) are reviewed. Four aphids, Toxoptera citricidus, T. aurantii, Aphis gossypii and A. spiraecola, are all common species, and all of them transmit CTV. Their occurrence varies in different countries and localities. T. citricidus and A. gossypii are particularly dangerous vectors of CTV. The aphid life cycle in general, and that of the four species listed above in particular, are described, together with the seasonal occurrence of major citrus aphids in Japan and the virus diseases they transmit. The control of aphids in order to prevent virus disease is also discussed.

APHID SPECIES AND VIRUS TRANSMISSION

Several aphid species attack citrus in different parts of the world (Barbagallo 1966, Komazaki 1981, Niet Nafria et al. 1984, Blackman and Eastop 1984, Viggiani 1988, Yokomi et al. 1992). All of these belong to the families Aphidinae and Aphididae. Four important species are Toxoptera citricidus, Toxoptera aurantii, Aphis gossypii and Aphis spiraecola (= citricola) (Table 1). Species composition and seasonal occurrence vary in different countries and regions. T. citricidus is not found in the Mediterranean area or North America, while A. spiraecola invaded the Mediterranean region in the 1960s and has become a serious citrus pest there (Viggiani 1988). T. aurantii is not a major species, although it is abundant on tea in Japan (Komazaki et al. 1985).

Citrus tristeza virus (CTV) can only be transmitted by aphids, including the four important aphid species listed above (Costa and Grant 1951, Norman and Grant 1956, Sasaki 1974, Ahlawat and Raychaudhuri 1988). CTV is transmitted by the aphids in a semi-persistent manner. It can be acquired by the aphid as it feeds for 30 minutes on a plant infected with virus, and is transmitted as the aphid feeds for 30 minutes on a healthy plant. Transmissibility rises as the feeding period is prolonged up to 24 hr, but the aphid loses its ability to transmit CTV after it has fed for two days on healthy plants (Sasaki 1974) or a synthetic diet (Komazaki 1984). In some cases, the virus is transmitted non-persistently (Retuerma and Price 1972, Manjunath 1985). Aphid transmissibility of the virus varies with different aphid species (Sasaki 1974, Raccah et al. 1977, Roistacher and Bar-Joseph 1989) and virus strains (Bar-Joseph and Loebenstein 1973, Yokomi et al. 1989). T. citricidus is the most potent vector of CTV (Costa and Grant 1951, Sasaki 1974, Ahlawat and Raychaudhuri 1988). A. gossypii was not formerly a potent vector (Dickson et al. 1956, Norman and Grant 1956), but has now become a dangerous one in USA and Israel (Raccah et al. 1980, Roistacher et al. 1984). A. spiraecola and T. aurantii are much less effective vectors (Roistacher and Bar-Joseph 1989), with the exception of T. aurantii in India (Manjunath 1985). With regard to T. citricidus, there is no difference in virus transmissibility between alate and apterous aphids, or between adults and nymphs (Costa and Grant 1951, Sasaki 1974). Similarly, the adults and nymphs of A. gossypii can both transmit the virus equally (Norman and Sutton 1969, Roistacher et al. 1984). Transmission curves of T. citricidus are shown in Fig. 1. This is based on experimental data using Mexican lime, and a two-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 a single aphid. In this formula, the transmissibility of a single T. citricidus

Key words: Toxoptera citricidus, Toxoptera aurantii, Aphis gossypii, Aphis spiraecola, life-cycle, citrus tristeza virus, seasonal occurrence, insecticide resistance.
Table 1. Aphid species attacking citrus

<table>
<thead>
<tr>
<th>Species</th>
<th>Distribution</th>
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<tr>
<td><strong>Major species</strong></td>
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<tr>
<td><em>Toxoptera citricidus</em></td>
<td>Asia, South Africa, Central and South America,</td>
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<td></td>
<td>Australia, New Zealand</td>
</tr>
<tr>
<td><em>Toxoptera aurantii</em></td>
<td>Worldwide</td>
</tr>
<tr>
<td><em>Aphis gossypii</em></td>
<td>Worldwide</td>
</tr>
<tr>
<td><em>Aphis spiraecola</em></td>
<td>Worldwide</td>
</tr>
<tr>
<td>(= <em>A. citricola</em>)</td>
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</tr>
<tr>
<td><strong>Minor species</strong></td>
<td></td>
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<tr>
<td><em>Aphis craccivora</em></td>
<td>Worldwide</td>
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<tr>
<td><em>Aphis fabae</em></td>
<td>Almost worldwide</td>
</tr>
<tr>
<td><em>Aphis nerii</em></td>
<td>Tropics of the Old and New World</td>
</tr>
<tr>
<td><em>Aulacorthum magnoriae</em></td>
<td>Japan, Korea, India</td>
</tr>
<tr>
<td><em>Aulacorthum solani</em></td>
<td>Worldwide</td>
</tr>
<tr>
<td><em>Brachychytris harmalae</em></td>
<td>Israel, Sudan</td>
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<tr>
<td><em>Brachycaudus helichrysi</em></td>
<td>Worldwide</td>
</tr>
<tr>
<td><em>Myzus persicae</em></td>
<td>Worldwide</td>
</tr>
<tr>
<td>* Macrosiphum euphorbiae*</td>
<td>Worldwide</td>
</tr>
<tr>
<td><em>Toxoptera odinace</em></td>
<td>South and East Asia, South Africa</td>
</tr>
<tr>
<td><em>Uroleucon jaceae</em></td>
<td>Europe, the Middle East and Central Asia</td>
</tr>
</tbody>
</table>

