Specificity of the Helper-Component-Mediated Aphid Transmission of Three Potyviruses Infecting Muskmelon

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ABSTRACT

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Aphids (*Myzus persicae*) transmitted purified watermelon mosaic virus 1 strain of papaya ringspot virus (WMV 1), watermelon mosaic virus 2 (WMV 2), and zucchini yellow mosaic virus (ZYMV) in the presence of extracts from plants infected by the homologous virus and which contained helper component (HC). When heterologous combinations were tested, some degree of specificity was revealed in the virus-HC interaction even though in all cases some transmission occurred. WMV 1-HC allowed high transmission rates of WMV 2 but not of ZYMV, WMV 2-HC permitted high transmission rates of ZYMV and slightly less of WMV 1, while ZYMV-HC was efficient in promoting WMV 2 transmission but not that of WMV 1. When two viruses were mixed in the presence of one HC some competition did occur. In five of the six combinations tested, transmission rates of the homologous virus from the mixture were not significantly different (although usually slightly less) from that observed when alone, while transmission rates of the heterologous virus from the mixture were drastically reduced (four to six times). In these cases, a competition seemed to occur in favor of the homologous virus. When WMV 2 and ZYMV were mixed with WMV 2-HC the situation was different: ZYMV transmission rate was not affected by the presence of WMV 2, but the WMV 2 transmission rate was significantly reduced. In this case, competition also occurred but in favor of the heterologous virus. The high affinity between ZYMV and WMV 2-HC may provide some epidemiological advantage to ZYMV.

RESUMÉ

Les pucerons (*Myzus persicae*) ont transmis les virus de la mosaïque de la pastèque 1 et 2 (WMV 1 et WMV 2) et de la mosaïque jaune de la courgette (ZYMV) purifiés en présence d'extraits de plantes infectées par ces virus. Ces extraits contiennent donc le facteur assistant (FA) nécessaire à l'acquisition des potyvirus par les pucerons. L'étude de combinaisons hétérologues virus-extraits de plantes infectées a montré qu'une certaine spécificité existait dans la relation particules virales-FA. Le FA du WMV 1 a ainsi assuré des taux de transmission élevé pour le WMV 2 et faible pour le ZYMV. Le FA du WMV 2 a assuré des taux de transmission élevé pour le ZYMV et légèrement plus faible pour le WMV 1. Enfin le FA du ZYMV a assuré des taux de transmission élevé pour le WMV 2 et très faible pour le WMV 1. En cas de mélange de virus en présence du FA homologue de l'un d'entre eux est apparue une compétition dans la transmission des virus. Dans cinq des six combinaisons éprouvées, le taux de transmission du virus homologue du FA n'a pas été significativement modifié par rapport au taux observé lorsqu'il était seul. Par contre, le taux de transmission du virus hétérologue a été considérablement réduit (4 à 6 fois moins que lorsqu'il était seul). Dans ce cas la compétition est favorable au virus homologue. Lorsque les WMV 2 et ZYMV ont été mis en présence du FA du WMV 2, la situation a été différente: c'est le taux de transmission du virus homologue qui s'est trouvé considérablement réduit alors que le taux de transmission du virus hétérologue (ZYMV) demeurait élevé. Cette propriété peut conférer au ZYMV un certain avantage épidémiologique.

Watermelon mosaic virus 1 strain of papaya ringspot virus (16) (WMV 1), watermelon mosaic virus 2 (WMV 2), and zucchini yellow mosaic virus (ZYMV) are potyviruses that cause major diseases in cucurbit crops in southern France (7–9,11) as well as in many other parts of the world (12). These viruses are transmitted by several aphid species in a nonpersistent manner and differ in symptomatology, host range, and serological properties. Serological relationships have been established between ZYMV and WMV 2 (10), and between some WMV 1 and WMV 2 isolates (1), but not between other isolates (17).

The transmission of several potyviruses by aphids has been shown to be dependent on the presence of a helper component (HC) which is present in infected, but not in healthy plants (2,13,14,18). HCs from different potyviruses may differ either in their biological activities (13,18) or in their serological properties (19). HC has been detected among cell-free translation products of tobacco vein mottling virus (TVMV) RNA indicating its viral origin (4). More recently, using an antiserum against TVMV-HC, HC-related polypeptides have been identified in cell-free translation products of 16 other potyviruses including WMV 1, WMV 2, and ZYMV (5). As the evidence that HC is virus coded is now unequivocal, this substance may provide a new approach to investigate relationships between viruses.

