Physical and Serological Properties of Maize Dwarf Mosaic and Sugarcane Mosaic Viruses

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ABSTRACT

The physical properties [thermal inactivation point (TIP), longevity in vitro (LIV), and dilution end point (DEP)] of all known strains of maize dwarf mosaic virus (MDMV) and sugarcane mosaic virus (SCMV) were compared under a uniform set of experimental conditions. TIP was very uniform (56-58 C) for all viruses. DEP and LIV were variable. None of these properties is different or uniform enough to be diagnostic. The A-strain of both MDMV and SCMV retains infectivity longest at pH 8.0. All strains were most infective between pH 7 to 9. Sedimentation coefficients were 170 ± 5 S for MDMV-A and -B, and 176 ± 5 S for SCMV-D. In buoyant density determinations $\rho = 1.3421$ for MDMV-A, 1.3427 for MDMV-B, and 1.3327 for SCMV-D. Serological tests show MDMV-A distinct from MDMV-B. MDMV-B is more closely related to the SCMV strains than to MDMV-A.

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A number of viruses which are infective to corn and mechanically transmitted have been described worldwide by different authors and under various conditions; thus, their relationships need clarification. Among these in the USA are the maize dwarf mosaic (MDMV) and sugarcane mosaic viruses (SCMV). Our purpose was to compare physical properties and serological relationships of MDMV and SCMV isolates under uniform test conditions. In addition to a preliminary report (17) some new physical properties are reported.

MATERIALS AND METHODS.—The viruses, strains, and isolates used in this study were: (i) MDMV, strain A (M-A) isolates which included local isolates from Iowa [Iowa 65-74 (Ia. 74), Hamburg, 68-58] and isolates provided by numerous cooperators in Illinois, Indiana, Tennessee, Kentucky [Ohio A, Pennsylvania 3, and isolate "24"] all of which infected Johnsongrass; (ii) MDMV, strain B (M-B) isolates which included Iowa 66-188 (Ia. 188), Pennsylvania 1, and Ohio 13, none of which infected Johnsongrass; and (iii) SCMV strains (S), which included A, B, D, H, and I obtained from A. G. Gillaspie, Jr., Houma, La., and Jg obtained from R. J. Shepherd, Davis, Calif. These isolates were maintained in *Zea mays* L. sweet corn cultivars 'Seneca Chief' or 'Golden Bantam'.

All tests were assayed for infectivity on 10-day-old sweet corn by a systemic assay technique (20). Corn seedlings [10 per 10-cm (4-inch) diam clay pot] were grown in a loam:sand: peat mixture (2:1:1, v/v) in a greenhouse at ca. 25 C. Each test dilution was assayed on 20 seedlings, and was repeated at least twice. All results are means of three experiments. Assay data were recorded 2 wk after inoculation.

All inoculations were made by rubbing crude, or buffer-diluted, infective sweetcorn sap on leaves previously dusted with 600-mesh silicon carbide.

Physical properties of MDMV and SCMV.—Thermal inactivation point (TIP), dilution end point (DEP), and longevity in vitro (LIV) were tested for each strain and isolate. TIP was determined by heating inocula for 10 min, at successively increased 2-C increments in a water bath, cooling them, and then inoculating test plants. The inoculum preparation was infective sap diluted 10-fold with 0.01 M phosphate buffer pH 7.0.

Dilution end points were determined by serially diluting infective sap with 0.01 M phosphate buffer (pH =

7.0) and inoculating test plants.

Longevity in vitro was determined by using crude sap extracted from infected plants, as well as sap diluted 10-fold in phosphate buffer. Both inocula were kept at room temperature, about 23 C, during the test, and test plants were inoculated at certain intervals.

pH.—The effect of pH on the longevity of MDMV and SCMV was studied by using citrate-phosphate-borate buffer (16). The sap was mixed with this buffer in the ratio 1:9 (v/v) to give final pH levels of 3.0 through 10.0 in unit intervals; mixing buffer at pH 2.3, 2.85, 5.0, 6.5, 7.9, 9.1, 9.95, or 11.35 with the crude infective sap provided the desired unit intervals. Infectivity of the treated sap was assayed at intervals after preparation.

