A Non-Aphid-Transmissible Isolate of Bean Yellow Mosaic Virus-Scott That Is Transmissible from Mixed Infections with Pea Mosaic Virus-204-1

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ABSTRACT

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An isolate of bean yellow mosaic virus (BYMV-Scott) that was not transmissible from single infections of pea (*Pisum sativum* 'Dwarf Gray Sugar') by *Aphis craccivora* was transmissible from mixed infections with pea mosaic virus (PMV-204-1). The relative transmission efficiency of BYMV-Scott compared with PMV-204-1 averaged 20% from mixed infections (8–14% transmission of BYMV-Scott versus 39–70% transmission of PMV-204-1). BYMV-Scott seldom was transmitted alone from mixed infections. Sequential probing by aphids on PMV-204-1-infected pea tissue, then on BYMV-Scott-infected pea tissue, resulted in transmission of PMV-204-1 only. Aphids probing sequentially on BYMV-Scott-infected pea tissue and then through membranes on purified virions of PMV-204-1 or clover yellow vein virus (CYVV-Pratt) transmitted PMV-204-1 and CYVV-Pratt to 35 and 45% of test plants, respectively, indicating that an active helper component was available in BYMV-Scott-infected pea. Aphids that sequentially probed on BYMV-Scott or PMV-204-1-infected pea tissue and then through membranes on purified BYMV-Scott transmitted BYMV-Scott at very low levels (2–7%). The specific infectivity of BYMV-Scott was lower than those of PMV-204-1 and CYVV-Pratt. Virion properties of this isolate of BYMV-Scott apparently are responsible for its lack of aphid transmissibility from single infections.

Bean yellow mosaic virus (BYMV-Scott), pea mosaic virus (PMV-204-1), and clover yellow vein virus (CYVV-Pratt) are members of the BYMV subgroup of potyviruses. Isolates PMV-204-1 and CYVV-Pratt typify BYMV subgroup viruses that cause important diseases of forage legumes in the southeastern United States (8,9). BYMV-Scott is typical of isolates that commonly infect gladiolus in the United States (2,10). Isolates similar to CYVV-Pratt and BYMV-Scott also infect various legumes and *Gladiolus* spp., respectively, in Australia (2). Based on molecular hybridization analysis and enzyme-linked immunosorbent assay (ELISA) studies, BYMV-Scott, PMV-204-1, and CYVV-Pratt represent three related but distinct viruses (1,2).

Aphid transmission of PMV-204-1 has been shown to be dependent on a helper component (HC) (12), as is characteristic of the potyvirus group. Purified potyvirus virions can be transmitted mechanically or by aphids that have prior or simultaneous access to HC. Aphids can acquire HC through probing on infected plant tissue or on purified or partially purified HC preparations derived from infected plant tissue.

Several non-aphid-transmissible isolates of BYMV subgroup potyviruses have been reported (5,15). Evans and Zettler (5) described a bean yellow mosaic virus isolate from Wisconsin that was nontransmissible using several different aphid vectors and plant species. In contrast, both a Florida isolate and a Kentucky isolate were readily transmissible.

Non-aphid-transmissible isolates of several potyviruses have been transmitted when in mixed infection with transmissible isolates of the same or another potyvirus (6,11,14). Alternatively, sequential probing of aphids on leaf tissue of the transmissible isolate first, followed by probing on the non-aphid-transmissible isolate, often has yielded transmission of the non-aphid-transmissible isolate (6,11,14). Pirone and Thornbury (13) described a non-aphid-transmissible isolate of tobacco etch virus, which could be transmitted when purified non-aphid-transmissible virions were mixed with purified HC from a transmissible isolate, although transmission levels were lower than for the transmissible isolate. HC purified from plants infected with the non-aphid-transmissible isolate enabled transmission of an aphid-transmissible isolate. The authors concluded that both HC and virion properties could be involved in the nontransmissibility of the non-aphid-transmissible isolate.

