Inheritance of Resistance to Cucumber Mosaic Virus Transmission by *Aphis gossypii* in *Cucumis melo*

M. Pitrat and H. Lecoq

Chargés de Recherches, Station d'Amélioration des Plantes Maraîchères and Station de Pathologie Végétale respectively, Domaine Saint Maurice 84140 – MONTFAVET, France.

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ABSTRACT

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Melon (*Cucumis melo*) line PI 161375 (SC), which is resistant to cucumber mosaic virus (CMV) transmission by *Aphis gossypii*, was crossed with two susceptible lines to study the inheritance of its resistance. According to the behavior of the F_1, F_2, and BC_1 progenies, resistance to CMV transmission by *A. gossypii* is controlled by one dominant gene that appears to be associated with nonpreference for these plants by *A. gossypii*. The resistance to CMV transmission by the melon aphid is independent of the resistance to CMV "common" strains which is under an oligogenic recessive genetic control. The study of a varietal collection has shown that five melon lines other than SC (viz. PI 164320 and PI 414723 from India and Ginsen makuwa, Kanro makuwa, and Shiroubi okayama from Japan) are resistant to CMV transmission by *A. gossypii* regardless of their resistance or susceptibility to CMV "common" strains.

RESUME

La lignée de melon (*Cucumis melo*) PI 161375 est résistante à la transmission du virus de la mosaïque du concombre (CMV) par *Aphis gossypii.* D'après l'étude des générations F_1, F_2 et BC_1 entre PI 161375 et deux lignées sensibles, la résistance à la transmission est gouvernée par un gène dominant. Cette résistance est associée à une résistance des plantes par non préférence à *A. gossypii* et est indépendante de la résistance aux souches "communes" de CMV qui est sous un contrôle génétique oligogénique récessif. L'étude d'une collection variétale montre que cinq lignées de melon autres que PI 161375 sont résistantes à la transmission du CMV par *A. gossypii* à savoir PI 164320 et PI 414723 originaires de l'Inde et Ginsen makuwa, Kanro makuwa, et Shiroubi okayama originaires du Japon.

Cucumber mosaic virus (CMV) causes a severe disease in France's muskmelon (*Cucumis melo* L.) fields (16,18). A breeding program has been developed to introduce into Charentais-type muskmelons (*C. melo* var. *cantalupensis* Naud) the oligogenic recessive resistance to CMV "common" strains found in PI 161375 (= Songwhan charmi = SC) (19). However, CMV isolates (grouped in the "Song" pathotype) able to systemically infect SC after mechanical inoculation have been reported to be frequent in naturally infected weeds and vegetables (13). The additional resistance mechanism recently found in SC (12) (which prevents transmission by *Aphis gossypii* Glov., a major CMV vector in southeastern France from transmitting CMV "Song" pathotype strains to SC) may contribute to the good performance of this cultivar under our field conditions, a performance better than that of cultivars possessing only the resistance to CMV "common" strains (12,19). Therefore, it is important to keep this resistance component together with the resistance to CMV "common" strains in a muskmelon breeding program for resistance to CMV.

The aim of this work was to study the inheritance of resistance to CMV transmission by *A. gossypii* and its possible relation to the resistance of SC to *A. gossypii* (1). Resistance of melon to *A. gossypii* has been recognized to involve three partly independent mechanisms (2): "nonpreference," "antibiosis," and "tolerance" according to Painter's definitions of plant resistance to insects (17). SC has been reported to possess some antibiosis and tolerance to *A. gossypii* (1). In the present study an attempt is made to relate the resistance to CMV transmission by *A. gossypii* to a tendency of the aphid not to accept a resistant melon plant even if there is no alternative source of food.

MATERIALS AND METHODS

Plants. Melon seeds were sown in flats and plantlets were transplanted 1 wk later into 10 × 10-cm pots filled with a potting soil. Plants were maintained in an insect-proof greenhouse at 18–25 C; the greenhouse was regularly fumigated with aphicides, but not within 5 days of each test. Plants to be tested were used 15–20 days after sowing when the first leaf had started to expand. In this study, varieties, breeding lines, and accessions will be referred collectively as cultivars. LJ. numbers identify CMV-resistant breeding lines supplied by G. W. Bohn; plant introduction (PI) numbers identify lines furnished by the Plant Introduction Service of the USDA.

Virus strain. CMV strain 14 (CMV-14) (12), a "Song" pathotype, was used throughout this study. Mechanical inoculations were done by the method currently used in our laboratory (15). Under these conditions, CMV-14 induces mosaic symptoms in all cultivars within 5–7 days.

