

Infection Cycle of Watermelon Mosaic Virus

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Among the viruses occurring in cucurbits in Japan, the most prevalent ones are watermelon mosaic virus (WMV) and cucumber mosaic virus (CMV). Of them, WMV occurs mainly in the summer season in the Kanto region and westward. The WMV diseases in cucurbits cause not only systemic symptoms such as mosaic, dwarf, etc. but also fruit malformation, thus giving severe damage to crops. In addition, the control of WMV is quite difficult as the virus is transmitted by aphids and that carried by plant sap is also infectious. Thus, WMV is one of the greatest obstacles to the production of cucurbits.

The infection cycle of the WMV, including the routes of transmission of the virus by aphids, which is the most important in controlling the virus is briefly presented in this paper, based on the research results reported in the "Epidemiological studies of watermelon mosaic virus".¹⁹⁾

Species of the vector aphids

The main route of infection with WMV is through aphids. As shown in Table 1, many kinds of aphids transmit the virus in a non-persistent manner. Of them, 23 species have been reported as vectors in Japan. Furthermore, by adding several species distributed in Japan, the total number reaches as many as nearly 30. Among them, *Aphis gossypii* and *Myzus persicae* are highly capable of transmitting WMV.¹⁸⁾ Particularly, *Aphis gossypii* occurs abundantly on cucurbits, and is regarded to play a principal role for the virus

transmission. As to other vectors, many of them showed low parasitism to cucurbits and low ability of transmitting WMV, so that their role for the spread of WMV in the field was not clear. A survey conducted in fields of cucurbits in 1981 spring to know the kinds of aphids which fly to the cucurbits at the initial incidence of WMV showed that more than a half of the aphid species sampled were vector species (Table 2). The initial incidence of WMV occurs usually in the period from mid-May to early-June at the survey site (west part of Kagawa Prefecture), and this period coincides with the period of abundant appearance of aphids. In this period, vector species less parasitic to cucurbits also flew in plenty to cucurbits. It is inferred that these aphids may take part greatly in the primary infection of WMV, namely, the infection to cucurbits from wintered hosts (virus-source plants).

Wintered host plants as the source of the first infection of WMV

The range of WMV hosts is limited: mainly Cucurbitaceae, and few other plants such as those of Pedaliaceae, Leguminosae, Chenopodiaceae, and Amaranthaceae. In areas where cucurbits are cultivated throughout the year under structures** in Shikoku, Kyushu, and other regions, WMV is transferred from cucurbits to cucurbits. Namely, the wintering infection-source plants are cucurbits. However, in the regions of the open culture where no cucurbits are grown in winter, it has not been fully clarified that what kind of plant serves as the wintering host. Major winter crops which are infected with

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** Glasshouses or vinylhouses

Table 1. Aphid species reported to be vectors of WMV-2 (1982)

