Susceptibility of Representative Native Mississippi Grasses in Six Subfamilies to Maize Dwarf Mosaic Virus Strains A and B and Sugarcane Mosaic Virus Strain B

Eugen Rosenkranz

Research plant pathologist, Agricultural Research Service, U.S. Department of Agriculture and professor, Department of Plant Pathology and Weed Science, Mississippi State University, Mississippi State 39762.

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ABSTRACT

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A representative collection of the Mississippi grass flora, consisting of 42 annual and 71 perennial grasses, contained 79 host species and 34 nonhost species of maize dwarf virus strain A (MDMV-A), strain B (MDMV-B), and sugarcane mosaic virus strain B (SCMV-B). Of the 79 host species, 68 were new hosts which were divided into 63 species susceptible to MDMV-A, 47 species susceptible to MDMV-B, and 48 species susceptible to SCMV-B; 40 species were susceptible to all three strains. Among the 34 insusceptible species, 29 were new nonhosts. Host species were found in all six subfamilies of the Gramineae, in 14 of 16 tribes, and in 40 of 51 genera included in this study. The subfamily Festucoideae had the highest percentage of species with latent infection, and the festucoid species also exhibited the least differential reaction to the three virus strains. The tribe Andropogoneae in the subfamily Panicoideae had the highest proportion of hosts to nonhosts, but species with the greatest susceptibility were in the tribe Paniceae. The subfamily Eragrostoideae had twice as many species susceptible to MDMV-A as to MDMV-B or SCMV-B. Of the two Mississippi species in the subfamily Bambusoideae, one was latently susceptible to MDMV-A, the other insusceptible to all three strains. Eight of the nine species in the subfamily Oryzoideae occurring in Mississippi were hosts of MDMV or SCMV. Species in the subfamily Arundinoideae were evenly divided between hosts and nonhosts. Host species made up 88% of the annual and 61% of the perennial grasses tested. Infectivity profile of MDMV-B resembled more closely that of SCMV-B than that of MDMV-A. Genera with the closest taxonomic position to corn seem less susceptible to these viruses than genera somewhat more distant to corn in the phylogeny of the Gramineae.

Additional key words: corn, differential host, host range, symptomless host, *Zea mays*.

Maize dwarf mosaic virus (MDMV) causes an important disease in a major crop and has an extensive geographic distribution in the USA. Of the two principal strains, strain A (MDMV-A) occurs over a larger area and infects more species in the Gramineae than strain B (MDMV-B) (21). The latter strain tends to have a more northern range than MDMV-A. Only 66 genera of the 122 grass genera with representative species in the USA have been tested for reaction to MDMV. Even fewer genera have been included in host range studies of the closely related sugarcane mosaic virus (SCMV), which also infects corn (*Zea mays* L.).

Previous investigations of the host ranges of MDMV and SCMV emphasized festucoid grasses (4,5,12,15,16,22,23,25) and panicoid grasses (17,19). Therefore, reaction of species in the subfamilies Eragrostoideae, Bambusoideae, Oryzoideae, and Arundinoideae requires further evaluation. Eragrostoideae constitute 28.5% of all U.S. grass species and are widely distributed in all parts of the USA (6).

Mississippi grass flora includes ~315 grass species. Half of them belong to the subfamily Panicoideae, one quarter to the subfamily Eragrostoideae; the remainder are distributed unevenly among the other four subfamilies, with the greatest number of these belonging to the Festucoideae. This investigation provides information on the reaction to MDMV and SCMV of grass species in subfamilies and tribes that received insufficient attention in earlier studies.

The objectives of this research were: to locate and identify as many wild grass species as possible not yet tested for reaction to MDMV and SCMV; to produce wild grass seed in the greenhouse; to concentrate the testing on species from the previously underrepresented subfamilies Eragrostoideae, Bambusoideae, Oryzoideae, and Arundinoideae; to determine the concentration and distribution of the susceptible species in the six subfamilies of Gramineae; to further characterize MDMV-A, MDMV-B, and strain B of SCMV (SCMV-B) by host range studies; to search for potential overwintering hosts of MDMV-B; to find more suitable differential hosts for these viruses; and to gain a better understanding of the relationship among the three virus strains.

MATERIALS AND METHODS

Except for *Chloris floridana* and *Heteropogon melanocarpon* found by the author in Alabama and six species (*Brachiaria plantaginea*, *Chloris gayana*, *Eragrostis curvula*, *Eragrostis diffusa*, *Leptochloa scabra*, and *Setaria adhaerans*) acquired from various sources, all grasses were collected by the author in the wild in Mississippi. The plants were dug with sufficient soil around the roots to fill a 15- to 20-cm (6- to 8-inch)-diameter clay pot and grown in a greenhouse for seed production. The grasses were identified with the help of A. S. Hitchcock's Manual of the Grasses of the United States (9), F. W. Gould's The Grasses of Texas (7), or A. E. Radford's et al Manual of the Vascular Flora of the Carolinas (14). Uncertain identifications were verified by S. T. McDaniel, Department of Biological Sciences, Mississippi State University.

The harvested seeds were stored at 3 C for a minimum of 6 mo to break the dormancy of perennial grasses, then plated out on moist, sulfur-free germination paper in petri dishes, and placed in a germinator programmed for 30 C/light 10 hr and 20 C/dark 14 hr. Germination ranged from 0 to 100%. Seedlings were transplanted individually into round 7.5-cm (3-inch)-diameter peat pots containing a soil-sand-peat moss mixture (3:1:1, v/v) and were fertilized weekly with a 12-6-6 (N-P-K) liquid fertilizer. The few grasses that did not produce viable seed in the greenhouse were propagated vegetatively.