We discovered through initial aphid transmission tests with BYMV subgroup virus isolates that our isolate of BYMV-Scott was not transmissible under the same conditions that the CYVV-Pratt and PMV-204-1 isolates were efficiently transmitted. We subsequently began researching the mechanism of nontransmission with BYMV-Scott. This paper reports results of that research. The purpose of the research was to characterize this nontransmissibility, including involvement of HC and virion properties. This characterization involved a series of experiments to determine whether the nontransmissible isolate of BYMV-Scott could be transmitted from mixed infections or sequential probings with the transmissible isolate PMV-204-1. The results provide insight into the reason(s) for the nontransmissibility of this isolate and clues concerning the mechanism of nonpersistent aphid transmission of some plant viruses.

MATERIALS AND METHODS

Virus cultures. Isolates of BYMV-Scott, PMV-204-1, and CYVV-Pratt were obtained originally from O. W. Barnett, Clemson University, Clemson, SC. They were passed through three consecutive single-lesion transfers from *Chenopodium amaranticolor* (Coste & A. Reynier) Coste & A. Reynier to *Pisum sativum* L. 'Dwarf Gray Sugar' (S. W. Scott, *unpublished*) and maintained in Dwarf Gray Sugar pea by mechanical inoculations in the greenhouse. Viruses were purified from mechanically inoculated Dwarf Gray Sugar pea by a method slightly modified from that described by Baum and Barnett (3). Virus bands collected from cesium sulfate gradients were dialyzed in the final step against 0.5 M potassium phosphate buffer, pH 7.0 (instead of Tris buffer), and stored at −70 C at a concentration of 1 mg/ml (A_{260nm} = 2.4, 1 mg/ml, 1-cm light path). Acquisition host plants were inoculated with 100 μg/ml of purified virus in 0.03 M sodium phosphate buffer, pH 7.3, containing 0.15% 2-mercaptoethanol and with Carborundum as abrasive.

Aphid maintenance. *Aphis craccivora* Koch was maintained on cowpea (*Vigna unguiculata* (L.) Walp. subsp. *unguiculata* 'California Blackeye No. 5'). Nymphs and wingless adults were starved in plastic petri dishes 2–6 hr before acquisition probing.

Transmission from mixed infections. Dwarf Gray Sugar pea acquisition host plants were mechanically inoculated with PMV-204-1 or BYMV-Scott as above, then mechanically inoculated with the other virus 6–7 days later. Nine to twelve days after the second inoculation, aphid transmission tests were carried out using detached infected leaves for acquisition probing periods of 4 min. Presence of both viruses in acquisition hosts was confirmed by double antibody sandwich (DAS)-ELISA (4). Dwarf Gray Sugar pea plants with single 9- to 19-day-old infections of PMV-204-1 and BYMV-Scott also were used as acquisition hosts in the same experiments. Ten aphids were transferred to each Dwarf Gray Sugar pea test plant, allowed to probe overnight, then killed with insecticide.

Mixed infection serial transmission test. Several test plants infected by aphid transmission with both viruses in the above tests were used as initial acquisition hosts in a subsequent test. Test plants subsequently infected with both viruses by this process of serial aphid transmission were in turn used as acquisition hosts. This process was repeated through three cycles of serial transmission, 3–5 wk apart. Acquisition and test probing were as described above.

Sequential probing tests with tissue. In sequential probing tests involving only leaf tissue, aphids probed for 2 min on detached leaves of Dwarf Gray Sugar pea plants inoculated 6–10 days earlier with PMV-204-1, then probed for 2 min on leaves of Dwarf Gray Sugar pea plants inoculated 13–17 days earlier with BYMV-Scott. Test probing was as described above. Ten aphids were used per test plant.

Sequential probing tests with tissue and membrane probing. Aphids were given 2-min acquisition probing on detached leaves of Dwarf Gray Sugar pea inoculated with PMV-204-1 (9–17 days earlier) or BYMV-Scott (11–22 days earlier). They then were given 10-min probing access on Parafilm membranes to purified virus suspensions of BYMV-Scott, PMV-204-1, or CYVV-Pratt. Control aphids probed for 2 min on healthy Dwarf Gray Sugar pea tissue before being given 10-min access to purified virus suspensions. Virus suspensions of 400 μg/ml were in 0.2 M potassium phosphate buffer, pH 7, and suspensions of 1 mg/ml were in 0.5 M potassium phosphate buffer, pH 7. Sucrose was added to 20% in all virus suspensions. Ten to 15 aphids were used per Dwarf Gray Sugar pea test plant.

