Sugarcane Mosaic Virus Strain Maize Dwarf Mosaic Virus B as a Pathogen of Eastern Gamagrass

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ABSTRACT

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Eastern gamagrass (EGG) (*Tripsacum dactyloides*) is a high-quality, high-production native forage grass with potential as a high-protein, perennial grain crop. We used enzyme-linked immunosorbent assay to test EGG samples for virus infection. Over a 2-yr period, we found five instances of maize dwarf mosaic virus (MDMV) and a high incidence (12 and 72% in 3-mo-old and 5-yr-old plantings, respectively) of sugarcane mosaic virus strain MDMV-B (SCMV-MDMV-B) in experimental breeding nurseries in Kansas. Incidence of SCMV-MDMV-B was higher in older breeding nurseries. SCMV-MDMV-B, but not MDMV, was found in three of 42 natural EGG stands. EGG plants infected by SCMV-MDMV-B showed no symptoms or a range of symptoms from mild mosaic to extensive chlorotic spots that became necrotic. EGG seedlings grown from two seed sources and inoculated in the greenhouse were infected by four MDMV and five SCMV-MDMV-B isolates. SCMV-MDMV-B apparently overwinters in infected EGG and has the potential to be a serious disease problem for this crop.

Eastern gamagrass (EGG) (*Tripsacum dactyloides* (L.) L.) has been reported to be a host for maize dwarf mosaic virus (MDMV) (18), but natural infection of EGG by sugarcane mosaic virus strain MDMV-B (SCMV-MDMV-B) has not been reported. In the spring of 1990, EGG with mosaic symptoms from a breeding nursery in Saline County, KS, reacted in enzyme-linked immunosorbent assay (ELISA) to antisera made to MDMV and SCMV-MDMV-B (8).

Two studies reported infection of EGG by MDMV under greenhouse conditions (14,18), but MDMV failed to infect EGG in the greenhouse in three studies (5,11,13). Efforts to infect EGG with SCMV-MDMV-B have been unsuccessful (5,13,20), with one exception (10).

Because infection at the nursery site in Kansas appeared to be extensive, we began to investigate whether MDMV and SCMV-MDMV-B are potentially serious pathogens of EGG. This problem is relevant because EGG is being developed as a new forage crop (4) and is being studied as a potential perennial grain crop (23).

We surveyed EGG of different ages in nurseries and natural stands to determine incidence of infection and symptoms caused by MDMV and SCMV-MDMV-B. We also investigated the susceptibility of EGG seedlings to infection by isolates of MDMV and SCMV-MDMV-B.

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MATERIALS AND METHODS

Virus isolates and source plants. Virus isolates were maintained in sorghum (*Sorghum bicolor* (L.) Moench) cultivar Bugoff (Asgrow) in a greenhouse at 27 ± 4 C. Sorghum planting conditions, inoculum preparation, and inoculation procedures were as described by Seifers (15). This cultivar was chosen for virus maintenance and infectivity assays because it is easily infected by MDMV and SCMV-MDMV-B (16) and is reportedly resistant to maize chlorotic mottle virus (MCMV) (22). The latter trait we considered important because EGG is reportedly susceptible to MCMV (2). The sources and characteristics of the virus isolates used in this study are given in Table 1.

Enzyme-linked immunosorbent assay. Antisera and buffers used for double-antibody sandwich enzyme-linked immunosorbent assay (ELISA) were prepared as described by Seifers and Caceres (16). The immunoglobulin G (IgG) was used at 2.5 μg/ml, and the sample was ground in phosphate-buffered saline (1:25, w/v) containing 0.05% Tween 20 and 2% polyvinylpyrrolidone (average molecular weight 40,000), pH 7.4. Absorbance values were compared against those of healthy EGG or sorghum. Except where otherwise stated, values at 405 nm four times greater than those of healthy checks were considered positive.

All extracts from EGG were tested against antisera to MDMV and SCMV-MDMV-B, and some were tested against antisera to johnsongrass mosaic virus (JGMV) (formerly MDMV-0) (8), wheat streak mosaic virus, MCMV (PVAS 262), and barley yellow dwarf virus (BYDV) (the latter were sent to Agdia, Elkhart, IN). Antiserum to JGMV was prepared in our laboratory using an isolate collected at Hays, KS. Positive controls for JGMV and MCMV were infected sorghum and corn, respectively, previously dried and maintained at −20 C.