Aphid colonies. Nonviruliferous colonies of *A. gossypii* were maintained on muskmelon cultivar Cantaloup Charentais (CH) in a growth chamber with 16 hr of continuous light at 21 C and 8 hr of darkness at 16 C. To get homogeneous aphid populations for the experiments, 10 adults were placed on healthy plants and allowed to produce larvae for 2–3 days. The adults were then removed and the remaining larvae were used 7–8 days later, when they had reached the adult stage. Only apterous young adults were used in all experiments (nonpreference and virus transmission).

Experimental procedure. This study included two independent experiments: (i) the analysis of crosses between susceptible and resistant parental lines; (ii) the study of a varietal collection of *C. melo*.

The first experiment included three tests: one involving five replicates each containing five SC, five Doublon, five F_1 (Doublon × SC) and 20 F_2 (Doublon × SC; selfed); a second involving four replicates each containing five SC, five Doublon, 20 BC_1 (F_1 × Doublon); and a third with two replicates of five SC, five Freeman's cucumber (= FC), five F_1 (SC × FC) and 25 F_2 (SC × FC; selfed) and two replicates of five SC, five FC, five F_1 (SC × FC) and 20 F_2 (SC × FC; selfed).

The second experiment involved 22 cultivars. Four tests were done, each including four replicates containing five plants of the

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five or six cultivars under study.

Every tested plant was submitted consecutively to two assays: the first to evaluate the nonpreference for the plant by *A. gossypii* and the second to check the resistance to CMV transmission by this aphid.

Nonpreference by *A. gossypii*. Assays were done in a growth chamber with 16 hr of light at 21 C and 8 hr of darkness at 16 C. After a 30–60 min starvation period, 10 nonviruliferous aphids were deposited on the first leaf of each plantlet. Twenty-four hours later the remaining adults on each plant were counted and removed with a camel's hair paint brush. To prevent aphids leaving a plant from reaching another one, plants were isolated by putting each of them on a petri dish placed in a water-filled tray. Under these conditions plants fell within two classes: (i) susceptible to *A. gossypii* in regard to nonpreference if very few aphids (0 – 2 of 10) left the plant on which they had been deposited 24 hr earlier; (ii) resistant to *A. gossypii* by nonpreference if most of them (3 – 10 of 10) had left the plant by this time.

Resistance to CMV transmission. Assays were done 1–3 hr after the end of the nonpreference assay. Terminal leaves of CMV-susceptible CH muskmelon that had been mechanically inoculated 6–8 days prior to the transmission experiments and that showed mosaic symptoms were used as virus sources for the aphids. Following a 2–4 hr starvation period, groups of 10–15 aphids were placed in a small leaf cage which was affixed for 3.5 min to young infected leaves. Then the leaf cage was removed, and aphids found in probing position, were carefully transferred to healthy plants with a small paint brush. To get the highest virus transmission in the susceptible parent for the inheritance study, four viruliferous aphids were deposited on the first leaf of each plantlet. After 15 days, each plant showing no virus symptoms was exposed to a second inoculation by depositing four viruliferous aphids on the youngest leaf. At least 3 hr after the deposition of viruliferous aphids, plants were fumigated with an insecticide. After the 2nd inoculation, plants were allowed an additional 3 wk incubation periods, before final reading was made. Regular aphicide fumigations were done in the greenhouse during the incubation period to control aphids. Each symptomless plant was individually mechanically back inoculated to a *Vigna sinensis* 'Black' plant to check for the absence of CMV. Under these conditions, plants found to be virus-infected and virus-free were rated as "susceptible" and "resistant," respectively to CMV transmissions by *A. gossypii*.

Virus transmission was achieved, for the cultivar collection study, in similar conditions except that three viruliferous aphids were used for both inoculations. At the end of the experiment symptomless plants were grouped by 5 (or less) within each tested cultivar before being inoculated by *V. sinensis* 'Black' to check for the absence of CMV.

RESULTS

Inheritance of resistance to CMV transmission by *A. gossypii*. The study of the F_1, F_2, and BC_1 progenies between Doublon (Charentais cultivar which is susceptible to CMV "common" strains and to CMV transmission by *A. gossypii*) and SC shows that the resistance to CMV transmission by the melon aphid is controlled by one dominant gene (Table 1). The chi-square values in the F_2 progeny for an expected ratio 1 susceptible: 3 resistant is $\chi^2 = 0.853$ ($P = 0.30–0.50$), and in the BC_1, for an expected ratio 1 susceptible : 1 resistant is $\chi^2 = 1.800$ ($P = 0.10–0.20$).