The purpose of the experiments reported here was to confirm, by biological means, the dependence of WMV 1, WMV 2, and ZYMV on an HC system for aphid transmission, and to test the specificity of the HC associated with these viruses using extracts and purified virus preparations from a common host.

MATERIALS AND METHODS

Virus isolates. The isolates of watermelon mosaic virus 1 strain of papaya ringspot virus (WMV 1 isolate E2), watermelon mosaic virus 2 (WMV 2 isolate MAR), and zucchini yellow mosaic virus (ZYMV isolate E9) used in this study were already described (8,9,11). All are very efficiently transmitted from plant to plant by *Myzus persicae* Sulz.

Virus purification. A standard method modified from that of Lisa et al (10) was used for purifying the three viruses. Infected melon (*Cucumis melo* L. 'Védrantais') leaves were harvested 3–4 wk after inoculation with each virus and homogenized with four volumes (w/v) of an extraction solution consisting of 0.3 M K_2HPO_4, 0.2% Na-diethyldithiocarbamate (DIECA), and 0.1% 2-mercaptoethanol, pH 8.5. The slurry was emulsified with an equal

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volume of Freon 113 (1,1,2-trifluoro-1,2,2-trichloroethane). After centrifugation at 5,000 *g* for 10 min, 1% Triton-X100 was added to the aqueous phase and stirred for 20 min at 4 C. The virus was recovered by ultracentrifugation at 20,000 rpm for 3 hr in a Beckman R30 rotor. The pellets were suspended in 0.02 M potassium phosphate buffer, pH 7.4, and left 6 hr at 4 C with occasional stirring.

The suspensions were submitted to a slight clarification (1 min, 2,500 *g*) before adding Cs_2SO_4 to reach a final density $\rho = 1.27$ g/cm^3, and centrifuging 16 hr at 35,000 rpm at 10 C in a Beckman R50Ti rotor. The opalescent virus containing zone was removed, diluted 10–15 times in phosphate buffer, pH 7.4, and centrifuged at 5,000 *g* for 10 min. The supernatant was then ultracentrifuged at 37,000 rpm for 2 hr in a Beckman R50Ti rotor. The final pellet was resuspended in a small volume of phosphate buffer, pH 7.4. Virus concentration was determined spectrophotometrically by using an approximate extinction coefficient $E_{260\,nm}^{0.1\%} = 2.5$. Final yields varied according to the virus and the purification from 10 to 200 mg of virus per kilogram of fresh infected leaves.

Preparation of extracts containing the helper components. Crude HC-containing preparations for the three viruses were obtained by a standard method similar to that described by Sako and Osaka (18). Three grams of infected leaves 3–4 wk after inoculation were ground with a mortar and pestle in 10 ml of 0.3 M K_2HPO_4, pH 9. The homogenate was strained through gauze and the filtrate was centrifuged at 5,000 *g* for 10 min. The resulting supernatant was centrifuged at 40,000 rpm for 3 hr in a Beckman R50Ti rotor. The upper part of the supernatant was then carefully collected and used as a soluble fraction containing HC.

In preliminary tests, these fractions were found to be devoid of infectious virus particles and to be highly effective for mediating virus transmission. Therefore, no attempts were made to further purify the HC. For clarity in the text these soluble fractions containing HC will be referred thereafter as HC.

Transmission tests. *Myzus persicae* were reared as previously described (6). Transmission tests were done using a method similar to that of Govier et al (3). Groups of aphids were starved for a 2- to 4-hr period and then allowed a 10-min acquisition access period to the test solution through a stretched Parafilm membrane. Unless otherwise stated, the test solution contained 80 μg of purified virus per milliliter, fresh HC prepared within the same day, and 20% sucrose. Ten aphids were placed on each of five plantlets of *C. melo* cultivar Védrantais at the first-leaf stage for each treatment except in the competition tests, in which a single aphid was deposited on each of 30 plantlets for each treatment. Aphids were allowed to remain on the test plants for 2–4 hr, then the plants were fumigated with an insecticide and maintained in an insect-proof greenhouse for 3–6 wk. When homologous virus-HC combinations were tested, transmission percentage was determined on the basis of number of plants developing symptoms. With heterologous virus-HC combinations or with combinations containing more than one virus, symptom-expressing plants were individually tested by using the SDS immunodiffusion method (15) and antisera that did not detect cross reactions between WMV 2 and ZYMV (9).