Detection of virus transmission. Ten days to 2 wk after test probing, test plants were assayed for presence of virus(es) by DAS-ELISA (4). Antisera specific to each of the three viruses were used.

TABLE 1. Transmission of pea mosaic virus (PMV-204-1) and bean yellow mosaic virus (BYMV-Scott) by *Aphis craccivora* from single and mixed infections of pea cultivar Dwarf Gray Sugar

Acquisition source[a]	Transmission record:[b] No. infected plants/No. test plants (% transmission)	
	PMV-204-1	BYMV-Scott[c]
PMV-204-1 single infection	50/67 (75%)	...
BYMV-Scott single infection	...	0/87 (0%)
Mixed infection, PMV-204-1 mechanically inoculated 6–7 days before BYMV-Scott	28/50 (56%)	4/50 (8%)
Mixed infection, BYMV-Scott mechanically inoculated 6–7 days before PMV-204-1	22/56 (39%)	7/56 (13%)
Mixed infection, aphid inoculation (serial transmission tests)	90/128 (70%)	18/128 (14%)

[a] Acquisition access on detached infected leaves of 4 min. Ages of single infections were 9–19 days. For mixed infections, transmission tests were 9–12 days after inoculation of second virus. Serial transmission tests from mixed infections were repeated through three cycles at 3- to 5-wk intervals.

[b] Ten aphids per test plant. Combined results of three to six experiments.

[c] All BYMV-Scott-infected plants were doubly infected with PMV-204-1, except for one plant inoculated from the mixed infection in which PMV-204-1 had been mechanically inoculated 6–7 days before BYMV-Scott.

Mechanical inoculation infectivity tests. Dilutions of purified PMV-204-1, BYMV-Scott, and CYVV-Pratt virions were made in 0.03 M sodium phosphate buffer, pH 7.3, plus 0.15% 2-mercaptoethanol. Celite was mixed with inocula at a 1% concentration. Dwarf Gray Sugar pea plants were inoculated with cotton-tipped swabs. For each treatment, 8–10 plants were inoculated in each of three experiments. Plants were observed for 10 days to 2 wk for symptom development.

ELISA comparison of virus concentration in single and mixed infections. Dwarf Gray Sugar pea plants were inoculated mechanically with PMV-204-1 and BYMV-Scott using schedules and procedures like those for mixed infection acquisition host plants. Plants were mechanically inoculated with one virus, then 7–8 days later were mechanically inoculated with the other. Nine to twelve days after inoculation of the second virus, DAS-ELISA comparisons of virus concentration were made by weighing and extracting upper portions of individual plants (youngest two to three leaves plus bracts, petioles, and stem). Samples were triturated with mortar and pestle in 0.02 M potassium phosphate buffer, pH 7.3, containing 0.05% (v/v) Tween 20 and 0.01 M sodium diethyldithiocarbamate (PB-Tween-DIECA) at a 1:10 (w/v) ratio of tissue to buffer. Tissue from plants singly infected with PMV-204-1 or BYMV-Scott 17–20 days earlier also was extracted. Each sample was tested against antisera to PMV-204-1 and BYMV-Scott. Aliquots of individual plant extracts were tested in two separate wells on each of three ELISA plates (six replicate wells total). Sample and reagent volumes, reagent concentrations, and incubation times were kept constant. Absorbance at 405 nm after 1-hr substrate incubation was determined with a Bio-Tek model 309 microplate reader (Bio-Tek Instruments, Inc., Burlington, VT).

RESULTS

Transmission from mixed infections. Aphid transmission of BYMV-Scott from mixed infections of PMV-204-1 and BYMV-Scott occurred from acquisition hosts mechanically inoculated first with either virus (Table 1). Rates of BYMV-Scott transmission were 8% from acquisition hosts inoculated first with PMV-204-1 and 13% from those inoculated first with BYMV-Scott. Of 11 plants infected with BYMV-Scott in these two groups, only one (in the former group) was singly infected. The other 10 plants also were infected with PMV-204-1. Overall, the relative transmission efficiency of BYMV-Scott from mixed infections in this experiment compared with PMV-204-1 was 22% (11 BYMV-Scott transmissions versus 50 PMV-204-1 transmissions).

