Grasses Native or Adventive to the United States as New Hosts of Maize Dwarf Mosaic and Sugarcane Mosaic Viruses

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ABSTRACT

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One hundred gramineous species, comprising 51 native and 49 adventive grasses, were tested for reaction to inoculation with maize dwarf mosaic virus strains A (MDMV-A) and B (MDMV-B) and sugarcane mosaic virus strain B (SCMV-B). Among these, 57 grasses, belonging to 26 genera, were found to be new hosts of MDMV-A, MDMV-B, and/or SCMV-B. Of the 57 new hosts, 54 were susceptible to MDMV-A, 44 were susceptible to MDMV-B, and 50 were susceptible to SCMV-B. The three virus strains had 42 hosts in common. Most of the common hosts were more susceptible, in terms of disease incidence and severity, to MDMV-A than to MDMV-B or SCMV-B. No differences were found in the host range of the Mississippi and the Ohio isolates of MDMV-A. New host species were found in the following eight genera not previously reported as containing hosts of MDMV or SCMV: *Arthraxon, Brachypodium, Hyparrhenia, Leersia, Tragus, Trichachne, Trichloris,* and *Vaseyochloa*. Many of the new grass species are perennial, and some are widely distributed. These could be reservoir hosts of MDMV and SCMV and could thus play a role in the epiphytology of these diseases. Differences in the host ranges of MDMV-A, MDMV-B, and SCMV-B make it possible to propose a set of grasses for identifying and separating these virus strains. Infectivity data indicate that MDMV-B may be more closely related to SCMV-B than is MDMV-A.

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

The host ranges of maize dwarf mosaic virus (MDMV) and sugarcane mosaic virus (SCMV) have been studied extensively, but the reaction to these viruses of many important wild grasses occurring in the USA remains unknown. Several studies were devoted exclusively to the determination of hosts of MDMV and SCMV (3, 4, 6, 10, 12, 15), whereas other studies included tests for host plants as part of broader investigations (1, 2, 5, 7, 8, 9, 11, 13, 14, 16). About 145 grass species, belonging to some 60 genera, were found to be hosts of MDMV, and a smaller number of grasses were found to be hosts of SCMV. All species outside the Gramineae so far tested have been immune to both viruses. Most researchers have used mechanical inoculation with MDMV, but a few (7, 9) have used aphids for inoculating prospective hosts.

Because of the almost universal occurrence of MDMV wherever corn is grown in this country, it is desirable to have for it as complete a host range among U.S. grasses as practically possible. In the present study, I determined the reaction to MDMV strains A (MDMV-A) and B (MDMV-B) and to SCMV strain B (SCMV-B) of some native and adventive grasses not tested before to further identify hosts of these two principal aphid-borne viruses infecting corn (*Zea mays* L.). Strain B of SCMV was chosen because it is the most common strain of SCMV in Mississippi. I included a small number of grasses for which information existed on their reaction to only one or another of these viruses. Also, an attempt was made to resolve a few discrepancies in the literature as to whether or not a particular species was a host of these viruses. A brief report listing a few of the new hosts of MDMV and SCMV has been made (10).

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MATERIALS AND METHODS

For comparison, two isolates of MDMV-A, one from Mississippi and one from Ohio, were used. The MDMV-B isolate was supplied by R. E. Ford, University of Illinois. The isolate of SCMV-B was acquired from the U.S. Sugar Crops Field Station, Meridian, Mississippi. The MDMV isolates were maintained in Seneca Chief sweet corn and SCMV-B was maintained in sweet sorghum [*Sorghum bicolor* (L.) Moench], cultivar Rio Sorgo. Viruses were transferred frequently to ensure a ready supply of young infected leaf tissue. Six to 12 grass species were inoculated with the four virus isolates at a time. With a few exceptions, at least 10 plants of each species were inoculated in the two- to three-leaf stage with each virus isolate. The grass seedlings were kept, before and after inoculation, in a greenhouse at about 25 C. Plants were maintained in a vigorous condition by weekly

TABLE 1. Susceptibility of new grass hosts to maize dwarf mosaic virus strains A (MDMV-A) and B (MDMV-B) and sugarcane mosaic virus strain B (SCMV-B)

