

Genetics of Resistance of Two Dent Corn Inbreds to Maize Dwarf Mosaic Virus and Transfer of Resistance into Sweet Corn

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ABSTRACT

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Based on inoculation tests, dent corn inbreds Pa405, B68, Oh1EP, and Ga209 are good sources of resistance to maize dwarf mosaic virus (MDMV). When the other inbreds were crossed to Pa405, little or no segregation for resistance to MDMV was observed in the F₁ or F₂ progeny. In crosses to sweet corn susceptible to MDMV, resistance to MDMV in the F₁ hybrids of sweet corn × Pa405, × B68, × Oh1EP, and × Ga209 was 97, 61, 69, and 0%, respectively, of the plants tested. Based on three years' data from F₂ [(sweet corn × Pa405)F₂] and testcross [(sweet corn × (sweet corn ×

Pa405)F₁] progeny, we estimated that three genes controlled resistance to MDMV. For effective resistance, one gene must be present with either of the other two. For F₂ and testcross progeny of (sweet corn × B68)F₂ and sweet corn × (sweet corn × B68)F₁, respectively, three genes were required for MDMV resistance. With selfing and selection of resistant plants from two-way (sweet corn × Pa405), three-way [(sweet corn × (sweet corn × Pa405)F₁)] and delayed three-way [(sweet corn × (sweet corn × Pa405)F₂)] crosses we have obtained homozygously resistant sweet corn lines.

Maize dwarf mosaic virus (MDMV) has caused significant yield loss in sweet corn in Illinois (8). Little information is known about resistance to MDMV in sweet corn, but sweet corn appears to be susceptible (8).

Genetic resistance to MDMV exists in dent corn. Estimates of the number of genes controlling MDMV resistance range from one to three based on studies involving several resistant genotypes. Scott and Rosenkranz (11) and Rosenkranz and Scott (10) reported: one gene for resistance to MDMV in Va35; two genes in Ga209, Mp339, Mp412, and Ark261; two to three genes in Mp71:222 and T232; and three genes in T240. Based on a diallel of 10 proprietary lines, Johnson (3) estimated that general combining ability variance accounted for most of the genetic variation and

that resistance appeared to be transmitted with nearly complete dominance among crosses. Josephson and Naidu (4), using a diallel set of crosses involving Ga209, Mo18W, T-E199, T105, T13, Ky27, and SE, found resistance to MDMV to be largely dominant and controlled by only a few major genes. Dollinger et al (2) found MDMV resistance in Oh07 to be largely dominant and controlled by two to three genes. Loesch and Zuber (5) reported MDMV resistance in 38-11 controlled by more than one gene.

In this study, we examined the genetics of resistance to MDMV for two dent corn inbreds, Pa405 and B68, and used the resistance to MDMV in Pa405 to obtain sweet corn lines resistant to MDMV.

MATERIALS AND METHODS

All experiments were conducted at the University of Illinois Vegetable Crops Research Farm, Urbana. Rows were spaced 97 cm apart and consisted of 25 kernels per row planted 33 cm apart within rows. Planting dates ranged from 12 May to 10 June over

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years and experiments. Plants were inoculated at several growth stages beginning at the three- to five-leaf stage. Secondary spread from aphid vectors also occurred. Unless otherwise stated, inoculation was with a mixture of MDMV strains A and B (1:1, v/v) introduced according to the mechanical inoculation technique described by Mikel et al (8). The criterion for separation of strains was infection of *Sorghum halepense*; MDMV strain A infects, and strain B does not infect *S. halepense*. In each experiment, one or more rows of sweet corn susceptible to MDMV were inoculated as control plots. Ratings for MDMV were by MDMV incidence; MDMV symptoms were either present or absent, with the former being susceptible and the latter being resistant. Ratings of the incidence of MDMV were conducted at weekly intervals following inoculation, expressed as days after inoculation (dai). Final ratings of MDMV, for which incidence was usually greatest, were used for fitting observed segregation of MDMV to genetic models, unless otherwise stated. In studies of the inheritance of resistance to MDMV for both Pa405 and B68, the resistant and susceptible parents, and the F₁, F₂, and testcross progeny were included within an experiment.