Species	References
* <i>Acyrtosiphon kondoi</i> Shinji et Kondo	Wyman, 1979 ¹⁰⁾
<i>A. lactucae</i> (Passerini)	Coubriet, 1962 ⁴⁾
** <i>A. pisum</i> (Harris)	Swift, 1949 ¹³⁾
** <i>Aphis citricola</i> van der Goot	Adlerz, 1978 ²⁾
** <i>A. clerodendri</i> Matsumura	Yonaha et al., 1979 ²⁰⁾
** <i>A. craccivora</i> Koch	Greber, 1969 ⁵⁾
<i>A. fabae</i> Scopoli	Molnar & Schmelzer, 1964 ¹¹⁾
<i>A. frangulae beccabungae</i> Koch	Karl & Proesler, 1976 ⁸⁾
** <i>A. glycines</i> Matsumura	Yamamoto et al., 1982 ¹⁸⁾
** <i>A. gossypii</i> Glover	Lindberg et al., 1956 ¹⁰⁾
<i>A. middletonii</i> Thomas	Komuro, 1956 ⁹⁾
<i>A. nasturtii</i> Kaltentbach	Adlerz, 1978 ²⁾
** <i>A. nerii</i> Boyer de Fonscolombe	Karl & Schmelzer, 1971 ⁷⁾
** <i>A. nerii</i> Boyer de Fonscolombe	Tewari, 1976 ¹⁵⁾
** <i>A. rumicis</i> Linné	Yamamoto & Ishii, 1980 ¹⁷⁾
* <i>A. sanbuci</i> Linné	Karl & Schmelzer, 1971 ⁷⁾
** <i>Aulacorthum magnoliae</i> (Essig et Kuwana)	Karl & Schmelzer, 1971 ⁷⁾
** <i>A. nipponicum</i> (Essig et Kuwana)	Yamamoto et al., 1982 ¹⁸⁾
** <i>A. solani</i> (Kaltenbach)	Yamamoto et al., 1982 ¹⁸⁾
* <i>A. (Neomyzus) circumflexum</i> (Buckton)	Karl & Schmelzer, 1971 ⁷⁾
<i>Brachycaudus (Acaudus) cardui</i> (Linné)	Karl & Schmelzer, 1971 ⁷⁾
** <i>Brevicoryne brassicae</i> (Linné)	Karl & Schmelzer, 1971 ⁷⁾
<i>Cryptomyzus ribis</i> (Linné)	Coubriet, 1962 ⁴⁾
<i>Dysaphis crataegi</i> (Kaltenbach)	Karl & Schmelzer, 1971 ⁷⁾
* <i>Hyalopterus pruni</i> (Geoffroy)	Karl & Schmelzer, 1971 ⁷⁾
* <i>Hysteroneura setariae</i> (Thomas)	Karl & Schmelzer, 1971 ⁷⁾
** <i>Lipaphis erysimi</i> (Kaltenbach)	Coubriet, 1962 ⁴⁾
** <i>Macrosiphum euphorbiae</i> (Thomas)	Adlerz, 1974 ¹⁾
* <i>Macrosiphoniella sanborni</i> (Gillette)	Greber, 1969 ⁵⁾
<i>Myzus cerasi</i> (Fabricius)	Karl & Schmelzer, 1971 ⁷⁾
** <i>M. (Nectarosiphon) persicae</i> (Sulzer)	Karl & Schmelzer, 1971 ⁷⁾
<i>Phorodon humuli</i> (Schrank)	Anderson, 1954 ³⁾
** <i>P. humuli japonensis</i> Takahashi	Karl & Schmelzer, 1971 ⁷⁾
** <i>Rhodobium porosum</i> (Sanderson)	Yamamoto et al., 1982 ¹⁸⁾
** <i>Rhopalosiphum maidis</i> (Fitch)	Yamamoto et al., 1982 ¹⁸⁾
** <i>R. padi</i> (Linné)	Coubriet, 1962 ⁴⁾
<i>Semiaphis dauci</i> (Fabricius)	Karl & Schmelzer, 1971 ⁷⁾
** <i>Sitobion akebiae</i> (Shinji)	Karl & Schmelzer, 1971 ⁷⁾
** <i>Toxoptera citricidus</i> (Kirkaldy)	Yamamoto et al., 1982 ¹⁸⁾
** <i>Uroleucon formosanum</i> (Takahashi)	Yamamoto et al., 1982 ¹⁸⁾
** <i>U. (Uromelan) gobonis</i> (Matsumura)	Yamamoto et al., 1982 ¹⁸⁾

* Aphid species occurring in Japan.

** Aphid species reported to be vectors of WMV in Japan.
(Sako et al., 1977¹²⁾; Tanaka et al., 1979¹⁴⁾)

Table 2. Aphid species collected from the cucumber and pumpkin fields during the approximate period of first infection of WMV in Kagawa (1981)

