Resistance Responses in Cowpea to Southern Bean Mosaic Virus Based on Virus Accumulation and Symptomatology

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ABSTRACT

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Southern bean mosaic virus accumulation and various other virus-host interactions were evaluated in cowpea. All cowpea lines became infected, but four major categories of disease reaction were observed: local chlorosis followed by systemic severe mosaic and stunting, local chlorosis followed by systemic mottle, no symptoms, and necrotization. Infrequently, one normally symptomless cultivar, Iron, exhibited local chlorosis. Virus accumulation was high in inoculated leaves of genotypes (e.g., California Blackeye) with severe symptoms (susceptible), and it was restricted about 10- to 25-fold in Early Pinkeye, which reacted with a mottle and little or no stunting (moderately resistant). Symptomless lines were divided into three subcategories; virus accumulation was restricted 40- to 50-fold in Iron (resistant), about 500-fold in Worthmore (highly resistant), and 10,000- to 1,000,000-fold in two plant introductions (147562 and 186465) (extremely resistant). Local necrotization occurred in two lines; virus accumulation was restricted over 300-fold in Clay (small local lesions) and was relatively unrestricted in PI 399419 (large local lesions). Systemic necrosis occurred frequently in PI 399419. Virus accumulation was similar in both inoculated and uninoculated tissue of three susceptible control cultivars; however, in all lines with resistance, virus production was less in uninoculated tissue than in inoculated. Also, spread of virus within inoculated leaves was more restricted in resistant lines than in susceptible ones. Plant growth and symptomatology were related to virus production. Both biological and physicochemical properties of virus from cowpea lines with different virus-host interactions were similar, if not indistinguishable.

Cowpea (*Vigna unguiculata* (L.) Walp. subsp. *unguiculata*) is grown on all continents and is an important food crop in tropical and subtropical areas. It is the second most important pulse in tropical Africa and in tropical America, particularly in Venezuela and Brazil. In the United States, cowpea is grown widely in California, the southeastern United States, and Puerto Rico (5). The cowpea strain (CP) of southern bean mosaic virus (SBMV) is one of several viruses that cause important diseases of cowpea (11,22). The virus has a narrow host range; it infects cowpea and a few other leguminous genera and species (21). It is a beetle-transmitted, seedborne virus with small isometric particles (25 nm). Geographic distribution of the virus includes the United States (8), western Africa (14), and India (22).

Resistance to SBMV in cowpea and a variety of disease reactions have been noted previously (10,17). Resistance related to necrotic local lesions is dominant and controlled by a single gene (2). Insusceptibility to SBMV has not been found in cowpea, but several lines are known to be symptomless or to react with mild, nonstunting symptoms (10,17). Objectives of this study were to determine virus production in cowpea lines exhibiting different disease reactions, virus spread in inoculated primary and systemically infected leaves, effect of virus infection on plant growth and seed transmission, and properties of SBMV produced in plants with different disease reactions.

MATERIALS AND METHODS

Virus source and plant manipulation. The cowpea strain of SBMV was maintained in cowpea cultivar California Blackeye. An isolate of strain CP was selected for these studies by serial passage through necrotic local lesions in cowpea cultivar Clay. The reaction of the CP isolate was checked periodically by its necrotization reaction on cowpeas Clay and plant introduction (PI) 399419, and by immunodiffusion tests with four other strains of SBMV (16).

For most studies, the primary leaves of 8- to 10-day-old cowpea seedlings were mechanically inoculated with 100 μg/g of purified virus in 0.01 M potassium phosphate buffer, pH 7.0, containing 1% diatomaceous earth. Two to three plants per pot were grown in 10-cm-diameter plastic pots containing a mixture of soil, sand, and vermiculite (2:1:1, v/v/v) previously treated with methyl bromide. The soil was about pH 6.8, and the plants were fertilized weekly with a complete fertilizer (20-20-20, N-P-K). Greenhouse temperatures ranged from 21 to 35 C in the daytime and from 18 to 24 C at night.

Virus accumulation studies. Inoculated primary leaves were harvested 18–21 days after inoculation, and uninoculated leaves (first two trifoliolates) were harvested at 28–32 days. Pots were randomized on greenhouse benches, and a minimum of 10 leaves or leaflets, each from a different plant, was collected at random and combined for one sample. In some experiments, four replications per treatment were purified and analyzed statistically, using Duncan's multiple range.