Screening for resistance to MDMV. Over 500 sugary genotypes were screened for resistance to MDMV in 1978 and 1979. They ranged from commercial F₁ hybrids to lines at varying levels of inbreeding, many of which contained exotic maize germ plasm in their pedigrees. Dent corn inbreds Pa405, B68, Oh1EP, 1LA, Ga209, and T232 were also screened as sources of resistance to MDMV.

Inheritance of resistance to MDMV. Several resistant dent corn inbreds were crossed to Pa405 and observed in the F₁ and F₂ for incidence of MDMV. Two phenotypic classes were observed: those showing symptoms of infection by MDMV and those not showing symptoms. Symptoms consisted of a systemic mosaic and, occasionally, a streak or stripe-type mosaic restricted to a narrow portion of the leaf. However, plants with streaks almost always developed systemic mosaic symptoms and thus were considered susceptible. The crosses screened were: Pa405 × Oh1EP, Oh1EP × Pa405, Pa405 × B68, B68 × Pa405, and Pa405 × Ga209. The MDMV-resistant sweet corn line NYMDM1, derived from B68

× Silver Queen, was also crossed with Pa405 and screened.

Several F₁ hybrids of dent corn lines susceptible and resistant to MDMV were screened for incidence of MDMV. The sweet corn genotypes Gold Cup, Banner, Golden Gleam, 59710, and 1L677a were all crossed with Pa405 and B68. In addition, Pa405 was crossed with the following sweet corn genotypes: B5713, B5890, 58374, 58325, 58359, and 58398. Included in the same test were the crosses Gold Cup × T232, 58325 × Ga209, 1L677a × Oh1EP, and Gold Cup × Oh1EP.

Testcross and F₂ progeny of sweet corn lines × Pa405 [sweet corn × (sweet corn × Pa405)F₁ and (sweet corn × Pa405)F₂, respectively] were evaluated for the incidence of MDMV in 1980, 1981, and 1982. Segregation for incidence of MDMV was tested for goodness of fit to several Mendelian genetic models with the chi-square goodness of fit test. The F₂ progenies were derived from MDMV-resistant F₁ crosses of Gold Cup × Pa405, Banner × Pa405, Golden Gleam × Pa405, and 59710 × Pa405. The testcross progeny were derived from the same F₁ progeny with resistance to MDMV and were testcrossed to several sweet corn tester lines susceptible to MDMV. Observed segregations were tested for fit to genetic models for each of the four crosses for both generations individually, for 1-yr totals of summed crosses (tested for homogeneity by a chi-square homogeneity test prior to pooling), and for 3-yr totals (tested for homogeneity prior to pooling). In 1981 and 1982, seeds with sugary and starchy endosperms were planted separately and the incidence of MDMV of plants from each were tested for homogeneity. Testcross and F₂ progeny for 1981 and 1982 were also tested for fit to several genetic models at each weekly rating. The backcross to the resistant parent (Pa405) was also examined for Pa405 × (Gold Cup × Pa405)F₁ and Pa405 × (Golden Gleam × Pa405)F₁. In addition, MDMV-resistant and -susceptible parents, F₁, F₂, and testcross progeny were planted in an isolated plot and inoculated with MDMV strain A in 1981 and 1982. Random plants showing MDMV symptoms within the plot were indexed for MDMV-A and MDMV-B by enzyme-linked immunosorbent assay (ELISA).

During 1982, the inheritance of resistance to MDMV-A and -B was also studied in a second source of resistance to MDMV, B68.