Sedimentation coefficients and buoyant density.—Viruses were partially purified as previously described (19), except that a sucrose gradient was not used, and their sedimentation coefficients and buoyant densities were measured.

MDMV-A (Ia. 74), MDMV-B (Ia. 188), and SCMV-D were centrifuged in a Beckman Model E analytical ultracentrifuge with diagonal Schlieren or ultraviolet (UV) optics, using the An-D rotor. The interference angle for Schlieren optics was 60 degrees of arc. Virus was prepared in 0.01 M phosphate buffer pH 7.0 for the Schlieren optics, and in 0.005 M borate buffer pH 8.2 for UV optics. Centrifugation was at 20 C and 31,410 rpm, with Schlieren optics and 32,000 rpm with UV optics. The sedimentation coefficients were determined by using the graphic method described by Markham (9).

Buoyant densities of MDMV-A, MDMV-B, and SCMV-D were determined by sedimenting to equilibrium in CsCl. Centrifugation was at 25 C in a Beckman Model E analytical ultracentrifuge, using an An-D rotor at 44,000 rpm. Mixtures of cesium chloride solution and virus with a refractive index of 1.3605, 1.36525, and 1.36525 were prepared for MDMV-A, MDMV-B, and SCMV-D, respectively. Tobacco mosaic virus (TMV) was the reference (ρ = 1.3248) marker in each determination (11). Buoyant densities were calculated by the formula of Mandel et al. (8) after scanning the equilibrium photos with a Joyce-Loebel Scanner.

Serology.—Serological relationships between maize dwarf mosaic and sugarcane mosaic viruses were investigated by preparing antisera specific for MDMV-A (Ia. 74), MDMV-B (Ia. 188), and SCMV-D. All virus isolates studied were reacted with these antisera in a slide agglutination-precipitin test.

The viruses were purified (11, 19) from sweet corn plants (cultivar Seneca Chief) 2 wk after inoculation. This partially purified virus preparation was injected into New Zealand white rabbits and used as the antigen source for the serological tests. Rabbits received four intravenous injections of 0.5 ml each at 2-day intervals, three subcutaneous injections of 2 ml each (1 ml of virus + 1 ml of Difco incomplete adjuvant) at 5-day intervals, followed, after 6 wk, by an intramuscular booster injection of 2 ml (1 ml of virus + 1 ml of adjuvant). Five days later the rabbits were bled by cardiac puncture at 2-day intervals for 10 days. Antisera titers were determined by the microprecipitin test in plastic petri dishes, with partially purified virus preparations and by the slide agglutination test with crude infective sap.

For the slide agglutination-precipitin tests, we used crude sap extracted from plants infected for 10-12 days and clarified it by low-speed centrifugation (2,500 *g* for 15 min) (Table 5). One drop of antiserum and one drop of virus preparation were placed on a glass slide, mixed, and covered with a cover glass. All antisera were used at a titer of about 1/16. This allowed for dilutions which occurred during healthy sap absorption and/or cross-absorption with different virus isolates. The reaction was read 10 to 30 min later by using indirect light in a light microscope with ×20 magnification. Precipitations were flocculent with different sizes and shapes and very often consisted of net patterns. When the cover slip was touched, the flocculant precipitant moved, but it was stable. Nonspecific precipitations were granular in nature, were not stable, and they readily dispersed when the cover slip was touched.

Serological reactions between antisera and viruses were studied before, but most extensively after absorbing the antisera with juice of healthy plants, and after cross-absorption with heterologous viruses.

Controls included sap from healthy plants and antisera, plus normal sera, saline, and all the virus strains and isolates. All combinations with saline and normal sera were negative.

