Interactions of Peanut Mottle Virus Strains and Soybean Germ Plasm

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ABSTRACT

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The reactions of selected soybean cultivars and plant introductions to peanut mottle virus (PMV) varied with virus isolate. Twelve isolates were classified into five strain groups (P1–P5) based on reactions of soybean cultivars Lee 68, York, Virginia, and Cumberland. Strain group P1 members caused severe symptoms in Lee 68, Virginia, and Cumberland but caused no symptoms in York. Strain group P2 members caused severe symptoms in Lee 68, mild symptoms in Virginia and Cumberland, and no symptoms in York. Strain group P3 members caused mild symptoms in Lee 68, Virginia, and Cumberland and none in York. Strain group P4 members caused mild symptoms in Cumberland, severe symptoms in Lee 68, and none in Virginia and York. Strain group P5 members caused mild symptoms in only Lee 68 and York. Of 37 additional cultivars and lines tested, 26 responded like Lee 68, except symptom severity varied in plants infected with P2 and P4 strains, four responded like York, and seven were resistant to all strains. The reaction of certain soybean germ plasm to the five strains could be used to determine the identity of known genes for resistance to PMV.

Peanut mottle virus (PMV) causes significant yield losses in soybean (*Glycine max* (L.) Merr.) in the southeastern United States (6,11,16,19). There is resistance in soybeans to PMV that is being incorporated into cultivars for management of the disease. Resistance, in this case, is defined as a lack of virus infection of the plant. Demski and Kuhn (5) tested 70 cultivars for resistance to PMV in the greenhouse and found 14 that were resistant. Shipe et al (20) tested 2,161 soybean plant introductions in maturity groups II, III, and IV for resistance to PMV and identified seven resistant entries in group II, 16 in group III, and 122 in group IV.

Inheritance of the reaction to PMV in soybean has been investigated. Boerma and Kuhn (2) found that a single dominant gene designated *Rpv* conditioned resistance in the cultivars Dorman and CNS. Shipe et al (21) concluded that resistance in the cultivar Peking is conditioned by a single recessive gene, designated rpv_2. Shipe et al (21) also demonstrated that Arksoy, PI 89784, and PI 219789 contained single dominant genes for PMV resistance, but they did not test allelic relationships among the genes. Buss et al (3) determined that the cultivars York, Arksoy, Dorman, and Shore contain the *Rpv* gene for resistance to PMV but that it differs from the gene in the cultivar CNS. The cultivar York is also resistant to the type or G1 strain of soybean mosaic virus (SMV) (4,16). This resistance is conditioned by a gene closely linked to *Rpv* (18), but several SMV strains are capable of infecting York (4).

The V74S isolate of PMV, which was used in inheritance studies in Virginia, has characteristics typical of other described isolates of the virus (1). This isolate occasionally produced atypical symptoms on some soybean plants and infected cultivars previously noted as resistant. To determine if the culture contained variants, subcultures were produced from single necrotic lesions on bean (*Phaseolus vulgaris* L. cv. Topcrop). Most of the resulting virus subcultures produced symptoms in susceptible soybean cultivars typical of those induced by PMV-V74S, but some subcultures clearly differed in types of symptoms, symptom severity, and host range in soybeans. Although symptomatologically differing PMV strains occur in peanut (*Arachis hypogaea* L.), their effects on soybean are unknown (14). The purpose of our study was to characterize PMV-V74S variants and natural isolates for reactions on soybean, to select a set of soybean cultivars for differentiating PMV strains, and to determine the interactions of known host genes with the PMV strains.