Two isolates of MDMV-A, one from Mississippi and one from Ohio; an MDMV-B isolate from R. E. Ford, University of Illinois, Urbana; and an isolate of SCMV-B from the U.S. Sugar Crops Field Station, Meridian, MS, were used in the tests described. Strain B of SCMV was selected because it is the most common strain of SCMV in MS. The MDMV strains were maintained in

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plants of sweet corn cultivar Seneca Chief and SCMV-B was maintained in plants of sweet sorghum (*Sorghum bicolor* (L.) Moench) 'Rio'. Viruses were transferred monthly to new source plants.

Grasses were manually inoculated at the three- to four-leaf stage with all four virus isolates on the same day. Five to eight grass species were tested at a time. An attempt was made to have at least 10 seedlings of each species inoculated with each virus isolate and two to five seedlings left uninoculated as checks. Inocula were prepared by triturating succulent leaf tissue with pronounced mosaic symptoms in a mortar with a pestle and expressing sap from the pulp through gauze. The undiluted sap was rubbed with a gauze pad onto leaves dusted with 600-grit silicon carbide. All plants were inoculated only once to reduce loss due to mechanical damage of seedlings among the more delicate species. Grasses were kept before and after inoculation in a greenhouse at 20–30 C under natural light conditions. The inoculated plants were inspected daily during the first 2 wk for the appearance of first symptoms, and the final reading was made ~6 wk after inoculation, when the incidence and severity of disease were recorded. Grasses that remained symptomless in response to one or more virus isolates were back-assayed to 10 sweet corn plants per isolate 6 wk after inoculation, and the sweet corn was observed for 4 wk. Grass species that showed immunity to all three viruses were tested again at a different time of the year.

Aphids were controlled in the greenhouse by fumigation with Plantfume 103 (Plant Products Corp., Blue Point, L.I., NY 11715) and by spraying plants with Pyrenone (Fairfield American Corp., 3932 Salt Rd., Medina, NY 14103).

RESULTS

This collection of 113 grass species in 51 genera, 16 tribes (of 19 represented in Mississippi), and all six subfamilies of the Gramineae contained 79 hosts and 34 nonhosts. Nine of the grasses were tested in the preceding study (19) but are included here to assemble all Mississippi species in the three small subfamilies Bambusoideae, Oryzoideae, and Arundinoideae. Of the 79 host grasses, 68 were new hosts, and these were composed of 63 species susceptible to MDMV-A, 47 species susceptible to MDMV-B, and 48 species susceptible to SCMV-B. The three virus strains had 40 new hosts in common. Among the 34 grasses that reacted with immunity to all virus strains, 29 were new nonhosts.

Species in this study were distributed among 51 genera of the 89 grass genera represented in Mississippi. The 89 genera gathered into 19 tribes, which comprise the Mississippi grass flora, are arranged in Table 1. This is the first time that species in the following 13 genera have been tested for reaction to MDMV and SCMV: *Aira*, *Anthaenantia*, *Cinna*, *Glyceria*, *Hackelochloa*, *Heteropogon*, *Hydrochloa*, *Luziola*, *Sphenopholis*, *Triplasis*, *Zizania*, *Zizaniopsis*, and *Zoysia*. All of these genera, except *Cinna* and *Sphenopholis*, include species susceptible to MDMV or SCMV. Additionally, new host species were found for the first time in *Anthoxanthum*, *Bouteloua*, and *Festuca*, genera that were represented in prior studies without yielding any hosts of MDMV or SCMV. Besides *Cinna* and *Sphenopholis*, other genera that had no susceptible species were *Arundo*, *Axonopus*, *Danthonia*, *Hordeum*, *Melica*, *Paspalum*, *Tripsacum*, *Trisetum*, and *Vulpia*. Thus, the 51 genera represented in this investigation can be classified into 40 genera with host species and 11 without.

Grasses with various degrees of susceptibility to MDMV and SCMV were found in all six subfamilies and in 14 of 16 tribes (Table 2). Member species of the subfamily Festucoideae exhibited the least variability in their response to the three virus strains. If a festucoid grass was susceptible to one virus strain, it usually was susceptible to all three, and conversely, if a species was immune to one strain, it generally was immune to all three. Of the 23 festucoid species tested, the only exceptions were *Festuca rubra*, a symptomless host of only MDMV-A, and *Lolium multiflorum* which produced weak symptoms on very few plants only in response to SCMV-B. The Festucoideae also had the highest percentage of species with latent infection of any subfamily. Nine of the 13 host species found in this taxon were symptomless hosts.

Panicoideae, the largest subfamily of the Mississippi grass flora, is classified into two tribes, Paniceae and Andropogoneae. The 38 species in the tribe Paniceae separated into 26 hosts and 12 nonhosts. Of the 10 species belonging to Andropogoneae, nine were hosts and one was not. Although the Panicoideae had species with the greatest susceptibility to MDMV and SCMV of any subfamily, some genera (*Axonopus*, *Paspalum*, and *Tripsacum*) contained only immune species. The only panicoids with sufficiently different reactions to MDMV and SCMV to qualify as differential hosts were *Andropogon virginicus* and *Setaria glauca*, both of which were susceptible to MDMV-A and MDMV-B but immune to SCMV-B.

The 25 species of the subfamily Eragrostoideae tested were distributed among nine genera, all of which contained host species. However, the 18 host species found were differentially susceptible to the three virus strains. MDMV-A infected all 18 species, whereas MDMV-B infected nine and SCMV-B infected eight of the same grasses. Thus, the infectivity data of MDMV-B in the Eragrostoideae resembled more closely those of SCMV-B than those of MDMV-A. Unlike festucoid grasses, eragrostoids showed no tendency for symptomless infection. Only one species, *Leptochloa panicoides*, was latently infected with MDMV-A while being immune to MDMV-B and SCMV-B.