Freeman's cucumber shares with SC the same oligogenic recessive resistance to CMV "common" strains (7,19) but is susceptible to CMV-14 transmission by *A. gossypii* (Tables 1 and 2). The observation of the F_1 and F_2 progenies between SC and Freeman's cucumber gave similar results (Table 1): one dominant gene appears to be involved in SC resistance to CMV transmission by *A. gossypii*. The chi-square value for an expected ratio 1 susceptible: 3 resistant in the F_2 progeny is $\chi^2 = 0.726$ ($P = 0.30–0.50$).

Therefore resistance to CMV "common" strains and to CMV transmission by *A. gossypii* are governed by different genes. The independence of these two resistance mechanisms is confirmed by the study of a varietal collection, among which 11 entries are susceptible to CMV "common" strains and 11 resistant (7,19,22, and authors' *unpublished*). Table 2 indicates that 16 are susceptible to CMV-14 transmission by *A. gossypii* (transmission rate ≥ 85 %) and six are resistant to CMV-14 transmission (five with a transmission rate 0 %, one with 5 %). Among these, two (PI 164320 and PI 414723) are susceptible to CMV "common" strains and four (SC, Ginsen makuwa, Kanro makuwa, and Shiroubi okayama) are resistant to these strains.

Resistance to *A. gossypii* by nonpreference and its relation to resistance to CMV transmission. It was previously reported (12) that within a few hours after deposition on SC plants, apterous *A. gossypii* tended to leave the plants and that such was not the case with CH.

In a preliminary trial, 10 nonviruliferous apterous adult *A. gossypii* were deposited on 30 CH and 30 SC. Fig. 1 indicates that 24 hr later seven or more aphids had left each of the 30 SC plants and only one aphid had left a CH plant. Therefore, this test was applied to 22 melon cultivars. Results expressed in Table 2 indicate that the cultivars fall within one of two classes: susceptible or preferred by *A. gossypii* if most of the aphids remain on the plants 24 hr after deposition (sixteen cultivars were classified as susceptible with a mean number of adults per plant ranging 9.75 – 10.0); resistant or nonpreferred by *A. gossypii* if the aphids have a strong tendency to leave the plants (six cultivars were resistant with a mean number of aphids remaining per plant ranging 1.1–3.1

TABLE 1. Inheritance of resistance in *Cucumis melo* to the transmission of cucumber mosaic virus (CMV) by *Aphis gossypii* and the relation of resistance by nonpreference of this aphid for *Cucumis melo*

Generations	Total number of plants	Plants (no.) susceptible to CVM transmission[a]		Plants (no.) resistant to CMV transmission	
		preferred by *A. gossypii*[b]	nonpreferred by *A. gossypii*	preferred by *A. gossypii*	nonpreferred by *A. gossypii*
PI 161375 (=SC)	25	0	0	0	25
Doublon	25	25	0	0	0
F_1 : Doublon × SC	25	0	1	0	24
F_2 : (Doublon × SC)⊕	100	28	1	0	71
SC	20	0	0	1	19
Doublon	20	20	0	0	0
BC_1 : F_1 × Doublon	80	46	0	0	34
SC	20	0	0	1	19
Freeman's cucumber (=FC)	20	20	0	0	0
F_1 : SC × FC	20	0	0	2	18
F_2 : (SC × FC)⊕	90	18	1	3	68

[a] Plants were rated "resistant" to CMV transmission if they were not infected following two successive exposures to inoculation by four viruliferous aphids. They were rated "susceptible" if they were infected after one or two exposures to inoculation under the same conditions.
[b] Plants were rated "preferred" or "nonpreferred" by *A. gossypii*, if 24 hr after their deposition, respectively, 8 – 10 of 10 or 0 – 7 of 10 adults apterous aphids were found on the plants.

adults). On each plant on which aphids remained after 24 hr there were 7 or less adults (except for two plants of Kanro makuwa with eight adults). The resistant cultivars are: SC, PI 164320, PI 414723, Ginsen makuwa, Kanro makuwa, and Shiroubi okayama.

In the F_2 and BC_1 progenies of the crosses between SC and the two susceptible Doublon and Freeman's cucumber parents (Table 1), 175 plants carried seven or less adult *A. gossypii* per plant after 24 hr; among them 173 were resistant to CMV transmission. Among 95 plants on which eight to 10 adults per plant were found, 92 were susceptible to CMV transmission. Correlation between resistance to CMV transmission by *A. gossypii* and nonpreference appears to be very high.

A study of the cultivar collection leads to the same conclusion (Table 2). The six cultivars resistant to CMV transmission also are nonpreferred by *A. gossypii*. The other 16 cultivars are susceptible to CMV transmission and are preferred by *A. gossypii*.