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MATERIALS AND METHODS

Source and propagation of virus. The PMV isolates used in these experiments were obtained from soybean plants growing in

TABLE 1. Origins of peanut mottle virus isolates

Isolate designation	Origin
V74S[a]	Original isolate from field samples 80 and 81 collected in 1974 from Holland, VA[b]
V74S/473	Culture accession number 473, a direct derivative of V74S appearing biologically identical to V74S
V74S/348-1	Selected in 1978 from a single lesion[c] from culture accession 348, a derivative of V74S
V74S/495-1	Selected in 1978 from a single lesion from culture accession 495, a derivative of V74S
V74S/10B-1	Selected in 1978 from a single lesion after 10 transfers of V74S in soybean cultivar Essex
V74S/73-178	Selected in 1980 from single lesions after maintenance of V74S/473 in soybean breeding line V73-178
V74S/73-741	Selected in 1980 from single lesions after maintenance of V74S/473 in soybean breeding line V73-741
V79S/20	Field isolate collected from Warsaw, VA
V79S/33	Field isolate collected from Holland, VA
V79S/38-2	Field isolate collected from Blacksburg, VA
V81S/29	Field isolate collected from Holland, VA
V81S/30	Field isolate collected from Holland, VA
V81S/31	Field isolate collected from Holland, VA

[a] Isolates were designated by the year collected (74 = 1974), the plant from which collected (S = soybean), and an identification number. Each of the V79S and V81S isolates was subjected to two or more single-lesion isolations on the bean cultivar Topcrop.
[b] Culture considered to be the predominant Virginia isolate with characteristics typical of previous descriptions of the virus (1).
[c] All local lesions were selected from the bean cultivar Topcrop.

experimental plots or commercial fields in Virginia from 1974 through 1981 or were derivatives of these isolates (Table 1). Samples were mechanically inoculated to the soybean cultivars Essex or Lee 68 as described previously (22), using seed lots specifically selected for freedom from seedborne SMV. The isolates were maintained in soybean by transfer about once every 2 wk in the greenhouse or by storage of dried infected soybean leaves over $CaCl_2$ at 4 C. Each isolate was subjected to two or more successive isolations from single lesions on bean cultivar Topcrop (10).

Biological testing. Seeds of the soybean cultivars and plant introductions were provided by G. R. Buss, Department of Agronomy, Virginia Polytechnic Institute and State University. The responses of plant introductions to four derivatives of PMV-74S were tested in field plots at Blacksburg, VA, in 1979. The field plot was divided into seven blocks, one each for the six virus isolates and an uninoculated control. Each block consisted of four repetitions of all 19 entries randomized within the block, and each entry had 15 plants in a 90-cm-long row. The plant introductions were included because each contained resistance to PMV isolate V74S (20). The test also included two resistant cultivars, Virginia and Peking, and two susceptible entries, Essex and PI 229315 (5,20,21). Plants were inoculated with an artist's airbrush as described previously (18). Entries were evaluated for disease and rated for symptom severity 50 days after inoculation.

Greenhouse tests were conducted to identify soybean cultivars that would give differential responses to PMV isolates and to establish strain groups based on these responses. The PMV-resistant cultivars Cumberland, York, and Virginia and the susceptible cultivar Lee 68 were selected as the soybean differentials. Plants were prepared by planting six to eight seeds in clay pots containing a soilless potting mix and growing them until unifoliolate leaves were fully expanded. Inocula were prepared by grinding Essex or Lee 68 soybean or pea (*Pisum sativum* L. cv. Little Marvel) tissue collected 2–3 wk after inoculation in 0.01 M phosphate buffer, pH 8.0 (22). Unifoliolate leaves were inoculated and symptom development was observed over a 4-wk period.

Serological testing. Antisera were prepared to PMV isolate V74S/473 by injecting rabbits intramuscularly and intravenously with 5 mg of purified virus (22), then injecting them intervenously 4 wk later with 0.1 mg of purified virus. Bleedings were made 6 wk after the initial injection, and sera were stored frozen at −20 C. Homologous microprecipitin titers of the antisera were 1:128–1:256. Isolates were tested serologically using either agar immunodiffusion with sodium dodecyl sulfate (SDS) (22) or indirect enzyme-linked immunosorbent assay (ELISA) (13). Antigens for ELISA were prepared in phosphate-buffered saline, pH 7.4, containing 2% polyvinylpyrolidone 40 and 0.2% ovalbumin. Purified virus used in ELISA was prepared by the method of Tolin and Ford (22). The isolates were also tested against SMV antiserum (8) to detect any contamination.