TABLE 1. Effect of inbreeding with selection for resistance to maize dwarf mosaic virus (MDMV) strains A and B in populations from susceptible × resistant corn crosses

	F ₁		F ₂		F ₃		F ₄	
	Tot ^a	%R	Tot	%R	Tot	%R	Tot	%R
Two-way cross^b								
Gold Cup × Pa405	26	96	60	72	19	84	17	65
Banner × Pa405	26	100	58	76	15	87	23	100
Golden Gleam × Pa405	21	90	55	78	19	74	34	82
59710 × Pa405	26	77	64	64	24	75	45	100
Total	99	91	237	72	77	79	119	90
Three-way cross								
58359 × (Gold Cup × Pa405)F ₁	18	72	18	67	108	81		
B5695 × (Gold Cup × Pa405)F ₁	22	27	21	52	17	100		
B5769 × (Gold Cup × Pa405)F ₁	18	39	53	55	191	74		
B5717 × (Banner × Pa405)F ₁	20	55	21	67	36	50		
58325 × (Banner × Pa405)F ₁	23	39	19	16	10	60		
58338 × (Banner × Pa405)F ₁	23	65	20	60	52	56		
B5829 × (Banner × Pa405)F ₁	18	56	22	68	41	71		
B5699 × (Golden Gleam × Pa405)F ₁	17	47	24	63	58	74		
1L677a × (Golden Gleam × Pa405)F ₁	25	20	22	64	81	53		
58323 × (59710 × Pa405)F ₁	20	65	21	67	71	63		
B5705 × (59710 × Pa405)F ₁	15	20	19	79	128	69		
Total	219	46	260	59	793	69		
Delayed three-way cross								
(Gold Cup × Pa405)F ₃ × 59829	40	33	130	45	425	71		
(Gold Cup × Pa405)F ₃ × 59872	43	30	142	56	353	84		
Total	83	31	272	51	778	77		

^aTot = total number of plants inoculated; %R = percentage of MDMV-resistant plants.

^bTwo-way cross is MDMV-susceptible sweet corn × Pa405 (MDMV-resistant). Three-way cross is MDMV-susceptible sweet corn × resistant (MDMV-susceptible sweet corn × Pa405)F₁. Delayed three-way cross is two-way cross selected and inbred for MDMV resistance and crossed to MDMV-susceptible sweet corn. In all crosses only resistant plants were selected for further inbreeding. Gold Cup, Banner, Golden Gleam, and 59710 are MDMV-susceptible sweet corn hybrids; 58359, B5695, B5769, B5717, 58325, 58338, B5829, B5699, 1L677a, 58323, B5705, 59829, and 59872 are MDMV-susceptible sugary corn lines.

The F₂ progeny were from selfed resistant F₁ progeny of Gold Cup × B68, Banner × B68, Golden Gleam × B68, and 59710 × B68. The testcross progeny were derived from the previous F₁ progeny resistant to MDMV and testcrossed to sweet corn tester lines susceptible to MDMV. As with the Pa405 study, the observed segregation was fit to genetic models for each cross, and for the total of all four crosses (tested for homogeneity prior to pooling). Sugary and starchy kernels were planted separately and the incidence of MDMV among plants from each group was tested for homogeneity, as with the previous experiments with Pa405.

Breeding for MDMV resistance. The effect of inbreeding with selection for resistance to MDMV was examined for various crosses. The lines used were from our sweet corn developmental nursery (Table 1). Two-way crosses were MDMV-susceptible sweet corn × Pa405, with MDMV-resistant plants selected for selfing to the next generation. Three-way crosses were sweet corn × (sweet corn × Pa405)F₁, with sweet corn × Pa405 being either Gold Cup, Banner, Golden Gleam, or 59710 × Pa405, with plants resistant to MDMV selected for selfing to the next generation. The delayed three-way cross was the Gold Cup × Pa405 two-way cross selfed with selection for resistance to MDMV to the F₅, and then crossed to sweet corn lines. MDMV-resistant progeny from this cross were selected for selfing to the next generation. Other delayed three-way crosses used (but not shown in Table 1) were 58422 × (Gold Cup × Pa405)F₂, and IL677a × (Gold Cup × Pa405)F₄. All delayed three-way crosses had one generation per year in the field and either one or two generations per year in the greenhouse.

Evaluation of effects of environmental stress on lines resistant to MDMV. An early planting (12 May) and a moisture- and heat-stressed late planting (14 July) of sweet corn lines resistant to MDMV were compared in 1982. The late-planted lines were remnant seed from the lines in the early planting which were considered 100% resistant to MDMV. The lines tested and their pedigrees are shown in Table 2.

