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Resistance

Differential Field Infection of Cowpea Genotypes by Southern Bean Mosaic Virus

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ABSTRACT

Hobbs, H. A., and Kuhn, C. W. 1987. Differential field infection of cowpea genotypes by southern bean mosaic virus. Phytopathology 77:136-139.

Natural spread of the cowpea strain of southern bean mosaic virus (SBMV) from infected cowpea to several cowpea genotypes, including susceptible ones and those with different levels of resistance, was studied under field conditions. Little spread (0–2%) occurred in three lines with different levels of resistance (resistance based on virus concentration and symptomatology). Disease incidence was about twofold higher in the susceptible cultivar California Blackeye than in two other cultivars, Knuckle Purple Hull and Coronet, believed to be similarly susceptible. Both older plant age at time of inoculation and lower inoculum concentration caused decreases in virus accumulation and infectibility (proportion of plants becoming infected after mechanical inoculation) among susceptible lines and between susceptible and resistant lines. Inoculation by needle pricking showed similar levels of infectibility among the susceptible cultivars but a higher virus concentration in California Blackeye. Lateral spread and virus accumulation into an uninoculated leaf portion were greater in California Blackeye than in Knuckle Purple Hull and Coronet. We conclude that virus concentration and spread within plants contribute to differences in field incidence of SBMV because of effect on virus acquisition by beetles. Evidence is also presented showing that susceptible Coronet and resistant Early Pinkeye are more difficult to infect than susceptible California Blackeye and Knuckle Purple Hull.

Resistance in cowpea (*Vigna unguiculata* (L.) Walp. subsp. *unguiculata*) to the cowpea strain of southern bean mosaic virus (SBMV) has been reported (12). In addition to the resistance related to necrotic local lesions (2), resistance in hosts with nonnecrotic reactions has been associated with reduced virus concentration (11), and host genes controlling virus concentration have been identified (7).

The purpose of this study was to compare field transmission of SBMV in susceptible and nonnecrotic resistant cowpea lines and to explore possible reasons for differences in field incidence involving these virus-host interactions. SBMV is efficiently transmitted by the bean leaf beetle, *Cerotoma trifurcata* Forst., from cowpea to cowpea (14,15). Individual beetles can transmit the virus after a 24-hr acquisition feeding and can continue for at least 5 days (14). Preliminary results (8) showed a very low incidence of SBMV in resistant cowpeas and differential levels of incidence among cowpea cultivars that were believed to be equally susceptible.

MATERIALS AND METHODS

Field transmission, 1982. Six cowpea genotypes were used in the experiment: California Blackeye, Coronet, and Knuckle Purple Hull (all susceptible to SBMV); Early Pinkeye (moderately resistant); Iron (resistant); and PI 186465 (extremely resistant).

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Classification of genotypes with respect to resistance to SBMV was based on virus accumulation (11).

The experimental plot was located at the University of Georgia Plant Sciences Farm, Athens. The overall plot consisted of a central row of the susceptible cultivar California Blackeye plus four blocks (replications) of the six cowpea lines. Two blocks were planted on each side of the central row, each block containing three rows planted 2, 4, and 6 m from the central row. Each row had six (each genotype) 3-m subrows separated by 1.2-m alleys. Each subrow had 7–10 plants (averaging eight) spaced at 0.3-m intervals. For each cowpea line, there were three subplots/block (one subplot at each distance from the central row) and therefore 12 subplots with about 100 plants total. The six cowpea lines were randomized within each row. Border rows of 1.5 m were planted at the ends of the plot.

One month after seeding, the central row was inoculated with SBMV. Infected California Blackeye leaf tissue was ground in 0.01 M potassium phosphate buffer (pH 7.0) containing 1% Celite and applied with cheesecloth pads to the youngest trifoliolate leaves.

Field transmission, 1983. Procedures and experimental design were similar to the 1982 field experiment, with two main differences: only four cowpea lines were used (California Blackeye, Knuckle Purple Hull, Coronet, and Early Pinkeye) and four distances (2, 4, 6, and 8 m) from the central row were used instead of three.

Virus incidence. Incidence (percentage of uninoculated plants that became infected) of SBMV-infected plants in the field was determined by enzyme-linked immunosorbent assays (ELISA) (4). One month after mechanical inoculation of the central row, a single leaf or leaflet of the youngest expanded leaves was collected from all plants in the field, except those in the central row. Each sample was ground in 3–5 ml of PBS-Tween-PVP (0.02 M potassium phosphate buffer [pH 7.3], 0.15 M NaCl, 0.003 M KCl; 0.05% Tween 20; 2% polyvinylpyrrolidone). Antibody coating protein and enzyme-linked conjugates were diluted 1/4,000 and 1/800 for the susceptible and resistant cowpea lines, respectively. Furthermore, because of the high level of reactivity to the SBMV conjugate, sap from uninoculated greenhouse plants was placed in every other well in ELISA plates with sap from susceptible plants. The absorbance of substrate reactions was determined at 405 nm with a Dynatech Microelisa Minireader. Plants were considered infected when the absorbance reading was at least two times higher than readings for uninoculated plants.