The antisera obtained had titers of 1/128 for MDMV-A, 1/256 for MDMV-B, and 1/512 for SCMV-D. When undiluted and unabsorbed, these antisera reacted with sap from healthy plants. This reaction was eliminated in all cases by absorbing the antisera with healthy juice (1:1 ratio). For cross-absorption, the ratio of antiserum to infective sap varied. It was lower for MDMV-A antiserum than for MDMV-B and SCMV-D antisera. Antiserum of MDMV-A was cross-absorbed with an equal volume of MDMV-B or SCMV-D infective plant sap. Thereafter, antiserum of MDMV-A did not react with MDMV-B or SCMV-D infective sap, but did react with all isolates of MDMV-A. MDMV-B antiserum was completely absorbed (reacted homologously but not heterologously) by adding sequentially five lots of MDMV-A infected sap. Each absorption step involved addition of an equal volume of sap. The reaction between this antiserum and Ia. 74 was checked after each absorption and was negative after the fifth absorption. Absorption of MDMV-B antiserum with SCMV-D was sufficient after adding equal volumes of SCMV-D juice in six repetitions. Thereafter, the absorbed antiserum did not react with SCMV-D, but did react with MDMV-B. Antiserum of SCMV-D was sufficiently absorbed (reacted homologously but not heterologously) with four volumes of MDMV-A (Ia. 74) juice and with five volumes of MDMV-B (Ia. 188).

MDMV-A, MDMV-B, and SCMV-D antisera (unabsorbed, absorbed with healthy sap, or cross-absorbed) plus SCMV-A and SCMV-H antisera prepared by T. P. Pirone, Lexington, Ky., and SCMV-H antiserum prepared by R. E. Ford, were tested with all the virus strains and isolates in all combinations. Data were recorded as "plus" (+) or "minus" (−) and are compilations of three complete tests. When data could not be readily interpreted, tests were run two or more additional times.

RESULTS.—*Physical properties.*—The TIP for all

TABLE 1. Thermal inactivation point (TIP) of isolates of strains M-A and M-B of maize dwarf mosaic virus and sugarcane mosaic virus strains (S)

TIP	M-A isolates	M-B isolates	S strains
56 C	Ia 74, Oh A, Pa 3[a]	Oh 13	A
58 C	Ia Hamb., Ia 68-58, Ill., Ind., Tenn., Ky., "24."	Ia 188, Pa 1	B, D, H, I, Jg

[a]Sources of strains and isolates listed in Materials and Methods.

TABLE 2. Dilution end point (DEP) of isolates of strains M-A and M-B of maize dwarf mosaic virus and sugarcane mosaic virus strains (S)

DEP Reciprocal	M-A isolates	M-B isolates	S strains
100	Ia Hamb[a]		I
1,000		Pa 1, Oh 13	
5,000	Tenn, Oh A		A, D, H
10,000	Ia 74, Ind, Pa 3, Ia 68-58		Jg
20,000	Ill, Ky, "24"	Ia 188	B

[a]Sources of strains and isolates listed in Materials and Methods.

isolates tested was 56 to 58 C (Table 1). The DEP of the various strains and isolates ranged from 10^{-2} to 2×10^{-4} (Table 2). No strain or isolate retained infectivity longer than 72 h in the LIV tests (Table 3). Some were rendered noninfective sometime between 1 and 12 h.

pH.—Only MDMV-B was infective at pH 10. All the virus strains were infective at pH 9.0 and 4.0; only four strains were infective at pH 3.0 (Table 4). Loss of infectivity of all viruses tested was more gradual; i.e., over a broader pH range, below pH 7.0 than above pH 8.0. Optimum pH for the MDMV and SCMV strains and isolates was between pH 7 and 9.

