Disease Reactions, Resistance, and Viral Antigen Content in Six Legume Species Infected with Eight Isolates of Peanut Mottle Virus

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ABSTRACT

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Disease reactions to eight isolates of peanut mottle virus (PMV) were determined in peanut, pea, bean, cowpea, lima bean, and soybean. No resistance to any of the isolates was found in 70 peanut and seven pea genotypes. Four bean genotypes and four cowpea genotypes were extremely resistant to all eight PMV isolates; the virus was localized in inoculated leaves of bean, and no virus could be detected in uninoculated leaves of resistant cowpea. In soybean, reactions were variable; specific genotypes were susceptible to some PMV isolates and extremely resistant (no symptoms and virus not detectable in uninoculated leaves) to others. A differential host range utilizing four plant species (bean, Chenopodium amaranticolor, peanut, and soybean) provided a means to distinguish the eight PMV isolates. Viral antigen content of all PMV isolates was higher in pea, peanut, and bean than in lima bean, soybean, and cowpea. More viral antigen was detected in all six plant species infected with the necrosis isolate than with any of the other PMV isolates. We conclude that four isolates are distinct enough to be considered strains of PMV: mild (type), chlorotic stunt, necrosis, and necrosis/chlorosis. Disease reactions of the other four isolates are similar to each other and to the mild strain on all hosts except soybean and C. amaranticolor.

In general, peanut mottle virus (PMV) is found wherever peanut (Arachis hypogaea L.) is grown, primarily because it is seed-transmitted (14). It causes diseases in peanut (14) and other important agronomic hosts such as soybean (Glycine max (L.) Merr.) (15) and bean (Phaseolus vulgaris L.) (2). In 1973, loss in peanut in Georgia alone was estimated at \$11.3 million (22). Other than tolerance (17), no significant resistance to PMV has been found in A. hypogaea.

Several variants of PMV, referred to as strains or isolates, have been recovered from naturally infected peanut and soybean (1,4,14,16,26). The first isolate reported caused a mild mottle on peanut and is considered the type strain (M) (14). Among the variants of PMV, mild mottle predominates on peanut worldwide (4,11, 14,26), but the reactions to most of the causal isolates of these mild diseases have not been compared directly to determine their similarity or variability to strain M. In all cases, it appears that the variants are serologically indistinguishable (1,3,27). The variants were classified into isolates or strains on the basis of symptoms on

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peanut (21) and soybean genotypes (1).

In this paper, terminology to define resistance will follow the scheme proposed by Fraser (13). In particular, nonhost resistance (immunity) relates only to an entire plant species that is completely unaffected by a particular virus (no replication and no symptoms). Therefore, when some genotypes within a species are susceptible, we define genotypes with no detectable virus (infectivity and serological tests) in either inoculated or uninoculated leaves as being extremely resistant.

In this study, eight isolates of PMV were used to inoculate peanut and five other legumes. The objectives were to test for resistance, to compare biological reactions and virus concentration, and to establish a small host range that could be used to identify variants of PMV.

MATERIALS AND METHODS

Virus isolates. Eight PMV isolates were obtained from various sources (Table 1), mostly in Georgia. Four isolates were found in commercial peanut fields, two were obtained from other crops, one was derived from a weed, and one was selected in the greenhouse because of an unusual disease reaction on Topcrop bean (Table 1). They were subjected to one single lesion transfer in Topcrop bean and thereafter maintained in pea (*Pisum sativum* L. 'Little Marvel') under greenhouse conditions.

Plant maintenance. Plants were grown in a greenhouse in 10-cm-diameter plastic pots in a mixture of soil:sand:vermiculite: perlite (6:2:1:1, v/v) fumigated with methyl bromide. Plants were fertilized with a 20-20-20 (N-P-K) solution at weekly intervals. Greenhouse temperatures were maintained between 20-28 C (natural light supplemented with 14 hr of illumination with fluorescent lights, 3,000-6,000 lx) in winter and 25-35 C in summer.

Inoculation procedure. Infected leaf tissue was ground in a mortar with 0.01 M potassium phosphate buffer (pH 8.0) containing 0.2% sodium diethyldithiocarbamate, 0.2% sodium bisulfite, and 1% Celite. Plants were inoculated 9–12 days after seeding by rubbing the upper surface of young leaves of test plants with a cheesecloth pad dipped into a solution of sap with virus.