Bambusoideae is the smallest of the six subfamilies of Gramineae, and is represented in the USA by only three species in two genera. Of the two species of *Arundinaria* endemic to Mississippi, *A. tecta* was infected by only MDMV-A (latently), whereas *A. giganteae* was immune to all three virus strains. It is remarkable that a bamboo would support the multiplication of

TABLE 1. Subfamilies, tribes, and genera of Gramineae represented in Mississippi[a]

Subfamily Festucoideae
- Festuceae: *Bromus*[b], *Festuca*[b], *Vulpia*[b], *Lolium*[b], *Catapodium*, *Poa*, *Briza*, *Dactylis*
- Aveneae: *Sphenopholis*[b], *Trisetum*[b], *Aira*[b], *Avena*, *Holcus*, *Agrostis*[b], *Polypogon*, *Cinna*[b], *Limnodea*, *Anthoxanthum*[b], *Phalaris*[b], *Alopecurus*[b], *Phleum*
- Triticea: *Elymus*, *Hordeum*[b], *Triticum*, *Secale*
- Melicea: *Melica*[b], *Glyceria*[b]
- Stipeae: *Stipa*[b]
- Brachyelytreae: *Brachyelytrum*

Subfamily Panicoideae
- Paniceae: *Digitaria*[b], *Leptoloma*, *Anthaenantia*[b], *Stenotaphrum*, *Brachiaria*[b], *Axonopus*[b], *Eriochloa*[b], *Paspalum*[b], *Panicum*[b], *Oplismenus*, *Echinochloa*[b], *Sacciolepis*, *Setaria*[b], *Cenchrus*[b]
- Andropogoneae: *Imperata*, *Miscanthus*, *Saccharum*, *Erianthus*, *Sorghum*, *Sorghastrum*, *Andropogon*[b], *Arthraxon*, *Microstegium*, *Bothriochloa*, *Eremochloa*, *Elyonurus*, *Manisuris*[b], *Hackelochloa*[b], *Tripsacum*[b], *Zea*[b]

Subfamily Eragrostoideae
- Eragrosteae: *Eragrostis*[b], *Tridens*, *Triplasis*[b], *Muhlenbergia*[b], *Sporobolus*
- Chlorideae: *Eleusine*, *Dactyloctenium*, *Leptochloa*[b], *Gymnopogon*, *Cynodon*, *Chloris*[b], *Bouteloua*[b], *Spartina*[b], *Ctenium*
- Zoysieae: *Zoysia*[b]
- Aeluropodeae: *Distichlis*
- Unioleae: *Uniola*
- Aristideae: *Aristida*[b]

Subfamily Bambusoideae
- Bambuseae: *Arundinaria*[b]

Subfamily Oryzoideae
- Oryzeae: *Oryza*[b], *Leersia*[b], *Zizania*[b], *Zizaniopsis*[b], *Luziola*[b], *Hydrochloa*[b]

Subfamily Arundinoideae
- Arundineae: *Arundo*[b], *Phragmites*, *Cortaderia*
- Danthonieae: *Danthonia*[b]
- Centotheceae: *Chasmanthium*[b]

[a] Adapted and modified by the author from F. W. Gould (6).
[b] Genera represented in this study of the susceptibility.

TABLE 2. Response of native Mississippi grasses in all six subfamilies of Gramineae to inoculation with maize dwarf mosaic virus strain A (MDMV-A) and strain B (MDMV-B) and sugarcane mosaic virus strain B (SCMV-B)

Grass subfamilies, tribes, species, and common names	Growth habit[b]	Number of plants showing symptoms following inoculation with:[a] MDMV-A (Miss.)[c]	Back assay to corn[d]	MDMV-A (Ohio)	Back assay to corn	MDMV-B	Back assay to corn	SCMV-B	Back assay to corn
Subfamily Festucoideae									
Agrostis elliottiana Schult. Elliott bentgrass	A	14/17	10/10	11/17	10/10	13/17	10/10	9/17	10/10
A. hiemalis (Walt.) B.S.P. Winter bentgrass	P	0/22	0/10	0/22	0/10	0/22	0/10	0/22	0/10
Aira elegans Willd. ex Gaud. Annual hairgrass	A	0/24	5/10	0/24	10/10	0/24	10/10	0/24	4/10
Alopecurus carolinianus Walt. Carolina foxtail	A	0/24	4/10	0/24	6/10	0/24	1/10	0/24	4/10
Anthoxanthum aristatum Boiss. Annual sweetgrass	A	0/18	10/10	0/18	9/10	0/18	10/10	0/18	9/10
Bromus commutatus Schrad. Hairy chess	A	0/13	0/10	0/13	0/10	0/13	0/10	0/13	0/10
B. japonicus Thunb. Japanese chess	A	0/23	10/10	0/23	6/10	0/23	8/10	0/23	6/10
B. tectorum L. Downy chess	A	0/19	3/10	0/19	6/10	0/19	3/10	0/19	2/10
Cinna arundinacea L. Stout woodreed	P	0/22	0/10	0/22	0/10	0/22	0/10	0/22	0/10
Festuca rubra L. Red fescue	P	0/24	5/10	0/24	6/10	0/24	0/10	0/24	0/10
Glyceria septentrionalis Hitchc. Eastern mannagrass	P	2/24	2/10	5/24	6/10	4/24	8/10	3/24	2/10
G. striata (Lam.) Hitchc. Fowl mannagrass	P	0/16	9/10	0/16	10/10	0/16	6/10	0/16	2/10
Hordeum pusillum Nutt. Little barley	A	0/24	0/10	0/24	0/10	0/24	0/10	0/24	0/10
Lolium multiflorum Lam. Italian ryegrass	P	0/24	0/10	0/24	0/10	0/24	0/10	2/24	0/10
Melica mutica Walt. Two-flower melic	P	0/21	0/10	0/21	0/10	0/21	0/10	0/21	0/10
Phalaris canariensis L. Canarygrass	A	2/18	7/10	2/18	10/10	8/18	10/10	3/18	5/10
P. caroliniana Walt. Maygrass	A	0/15	10/10	0/15	10/10	7/15	10/10	0/15	7/10
Sphenopholis nitida (Biehler) Scribn. Shiny wedgescale	P	0/24	0/10	0/24	0/10	0/24	0/10	0/24	0/10
S. obtusata (Michx.) Scribn. Prairie wedgescale	P	0/23	0/10	0/23	0/10	0/23	0/10	0/23	0/10
Stipa avenacea L. Blackseed needlegrass	P	0/17	10/10	0/17	4/10	0/17	7/10	0/17	9/10
Trisetum pennsylvanicum (L.) Beauv. Swamp oats	P	0/24	0/10	0/24	0/10	0/24	0/10	0/24	0/10
Vulpia myuros (L.) K. C. Gmelin Mousetail sixweeksgrass	A	0/24	0/10	0/24	0/10	0/24	0/10	0/24	0/10
V. sciurea (Nutt.) Henr. Squirrel sixweeksgrass	A	0/20	0/10	0/20	0/10	0/20	0/10	0/20	0/10
Subfamily Panicoideae									
Tribe Paniceae									
Anthaenantia rufa (Ell.) Schult. Purple silkyscale	P	0/10	1/10	0/10	0/10	0/10	1/10	0/10	0/10
Axonopus affinis Chase Carpetgrass	P	0/19	0/10	0/19	0/10	0/19	0/10	0/19	0/10
A. furcatus (Flugge) Hitchc. Big carpetgrass	P	0/17	0/10	0/17	0/10	0/17	0/10	0/17	0/10
Brachiaria plantaginea (Link) Hitchc. Plantain signalgrass	A	20/20	···	20/20	···	20/20	···	6/20	···
Cenchrus echinatus L. Southern sandbur	A	0/17	0/10	0/17	0/10	0/17	0/10	0/17	0/10
C. longispinus (Hack.) Fern. Longspine sandbur	A	3/20	7/10	1/20	2/10	0/20	0/10	0/20	0/10
C. tribuloides L. Dune sandbur	A	14/15	···	9/15	···	3/15	···	5/15	···
Digitaria ciliaris (Retz.) Koel. Southern crabgrass	A	20/24	···	10/24	···	22/24	···	19/24	···
D. filiformis (L.) Koel. Slender crabgrass	A	9/10	···	5/10	···	5/10	···	6/10	···
D. villosa (Walt.) Pers. Shaggy crabgrass	P	14/20	···	16/20	···	20/20	···	20/20	···