Virus purification and quantitation. Infected tissue of each sample (4–9 g) was placed in a 40-ml plastic tube and processed with a Tekmar homogenizer in 10 ml of 0.1 M acetate buffer (pH 4.5) containing 0.02 M sodium bisulfite and 5 ml each of chloroform and butanol. The samples were then centrifuged at 10,000 *g* for 10 min and the aqueous layer was frozen. After thawing, the low-speed centrifugation was repeated, the supernatant was centrifuged at 165,000 *g* for 75 min, and the virus was suspended in 0.01 M potassium phosphate buffer, pH 7.0.

A second cycle (or more) of ultracentrifugation caused a significant loss of virus, particularly for samples with less than 1,000 μg, that resulted in less accurate virus quantitation than the one-cycle purification. The concentration of virus in these partially purified samples was estimated by ultraviolet (UV) spectrophotometry [extinction coefficient = 5.8 $(mg/ml)^{-1}$ cm^{-1} at 260 nm]. The concentration of each sample was reduced by 15 μg/g; this is an average estimate for nonspecific UV-absorbing constituents, which was determined by treating healthy cowpea tissue according to the purification procedure described above.

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When partially purified virus samples contained less than 100 μg/g, they were subjected to sucrose gradient centrifugation, which allowed separation of virus and host material and detection of 1 μg of virus per sample. Concentrated virus preparations (1 ml) were layered on 10–40% sucrose columns and centrifuged for 2 hr at 95,000 *g*. Gradients were analyzed by UV absorbance, and profiles from recorder chart paper were measured with a planimeter to determine virus quantity. The areas under the profiles were correlated with known quantities (absorbance at 254 nm) of highly purified virus. When this procedure failed to detect virus in some samples, the sandwich method of the enzyme-linked immunosorbent assay (ELISA) (4) was used to estimate virus quantity to 10 ng/ml.

Spread within inoculated leaves. Each half leaf of primary leaves of 9-day-old seedlings of California Blackeye, Early Pinkeye, Iron, and Clay was divided into three sections, each parallel to the midrib, with waterproof ink lines. The center section, about 5-mm wide, was rubbed with a glass rod dipped in SBMV inoculum (1 mg/ml) containing 1% diatomaceous earth. At harvesttime (2–3 wk after inoculation), the midrib was removed and the three sections were separated with scissors. Virus quantitation was made using the procedure described above. Three similar tests were conducted.

Inoculum concentration and plant age. Three cultivars (California Blackeye, Early Pinkeye, Iron) were inoculated with three concentrations of purified SBMV: 11, 33, and 100 μg/ml. For young plant tissue, primary leaves of 10-day-old seedlings were inoculated; for older tissue, primary leaves on 30-day-old plants were inoculated. Pots with two plants each were randomized on a greenhouse bench, and new growth was removed weekly to prevent abscission of the inoculated leaves. Virus was purified and quantitated from inoculated leaves only, which were harvested 3 wk after inoculation.

Plant growth. For shoot and root growth experiments, single plants were grown in plastic pots (10 cm diameter) in the greenhouse. A methyl bromide-fumigated 3:1:1:1 (v/v/v/v) mixture of soil:sand:vermiculite:perlite was used. Plants were fertilized weekly with a complete fertilizer (20-20-20,N-P-K). Eight days after planting, 15 plants per line were inoculated with SBMV at a concentration of 170 μg/ml, whereas 15 were left uninoculated. The plants of each treatment were separated into groups of five plants, which were randomized on two greenhouse benches (area of 22 m^2). Three and six weeks after inoculation, plants were harvested, the roots were washed free of the soil mix, and plants were cut into root and shoot portions at the soil line. Dry weights were determined after samples were oven dried at 80 C for 2 days.

Seed transmission. Six cowpea lines were planted in the field and mechanically inoculated with SBMV (100 μg/ml) 3 wk after seeding. Seeds harvested from infected plants were planted in plastic pots (10 cm diameter) in the greenhouse. Plants were observed weekly and those with symptoms were removed from the pots and tested serologically (immunodiffusion) for SBMV. At the end of 4 wk, the newest expanded leaf of numerous symptomless plants of each line was tested by ELISA for SBMV.