Virus purification and quantitation. Infected leaf tissue of Little Marvel pea was usually harvested 6-10 days after inoculation and purified by the method of Demski et al (10). Because of rapid

Table 1. Origin of eight isolates of peanut mottle virus

Isolate	Abbreviation	Origin and host ^a	Reference		
Arrowleaf	AR	Commercial clover field	Demski ^b		
Chlorotic stunt	CS	Commercial peanut field	Kuhn et al (16)		
Desmodium	DE	Near commercial peanut field	Demski ^b		
India	ĪN	Commercial peanut field	Rajeshwari et al (25)		
Lima bean	LB	Commercial lima bean field	Demski ^b		
Mild ^c	M	Commercial peanut field	Kuhn (14)		
Necrosis	N	Commercial peanut field	Paguio and Kuhn (21)		
Necrosis/chlorosis	N.C	Greenhouse	Kuhn ^d		

^a All isolates except IN were from Georgia.

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^bJ. W. Demski, University of Georgia (unpublished).

^cType strain reported in 1965.

^dC. W. Kuhn (*unpublished*). Isolate NC was derived from a peanut plant inoculated with isolate N and showing typical necrosis symptoms. Subsequent inoculation on Topcrop bean gave local chlorosis and no systemic symptoms.

yellowing and senescence of leaves, plants that were inoculated with the chlorotic stunt isolate (PMV-CS) were harvested about 3 days earlier than those inoculated with the other PMV isolates (AR = arrowleaf, DE = Desmodium, IN = India, LB = lima bean, M = mild, N = necrosis, NC = necrosis/chlorosis). Quantitation of the purified virus was by the spectrophotometric method: E ^{0.1%}_{260nm} = 2.6) (6).

Disease reactions in selected plant species. Disease reactions to seven PMV isolates were evaluated using 70 peanut genotypes simultaneously under the same environmental conditions in the greenhouse so that critical comparisons could be made. An eighth isolate, CS, was found in commercial peanut fields (16) after the 70 peanut genotypes had been evaluated, and tests were confined to only eight peanut genotypes. Peanut seeds of advanced breeding lines and commercial cultivars currently used in the southeastern United States were obtained from peanut breeders. Six plants per genotype were inoculated with each PMV isolate, and three plants per genotype were rubbed with inoculation buffer (uninfected controls). Observations on disease reactions were made from 5 to 30 days after inoculation.

Studies similar to the peanut experiment were conducted with bean, Chenopodium album L. subsp. amaranticolor Coste & Reyn. (=C. amaranticolor), cowpea (Vigna unguiculata (L.) Walp.), lima bean (Phaseolus lunatus L.), pea, and soybean.

ELISA. The relative viral antigen content of seven isolates of PMV in six legume hosts was compared quantitatively in enzyme-linked immunosorbent assays (ELISA). The antiserum was prepared against the necrosis (N) PMV isolate. Antisera to other isolates have been used in other serological studies and no differences among isolates have been noted in either ELISA or immunodiffusion tests (3,27). The double-antibody sandwich procedure described by Clark and Adams (8) was followed. The concentration of PMV antibody protein was 1.25 $\mu g/ml$, and the alkaline phosphataselinked PMV antibody protein was diluted 1/400 after the conjugation step in which $1,000 \mu g$ of each of the reactants were mixed together. Incubation periods were 3 hr at 30 C, overnight at 4 C, and 4 hr at 4 C for the immunoglobulin, the antigen samples, and the enzyme-linked antibody, respectively. Absorbance values (405 nm) were determined with a MICROELISA Mini Reader MR 590 (Dynatech Laboratories, Chantilly, VA).

Leaf tissue from six plant species was selected 14 days after inoculation and consisted of uninoculated new growth of Clay cowpea, Henderson lima bean, Little Marvel pea, Florunner peanut, and Bragg soybean and of inoculated unifoliate leaves of Bountiful bean. Four

replications, each consisting of one pot with three plants, of each genotype were located on a greenhouse bench in a randomized complete block design. Tissue (3-5 g per replication) was macerated in 0.02 M potassium phosphate buffer (pH 7.3) containing 150 mM sodium chloride, 30 mM potassium chloride, 0.05% (v/v) Tween 20, 2% (w/v) polyvinylpyrrolidone $(M_r =$ 40,000), and 10 mM diethyldithiocarbamate (ratio of 1 g of tissue to 9 ml of buffer). Antigen samples were placed in the ELISA plates in a randomized complete block design, four wells (replicates) per treatment.