Field sampling of natural stands and nurseries. Nurseries in Saline and Riley counties, KS, were sampled in spring and early summer of 1990 and 1991 and again in late summer and early fall of 1991. Saline County nurseries were monoculture plantings of diverse EGG germ plasm collected from six states and established in the springs of 1986, 1988, 1989, 1990, and 1991. Riley County nurseries were 1- and 11-yr-old plantings of diverse origin. The EGG samples were placed on ice for transport to the laboratory for ELISA. Some samples were mailed to the laboratory and arrived in good condition.

In addition to the nurseries, 42 natural stands of EGG were sampled in the spring and early summer of 1990 and 1991. Five samples were taken from each stand. Each sample consisted of two leaves from separate plants with obvious or apparent mosaic symptoms.

Infectivity assays. Six days after planting, sorghum plants were manually inoculated (9) with EGG tissue ground (1:4, w/v) in 20 mM potassium phosphate buffer, pH 7, with 1 g of abrasive (Crystolon flour B, 600-mesh; Norton Co., Worcester, MA) added per 100 ml of inoculum. Inoculated plants were maintained in a greenhouse under natural light conditions at 27 ± 5 C.

Infection of EGG by MDMV and SCMV-MDMV-B isolates. The EGG seed sources were a Kansas cultivar, Pete (4), and a Missouri source (Sharp Bros. Seed Co., Clinton, MO). The seed cases (modified spikelets) were removed, and seeds were planted into soil-filled metal

flats (30 × 70 cm), with 11 rows per flat and 10 seeds per row. All flats were maintained in a greenhouse under natural lighting. The experiment was repeated three times. The temperature ranges were 24–37, 27–39, and 28–38 C for experiments 1, 2, and 3, respectively.

At 21, 16, and 16 days after planting for experiments 1, 2, and 3, respectively, plants of uniform size (second leaf 10% [range 8–12%] as long as the first leaf) were selected, and equal numbers were inoculated (1:10, w/v) with each of the nine virus isolates on the first leaf with a DeVilbiss atomizer (4.2 kg/cm^2 air pressure) held 1–2 cm from the plants until water-soaked lesions could be seen on the inoculated leaves. Inoculated plants were inspected daily for symptoms and were harvested for ELISA 14 days after inoculation. The inoculated leaf was removed and discarded, and a portion of the remaining foliage was weighed (some was retained for infectivity assays) and processed for ELISA. Plants that had been rubbed with buffer and abrasive served as negative ELISA controls and were harvested and treated in an identical manner.

Relationship of virus infection to necrotic spot symptom. Some nursery-grown EGG plants exhibited chlorotic spots, which later became necrotic (typically 1–10 × 1–3 mm in size). Some of the necrotic lesions appeared water-soaked. Necrotic spots were usually discrete, but confluent lesions were also common. Plants with necrotic spots usually tested positive for SCMV-MDMV-B. However, initial inoculation experiments to the cultivar Pete resulted in mosaic symptoms but no necrotic spots.

To try to clarify the relationship between the development of necrotic spots and infection with SCMV-MDMV-B, we selected a plant (designated 2-4-14-3) from the nursery in Saline County that consistently exhibited a severe necrotic spot symptom (based on field notes of 1989 and 1990) and that tested positive in ELISA for SCMV-MDMV-B. It was removed while dormant in April 1991 and divided into 13 pieces, each having a single tiller with axillary buds. Each piece was potted in a separate pot containing a peat-vermiculite mixture and grown in the greenhouse at 22–32 C under natural light conditions. Six of the clones developed mosaic symptoms, which later became necrotic spots. The leaves from these plants tested positive for SCMV-MDMV-B in ELISA. Isolations were made from both chlorotic and necrotic spots excised from the ELISA-positive tissue to determine whether fungal pathogens were present.

The other seven EGG clones were symptomless and tested negative in ELISA for MDMV and SCMV-MDMV-B. These were propagated to yield a total of 14 plants. In March 1992, the leaves on all tillers were cut off 1 cm from the rhizome, and 10 of the plants were inoculated with SCMV-MDMV-B in two ways. One set of five plants was inoculated at the cut end of the leaf tissue with a 1:10 (w/v) dilution of inoculum (from source plants inoculated 14 days earlier with the isolate 1990-3 from EGG). The other five plants were inoculated over a period of 1 wk at the tip 1-cm section of each of three consecutive leaves as they emerged on each tiller (1:10 [w/v] dilution of inoculum). The remaining four plants were mock-inoculated as controls (two for each inoculation treatment). Plants were incubated at 15–39 C for 5 wk under natural light conditions in a greenhouse.