DISCUSSION

Resistance to CMV transmission by *A. gossypii* found in melon line SC (12) is determined by one dominant gene which appears to be associated with nonpreference for this host by *A. gossypii*. This association has been established by studying a varietal collection of *C. melo* and F_1, F_2, and BC_1 progenies between resistant (ie, possessing both types of resistance) and susceptible lines. In the F_2 and BC_1 progenies (Table 1) two plants of 270 were found to be nonpreferred hosts and susceptible to CMV transmission while three were preferred and resistant to CMV transmission. These plants may have resulted from a recombination process between the two genes. However, they may also result from imperfection of the testing procedure: the first two plants may represent cases where resistance to CMV transmission was broken (12) and the three others, plants which had escaped infection (a single inoculation in these experiments led to only 81% infection of the susceptible Doublon and Freeman's cucumber). It cannot yet be concluded whether these two types of resistance are governed by the same gene or by two very closely linked genes. The mean aphid number after 24 hr on SC was 1.9 vs 3.2 on the two F_1 (SC with Doublon and Freeman's cucumber). It seems that when aphid resistance is concerned, the dominance is not absolute though it is sufficient for breeding purposes.

Five melon cultivars, other than SC, among the 22 tested were found to be resistant to CMV transmission and not preferred by *A. gossypii*: PI 164320 and PI 414723 from India and Ginsen makuwa, Kanro makuwa, and Shiroubi okayama from Japan. No cultivar was found to possess only one of these two types of resistance, confirming their possible linkage.

The relation between nonpreference and resistance to transmission is puzzling. Indeed it had been previously observed (12) that soon after being deposited on SC plants, *A. gossypii* quickly started to make probes. An additional proof that *A. gossypii* probes on SC is the fact that this aphid may acquire CMV from an infected SC plant (12). It is likely that these probes help *A. gossypii* to determine whether a plant will be a suitable host. Therefore if *A. gossypii* probes on SC, the question is why CMV, which is a stylet-borne virus and which may be transmitted during very short probes is not transmitted to SC. The mechanism of nontransmission is not fully understood; it may be associated with a particular probing behavior of *A. gossypii* on SC (9), which would prevent CMV from reaching sites from which the virus would spread in the plant, or it could also be associated with a reaction of the plant to the aphid probes which would indirectly prevent the virus spread. Similar to what is observed in SC, resistance to aphids in some crops has been reported to also confer field resistance to the viruses they transmit (3,5,6,23).

Different forms of melon resistance to *A. gossypii* have been described and PI 414723 (studied under the symbol LJ 90234) was found to exhibit nonpreference, tolerance, and antibiosis to a western biotype of this aphid (2,10). In this line, absence of leaf curling (an aspect of tolerance) is controlled by one dominant gene (symbol *Ag*). Resistance to stunting (another aspect of tolerance) seems to have a more complex heredity, but is at least partly independent of *Ag* (1). A major partly dominant gene, probably different from *Ag*, confers antibiosis but minor genes can modify the antibiosis level (11). SC possesses the gene *Ag* for leaf curling

TABLE 2. Resistance in *Cucumis melo* to the transmission of cucumber mosaic virus (CMV) by *Aphis gossypii* in relation to host preference by this aphid

Cultivar	Total number of plants	Number of plants susceptible to CMV transmission[a]		Number of plants resistant to CMV transmission		Adult aphids per plant[e] (mean no.)
		preferred by *A. gossypii*[b]	nonpreferred by *A. gossypii*	preferred by *A. gossypii*	nonpreferred by *A. gossypii*	
Doublon	20	20	0	0	0	9.80
Charentais T	20	20	0	0	0	10.00
Cantaloup Charentais (=CH)	20	20	0	0	0	10.00
Smith's Perfect[c]	20	18	0	2	0	10.00
Texas MR 1[c]	20	17	0	3	0	10.00
Kanro makuwa[d]	20	0	0	2	18	3.10
Ginsen makuwa[d]	20	0	0	0	20	1.75
Shiroubi okayama[d]	20	0	0	0	20	1.10
Freeman's cucumber (=FC)[d]	20	20	0	0	0	10.00
B 63-3	20	20	0	0	0	9.90
69-G-61[d]	20	19	0	1	0	9.80
L.J. 34340[d]	20	20	0	0	0	10.00
L.J. 90279[d]	20	20	0	0	0	9.75
L.J. 90386[d]	20	20	0	0	0	9.95
L.J. 90389[d]	20	20	0	0	0	9.95
L.J. 90436[d]	20	19	0	1	0	9.85
PI 124112[c]	20	20	0	0	0	9.95
PI 161375 (=SC)[cd]	20	0	0	0	20	1.55
PI 164320[c]	20	0	0	0	20	1.10
PI 179671[c]	20	20	0	0	0	10.00
PI 180280	20	17	0	3	0	9.95
PI 414723[c]	20	0	0	0	20	2.40