Virus properties. Several biological and physicochemical properties of SBMV purified from different cowpea lines were studied using standard, previously described procedures. Serological comparisons were made with 1.0% immunodiffision gels in 0.01 M potassium phosphate buffer (pH 7.0) (16) and by ELISA. Specific infectivity tests used cowpea PI 399419 for half leaf necrotic local lesion assays, 6–12 replications per treatment (9). Banding in Cs_2SO_4 followed the procedure of Hull (7). RNA was isolated by dissociating virions in 2% sodium dodecyl sulfate followed by treatment with phenol:chloroform according to Zimmern's method (25). The RNA's were analyzed by UV absorption after centrifugation on 5–20% sucrose gradients (16).

RESULTS

Disease reactions. The range of disease reactions in cowpea to SBMV was determined by screening about 100 cultivars and plant introductions. Entries were selected on the basis of two previous studies (10,17). Although a continuum of symptoms from none to severe was observed, four categories were relatively easy to discern: local chlorosis followed by systemic mosaic, leaf distortion, and stunt; local chlorosis followed by systemic mild mottle; no symptoms; and necrosis. Infrequently, one genotype (Iron) in the no symptoms category developed faint chlorotic spots on inoculated leaves, particularly during the spring months (March to May). Lines with necrosis were subdivided into two groups, local lesions only and local lesions followed by systemic necrosis. Eleven cowpea lines, representative of the different reactions, were selected for further study (Table 1). During a period of 4 yr, the lines were observed throughout the year in the greenhouse and in the field; the reactions were consistent and the categories, except for the no symptoms category, were clearly distinguishable under all growing conditions.

Time course assays. Virus accumulation in inoculated primary

TABLE 1. Symptoms and virus accumulation in cowpea lines inoculated with southern bean mosaic virus

Cowpea line	Symptoms[c]	Virus accumulation (μg/g)[a] Inoculated leaves[b] Tests (no.)	Range	Average	Uninoculated leaves[b] Tests (no.)	Average	Virus accumulation classification
California Blackeye	C,M,S,D	17	917–1,870	1,362	4	1,201	Control[d]
Knuckle Purple Hull	C,M,S,D	7	1,057–2,340	1,392	4	1,289	Control[d]
Coronet	C,M,S,D	6	900–1,610	1,093	4	1,183	Control[d]
PI 399419[e]	NLL,SN	3	506–658[f]	557	4	...[g]	Variable
Early Pinkeye	C,Mt	7	38–237	136	2	50	Restricted
Iron	None[h]	17	6–91	30	6	8	Highly restricted
Worthmore	None	3	1–6	3	2	<1	Highly restricted
Blue Goose	None	3	1–3	2	2	<1	Highly restricted
Clay	NLL	4	1–6	4	4	<1	Highly restricted
PI 147562	None	6	<0.1	<0.1	2	Det[i]	Extremely restricted
PI 186465	None	6	<0.1	<0.1	2	Det	Extremely restricted

[a] μg of virus per gram of leaf tissue.
[b] Virus purified from inoculated and uninoculated leaves 18–22 and 30–40 days after inoculation, respectively.
[c] C = local chlorosis, D = leaf distortion, M = mosaic, Mt = mild mottle, NLL = necrotic local lesions, S = stunt, SN = systemic necrosis.
[d] These susceptible control plants had the highest level of virus concentration in the study.
[e] At 21 and 24 C, the symptoms and virus accumulation were similar to Clay.
[f] Leaves harvested at 4–8 days because of leaf necrosis and abscission. In three tests virus accumulation was simlar to that in California Blackeye when leaves were harvested at the same time after inoculation.
[g] Leaves became necrotic and frequently dropped from plant within 10 days.
[h] Infrequently, faint chlorotic spots occurred on inoculated primary leaves, but no systemic symptoms developed.
[i] Virus detectable by infectivity test to California Blackeye.

TABLE 2. Lateral spread of southern bean mosaic virus from an inoculated section of half leaves of cowpea cultivars[a] characterized by different levels of resistance

Plant tissue[c]	Virus concentration (μg/g)[b]											
	Test 1				Test 2				Test 3			
	CB	EP	IR	CL	CB	EP	IR	CL	CB	EP	IR	CL
Toward margin	253	19	1	D[d]	540	D	1	D	217	9	N[d]	N
Center, inoculated	947	162	44	6	1,101	67	42	1	357	150	5	1
Toward midvein	537	23	1	0.02	872	2	1	D	264	28	0.02	N

[a] CB = California Blackeye, EP = Early Pinkeye, IR = Iron, CL = Clay.
[b] Virus was purified and quantitated at 21 days after inoculation.
[c] The center of each half leaf was inoculated.
[d] Virus detectable (D) or not detectable (N) by ELISA.

leaves from 5–50 days after inoculation was studied in six cowpea lines representing different classes in Table 1: California Blackeye, Early Pinkeye, Iron, Blue Goose, Clay, and PI 147562. For the first three lines, the virus concentration peaked between 14 and 20 days, similar to a previous report (12) for susceptible cultivar California Blackeye. There was no indication of continued accumulation, presumably virus replication, beyond 20 days, even in the latter three lines, which produced very low quantities of virus.