Tillers of plants that developed chlorotic and necrotic spots were tested for MDMV and SCMV-MDMV-B by ELISA as described previously. Leaves from plants that tested positive for SCMV-MDMV-B were cut into sections containing one to four chlorotic or necrotic spots (at least 50 chlorotic or necrotic spots were tested). Leaf pieces were taken for fungal isolations. Mock-inoculated controls were treated in an identical manner.

Table 1. Sources and characteristics of isolates of maize dwarf mosaic virus (MDMV) and sugarcane mosaic virus strain MDMV-B (SCMV-MDMV-B) used in this study

Strain or isolate	Supplier[a]	Plant source	Infection of johnsongrass
1990-2	DS	EGG (Saline Co., KS)	No
1990-8	DS	EGG (Riley Co., KS)	No
SCMV-MDMV-B_{KS}	DS	Sorghum (Kansas)	No
SCMV-MDMV-B_{NB}	SJ	Sorghum (Nebraska)	No
SCMV-MDMV-B_{TX}	RT	Sorghum (Texas)	No
MDMV-1990-1A	DS	EGG (Saline Co.)	Yes
$MDMV_{KS}$	DS	Sorghum (Kansas)	Yes
$MDMV_{MS}$	GS	Corn (Mississippi)	Yes
$MDMV_{TX}$	RT	Sorghum (Texas)	Yes

[a] DS = Dallas Seifers, Kansas State University, Hays; SJ = Stanley Jensen, USDA-ARS, Lincoln, NB; RT = Robert Toler, Texas A&M University, College Station; GS = Gene Scott, USDA-ARS, Mississippi State, MS.

Table 2. Enzyme-linked immunosorbent assay values[a] for 1:25 (w/v) dilutions of eastern gamagrass (EGG) extracts reacted against antisera to maize dwarf mosaic virus (MDMV) and sugarcane mosaic virus strain MDMV-B (B)

	Antiserum		Symptoms on EGG[c]	
Sample[b]	MDMV	B	Mosaic	Necrotic spots
1990-1	0.781	0.958	+	−
1990-2	0.031	1.019	+	+
1990-3	0.018	0.578	+	+
1990-4	0.044	1.030	+	+
1990-5	0.024	0.737	+	−
MDMV	0.332	0.097	NT	NT
B	0.055	0.540	NT	NT
Healthy EGG	0.057	0.057	−	−

[a] Values were considered positive if they were three times the value for the equivalent healthy extract.

[b] Extracts from the EGG tissue from the Saline County nursery were also tested for infection by wheat streak mosaic virus and johnsongrass mosaic virus. Samples 1990-2, 1990-3, 1990-4, and 1990-5 were tested for barley yellow dwarf virus infection, and sample 1990-3 tested positive for this virus (strain MAV). MDMV and B were isolated in Kansas.

[c] NT = not taken.

RESULTS

Field sampling of EGG nurseries and natural stands. The initial samples of EGG (1990-1 to 1990-5) were all positive for SCMV-MDMV-B (Table 2). In addition, 1990-1 reacted to MDMV serum and 1990-3 was positive for BYDV. The reaction to both MDMV and SCMV-MDMV-B sera indicated a probable double infection of plant 1990-1 by these viruses. This was verified by successful transmission to johnsongrass (nonhost for SCMV-MDMV-B) (7) and sorghum (host for both viruses), followed by confirmatory ELISA tests. No healthy control showed symptoms, and extracts from these controls were never positive in ELISA and did not infect johnsongrass or sorghum.

In 1990 and 1991, 300 plants in Saline County and 89 in Riley County were sampled. In Saline County, infection ranged from 12% in a 3-mo-old planting to 72% in the 5-yr-old planting (Table 3). Infection percentages indicated by symptoms were similar to those determined by ELISA, differing by 4–11% (Table 3). Three samples were positive for MDMV, whereas the remainder were infected by SCMV-MDMV-B. Three of the MDMV positives were first tested in 1990. The plants were symptomless and gave negative results in ELISA in 1991. Tissue from the plants that had been frozen in 1990 was positive in 1991.