Statistical analysis was by means comparison using Student's *t*-test following arc sine transformation for the proportion of transmission (specificity experiments) or after the same transformation by analysis of variance and using Duncan's multiple range test (competition experiments).

RESULTS

Transmission of WMV 1, WMV 2, and ZYMV. *M. persicae* efficiently transmitted purified WMV 1, WMV 2, and ZYMV at concentrations of 8 or 80 μg/ml in the presence of HC from plants infected by the same viruses (Table 1). At a virus concentration of 0.8 μg/ml, transmission rates were still over 50% in all cases. No transmission occurred when extracts from infected plants were replaced by similar extracts from healthy plants or by the extraction solution (K_2HPO_4, 0.3 M, pH 9), or when purified viruses were omitted.

Specificity experiments. The results of the previous experiments indicated that transmission of purified WMV 1, WMV 2, and ZYMV was dependent on HC-containing extracts from infected plants. A comparison of heterologous HC-virus combinations indicated some level of specificity in the HC-virus interactions (Table 2). HC from WMV 1-infected plants allowed a high transmission rate for WMV 1 and WMV 2 but was inefficient for ZYMV. HC from WMV 2-infected plants, in contrast, permitted high transmission rates for the three viruses although that of WMV 1 was slightly less, while HC from ZYMV was very efficient for WMV 2 and ZYMV transmission but allowed a significantly lower transmission of WMV 1. In all cases higher transmission rates were obtained with homologous combinations.

Competition experiments. The specificity of the HC-virus interactions was further studied in experiments in which aphids were allowed to acquire virus from suspensions containing mixtures of viruses. This was done by comparing viruses and HC in pairs. A single aphid was deposited per test plant to detect double transmission and to determine the actual virus transmission rates.

Results of the WMV 1-WMV 2 combinations are reported in Table 3. Transmission rates of both viruses from mixtures, in the presence of homologous HC, were only slightly less (although not significantly) to those observed when these viruses were alone. In contrast, transmission of WMV 1 or of WMV 2 from mixtures in the presence of heterologous HC was greatly reduced (about four times). In most cases, transmission of heterologous virus occurred jointly with the transmission of the homologous virus.

Results of the WMV 1-ZYMV combinations are similar (Table 4) except that no transmission at all of WMV 1 or ZYMV occurred from mixtures of these viruses in the presence of heterologous HC. When alone, these viruses were very poorly transmitted in the presence of heterologous HC, confirming results presented in Table 2.

TABLE 1. Aphid transmission of purified watermelon mosaic virus 1 and 2 (WMV 1 and WMV 2) and zucchini yellow mosaic virus (ZYMV) in the presence of extracts from plants infected by the same virus

Aphid feeding source[a]		Transmission[b] of:		
Virus concentration (μg/ml)	Extract from plant[c]	WMV 1	WMV 2	ZYMV
80	Infected	29/30[d]	28/30	28/30
8	Infected	28/30	27/30	30/30
0.8	Infected	23/30	17/30	16/30
0	Infected	0/30	0/30	0/30
80	Healthy	0/20	0/20	0/20
80	Buffer	0/20	0/20	0/20

[a] All solutions contained 20% sucrose.
[b] Aphids (*Myzus persicae*) allowed a 10-min acquisition access period, five test plants per treatment and 10 aphids per test plant.
[c] Extracts were made from muskmelon. Buffer is the extraction solution alone.
[d] Results are expressed as number of plants infected divided by the number of plants inoculated. Cumulative data of four or six independent experiments.

TABLE 2. Aphid transmission of three purified viruses: watermelon mosaic virus 1 and 2 (WMV 1 and WMV 2) and zucchini yellow mosaic virus (ZYMV) in the presence of extracts containing homologous or heterologous helper component (HC)[w]

HC from plants infected with:	Transmission[x] (%) of:		
	WMV 1	WMV 2	ZYMV
WMV 1	97[y]a[z]	97 a	30 d
WMV 2	67 bc	93 ab	90 abc
ZYMV	13 d	87 abc	93 ab

[w] No transmission was observed in the absence of either HC or virus.
[x] Aphids (*Myzus persicae*) allowed a 10-min acquisition access period, five test plants per treatment and 10 aphids per test plant. Virus concentrations were 80 μg/ml and feeding sources contained 20% sucrose.
[y] Cumulative data of six independent experiments.
[z] Means followed by the same letter are not significantly different, $P = <0.05$, according to Student's *t*-test.