Virus purification and quantification. Virus purification procedures were similar in all experiments. In experiments with 5 g or less of leaf tissue, tissue was extracted in 10 ml of 0.1 M sodium acetate buffer (pH 4.5) containing 0.02 M sodium bisulfite, 5 ml of chloroform, and 5 ml of butanol, using a Tekmar Tissumizer. Larger tissue samples were extracted in acetate buffer with sodium bisulfite, chloroform, and butanol (one volume of each per gram of tissue) using a Virtis homogenizer. Additional steps in SBMV purification have been described previously (11) and include clarification by low-speed centrifugation and freezing and one or more cycles of ultracentrifugation.

Quantitative procedures to analyze a range of virus concentrations from 1 to more than 1,000 μg/g of tissue were developed previously (11). Virus samples with more than 500 μg were measured spectrophotometrically, and smaller samples were analyzed by ultraviolet optics after centrifugation of the virus into sucrose gradients.

Needle-pricking experiment. A needle-pricking experiment was designed to compare infectibility and virus accumulation in the susceptible cultivars infected by puncturing holes in leaves. Plants for this and the following two experiments were maintained in the greenhouse in a methyl bromide-fumigated mixture of soil:sand:vermiculite:perlite (3:1:1:1, v/v). Plants grown in 10-cm plastic pots were fertilized weekly with a 20-20-20 (N-P-K) solution. Greenhouse temperatures ranged from 20 to 30 C in winter and from 25 to 35 C in summer.

Four infected leaves from California Blackeye were placed together and held over the surface of each primary leaf to be inoculated. A dissecting needle was used to puncture the infected leaves and then the primary leaf of the test plant. Three punctures were made per one-half leaf of the test plants. Thirty plants were inoculated per cultivar at each of two plant ages, 8 and 14 days after seeding. Inoculated leaves only from plants showing systemic symptoms were harvested at 12 and 18 days after inoculation for the 8- and 14-day-old groups, respectively, and virus was extracted and quantified. One leaf each from five plants, randomly selected, was used per replication, with four replications per cultivar.

Inoculum concentration and plant age. In the first experiment, the first trifoliolate leaf above the primary leaves of plants 20 and 30 days old were inoculated with purified SBMV (0.0001, 0.01, 1, and 100 μg/ml) in 0.01 M potassium phosphate buffer (pH 7.0) containing 1% Celite. Fifteen plants per inoculum concentration per plant age of four cultivars (California Blackeye, Knuckle Purple Hull, Coronet, and Early Pinkeye) were rubbed with a cheesecloth pad. Infectibility (percentage of infection after plants inoculated mechanically) was determined by observing symptoms 4 wk after inoculation.

In a second experiment, primary leaves of California Blackeye, Knuckle Purple Hull, and Coronet plants of two ages, 10 and 30 days after seeding, were mechanically inoculated with SBMV at three concentrations (0.1, 3.3, and 100 μg/ml). There were two plants per pot, with 72 pots (three cultivars × two plant ages × three inoculum concentrations × four replications) arranged randomly on a greenhouse bench. Virus concentration was determined from four inoculated leaves per replication.

Lateral virus movement and replication. Primary leaves of 13-day-old seedlings of California Blackeye, Knuckle Purple Hull, and Coronet were marked with waterproof ink lines extending halfway between the midrib and the outer margin of the leaves. The outer portion of each leaf was inoculated with a cotton-tipped swab dipped in SBMV inoculum (1,000 μg/ml in 0.01 M potassium phosphate buffer [pH 7.0] containing 1% Celite). Twenty days after inoculation, leaves were cut and divided into inoculated outer and uninoculated inner portions, and virus concentration was determined. Two to four replications with 5–20 leaves per replication were used in test 1 and four replications with eight leaves per replication in test 2.

