Soybean Mosaic Virus: Infection of Soybean Seed Parts and Seed Transmission

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ABSTRACT

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The presence of soybean mosaic virus (SMV) (Illinois severe isolate) in reproductive plant parts was compared in field-grown, manually inoculated soybean (*Glycine max*) cultivars Merit and Midwest. Soybean mosaic virus was detected in 100% of the flowers, immature seeds, and green pods that were tested but not in any of the dry pods. The percentage of Merit seeds containing detectable virus was 58% at physiological maturity and 0.8% at harvest maturity; the corresponding values for Midwest were 94 and 66%, respectively. The percentage of mature seeds containing SMV was the same as the percentage of SMV-infected seedlings arising from those seeds. The incidence of SMV transmission through seed was only slightly reduced after storage for 6 mo at 14 C. Infectious SMV was detected in the testas, cotyledons, and embryos from immature seeds of both Midwest and Merit. In mature seeds, infectious virus was detected in embryos of Midwest seeds but not in those of Merit seeds. Infectious virus was not detected in testas from mature Midwest seeds by a local lesion index, but the same testas contained viral antigen detectable by enzyme-linked immunosorbent assay. The relationship between the time during the growing season when the plants were inoculated with SMV and the incidence of seed coat mottling, percent germination, and the incidence of SMV transmission through seed was tested in field-grown Williams soybeans. Time of inoculation affected only virus transmission through seed, which averaged 16 or 3% if inoculation was before or after the onset of flowering, respectively.

Additional key words: embryo infection, seed transmission.

Transmission of soybean mosaic virus (SMV) through soybean (*Glycine max* [L.] Merr.) seed occurs at relatively low frequencies (3,12). Previous investigations suggested the importance, but did not entirely resolve the roles, of several factors that may influence the incidence of SMV seed transmission. For example, time of inoculation relative to time of flowering may (14) or may not (15) affect the incidence of transmission of SMV through seed. Evidence for variation in seed transmission of SMV in different soybean germplasms has been documented (14,15,18,21), but little is known about its cause.

Embryo infection appears to be an important factor affecting the seed transmissibility of other plant viruses (2,23). Working with a Brazilian isolate of SMV, Porto and Hagedorn (21) were able to detect the virus in embryos from mature Bansei soybean seeds in which SMV is seed transmitted (4).

We report here the results of studies on the infection by SMV of reproductive tissues of two soybean cultivars, Merit and Midwest, previously shown to exhibit high and low incidences, respectively, of SMV transmission through mature seed (15,16). We show that this variation is not due to differences in the incidence of flower or immature seed infection and that SMV infection of mature soybean seed embryos is confined to the seed-transmitting genotype. We also report results indicating that the incidence of SMV transmission through seed of Williams soybeans is lower in plants that become infected after the onset of flowering. A preliminary report of part of this work has been published (5).

MATERIALS AND METHODS

Effect of inoculation time. Soybean plants were inoculated at different reproductive stages to determine the effect of time of inoculation upon rates of seed mottling and seed transmission. Two hills (10 plants per hill) of Williams soybeans were inoculated with the Illinois severe isolate of SMV (SMV-Il-S) (24) 3 wk after planting in the field on 21 May 1976. The plants were inoculated by manually rubbing the leaves with inoculum prepared from SMV-Il-S infected soybeans (cultivar Rampage) which had been inoculated 14–21 days previously. The inoculum contained 4 ml of 0.05 M sodium phosphate buffer, pH 7.0, per gram of tissue (fresh weight) plus a small amount of 22-μm (600-mesh) Carborundum and was applied with a sterilized gauze pad. Similarly, 20 plants were inoculated weekly for 8 wk. The first two inoculations preceded flowering and the others were done during various reproductive stages identified according to Fehr et al (11). The third inoculation was at stage R1 in which there is one flower at any node. The fourth inoculation was at stage R2 when there is a flower at the node immediately below the uppermost node with a completely unrolled leaf. The fifth inoculation was at R4 when there is a 2-cm-long pod at one of the four uppermost nodes with a completely unrolled leaf. By the seventh inoculation the plants were at stage R6 (possessing a pod containing full-size beans at one of the four uppermost nodes with a completely unrolled leaf).