TABLE 3. Aphid transmission of watermelon mosaic virus 1 and 2 (WMV 1 and WMV 2) alone or from mixtures, in the presence of extracts containing helper component (HC) of these viruses

HC from	WMV 1					WMV 2				
Virus in feeding[x]	WMV 1	WMV 2	WMV 1 + WMV 2			WMV 1	WMV 2	WMV 1 + WMV 2		
Transmission of[w]	WMV 1	WMV 2	WMV 1	WMV 2	Both[x]	WMV 1	WMV 2	WMV 1	WMV 2	Both
Experiment 1[y] A	27	22	23	3	3	6	12	2	12	1
1 B	26	22	22	4	3	6	17	1	13	1
2 A	25	11	23	8	7	3	17	1	14	1
2 B	22	13	20	4	4	7	17	3	8	3
3 A	18	17	17	4	4	9	20	1	18	1
3 B	14	18	17	2	2	11	14	3	18	3
Transmission (avg %)	73.3 a[z]	57.2 ab	67.8 ab	13.9 cd	12.8	23.3 c	53.9 ab	6.1 d	46.1 b	5.6

[x] Concentration of each virus was 80 μg/ml in all cases. Feeding solution contained 20% sucrose.
[w] Aphids (*Myzus persicae*) were allowed a 10-min acquisition access period; 30 test plants with one aphid per plant were used with each virus-HC combination. Results are expressed as number of plants infected out of 30 tested.
[x] Data included in columns for individual viruses.
[y] Experiments with the same numbers were done with the same virus and HC preparations. Every HC preparation was checked for the presence of contaminant virus.
[z] Means followed by the same letter are not significantly different, according to Duncan's multiple range test, $P = <0.05$. For statistical analysis data from experiments with the same HC and virus preparations were cumulated.

TABLE 4. Aphid transmission of watermelon mosaic virus 1 (WMV 1) and zucchini mosaic virus (ZYMV) alone or from mixtures, in the presence of extracts containing helper component (HC) of these viruses

HC from	WMV 1					ZYMV				
Virus in feeding source[x]	WMV 1	ZYMV	WMV 1 + ZYMV			WMV 1	ZYMV	WMV 1 + ZYMV		
Transmission of[w]	WMV 1	ZYMV	WMV 1	ZYMV	Both[x]	WMV 1	ZYMV	WMV 1	ZYMV	Both
Experiment 1[y] A	25	1	18	0	0	3	17	0	17	0
1 B	22	3	18	0	0	7	15	0	15	0
2 A	18	1	10	0	0	0	14	0	9	0
2 B	12	3	10	0	0	0	16	0	11	0
3 A	3	3	4	0	0	1	20	0	20	0
3 B	7	3	6	0	0	0	24	0	21	0
Transmission (avg %)	48.3 a[z]	7.8 b	36.7 a	0 c	0	6.1 b	58.9 a	0 c	51.7 a	0

[x] Concentration of each virus was 80 μg/ml in all cases. Feeding solution contained 20% sucrose.
[w] Aphids (*Myzus persicae*) were allowed a 10-min acquisition access period; 30 test plants with one aphid per plant were used with each virus-HC combination. Results are expressed as number of plants infected out of 30 tested.
[x] Data included in columns for individual viruses.
[y] Experiments with the same numbers were done with the same virus and HC preparations. Every HC preparation was checked for the presence of contaminant virus.
[z] Means followed by the same letter are not significantly different, according to Duncan's multiple range test, $P = <0.05$. For statistical analysis data from experiments with the same HC and virus preparations were cumulated.

TABLE 5. Aphid transmission of watermelon mosaic virus 2 (WMV 2) and zucchini yellow mosaic virus (ZYMV) alone or from mixtures, in the presence of extracts containing helper component (HC) of these viruses