is estimated to be 0.04, and of *A. gossypii* 0.03 according to data in Roistacher *et al.* 1984 and within the range 0.01 - 0.11 according to other estimates (Yokomi *et al.* 1989).

**BIOLOGY OF APHIDS**

Aphids can propagate parthenogenetically, their parthenogenesis being linked with viviparity. Sexual and parthenogenetic reproduction alternate in the life cycle (cyclical parthenogenesis). Sexual forms usually appear in fall and oviposit overwintering eggs on the primary host (holocycle) (Fig. 2). Eggs hatch in spring, and each hatched larva develops into a mother which reproduces parthenogenetically (fundatrix). Several aphid species and strains of species reproduce parthenogenetically all year round (anholocycle). Host alternation is another characteristic of aphids. Most alternate between host plants belonging to different families. Overwintering eggs are deposited on one host (the primary host), while nymphs of the parthenogenetically reproducing generation are on another host (the secondary host, usually the summer one). However, some aphid species do not change their hosts, and live on a single species of plant or a group of closely related species. 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 have many morphs (Hille Ris Lambers 1966), including winged and wingless forms. Winged parthenogenetic females (alate vivipara or virginopara) disperse and search for new host plants, while the wingless parthenogenetic females (apterous vivipara) can quickly reproduce on host plants. In host alternating species, the winged female migrates between primary and secondary hosts: the fundatrix or her daughter on the primary host produce winged females which fly to the secondary host. Some morphs appear in a particular season. The gynopara appear in fall, producing sexually reproducing females (ovipara) which lay overwintering eggs. The males also appears in fall, and mate with the ovipara. The fundatrix appears in spring. In some species, the parthenogenetic female produces both ovipara and male (sexupara). Aphid life cycles are complex because of their range of hosts and their polymorphism.
Fig. 1. CTV transmission by *T. citricidus*. Circles show observed data and the line is \( Y = 1 - \exp(-np) \) when \( n = \) number of aphids, \( p = \) transmissibility by one aphid (= 0.04).

Fig. 2. The life cycle of aphids
Life Cycles of Major Citrus Aphids

*T. citricidus*

This aphid has holocyclic and anholocyclic life-cycles. In Japan, the aphid overwinters holocyclically on citrus (Komazaki *et al.* 1979), but overwintering eggs have not been found in other countries (Blackman and Eastop 1984). Host plants are almost completely restricted to species belonging to the family Rutaceae.

*T. aurantii*

This species is almost completely anholocyclic. This aphid has a wide host range, and in Japan, overwintering eggs have been reported on tea.

*A. gossypii*

The taxonomic status of this species is complicated. In Europe, it is distinguished from the *Aphis frangulae* group by the absence of sexual reproduction (Thomas 1968). In East Asia, Japan and China, however, it has a holocyclic life-cycle in addition to an anholocyclic one (Komazaki 1979), Inaizumi 1980; Zhang and Zhong 1990). Primary hosts belong to four families, and parthenogenetic overwintering populations are reported from Japan (Inaizumi 1980). It is a highly polyphagous species.

*A. spiraecola*

This aphid may be holocyclic (North America and Japan) or anholocyclic. In Japan, citrus is one of the primary hosts (Komazaki *et al.* 1979) for one type, and can be distinguished from another type which overwinters on spirea (Komazaki 1983). The former attacks mainly citrus, and the latter attacks other fruit trees belonging the family Rosaceae (Komazaki 1990). The two types can also be distinguished by the esterase banding patterns when electrophoresis is carried out (Komazaki 1991). This aphid is polyphagous.

Seasonal Occurrence of Major Citrus Aphids in Japan

The three most important citrus aphid species in Japan are *T. citricidus*, *A. spiraecola* and *A. gossypii*. *T. aurantii* also attacks citrus, but does not do serious damage (Table 2). These three major aphid species occur continuously on citrus from spring to fall (Fig. 3) and overwinter on citrus as eggs. *A. gossypii* appears on citrus first in the spring, followed by *A. spiraecola*, and finally *T. citricidus*. The early appearance of *A. gossypii* is explained by the fact that the aphid has a wide range of overwintering hosts other than citrus, such as vegetables and weeds, on which it overwinters parthenogenetically. The role of the citrus overwintering population in spring infestation may be comparatively slight, be-

