Strains of Soybean Mosaic Virus: Classification Based on Virulence in Resistant Soybean Cultivars

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ABSTRACT

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Ninety-eight isolates of soybean mosaic virus (SMV) from seeds in the USDA soybean germplasm collections were classified into seven strains based on disease reactions of inoculated differential soybean cultivars. Two susceptible soybean cultivars (Clark and Rampage) and six putatively resistant cultivars (Buffalo, Davis, Kwanggyo, Marshall, Ogden, and York) were used. The results showed differences in virulence among SMV strains and in the susceptibility and reactions of soybean cultivars to these strains. Cultivars resistant to less virulent strains in most cases exhibited severe necrotic symptoms when inoculated with more virulent strains. All SMV strains tested caused infection and typical mosaic symptoms in cultivars Clark and Rampage. Strain G1 (including ATCC PV-94) did not infect any of the resistant cultivars. Strain G2 caused local and systemic necrosis in Marshall but did not infect other resistant cultivars. Strain G3 and strain G4 caused local and systemic necrosis in both Ogden and Marshall; strain G4 also infected Davis and York, causing either local and systemic necrosis or mosaic symptoms. Strains G5, G6, and G7 all caused mosaic symptoms in Davis and York; strain G5 also caused necrosis in Kwanggyo, strain G6 caused necrosis in both Kwanggyo and Marshall, and strain G7, which infected all cultivars tested, caused necrosis in Marshall, Odgen, Kwanggyo, and Buffalo. The incidence of SMV and the presence of highly virulent strains in germplasm collections call for use of a range of SMV strains in soybean breeding programs in which SMV resistance is an objective.

Soybean mosaic (caused by soybean mosaic virus [SMV]), probably the most common virus disease of soybeans, may cause severe damage and is considered one of the more serious threats to soybean production in some areas (4,5). Since Clinton first described soybean mosaic in 1915 (7), it has been found wherever soybeans are cultivated and disease surveys have been conducted (9,20). The primary factor affecting the world-wide distribution of SMV is that it is seedborne (3,14).

A variety of symptoms caused by various isolates of SMV (2,4,5,7–12,14,15,19) has been observed in various soybean cultivars by previous workers. Symptoms range from mild mosaic that may be masked during periods of high temperature to severe necrosis. Necrosis caused by strains of SMV is a serious problem for soybean production in some Far East countries, particularly in Korea where a strain designated SMV-N (4,5) has hampered efforts to increase production of leading soybean cultivars because plants infected when young produce virtually no seeds. The lethal effect of SMV-N in soybean was considered important in Korea because the affected cultivars were supposed to have been resistant to SMV (4).

Our study was undertaken to identify and classify isolates of SMV present in the U.S. Department of Agriculture (USDA) soybean germplasm collections, and to investigate the virulence of these isolates on soybean cultivars previously reported to be resistant to some isolates of SMV.

MATERIALS AND METHODS

Sources of soybean mosaic virus isolates. Seeds of 23 soybean accessions from the collection at Urbana, IL (11 from Japan, four from Rumania, two from the USSR, and six from Sweden) and 53 accessions from the collection at Stoneville, MS (four from China, three from Thailand, four from India, five from Pakistan, two from the Philippines, seven from Australia, seven from Angola, four from Uganda, six from South Africa, one from Liberia, two from Rhodesia, two from the Sudan, three from Tanzania, one from Argentina, and two from Brazil) were provided by R. L. Bernard, USDA and Department of Agronomy, University of Illinois, Urbana, IL, and E. E. Hartwig, Delta Branch Experiment Station, Stoneville, MS, respectively.

Fifty-five to 100 seeds of each accession were planted in a greenhouse sand bench. SMV-infected seedlings were identified at the primary leaf stage and used for virus isolation.