All symptomless plants were removed at the end of August. When the plants reached maturity, each of the eight inoculation sets were harvested and threshed separately. Two samples of 200 seeds were counted from each inoculation set, and the percentage of mottling was determined. Two hundred seeds from each set were germinated and 100 seedlings were randomly selected and indexed on the detached primary leaves of bean (*Phaseolus vulgaris* 'Top Crop') as described by Quantz (22) and refined by Milbrath and Soong (20).

Presence of SMV in reproductive tissue during plant development. Merit and Midwest soybeans each were planted in 10 hills in a field near Urbana, IL on 22 May 1976. Plants were manually inoculated with SMV-Il-S on June 17, 25 days before the onset of flowering for Merit and 50 days for Midwest. Ten plants from each cultivar were sampled during reproductive states R1, R2, R4, R6, R7, and R8. At stage R7 the plant is at physiological maturity with the pods and 50% of the leaves yellow. At stage R8 (harvest maturity) 95% of the pods are brown. Both cultivars also were sampled after the seeds were germinated immediately after

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harvesting and again after 6 mo of storage at 14 C. A sample was taken from every node of each of the 10 plants, one plant being randomly selected from each of 10 hills during each stage for both cultivars. These samples are considered as 'node-plant' positions. The samples were indexed for the presence of SMV as described above. Individual plants were considered as replications. In stages R1 and R2 entire flowers were indexed, but in stage R4 pods and immature green seeds were indexed together. During R6, R7, and R8 the pods and seeds were indexed separately. For the germination sample, two seeds from each 'node-plant' position were placed on moist cellulose pads under continuous light in a germinator operating at 25 C and 100% RH. When the seedlings had fully-expanded primary leaves, a leaf from one plant from each 'node-plant' position was indexed individually. Seeds also were stored in the cold room at 14 C for 6 mo after which they were germinated and indexed as above. The percentage of seed coat mottling from each 'node-plant' position was determined by examining all of the seeds from the plants that produced the seeds used in the germination sample.

Presence of SMV in seed parts. Merit and Midwest soybeans were planted in five 1-m rows in a field near Urbana, IL. On 14 June 1977, 3 wk after planting, the plants were inoculated with SMV-Il-S. Seed samples were taken from plants at three stages of plant reproductive development (11). The first sampling was at stage R6, a second was at stage R7, and the third was at stage R8. At each sampling time, five plants with symptoms of each cultivar were randomly selected from each of the five rows. Three seeds were taken from each of these 25 selected plants, one from a node near the top, a second from a node near the middle, and a third from a node near the bottom of each plant. The seeds were placed overnight on moist cellulose pads under continuous light in a germinator operating at 25 C and 100% RH. Each seed was then carefully and cleanly dissected into embryo, testa, and cotyledon. These seed parts were separately surface-decontaminated by immersion in 10% (w/v) Na_3PO_4 for 1 min, followed by several washes with distilled water (26), and each was separately indexed on the detached primary leaves of Top Crop beans.

Immediately after harvesting and again after 6 mo of storage at 14 C, two seeds from each of the three sampling positions (as described above) from 25 plants of each cultivar were germinated as described above. When the seedlings had fully expanded primary leaves, a leaf from one plant from each sampling position was indexed individually as above.

Twenty-five seeds from SMV-infected Midwest soybean plants were harvested at stage R8 and germinated as above. The testa was removed from each seed and cut in half; one half was surface-decontaminated as described above and the other half was only rinsed in distilled water. Each testa half was then homogenized in 0.5 ml of buffer. One half of the extract from each testa half was indexed for the presence of infectious SMV on the detached primary leaves on Top Crop beans. The remaining half of the extract from each testa half was indexed for the presence of viral antigen with an enzyme-linked immunosorbent assay (ELISA). The above procedure was repeated three times.

TABLE 1. The effect of the time of inoculation with soybean mosaic virus (Illinois severe isolate) upon seed coat mottling, germination, and seed transmission in Williams soybeans

Week of inoculation	Developmental stage[a]	Seed coat mottling (%)[b]	Germination (%)[c]	Seed Transmission (%)[d,e]
1		69.0	90.5	18.0
2		65.8	91.5	19.0
3	R1	80.5	89.5	11.0
4	R2	72.3	85.0	2.0
5	R4	80.0	88.0	4.0
6		69.8	87.0	4.0
7	R6	77.0	85.0	3.0
8		78.5	92.0	4.0

[a] According to the descriptions in reference 11.
[b] Sample of 400 seeds.
[c] Sample of 200 seeds.
[d] Sample of 100 seeds.
[e] The r value between the week of inoculation and rate of seed transmission was −0.826.