Evaluation of F₁ hybrids of MDMV-susceptible sweet corn lines × developed MDMV-resistant sweet corn lines. Experimental F₁ hybrids were evaluated for resistance to MDMV in 1982. The female parent was a sweet corn line susceptible to MDMV and the male parent a sweet corn line from our MDMV nursery (Table 3) resistant to MDMV at some level of inbreeding. Several

TABLE 2. Comparison of early versus late plantings of corn lines resistant to maize dwarf mosaic virus (MDMV) strains A and B

Line	Early planting ^a		Late planting	
	R/Total ^b	%R	R/Total	%R
(Gold Cup × Pa405)F ₅ ^c	13/13	100	21/25	84
(Banner × Pa405)F ₄	23/23	100	23/29	79
(59710 × Pa405)F ₄	21/21	100	24/27	89
(59710 × Pa405)F ₄	24/24	100	22/27	81
[B5695 × (Gold Cup × Pa405)F ₁]F ₃	17/17	100	25/31	81
[58325 × (59710 × Pa405)F ₁]F ₃	16/16	100	13/18	72
[58325 × (59710 × Pa405)F ₁]F ₃	18/18	100	13/20	65
[B5705 × (59710 × Pa405)F ₁]F ₃	17/18	94	15/25	60
[B5705 × (59710 × Pa405)F ₁]F ₃	20/20	100	8/22	36
[58422 × (Gold Cup × Pa405)F ₂]F ₄	14/14	100	13/19	68
[58422 × (Gold Cup × Pa405)F ₂]F ₆	19/19	100	12/17	71
[58422 × (Gold Cup × Pa405)F ₂]F ₆	18/18	100	26/30	87
[IL677a × (Gold Cup × Pa405)F ₄]F ₄	17/17	100	9/21	43
[(Gold Cup × Pa405)F ₅ × 59829]F ₃	13/13	100	5/20	25
[(Gold Cup × Pa405)F ₅ × 59829]F ₃	19/19	100	6/29	21
[(Gold Cup × Pa405)F ₅ × 59829]F ₃	16/16	100	8/22	36
[(Gold Cup × Pa405)F ₅ × 59829]F ₃	19/19	100	6/24	25
[(Gold Cup × Pa405)F ₅ × 59829]F ₃	18/18	100	5/26	19
[(Gold Cup × Pa405)F ₅ × 59872]F ₃	22/22	100	8/25	32
[(Gold Cup × Pa405)F ₅ × 59872]F ₃	13/13	100	8/26	31
[(Gold Cup × Pa405)F ₅ × 59872]F ₃	13/13	100	5/20	25

^aEarly planting 12 May 1982; late planting 14 July 1982.

^bNumber of MDMV-resistant (R) plants over total number inoculated.

^cSweet corn hybrids Gold Cup, Banner, and 59710 are susceptible to MDMV; sweet corn lines B5695, 58325, B5705, 58422, IL677a, 59829, and 59872 are susceptible to MDMV.

commercial hybrids thought to have some MDMV resistance were included: BVX819, BVX849, PVX100, VX719 (all from Joseph Harris Company, Inc., Rochester, NY 14624), and RXP258 from Robson Seed Farms, Hall, NY 14461. The MDMV-susceptible commercial sweet corn hybrids Seneca Chief, Mirada, and Gold Cup were included as MDMV-susceptible checks. Data on MDMV disease incidence were recorded for the experimental hybrid and when present, the resistant parent selfed.

Indexing for resistance to MDMV by ELISA. An experiment was conducted in 1981 to determine how visual ratings of the incidence of MDMV were correlated to ELISA of the plants. The methods used were the ELISA leaf disk assay of Romaine et al (9) with the ELISA systems for MDMV-A and MDMV-B described by Mikel et al (7). All resistant plants and one susceptible plant per row of either testcross [sweet corn × (sweet corn × Pa405)F₁] or F₂ progeny (sweet corn × Pa405) were assayed for a total of 955 observations. A correlation was calculated between late visual ratings (42–43 dai) and ELISA values (42–59 dai) for resistant plants. In addition, 61 Pa405 and 15 Oh1EP plants were assayed for MDMV by ELISA on flag leaf samples from plants at anthesis, but plants were not sampled on the lower inoculated leaves.