In Riley County, all seven plants with mosaic symptoms that were sampled in July 1990 and 13 of 25 (56%) sampled in August 1990 were infected by SCMV-MDMV-B. All but one plant in the July sample had symptoms (one plant, 1990-14, was the original gynomonoecious sex form used in both the Riley and Saline county breeding programs [3]). In the August sample, 11 plants rated as having symptoms tested negative and the only symptomless plant tested positive. Two of the seven plants sampled in July were from a natural population 2.4 km from the nursery. One plant was also infected by MDMV. In 1991, 29 of 57 (50.8%) plants sampled from the nursery were infected by SCMV-MDMV-B; 39 plants were symptomless, but 11 of these reacted positively in ELISA; the remaining plants showed symptoms and had positive ELISAs).

Three of the 42 natural stands of EGG in 25 Kansas counties sampled during 1990 and 1991 had plants (with symptoms) that tested positive in ELISA for SCMV-MDMV-B. None of the plants tested positive for MDMV. Fifty-eight percent of the 100 plants surveyed in one of the infected stands (from a population of more than 1,000) and 100% of the 50 plants sampled in a second had mosaic and necrotic symptoms. The number of plants with symptoms was not recorded for the third stand, but all five of the samples taken tested positive in ELISA.

Symptoms of SCMV-MDMV-B infection on EGG. Symptoms exhibited by infected EGG varied from a general mosaic to oblong chlorotic spots and oblong necrotic spots (1–10 × 1–3 mm) dispersed throughout the leaf (Fig. 1). In many leaves, a gradation was observed in the development of the necrotic spots: at the base of the leaf, chlorotic spots were evident; toward the middle of the leaf, chlorotic spots often became water-soaked in appearance; and at the tip of the leaf, the spots were necrotic. In the field, mosaic symptoms were most pronounced early in the season as plants emerged from dormancy. The mosaic symptoms varied from a pale green, very mild mosaic on just a few of the youngest leaves to a very distinct, bright mosaic on the entire plant. Dwarfing was observed in some plants. Water-soaked lesions and necrotic spots developed later than mosaic symptoms and were most pronounced in midsummer. Occasionally, symptomless plants tested positive by ELISA for SCMV-MDMV-B.

In an effort to sort out inconsistencies between symptoms and ELISA results, 19 EGG plants that were symptomatic (whole-plant rating) in May 1991 and then symptomless and negative in ELISA in August 1991 were rated for symptoms and tested by ELISA again in September. In September, 12 of the 19 were positive in ELISA, 11 with symptoms and one without. Symptom ratings for August and September were taken from leaves used for ELISA. The remaining seven symptomless plants tested negative in ELISA.

Relationship of virus infection to necrotic spot symptom. The cloned EGG tested positive only to SCMV-MDMV-B antiserum. Twenty chlorotic spots and 100 necrotic spots from five EGG clones (testing positive for SCMV-MDMV-B) were excised for fungus isolation. Only one fungus (unknown identity) was isolated from one of 20 chlorotic spots. No fungi were isolated from 91 of the 100 necrotic spots, and saprophytic fungi were isolated from the other nine spots. No pathogenic fungi were isolated from the leaf tissue.

Four of the 10 cloned EGG that tested negative for MDMV and SCMV-MDMV-B and were then reinoculated with SCMV-MDMV-B developed symptoms within 4–5 wk after inoculation (two plants from each inoculation treatment). Two additional plants developed symptoms 9 wk after inoculation and tested positive in ELISA for SCMV-MDMV-B only. Chlorotic spots in all infected plants later became necrotic. Mock-inoculated EGG clones remained

Table 3. Estimates of infection of eastern gamagrass (EGG) in breeding nurseries in Saline County by sugarcane mosaic virus strain maize dwarf mosaic virus-B as determined by symptom expression and enzyme-linked immunosorbent assay[a] (ELISA)

Year	Planting age (yr)	Planting size (no.)	Percentage infection (symptoms)	Number tested by ELISA	Percentage infection (ELISA)
1990	5	900	NT[b]	50	72
1990	2	1,780	20	25	16
1990	0.25	3,223	NT	25	12[c]
1991	3	1,637	44	81	37
1991	2	3,223	33.9	80	30
1991	0.25	952	25	25	36
1991	0.25	NT	NT	25	24

[a] Samples (1:25 [w/v]) were also tested for wheat streak mosaic virus and johnsongrass mosaic virus. Positive values were greater than eight times the value for the healthy control. The lowest positive value from EGG was 0.097, with a value from an equivalent extract of healthy EGG of 0.011.
[b] NT = not taken.
[c] Three (12%) of the EGG samples reacted to maize dwarf mosaic virus antiserum.