RESULTS

Time of inoculation. A significant correlation ($P = 0.05$) was found between the incidence of seed transmission of SMV and the time of inoculation (r = −0.826), which indicated that early infection resulted in more seed transmission than did later infections. The incidence of seed transmission was higher when infection occurred prior to the onset of flowering (Table 1). However, the seed produced by plants inoculated after flowering exhibited a low but detectable incidence of seed transmission of SMV. The time of inoculation had no effect upon the incidence of seed coat mottling or germination (Table 1).

Effect of stage of reproductive development. Virus was detected in all of the young reproductive parts tested from both cultivars. Maturation of SMV-infected Merit and Midwest soybean seeds was accompanied by a decrease in the proportion of seeds from which virus was detected by indexing (Fig. 1). Statistical analysis according to Fisher's least significant difference, (FLSD) for comparison between any two means indicated significant differences ($P = 0.05$) between stages R6, R7, and R8 for Merit and between stages R7 and R8 for Midwest. No significant difference ($P = 0.05$) existed, however, between the percentage of seeds from which virus was detected before and after germination. Storage of Midwest soybean seeds for 6 mo resulted in a slight, but significant, decrease in percentage of virus detected in seeds ($P = 0.05$) (Table 2).

Effect of node position. Analysis of FLSD indicated a significant difference ($P = 0.05$) for the presence of virus in seed from different node positions only when Midwest soybean seeds were germinated immediately after harvesting (Table 2). However, no pattern could be established.

Analysis by FLSD showed no significant difference ($P = 0.05$) for the percentage of mottled seed taken from different node positions of Merit soybean plants. A significant difference ($P =$

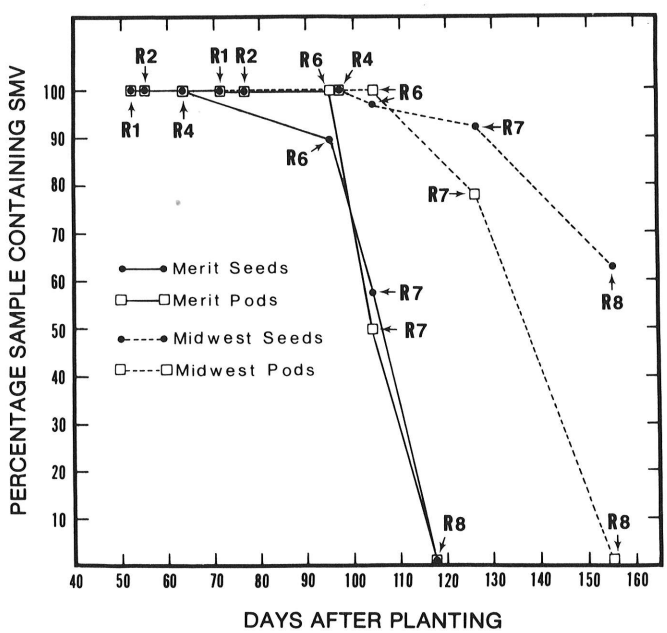

Fig. 1. Detection of the Illinois severe isolate of soybean mosaic virus (SMV-Il-S) from Midwest and Merit soybean flowers, pods, or seeds at various stages of reproductive growth of artificially inoculated plants. Points correspond to developmental reproductive stages R1 to R8 (see reference 11). Flowers were indexed in stages R1 and R2. Seeds and pods were indexed together in stage R4. Pods and seeds were separately indexed in stages R6, R7, and R8.

0.05) was found in the percentage of mottled seed from various node positions of Midwest soybeans, but again we could not establish a pattern (Table 3).

Presence of SMV in seed parts. Infectious virus was detected in the testas, cotyledons, and embryos dissected from immature seeds of both Merit and Midwest soybeans (Table 4). The virus was present in a higher proportion of testas than of either embryos or cotyledons for both cultivars. More cotyledons and embryos contained infectious virus when sampled from Midwest seeds at stage R7 than at stage R6. This result may be due to the smaller amount of tissue indexed at the latter stage. The proportion of Midwest seeds in which infectious virus was detected in the testa declined as the plants matured from stage R7 to R8. Germination and storage did not decrease the proportion of seeds from which infectious virus was detected. For all seed parts indexed, the proportion of Merit seeds from which virus was detected decreased as the seeds matured. Infectious virus was absent from all parts of mature Merit seeds and the virus was not seed transmitted.