TABLE 3. Evaluation of F₁ sweet corn hybrids for resistance to maize dwarf mosaic virus (MDMV) strains A and B

Hybrids (S × R) ^a	F ₁ Hybrids		R parent selfed	
	R/Total ^b	%R	R/Total	%R
IL788a × B6008F ₃	11/21	52		
IL677a × B6008F ₅	6/13	46		
ILT55 × B6009F ₃	14/15	93		
BES × B6011F ₃	17/18	94	24/24	100
IL758a × M6018F ₂	23/23	100	11/11	100
B5885 × M6030F ₂	21/22	95	14/14	100
BES × M6036F ₂	5/21	24		
IL14h × M6036F ₅	21/21	100	18/18	100
IL778b × M6036F ₅	15/16	94	16/16	100
IL778e × M6036F ₅	12/21	57		
H6048 × M6036F ₅	6/15	40	13/20	65
IL759a × M6065F ₂	15/24	63	20/21	95
IL760a × M6065F ₂	25/25	100	19/21	90
BES × M6073F ₂	0/22	0	2/20	10
IL757c × M6117F ₂	23/23	100	8/8	100
I2132 × M6117F ₂	23/23	100	17/17	100
BES × M6117F ₂	14/16	88		
IL731a × M6161F ₃	3/19	16	9/13	69
IL766a × M6222F ₂	9/19	47	12/18	67
IL774a × M6222F ₂	2/11	18	10/20	50
IL767b × M6223F ₂	2/15	13	23/23	100
IL772a × M6223F ₂	3/23	13	8/17	47
IL772b × M6223F ₂	2/22	9	14/15	93
IL773a × M6223F ₂	8/23	35		
IL764a × M6224F ₂	5/18	28		
IL774a × M6224F ₂	11/12	92	18/18	100
IL764b × A10613F ₂	4/14	29		
BES × A10613F ₂	10/19	53		
BVX 819	1/20	5		
BVX 849	4/23	17		
VX 719	2/11	18		
PVX 100	1/22	5		
Seneca RXP258	0/22	0		
Seneca Chief	0/16	0		
Mirada	0/19	0		
Gold Cup	0/20	0		

^aAll hybrids are MDMV-susceptible (S) sweet corn line × MDMV-resistant (R) sweet corn line. MDMV-resistant sweet corn lines are B6008 (Gold Cup × Pa405), B6009 (Banner × Pa405), B6011 (59710 × Pa405), M6018 (58359 × B6008F₁), M6030 (IL677a × Pa405), M6036 (58323 × B6011F₁), M6043 (58422 × B6008F₂), M6065 (B5769 × B6008F₁), M6073 (B5717 × B6009F₁), M6117 (Pa405 × NYMDM1), M6161 (IL677a × B6008F₄), M6222 (B6008F₅ × 59829), M6223 (B6008F₅ × 59872), M6224 (M6043F₃ × 59829), and A10613 (VX 719) a commercial F₁ hybrid for MDMV resistance.

^bR/Total = the number of MDMV-resistant (R) plants over the total number inoculated.

RESULTS

Screening for resistance to MDMV. All 510 sweet corn lines screened for resistance to MDMV were equally susceptible. Incidence of MDMV in the field corn inbreds was 0% for Pa405 (279 plants tested), 1% for B68 (68 plants), 2% for Oh1EP (118 plants), 100% for ILA (16 plants), 12% for Ga209 (25 plants), and 94% for T232 (18 plants).

Inheritance of resistance to MDMV. The F₁ and F₂ progeny of the dent corn sources crossed to Pa405 were highly resistant to MDMV (Table 4). Among crosses of sweet corn lines to resistant dent corns, F₁ hybrids involving Pa405 were most resistant (Table 5).

Inheritance of the MDMV resistance of Pa405, based on final MDMV incidence ratings, fit a three-gene model where one gene must be present with either of the other two (referred to as the Pa405 three-gene model) for resistance. The F₂ and testcross progeny fit a 45 resistant(R):19 susceptible(S) and a 3R:5S ratio, respectively, of the same three-gene model (Tables 6 and 7).