SMV samples also were collected from field-grown soybeans. Leaves from 34 SMV-infected plants found in the soybean germplasm field trial at Urbana were collected on 7 July 1977, when the plants had produced three trifoliolate leaves. A similar collection of 27 samples was made from a soybean germplasm field trial at Stoneville on 10 June 1977, when the plants were at the primary leaf stage. Leaf samples were kept in vinyl bags in the refrigerator before inoculations were made on Rampage soybeans in the greenhouse.

Of the 27 soybean accessions from which samples were collected at Stoneville, 24 were introduced from Korea and one from Japan in 1976; the origin of the two remaining accessions was unknown. All 34 accessions from which field collections were made at Urbana were introduced from Korea in 1974 or 1976.

Isolation of soybean mosaic virus. Two weeks after planting of seeds, soybean seedlings with mosaic symptoms were transplanted into composted, autoclaved soil in clay pots (11 cm in diameter); from one to several weeks later, these plants were used to prepare inoculum for inoculation to Rampage soybeans. Leaves from infected Rampage soybeans were used for further studies and maintenance of stock cultures of the isolates.

Diseased soybeans collected from the field were used to inoculate

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the primary leaves of Rampage soybeans, and Rampage soybean leaves showing mosaic symptoms about 10 days after inoculation were used as inoculum to inoculate soybean differentials. Inoculum prepared from field-collected samples also was indexed by the Top Crop bean index method (16) to confirm that SMV was present. Isolates showing symptoms on Rampage soybeans and inducing local lesions on the detached leaves of Top Crop beans were used for further differentiation on the basis of the reactions on soybean differentials.

Soybean differentials. The SMV-resistant soybean cultivars used were Buffalo, Davis, Kwanggyo, Marshall, Ogden, and York (5,17–19 [the observation that Marshall possesses SMV resistance is the unpublished work of M. R. McLaughlin in our laboratory]). Rampage and Clark soybeans, which are susceptible to SMV (9), also were used as differentials. Plants for use as differentials were prepared by seeding five to six seeds in clay pots containing autoclaved, composted soil.

Inoculation procedures. Four or five trifoliolate leaves from diseased plants showing mosaic symptoms were homogenized with a sterilized, ice-chilled mortar and pestle in 3–5 ml of chilled 0.01 M potassium phosphate (pH 7.0). A small amount of 22-μm (600-mesh) Carborundum was added to the inoculum or dusted on the leaves to be inoculated. Inoculum was applied by rubbing a cotton-tipped applicator or a pestle dipped in the inoculum on the leaves of test plants. Inoculated leaves were washed with running tap water.

In all cases, primary leaves were inoculated just before trifoliolate leaves developed. Rampage soybeans were used as test plants as well as sources of the virus throughout the experiments.

Most experiments were conducted in a greenhouse in which temperatures ranged between 18 and 30 C, depending upon the season and other weather conditions. In preliminary tests carried out in the greenhouse between April and September in 1977, each of the 98 isolates was inoculated to one or two plants of each differential cultivar. Notes on symptom development were taken daily. Based on these results, provisional groupings were made and isolates representative of each group were selected for further testing. The representative isolates were inoculated in the greenhouse during November and December, 1977, to 50 or 60 plants of each cultivar in one test and 25 to 30 plants of each cultivar in a second test, respectively. To test whether temperature affected symptom development in soybean differentials, experiments also were conducted with a representative isolate of each strain in growth chambers maintained at 23 ± 1 C or 30 ± 1 C with 14 hr of light and 10 hr of dark daily.

Host range tests and serological determinations. Whenever obscure or atypical mosaic symptoms were encountered on plants grown in the sand bench or on Rampage soybeans inoculated from field samples, or if the reactions on soybean differentials were suspected of being caused by viruses other than SMV, cowpea (*Vigna unguiculata* [L.] Walp.), and tobacco (*Nicotiana tabacum* L.) were inoculated. Isolates that proved not to be SMV by that host range test were not used further.

Enzyme-linked immunosorbent assay (ELISA) was conducted with the representative isolates of SMV groups (6). For ELISA, 0.8 g of diseased tissue was homogenized in 2 ml of 0.05 M Tris-HCl, 0.85% NaCl (pH 7.0), and a few drops of the juice were added to sensitized wells (6) with disposable pipettes. To determine whether the isolates contained tobacco ringspot or bean pod mottle virus, Ouchterlony agar double diffusion tests were conducted (1).

