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Field Spread of Soybean Mosaic Virus Strains

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콩모자익바이러스 系統의 圃場傳染

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ABSTRACT

Isolates of soybean mosaic virus (SMV) strains classified based on virulence in six resistant soybean cultivars caused the same reactions in soybean cultivars used as differentials as those obtained by sap inoculations to the same cultivars. Five species of aphids (*Myzus persicae* SULZ., *Aphis craccivora* KOCH, *Aphis citricola* VAN., *Rhopalosiphum maidis* FIT., and *R. padi* L.) were able to transmit each of SMV strains. However, *R. maidis* and *R. padi* were inefficient vectors for transmission of SMV strain G3.

Spread of four SMV strains (G2, G3, G6, and G7) was monitored in the field from sap-inoculated plants in a one meter row of Williams soybeans (source plants) to plants in an adjacent row of Williams 80cm away (test plants). Test plants were downwind from the source plants. A complete block design was used. Spread of strain G6 was significantly greater than that of other three strains.

Two hundred six aphids were collected from June 27, 1979 to August 2, 1979 in the same field. *A. citricola* was the most prevalent, comprising 68% of the total aphids. Yields of Williams inoculated with each strain were also compared. Yields were the least from plants inoculated with strain G2 following G6, G3, and G7 in that order.

INTRODUCTION

SMV is a member of potato virus Y group which includes a large number of agriculturally important viruses (8). SMV is transmitted through seeds of soybean plants producing mosaic symptoms; the rate of seed transmission was reported as high as 68.4% in soybean cultivar Midwest (15), but generally ranges from 0 to 35% in most soybean cultivars (6, 13). Seedborne SMV is the primary inoculum source in epidemics of soybean diseases caused by SMV; none of the 33 species of host plants other than soybean are known to carry SMV over winter in nature (2, 8).

Based on virulence to six resistant soybean cultivars, more than 100 SMV isolates obtained from USDA germplasm collections were classified into seven strains (2, 4). Depending upon combinations of soybean genotype and SMV strain, SMV causes either mosaic or necrotic symptoms during systemic infection. The necrotic reaction occurs in soybean

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cultivars resistant to less virulent SMV strains when infected with more virulent SMV strains, while all strains cause mosaic symptoms in soybeans susceptible to less virulent strains (4). It is important to know whether the necrotic reaction obtained by mechanical sap inoculation is the result simply of a genetic interaction between soybean genotype and virus strain or possibly the result of a heavy dosage of inoculum.

SMV is transmitted by as many as 31 species of aphids in a nonpersistent manner (14); five species, *Aphis craccivora*, *Macrosiphum euphorbiae*, *Myzus persicae*, *Rhopalosiphum maidis*, and *R. padi*, were responsible for 93% of all transmission of SMV in tests conducted in Illinois (14). Using four of the seven SMV strains, differences in the extent of spread under field conditions were investigated in this study. Our results indicate that virulent strains spread efficiently under field conditions and that *A. citricola* was the most prevalent species of aphids and might be responsible for the spread.

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MATERIALS AND METHODS

Virus strains: For each of the SMV strains G1, G2, G3, G4, G5, G6 and G7 described previously (4), a single isolate was used in this study. Since the original isolate of strain G4 was subsequently found to contain a mixture of variants (3), a new type isolate obtained from soybean accession PI 171451 grown at Champaign, IL. in 1978 was used to determine virulence of SMV strains by aphid trans missions. Strains G2, G3, G6 and G7 were used for monitoring virus spread in the field.

Soybean test plants: Soybean cultivars Rampage, Williams, Davis, Marshall, Ogden, Kwanggyo, and Buffalo were used as differentials for virulence of SMV strains by aphid transmission tests. Plants for use as differentials were prepared by seeding five or ten seeds in clay pots containing autoclaved, composted soil. For monitoring field spread of SMV strains, Williams soybeans were used.

Vectors: The aphid species in this study were obtained from Dr. M.E. Irwin, University of Illinois at Urbana-Champaign. *Aphis citricola* VAND DER GOOT was maintained on celery (*Apium graveolens* cv. Utah Pascal), *A. craccivora* KOCH on broad bean (*Vicia faba* cv. Long Pod), *Myzus persicae* SULZER on radish (*Rhapanus sativus* L. cv. Scarlet Globe), *Rhopalosiphum maidis* on sweet corn (*Zea mays* cv. Gold Cup), and *R. padi* L. on barley(*Hordeum vulgare* cv. Larker). All Aphids were originally collected from Champaign county in Illinois except *R. padi* which was originally obtained from Dr. H. Jedlinski, USDA, Department of Plant Pathology, Uni versity of Illinois, Urbana (M.E. Irwin, 1980, personal communicatcn). All colonies were maintained in a growth chamber at 24±1°C with 14hr of light and 10hr of dark daily.