Testing of soybean cultivars and lines. Forty-one soybean cultivars and lines were screened for their reactions to PMV. Seeds were obtained from G. R. Buss except for those known to respond differentially to strains of SMV (cultivars Buffalo, Davis, Kwanggyo, Marshall, Ogden, and Rampage) (4) which were received in 1981 from R. M. Goodman (University of Illinois, Urbana). All tests were conducted in a greenhouse, using conditions and procedures described previously. Within 12–14 days of seeding, when unifoliolate leaves were just fully expanded, plants were inoculated with the virus isolates. When symptoms became apparent, usually within 2–3 wk, the number of symptomatic and healthy plants was recorded and symptom severity was noted.

RESULTS

Reactions of soybean plant introductions and cultivars to four PMV isolates. Several reactions were observed on soybean plant introductions and cultivars grown in field plots that were inoculated with the four PMV isolates (V74S/473, V74S/348-1, V74S/495-1, and V74S/10B-1) (Table 2). The susceptible controls (Essex and PI 229315) and two plant introductions (PI 91733-1 and PI 171427) were infected by all four isolates. Seven plant introductions and the cultivar Peking were resistant to all of the isolates. The six remaining plant introductions and the cultivar Virginia gave various responses. The cultivar Virginia was resistant to isolate V74S/10B-1 but was susceptible to isolates V74S/473, V74S/348-1, and V74S/495-1. Six plant introductions were resistant to V74S/473, V74S/348-1, and V74S/495-1 but were susceptible to V74S/10B-1.

Symptom severity also varied among plant introductions and cultivars inoculated with the same isolate and among the PMV isolates on the same plant introduction or cultivar (Table 2). Any symptoms observed on uninoculated control plants were negative serologically to PMV antiserum.

TABLE 2. Reactions of selected soybean plant introductions and cultivars to four peanut mottle virus (PMV) isolates

PI or cultivar	Virus isolates			
	V74S/473	V74S/348-1	V74S/495-1	V74S/10B-1
PMV-susceptible cultivars or lines				
Essex	S[a]	M	S	M
229315	S	M	S	M
PMV-resistant cultivars or lines				
91733-1	M	M	M	M
171427	M	M	M	M
54606-1	–	–	–	–
157492	–	–	–	–
205089	–	–	–	–
224271	–	–	–	–
235335	–	–	–	–
235340	–	–	–	–
264555	–	–	–	–
Peking	–	–	–	–
Virginia	S	M	S	–
19976-1	–	–	–	M
71506	–	–	–	S
82218	–	–	–	S
159923-1	–	–	–	S
274423	–	–	–	M
398990	–	–	–	M

[a] Designations represent the predominant reactions observed with four repetitions containing 15 plants each, using the following rating scale: S = severe mottle and leaf crinkling, M = mild mottle, and – = no symptoms produced, serological testing by ELISA negative, and no virus recovered.

TABLE 3. Differentiation of 12 peanut mottle virus (PMV) isolates into five strain groups based on symptom expression in four soybean cultivars

PMV strain group designation[a]	PMV isolates[b]	Soybean cultivars			
		Lee 68	Cumberland	Virginia	York
P1	V74S/473 V74S/495-1 V81S/29 V81S/30 V81S/31	S[c]	S	S	–
P2	V79S/33 V74S/73-178 V74S/73-741	S	M	M	–
P3	V79S/20 V74S/348-1	M	M	M	–
P4	V79S/38-2	S	M	–	–
P5	V74S/10B-1	M	–	–	M

[a] Strains were inoculated to the soybean cultivars at least once every 3 mo over a 3-yr period to ensure the reliability of the strain groupings. These tests were conducted at different times of the year to include a wide range of environmental conditions.