RESULTS

Field transmission studies. In 1982, all three resistant lines (Early Pinkeye, Iron, and PI 186465) had lower incidences of SBMV than any of the susceptible cultivars. Incidences among the three resistant lines did not differ. In both 1982 and 1983, California Blackeye had a higher SBMV incidence in the field than the other two susceptible cultivars, Knuckle Purple Hull and Coronet (Table 1). Virus incidence in Knuckle Purple Hull and Coronet did not differ. In 1983, Early Pinkeye again had a lower SBMV incidence than any of the susceptible cultivars. Distance from the source of inoculum had no effect on SBMV incidence in any cowpea line in either 1982 or 1983 (data not shown).

TABLE 1. Natural transmission of southern bean mosaic virus (SBMV) to cowpea genotypes in the field[x]

Cultivar	Resistance type[y]	Virus incidence (%)[z] 1982	1983
California Blackeye	Susceptible	86 a	75 a
Knuckle Purple Hull	Susceptible	41 b	31 b
Coronet	Susceptible	30 b	39 b
Early Pinkeye	Moderately resistant	2 c	2 c
Iron	Resistant	0 c	···
PI 186465	Extremely resistant	2 c	···

[x] California Blackeye in center row of experimental plot was mechanically inoculated with SBMV 30 days before test plants were analyzed for presence of SBMV by ELISA.

[y] Classified by virus accumulation (11).

[z] Means of four replications. Statistical analysis performed on arc sine-square root transformed data. Values in a column followed by same letter are not statistically different ($P = 0.05$) according to Duncan's new multiple range test.

Leaf mosaic and distortion symptoms were obvious on California Blackeye, Knuckle Purple Hull, and Coronet plants in the field, and a close relationship was noted between obviously diseased California Blackeye plants and the serology tests. However, 25–50% of the Knuckle Purple Hull and Coronet plants with positive ELISA readings did not have symptoms at 30 days after the central row in the plot was inoculated. Symptoms did develop later on Knuckle Purple Hull and Coronet plants and were similar to those on California Blackeye plants. Because no symptoms were observed on Early Pinkeye, Iron, and PI 186465 in the field, infected plants were identified by ELISA.

The bean leaf beetle was the most common of the beetles (presumably vectors of SBMV) found in plots in 1982 and 1983. The spotted cucumber beetle, *Diabrotica undecimpunctata howardi* Barber, was seen occasionally.

Needle-pricking experiment. Infectibility of the three susceptible cultivars by needle pricking was similar (Table 2). When 8-day-old seedlings were inoculated, virus accumulation also was similar for the three cultivars (Table 2). When plants were slightly older (14 days) at the time of inoculation, virus accumulation was four to eight times greater in California Blackeye than in Knuckle Purple Hull and Coronet.

Inoculum concentration and plant age. In the first experiment, infectibility was similar for California Blackeye and Knuckle Purple Hull, regardless of inoculum concentration or plant age (Fig. 1). Fewer plants of Coronet and Early Pinkeye became infected at lower inoculum concentrations and when older plants were inoculated, however. For example, in older plants inoculated with 0.01 μg/ml, all California Blackeye and Knuckle Purple Hull plants became infected, whereas only 30% of Coronet plants and no Early Pinkeye plants became infected.