			Number of plants infected when inoculated with:			
Grass species	Growth habit[a]	Habitat[b]	MDMV-A (Miss.)[c]	MDMV-A (Ohio)	MDMV-B	SCMV-B
Andropogon cirratus Hack.	P	N	10/10[d]	10/10	10/10	10/10
Andropogon hirtiflorus (Nees) Kunth.	P	N	3/16	3/16	1/16	1/16
Andropogon perforatus Trin. ex Fourn.	P	N	16/18	16/18	0/18	2/18
Arthraxon hispidus (Thunb.) Makino	A	A	7/15	6/15	1/15	3/15
Bothriochloa barbinodis (Lag.) Heter	P	N	12/20	16/20	2/20	12/20
Brachiaria erucaeformis (J. E. Smith) Griseb.	A	A	9/11	7/11	8/11	10/11
Brachiaria platyphylla (Griseb.) Nash[e]	A	N	21/21	21/21	21/21	21/21
Brachypodium distachyon (L.) Beauv.	A	A	10/16	9/16	12/16	4/16
Bromus brizaeformis Fisch. & Mey.	A	A	5/6	6/6	5/6	4/6
Bromus squarrosus L.	A	A	9/12	4/12	5/12	5/12
Bromus trinii Desv.	A	A	7/30	8/30	12/30	7/30
Chloris argentina (Hack.) Lillo & Parodi	P	A	9/10	8/10	0/10	0/10
Chloris canterai Arech.	P	A	7/20	6/20	0/20	2/20
Chloris cucullata Bisch.	P	N	14/30	14/30	10/30	5/30
Chloris distichophylla Lag.	P	A	12/14	12/14	1/14	1/14
Chloris radiata (L.) Swartz	A	A	33/34	33/34	23/34	27/34
Chloris submutica H.B.K.	P	A	10/16	9/16	11/16	5/16
Chloris truncata R. Br.	P	A	11/11	10/11	10/11	8/11
Chloris ventricosa R. Br.	P	A	6/11	6/11	0/11	0/11
Danthonia pilosa R. Br.	P	A	0/14	0/14	6/14	4/14
Danthonia semiannularis (Labill) R. Br.	P	A	0/10	0/10	1/10	2/10
Digitaria longiflora (Retz.) Pers.	P	A	7/20	1/20	18/20	17/20
Echinochloa polystachya (H.B.K.) Hitchc.	P	N	22/22	22/22	22/22	22/22
Eragrostis bahiensis Schrad.	P	A	14/17	8/17	0/17	0/17
Eragrostis chariis (Schult.) Hitchc.	P	A	11/15	3/15	2/15	7/15
Eragrostis intermedia Hitchc.	P	N	3/20	8/20	13/20	2/20
Eragrostis mexicana (Hornem.) Link	A	N	18/18	18/18	6/18	18/18
Eragrostis poaeoides Beauv. ex Roem.	A	A	9/18	8/18	6/18	4/18
Eragrostis tef (Zuccagni) Trotter	A	A	32/32	32/32	32/32	32/32
Eragrostis unioloides (Retz.) Nees	A	A	20/20	16/20	20/20	15/20
Eragrostis virescens Presl.	A	A	13/17	13/17	9/17	6/17
Eriochloa punctata (L.) Desv.	P	N	12/18	11/18	0/18	0/18
Hyparrhenia rufa (Nees) Stapf	P	A	0/9	0/9	0/9	2/9
Leersia virginica Willd.	P	N	11/20	16/20	18/20	7/20
Leptochloa virgata (L.) Beauv.	P	N	20/20	20/20	0/20	1/20
Panicum bergi Arech.	P	A	8/11	10/11	7/11	5/11
Panicum coloratum Walt.	P	N	3/9	3/9	3/9	6/9
Panicum hallii Vasey	P	N	15/15	15/15	15/15	15/15
Panicum havardii Vasey	P	N	6/10	5/10	6/10	2/10
Paspalum almum Chase	P	N	6/26	4/26	0/26	0/26
Paspalum malacophyllum Trin.	P	N	6/13	7/13	0/13	1/13
Paspalum scrobiculatum L.	A	A	3/25	1/25	6/25	8/25
Pennisetum alopecuroides (L.) Spreng.	P	A	1/19	4/19	0/19	0/19
Pennisetum latifolium Spreng.	P	A	3/9	2/9	2/9	2/9
Phleum paniculatum Huds.	A	A	19/30	18/30	16/30	24/30
Rhynchelytrum repens (Willd.) Hubb.	P	A	25/25	25/25	25/25	25/25
Rhynchelytrum roseum (Nees) Stapf & Hubb.	P	A	9/25	9/25	15/25	6/25
Setaria grisebachii Fourn.	A	N	20/20	20/20	20/20	20/20
Setaria palmifolia (Koen.) Stapf	P	A	6/12	10/12	12/12	10/12
Setaria verticillata (L.) Beauv.	A	N	9/12	9/12	9/12	10/12
Sporobolus contractus Hitchc.	P	N	7/14	2/14	0/14	0/14
Sporobolus cryptandrus (Torr.) A. Gray	P	N	7/15	10/15	6/15	10/15
Sporobolus texanus Vasey	P	N	10/15	8/15	15/15	5/15
Tragus berteronianus Schult.	A	N	1/15	2/15	8/15	4/15
Trichachne californica (Benth.) Chase	P	N	5/14	6/14	5/14	8/14
Trichloris crinita (Lag.) Parodi	P	N	14/14	14/14	2/14	1/14
Trichloris pluriflora Fourn.	P	N	14/17	11/17	0/17	1/17
Vaseyochloa multinervosa (Vasey) Hitchc.	P	N	15/20	9/20	18/20	12/20
Zea mays L. 'Mp486'[e]	A	N	11/12	10/12	12/12	12/12
'GA203'			5/12	2/12	10/12	0/12