Combined results from the three cycles of mixed infection serial transmission tests were similar to the other mixed infection tests (Table 1). BYMV-Scott was transmitted to 14% of the combined total test plants compared with 70% for PMV-204-1, an average relative transmission efficiency of 20% (18 BYMV-Scott transmissions versus 90 PMV-204-1 transmissions). The relative transmission efficiencies of BYMV-Scott compared with PMV-204-1 were 13% in the first cycle (4 versus 30 transmissions, respectively), 30% in the second cycle (6 versus 20 transmissions, respectively), and 20% in the third cycle (8 versus 40 transmissions, respectively). All of the 18 test plants infected with BYMV-Scott in this experiment also were infected with PMV-204-1.

Sequential probing tests with leaf tissue. Aphids that probed first for 2 min on PMV-204-1-infected pea tissue, then for 2 min on BYMV-Scott-infected tissue, did not transmit BYMV-Scott to any of 80 test plants. Forty-four of the 80 test plants (55%) were infected with PMV-204-1.

Sequential probing tests with leaf tissue and purified virus. Aphids that probed on PMV-204-1-infected tissue and then through membranes into BYMV-Scott purified virus at a concentration of 400 μg/ml, transmitted BYMV-Scott to only 2% (one of 44) of the test plants (Table 2). Aphids that probed on purified CYVV-Pratt at 400 μg/ml after probing on PMV-204-1-infected pea tissue transmitted CYVV-Pratt to 27% (nine of 34) of the test plants. Two of the nine plants positive for CYVV-Pratt contained CYVV-Pratt only, whereas the remaining seven were doubly infected with PMV-204-1. The relative transmission efficiency of BYMV-Scott compared with CYVV-Pratt in this experiment was 9%.

Aphids that probed BYMV-Scott tissue before having membrane probing access to purified PMV-204-1 at 400 μg/ml transmitted PMV-204-1 to 35% of the test plants (seven of 20) with no transmissions of BYMV-Scott (Table 2). Aphids that

TABLE 2. Aphid sequential probing transmission tests with pea mosaic virus (PMV-204-1)-infected and bean yellow mosaic virus (BYMV-Scott)-infected tissue of pea cultivar Dwarf Gray Sugar and purified PMV-204-1, BYMV-Scott, and clover yellow vein virus (CYVV-Pratt) virions

Probing sequence		Transmission record:[a] No. infected plants/No. test plants (% transmission)		
First	Second	PMV-204-1	BYMV-Scott	CYVV-Pratt
PMV-204-1 tissue[b]	Purified BYMV-Scott[c]			
	400 μg/ml	20/44 (45%)	1/44 (2%)	...
	1 mg/ml	23/30 (77%)	1/30 (3%)	...
PMV-204-1 tissue	Purified CYVV-Pratt			
	400 μg/ml	19/34 (56%)	...	9/34 (27%)
BYMV-Scott tissue	Purified PMV-204-1			
	400 μg/ml	7/20 (35%)	0/20 (0%)	...
	1 mg/ml	7/20 (35%)	0/20 (0%)	...
BYMV-Scott tissue	Purified BYMV-Scott			
	400 μg/ml	...	1/44 (2%)	...
	1 mg/ml	...	2/30 (7%)	...
BYMV-Scott tissue	Purified CYVV-Pratt			
	400 μg/ml	...	0/20 (0%)	9/20 (45%)
Purified PMV-204-1				
400 μg/ml	BYMV-Scott tissue	0/20 (0%)	0/20 (0%)	...
Purified CYVV-Pratt				
400 μg/ml	BYMV-Scott tissue	...	0/20 (0%)	0/20 (0%)
Healthy tissue	Purified virus[d]	0/40 (0%)	0/138 (0%)	0/44 (0%)

[a] Combined results of two to four experiments with viruses at 400 μg/ml and two to three experiments with viruses at 1 mg/ml. Ten to 15 aphids were used per Dwarf Gray Sugar pea test plant.

[b] Two-minute acquisition access on detached leaf tissue. Age of infection for PMV-204-1 acquisition host plants was 9–17 days; for BYMV-Scott plants it was 11–22 days.