TABLE 4. Segregation for resistance to maize dwarf mosaic virus (MDMV) strains A and B among progenies from resistant corn crosses

Cross	Incidence ^a			
	F ₁		F ₂	
	R	S	R	S
Pa405 × NYMDMI	58	0	88	1
Pa405 × Oh1EP	79	0	87	0
Oh1EP × Pa405	13	1	16	1
Pa405 × B68	16	0	11	8
B68 × Pa405	49	0	162	1
Pa405 × Ga209	63	0	89	0

^a Incidence of plants resistant (R) and susceptible (S) to MDMV strains A and B.

TABLE 5. Resistance to maize dwarf mosaic virus (MDMV) strains A and B in corn F₁ (sweet corn × dent corn) progeny

Cross ^a	Number of plants		R ^c (%)
	R ^b	S	
Gold Cup × Pa405	198	7	97
Banner × Pa405	130	2	98
Golden Gleam × Pa405	110	5	96
59710 × Pa405	123	10	92
IL677a × Pa405	61	4	94
B5713 × Pa405	25	0	100
B5890 × Pa405	17	0	100
58374 × Pa405	71	0	100
58325 × Pa405	22	0	100
58359 × Pa405	24	0	100
58398 × Pa405	48	0	100
Total	829	28	97
Gold Cup × B68	42	21	67
Banner × B68	14	9	61
Golden Gleam × B68	18	9	67
59710 × B68	14	13	52
B68 × IL677a	25	21	54
Total	113	73	61
IL677a × Oh1EP	33	30	52
Gold Cup × Oh1EP	40	3	93
Total	73	33	69
58325 × Ga209	0	48	0
Gold Cup × T232	0	48	0

^a All crosses are MDMV strains A- and B-susceptible sweet corn × MDMV-resistant dent corn, except B68 × IL677a, which is resistant dent × sugary corn.

^b R = resistant, S = susceptible.

^c R = percentage of resistant plants.

Testcross and F₂ progeny did not both fit any other genetic models tested. The two phenotypes of the F₂ progeny consisted of the following genotypes: 45R (27/64 *A-B-C-* + 9/64 *A-B-cc*, + 9/64 *A-bbC-*):19S (9/64 *aaB-C-* + 3/64 *A-bbcc* + 3/64 *aaB-cc* + 3/64 *aabbC-* + 1/64 *aabbcc*). Allele *A* for resistance is only expressed when one or both of alleles *B* and *C* are present. The two phenotypes of the testcross progeny consisted of the following genotypes: 3R (1/8 *AaBbCc* + 1/8 *AaBbcc* + 1/8 *AabbCc*):5S (1/8 *aaBbCc* + 1/8 *Aabbcc* + 1/8 *aaBbcc* + 1/8 *aabbCc* + 1/8 *aabbcc*).

Each cross within each year fit the Pa405 three-gene model for both F₂ and testcross progeny generations, except for one testcross [sweet corn × (sweet corn × Pa405)F₁] in 1981. The sum of all crosses for each of the three years (found homogeneous prior to pooling) and the combined total for all 3 yr (found homogeneous prior to pooling) fit the Pa405 three-gene model for both generations. As shown in Table 8, resistance to MDMV in both F₂ and testcross progeny segregated independently of the starch/sugary locus. The backcrosses to the MDMV resistant parent (Pa405) for (Gold Cup × Pa405)F₁ and (Golden Gleam × Pa405)F₁ were 94% (31R/33) and 100% (40R/40) resistant to MDMV, respectively.

When the F₂ and testcross progeny described above were inoculated with MDMV-A, instead of MDMV-A and -B as previously used, the segregation fit the Pa405 three-gene model (Table 9). In 1981, ELISA showed that none of 29 plants sampled were infected by MDMV-B and all were infected by MDMV-A. In 1982, one of 17 samples was infected by MDMV-B and the other 16 were infected by MDMV-A.