Cucumber field (May 2, 9, 16, 23, 30) ^{a)}		Pumpkin field (May 20, 27, June 3, 7) ^{b)}	
Aphid species ^{c)}	No. of aphid collected (% of total)	Aphid species ^{c)}	No. of aphid collected (% of total)
* <i>Acyrtosiphon pisum</i>	1 (0.4)	* <i>Acyrtosiphon pisum</i>	6 (1.0)
* <i>Aphis citricola</i>	2 (0.9)	* <i>Aphis citricola</i>	9 (1.5)
* <i>A. craccivora</i>	5 (2.2)	* <i>A. craccivora</i>	63 (10.3)
* <i>A. gossypii</i>	30 (13.1)	* <i>A. gossypii</i>	123 (20.1)
<i>A. odorikonis</i>	64 (28.0)	<i>A. odorikonis</i>	316 (51.7)
<i>A. sp.</i>	1 (0.4)	<i>A. sp.</i>	3 (0.5)
* <i>Aulacorthum magnoliae</i>	3 (1.3)	* <i>Aulacorthum nipponicum</i>	1 (0.2)
* <i>A. solani</i>	31 (13.6)	* <i>A. solani</i>	14 (2.3)
* <i>Brevicoryne brassicae</i>	5 (2.2)	* <i>Brevicoryne brassicae</i>	2 (0.3)
* <i>Macrosiphum euphorbiae</i>	33 (14.5)	<i>Capitophorus hippophaes</i>	
<i>Megoura crassicauda</i>	7 (3.1)	<i>javanicus</i>	4 (0.7)
* <i>Myzus (Nect.) persicae</i>	30 (13.1)	<i>Eumyzus impatiensae</i>	2 (0.3)
* <i>Rhopalosiphum maidis</i>	3 (1.3)	<i>Megoura crassicauda</i>	8 (1.3)
* <i>R. padi</i>	7 (3.1)	* <i>Myzus (Nect.) persicae</i>	35 (5.7)
* <i>R. rufiabdominalis</i>	5 (2.2)	* <i>Phorodon humuli japonensis</i>	1 (0.2)
* <i>Sitobion akebiae</i>	1 (0.4)	<i>Pleotrichophorus glandulosus</i>	1 (0.2)
Total 228		<i>Rhopalosiphum nymphaeae</i>	9 (1.5)
		* <i>R. padi</i>	6 (1.0)
		<i>Semiaphis heraclei</i>	1 (0.2)
		* <i>Sitobion akebiae</i>	1 (0.2)
		<i>S. ibarae</i>	1 (0.2)
		Total 609	

a) First incidence of WMV in the field; June 4.

b) First incidence of WMV in the field; May 27.

c) * : Vector aphid of WMV

Table 3. Reciprocal transmission of WMV between cucumber and wintering crops by aphid species

Aphid species	Transmission*
<i>Acyrtosiphon pisum</i>	Garden pea → Cucumber
<i>Aphis craccivora</i>	Broadbean } → Cucumber
	Garden pea } ← Cucumber
<i>Aphis gossypii</i>	Broadbean } → Cucumber
	Garden pea } → Cucumber
	Spinach } ← Cucumber
	Sweet pea } ← Cucumber
<i>Myzus (Nect.) persicae</i>	Spinach → Cucumber

* Arrows indicate direction of transmission.

Table 4. WMV-transmission efficiency of *Aphis gossypii*

Factor	Optimum condition
Morph, Age	No significant difference
Host plants	Cucumber > Taro, Sweet pepper > Egg plant, Pokeweed
Pre-acquisition fasting period	Cucumber > Okra, Loquat, Weeds
Acquisition feeding period	1-2 hr
Inoculation feeding period	1-2 min (5 sec)
Transmission by groups	> 1 hr (5 sec)
Virus retention period	$p=1-Q^x$
Starved	> 4 hr
Released on plant	> 15 min
Serial transmission by single aphid	2-5 plants
Temperature	25°C

WMV are spinach, garden pea, broad bean, etc.^{5,18)} As garden pea plants with natural infection of WMV were collected everywhere,^{6,19)} garden pea can be regarded as the major wintering source of infection of WMV. Since broad bean and spinach are also cultivated abundantly like garden pea and their growth duration overlaps with that of cucurbits of outdoor culture for certain periods in autumn and spring, and WMV is reciprocally transmitted between cucumber and these crops by aphids as shown in Table 3, it is highly possible that these crops also serve as the wintering source of WMV.

As given in Table 2, the first incidence of WMV occurs 1-2 weeks after the peak emergence of aphids in spring, i.e. from mid-May to early-June. This time is later by more than one month than the time of incidence of CMV which is also transmitted by aphids like WMV. Furthermore, the number of hills which show the first incidence of WMV is quite few in the field. These facts suggest that even in areas where WMV prevails, wintering host plants (infection source) of the virus are extremely few, with limited kinds and quantity. It seems to show that viruriferous aphids do not emerge unless the aphid population increases to a considerably high level and the number of viruriferous aphids reaching cucurbits is also small.