Infectious virus was present in the majority of immature testas of both Merit and Midwest but absent from testas of mature seeds, which made it of interest to determine whether viral antigen remained in mature testas. To test this, we dissected Midwest seeds and tested testas for infectivity and by ELISA. Viral antigen was detected by ELISA in all testas taken from 75 Midwest seeds sampled at stage R8, but infectious virus was not detected by local lesion index in any of the same testas. Surface-decontamination of half-testas taken from the same seeds did not alter the above results.

TABLE 2. Detection of soybean mosaic virus (Illinois severe isolate) in seedlings of Midwest and Merit soybeans

	Germinated seedlings			
	Midwest		Merit	
Plant node[a]	H[b]	S[b]	H	S
1	6/10[c] B[d]	7/10	0/8	0/6
2	6/10 B	5/10	0/9	0/7
3	8/10 AB	5/9	0/8	0/9
4	8/10 AB	5/10	0/9	0/8
5	6/10 B	6/9	0/8	0/8
6	10/10 A	4/10	0/9	0/10
7	4/8 BC	6/9	0/10	0/9
8	1/6 C	5/8	0/10	0/9
9	6/8 AB	5/8	0/7	0/7
10	4/6 AB	2/3	0/8	0/8
11	8/8 AB	1/3	0/9	0/8
12	4/8 BC	3/3	0/9	0/8
%[e]	67.6 I	58.4 J		

[a] Node positions are numbered starting at the bottom of the plant.
[b] Abbreviations: H = seedlings derived from seeds germinated immediately after harvesting. S = seedlings derived from seeds stored for 6 mo at 14 C before germination.
[c] The fraction indicates the number of positive reactions for SMV divided by the total number of samples indexed.
[d] Entries followed by a common letter are not significantly different ($P = 0.05$) according to Fisher's least significant difference test.
[e] Percentage of seeds or seedlings for each stage from which virus could be detected by indexing (20).

DISCUSSION

The reproductive stage of Williams soybeans when inoculated with SMV affected the incidence of seed transmission. Incidence of seed transmission was much lower from plants inoculated after flowering. However, plants inoculated while bearing immature green seeds produced infected seed. Our results do not agree with reports (14,18) that inoculations after flowering do not result in seed transmission and also are not in complete agreement with those of Kendrick and Gardner (15) who reported that the percentage of seed transmission was unaffected by time of inoculation. Seed transmission following late inoculations could have come from seed produced by late flowers. Iizuka (14) showed SMV transmission in pollen produced on infected plants. Transmission of SMV in seeds produced on plants inoculated after flowering may have resulted from outcrossing with infected pollen from early infected plants growing nearby.

Transmission of SMV through seed occurs in only a portion of the seeds produced by an infected plant. Koshimizu and Iizuka (18) found virus in almost all immature seeds of infected plants of soybean cultivar Kawanagare and concluded that during seed maturation, especially during drying, the virus may be inactivated in some seeds when they are mature (18). Our experiment further explored this question by comparing a line with a low incidence of seed transmission with one having a relatively high incidence of seed transmission. We also indexed for virus more often during seed development to determine the timing of virus inactivation. Our results appear to confirm those of Koshimizu and Iizuka (18) that varying rates of flower or immature seed infection do not account for differences in rates of seed transmission. Since SMV was present in 100% of the young reproductive parts from both cultivars, variation in the inital rates of infection of these reproductive parts does not explain the observed differences in the percentage of seed transmission. As seeds from Midwest and Merit soybeans matured and

TABLE 3. The percentage seed coat mottling of seeds taken from different nodes of Merit and Midwest soybean plants infected with the Illinois severe isolate of soybean mosaic virus

	Seed coat mottling (%) in cultivars:	
Plant node	Merit	Midwest
1	63.8 a	89.9 abc[z]
2	63.5 a	94.1 ab
3	53.9 a	88.2 abc
4	84.2 a	98.2 a
5	62.5 a	79.8 cd
6	80.0 a	95.9 ab
7	71.7 a	85.0 bcd
8	69.7 a	84.9 bcd
9	71.6 a	88.3 abc
10	70.6 a	84.1 bcd
11	78.9 a	91.5 abc
12	70.9 a	75.5 d

[z] Entries followed by a common letter are not significantly different ($P = 0.05$) according to Fisher's least significant difference test.