MDMV incidence for both F₂ and testcross progeny at earlier rating dates showed that MDMV resistance fit a one-gene model and then MDMV incidence increased with time until at the last rating it fit the previous Pa405 three-gene model. In 1981, the F₂ progeny were 79% (445 resistant/563 total), 74% (417/563), 72% (405/563), and 69% (387/563) resistant to MDMV at 21, 28, 35, and 42 dai, respectively. The F₂ progeny fit a one-gene model

TABLE 6. Resistance to maize dwarf mosaic virus (MDMV) strains A and B in corn F₂ progeny (sweet corn × Pa405) for a three-gene model of 45 resistant:19 susceptible

Cross and year ^a	Incidence ^b				Chi-square ^c	P
	Observed		Expected			
	R	S	R	S		
Gold Cup × Pa405						
1980	43	17	42	18	0.051	0.9-0.5
1981	143	67	148	62	0.505	0.5-0.1
1982	62	31	65	28	0.592	0.5-0.1
Banner × Pa405						
1980	44	14	41	17	0.846	0.5-0.1
1981	83	31	80	34	0.330	0.9-0.5
1982	72	25	68	29	0.713	0.5-0.1
Golden Gleam × Pa405						
1980	43	12	39	16	1.612	0.5-0.1
1981	76	42	83	35	1.990	0.5-0.1
1982	84	29	79	34	0.878	0.5-0.1
59710 × Pa405						
1980	41	23	45	19	1.198	0.5-0.1
1981	85	36	85	36	0.000	1.0-0.9
1982	81	25	75	31	1.892	0.5-0.1
Total 1980 ^d	171	66	167	70	0.391	0.9-0.5
Total 1981	387	176	396	167	0.674	0.5-0.1
Total 1982	299	110	288	121	1.527	0.5-0.1
Three-year total	857	352	850	359	0.189	0.9-0.5

^a Segregates of F₂ progeny from MDMV-susceptible sweet corn × Pa405 (MDMV-resistant). Presented are field data from 1980 through 1982.

^b Number of MDMV-resistant (R) and -susceptible (S) plants.

^c Chi-square value of fit to the expected 45 resistant:19 susceptible ratio with one degree of freedom.

^d Total of crosses pooled within years and totaled over 3 yr.

(3R:1S) (chi-square = 0.291, 1 df, $0.9 > P > 0.5$) at 28 dai. In 1982, the F₂ progeny were 87% (355 resistant/409 total), 76% (310/409), 73% (300/409), and 73% (299/409) MDMV resistant at 14, 21, 28, and 35 dai, respectively. At both 21 and 28 dai, the segregation fit a one-gene model (3R:1S), chi-square = 0.137, 1 df, $0.9 > P > 0.5$, and chi-square = 0.595, 1df, $0.5 > P > 0.1$, respectively. In 1981, the testcross progeny were 60% (341 resistant/568 total), 46% (261/568), 42% (239/568), and 37% (209/568) resistant to MDMV at 21, 28, 35, and 42 dai, respectively. The testcross progeny fit a 1R:1S ratio of a one-gene model (chi-square = 2.098, 1 df, $0.5 > P > 0.1$) at 28 dai. In 1982, the testcross progeny were 79% (295 resistant/376 total), 41% (153/376), 36% (136/376), and 35% (132/376) resistant to MDMV at 14, 21, 28, and 35 dai, respectively. None of the 1982 testcross MDMV incidence ratings fit a one-gene model.

Inheritance of MDMV resistance for B68 fit a three-complementary gene model (referred to as the B68 three-complementary gene model) for resistance. The F₂ and testcross progeny fit a 27R:37S and a 1R:7S ratio, respectively, of the B68 three-complementary gene model (Tables 10 and 11). The F₂ and testcross progeny did not both fit any of the other genetic models tested. The two phenotypes of the F₂ progeny consisted of the following genotypes: 27R (27/64 A-B-C):37S (9/64 A-B-cc + 9/64 A-bbC- + 9/64 aaB-C- + 3/64 A-bbcc + 3/64 aaB-cc + 3/64 aabbC- + 1/64 aabbcc), in which A, B, and C designate alleles for MDMV resistance. The two phenotypes of the testcross progeny consisted of the following genotypes: 1R (1/8 AaBbCc):7S (1/8 AaBbcc + 1/8 AabbCc + 1/8 aaBbCc + 1/8 Aabbcc + 1/8 aaBbcc + 1/8 aabbCc + 1/8 aabbcc). Each cross fit the B68 three-complementary gene model for both F₂ and testcross progeny generations. The sum