Aphid transmission tests: Aphids were starved 2~6 hours in glass bottles before being allowed acquisition access to SMV-infected leaves (source leaves) of Rampage or Williams soybeans. All leaves used for acquisition access were systemically infected and exhibited typical SMV symptoms. Leaves were used 14~17 days after sap inoculations of the plants as described by Cho and Goodman (4). The source leaves were detached and placed singly in a Petri dish. A small amount of water was added to each Petri dish to keep the leaf fresh and prevent aphids from wandering off the leaf.

Twenty to 30 aphids placed on each leaf were observed under a dissecting microscope. Five or ten aphids that had probed the infected leaf were transferred with a camel's hair brush to each soybean test seedling and the plants in the pot enclosed with a cage. Cages were made from cellulose nitrate cylinders (9cm×25cm) provided with a nylon screen on top for ventilation.

For tests of transmission of SMV strains by different species of aphids, an SMV-infected Williams plant(source plant) was transplanted to the center of a 10-cm clay pot (usually 3~4 days after inoculation) and around the source plant ten seeds of Williams soybeans were planted (test plants). When test plants had grown to the primary leaf stage (usually 10 days after seeding), 20 aphids were placed on a leaf of the source plant, and all source and test plants in the pot were caged as above. The acquisition and inoculation access period in this type of experiment was 12~24 hours, after which aphids were killed by fumigation with the insecticide dichlorvos (dimethyl dichloro vinyl phosphate).

On each occasion when aphid transmission tests were attempted, the same leaves that were used for acquisition access by aphids were also used to test on differentials by sap inoculations to confirm that the strain being used was correctly identified.

Field experiment design: A soybean field (22.5m²) planted to Williams soybeans on 29 May 1979 was used for monitoring spread of SMV strains. The field was located near Urbana, IL, and consisted of 14 rows planted in pairs with 80cm between rows; each pair of two rows was 240cm apart.

In the alternate pair, the upwind row was used as spreader row (source row), and the downwind row was used as to read for infected plants (test row). The experimental design was a randomized split complete block with four replications. Prior to inoculation, the field was inspected visually and no plants were found to be infected with seedborne virus.

In the source row, an average of 20 plants in one meter of row were inoculated with one of four SMV strains (G2, G3, G6, or G7); plants inoculated with the different strains were four meter apart. Inoculations were on June 8, 1979 as described by Cho and Goodman (4). Readings of number of plants infected in one meter of a test row located downwind from and in parallel with each source row were made by visual observations for symptoms development every three days from June 16, 1979 to August 2, 1979, and each infected plant was marked with a label when it was first found.

The number of plants infected per total observed was recorded, the percentage infection calculated and then the percentage was transformed into the multiple infection rate (9). Soybeans were harvested from plants inoculated with each of four strains and yields were compared among strains.

Aphids were collected at the center of the field at canopy level with horizontal ermine lime traps described by Irwin and Goodman (14). Aphids in the trap were removed weekly and aphid species were identified in the laboratory. Aphids were collected with the help of G.E. Kampmeier and M.E. Irwin, University of Illinois, and aphids were identified with the help of S.W. Halbert, University of Illinois.

RESULTS

Virulence of SMV strains by aphid transmission: Reactions of soybean differentials to the seven SMV strains transmitted by aphids were similar to those obtained following mechanical inoculations (Table 1). The minor differences noted were probably due to the relative inefficiency of virus transmission by aphids. For example, Marshall tested with strain G2 or G6 sometimes did not produce symptoms by aphid transmissions. The expected necrotic reaction was observed, however, following sap inoculations with inoculum prepared from source leaves used for aphid transmission and from leaves of Rampage inoculated by aphid transmission.

Transmissibility of SMV strains by different species of aphids: SMV strains G1, G2, G4, G5, G6, and G7 were transmitted by aphids of the species *A. citricola*, *A. craccivora*, *M. persicae* *R. maidis*, and *R. padi* (Table 2).

In one test, *R. maidis* and *R. padi* failed to transmit the isolate of SMV strain G3 whereas *A. citricola*, *A. craccivora*, and *M. persicae* transmitted it. However, when a Williams plant infected with G3 transmitted by *M. persicae* was used as a source plant, both *R. maidis* and *R. padi* transmitted the isolate (Table 2).