Symptomless inoculated plants were assayed by indexing on detached Top Crop bean leaves (16). Ten trifoliolate leaves, each from a different plant, were collected and stacked. A sample containing approximately equal amounts of tissue from each leaf was taken by cutting a narrow strip (1–2 mm wide) crosswise through the stacked leaves. Preliminary experiments showed the test to be sufficiently sensitive to detect one infected leaf among the ten.

RESULTS

Soybean mosaic virus isolates from germplasm collections. Twelve of 53 soybean accessions from the Stoneville germplasm collection and seven of 23 soybean accessions from the Urbana germplasm collection produced one or more seedlings with virus symptoms. From these 19 accessions, 37 isolates of SMV were obtained. Each isolate was obtained from a single plant showing mosaic symptoms.

Twenty-seven isolates from 20 soybean accessions in the collection grown at Stoneville, Mississippi, and 34 isolates from 34 soybean accessions in the collection grown at Urbana, Illinois, were obtained. All isolates produced mosaic symptoms in Rampage soybeans.

Classification of SMV isolates. Ninety eight isolates of SMV, 37 from seeds and 61 from field samples, were classified into seven strains based on the symptoms caused in soybean differentials (Table 1). SMV-G1 included 27 isolates, 11 from seeds and 16 from field samples; SMV-G2 included 24 isolates, eight from seeds and 16 from field samples; SMV-G3 included 17 isolates, eight from seeds and nine from field samples; SMV-G4 included three isolates, all from seeds; SMV-G5 included eight isolates, one from seed and seven from field samples; SMV-G6 included 17 isolates, all from field samples, and SMV-G7 included two isolates from field samples.

The classification given in Table 1 is based on the results of numerous preliminary tests with all 98 isolates followed by four large-scale tests in which representative isolates were used; in each of the latter four tests all seven strains were inoculated at the same time, under the same conditions, on numerous plants of each differential cultivar (see Materials and Methods). The results from a test conducted in the growth chamber held at 24 ± 1 C were similar to those obtained in the two greenhouse tests. Necrosis was more conspicuous on the plants held in a growth chamber at 30 ± 1 C than on those held at 24 ± 1 C, but no qualitative differences in reactions were noted at the higher temperature. The reactions described (Table 1) were consistent and reproducible.

Reactions of soybean differentials to seven strains of soybean mosaic virus. All virus strains produced mosaic symptoms on Clark and Rampage. No local lesions or veinal necroses were observed on the inoculated primary leaves or on the noninoculated trifoliolate

TABLE 1. Reactions of soybean cultivars to seven soybean mosaic virus (SMV) strains obtained from seeds in the U.S. Department of Agriculture soybean germplasm collections[a]

Soybean cultivars	Symptoms caused by SMV strains[b]						
	SMV-G7	SMV-G6	SMV-G5	SMV-G4	SMV-G3	SMV-G2	SMV-G1
Clark	−/M[c]	−/M	−/M	−/M	−/M	−/M	−/M
Rampage	−/M	−/M	−/M	−/M	−/M	−/M	−/M
Davis	−/M	−/M	−/M	−,N/M,N	−/−	−/−	−/−
York	−/M	−/M	−/M	−,N/M,N	−/−	−/−	−/−
Marshall	N/N	N/N	−/−	N/N	N/N	N/N	−/−
Ogden	N/N	−/−	−/−	N/N	N/N	−/−	−/−
Kwanggyo	N/N	N/N	N/N	−/−	−/−	−/−	−/−
Buffalo	N/N	−/−	−/−	−/−	−/−	−/−	−/−

[a] A list of accessions from which SMV isolates were obtained is available on request from the authors.
[b] Symbols for symptoms: − = symptomless, no virus was detected in noninoculated tissue by Top Crop indexing; M = mosaic symptoms; N = necrosis.
[c] Format for symptom symbols: (Reactions on inoculated primary leaves)/(reactions on noninoculated trifoliolate leaves).

leaves. There was variation in the severity of mosaic symptoms depending upon the strains. However, the more virulent SMV strains did not necessarily cause the more severe mosaic symptoms in the susceptible cultivars tested. Stunting of the plants was not severe in SMV-inoculated Clark and Rampage soybeans regardless of which strain was used.