Secondary infection

Although the number of diseased plants caused by the first infection of WMV is not necessarily large, the disease spreads rapidly after the first incidence through the vector, *A. gossypii* and by the infection through plant sap, occurring during crop management practices. Particularly, the role of *A. gossypii* seems to be very large.

As shown in Table 4, *A. gossypii* is able to acquire and transmit WMV quite easily. The viruriferous insects maintain stable transmissibility for many hours. Many of them can cause the disease in several seedlings of cucumber by one insect. The large number of *A. gossypii* emerged on cucurbits can explain how rapid is the spread of secondary infection. It is considered that highly movable alate insects spread WMV to a wider extent, but apterous-form insects play an important role to spread WMV within the fields. Therefore, it is extremely important to suppress the emergence of aphids in the field from the standpoint of preventing the infection within the fields and of the large area control of WMV disease.

In addition to the high virus transmissibility of *A. gossypii*, other factor for the severe occurrence of WMV seems to be that many of cucurbits infected with WMV serve as good virus-source plants. As shown in Table 5, WMV is transmitted through aphids

Table 5. WMV transmission by *Aphis gossypii* from diseased plants to cucumber seedlings

Virus source plant (var.)	Transmission rate (%) ^{a)}	
	I	II
<i>Cucumis sativus</i> (Sagami-hajiro)	64	72
<i>C. melo</i> (Earl's Favourite)	52	72
<i>C. melo makuwa</i> (Shunka)	40	32
<i>C. melo conomon</i> (Katsura-ohshirouri)	64	40
<i>Cucurbita maxima</i> (Chikanari-ebisu)	64	80
<i>C. moschata</i> (Heian-kogiku)	52	72
<i>Citrullus vulgaris</i> (Shinyamoto 2)	44	28
<i>Lagenaria siceraria</i> (Sakigake)	8	12
<i>Lagenaria siceraria</i> (Hyo-tan)	20	24
<i>Luffa cylindrica</i>	32	40
<hr/>		
<i>Sesamum indicum</i> (Suigen-kuro)	5	
<i>Sesamum indicum</i> (Biroodo)	5	
<i>Gomphrea globosa</i> ^{b)}	4	
<i>Spinacia oleracea</i> (King of Denmark)	43	

a) Test plant: Each 25 seedlings, 2 aphids were placed on each test plant.

b) Inoculum: Inoculated leaves.

at a high rate from many kinds of cucurbit crops infected with WMV. In cucumber, even from resistant cultivars which do not show symptoms, WMV is transmitted at a high rate similar to that of susceptible cultivars. Weeds of Cucurbitaceae infected with WMV are considered to serve as virus-source plants, like diseased cucurbits. As these weeds and cucurbits in home gardens remain growing until late autumn, they are regarded important as the virus-source for wintering host plants.

As mentioned above, WMV can spread rapidly among cucurbits by an efficient mutual infection through aphids, and spread to wider areas by repeating it, resulting in severe outbreak of WMV disease. Particularly during the period from summer to autumn, there are infection-source plants everywhere, so that cucurbit crops in the fields are always exposed to the infection with WMV. In autumn, WMV is transmitted by aphids from diseased cucurbit crops to plants which are going to winter outdoors or cucurbit crops under structure. These plants and crops infected in autumn become the sources of WMV for the succeeding year.

Infection cycle of WMV

On the basis of the above-mentioned results, the infection cycle of WMV is summarized as follows:

1) Transmission of WMV from wintering host plants (virus source plants) to cucurbits (the primary infection, i.e., the initial incidence of WMV in the fields).

2) The secondary infection due to mutual infection among cucurbit plants.

3) Transmission of WMV from diseased crops to wintering plants.