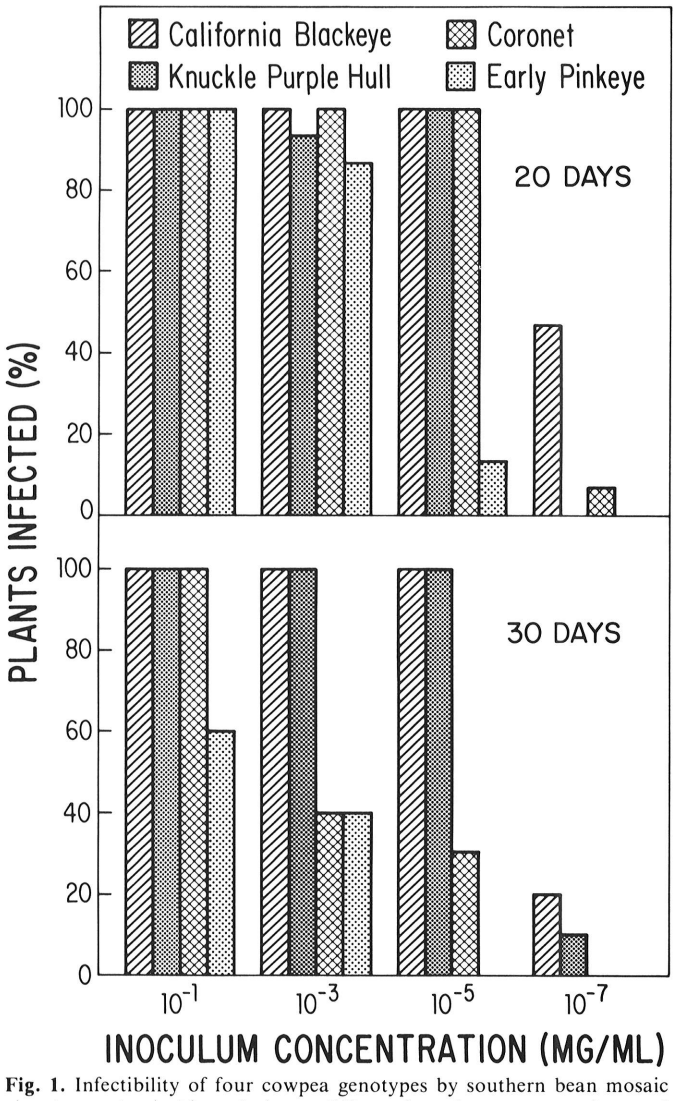

Fig. 1. Infectibility of four cowpea genotypes by southern bean mosaic virus by mechanical inoculation at different inoculum concentrations and different age of plants at time of inoculation (20 and 30 days after seeding) (15 plants/treatment).

In experiment two, both inoculum concentration and plant age at time of inoculation affected virus concentration in three cultivars. More virus was produced in plants inoculated with high virus concentrations and in young plants (Table 3). Differences in virus concentration among the three susceptible cultivars were also observed (Table 3), with the largest differences occurring at low concentrations of inoculum and usually in older plants. The most virus was produced in California Blackeye. Knuckle Purple Hull consistently had more virus than Coronet, but a statistical difference was noted in only one of six comparisons.

Lateral spread and replication of virus. More virus accumulated in inoculated portions of cowpea leaves than in uninoculated portions (Table 4). Some differences in virus concentration were

TABLE 2. Southern bean mosaic virus infection and accumulation in three susceptible cultivars inoculated by needle pricking[x]

Cultivar	No. of plants (infected/inoculated)		Virus accumulation (μg/g)	
	8 days[y]	14 days	8 days	14 days
California Blackeye	27/28	30/30	109 a[z]	52 a
Knuckle Purple Hull	27/28	26/29	70 a	6 b
Coronet	26/27	27/30	83 a	13 b

[x] A dissecting needle was passed through detached infected leaves to puncture primary leaf of test plant. Virus was extracted and quantified from inoculated leaves.
[y] Age of seedlings at time of inoculation.
[z] Values in a column followed by the same letter are not statistically different ($P = 0.05$) according to Duncan's new multiple range test.

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

Cultivar	Virus accumulation (μg/g)[x]					
	100 μg/ml[y]		3.3 μg/ml		0.1 μg/ml	
	10 days[z]	30 days	10 days	30 days	10 days	30 days
California Blackeye	1,558 a	1,125 a	1,045 a	513 a	161 a	237 a
Knuckle Purple Hull	1,207 b	1,125 a	830 a	337 a	42 b	62 b
Coronet	821 b	835 a	176 b	298 a	30 b	16 b

[x] Virus was purified and quantified from inoculated leaves 14 days after inoculation (average of four replications with two plants per replication). Values in a column followed by same letter are not statistically different ($P = 0.05$) according to Duncan's new multiple range test.
[y] Inoculum concentration.
[z] Plant age at time of inoculation of primary leaves.

TABLE 4. Lateral movement and replication of southern bean mosaic virus from inoculated (I) to uninoculated (U) areas of leaves in three susceptible cultivars[y]

Cultivar	Virus accumulation (μg/g)[z]					
	Test 1			Test 2		
	I	U	Ratio U/I	I	U	Ratio U/I
California Blackeye	1,110 a	270 a	0.243 a	2,363 b	1,084 a	0.459 a
Knuckle Purple Hull	715 b	96 b	0.134 b	2,737 a	875 a	0.324 b
Coronet	531 b	26 c	0.049 c	2,412 b	324 b	0.132 c

[y] Twenty days after outer portions of primary leaves were rubbed with a cotton-tipped swab dipped in inoculum (1,000 μg/ml), leaves were divided into inoculated outer and uninoculated inner portions.
[z] Test 1: two to four replications, each with 5–20 leaves; test 2: four replications, each with eight leaves. Values in a column followed by same letter are not statistically different ($P = 0.05$) according to Duncan's new multiple range test.

observed among the three susceptible cultivars (California Blackeye, Knuckle Purple Hull, and Coronet) in both inoculated and uninoculated leaf sections. In general, California Blackeye had the highest concentration and Coronet the lowest. In both tests (Table 4), the ratio of virus in inoculated portions of leaves to that in uninoculated portions was different for the three cultivars. Again, California Blackeye had the highest ratio and Coronet the lowest. The relative values of the uninoculated to inoculated ratios among the three cultivars were similar regardless of the amount of virus produced in the inoculated sections of leaves (Table 4).