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TABLE 2 (continued)

Grass subfamilies, tribes, species, and common names	Growth habit[b]	Number of plants showing symptoms following inoculation with:[a] MDMV-A (Miss.)[c]	Back assay to corn[d]	MDMV-A (Ohio)	Back assay to corn	MDMV-B	Back assay to corn	SCMV-B	Back assay to corn
Echinochloa muricata (Beauv.) Fern. Rough barnyardgrass	A	9/10	···	7/10	···	7/10	···	10/10	···
E. walteri (Pursh) Heller Walter barnyardgrass	A	24/24	···	24/24	···	24/24	···	24/24	···
Eriochloa contracta Hitchc. Prairie cupgrass	A	0/10	6/10	0/10	5/10	0/10	0/10	0/10	5/10
E. gracilis (Fourn.) Hitchc. Southwestern cupgrass	A	18/18	···	18/18	···	18/18	···	9/18	···
Panicum aciculare Desv. ex Poir.	P	5/11	···	5/11	···	1/11	···	3/11	···
P. dichotomum L.	P	3/10	···	3/10	···	1/10	···	4/10	···
P. gymnocarpon Ell.	P	0/15	0/10	0/15	0/10	0/15	0/10	0/15	0/10
P. lancearium Trin.	P	0/13	0/10	0/13	0/10	0/13	0/10	0/13	0/10
P. lanuginosum Ell. Wooly panicum	P	10/22	···	14/22	···	3/22	···	10/22	···
P. lanuginosum var. *tennesseense (Ashe) Gleason*	P	10/16	···	5/16	···	4/16	···	13/16	···
P. longifolium Torr. Longleaved panicum	P	0/19	0/10	0/19	0/10	0/19	0/10	0/19	0/10
P. oligosanthes Schult. Few-flowered panicum	P	12/20	···	14/20	···	10/20	···	8/20	···
P. philadelphicum Bern. ex Trin. Philadelphia witchgrass	A	5/24	···	11/24	···	2/24	···	4/24	···
P. portoricense Desv. ex Hamilt.	P	3/15	···	5/15	···	1/15	···	5/15	···
P. scabriusculum Ell.	P	2/23	···	1/23	···	0/23	0/10	0/23	0/10
P. scribnerianum Nash Scribners panicum	P	18/20	···	18/20	···	14/20	···	20/20	···
P. sphaerocarpon Ell. Roundseed panicum	P	10/17	···	3/17	···	7/17	···	4/17	···
P. tenerum Beyr. ex Trin.	P	0/16	0/10	0/16	0/10	0/16	0/10	0/16	0/10
P. villosissimum Nash Hairy panicum	P	6/10	···	5/10	···	1/10	···	2/10	···
Paspalum distichum L. Knotgrass	P	0/24	0/10	0/24	0/10	0/24	0/10	0/24	0/10
P. laeve var. *pilosum* Scribn.	P	0/12	0/10	0/12	0/10	0/12	0/10	0/12	0/10
P. pubiflorum var. *glabrum* Vasey ex Scribn., beadgrass	P	0/24	0/10	0/24	0/10	0/24	0/10	0/24	0/10
P. quadrifarium Lam.	P	0/17	0/10	0/17	0/10	0/17	0/10	0/17	0/10
P. setaceum var. *longepedunculatum* (Le Conte) Wood	P	0/19	0/10	0/19	0/10	0/19	0/10	0/19	0/10
Setaria adhaerans (Forsk.) Chiov.	A	1/21	···	1/21	···	15/21	···	15/21	···
S. faberi Herrm. Nodding foxtail	A	18/18	···	18/18	···	18/18	···	18/18	···
S. glauca (L.) Beauv. Yellow foxtail	A	5/19	···	6/19	···	4/19	···	0/19	0/10
S. magna Griseb. Giant foxtail	A	15/15	···	15/15	···	15/15	···	15/15	···
Tribe Andropogoneae									
Andropogon elliottii Chapm. Elliott beardgrass	P	0/20	2/10	0/20	1/10	0/20	0/10	0/20	0/10
A. maritimus Chapm. Sea beardgrass	P	1/20	0/10	1/20	0/10	1/20	0/10	1/20	0/10
A. mohrii Hack. Mohr's beardgrass	P	0/15	0/10	4/15	0/10	4/15	1/10	0/15	0/10
A. tracyi Nash	P	1/24	10/10	1/24	10/10	0/24	0/10	0/24	0/10
A. virginicus L. Broomsedge	P	13/14	···	7/14	···	8/14	···	0/14	0/10
Hackelochloa granularis (L.) Kuntze Hackelgrass	A	4/12	···	1/12	···	2/12	···	6/12	···
Heteropogon melanocarpon (Ell.) Benth. Sweet tanglehead	A	2/12	···	2/12	···	0/12	0/10	1/12	···
Manisuris cylindrica (Michx.) Kuntze Carolina jointgrass	P	1/18	···	1/18	···	1/18	···	1/18	···