HC from	WMV 2					ZYMV				
Virus in feeding source[x]	WMV 2	ZYMV	WMV 2 + ZYMV			WMV 2	ZYMV	WMV 2 + ZYMV		
Transmission of[w]	WMV 2	ZYMV	WMV 2	ZYMV	Both[x]	WMV 2	ZYMV	WMV 2	ZYMV	Both
Experiment 1[y] A	13	9	2	5	1	18	12	4	11	3
1 B	12	7	2	5	0	11	10	1	10	1
2 A	15	6	5	11	3	7	17	3	11	2
2 B	15	13	7	11	2	15	21	1	11	1
3 A	8	14	0	8	0	7	17	1	10	0
3 B	9	17	1	12	1	2	20	0	13	0
Transmission (avg %)	40 ab[z]	36.7 ab	9.4 c	28.9 b	3.9	33.3 ab	53.9 a	5.6 c	36.7 ab	3.9

[x] Concentration of each virus was 80 μg/ml in all cases. Feeding solution contained 20% sucrose.
[w] Aphids (*Myzus persicae*) were allowed a 10-min acquisition access period; 30 test plants with one aphid per plant were used with each virus-HC combination. Results are expressed as number of plants infected out of 30 tested.
[x] Data included in columns for individual viruses.
[y] Experiments with the same numbers were done with the same virus and HC preparations. Every HC preparation was checked for the presence of contaminant virus.
[z] Means followed by the same letter are not significantly different, according to Duncan's multiple range test, $P = <0.05$. For statistical analysis data from experiments with the same HC and virus preparations were cumulated.

Results of the WMV 2-ZYMV combinations (Table 5) differ from those of previous combinations: in the presence of both homologous or heterologous HC, ZYMV was transmitted from mixture with WMV 2 almost as well as alone. Conversely, WMV 2 transmission rates were drastically reduced (four to six times) in the presence of ZYMV whatever the HC.

DISCUSSION

The results presented here indicate that WMV 1, WMV 2, and ZYMV require HC for aphid transmission, confirming earlier results obtained with a strain of WMV—probably WMV 2—in Japan (18). They bring also a biological support to the recent identification of polypeptides serologically related to TVMV-HC in cell-free translation products of WMV 1, WMV 2, and ZYMV RNAs (5). HC-containing extracts proved to be very efficient in virus transmission assays even at low virus concentrations (0.8 μg/ml), and the transmission rates were similar to those obtained with potato virus Y (PVY) and purified PVY-HC (13).

Specificity in HC-virus interactions has been observed in several virus combinations (13,18) but in these experiments sources of HC as well as test plants were from different species. As pointed out by Pirone (13), this may affect to some extent transmission efficiency. Therefore, in our experiments, sources of HC or purified virus and test plants were of the same cultivar. In these conditions, the study of homologous and heterologous virus and HC combinations revealed some degree of specificity in virus-HC relationship even though at least some virus transmission occurred in all combinations. When comparing viruses and their related HC by pairs in two cases a reciprocal situation was observed: WMV 2 and ZYMV were very efficiently transmitted both in homologous or heterologous combinations, while WMV 1 and ZYMV were very efficiently transmitted in homologous combinations but very poorly transmitted in heterologous combinations. In terms of virus-HC interactions ZYMV appears to be related to WMV 2 and different from WMV 1. In combinations between WMV 1 and WMV 2 the situation was slightly different; transmission rates were high in three combinations and only moderate in one case. From these data, WMV 2-HC appears as the more polyvalent and WMV 2 the more efficiently transmitted virus whatever the HC. However, it should be pointed out that differences in HC efficiencies may occur among different isolates of the same virus (14).

When two viruses were mixed in equal amounts in the presence of one of their HCs, selective transmission of one component of the mixture was consistently observed. In five of the six combinations tested, transmission rates of the homologous virus from the mixture were not significantly different from those obtained when alone in the feeding source (Tables 3–5). In contrast, transmission of the heterologous viruses was drastically reduced (four to six times) and happened mainly in cotransmission with the homologous virus. The situation was reversed in the sixth combination: from the mixture containing purified WMV 2 and ZYMV with WMV 2-HC, aphids consistently transmitted ZYMV better than WMV 2. ZYMV transmission was not significantly different in the presence of WMV 2 or alone, while WMV 2 transmission was significantly reduced. Since little is known on the nature of virus-HC relationship, interpretation of this competition may only be speculative. However, it appears that generally there are higher affinities in homologous virus HC combinations, and preferential transmission of the homologous virus was also noticed from mixtures containing TVMV, PVY and only one HC (13). It is of interest that, in mixture with WMV 2, ZYMV is transmitted better than WMV 2 regardless of the HC. If this also happens from plants with double infections it could provide an important epidemiological advantage to ZYMV and contribute to the rapid spread of this newly recognized virus in several parts of the world.

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