DISCUSSION

Cowpea resistance to SBMV characterized under greenhouse/laboratory conditions proved to be highly effective under field conditions (11). Early Pinkeye, Iron, and PI 186465 represent three levels of resistance to SBMV on the basis of disease reaction and virus concentration. All three genotypes had similarly low virus incidence in the field, with incidences 15–43 times lower than those in susceptible cultivars. Surprisingly, differential levels of SBMV incidence were found in three cowpea cultivars believed to be similarly susceptible (11). Incidence was about twofold greater in California Blackeye than in Knuckle Purple Hull and Coronet 1 mo after a source of inoculum was available.

The differential field infection of susceptible cowpea genotypes by SBMV is significant for two reasons: 1) a dilatory resistance (3) in susceptible cultivars may be acceptable for commercial use and 2) new factors involved in virus-host interactions and host resistance to viruses may be revealed. In general, delaying the onset of infection or reducing the rate of virus spread in the field will result in a lower virus incidence at harvest and presumably in a higher yield (6). Field spread of SBMV was less in the susceptible cultivars Knuckle Purple Hull and Coronet than in California Blackeye during the early part of the growing season, but more studies are needed to determine if this delay represents a practical and usable type of resistance.

Browning et al (3) have reviewed how plant hosts can vary in levels of virus concentration and consequently in ability to serve as virus acquisition sources for vectors. Jansen and Staples (9) found that the bean leaf beetle could retain the ability to transmit cowpea mosaic virus longer if the acquisition source was cowpea rather than soybean. They speculated that virus titer was higher in cowpea than in soybean. Evidence supporting such a hypothesis was presented by Kopek and Scott (10). The Mexican bean beetle, *Epilachna varivestis* Mulsant, and the bean leaf beetle retained the ability to transmit SBMV (bean strain) to bean longer after feeding on leaf segments dipped in 10 mg of virus per milliliter than on segments dipped in 1 mg per milliliter. Furthermore, more SBMV occurred in the regurgitant of beetles fed on the higher virus concentration and transmission levels could be associated with the amount of virus in the regurgitant. For beetle-transmitted viruses in general, the amount of tissue consumed (presumably also the amount of virus) in acquisition feeding affects retention of the ability to transmit over time (5).

We believe host factors affecting SBMV replication and internal spread were at least partially responsible for the differences in field incidence that occurred among the susceptible cowpea cultivars. Four studies that compared virus accumulation in three cowpea genotypes support this contention: plant age, inoculum concentration, needle-pricking inoculation, and lateral virus movement into uninoculated leaf tissue. In all four cases, virus accumulation was greater in California Blackeye than in Knuckle Purple Hull and Coronet, and the latter two cultivars had a twofold lower incidence of virus in the field. The more quickly the virus moves to all parts of a plant and the faster it accumulates, the more likely a beetle will acquire and transmit the virus.

It is tempting to speculate that Knuckle Purple Hull and Coronet can inhibit internal spread of SBMV in some manner. In the study in which California Blackeye, Knuckle Purple Hull, and Coronet were determined to be similarly susceptible (11), conditions for inoculation and infectivity were optimal: very high inoculum concentration and thorough, repeated inoculum coverage of the leaf surface. Differences in virus concentration among cultivars were greatest when conditions were least optimal, such as older plants, low inoculum concentration, and required spread of virus into uninoculated leaf tissue for concentration evaluation. Less-than-optimal conditions should exist under field conditions when beetles feed on a limited amount of plant leaf tissue.

The suggestion that differences in SBMV incidence in the field may have been mostly due to differences in the cultivars as virus acquisition sources does not mean that other host factors could not have played a significant role. Cowpea genotypes could have varied in resistance to virus vectors, and that was not considered in this study. It should be noted that cowpea preference by the beetle *Cerotoma ruficornis rogersi* Oliver has been reported (13). Furthermore, resistance to virus inoculation (infectibility) (1) was observed for Coronet (susceptible) and Early Pinkeye (resistant). Achieving 100% infection of these two cultivars by mechanical inoculation required 100- to 10,000-fold higher inoculum concentrations than for the susceptible cultivars California Blackeye and Knuckle Purple Hull. This represents a new type of resistance in cowpea to SBMV. We do not think infectibility alone can account for the differential reactions among the susceptible cultivars, however, because infectibility was similar for California Blackeye and Knuckle Purple Hull and field incidence differed significantly.

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