The same ELISA procedure was used for qualitative tests. Positive results were required to have a reading of at least 0.2 absorbance (405 nm) units and to be at least twofold greater than sap from uninoculated plants. Sometimes, infectivity tests were conducted by grinding leaf tissue in inoculation buffer and inoculating Topcrop bean.

RESULTS

Reactions in peanut. All peanut genotypes became infected when inoculated with the eight PMV isolates, and no resistance was observed. Symptoms varied from mild mottle to mosaic patterns, necrosis, chlorosis, and combinations of mottle, necrosis, and stunting. Each PMV isolate caused a similar reaction in all 70 genotypes. Within a genotype, however, the isolates caused different symptoms, similar to those in Florunner (Table 2). Severity of symptoms depended on the virus isolate. PMV-AR and PMV-DE caused the mildest symptoms, some of which were barely visible on most peanut genotypes. When symptoms were mild or not visible, ELISA tests confirmed the presence of virus. PMV-M and PMV-LB caused moderate mottle on all peanut genotypes, with no reduction in plant height. Severe mottle to mosaic was observed in all

peanut genotypes inoculated with PMV-IN. The most severe symptoms occurred on peanut plants inoculated with PMV-N, PMV-NC, and PMV-CS. The new isolate, CS, caused very strong symptoms: concentric rings, mosaic, and severe stunting on the eight commercial cultivars tested, including Florunner. Peanut plants infected with PMV-N and PMV-NC reacted with foliar and stem necrosis and severe stunting in most genotypes. Initial symptoms developed more slowly for isolates CS and N (7-10 days) than the other isolates (5-7 days).

Reactions in other legumes. In all eight bean genotypes, the PMV isolates caused necrotic lesions, chlorotic spots, or a combination of necrosis and chlorosis on inoculated unifoliate leaves (Table 3). In Bountiful, Bush Blue Lake, Topcrop, and Topnotch Golden Wax, either necrosis or chlorosis spread throughout the inoculated leaves. Uninoculated trifoliolate leaves, however, were symptomless, and virus could not be detected by ELISA or infectivity tests (Table 3); thus, they were considered resistant. Four susceptible cultivars (Genuine Cornfield, Kentucky Wonder, Spartan Half Runner, and Striped Half Runner) reacted systemically to all isolates with chlorosis, necrosis, and frequently death.

No symptoms were noted, and PMV infection (tested by ELISA) could not be detected in uninoculated trifoliolate leaves of four resistant cowpea cultivars: Corona, Early Pinkeye, Iron, and Worthmore (Table 3). Three or more PMV isolates caused a systemic mild mottle in four other cultivars: California Blackeye, Clay, Knuckle Purple Hull, and PI 186465.

Responses to PMV inoculation were more variable in eight soybean genotypes than in other legume species (Table 3). Bragg and Buffalo were susceptible (systemic mosaic) to all eight PMV isolates (Table 3). The other six genotypes were susceptible to some

Table 2. Disease reactions of four plant species to eight isolates of peanut mottle virus

Isolate ^a	Disease reaction ^b					
	Florunner peanut ^c	Topcrop bean	Chenopodium amaranticolor	Soybeand		
AR	MMt	NLL	CL	M/0		
CS	C,St	NLL	CL	0/0		
DE	MMt	NLL	CL	M/M		
IN	Mt	NLL	CL	0/0		
LB	Mt	NLL	ČL	0/ M		
M	Mt	NLL	0	0/0		
N	N	NLL	CL	0/ M		
NC	N,C	$CL^{\mathfrak{e}}$	CL	0/0		

^a AR = arrowleaf, CS = chlorotic stunt, DE = Desmodium, IN = India, LB = lima bean, M = mild, N = necrosis, NC = necrosis/chlorosis.

^bC = chlorosis, CL = chlorotic lesions (no systemic symptom), M = mosaic, Mt = mottle, MMt = mild mottle, NLL = necrotic local lesion (no systemic symptom), N = foliar and stem necrosis, 0 = no symptom, St = stunt.