[b] The first listed isolate in each strain group was chosen as the type strain of the group for further studies.

[c] S = severe mottle and crinkling, M = mild mottle, and – = no symptoms produced and no virus recovered.

Differentiation of PMV isolates into strain groups. Of the 12 PMV isolates selected for testing, six were derived over time from the original V74S isolate and six were unique isolations from naturally infected soybean plants (Table 1). All of the isolates produced typical necrotic lesions, 2–3 mm in diameter, on Topcrop bean and a strong positive reaction with antiserum to PMV in SDS-immunodiffusion tests (22). Some isolates that did not have both of these properties were not included in this study.

Four soybean cultivars, Lee 68, Virginia, York, and Cumberland, reacted differentially to the PMV isolates (Table 3). In addition, the cultivar Peking was resistant to all isolates. Lee 68 was susceptible to all isolates, but symptom severity varied. Nine isolates caused severe mottling and crinkling, and three isolates caused mild mottling (Table 3). York was susceptible to V74S/10B-1 but resistant to all other isolates. Virginia was susceptible to 10 isolates and Cumberland to 11, with variable symptom severity. The PMV isolates were thus placed in five strain groups designated P1–P5 (Table 3). One isolate of each group was chosen as the type strain for the group and used for further study. Repeated testing of these strain groups on the soybean cultivar series demonstrated the reproductibility of the strain grouping. No variation in reaction among the strains and cultivars was observed, regardless of the environmental conditions at different times of the year that the tests were conducted.

Serological relatedness. In SDS-immunodiffusion tests, no differences were detected among the type strains of each group. Each produced a strong precipitin band that coalesced with bands of other strains. In indirect ELISA with leaf extracts or purified virus preparations, the absorbance values of the five strains were nearly identical and increased as the virus concentration increased (1–1,000 μg/ml).

Reactions of selected soybean cultivars and lines to five PMV strains. A wide range of reaction types was observed after inoculating 41 soybean cultivars and lines with five PMV strains (Table 4). Twenty-seven soybean cultivars including Lee 68 were susceptible to all five PMV strains. Six patterns of variable

TABLE 4. Reactions of selected soybean cultivars and lines to five peanut mottle virus strains

Cultivars or lines	Strain group and virus isolate				
	P1 (V74S/473)	P2 (V79S/33)	P3 (V79S/20)	P4 (V79S/38-2)	P5 (V84S/10B-1)
Class 1-A					
AP-40	S[a]	S	M	S	M
AP-350	S	S	M	S	M
Essex	S	S	M	S	M
Lee 68	S	S	M	S	M
RA-480	S	S	M	S	M
RA-481	S	S	M	S	M
Rampage	S	S	M	S	M
V73-178	S	S	M	S	M
WS550	S	S	M	S	M
Class 1-B					
Bay	S	M	M	S	M
Bedford	S	M	M	S	M
Columbus	S	M	M	S	M
L74-609	S	M	M	S	M
V75-75	S	M	M	S	M
V76-595	S	M	M	S	M
Williams	S	M	M	S	M
Class 1-C					
Miles	S	M	M	M	M
V75-35	S	M	M	M	M
Class 1-D					
Forrest	M	S	M	M	M
Ogden	M	S	M	M	M
WS365	M	S	M	M	M
WS430	M	S	M	M	M
WS430A	M	S	M	M	M
Class 1-E					
Elf	M	M	M	S	M
Class 1-F					
Marshall	M	M	M	M	M
Will	M	M	M	M	M
Williams-79	M	M	M	M	M
Class 2					
Cumberland	S	M	M	M	–
Class 3					
Virginia	S	M	M	–	–
Class 4					
Arksoy	–	–	–	–	M
Dorman	–	–	–	–	M
Shore	–	–	–	–	M
Toano	–	–	–	–	M
York	–	–	–	–	M
Class 5					
Buffalo	–	–	–	–	–
CNS	–	–	–	–	–
Davis	–	–	–	–	–
Haberlandt	–	–	–	–	–
Kwanggyo	–	–	–	–	–
Peking	–	–	–	–	–
Ware	–	–	–	–	–