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[a] Fraction expresses disease incidence in response to manual inoculation; the numerator denotes the number of plants with symptoms and the denominator the number of plants inoculated.

[b] Abbreviations: A = annual species, p = perennial species.

[c] Two isolates of MDMV-A, one from Mississippi and one from Ohio, were used.

[d] Back assay to Seneca Chief sweet corn was made from each inoculated grass species that remained symptomless or showed uncertain symptoms; in the fraction, the numerator indicates the number of corn plants with symptoms and the denominator (constant:10) the number of corn seedlings inoculated; each such fraction refers to the virus isolate to its left.

TABLE 2. (continued). Response of native Mississippi grasses in all subfamilies of Gramineae to inoculation with maize dwarf mosaic virus strain A (MDMV-A) and strain B (MDMV-B) and sugarcane mosaic virus strain B (SCMV-B)

		Number of plants showing symptoms following inoculation with:[a]							
Grass subfamilies, tribes, species, and common names	Growth habit[b]	MDMV-A (Miss.)[c]	Back assay to corn[d]	MDMV-A (Ohio)	Back assay to corn	MDMV-B	Back assay to corn	SCMV-B	Back assay to corn
Tripsacum dactyloides L.									
Eastern gamagrass	P	0/11	0/10	0/11	0/10	0/11	0/10	0/11	0/10
Zea mays L.									
Corn, maize 'Ab24E'	A	20/20	...	20/20	...	20/20	...	20/20	...
'Pa405'		0/20	...	0/20	...	0/20	...	0/20	...
Subfamily Eragrostoideae									
Aristida intermedia Scribn. & Ball	A	12/21	...	6/21	...	0/21	0/10	0/21	0/10
A. stricta Michx.									
Wiregrass	P	0/14	0/10	0/14	0/10	0/14	0/10	0/14	0/10
A. virgata Trin.									
Slender three-awn	P	0/13	0/10	0/13	0/10	0/13	0/10	0/13	0/10
Bouteloua curtipendula (Michx.) Torr.									
Sideoats grama	P	2/10	1/10	2/10	1/10	0/10	0/10	0/10	0/10
Chloris floridana (Chapm.) Wood	P	6/20	...	8/20	...	2/20	...	0/20	0/10
C. gayana Kunth									
Rhodesgrass	P	14/20	...	12/20	...	0/20	0/10	1/20	2/10
Eragrostis capillaris (L.) Nees									
Lacegrass	A	15/22	10/10	9/22	4/10	6/22	10/10	5/22	4/10
E. curvula (Schrad.) Nees									
Weeping lovegrass	P	0/20	0/10	0/20	0/10	0/20	0/10	0/20	0/10
E. diffusa Buckl.									
Spreading lovegrass	A	15/18	...	10/18	...	6/18	...	3/18	...
E. elliottii S. Wats.									
Elliott lovegrass	P	24/24	...	24/24	...	18/24	...	18/24	...
E. intermedia Hitchc.									
Plains lovegrass	P	22/24	...	10/24	...	0/24	0/10	0/24	0/10
E. pectinacea (Michx.) Nees									
Tufted lovegrass	A	17/22	...	13/22	...	17/22	...	18/22	...
E. spectabilis (Pursh) Steud.									
Purple lovegrass	P	0/21	0/10	0/21	0/10	0/21	0/10	0/21	0/10
Leptochloa fascicularis (Lam.) A. Gray									
Bearded sprangletop	A	10/22	10/10	5/22	10/10	0/22	0/10	0/22	0/10
L. filiforms (Lam.) Beauv.									
Red sprangletop	A	7/22	10/10	2/22	8/10	6/22	10/10	0/22	0/10
L. panicoides (Presl) Hitchc.									
Amazon sprangletop	A	0/10	8/10	0/10	6/10	0/10	0/10	0/10	0/10
L. scabra Nees									
Rough sprangletop	A	7/10	...	10/10	...	0/10	...	7/10	...
L. uninervia (Presl) Hitchc. & Chase									
Mexican sprangletop	A	14/14	...	13/14	...	0/14	0/10	0/14	0/10
Muhlenbergia capillaris (Lam.) Trin.									
Hairyawn muhly	P	7/17	...	5/17	...	2/17	...	11/17	...
M. expansa (DC) Trin.	P	0/15	0/10	0/15	0/10	0/15	0/10	0/15	0/10
Spartina spartinae (Trin.) Merr.									
Gulf cordgrass	P	2/24	4/10	0/24	0/10	0/24	0/10	0/24	0/10
Triplasis americana Beauv.									
American sandgrass	P	0/15	...	0/15	...	7/15	...	0/15	...
T. purpurea (Walt.) Chapm.									
Purple sandgrass	A	14/21	10/10	7/21	10/10	5/21	9/10	3/21	10/10

(continued on next page)

MDMV, a "panicoid virus," while many species belonging to the Panicoideae, where the virus apparently originated, are immune to it.