TABLE 4. Detection of infectious soybean mosaic virus (SMV) in the different parts of Midwest and Merit soybean seeds and in germinated seedlings

	Ratio of SMV-infected to total observed seed parts:							
	Testa		Cotyledon		Embryo		Seedling	
Stage[a]	Midwest	Merit	Midwest	Merit	Midwest	Merit	Midwest	Merit
R6	61/75[b]	67/75	13/75	16/75	16/75	12/75		
R7	65/75	65/75	27/75	7/75	32/75	5/75		
R8	2/75	0/75	24/75	0/75	25/75	0/75		
At harvest							39/72	0/53
After storage							28/66	0/49

[a] Stages R6, R7, and R8 correspond to developmental reproductive stage descriptions in reference 11. 'Harvest' means seedlings derived from seeds that were germinated immediately after harvesting. 'Storage' means seedlings derived from seeds that were stored for 6 mo at 14 C before germination.
[b] Number of positive reactions for SMV per number of samples indexed.

dried, the percentage of seeds containing virus decreased significantly. Inactivation during maturation could account for the lack of, and variation in, rates of seed transmission in soybeans. The rate of decrease in detectable infectious virus in pods was similar for both Merit and Midwest. Merit seeds began to mature sooner and lost detectable infectious virus more rapidly than did Midwest seeds (Fig. 1). The largest daily decrease in the percentage of seeds with detectable infectious virus occurred between stages R7 and R8 for both Merit and Midwest. The average daily decrease in the percentage of seeds from which infectious virus could be detected from stage R4 and R8 is 1.07% for Midwest and 2.77% for Merit.

Infectious SMV previously was found associated with the testas of immature seeds (14,18), but Porto and Hagedorn (21) were unable to detect the presence of infectious virus in surface-decontaminated testas from mature seeds.We confirmed these results and also showed that viral antigen is detectable after infectivity is lost. It has been suggested that virus particles present in the testa are inactivated during the process of seed maturation (21). Our results may support the idea that virus may be inactivated within the testas of maturing seeds. The technique used for surface decontamination was not the cause of the virus inactivation within the testas tested. In fact, testas from mature seeds apparently were not contaminated with infectious virus.

Seed transmission, with a few possible exceptions (6,19,25), is dependent on infection of the embryo (2,23). We found infectious virus associated with cotyledons and embryos from both immature and mature seeds of Midwest, a cultivar that transmits SMV through its seeds. The soybean cultivar 'Merit', in which SMV is not seed transmitted, had infectious virus in embryos and cotyledons of immature seeds but not in mature seeds. This supports a previous report (18) that SMV in immature soybean embryos is inactivated during seed maturation in certain cultivars. SMV resembles the majority of seed transmitted viruses in that embryo infection is a prerequisite for seed transmission. Our results (Table 4) also indicate that the mechanism preventing seed transmission in certain genotypes is not caused by the resistance of the immature embryo to virus infection.

Germination of mature seeds had no effect upon the percentage of Midwest seeds transmitting SMV, which agrees with a previous report (18). Storage for 6 mo reduced the percentage of seed transmission in Midwest soybeans. This is not in disagreement with previous work showing that SMV can be recovered from 2-yr-old soybean seeds (15) since the reduction found here, although significant, was small (Table 2).

Cooper (7) reported that Merit possesses a major gene (*Im*) for resistance to SMV-induced seed mottling and Kiihl (17) cited reports that in Merit inoculated with the isolate SMV-1, 40% of the seeds were lightly mottled. In our work, Merit plants inoculated with SMV produced mottled seed, but no significant difference was found in the percentage of mottled seeds taken from different nodes on the same plant. However, a significant difference was found for Midwest node position and seed coat mottling but no pattern was discerned. In previous work, no correlation was found between the incidence of seed transmission and the seed's position on the plant for soybean mosaic (9,15) and tobacco ringspot (1) viruses in soybean, lettuce mosaic virus in lettuce (8), cowpea chlorotic mottle virus in cowpea (13), and bean common mosaic virus in bean (10). With one exception, we found no significant difference in the incidence of SMV in seeds from different nodes of Merit and Midwest soybeans.

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