Sedimentation coefficients and buoyant densities.—Spectrophotometric analyses following purification indicated a small amount of nucleic acid, for the three viruses studied, about 5% (which is an approximation for descriptive purposes, not a specific determination). The 260/280 ratios were: 1.13 to 1.16 for MDMV-A (Ia 74); 1.14 to 1.17 for MDMV-B (Ia 188); and 1.10 to 1.15 for SCMV-D. For preparations from sucrose density-gradient centrifugations, after purification (19), this ratio was 1.10 for MDMV-A (Ia 74), 1.06 for MDMV-B (Ia 188), and 1.10 for SCMV-D.

Only one virus component was observed with Schlieren and UV optics in each virus preparation of MDMV-A, MDMV-B, and SCMV-D. The sedimentation coefficient was 170 ± 5 S for both MDMV-A and MDMV-B, and 176 ± 5 S for SCMV-D. Each value is based on data from three or more runs.

Buoyant density tests detected only single bands of MDMV and SCMV, plus the TMV marker band. MDMV-B and SCMV-D bands were sharp and narrow. The MDMV-A band was broader. Furthermore, in a CsCl solution with a refractive index of 1.3656, the MDMV-A band was broader, and at 1.3710, the band of MDMV-A did not appear. The same virus preparation, run for the same length of time at a 1.3605 refractive index, however, developed a band as mentioned earlier.

The buoyant density for MDMV-A was 1.3421; for MDMV-B, 1.3427; and for SCMV-D, 1.3327. Each value is based on three or more runs. There was small variation and only once did the values for MDMV-A and MDMV-B overlap.

Serology.—All MDMV and SCMV isolates and strains tested reacted positively with antisera specific for MDMV-A, MDMV-B, and SCMV-D, as well as with these same antisera absorbed with healthy sap (Table 5). All combinations of viruses and antisera with saline were negative. When antisera specific for MDMV-A were cross-absorbed with MDMV-B or SCMV-D, the only positive reaction was the homologous one (MDMV-A, and SCMV-Jg, which we consider identical). Conversely,

TABLE 3. Longevity in vitro (LIV) of isolates of strains M-A and M-B of maize dwarf mosaic virus and sugarcane mosaic virus strains (S)

	Virus strains and isolates					
	In crude sap			In sap diluted 10-fold with 0.01 M phosphate buffer, pH 7.0		
LIV (h)	M-A Isolates	M-B Isolates	S strains	M-A Isolates	M-B Isolates	S Strains
1		Ia 188	D		Oh 13	
		Pa 1			Pa 1	
12	Ia 74, Ill,	Oh 13	A	Ia Hamb		B
	Ky, Ind		B			
	Ia Hamb,		H			H
	Ia 68-58[a]					
	"24"		I			I
24	Tenn, Pa 3			Ia 74, Ill, Ind, Oh A	Ia 188	
48	Oh A		Jg	Tenn, Pa 3, Ky,		A
				Ia 68-58, "24"		D
72						Jg

[a]Sources of strains and isolates listed in Materials and Methods.

when antisera specific for MDMV-B were cross-absorbed with MDMV-A, all SCMV strains, except I, and MDMV-B reacted positively. When the MDMV-B antisera were cross-absorbed with SCMV-D, they reacted with all SCMV strains, except SCMV-D and I. When antisera specific for SCMV-D were cross-absorbed with MDMV-A, they reacted with all SCMV strains, except SCMV-I. When antisera specific for SCMV-D were cross-absorbed with MDMV-B, they reacted positively with all SCMV strains, except I, and negatively with MDMV-A, and MDMV-B isolates. Antisera specific for SCMV-A and SCMV-H reacted positively with all SCMV strains, except I, and MDMV-B, and they reacted negatively with MDMV-A and SCMV-Jg (Table 5).

DISCUSSION.—There are no significant differences in physical properties amongst MDMV-A, MDMV-B, and SCMV strains; thus their diagnostic usefulness is limited. The DEP will vary depending on virus-propagative host combination and environmental factors. The LIV varies, depending on whether the test is done in crude sap or whether a 1:10 dilution is made with a buffer (note shift in position in Table 3 of some isolates when phosphate buffer was used).