Field spread of SMV strains: The field plot was carefully inspected twice before inoculation (on June 8 and June 16, 1979) for evidence of SMV-infected plants that might be present due to seed transmission, but no infected plants were found. The first infected

Table 1. Reactions of soybean cultivars to soybean mosaic virus strains transmitted by *Myzus persicae* SULZ.

Soybean cultivar	Aphid transmissibility of soybean mosaic virus strains[a]						
	G1	G2	G3	G4	G5	G6	G7
Rampage	5/7(M)[b]	4/10(M)	3/5(M)	3/8(M)	9/12(M)	4/6(M)	7/7(M)
Davis	0/7	0/8	0/2	1/5(N)	2/5(M)	3/4(M)	4/6(M)
Marshall	0/10	1/9(N)	2/4(N)	0/5	0/5	2/23(N)	1/9(N)
Ogden	0/9	0/10	2/6(N)	0/5	0/8	0/7	3/9(N)
Kwanggyo	0/9	0/10	0/8	0/3	1/6(N)	4/8(N)	3/9(N)
Buffalo	0/5	0/9	0/5	0/4	0/6	0/6	4/7(N)

[a] SMV strains except strain G4 were as described by Cho and Goodman (4). Strain G4 was redesignated as causing mosaic in Rampage, necrosis in Davis, no infection in Marshall, Ogden, Kwanggyo, and Buffalo by sap inoculations, since the original G4 contained a mixture of variants. The results were similar to those following sap inoculations.

[b] Number of plants infected/number of plants tested. Five or ten aphids were used per test plant. Symbols for reaction (in parenthesis): M signifies mosaic symptoms and N signifies symstemic necrosis.

Table 2. Transmissibility of seven soybean mosaic virus (SMV) strains by five species of aphids to soybean cultivar Williams

Aphid species	Aphid transmissibility of SMV strains[a]						
	G1	G2	G3	G4	G5	G6	G7
Aphis citricola VAN.	9/12[b]	5/14	1/7	4/6	5/9	5/7	5/7
Aphis craccivora KOCH	3/16	3/15	2/10	2/9	6/10	5/7	3/7
Myzus persicae SULZ.	13/15	16/16	1/10	9/9	8/8	9/9	5/6
Rhopalosiphum maidis FIT.	2/17	4/12	0/6[c]	4/10	4/8	4/6	2/7
Rhopalosiphum padi L.	5/12	5/16	0/9[c]	7/10	4/10	7/8	7/9

[a] SMV strains except strain G4 were as described by Cho and Goodman (4). Strain G4 was redesignated as causing mosaic in Rampage, necrosis in Davis, no infection in Marshall, Ogden, Kwanggyo, and Buffalo by sap inoculations, since the original G4 contained a mixture of variants. An SMV-infected Williams plant was transplanted to the center of 10-cm clay pot and around the infected plant (source plant) ten seeds of Williams were planted (test plants). When test plants had grown to the primary leaf stage, 20 aphids were placed on a leaf of the source plant and allowed an acquisition and inoculation access period of 24 hr.

[b] Number of plants infected/number of plants tested.

[c] Strain G3 was found to be transmissible by *R. maidis* and *R. padi* when a Williams plant infected with G3 transmitted by *M. persicae* was used as a source plant in a later test.

plants were found on June 23, 1979 two weeks after inoculations.

Thirty-three days after inoculations, the infection incidences were 1.4%, 1.4%, 3.3%, 1.4% for G2, G3, G6 and G7, respectively. Forty days after inoculations, the infection incidences were 11.1%, 11.3%, 26.3%, 12.3% for G2, G3, G6 and G7, respectively. Forty seven days after inoculations, the infection incidences were 24.3%, 15.5%, 43.3%, and 16.4% for G2, G3, G6 and G7, respectively. Fifty five days after inoculations, the infection incidences were 51.4%, 35.5%, 80%, and 42.5% for G2, G3, G6 and G7, respectively. Virus spread differed among SMV strains. Spread of strain G6 was significantly greater than that of G2, G3, and G7, but there was no significant differences in virus spread among strains G2, G3, and G7 (Table 3 and 4). Considering the spread of SMV strains together,

Table 3. Field spread of four soybean mosaic virus strains

Soybean mosaic virus strains[a]	Multiple infection[b] transformation
G6	179.1
G2	77.2
G7	57.7
G3	45.4
L.S.D. (.05)	65.5

[a] Soybean mosaic virus strains were described by Cho and Goodman (4).

[b] Percentage of total infection was transformed by the multiple infection transformation (9).

virus spread increased rapidly between 47 days and 55 days after inoculations (July 23-August 1).