Based on the growing season of major crops which are liable to be suffered from WMV and the occurrence pattern of WMV in Kagawa Prefecture (Fig. 1), the infection cycle of the virus was drawn schematically in Fig. 2. In a word, WMV is transmitted through its vector aphids from wintering host plants to cucurbits in spring, and conversely from the cucurbits to wintering plants in autumn. Accordingly, the method of controlling the virus should be based on such infection routes. The control of WMV appears to be extremely difficult because WMV is carried by many kinds of aphids. However, its host range is so limited that the

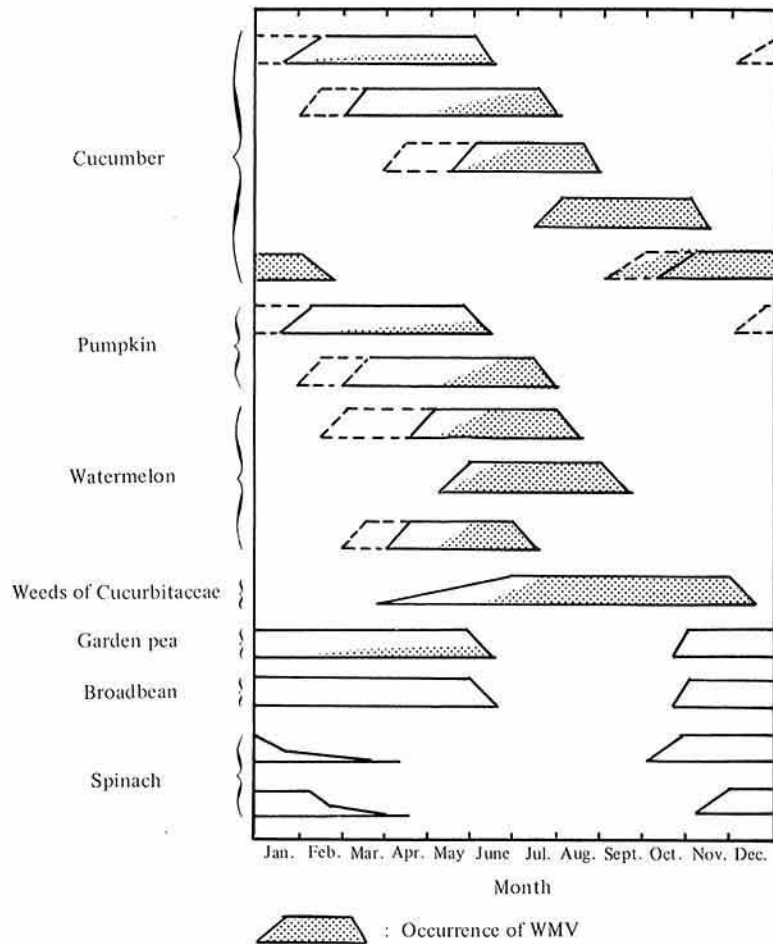


Fig. 1. Cropping pattern of host plants of WMV and occurrence of the virus

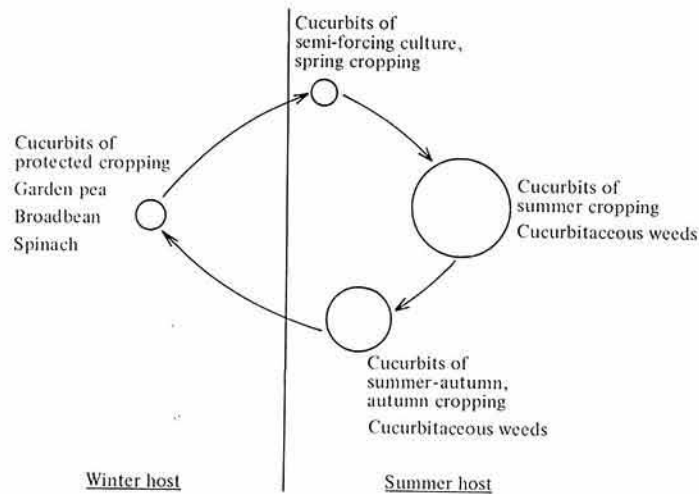


Fig. 2. Schematic presentation of infection cycle of WMV in western Japan

interruption of the infection cycle will be possible. For the culture under structures, prevention of aphids entering into structures, early removal of infection-source plants, prevention of sap transmission, etc. are effective in reducing the WMV occurrence. In the fields, control of aphids and prevention of aphids from flying to crops, together with early removal of virus-source plants in large areas and avoiding the overlapping of growing seasons of cucurbits and wintering host plants, etc. may be able to suppress WMV occurrence to a considerable extent. In addition, the use of resistant cultivars is an important practice for cucumber.

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