All virus strains were detected easily by Top Crop bean indexing when infected Clark or Rampage was used as the inoculum source.

All 302 Rampage plants inoculated (48, 28, 51, 42, 45, 43, and 45 plants were inoculated with SMV-G7, SMV-G6, SMV-G5, SMV-G4, SMV-G3, SMV-G2, or SMV-G1, respectively) showed mosaic symptoms.

Davis and York reacted similarly to each strain. A total of 254 Davis plants inoculated with more virulent strains (74, 29, 78, and 73 plants were inoculated with SMV-G7, SMV-G6, SMV-G5, or SMV-G4, respectively) produced mosaic symptoms. Ten plants inoculated with an SMV-G4 strain in early tests showed necrosis but in later tests 73 plants inoculated with the same isolate showed mosaic symptoms. Top Crop indexing gave positive results with leaves showing mosaic or necrosis. The 293 Davis plants tested with less virulent strains (79, 76, and 138 plants were inoculated with SMV-G3, SMV-G2, or SMV-G1, respectively) remained symptomless and no virus was detected by Top Crop indexing. The 226 York plants tested with SMV-G7, SMV-G6, SMV-G5, or SMV-G4 (71, 24, 63, and 68 plants were inoculated with these isolates, respectively) all showed mosaic symptoms, but 279 York plants inoculated with SMV-G3, SMV-G2, or SMV-G1 (71, 74, and 134 plants, respectively) remained symptomless and no virus was detected by indexing.

All 337 Marshall plants tested by inoculation with SMV-G7, SMV-G6, SMV-G4, SMV-G3, or SMV-G2 (76, 26, 80, 79, and 76 plants, respectively) showed necrosis; of 213 Marshall plants inoculated with SMV-G5 or SMV-G1 (76 and 137 plants, respectively) all remained symptomless and no virus was detected by Top Crop bean indexing.

Ogden showed necrotic symptoms in response to infection by some strains, but generally it was more resistant than was Marshall. The 205 Ogden plants inoculated with SMV-G7, SMV-G4, or SMV-G3 (62, 73, and 70 plants, respectively) all showed necrosis; none of the 274 plants inoculated with SMV-G6, SMV-G5, SMV-G2, or SMV-G1 (20,70,70, and 114 plants, respectively) showed symptoms and no virus was detected by Top Crop indexing.

Kwanggyo showed necrotic symptoms when inoculated with isolates from strains SMV-G7, SMV-G6, or SMV-G5; of the 172 Kwanggyo plants inoculated with these strains (69, 23, and 80 plants, respectively) all showed necrosis. None of 333 Kwanggyo plants inoculated with SMV-G4, SMV-G3, SMV-G2 or SMV-G1 (69, 68, 69, and 127 plants, respectively) showed symptoms, and no virus was detected by Top Crop indexing.

Buffalo was infected only when inoculated with isolates of strain G7. All 64 Buffalo plants inoculated with SMV-G7 showed necrosis. Of 386 Buffalo plants tested with other strains (17, 69, 63, 61, 59, and 117 plants were inoculated with SMV-G6, SMV-G5, SMV-G4, SMV-G3, SMV-G2, and SMV-G1, respectively), all remained symptomless, and no virus was detected by Top Crop indexing.

All soybean cultivars that showed necrotic symptoms when infected with SMV had necrotic local lesions on the inoculated leaves (Fig. 1) and necrotic lesions on the noninoculated leaves, veinal necrosis both on inoculated and noninoculated leaves, necrotic mosaic symptoms on the newly developed leaves, and bud blight.