All six U.S. genera and nine of the 12 U.S. species of the subfamily Oryzoideae (6) are represented in Mississippi. Data are presented on all nine species. Only *Leersia oryzoides* was immune to all the virus strains that were tested. The other three *Leersia* species, *L. hexandra*, *L. lenticularis*, and *L. virginica*, were susceptible to MDMV-A, MDMV-B, and SCMV-B, as was wild rice, *Zizania aquatica*. The two aquatic grasses, *Hydrochloa caroliniensis* and *Luziola bahiensis* were susceptible to only SCMV-B, but the latter was symptomless. *Zizaniopsis miliacea* was mildly susceptible to MDMV-A and immune to MDMV-B and SCMV-B. Of the three cultivars of rice, *Oryza sativa*, only one was infected by MDMV-A, but not by MDMV-B or SCMV-B.

The subfamily Arundinoideae was represented here by six of the eight species found in Mississippi. Three species supported the multiplication of MDMV or SCMV while three species did not. There was a wide diversity in the response to these viruses among four species of one genus. *Chasmanthium latifolium* was susceptible to MDMV-A, MDMV-B, and SCMV-B; *C. sessiliflorum* was susceptible to MDMV-A and MDMV-B but immune to SCMV-B; *C. laxum* was immune to MDMV-A but susceptible to MDMV-B and SCMV-B; and *C. ornithorhynchum* was immune to all three strains.

The grass collection for this study was composed of 42 annual and 71 perennial species. More annual species (88%) than perennial grasses (61%) were susceptible to MDMV and SCMV. Among the host species, the annuals also showed a greater susceptibility in terms of both disease incidence and disease severity than the perennials. All four grasses (*Echinochloa walteri*, *Setaria faberi*, *S. magna*, and *Zea mays*) that reacted with 100% infection to all four virus isolates were annuals, as were two additional grasses (*Brachiaria plantaginea* and *Eriochloa gracilis*) that were 100%

TABLE 2 (continued)

Grass subfamilies, tribes, species, and common names	Growth habit[b]	MDMV-A (Miss.)[c]	Back assay to corn[d]	MDMV-A (Ohio)	Back assay to corn	MDMV-B	Back assay to corn	SCMV-B	Back assay to corn
		Number of plants showing symptoms following inoculation with:[a]							
Zoysia japonica Steud. Japanese lawngrass	P	0/13	0/10	0/13	0/10	0/13	0/10	0/13	0/10
Z. matrella Merr. Manilagrass	P	0/12	2/10	0/12	3/10	0/12	0/10	0/12	0/10
Subfamily Bambusoideae									
Arundinaria gigantea (Walt.) Muhl. Giant cane	P	0/13	0/10	0/13	0/10	0/13	0/10	0/13	0/10
A. tecta (Walt.) Muhl. Switch cane	P	0/20	10/10	0/20	0/10	0/20	0/10	0/20	0/10
Subfamily Oryzoideae									
Hydrochloa caroliniensis Beauv. Southern watergrass	P	0/24	0/10	0/24	0/10	0/24	0/10	8/24	7/10
Leersia hexandra Swartz Southern cutgrass	P	18/23	···	20/23	···	6/23	···	15/23	···
L. lenticularis Michx. Catchfly grass	P	4/18	···	3/18	···	2/18	···	2/18	···
L. oryzoides (L.) Swartz Rice cutgrass	P	0/20	0/10	0/20	0/10	0/20	0/10	0/20	0/10
L. virginica Willd. Whitegrass	P	11/20	···	17/20	···	19/20	···	7/20	···
Luziola bahiensis (Steud.) Hitchc.	P	0/24	0/10	0/24	0/10	0/24	0/10	0/24	7/10
Oryza sativa L. Rice 'Labelle'	A	0/20	0/10	0/20	0/10	0/20	0/10	0/20	0/10
'Lebonnet'		1/18	2/10	0/18	0/10	0/18	0/10	0/18	0/10
'Starbonnet'		0/23	0/10	0/23	0/10	0/23	0/10	0/23	0/10
Zizania aquatica L. Wild rice	A	18/30	10/10	2/30	10/10	1/30	10/10	3/30	10/10
Zizaniopsis miliacea (Michx.) Doll. & Aschers., Southern wildrice	P	0/11	0/10	1/11	3/10	0/11	0/10	0/11	0/10
Subfamily Arundinoideae									
Arundo donax L. Giant reed	P	0/20	0/10	0/20	0/10	0/20	0/10	0/20	0/10
Chasmanthium latifolium (Michx.) Yates Broadleaf uniola	P	8/19	···	6/19	···	3/19	···	3/19	···
C. laxum (L.) Yates Loose spanglegrass	P	0/10	0/10	0/10	0/10	1/10	6/10	2/10	10/10
C. ornithorhynchum (Steud.) Yates Birdsbeak spanglegrass	P	0/15	0/10	0/15	0/10	0/15	0/10	0/15	0/10
C. sessiliflorum (Poir.) Yates Shortflower spanglegrass	P	6/20	···	2/20	···	1/20	···	0/20	···
Danthonia spicata (L.) Beauv. Poverty oatgrass	P	0/18	0/10	0/18	0/10	0/18	0/10	0/18	0/10

[a] Fraction expresses disease incidence in response to manual inoculation; the numerator denotes the number of plants with symptoms and the denominator the number of plants inoculated.
[b] Abbreviations: A = annual species, P = perennial species.
[c] Two isolates of MDMV-A, one from Mississippi and one from Ohio, were used.
[d] Back assay to Seneca Chief sweet corn was made from each inoculated grass species that remained symptomless or showed uncertain symptoms; in the fraction, the numerator indicates the number of corn plants with symptoms and the denominator (constant: 10) the number of corn seedlings inoculated; each such fraction refers to the virus isolate to its left.

susceptible to both isolates of MDMV-A and to MDMV-B (but not to SCMV-B). By comparison, of the 42 perennial hosts, only two species showed complete susceptibility to one or two virus strains but not to all three. *Eragrostis elliotii* was 100% susceptible to MDMV-A while *Digitaria villosa* was 100% susceptible to MDMV-B and SCMV-B.