[a] S = severe mottle and crinkling, M = mild mottle, and – = no symptoms produced, serological testing by ELISA negative, and virus not recovered.

symptom severity were observed; these variations were considered minor, and this group formed one major class reaction (class 1-A to 1-F). Seven cultivars including Peking were resistant to all strains tested (class 5). No symptoms developed, serological testing by ELISA was negative, and infectious virus could not be recovered from any of these plants. The remaining seven cultivars were susceptible to at least one virus strain group. Five of the cultivars, Arksoy, Dorman, Shore, Toano (formerly breeding line V75-183), and York, were susceptible to only PMV strain group P5 and resistant to the other four (class 4). Cumberland reacted in an exactly converse manner and hence was infected by all strain groups except P5 (class 2). Virginia (class 3) was susceptible to strain groups P1, P2, and P3 but resistant to P4 and P5 (Table 4).

DISCUSSION

Our results demonstrate that PMV strains can be differentiated by variable reactions of soybean germ plasm. Twelve isolates, six of which were derived from a single isolate, could be differentiated into five strain groups, designated P1–P5. The members of each group were differentiated by their ability to infect selected soybean cultivars and by the severity of symptoms they induced.

The strain group that contained the original Virginia isolate (V74S/473) was designated P1. Most field isolates collected from the peanut- and soybean-growing areas of Virginia could be placed in this group. In contrast, the PMV strain M-2 found commonly in Georgia, which produces a mild mottle in peanut, would be placed in the strain group P4 because it was reported to cause systemic symptoms in Lee 68 but did not infect the cultivar Virginia (6,14).

Three strain groups, P2, P3 and P4, demonstrate that other strains are found in nature, because they contained isolates collected from soybean growing in the field. Two of the three field isolates (V79S/20 and V79S/38-2) were collected outside the peanut-growing areas of Virginia, at Warsaw and Blacksburg, respectively. Their source is not known, but perhaps they could have resulted from a rare seed transmission event or transmission from an unknown wild host species. In both cases, only a single infected plant was found at the collection site.

The single member of the P5 strain group, V74S/10B-1, was the most strikingly different isolate tested. It infected the cultivar York, which is resistant to the commonly occurring P1 strain group (17,18). If this new PMV strain were to become prevalent in nature, it could result in disease in resistant soybean cultivars such as York, Shore, and others that have the York gene for resistance.

It was of interest that no PMV strain-soybean host combination resulted in a necrotic reaction. The reaction of resistant legumes to viruses in many instances is a hypersensitive response of the host resulting in a necrotic local lesion (15) or a systemic, often lethal necrosis (4,7). The systemic necrotic reaction has been recognized in resistant soybeans infected by certain resistance-breaking strains of SMV (4), but these same cultivars responded to PMV strains with no symptoms and no detectable virus (Davis, Kwanggyo, and Buffalo) or with a systemic mottle and mosaic (Marshall, Ogden, and Rampage). Kiihl and Hartwig (9) noted a systemic necrotic response in Ogden to a strain of SMV. This cultivar, however, was susceptible to all PMV strains tested.

Some PMV-V74S derivatives (V74S/348-1, V74S/10B-1, V74S/73-178, and V74S/73-741) were found to differ from the parent strain (Table 3). We can only speculate that the variants arose after propagation in soybean, a host not known to perpetuate PMV in nature (1,6). The mechanism causing this change is not known, but it could have been caused by any number of factors including selection, random mutation, host-directed mutation, or host passage effects (12,23). Once these strains were isolated, however, they remained stable throughout the study. In one experiment to try to select additional variants, we isolated from more than 150 lesions induced by V74S/473 but failed to detect any subcultures that infected the cultivar York. Additionally, during passage of the PMV isolates through the cultivar Lee 68 for maintenance, no systemic symptoms were induced when the cultures were periodically inoculated to the cultivar York.