Aphid species in the experimental field: Aphids were collected every week from June 27, 1979. Of 206 aphids collected, there were 18 different species (Table 4). *A. citricola* was the most prevalent, comprising 68% of the total aphids collected. *Capitophorus elaeagni* (del. Guer.) was 9% of aphids collected.

By 35 days after SMV inoculation of plants in the source row, 79 aphids had been collected, or about 38% of the total aphids collected. At 49 days after SMV inoculations, 185 aphids had been collected, which amounted to 90% of the total aphids collected. Since the multiple infection rate increased from 29.4% to 89.8% between 47 days and 55 days after inoculations, the proportion of aphids collected appeared to be highly correlated with the increase of virus spread (r=0.82) (Fig. 1).

Yield from Williams infected with SMV strains: Plants inoculated with strain G2 suffered severe stunting and more severe mosaic symptoms than plants inoculated with G3, G6 or G7. Plants inoculated

Table 4. Number of aphids landing on a trap set up at the experimental field for monitoring the spread of soybean mosaic virus strains.

Aphid species[a]	Number of aphids collected on dates shown					
	7/4(28)[b]	7/11(35)	7/18(42)	7/25(49)	8/2(56)	Total
Aphis citricola	7	56	36	30	10	139
Capitophorus elaeagni	1	7	8	1	2	19
Aphis spp.	2		5	5	2	14
Therioaphis maculata	2		2	2	1	7
Dactynotus sp.			2	2	1	5
Aphis craccivora		2	1	1		4
Capitophorus hippophaes		1	2	1		4
Aphis nerii			2			2
Lipaphis erysimi			1		1	2
Myzocallis punctatus				2		2
Aphis fabae					1	1
Aphis gossypii			1			1
Aphis illinoisensis					1	1
Aphis polygonata			1			1
Macrosiphum euphorbiae					1	1
Myzus persicae				1		1
Pemphigus populi-transversus		1				1
Rhopalosiphum maidis					1	1
Total	12	67	61	45	21	206

[a] Aphids were collected with the help of G.E. Kampmeier, and identification of aphids was made with the help of S.E. Halbert and M.E. Irwin.

[b] Number signifies month/day (and day after SMV inoculation).

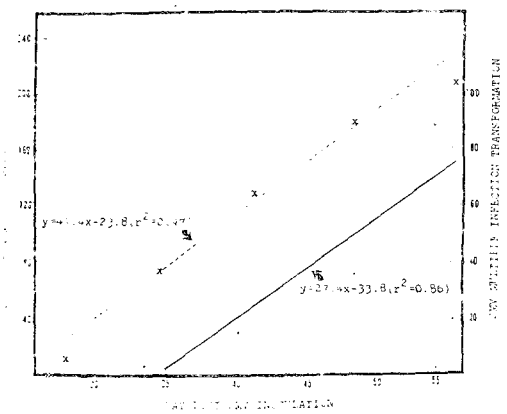

Fig 1. Relationships between cumulative number of aphids (·····) or multiple infection transformation of soybean mosaic virus (——) in soybean cultivar Williams spread from the infection focus during the season in a field at Urbana, Illinois, USA in 1979.

Table 5. Yield comparison in soybean cultivar Williams inoculated with isolates of four soybean mosaic virus strains.

Soybean mosaic virus strains[a]	g seeds / m row
G7	331.8[b]
G3	264.5
G6	204.0
G2	18.5
L.S.D. (.025)	62.0

[a] Soybean mosaic virus strains were described by Cho and Goodman (4).

[b] Average yield from four replications.

with G3 or G6 did not suffer conspicuous stunting but produced obvious mosaic symptoms which remained during the season. Plants inoculated with G7 produced mild mosaic symptoms when young but as the plants grew older, symptoms were masked, and the plants looked like healthy soybeans.

Yields from plants inoculated with each of the above four strains were compared among strains. The results showed significant differences between yields from plants inoculated with each strain (Table 5). Strain G2, which appeared to be the most prevalent when SMV isolates obtained from USDA germplasm collection were classified (4), caused the most severe yield reduction.

DISCUSSION

The results showed that all isolates of the SMV strains tested were aphid transmissible and that the virulence of each strain transmitted by aphids to soybean differentials was similar to the results obtained by sap inoculations. Therefore, the necrotic reaction observed in some soybean cultivars following infection by SMV did not appear to be a response of the plant to dosage of virus inoculum. This conclusion differs from that reached by Kiihl and Hartwig (16) but is similar to that reached, on the basis of less conclusive evidence, by Ross (19, 20) and Cho and Goodman (4).