[a] Plants were rated "resistant" to CMV transmission if they were not infected following two successive inoculations by three viruliferous aphids. They were rated "susceptible" if they were infected after one or two inoculations under the same condition.
[b] Plants were rated "preferred" or "nonpreferred" by *A. gossypii*, if 24 hr after their deposition, respectively, 8 − 10 of 10 or 0 − 7 of 10 adults apterous aphids were found on the plants.
[c] Described as resistant to *A. gossypii* or *Aphis* sp. (1,4,10,20)
[d] Described as resistant to CMV "common" strains (7,19,22, and author's *unpublished*)
[e] Mean number of adult aphids remaining per plant 24 hr after the deposition of 10 adult aphids.

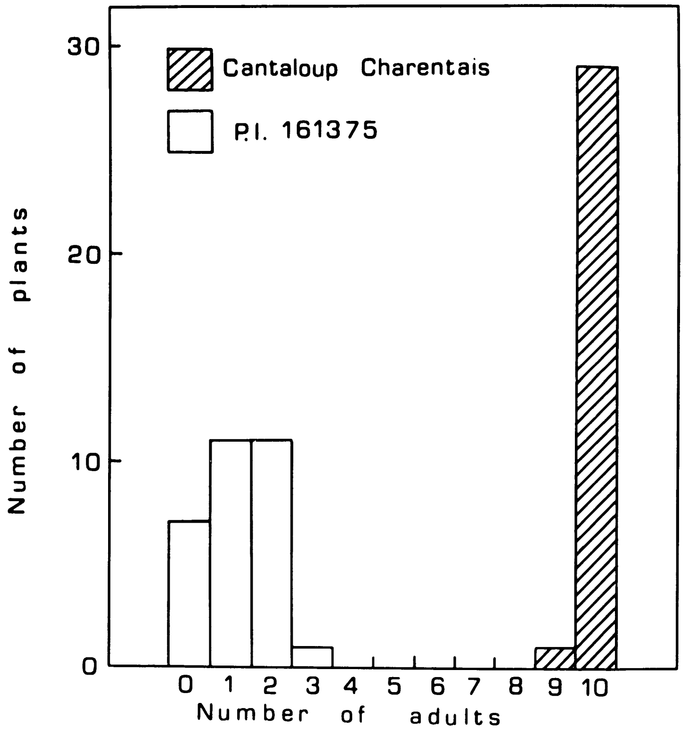

Fig. 1. Distribution of plants of two melon cultivars tested for nonpreference by *Aphis gossypii*. Plants are grouped by number of adults remaining 24 hr after deposition of 10 adults per plant (30 plants per cultivar were inoculated).

resistance and exhibits some antibiosis towards *A. gossypii* but it lacks the gene(s) conferring resistance to stunting (1). It is not yet known whether the dominant gene(s) controlling nonpreference and resistance to CMV transmission by *A. gossypii* is (are) the gene *Ag*, a gene controlling antibiosis, or a third undescribed one. An allelism test will be done to clarify this point.

Among resistant lines, PI 164320 also was previously described as resistant to *A. gossypii* in Florida (14). Cultivars Smith Perfect and Texas MR1, however, described as resistant to *A. gossypii* (4), and PI 124112 and 179671, described as resistant to *Aphis* sp. (20), were susceptible to both CMV transmission and *A. gossypii* under our conditions.

Resistance to CMV "common" strains in melon is under oligogenic recessive control (7,19,21) and may be overcome by the "Song" pathotype (13). Resistance to CMV aphid transmission is under monogenic dominant determinism and is not strain-specific (12). Therefore, it represents an additional resistance mechanism independent of the first one. The association of these two mechanisms in the same cultivar should contribute to better protection. However, CMV may be transmitted by over 60 aphid species (8); therefore, field efficiency of the CMV transmission resistance by *A. gossypii* will depend on the relative importance of this aphid among the other efficient vector species involved in virus spread in the crop. Indeed, resistance to CMV transmission in SC is only partial with efficient CMV vectors such as *Myzus persicae* (12).

In a breeding program for resistance to CMV, transmission assays can be advantageously replaced by nonpreference assays. Indeed, virus transmission to the susceptible controls is not always 100%, and a second transmission is often necessary to reach that level; experiments to measure virus transmission by aphids take time and require space to keep plants during the incubation period. In contrast, assays for nonpreference require only 24 hr.

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