<table>
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<th>Table 2. Citrus aphid species and their occurrence in Japan</th>
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<tr>
<td><strong>Species</strong></td>
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<tr>
<td><em>Toxoptera citricidus</em></td>
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<td><em>Toxoptera aurantii</em></td>
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<td><em>Aulacorthum magnoliae</em></td>
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<td><em>Aphis craccivora</em></td>
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<td><em>Myzus persicae</em></td>
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<tr>
<td><em>Aulacorthum solani</em></td>
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<tr>
<td><em>Sinomegoura citricola</em></td>
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<sup>a</sup> temporary in other seasons
cause the invasion from other hosts begins earlier than the appearance of 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 occurrence of invasion. This means that the population overwintering on citrus is an important source of infestation in spring. This is supported by the fact that migrants from spirea plants cannot reproduce well on citrus (Komazaki 1991). 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 then begins to decrease (Fig. 4). *A. gossypii* peaks in late May, then populations fall, to rise again to a second peak in September. *T. citricidus* peaks between July and September. The capacity of this species to increase may affect its distribution. *T. citricidus* and *A. spiraecola* realize their maximum increase at 27°C, while optimum temperatures for *A. gossypii* are 22 or 23°C (Komazaki 1982). The aphids increase on young shoots, so their numbers also depend on the number of new shoots (Komazaki 1981). The range in annual fluctuations is large in the case of *A. spiraecola*, but relatively small for *T. citricidus* and *A. gossypii* (Komazaki *et al.* 1985). These fluctuations are brought about by the availability of new shoots, climatic conditions and the activity of natural enemies.

Many natural enemies attack citrus aphids, and may sometimes be abundant. The parasitoid *Lysiphlebus japonicus* attacks the three main aphid species, especially *T. citricidus*. The coccinellid *Scymnus hilalis* also attacks these aphids, especially *A. spiraecola*. Many other species, including Syrphids, Crysopids and mites, are also known to attack...
citrus aphids. It is true that natural enemies have an important role in controlling aphid populations. However, they generally appear after aphid populations have already become high, so that by the time they act as control agents the citrus trees have already been damaged. Because virus transmission occurs a short time after infestation by aphids, natural enemies cannot prevent the spread of virus disease.

**SPREAD OF VIRUS IN JAPAN**

The aphid *T. citricidus* is a highly efficient vector of CTV in Japan, transmitting it in a semi-persistent manner. The aphid overwinters on citrus trees in the form of eggs. Parthenogenetic females cannot survive during the winter, because of the lack of new shoots on citrus trees. In spring, the eggs hatch and aphids reproduce parthenogenetically. The aphid population does not increase very much in the first and second generations, during which time a small number of alates appear and the aphids scarcely move from the tree on which they have overwintered. In the third generation, many alate aphids appear and disperse to other citrus trees. Alate aphids spend the teneral period (one or two days after the final molt), on the host plant where they have developed. If the overwintering host is infected with virus, they acquire virus during this period and fly to other hosts to which they transmit the virus. In the same way, many alates appear in summer and disperse the virus. It has been noted that *T. citricidus* is restricted to citrus hosts and migrates only between citrus trees, which increases the possibility of virus spread. In contrast, *A. gossypii* has many host plants, and only a small percentage of the aphids transmit CTV (Ieki 1986). *A. gossypii* is not very important as a CTV vector, and *A. spiraecola* does not transmit CTV at all (Ieki 1986).

**CONTROL**

Natural enemies cannot prevent virus transmission, for the reasons explained above. Nor can repeated spraying suppress aphid populations at a low level, because winged aphids continuously re-colonize citrus trees, and insecticide sprays do not remain active for long on growing shoots. If insecticide were to take effect quickly and remain for a long time, aphids and CTV disease could be controlled, because CTV is transmitted in a semi-persistent manner. However in practice, there are several difficulties:

- Determining the timing of spray applications is very difficult, because insecticide should be applied at an early stage of the spring flush, and flushing of shoots of different trees within a orchard is not synchronized.
- Aphid occurrence cannot be precisely

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**Fig. 4. Seasonal occurrence of major citrus aphids**

Source: Komazaki et al. 1985
Citrus trees are a perennial crop, and are attacked by aphids repeatedly. Insecticide resistance has developed in *A. gossypii* (Furk et al. 1980, Sun et al 1987, Takada and Murakami 1988, Saito 1991, Hosoda et al. 1992) and probably also in *A. spiraecola*. Resistance to organophosphates, carbamates and pyrethroids has developed in *A. gossypii*, and insecticide application is not a recommended way of controlling this aphid and the virus disease it transmits. Cross-protection with mild strains of CTV may be a practical and effective method (Ieki 1989).

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Zhang, G.X. and T.S. Zhong. 1990. Experi-

**DISCUSSION**

Dr. Choi asked for more information on the natural enemies of the citrus aphids. Dr. Komazaki explained that there are some species of parasitoid which have a wide host range but which mainly attack citrus aphids. The rate of predation had not yet been studied very much, but *Coccinella* spp. (ladybugs) and other predator species are abundant in Japan in summer, while *Circad* spp. (hoverflies) may also be abundant under favorable conditions.