[a]Abbreviations: P = perennial species, A = annual species.
[b]Abbreviations: N = native grass, A = grass adventive to the USA.
[c]Two isolates of MDMV-A, one from Mississippi and one from Ohio, were used.
[d]Fraction expresses disease incidence in response to inoculation; the numerator denotes number of plants with symptoms and the denominator the number of plants inoculated.
[e]Previously reported as hosts of these viruses; included in this study as controls.

application of liquid fertilizer.

Inocula were prepared by triturating succulent leaf tissue showing pronounced mosaic symptoms in a mortar with a pestle and expressing the crude sap through several layers of gauze. The strained juice was used undiluted to rub the Carborundum-dusted leaves of grasses with a gauze pad. To distinguish between highly susceptible and less susceptible species, the plants were inoculated only once. Those species that had few or no diseased plants after one application of the inoculum were not reinoculated but were tested again, usually during a different season. Grasses that remained symptomless to all virus strains were back-assayed to sweet corn.

Grasses were inspected daily for 3 wk for the appearance of first symptoms, and the final reading was made 6 wk after inoculation. At that time, the number of diseased plants and the severity of infection were recorded.

RESULTS

In this study, 102 grass species, comprising 46 genera, were tested for reaction to MDMV-A, MDMV-B, and SCMV-B. The two known hosts of MDMV and SCMV, maize and *Brachiaria platyphylla* (Griseb.) Nash, were included to provide continuity between this and previous investigations. Of the other 100 grasses tested and reported here, 57 species were new hosts of MDMV, SCMV, or both viruses. These are listed in Table 1. The remaining 43 grasses were immune to the two strains of MDMV and to SCMV-B. The reaction of nine of the 57 new hosts to MDMV-A and SCMV-B, but not to MDMV-B, was reported earlier (10). Of the 57 new host species contained in Table 1, 54 were susceptible to MDMV-A, 44 were susceptible to MDMV-B, and 50 were susceptible to SCMV-B. The three virus strains had 42 hosts in common.

The following 25 native grasses were immune to MDMV-A, MDMV-B, and SCMV-B (the number preceding each species name denotes the number of plants inoculated with each of the four virus isolates): 7 *Alopecurus alpinus* J. E. Smith, 12 *Andropogon hallii* Hack., 20 *Bromus ciliatus* L., 18 *Buchloë dactyloides* (Nutt.) Engelm., 24 *Calamovilfa longifolia* (Hook.) Scribn., 6 *Cenchrus myosuroides* H. B. K., 20 *Danthonia intermedia* Vasey, 12 *Deschampsia caespitosa* (L.) Beauv., 13 *Deschampsia flexuosa* (L.) Trin., 32 *Hilaria jamesii* (Torr.) Benth., 11 *Hilaria swalleni* Cory, 8 *Melica imperfecta* Trin., 12 *Muhlenbergia wrightii* Vasey, 6 *Panicum obtusum* H. B. K., 8 *Pappophorum bicolor* Fourn., 10 *Paspalum virgatum* L., 24 *Pennisetum setosum* (Swartz) L. Rich, 9 *Phleum alpinum* L., 20 *Puccinellia distans* (L.) Parl., 11 *Setaria macrostachya* H. B. K., 7 *Sitanion hystrix* (Nutt.) J. G. Smith, 17 *Stipa richardsoni* Link, 12 *Stipa speciosa* Trin. ex Rupr., 8 *Tripsacum lanceolatum* Rupr., and 13 *Trisetum spicatum* (L.) Richt.