Virus accumulation in inoculated leaves. In inoculated primary leaves of 8- to 9-day-old seedlings, virus accumulation was high in three cultivars (California Blackeye, Knuckle Purple Hull, Coronet), which had mosaic and stunt symptoms (Table 1). The time course assays demonstrated that virus replication was eventually inhibited in these susceptible control cultivars. Virus accumulation varied from experiment to experiment (range), but there was no difference ($P \leq 0.05$) among the three cultivars. As symptoms became progressively less severe in the various cowpea lines, there was a greater restriction of virus accumulation (Table 1). Compared with the control cultivars, accumulation was restricted about 10-fold in Early Pinkeye, 40- to 500-fold in Iron, about 500- fold in Worthmore, Blue Goose and Clay, and an estimated 10,000-fold in two PI's (186465 and 147562). Although the range of accumulation in Early Pinkeye and Iron overlapped, the two lines were clearly distinct statistically ($P \leq 0.05$) when compared in several individual experiments.

Although Clay reacted to SBMV with small necrotic local lesions, virus accumulation was similar to two lines (Worthmore and Blue Goose), which developed no symptoms. Necrotic local lesions, larger than on Clay, also developed on PI 399419; however, virus accumulation was relatively unrestricted, similar to California Blackeye, from time of inoculation until 4–8 days after inoculation, particularly when inoculated plants were maintained at 25–30 C. At lower temperatures, smaller lesions occurred on PI 399419 and virus accumulation was highly restricted. In order to detect virions in PI's 186465 and 147562, virus had to be purified and concentrated by ultracentrifugation from a minimum of 10 g of infected tissue, layered on sucrose gradients, and evaluated by ultraviolet analysis. We estimate about 10 ng of virus per gram of tissue.

Virus accumulation in uninoculated leaves. Virus accumulation in uninoculated leaves was high in the three control cultivars with severe symptoms (Table 1). Furthermore, the virus concentration was similar to the concentration in inoculated leaves. In all other lines accumulation was less in the uninoculated leaves than in inoculated ones. Even after purification and concentration, virus could not be detected by sucrose density gradient analysis or by ELISA from the PI's in the no symptom category. However, infectivity of concentrated preparations (3–10 g concentrated to 1 ml) was observed when California Blackeye was inoculated. We believe that uninoculated tissue of PI 147562 and PI 186465 contained 1 ng or less of virus per gram of plant tissue. In PI 399419, accumulation was highly dependent on temperature. Very little virus (1 μg/g) was found in uninoculated leaves when plants were incubated at 21 and 24 C. At 28 C, and frequently in the greenhouse, systemic necrosis developed, and these leaves had 50–300 μg of virus per gram of tissue, always less than virus accumulation in California Blackeye.

TABLE 3. Effect of inoculum concentration and plant age on southern bean mosaic virus accumulation in inoculated primary leaves of three cowpea cultivars

Cultivar	Virus accumulation (μg/g)[a]					
	100 μg/ml[b]		33 μg/ml		11 μg/ml	
	10[c]	30[c]	10	30	10	30
California Blackeye	1,983	361	2,405	153	1,995	143
Early Pinkeye	168	36	132	28	90	14
Iron	77	5	32	3	33	3

[a] Virus was purified and quantitated from inoculated leaves at 14 days after inoculation.
[b] Inoculum concentration.
[c] Primary leaves were inoculated at 10 and 30 days after planting.

Spread within inoculated leaves. Spread of SBMV in inoculated leaves was studied in four cowpea cultivars with different types of virus-host reaction. For the center, inoculated portion of half leaves, the relative accumulation in the four cultivars was similar to their rankings in Table 1 (Table 2). In general, virus accumulation was greater toward the midvein than toward the leaf margin. Furthermore, the relative amount of spread and accumulation was highest in California Blackeye. In the more resistant cultivars, there was a greater relative difference between the inoculated and uninoculated portions of the leaf than in California Blackeye. In two of three tests, virus moved from the necrotic local lesion area of Clay into uninoculated symptomless leaf portions.