Systemic reactions were observed numerous times; those listed occurred most frequently.

^dCultivars Davis and Dorman.

^eChlorotic lesions coalesced into general local chlorosis, but no systemic symptoms occurred.

isolates (systemic mosaic) and resistant to others (no detectable infection in uninoculated trifoliolate leaves). Thirtythree percent of the virus isolate/genotype reactions were resistant (Table 3).

Disease reactions caused by the PMV isolates were variable from test to test in eight lima bean cultivars: Can Green, Dixie Butterpea Speckled, Dixie Butterpea White, Florida Butter Pole, Fordhook, Henderson, Jackson Wonder, and Sieva. Necrotic etching occurred frequently on inoculated unifoliate leaves and mottle on uninoculated trifoliolate leaves. Cultivars with no systemic symptoms to infection by specific PMV isolates in an initial test sometimes reacted with mild mottle in subsequent tests.

No resistance to any PMV isolate was observed in the pea cultivars: Alaska, Blue Bantam, Dwarf Gray Sugar, Dwarf Sweet Snap, Green Arrow, Little Marvel, and Sugar Snap. The symptoms in all genotypes were similar to those in Little Marvel (Table 4).

Differential hosts. Four plant species were tested as potential differential hosts for the eight PMV isolates (Table 2). PMV-CS could be differentiated from the other isolates by the reaction it caused on peanut. PMV-N and PMV-NC were the only isolates to cause necrosis on peanut. PMV-NC was the only isolate to

cause local chlorosis on Topcrop bean. PMV-M was the only isolate that did not induce chlorotic lesions in C. amaranticolor. When the PMV-IN and PMV-M isolates were used to inoculate Topcrop bean and C. amaranticolor, each isolate caused about 350 lesions per half leaf on eight Topcrop plants. With the same inocula, PMV-IN caused 472 lesions on 22 half leaves of C. amaranticolor, while PMV-M caused no visible symptoms on the opposite half leaves of the same plants. It was necessary to use two soybean cultivars to differentiate isolates AR, DE, IN, and LB. Isolates AR and DE caused mottle on Davis, while IN and LB caused no symptoms (Table 2). Each pair of isolates could then be differentiated by their reaction on genotype Dorman (Table 2).

Virus quantitation. In general, viral antigen content of isolates N and NC was higher than that of the other five PMV isolates in all six legume hosts (Fig. 1). An exception was the LB isolate in Henderson lima bean. The viral antigen content of AR, DE, IN, LB, and M varied considerably from host to host.

The viral antigen content of all seven PMV isolates was higher in Little Marvel pea than in the other five hosts (Fig. 1). In general, lima bean, soybean, and cowpea had the lowest virus content, while peanut and bean had intermediate levels

Table 3. Systemic disease reactions of three legume species to eight isolates of peanut mottle virus

	Isolate ^a and systemic disease reaction ^b							
Genotype	AR	CS	DE	IN	LB	M	N	NC
Bean								
Bountiful (C) ^c	0	0	0	0	0	0	0	0
Bush Blue Lake (V)	0	0	0	0	0	0	0	0
Genuine Cornfield (V)	M,SN	M,SN	M,SN	M,SN	M,SN	M,SN	M,SN	M,SN
Kentucky Wonder (N)	M,SN	M,SN	M,SN	M,SN	M,SN	M,SN	M,SN	M,SN
Spartan Half Runner (V)	M,SN	M,SN	M,SN	M,SN	M,SN	M,SN	M,SN	M,SN
Striped Half Runner (V)	M,SN	M,SN	M,SN	M,SN	M,SN	M,SN	M,SN	M,SN
Topcrop (N)	0	0	0	0	0	0	0	0
Topnotch Golden Wax (C)	0	0	0	0	0	0	0	0
Cowpea								
California Blackeye	Mt	Mt	Mt	Mt	Mt	0	Mt	Mt
Clay	Mt	Mt	Mt	0	Mt	Mt	Mt	Mt
Corona	0	0	0	0	0	0	0	0
Early Pinkeye	0	0	0	0	0	0	0	0
Iron	0	0	0	0	0	0	0	0
Knuckle Purple Hull	0	Mt	Mt	Mt	0	0	0	0
PI 186465	0	Mt	Mt	Mt	Mt	0	Mt	Mt
Worthmore	0	0	0	0	0	0	0	0
Soybean								
Bragg	Mt	Mt	Mt	Mt	Mt	Mt	Mt	Mt
Buffalo	Mt	Mt	Mt	Μt	Mt	Mt	Mt	Mt
Davis	Mt	0	Mt	0	0	0	0	0
Dorman	0	0	Mt	0	Mt	0	Mt	0
Hardee	Mt	0	0	Mt	Mt	0	Mt	Mt
PI 96983	Mt	0	Mt	Mt	Mt	0	Mt	Mt
Virginia	Mt	Mt	Mt	Mt	Mt	0	Mt	Mt
York	Mt	0	Mt	0	0	0	Mt	0