By using indirect ELISA and SDS-immunodiffusion with antiserum to one strain (V74S/473), no serological differences were found among the strains. This was not surprising because the original isolates and variants were selected in part for their ability to react strongly with this antiserum in SDS-immunodiffusion tests. Additional testing with antisera to other strains was not pursued. In the early stages of this work, we occasionally obtained variants that resembled PMV biologically but reacted weakly with PMV-V74S antiserum. No further work has been done with these variants.

The implications of this work are that a soybean cultivar recognized as resistant to one strain of PMV may be susceptible to another strain. We suggest strain identity and stability should be monitored in plant breeding research to ensure that the biological properties of the virus strain used for screening soybean germ plasm are known and that the strain is representative of the virus the commercial soybean will ultimately encounter.

It appears that PMV strains may be used to recognize specific resistance genes in soybean. Three genes for resistance to PMV have been described in soybean: *Rpv*, found in the cultivars Arksoy, Dorman, Shore, and York (2); rpv_2, found in Peking (21); and a dominant gene found in the cultivar CNS (3). The CNS gene has been found to be independent of *Rpv* but has not been tested

TABLE 5. Genetics of peanut mottle virus resistance in soybeans

Reaction class	Resistance gene designation	Cultivars with gene	Reactions of soybean cultivars to peanut mottle virus strain groups				
			P1	P2	P3	P4	P5
1	None	Lee 68	S[a]	S	M	S	M
2	Unknown[b]	Cumberland	S	M	M	M	–
3	Unknown	Virginia	S	M	M	–	–
4	*Rpv*	Arksoy	–	–	–	–	M
	Rpv	Dorman	–	–	–	–	M
	Rpv	Shore	–	–	–	–	M
	Rpv	York	–	–	–	–	M
	Rpv	(Toano)[c]	–	–	–	–	M
5	rpv_2	Peking	–	–	–	–	–
	CNS gene	CNS	–	–	–	–	–
	Unknown	Buffalo	–	–	–	–	–
	Unknown	Davis	–	–	–	–	–
	Unknown	Haberlandt	–	–	–	–	–
	Unknown	Kwanggyo	–	–	–	–	–
	Unknown	Ware	–	–	–	–	–

[a] S = severe mottle and crinkling, M = mild mottle, and – = no symptoms produced.
[b] Resistance gene has not been identified.
[c] Hypothesized to be a member of this group on the basis of symptom expression, but genetic studies are lacking.

for allelism with rpv_2 (3,17). The results of this study show that the cultivars with *Rpv* were susceptible to the P5 strain group, whereas CNS was resistant (Table 5). Thus, differential reactions to certain virus strains confirm classical genetic studies demonstrating that the cultivars contain different genes for resistance to PMV. This study also suggests that the Peking gene (rpv_2) and the CNS gene may be allelic, and genetic studies to determine their relationship are in progress. Two additional cultivars, Cumberland and Virginia, also varied in their reactions to the PMV strains, suggesting that additional genes for resistance to PMV may exist in soybeans (Table 5). A genetic analysis of Cumberland and Virginia would be necessary before one could conclude confidently that a gene-for-gene relationship exists in this host-pathogen system and that PMV strains could be used to identify host genes. However, the PMV-soybean gene system appears to be similar to the well-described bean yellow mosaic virus and bean gene-for-gene system (7), except it appears simpler and involves the interactions of fewer genes.

The PMV-soybean interaction may prove to be an effective system for examining the genetic basis for resistance of soybeans to PMV because of the availability of defined virus strains and soybean genotypes with known variable responses, which are apparently inherited in a simple, Mendelian fashion (2,5,17,18,21).

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