Inoculum concentration and plant age. Reducing the level of the usual inoculum concentration (100 μg/ml) three- and ninefold decreased virus accumulation in Early Pinkeye and Iron but not in the susceptible control California Blackeye (Table 3). Increasing the age of leaves to be inoculated from 10 to 30 days reduced virus concentration in all three cultivars. In general, age of leaves had a greater effect (79–94% reduction in older leaves) on virus accumulation than inoculum concentration (0–58% reduction with the lowest inoculum concentration). Virus accumulation levels were different ($P \leq 0.05$) in California Blackeye, Early Pinkeye, and Iron at each inoculum concentration and at each plant age.

Plant growth. SBMV caused a significant reduction in both shoot and root growth of California Blackeye and PI 399419 at 21 and 42 days after inoculation (Table 4). For Early Pinkeye, growth reduction was observed at 21 days but not 42. No growth reduction occurred with Iron, Clay, and PI 147562. A second experiment with only three cultivars confirmed the shoot growth reduction in California Blackeye and no reduction in Iron; however, no shoot growth reduction was detected with Early Pinkeye.

Seed transmission. SBMV seed transmission occurred in only three of six cowpea lines (Table 5). Furthermore, the frequency of transmission was greater in California Blackeye than in Knuckle Purple Hull or Coronet.

Virus properties. Virus from California Blackeye, Early Pinkeye, and Iron was highly purified through four cycles of ultracentrifugation. Direct comparison of virus from these hosts with different virus-host interactions showed no differences in several properties. The UV absorption curves of virions were identical. Virions in Cs_2SO_4 occurred primarily as one peak (more

than 90%), similar to the light one as reported by Hull (7). No spurs developed in immunodiffusion plates when SBMV-CP antiserum was placed in a center well, and virus from all three hosts could be detected at 3 ng/ml by ELISA but not at 0.6 ng/ml. Specific infectivity was similar when virions from the three sources were equalized at 0.17 μg/ml. When RNA was extracted from virions from the three cultivars, the major peaks sedimented similar distances in sucrose gradients, and similar quantities of low-molecular-weight RNA species were observed (16,18). Virus from the three sources produced similar and expected reactions on the following cowpea lines: California Blackeye, Clay, Iron, Worthmore, and PI 186465.

DISCUSSION

Plant virus disease reactions and virus concentration may or may not be directly correlated. Skaria et al (23) report clear associations between content of barley yellow dwarf virus and symptomatic resistance in barley and oats but not necessarily in wheat. In cowpea, the concentration of cowpea chlorotic mottle virus is more in some genotypes with very mild symptoms than ones with bright chlorosis (13). In the SBMV-cowpea interaction, there was a close correlation between disease reactions and virus accumulation; levels of resistance could thus be based on virus accumulation. Genotypes with severe symptoms, including reduced plant growth, and high concentrations of virus (1,000 μg/g or more) were considered susceptible. Virus accumulation ceased in susceptible cowpeas (also resistant ones) between 14 and 20 days after inoculation. They had about 10–25 times more virus than cultivar Early Pinkeye, rated moderately resistant, which had mild, nonstunting symptoms. No intermediate group between susceptible and moderately resistant was observed in these studies.

Rigorous quantitative studies of virus accumulation established that symptomless genotypes do not all belong to one disease reaction group, particularly with regard to virus accumulation. Three distinct groups were noted with the SBMV-cowpea reactions. Cultivar Iron (resistant) had less virus (4–6 times) than Early Pinkeye, but about 10 times more than Worthmore and Blue Goose (highly resistant). Extreme resistance was noted in two PI's, which appeared to have 100 ng or less of virus per gram of tissue.

Cowpea genotypes responded to SBMV infection with two types of necrotization. In cultivar Clay, lesions are small and necrotization is controlled by one dominant gene (2); however, virus accumulation was similar to the low amount in highly resistant cultivars with no symptoms. From 20 to 24 C, the reaction in PI 399419 was similar to Clay. However, above 24 C, including both greenhouse and field conditions, virus accumulation in this PI was similar to susceptible cultivars and necrosis developed in all tissues, frequently killing the plants. It appears likely that the difference between Clay and PI 399419 is a temperature-related host factor that controls viral replication or spread or both.