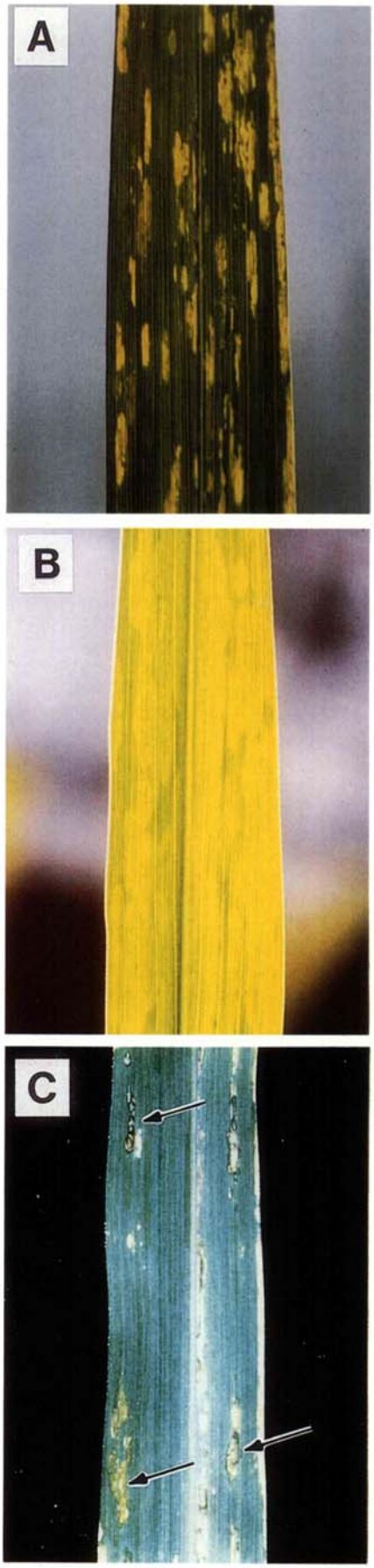

Fig. 1. Eastern gamagrass leaves showing symptoms associated with infection by sugarcane mosaic virus strain maize dwarf mosaic virus B: mosaic spots **(A)**, general mosaic (transmitted light) **(B)**, and mosaic spots that have become necrotic (arrows) **(C)**.

symptomless. No fungi were isolated from any spots from EGG clones inoculated with virus or from mock-inoculated tissue.

Infection of EGG by MDMV and SCMV-MDMV-B isolates. All MDMV and SCMV-MDMV-B isolates infected EGG seedlings from both seed sources (Table 4). The number of symptomatic seedlings varied among the three experiments for a given isolate. In all experiments, symptoms first appeared in some plants 7 days after inoculation and continued to appear in other plants until 14 days after inoculation, when plants were harvested for ELISA. Plants in all experiments with mosaic symptoms were tested against antisera to MDMV and SCMV-MDMV-B. Extracts from these plants reacted only to the homologous antiserum. All plants without symptoms were assayed by ELISA (1:10, w/v) against both MDMV and SCMV-MDMV-B antisera. No plant without symptoms reacted positively to MDMV antiserum. Some symptomless plants (two, two, and one in experiments 1, 2, and 3, respectively) reacted to SCMV-MDMV-B antiserum. Maximum and minimum ELISA values for symptomless plants were 0.323 and 0.093, respectively, compared to 0.014 for extract from healthy EGG.