A few minor differential host responses to the two isolates of MDMV-A were observed. Four species (*Anthaenantia rufa*, *Arundinaria tecta*, *Oryza sativa* 'Lebonnet,' and *Spartina spartinae*) reacted with susceptibility to MDMV-A from Mississippi but not to MDMV-A from Ohio, whereas two species (*Andropogon mohrii* and *Zizaniopsis miliacea*) exhibited immunity to MDMV-A from Mississippi, but susceptibility to MDMV-A from Ohio. Since the percentage of plants with symptoms among the six species (two species with symptomless infection) was relatively small, it is likely that the apparent differential responses would have disappeared upon inoculation of a larger number of plants than was available.

A taxonomic grouping of the grass flora of Mississippi into the six subfamilies shows the number of host species of MDMV and SCMV in each subfamily (Table 3). From these data it is evident that MDMV can infect every major taxon of the grass family. These and other (19) data seem to indicate that about two-thirds of the Mississippi grasses would be susceptible to MDMV-A. A summary of the number of new hosts and new nonhosts of the three viruses in each of the six subfamilies of the Mississippi Gramineae is contained in Table 4.

DISCUSSION

The native grass species chosen for this investigation approximate the relative taxonomic distribution of the Mississippi grass flora among the six subfamilies of the Gramineae (Table 3). For example, members of the subfamily Eragrostoideae constitute 24% of the Mississippi grass species and represent 22% of the species tested. Hosts of MDMV or SCMV were found throughout the entire phylogenetic spectrum of the grass family, from the native bamboos to the oryzoid aquatic grasses to corn.

The infectivity profile of MDMV-B among many diverse taxa showed a greater resemblance to that of SCMV-B than to that of MDMV-A. Ten species reacted similarly to MDMV-B and SCMV-B while five species reacted similarly to MDMV-B and MDMV-A. In the first group, eight grasses were susceptible to MDMV-A but immune to MDMV-B and SCMV-B, and two grasses were immune or highly resistant to MDMV-A but susceptible to MDMV-B and SCMV-B. In the second group, three species were susceptible to MDMV-A and MDMV-B but immune to SCMV-B, and two species were immune to MDMV-A and MDMV-B but susceptible to SCMV-B. Although most grasses responded similarly to all three virus strains, either with susceptibility or immunity, there were many instances of similar infectivity of MDMV-B and SCMV-B to suggest a closer relationship between MDMV-B and SCMV-B than between MDMV-B and its "sister" strain, MDMV-A.

Strain MDMV-B has a narrower host range, especially in the Eragrostoideae, than strain MDMV-A. In this investigation, 18 species susceptible to MDMV-A were immune to MDMV-B. In two other studies, there were 22 species in the same category (18,19). Furthermore, many grasses that are hosts of both strains are susceptible to a lesser extent to MDMV-B than to MDMV-A. The infectivity data from wild grasses contrast with the reaction of corn genotypes to the two strains of MDMV. Almost all corn inbred lines that show varying degrees of resistance to MDMV-A are highly susceptible to MDMV-B (*unpublished*).

The means by which MDMV-B overseasons is still unknown. The virus may survive in susceptible, possibly symptomless, perennial or winter-annual grasses or in the corn crop through infected corn seed or infected seed of wild grasses. Evidence exists that MDMV-B can be seedborne in corn at a very low rate (8,10), but no information is available on seed transmission of MDMV-B in wild grasses. The proposed northward flight of MDMV-B-inoculative aphids over hundreds of miles seems highly speculative (24).

Of the 28 perennnial grasses found susceptible to MDMV-B (Table 2), the following have the potential of being or becoming overwintering hosts of this virus because of their northern distribution: *Glyceria septentrionalis*, *Panicum lanuginosum* var. *tennesseense* (formerly *P. tennesseense* Ashe), *P. oligosanthes*, *P. sphaerocarpon*, *P. villosissimum*, and *Stipa avenacea*. Another four perennials, *Andropogon virginicus*, *Glyceria striata*, *Muhlenbergia capillaris*, and *Panicum scribnerianum* may also be reservoir hosts of MDMV-B (20). Additionally, *Leersia lenticularis* and *L. virginica* are experimental hosts of MDMV-B and are widespread in the midwestern USA as far north as Minnesota and Wisconsin (19).

Knowing whether MDMV-B can be transmitted via the seed of annual grasses (particularly *Bromus tectorum*, *B. japonicus*, *Echinochloa muricata, Eragrostis pectinacea, Panicum philadelphicum*, *Phalaris canariensis*, *Setaria glauca*, and *Zizania aquatica*) would be of special interest. All of these annual species were moderately to highly susceptible to MDMV-B, most were colonized by aphids in the greenhouse (observed on plants for seed production), and all have a very extensive distribution in the USA wherever corn is grown. Some of the annual as well as perennial hosts reacted with only latent infection to MDMV-B. Among the annual symptomless hosts of MDMV-B, attention should be focused on *B. japonicus* and especially on *B. tectorum*, as suggested by the author (18,21), because they are hardy winter annuals with geographic distributions that coincide with that of MDMV-B. Recently MDMV-B has been isolated from wild, symptomless plants of *B. tectorum* in Kansas (3).