Spread of SBMV occurred in cowpea, regardless of the type of virus-host interaction. Both lateral spread within inoculated leaves and systemic spread from inoculated to uninoculated leaves were evident in genotypes with leaf discoloration, ones with necrotic lesions, and ones with no symptoms. Virus was not restricted to the immediate area of necrotic lesions, even though the reaction in cowpea cultivar Clay appears to be similar to a number of virus-host combinations for which movement restriction has been reported (15,20). Furthermore, the extremely low virus concentration in PI's 147562 and 186465 is similar to previously reported subliminal infections (1,3,24); however, SBMV does not remain localized. It may be possible that the highly infectious nature of SBMV and its ease of purification may make it more easily detectable than some other viruses, or spread of SBMV may occur by a different mechanism than some other viruses, for example direct movement from xylem to parenchyma cells (19).

On the basis of virus accumulation, SBMV spread was more restricted in resistant genotypes than susceptible ones. Virus concentration was similar, or slightly less, in uninoculated tissue of susceptible lines than in inoculated tissue. For resistant lines, several times less virus was produced in uninoculated tissue. In another study with SBMV (6), lateral spread was different even for susceptible cowpea genotypes, and the difference appeared to be correlated with levels of virus incidence under field conditions where transmission probably was caused by beetles.

The frequency of seed transmission of SBMV in cowpea was lower in this study than in previous reports (8,17). No transmission occurred in the resistant genotypes, and the transmission level varied among the three susceptible cultivars. This may mean that some virus-host interaction, such as internal spread, other than virus replication may be responsible for seed transmission.

Results of several tests concerning inoculum concentration, age of plants at time of inoculation, and physicochemical and biological properties of virus purified from susceptible and resistant plants appeared to be relatively insignificant in elucidating the mechanism of resistance in cowpea to SBMV.

Previous studies (2,11) reported the local necrotization type of resistance in cowpea to SBMV. The current studies have established four degrees of resistance in cowpea associated with low levels of virus accumulation and nonnecrotic disease reactions. Virus production in one nonnecrotic genotype class (highly resistant) was similar to that in cultivar Clay, the most resistant necrotic genotype. In the extremely resistant, nonnecrotic genotype class, virus accumulation is even less than in Clay. From a horticultural standpoint, the nonnecrotic types of resistance (highly and extremely) may be more desirable than the local necrotization type of resistance which can develop into a systemic disease reaction, sometimes necrotic, under field conditions in Georgia (6) and Texas (18).

TABLE 4. Effect of southern bean mosaic virus on shoot and root growth of six cowpea lines[a]

Cowpea line	Time after inoculation[b] (wk)	Dry weight (g)			
		Shoots		Roots	
		U[c]	I	U	I
California Blackeye	3	1.43	0.92[d]	0.68	0.49[d]
	6	3.38	2.50[d]	1.25	1.02[d]
Early Pinkeye	3	1.47	1.28[d]	0.60	0.50[d]
	6	2.79	2.93	1.02	1.13
Iron	3	0.91	1.02	0.53	0.53
	6	1.96	1.71	1.07	1.00
Clay	3	0.88	0.87	0.64	0.69
	6	1.64	1.80	1.34	1.27
PI 147562	3	0.54	0.56	0.32	0.40
	6	0.84	1.13	0.70	0.84
PI 399419	3	1.29	1.04[d]	0.68	0.59[d]
	6	2.81	1.88[d]	1.35	1.05[d]

[a] Plants grown in pots (10 cm diameter) in the greenhouse.
[b] Plants harvested and processed at 3 and 6 wk after inoculation.
[c] U = uninoculated, I = inoculated.
[d] Significant growth reduction ($P = 0.05$) according to least significance difference test.

TABLE 5. Seed transmission of southern bean mosaic virus in cowpea lines with different levels of resistance

Cowpea line	Virus accumulation[a]	Seed transmission	
		Number[b,c]	Percent
California Blackeye	High level	33/595	5.5
Knuckle Purple Hull	High level	17/450	1.5
Coronet	High level	1/195	0.5
Early Pinkeye	Restricted	0/444	0
Iron	Highly restricted	0/425	0
PI 399419	Variable	0/490	0

[a] See Table 1.
[b] Number of plants infected per number of plants observed.
[c] ELISA detected no infection in the following number of symptomless plants: California Blackeye-37, Knuckle Purple Hull-50, Coronet-96, Early Pinkeye-359, Iron-425, and PI 399419-50.

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