Testing for sensitivity of viruses to pH levels is not standardized, although a procedure is being developed for standard use (R. E. Ford and C. Grau, *unpublished*). Although useful as a guide in developing purification procedures, the diagnostic value of pH sensitivity may be useful only for MDMV-B at the high pH range, especially since MDMV-B is not infective at pH 3.0, a level at which four of the strains or isolates are infective. The LIV test could easily be a routine part of the pH study. The similarity of reactions of viruses in phosphate buffer (Table 3) and in the citrate-phosphate-borate buffer (Table 4) is consistent.

The sedimentation coefficients of 170S for MDM-A and MDMV-B seem a little high, compared with results of other workers for MDMV-A [155S (1), 160S (S. A. Tolin, *personal communication*) and 168S (13)], for MDMV-B [167S (7)], for potato virus Y (PVY) [150S (15) and 154S (4)], and for tobacco etch virus (TEV) [154S (10)]. Several runs were made, however, and the values we report here were quite consistent. However, work in progress on the amount of RNA in MDMV-B and the size of the protein subunits, suggests that these values are reasonable (J. H. Hill, *personal communication*), in addition to the recent work of Langenberg (7).

The buoyant densities of $\rho = 1.33$ to 1.34 reported here compare very favorably with 1.3245 reported for MDMV-A (12), and with other viruses in this group [TEV $\rho = 1.332$ and turnip mosaic virus $\rho = 1.336$ (3)]. Since the MDMV-A band was broad under some experimental conditions, this may be evidence of the presence of more than one species of viral particle sedimenting. We, and

TABLE 4. The effect of pH on the infectivity of maize dwarf mosaic virus (M) and sugarcane mosaic virus (S) strains

Time of assay after treatment	pH of sap-buffer mixture[a]							
	3.0	4.0	5.0	6.0	7.0	8.0	9.0	10.0
1-2 min	S-H[b] S-I							
10 min								M-B[d]
30 min	M-A[c]	M-A	S-B					
1 h	S-Jg	M-B S-A S-B S-D S-H S-I	S-A M-B S-I	M-A S-D			S-I	
4 h		S-Jg	S-A S-D S-H	S-A S-B S-H S-I		S-I	S-B S-D	
12 h			S-Jg	M-B	M-A M-B S-A S-D S-H S-I	S-B S-D S-H	S-A S-H	
24 h					S-B	M-B	M-A M-B S-Jg	
48 h				S-Jg	S-Jg	M-A S-A		
72 h						S-Jg		

[a] Citrate-phosphate-borate buffer (15).

[b] Only the last time interval where the virus was still infective is reported. Viruses were infective at each pH level at shorter time intervals. Data are averages of three replicates.

[c] Ia 74 is the M-A isolate tested.

[d] Ia 188 is the M-B isolate tested.

other researchers, have had difficulty working with MDMV-A because the protein dissociates easily from RNA, relative to MDMV-B. Therefore, the broad band may be rather a manifestation of the rapid in vitro degradation of MDMV-A (5).

We did not try to establish the nearest dilution for which each virus-antiserum combination was specific because no one has defined critically what is a close or a distant serological relatedness (i.e., does a positive reaction 1 or 2 dilution steps less than the homologous reaction indicate a close relationship?).

From our data (Table 5), and by comparing recent work (14, 21), we conclude that the MDMV and SCMV strains are cross-reactive enough to be considered "related." Snazelle et al. (14) do not support this work entirely, but they did not cross-absorb any of the antisera they tested.