Symptomless hosts of a virus can be particularly troublesome if they act as overwintering hosts and remain unknown. The majority

TABLE 3. Taxonomic division of Mississippi (MS) grass flora and hosts of maize dwarf mosaic virus strain A (MDMV-A), strain B (MDMV-B), and sugarcane mosaic virus strain B (SCMV-B)

Subfamily (tribe)	Species in MS (no.)	Percent of MS species (%)	Species tested (no.)	Percent of species tested (%)	Hosts of MDMV and/or SCMV (no.)	Hosts of MDMV-A (no.)	Hosts of MDMV-B (no.)	Hosts of SCMV-B (no.)
Festucoideae	60	19.0	23	20.4	13	12	11	12
Panicoideae								
(Paniceae)	119	37.8	38	33.6	26	26	23	22
(Andropogoneae)	39	12.4	10	8.8	9	9	6	5
Eragrostoideae	77	24.4	25	22.1	19	18	9	8
Bambusoideae	2	0.6	2	1.8	1	1	0	0
Oryzoideae	9	2.9	9	8.0	8	6	4	6
Arundinoideae	9	2.9	6	5.3	3	2	3	2
Total	315	100.0	113	100.0	79	74	56	55

TABLE 4. New hosts and nonhosts of maize dwarf mosaic virus strain A (MDMV-A), strain B (MDMV-B), and sugarcane mosaic virus strain B (SCMV-B) among Mississippi grasses in all subfamilies of the Gramineae

Subfamily (tribe)	Species tested (no.)	New hosts of MDMV and/or SCMV (no.)	New hosts of MDMV-A (no.)	New hosts of MDMV-B (no.)	New hosts of SCMV-B (no.)	New hosts of MDMV-A MDMV-B and SCMV-B (no.)	New nonhosts of MDMV-A MDMV-B and SCMV-B (no.)
Festucoideae	23	11	10	9	10	9	10
Panicoideae							
(Paniceae)	38	25	25	22	22	21	12
(Andropogoneae)	10	8	8	5	4	3	0
Eragrostoideae	25	18	17	9	8	6	6
Bambusoideae	2	1	1	0	0	0	0
Oryzoideae	9	4	2	1	3	1	0
Arundinoideae	6	1	0	1	1	0	1
Total	113	68	63	47	48	40	29

of the 17 symptomless hosts found among the 113 species tested are members of the Festucoideae, and among these, most are annuals. However, the three perennial festucoids that are symptomless hosts (*Festuca rubra*, *Glyceria striata*, and *Stipa avenacea*) are widely distributed and may be important in the epiphytology of MDMV. The eight nonfestucoid symptomless hosts are of limited susceptibility or restricted geographic distribution. Several festucoid genera, *Bromus*, *Phalaris*, and *Stipa*, contain more than one species that react to MDMV or SCMV with symptomless infection (25). *Festuca rubra* is so far the only species in that genus known to be susceptible to MDMV. In the present study, this species proved to be a symptomless host of MDMV-A and a nonhost of MDMV-B and SCMV-B. Others reported *F. rubra* to be a symptomless host of brome mosaic virus (11) and barley stripe mosaic virus (13).

Differential hosts for MDMV-A, MDMV-B, and SCMV-B have been proposed earlier (18,19,25), but the practical use of these hosts in certain reaction categories is limited. Relatively few grasses are immune to MDMV-A and susceptible to MDMV-B, and those that fall into this category are impractical to use either because only a low percentage of MDMV-B-inoculated plants develop symptoms, or because they are difficult to grow. *Setaria adhaerans* and corn inbred line E663 (a South African corn strain) fill this need. However, reaction of these two hosts must be recorded within 7–14 days after inoculation because later 5–10% of MDMV-A-inoculated plants also may develop symptoms.

Andropogon virginicus, *Leptochloa filiformis*, and *Setaria glauca* proved suitable for separating MDMV-A and MDMV-B from SCMV-B. Immunity to MDMV-A and SCMV-B and susceptibility to MDMV-B was the rarest reaction among the grasses tested. The closest response to this desired category was produced by *Phalaris caroliniana* which responded with symptoms to infection by MDMV-B; however, the symptomless plants inoculated with MDMV-A and SCMV-B contained virus.

Andropogoneae, to which corn is assigned, contains proportionally more host species of MDMV than any other tribe. Species with the greatest susceptibility to this virus, however, are found in the tribe Paniceae. With the exception of *Andropogon cirratus* (18) and some genotypes of corn and sorghum, there are no known species with 100% susceptibility to MDMV among members of Andropogoneae. However, numerous species in the tribe Paniceae (including *Echinochloa crus-pavonis*, *E. polystachya*, *Panicum hallii*, and *Setaria grisebachii*) are 100% susceptible to MDMV (17). It is surprising that species phylogenetically related to corn should be less susceptible to MDMV than many species that are more distant relative to corn in the phylogeny of the Gramineae. Thus, except for teosinte [*Zea mexicana* (Schrade) Kuntze], species with the closest taxonomic position to corn are either immune or exhibit a high degree of resistance to MDMV. These include: *Tripsacum dactyloides*, *T. lanceolatum* (18), *Coix lacryma-jobi* (1), *Manisuris cylindrica*, *Rottboellia exaltata* (25), and *Themeda* spp. (Rosenkranz, *unpublished*). At the opposite extreme of the phylogenetic scale is the native bamboo *Arundinaria tecta* which supported symptomless multiplication of MDMV-A. Strain A of SCMV has been isolated from the naturally infected, close relative *Arundinaria gigantea* (2). Infectivity data of MDMV among the genera of the tribe Andropogoneae suggest that the virus may have originated in a taxon more remote from *Zea* than those close neighbors mentioned above, perhaps in *Saccharum* or *Sorghum*, and later became adapted to corn.

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