Sorghum plants were inoculated with extracts from one EGG plant (from each experiment) inoculated with each virus isolate that showed mosaic symptoms and tested positive in ELISA. In addition, all five plants with no symptoms but positive ELISA reactions and five plants with no symptoms and negative ELISA reactions were tested in a like manner. All extracts made from plants with symptoms infected sorghum. Extracts from two symptomless plants with positive ELISAs—one plant in experiment 1 ($A_{405nm} = 0.323$) inoculated with a Kansas isolate of SCMV-MDMV-B, and one plant in experiment 2 ($A_{405nm} = 0.215$) inoculated with the 1990-2 SCMV-MDMV-B isolate—infected two and one, respectively, of 10 sorghum plants. Extracts from the remaining symptomless plants (inoculated with the Kansas isolate of SCMV-MDMV-B) that were positive in ELISA (A_{405nm} values of 0.121, 0.101, and 0.093) did not infect sorghum. Extracts from symptomless plants negative in ELISA did not infect sorghum. Extracts from systemically infected sorghum assay plants were positive in ELISA to homologous antiserum.

DISCUSSION

This study confirms reports of the pathogenicity of MDMV (14,18) and SCMV-MDMV-B (10) to EGG. Inoculated seedlings from both EGG seed stocks could be infected with all four isolates of MDMV and five isolates of SCMV-MDMV-B tested (Table 4). Previous studies that failed to demonstrate infection could have been hampered if EGG clones used were resistant (resistant clones have yet to be documented). The consistent infection of EGG seedlings that we obtained with isolates of MDMV and SCMV-MDMV-B may have resulted from our use of a high-pressure inoculation system, as opposed to leaf rubbing techniques used in some previous studies (5,12,14,18,20).

SCMV-MDMV-B was the predominant virus found in 2 yr of sampling of nurseries and natural stands of EGG, with only five occurrences of MDMV (none in natural stands). This was unexpected for several reasons: the only previous report of natural infection of EGG was by MDMV (18), MDMV occurs over a larger area and infects more species in the Poaceae than does SCMV-MDMV-B (13), MDMV more readily infects EGG when plants are mechanically inoculated (10), SCMV-MDMV-B has a lower rate of transmission by vectors (1), and MDMV is much more prevalent than SCMV-MDMV-B on corn and sorghum in Kansas (D. L. Seifers, *unpublished*).

The anomalous dominance of SCMV-MDMV-B over MDMV on EGG suggests that the epidemiology of these viruses on this species differs significantly from their epidemiology on corn or sorghum in Kansas. SCMV-MDMV-B may overwinter in EGG more successfully than MDMV. Successful overwintering of SCMV-MDMV-B was demonstrated when winter-dormant plants were transplanted to the greenhouse: new growths on six of 13 divisions from a single field-grown plant were infected with SCMV-MDMV-B. We also found evidence that MDMV is less successful at overwintering: three plants that were positive for MDMV in 1990 were no longer infected when they were retested in 1991. However, this hypothesis could not explain the dominance of SCMV-MDMV-B in first-year stands (Table 3).

An alternative explanation for the dominance of SCMV-MDMV-B would be that, contrary to previous reports (10), EGG resists infection by MDMV more than it resists SCMV-MDMV-B. However, both viruses attain high titers in infected EGG (Table 2). When two sources of EGG germ plasm were challenged with five isolates of SCMV-MDMV-B and four isolates of MDMV, all virus isolates infected both seed sources (Table 4).

Another possibility is that the vector populations involved with EGG are different from those associated with corn or sorghum. Vectors of SCMV-MDMV-B include *Rhopalosiphum maidis, R. padi, Myzus persicae,* and *Schizaphis graminum* (1,17). *R. maidis* and *S. graminum* are important vectors for corn and sorghum (1,19). *S. graminum* nymphs reach maturity on excised EGG leaves, but EGG is one of the least effective hosts for this aphid (6). We observed colonies of *S. graminum, R. maidis,* and *R. padi* on EGG in the greenhouse, but in the field, small colonies of aphids occurred inside the boot of reproductive tillers only occasionally. Three such colonies collected from an EGG nursery in Riley County on 6 July 1992 were identified as *R. maidis.* Which aphid species are important vectors of SCMV-MDMV-B in EGG plantings remains uncertain.