Reports on the occurrence and spread of the necrotic disease in mainland China, (R.E. Ford, R.L. Bernard, 1980, personal communications), Siberia, Japan and Korea (5, 11) strongly suggest that the necrotic disease caused by SMV is not an experimental obsevation but should be considered a potential threat in soybean production. In Korea, the cultivar Kwanggyo, which was resistant to the prevalent SMV strain and was grown widely, was seriously damaged by necrotic symptoms and plants infected at an early stage gave virtually no yield (5, 7).

Since SMV is spread by aphids in the field from plants infected via seedborne virus to healthy plants, aphids are an important factor in the epidemiology of SMV (12). Swenson (22) indicated that, in most crops, virus spread is by an aphid species which colonizes the crop. However, transient aphids also can transmit a virus as efficiently as those aphids colonizing the host (7). Among those aphids transient in a crop, the most prevalent are not necessarily the most efficient vectors of the virus to the plants. For example, the green peach aphid, *M. persicae*, transmitted four strains of peanut mottle virus more efficiently than did *A. craccivora* (18) which was the most prevalent aphid species in peanut fields (1).

Among the thirty-one species of aphids known to transmit SMV, Irwin and Goodman (14) reported that five species, *A. craccivora*, *Macrosiphum*

phorbiae THOM., *M. persicae*, *R. maidis*, and *R. padi*, were responsible for 93% of all transmissions tests conducted in Illinois. These data were obtained by capturing aphids alive and testing them for transmission of SMV (10, 14). Among aphids prevalent in soybean fields, *A. craccivora*, *M. persicae* and *M. euphorbiae* were efficient vectors for SMV transmission, whereas *R. maidis* and *R. padi* were less efficient vectors (14). In one of our tests, *R. maidis* and *R. padi* failed to transmit an isolate of SMV strain G3 whereas *A. citricola*, *A. craccivora* and *M. persicae* transmitted it. Nontransmission of some SMV isolate by *R. maidis* and *R. padi* was suggested to be due to vector specificity (17). However, our results with strain G3 indicate the possibility that the aphids were inefficient transmitters rather than nontransmitters of SMV, especially when aphid transmissibility of the virus is low.

Eighty-nine percent of the total aphids was collected by 49 days after SMV inoculations and virus spread increased between 47 days and 55 days after SMV inoculations. Among aphids collected from the experimental field, *A. citricola* is known as a vector of SMV (14) and transmitted all four strains used in the experiments. *A. citricola* is probably primarily responsible for spread of the four SMV strains.

Our results on yield comparison showed that yield reduction could be different for SMV strains. However, it may be possible to get different results if different isolates for each SMV strain were used, since the data were obtained from the use of a single isolate for each strain. Also the data were simply collected from the study for virus spread, so we were not able to compare yield reduction with yield from noninoculated plants. This will require a more extensive study on yield loss potential by different SMV strains.

On the other hand, plants inoculated with strain G2, which appears to be the most prevalent strain in Illinois (21), resulted in significantly yield reduction compared to those by other strains. Moreover, strain G6, which is a virulent SMV strain causing necrosis in soybean cultivar Kwanggyo and Marshall and also mosaic disease in Williams, caused severe yield reduction second only to the yield reduction caused by strain G2.

Therefore, development of soybeans resistant to mosaic disease is indeed a requirement for improvement of soybean yield when SMV is prevalent. However, during development of soybeans resistant to mosaic disease, resistance to necrotic disease also has to be considered since the necrotic disease can cause severe yield losses in soybeans resistant to less virulent SMV strains and susceptible to virulent SMV strains.

摘 要

콩모자익바이러스(SMV) 7系統의 진딧물 傳染與否를 試驗한 結果 SMV 7系統 全部가 傳染되었으며 SMV의 진딧물 傳染에 依한 大豆判別品種의 反應도 汁液接種에 依하여 SMV系統을 分類하였을 때의 反應과 一致하였다.

供試한 5種의 진딧물중에서 복숭아혹진딧물, 아카시아진딧물, *Aphis citricola*는 SMV 7系統을 모두 잘 傳染시키는 媒介虫이었으나 옥수수네두리진딧물과 기장네두리진딧물은 SMV系統 G3를 傳染시키지 못하는 경우도 있었다.

圃場에서 SMV系統 G2, G3, G6 및 G7을 22.5m 이랑의 1m 內에 심겨진 콩品種 Williams에 接種한 後 80 cm 떨어진 이랑의 1m內 Williams의 發病率을 調査하였다. 供試한 SMV 4系統中 G6의 傳染率이 가장 높았고 調査期間에 採集된 206 마리의 진딧물중 *A. citricola*가 68%로서 優占種이었다. Williams의 收量은 G2로 接種하였을 때 가장 낮았다.

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