The following 18 grasses adventive to the USA were immune to both strains of MDMV and SCMV-B (number of plants tested with each of the four isolates precedes the species name): 10 *Alopecurus myosuroides* Huds., 15 *Andropogon nodosus* (Willem.) Nash, 16 *Brachypodium pinnatum* (L.) Beauv., 7 *Cenchrus biflorus* Roxb., 13 *Digitaria pentzi* Stent, 12 *Digitaria swazilandensis* Stent, 10 *Elymus caput-medusae* L., 19 *Eragrostis chloromelas* Steud., 18 *Eragrostis lehmanniana* Nees, 8 *Hyparrhenia hirta* (L.) Stapf, 15 *Lolium persicum* Boiss. & Hohen., 14 *Lolium remotum* Schrank., 11 *Melica ciliata* L., 20 *Oryzopsis miliacea* (L.) Benth., 12 *Pennisetum clandestinum* Hochst. ex Choiv., 10 *Phalaris brachystachys* Link, 20 *Sporobolus indicus* (L.) R. Br., and 10 *Vetiveria zizanoides* (L.) Nash.

The new hosts and nonhosts include 51 native and 49 adventive grasses. Among the host grasses that are adventive to the USA are some species that have become well naturalized and whose distribution is now fairly extensive in this country (e.g., *Bromus trinii, Eragrostis poaeoides, Rhynchelytrum roseum,* and *Setaria verticillata*).

There was a great variation in the degree of susceptibility of the new hosts. *Andropogon cirratus, Brachiaria platyphylla, Echinochloa polystachya, Eragrostis tef, Panicum hallii, Rhynchelytrum repens,* and *Setaria grisebachii* had 100% disease incidence when inoculated with any of the four virus isolates. On the other hand, there were hosts which reacted with only 5-10% infection (*Andropogon hirtiflorus, Pennisetum alopecuroides*). Some of the new host grasses were more susceptible to all three virus strains than some corn genotypes considered highly susceptible to these viruses. Incidence of disease among species was usually correlated with severity of infection in individual plants as expressed by the extent and intensity of symptoms which consisted primarily of various mosaic patterns.

A relationship was noticed between the degree of susceptibility of a host and the incubation periods of the viruses in that host. Grasses that showed the highest disease incidence and the highest accompanying severity of infection expressed the first symptoms in 5-7 days. The incubation period tended to become progressively more extended with decrease in the degree of susceptibility.

Although the Mississippi isolate of MDMV-A seemed at times slightly more virulent than the Ohio isolate, the overall reaction of the 102 grasses indicates that they are the same strain of MDMV. There were no instances in which a grass was infected by one of the MDMV-A isolates and could not be infected by the other.

From the differences in the host ranges of MDMV-A, MDMV-B, and SCMV-B, it was possible to select grasses that could be used to differentiate among these virus

TABLE 2. Differential grass hosts for the identification of maize dwarf mosaic virus strain A (MDMV-A), strain B (MDMV-B), and sugarcane mosaic virus strain B (SCMV-B)

	Reaction to inoculation with:		
Grass	MDMV-A	MDMV-B	SCMV-B
Brachiaria platyphylla	+[a]	+	+
Echinochloa polystachya	+	+	+
Pennisetum setosum	–	–	–
Setaria macrostachya	–	–	–
Eragrostis bahiensis	+	–	–
Eriochloa punctata	+	–	–
Andropogon perforatus	+	–	+
Chloris canterai	+	–	+
Danthonia pilosa	–	+	+
Hyparrhenia rufa	–	–	+

[a]Symbols: + = susceptible; – = immune.

strains. In Table 2, the first four species would help identify a mechanically transmissible corn virus, and the additional six species would distinguish among the three virus strains. No grass was found that was a host of MDMV-B without also being a host of MDMV-A and SCMV-B.

This paper adds the following eight genera, which contain new host species of MDMV-A, MDMV-B, and/or SCMV-B, to the list of genera previously reported as having susceptible species: *Arthraxon, Brachypodium, Hyparrhenia, Leersia, Tragus, Trichachne, Trichloris,* and *Vaseyochloa*.

DISCUSSION

Including those described here, there are now 201 gramineous species, distributed among 68 genera, reported to be hosts of MDMV. However, the known hosts of MDMV are not randomly distributed within the grass family. As might be expected, the vast majority of the MDMV-susceptible grasses are to be found in the subfamily Panicoideae, which is comprised primarily of the tribes Andropogoneae, Paniceae, and Tripsaceae (Maydeae). No hosts of this virus have been found yet in the important genera *Avena, Festuca, Hordeum, Melica, Oryzopsis, Poa, Secale,* and *Trisetum,* and only one species each has been reported to be a host of MDMV in *Agrostis, Agropyron, Alopecurus, Elymus, Lolium,* and *Stipa*. Further, most species tested in the genera *Aegilops, Phalaris, Phleum,* and *Triticum* are immune to infection by MDMV. All of the above genera belong to the subfamily Festucoideae.