Our survey of natural stands of EGG for virus infection revealed only three locations where plants were infected with SCMV-MDMV-B. Genetic resistance probably does not explain the low incidence of infection in natural stands: progeny from 37 of these stands were susceptible when grown in breeding nurseries (M. K. Handley, *unpublished*). Therefore, inoculum seems to be limiting in nature. However, once the virus is introduced into a planting, it appears to

Table 4. Number of eastern gamagrass (EGG) plants from two seed sources[a] with general mosaic symptoms after inoculation with isolates of maize dwarf mosaic virus (MDMV) and sugarcane mosaic virus strain MDMV-B (SCMV-MDMV-B)[b]

	Experiment 1		Experiment 2		Experiment 3	
Virus isolate[c]	MO	Pete	MO	Pete	MO	Pete
1990-2	2/9	5/6	3/8	2/4	2/10	1/5
1990-8	4/9	2/6	2/8	1/4	2/10	1/5
B_{KS}	6/9	3/6	3/8	1/4	1/10	3/5
B_{NB}	8/9	5/6	3/8	3/4	1/10	2/5
B_{TX}	6/9	2/6	2/8	2/4	2/10	2/5
1990-1A	5/9	3/6	1/8	1/4	8/10	4/5
$MDMV_{KS}$	6/9	2/6	1/8	1/4	7/10	3/5
$MDMV_{MS}$	8/9	2/6	3/8	2/4	10/10	3/5
$MDMV_{TX}$	5/9	6/6	4/8	3/4	9/10	2/5

[a] EGG seed sources were Missouri (MO) and Pete, a composite of 70 accessions originating as seed from native populations of EGG in Kansas and Oklahoma (4).

[b] The numerator is the number of EGG plants with mosaic symptoms; the denominator is the total number of EGG plants that were inoculated with the virus isolate.

[c] SCMV-MDMV-B isolates were 1990-2 and 1990-8 (isolated from EGG) and B_{KS}, B_{NB}, and B_{TX} (isolated in Kansas, Nebraska, and Texas, respectively, from sorghum); MDMV isolates were 1990-1A (isolated from EGG in Kansas) and $MDMV_{KS}$, $MDMV_{MS}$, and $MDMV_{TX}$ (isolated in Kansas, Mississippi, and Texas, respectively).

spread.

Detection of virus infection in EGG was often problematic. In some instances, ELISA tests detected SCMV-MDMV-B in symptomless plants, indicating that symptom expression is not always a reliable indicator of infection. Some of the symptomless plants may have had recent infections that were still latent. Also, some EGG genotypes may be symptomless carriers of SCMV-MDMV-B. Symptomless plants have been reported for other grasses infected by MDMV and SCMV-MDMV-B (12). However, environmental conditions may also play an important role in virus detection. Some plants that showed symptoms in the spring had no symptoms later in the summer, and extracts from those plants did not react in ELISA; however, in the fall some of these plants had mosaic symptoms and reacted positively in ELISA. The virus titer may decline, resulting in reduced expression of mosaic symptoms, under hot summer conditions.

The necrotic spots were initially attributed to fungal pathogens. However, no pathogenic fungi were isolated from symptomatic leaves in our studies. We also considered the possibility that the necrosis was the result of double infection with SCMV-MDMV-B and BYDV or MDMV, but we rejected this hypothesis because other viruses were uncommon and because only SCMV-MDMV-B was required to reproduce the symptom in inoculation studies. No plant infected with only MDMV was observed to have necrotic spots, but the sample size was small.

Although most EGG clones developed mosaic (at least in the spring) when infected with SCMV-MDMV-B, many did not express the necrotic symptom. The necrotic reaction is probably a genetic-environmental response of certain EGG genotypes to infection by SCMV-MDMV-B. A similar necrotic response was reported for *Setaria viridis* infected by MDMV, whereas infection by SCMV-MDMV-B resulted in mosaic spots or streaks (21). In addition, sorghum that is infected by SCMV-MDMV-B and exhibits mosaic symptoms may or may not develop necrosis, depending on genotype and environmental conditions (16).

SCMV-MDMV-B may threaten the production of EGG as a forage or grain crop in the central Great Plains. Incidence of virus infection ranged from 12 to 72% in EGG nurseries. Further studies will be required to elucidate the effects of SCMV-MDMV-B on agronomic performance of EGG and to seek sources of genetic resistance.

Because we found a low frequency of natural stands infected by SCMV-MDMV-B, and because we have not observed high populations of aphids on EGG in the field, it is unlikely that EGG is currently a significant reservoir of SCMV-MDMV-B that threatens corn or sorghum plantings. If EGG were more widely planted as a crop, it might become epidemiologically significant, especially if it sustained high populations of aphids.

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