We believe that the reason Snazelle et al. (14) were unable to get a positive serological reaction with SCMV-H was because they inadvertantly may have obtained the severe strain, which has been redesignated as SCMV-I. If this were the case, then their serological interpretations agree with ours. They reported that SCMV-H was especially severe (produced necrosis) in a number of sorghum varieties. In our laboratory, SCMV-H (originally obtained from H. H. Thornberry, Urbana, Ill., and a second collection obtained from A. G. Gillaspie, Jr., Houma, La., as a check on the biological purity of our first isolate) never reacted severely on sorghums (6). However, SCMV-I (also obtained recently from Gillaspie) reacted on sorghum exactly as reported by Snazelle et al. (14) causing severe necrosis and even killing plants. Some of the grasses we tested also reacted severely to infection with SCMV-I, but never in such a necrotic manner to the 2 SCMV-H isolates (6, 18).

MDMV-A differs markedly from other SCMV strains in symptom severity, host range, etc., and some researchers might suggest that it remain designated as MDMV, but MDMV-B likely is a strain of SCMV and should be made a member of that group. This contention is supported by the lack of a reaction between MDMV-A antiserum which had been cross-absorbed with SCMV-D, and isolates of MDMV-B (Table 5), and by positive reactions between SCMV-D antiserum which had been cross-absorbed with MDMV-A, and isolates of MDMV-B (Table 5). If there are enough differences to merit it, MDMV-B should be called SCMV-K since it was described after MDMV-A. It may in fact be one of the strains already described, although MDMV-B did not infect sugarcane in limited tests (6, 18).

Antigenic properties of SCMV-Jg (Table 5), plus host range studies (18) show it to be identical with MDMV-A. We concur with Bond and Pirone (2) that MDMV-A should henceforth be called SCMV-J, the "Johnsongrass infecting strain." Shepherd (13) suggested in 1965 that these California and Ohio viruses "should probably be considered as strains of the surgarcane mosaic virus."

The absence of serological reactions between SCMV-I and antisera after cross-absorption with heterologous virus probably is due to low concentration of strain I in extracted sap. This strain was difficult to purify and concentrate, probably because sweet corn was not the ideal host. Therefore, the conclusions about degree of relatedness of SCMV-I to other strains should be made cautiously. Titer data and reciprocal tests are needed to strengthen this conclusion. Since SCMV-I reacts so severely (6, 14) on sorghum and some grasses, it may be distinctly different from the other SCMV strains.

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TABLE 5. Reactions of selected maize dwarf mosaic (M) and sugarcane mosaic (S) virus antisera with purified strains and isolates of M and S in slide agglutination-precipitin tests

Virus Isolates[b]	Antisera[a] M-A h	M-B h	S-D h	M-A M-B	M-A S-D	M-B M-A	M-B S-D	S-D M-A	S-D M-B	S-A	S-H	N-S
M-A S-Jg	+	+	+	+	+	−	−	—	−	—	−	−
M-B	+	+	+	−	−	+	+	+	−	+	+	−
S-A	+	+	+	−	−	+	+	+	+	+	+	−
S-B	+	+	+	−	−	+	+	+	+	+	+	−
S-D	+	+	+	−	−	+	−	+	+	+	+	−
S-H	+	+	+	−	−	+	+	+	+	+	+	−
S-I	+	+	+	−	−	−	—	—	—	—	−	−
h	−	—	—	−	−	−	—	—	—	—	−	−

[a]Numerators indicate antisera specific against M-A = MDMV-A (Ia 65-74 isolate); M-B = MDMV-B (Ia 66-188 isolate); S-A = SCMV-A strain and S-H = SCMV-H strain from T. P. Pirone, Lex., Ky; (S-H antiserum produced by R. E. Ford reactions were identical). The denominator shows that the antiserum was absorbed with h = sap expressed from healthy corn − clarified; or purified M-A, M-B, or S-D. Controls are h = healthy sap or NS = normal serum.

[b]Viruses are strains or isolates of either M = MDMV or S = SCMV. The 10 isolates of M-A and the three of M-B are listed in Materials and Methods.

[c]Compilation of three complete experiments. Any questionable interpretations were run two or more additional times.

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