[c] Ten-minute acquisition access on Parafilm membranes.

[d] Control tests with aphids probing healthy tissue and then purified virus at 400 μg/ml included 20 test plants for PMV-204-1, 88 for BYMV-Scott, and 44 for CYVV-Pratt. Similar control tests with virus at 1 mg/ml included 20 test plans for PMV-204-1 and 50 for BYMV-Scott. CYVV-Pratt was not tested at 1 mg/ml.

probed BYMV-Scott tissue before having membrane probing access to purified CYVV-Pratt at 400 μg/ml transmitted CYVV-Pratt to 45% of the test plants (nine of 20) with no BYMV-Scott transmissions (Table 2). Reversal of the order of probing, with membrane probing on purified virus at 400 μg/ml followed by probing on BYMV-Scott tissue, resulted in no transmissions of either PMV-204-1 or CYVV-Pratt (Table 2).

After probing on BYMV-Scott tissue, aphids given membrane access to purified BYMV-Scott at 400 μg/ml transmitted BYMV-Scott to 2% of the test plants (one of 44) (Table 2). Aphids that were first allowed to probe on healthy Dwarf Gray Sugar pea tissue, then given membrane access to purified virus at 400 μg/ml, did not transmit any of the three viruses (Table 2).

Results with purified virus at 1 mg/ml were similar to those with 400 μg/ml (Table 2). Aphids that probed on either PMV-204-1-infected or BYMV-Scott-infected pea tissue before membrane access to purified BYMV-Scott transmitted BYMV-Scott to 3 and 7% of the test plants (one of 30 and two of 30), respectively. Aphids probing on BYMV-Scott tissue, then on purified PMV-204-1, transmitted PMV-204-1 to 35% of the test plants (seven of 20) (Table 2). The relative transmission efficiency of BYMV-Scott compared with PMV-204-1 from purified preparations at 1 mg/ml after probes of BYMV-Scott-infected tissue was 20%. Control aphids that probed on healthy Dwarf Gray Sugar pea tissue and then on purified virus did not transmit either BYMV-Scott or PMV-204-1. No tests were conducted with CYVV-Pratt at 1 mg/ml.

Mechanical inoculation infectivity tests. Infectivity of BYMV-Scott purified virus in mechanical transmission tests to Dwarf Gray Sugar pea was lower than that of either PMV-204-1 or CYVV-Pratt (Table 3).

Virus concentration in single and mixed infections. Against BYMV-Scott antiserum, ELISA absorbance readings for plants singly infected with BYMV-Scott were comparable to those of mixed infection plants in which BYMV-Scott had been inoculated before PMV-204-1 (Table 4). Absorbances against BYMV-Scott antiserum for mixed infection plants inoculated with PMV-204-1 first were generally lower than for the BYMV-Scott single infection plants (Table 4).

TABLE 3. Mechanical inoculation infectivity of purified virions of pea mosaic virus (PMV-204-1), bean yellow mosaic virus (BYMV-Scott) and clover yellow vein virus (CYVV-Pratt) to pea cultivar Dwarf Gray Sugar

Virus[a]	Infection percentage[b] at concentrations of:				
	40 (μg/ml)	4 (μg/ml)	0.4 (μg/ml)	0.04 (μg/ml)	0.004 (μg/ml)
PMV-204-1	100	83	10	10	3
BYMV-Scott	71	13	0	0	0
CYVV-Pratt	100	74	10	0	0

[a] Virus diluted in 0.03 M sodium phosphate buffer, pH 7.3, with 0.15% 2-mercaptoethanol. Celite at 1% was used as abrasive.
[b] Percentages based on totals in three experiments of 26–31 plants for each treatment.

DISCUSSION

We conclude that virion properties are at least partly responsible for the lack of aphid transmissibility of the BYMV-Scott isolate. It is apparent that BYMV-Scott tissue has some HC activity; however, direct comparisons of relative levels of HC activity in PMV-204-1-, CYVV-Pratt-, and BYMV-Scott-infected tissues were not possible by the techniques of this study.