SMV-G7 also caused necrotic symptoms in and death of the SMV-resistant PI 96983 while SMV-G5, SMV-G4, SMV-G3, and SMV-G1 did not infect this line. ISP-29, an isolate originating from Calland soybean seeds grown in 1975 at Seville, Spain, and grouped in SMV-G6, caused mosaic symptoms in PI 96983 but caused no symptoms in Buffalo. In addition, Tokyo, Norin No. 2, PI 360835 and PI 324068 showed necrosis when inoculated with SMV-G7. Tokyo soybeans also showed necrosis when inoculated with SMV-G3.

Serological tests with representative isolates of soybean mosaic virus groups. Reactions of all representative isolates of the seven SMV strains were positive in ELISA tests. No precipitin zones were formed in Ouchterlony agar double diffusion tests between any of the SMV strains and tobacco ringspot virus or bean pod mottle virus antisera, but in homologous tests with the same antisera precipitin zones were observed.

DISCUSSION

Seeds from the USDA soybean germplasm collections contain a wide variety of SMV strains, which differ in virulence. There were no apparent patterns of relationship between the virulence of the isolates collected and the origin of the soybean accessions from

Fig. 1. Local lesions and veinal necrosis on leaves of Kwanggyo soybeans inoculated with soybean mosaic virus strain SMV-G5. Strains G6 and G7 induce similar symptoms in this cultivar.

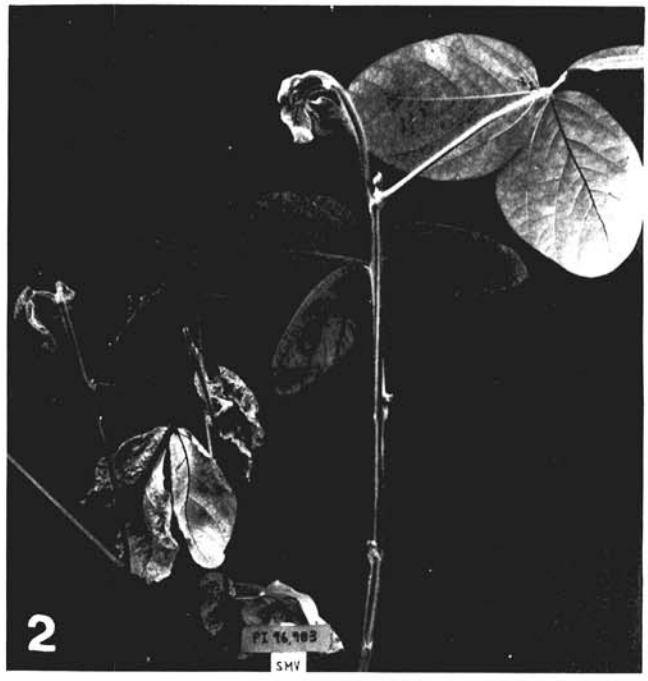

Fig. 2. Necrotic symptoms on noninoculated leaves of soybean PI 96983 inoculated with soybean mosaic virus strain SMV-G7. Bud blight and necrosis of trifoliolate leaves are conspicuous symptoms. Trifoliolate leaves become desiccated and fall from the plant.

which they were taken. This is probably the case because soybeans now in different regions of the world all originated in Asia. It is also possible that some accessions tested in our experiments were infected with SMV during cultivation in the United States, resulting in spread of SMV strains in plants from one area to those of soybean accessions of quite different geographical origin.

Symptomatology, Top Crop bean leaf indexing, serology, and host range tests produced no evidence that our SMV strains contained viruses other than SMV; thus the reactions observed are believed to unambiguously represent the range of symptoms induced by SMV on the cultivars tested. However, the possibility that one or more of the SMV strains could consist of a mixture of SMV strains, especially in isolates obtained from field samples, has not been completely eliminated, and will be the subject of continuing study.