With the addition of the new hosts of SCMV-B reported in this paper, it appears that about 150 grass species, representing 61 genera, are now known hosts of one or more strains of SCMV.

In a preliminary report, I (10) stated that *Bromus alopecuros* (not included in Table 1) and *Paspalum scrobiculatum* seemed immune to MDMV-A but reacted with infection to SCMV-B. More recent data show that *B. alopecuros* is immune to MDMV-A, MDMV-B, and SCMV-B. Upon retesting *P. scrobiculatum* and inoculating a greater number of plants than before, a few (4 and 12%) of the plants became infected with MDMV-A from Ohio and Mississippi, respectively, whereas 24 and 32% were infected with MDMV-B and SCMV-B, respectively.

There is some disagreement in the literature on the reaction to these viruses of a few of the grasses included in this study. Leisy and Toler (6) observed *Panicum coloratum* Walt. (Kleingrass) naturally infected with MDMV and confirmed the observation by artificial inoculation with that virus. According to the extensive data presented by Tosic and Ford (15), this species was immune to MDMV and SCMV. Sehgal [see Ford and Tosic (4)] also found this grass to be immune to infection by MDMV. Results presented in this paper show that my sample of *P. coloratum* was susceptible to both strains of MDMV and to SCMV-B. In the present study, *Rhynchelytrum repens* (Willd.) C. E. Hubb. [= *Tricholaena repens* (Willd.) Hitchc.] proved to be highly susceptible to MDMV-A, MDMV-B, and SCMV-B. In contrast, Tosic and Ford (15) found this species to be immune to the above three virus strains. However, Sehgal and Jean (12) were able to recover MDMV-A from symptomless plants of *R. repens* after they had been inoculated with this virus. Based on unpublished information provided by A. Q. Paulsen to Ford and Tosic, these authors (4) listed *Tricholaena rosea* Nees [= *Rhynchelytrum roseum* (Nees) Stapf & Hubb.] as being not susceptible to MDMV-A. My data, obtained in two tests, indicated that *R. roseum* was susceptible to the two isolates of MDMV-A as well as to MDMV-B and SCMV-B.

Among the new hosts common to all three virus strains, the infectivity profile of MDMV-B resembled that of SCMV-B more closely than that of MDMV-A. Seven of the grasses were immune to MDMV-B and SCMV-B but susceptible to MDMV-A. Additionally, only a few plants of *Chloris distichophylla* and *Trichloris crinita* became infected with MDMV-B and SCMV-B but these species were highly susceptible to MDMV-A. Conversely, two of the *Danthonia* species, immune to MDMV-A, were susceptible to MDMV-B and SCMV-B. By contrast, there were only five grasses that did not react similarly to MDMV-B and SCMV-B; these were highly susceptible to MDMV-A, showed no symptoms when inoculated with MDMV-B, and only a few (5-10%) of the plants became infected with SCMV-B.

Despite the fact that MDMV-B has been known to infect corn, especially in the northeastern USA, for many years, no means for its overwintering is known. In this study, MDMV-B infected *Leersia virginica* and *Sporobolus cryptandrus*, perennial native grasses that are found where this virus occurs in corn. The overseasoning of MDMV-B also may be sought in perennial ornamental grasses, such as *Pennisetum latifolium* and *Setaria palmifolia*, both of which are susceptible to MDMV-B (Table 1). Another means for MDMV-B survival may be through susceptible winter annuals. Some *Bromus* spp. fall into this category.

Many of the new host grasses are perennial. Among these are species belonging to *Chloris, Eragrostis,* and *Panicum,* all of which are colonized by aphids that are vectors of MDMV and SCMV. Furthermore, some of the new perennial hosts, including *Sporobolus cryptandrus* and *Leersia virginica,* have a very wide distribution in the USA, encompassing all the major corn-growing areas. Others among the new perennial hosts (e.g., *Chloris cucullata, Eragrostis intermedia, Paspalum malacophyllum,* and *Rhynchelytrum roseum*) occur predominantly in the southern corn-growing region, from Texas and Oklahoma to Georgia and Florida. Therefore, some of these grasses have the potential of becoming reservoir hosts of these viruses and of playing a role in the epiphytology of the diseases caused by MDMV and SCMV.

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