Direct comparisons of transmissibility of purified virions were possible, however. Using PMV-204-1 as HC source, BYMV-Scott purified virus yielded lower levels of transmission than CYVV-Pratt purified virus. Using BYMV-Scott tissue as HC source, BYMV-Scott purified virions yielded lower levels of transmission than either CYVV-Pratt or PMV-204-1 purified virus. In mechanical transmission testing of purified virus, the infectivity of BYMV-Scott to Dwarf Gray Sugar pea was lower than that of the other two viruses.

Lack of BYMV-Scott transmission from aphid acquisition probing on BYMV-Scott-infected tissue after prior acquisition probing on PMV-204-1-infected tissue also suggests that virion properties are involved. If low HC activity were the only factor responsible for nontransmissibility of BYMV-Scott, transmission of BYMV-Scott in the sequential probing tests might be expected because HC could be provided from the PMV-204-1 tissue. Other nontransmissible virus isolates have been transmitted successfully in similar sequential probing tests (6,11).

Higher BYMV-Scott concentration in mixed infections with PMV-204-1 as compared with BYMV-Scott single infections was ruled out as a possible explanation for BYMV-Scott transmission from mixed infections. Concentrations of BYMV-Scott in mixed infections as measured by ELISA were either similar to, or lower than, BYMV-Scott concentrations in single infections, depending upon whether BYMV-Scott or PMV-204-1 was inoculated first (Table 4).

Infectivity of PMV-204-1 is apparently greater than that of BYMV-Scott in Dwarf Gray Sugar pea (Table 3). Interestingly, this situation is the opposite of that reported by Evans and Zettler (5), who determined higher specific infectivity from a non-aphid-transmissible isolate of BYMV than from aphid-transmissible isolates.

Because relative HC activity of the three viruses was not measured, the possibility of lower BYMV-Scott HC activity cannot be ruled out. Lower HC activity could play a role in making the BYMV-Scott isolate nontransmissible from single

TABLE 4. Comparison of enzyme-linked immunosorbent assay absorbance values from single and mixed infections of *Pisum sativum* 'Dwarf Gray Sugar' with bean yellow mosaic virus (BYMV-Scott) and pea mosaic virus (PMV-204-1)

Experiment no.	Virus[a] treatment	Number of plants	Absorbance[b] (A_{405nm}) with antiserum to: PMV-204-1 Mean	PMV-204-1 Standard deviation	BYMV-Scott Mean	BYMV-Scott Standard deviation
1	H	9	0.091	0.025	0.049	0.003
1	P	12	0.658	0.124	0.056	0.005
1	S	5	0.116	0.026	0.357	0.037
1	P/S	7	0.670	0.110	0.241	0.051
1	S/P	4	0.271	0.028	0.336	0.030
2	H	8	0.096	0.028	0.049	0.002
2	P	12	0.940	0.132	0.057	0.004
2	S	12	0.139	0.033	0.371	0.017
2	P/S	9	0.766	0.193	0.310	0.045
2	S/P	19	0.355	0.153	0.377	0.029

[a] H = healthy, P = PMV-204-1 single infection, S = BYMV-Scott single infection, P/S = mixed infection of PMV-204-1 mechanically inoculated 7–8 days before BYMV-Scott, and S/P = mixed infection of BYMV-Scott mechanically inoculated 7–8 days before PMV-204-1. Single infections were evaluated 17–20 days after inoculation. Mixed infections were evaluated 9–12 days after inoculation of the second virus. Extracts were made in a 1:10 (w/v) ratio of plant tissue to extracting buffer.
[b] Six replicates (two wells in each of three plates) per individual plant extract. Absorbance measured after 1-hr substrate incubation.

infections. Helper component from PMV-204-1 and BYMV-Scott tissue assisted transmission of PMV-204-1, BYMV-Scott, and CYVV-Pratt purified virions. Given the close relationship of the viruses, this might be expected because PMV-204-1 HC was shown by Pirone and Thornbury (13) to assist transmission of two potyviruses, potato virus Y and tobacco vein mottling virus, which are serologically unrelated to PMV-204-1.

It is possible that our BYMV-Scott isolate is a laboratory curiosity, resulting from selection through single-lesion passages. Although our research provided no direct evidence for transcapsidation or phenotypic mixing (7) in mixed infections of PMV-204-1 and BYMV-Scott, these possibilities will be considered in future research with mixed infections of these two viruses.

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