^a AR = arrowleaf, CS = chlorotic stunt, DE = Desmodium, IN = India, LB = lima bean, M = mild, N = necrosis, NC = necrosis/chlorosis.

of virus.

Yield of purified PMV ranged from 29 to 160 mg/kg of infected pea tissue and was dependent on the PMV isolate (Table 4). The most virions were purified from plants infected with isolates CS and LB and the least with isolates DE and M. In general, virus yield was related to symptom severity on pea. Yield was considerably higher than previously reported (5–30 mg/kg) for purification of PMV by other methods (20,25,28).

DISCUSSION

Similar to findings in a previous study with PMV-M (18), no resistance to several variants of PMV was found in peanut cultivars and advanced breeding lines. Although most or all peanut genotypes reacted similarly to individual isolates of PMV, four general disease reactions to the eight isolates were noted. Mild mottle was induced by PMV-AR and PMV-DE and a slightly stronger mottle by PMV-M, PMV-IN, and PMV-LB. Severe symptoms of necrosis and stunting were induced by PMV-N and PMV-NC and chlorosis and stunting by PMV-CS.

Resistance to PMV has been reported in species of Arachis other than A. hypogaea (12,19). Since PMV-resistant species belonging to the taxonomic section Arachis are cross-compatible with the cultivated species, they represent very valuable germ plasm for interspecific gene transfer (19). For example, PMV could not be recovered from mechanically inoculated A. diogoi plants, thus indicating they are extremely resistant (1).

Table 4. Disease reactions and virus accumulation of eight isolates of peanut mottle virus (PMV) in the propagation host (*Pisum sativum* 'Little Marvel')

	Disease	Virus concentration (mg/kg) ^c			
Isolate ^a	reaction ^b	Range	Mean		
AR	SVC	54-155	101		
CS	SVC	86-154	128		
DE	MVC	32-62	48		
IN	SVC	50-87	72		
LB	SVC	89-160	131		
M	C	29-71	48		
N	SVC	51-107	73		
NC	SVC	52-133	100		

^aAR = arrowleaf, CS = chlorotic stunt, DE = Desmodium, IN = India, LB = lima bean, M = mild, N = necrosis, NC = necrosis/chlorosis.

^bC = chlorosis, MVC = mild veinal chlorosis, SVC = severe veinal chlorosis.

^b0 = No symptoms, M = mosaic, Mt = mottle, SN = systemic necrosis.

^cLocal reaction on inoculated unifoliate leaves of bean: C = chlorotic spots, N = necrotic local lesions, V = variable with virus isolates (some with chlorosis, some with necrosis, some with a mixture of chlorosis and necrosis).

^eEach isolate was purified four or five times, each time from a different group of plants; isolates were not compared directly with regard to time or virus inoculum concentration, however. Infected tissue was harvested 6–10 days after inoculation except that tissue inoculated with PMV-CS was harvested about 3 days earlier. PMV concentration was determined spectrophotometrically after purification.

Other sources of resistance, such as those found in bean, cowpea, and soybean, should not be ignored for use in peanut because of their potential for genetic engineering. In four bean genotypes, the resistant reaction involved localization of the virus in inoculated leaves, regardless of the virus isolate. Provvidenti and Chirco (23) observed a similar phenomenon and later determined that the resistance is conditioned by a single, incompletely dominant gene (24).