Of the previously described isolates or strains of SMV that were tested, the blister strain (19) belonged to SMV-G3; SMV-I1-S (3) belonged to SMV-G2; and ATCC PV-94 belonged to SMV-G1. Of six strains of SMV reported by Han and Murayama (11), SMV-T5 and SMV-T6 caused necrosis in Norin No. 2, Ou No. 3, and Enshiken. SMV-G5 and SMV-G7 also caused necrosis in Norin No. 2 in our tests, but it was not possible to make further comparisons of virulence because the other soybean cultivars used in the experiments of Han and Murayama were different from those used in our study. SMV-N (5) caused necrosis in Kwanggyo and mosaic symptoms in York (4) and thus might be similar to SMV-G5. None of the SMV strains reported by Ross (18) was able to infect Ogden, Davis, York, or PI 96983; thus our SMV-G3, SMV-G4, SMV-G5, SMV-G6, and SMV-G7 differ from any of the isolates investigated by Ross.

Most SMV isolates from field samples or seeds belonged to SMV-G1, SMV-G2, or SMV-G3. Isolates from field samples belonging to SMV-G5 or SMV-G6 constituted about 25% of the isolates and only two of 98 isolates were classified in SMV-G7.

Among the eight soybean differentials, Clark and Rampage showed the same reactions to all SMV strains. This is consistent with the common genetic background of Clark and Rampage (13). It was also not surprising that Davis and York reacted similarly to all SMV strains as they also have a similar genetic background (13). Ogden contributed to the parentage of Davis and York (13). Infections of Ogden by SMV-G3 resulted in severe necrotic symptoms while Davis and York were not susceptible to SMV-G3. Inoculation of SMV-G5 or SMV-G6 to Davis and York, on the other hand, resulted in mosaic symptoms but Ogden was not susceptible. SMV-G4, which caused necrosis in Odgen, was able to infect Davis and York, causing either mosaic or necrosis.

These results indicate that Odgen may possess SMV resistance that differs from that of Davis or York. Results with Marshall, Kwanggyo, and Buffalo also indicated that the genetic systems conferring SMV resistance in these cultivars differed from one another and from those of Odgen, Davis, and York.

The necrotic symptoms observed in SMV-infected Buffalo, Davis, York, Kwanggyo, Marshall, and Odgen soybeans were essentially the same regardless of the strain of SMV responsible and they also resembled those described earlier (5,8,11,12,14,15,19). Necrosis caused by SMV in resistant cultivars differed from that caused by tobacco ringspot virus which does not generally cause veinal necrosis. Our results confirm previous observations that necroses caused by SMV are associated with virulent strains infecting soybean cultivars that are resistant to less virulent strains (5,11,15). The occurrence of systemic necrosis caused by virulent strains of SMV is a threat to efforts to improve soybeans for SMV-resistance (4,5).

SMV isolates virulent to Davis, York, and Buffalo are reported here for the first time in the USA, since Davis, York, and Buffalo have been reported to be resistant to most isolates or strains of SMV used by previous investigators (9,17–19). In addition to the susceptibility of those soybean cultivars, it may be significant that the two isolates in SMV-G7 and one isolate in SMV-G6 caused severe necrosis (SMV-G7) or mosaic (SMV-G6) in PI 96983 (Fig. 2), which has been shown previously to have, and is presently in wide use as a source of, resistance to SMV (9,19).

If soybean cultivars resistant to less virulent strains of SMV are widely grown, and the more virulent strains are spread by an efficient means of dispersal, an epidemic of soybean necrosis caused by SMV similar to that rampant in Korea since 1974 (5) could occur in the USA. Also, the most widely grown soybean cultivars, such as Wayne, Clark, Lee, Amsoy, Corsoy, Bragg, Dare, Chippewa, Beeson, and Harosoy have a narrow genetic background and are related to Clark, Davis, Ogden, Rampage, or York which were susceptible to many of the SMV isolates used in our study (13). Our results therefore indicate that a range of SMV strains differing in virulence should be used in soybean breeding programs in which SMV resistance is an objective.

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