Several genotypes of cowpea and soybean reacted with extreme resistance (no symptoms and PMV not detectable by ELISA or infectivity tests). Four cowpea genotypes were resistant to all PMV isolates, while four other genotypes reacted with a mottle or no symptoms, depending on the isolate. Reactions in soybean to the PMV isolates were more variable than those in either bean or cowpea. No soybean genotype was resistant to all isolates, but six of eight were resistant to one or more of the isolates. Determination of the biochemical mechanisms related to PMV and extreme resistance, similar to those reported earlier for PMV in soybean (7,9), will require additional, more in-depth studies.

The lima bean genotypes became infected with all isolates of PMV. During fall months (October, November), many plants had extremely mild symptoms or were symptomless. In the spring, however, mottle symptoms were more obvious and occurred on most plants. The variability of the disease reaction made lima bean undesirable for a differential host of PMV isolates, and resistance to PMV was not evaluated.

Studies by ELISA of the quantitation of viral antigen revealed differences among both plant species and PMV isolates. PMV antigen content of all strains was consistently higher in pea, peanut, and bean than in lima bean, soybean, and cowpea. Isolate N antigen content was higher than that of the other isolates in all plant species, and that of isolate NC was usually second highest. In general, isolate AR produced the lowest viral antigen content. The ELISA quantitation results reaffirm that pea is the best culture host for PMV, regardless of the isolate (14). However, differences among the isolates were noted between the purification (Table 4) and ELISA (Fig. 1) methods of quantitation of virus content in pea tissue. The differences could be due to the lack of a direct comparison of tissue from the same plants for the two procedures or to the possibility that ELISA detected viral antigens not associated with virions.

Because serology with polyclonal antisera is not an effective method to distinguish isolates of PMV (1,3,27), a small differential host range appears to be the best method for identification. We suggest that four plant species—bean, C.

amaranticolor, peanut, and soybeanare probably sufficient. Specific symptoms on peanut, bean, and C. amaranticolor are highly useful diagnostic indicators. Reaction of PMV isolates in C. amaranticolor confirms Kuhn's first report (14) that the PMV type strain M does not induce symptoms in the host. Moreover, our data support other reports (5,27) that some isolates do induce symptoms on this host. Furthermore, we believe that most PMV isolates in nature cause only mild mottle symptoms on peanut and that soybean genotypes can distinguish such isolates. The number of soybean genotypes would depend on how critical a separation of isolates is desired by an investigator. A recent report by Bays et al (1) classified 12

isolates of PMV, found in Virginia, into five strain groups based on reactions in four soybean cultivars.

On the basis of our differential host range, we conclude that isolates CS, M, N, and NC are distinct enough to be classified as strains of PMV. Isolates AR, DE, IN, and LB are similar to isolate M in peanut, but they can be distinguished in soybean genotypes. We believe that isolates AR, DE, IN, LB, and M are distinct variants of PMV but too similar to each other to be considered strains.

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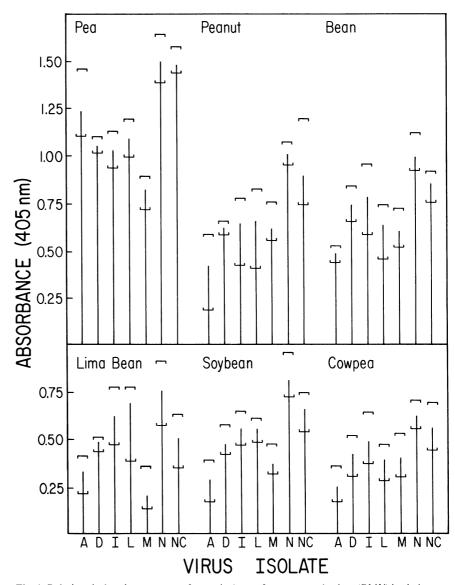


Fig. 1. Relative viral antigen content of seven isolates of peanut mottle virus (PMV) in six legume species, on the basis of enzyme-linked immunosorbent assays (ELISA). There were four replications (one pot with three plants) per treatment. The ELISA conjugate was prepared with PMV-N antiserum. Absorbance readings ranged from 0.01 to 0.10 for sap from uninoculated plants. The two brackets for each vertical line indicate the range of four absorbance readings for each treatment. Host species: Alaska pea, Florunner peanut, Bountiful bean, Henderson lima bean, Bragg soybean, Clay cowpea. Virus isolates: A = arrowleaf, D = Desmodium, I = India, L = lima bean, M = mild mottle, N = necrosis, NC = necrosis/chlorosis.

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