TABLE 7. Resistance to maize dwarf mosaic virus (MDMV) strains A and B in corn testcross progeny (tester × [sweet corn × Pa405]F₁) for a three-gene model of 3 resistant:5 susceptible

Testcross and year ^a	Incidence ^b				Chi-square ^c	P
	Observed		Expected			
	R	S	R	S		
Tester × (Gold Cup × Pa405)F ₁						
1980	62	135	74	123	3.066	0.1–0.05
1981	70	135	77	128	0.991	0.5–0.1
1982	31	69	38	62	1.803	0.5–0.1
Tester × (Banner × Pa405)F ₁						
1980	51	67	44	74	1.648	0.5–0.1
1981	61	70	49	82	4.613	0.05–0.025
1982	38	70	40	68	0.247	0.9–0.5
Tester × (Golden Gleam × Pa405)F ₁						
1980	54	65	45	74	3.161	0.1–0.05
1981	33	81	43	71	3.558	0.1–0.05
1982	30	55	32	53	0.177	0.9–0.5
Tester × (59710 × Pa405)F ₁						
1980	53	83	51	85	0.125	0.9–0.5
1981	45	73	44	74	0.021	0.9–0.5
1982	33	50	31	52	0.180	0.9–0.5
Total 1980 ^d	220	350	214	356	0.293	0.9–0.5
Total 1981	209	359	213	355	0.120	0.9–0.5
Total 1982	132	244	141	235	0.919	0.5–0.1
Three-year total	561	953	568	946	0.128	0.9–0.5

^aTestcross progeny are from resistant F₁ plants derived from MDMV-susceptible sweet corn × Pa405 (MDMV-resistant) testcrossed to MDMV-susceptible sweet corn. Presented are field data from 1980 through 1982.

^bNumber of MDMV-resistant (R) and -susceptible (S) plants.

^cChi-square value of fit to the expected 3 resistant:5 susceptible ratio with one degree of freedom.

^dTotal of crosses pooled within years and totaled over 3 yr.

of the four crosses for each generation (found homogeneous prior to pooling) fit the B68 three-complementary gene model. In both F₂ and testcross progeny MDMV resistance segregated independently of the sugary locus (Table 8).

The ratings of the incidence of MDMV for both F₂ and testcross progeny showed that segregation for resistance to MDMV fit a two-gene model earlier and then the incidence of MDMV increased with time until at the last rating it fit the B68 three-complementary gene model. The F₂ progeny were 71% (246 resistant/347 total), 54% (186/347), 46% (160/347), and 45% (156/347) resistant to MDMV at 14, 21, 28, and 35 dai, respectively. The 21 dai rating of the F₂ progeny did fit a 9R:7S two-complementary gene model for resistance to MDMV (chi-square = 0.989, 1 df, $0.5 > P > 0.1$). The testcross progeny were 54% (153 resistant/285 total), 24% (67/285),

TABLE 8. Homogeneity of resistance to maize dwarf mosaic virus (MDMV) strains A and B in corn derived from kernels with sugary and starchy endosperms in F₂ and testcross progeny of (sweet corn × Pa405 or B68)F₂ and tester × (sweet corn × Pa405 or B68)F₁, respectively

Generation/year	Incidence ^a				Chi-square ^c	P
	Sugary ^b		Starchy			
	R	S	R	S		
(Sweet corn × Pa405)F ₂						
1981	166	80	221	96	0.323	0.9–0.5
1982	118	54	181	56	3.057	0.1–0.05
Tester × (sweet corn × Pa405)F ₁						
1981	88	177	121	182	2.750	0.1–0.05
1982	52	121	80	123	3.582	0.1–0.05
(Sweet corn × B68)F ₂						
1982	62	82	94	109	0.360	0.9–0.5
Tester × (sweet corn × B68)F ₁						
1982	16	107	25	137	0.334	0.9–0.5

^aNumber of MDMV-resistant (R) and -susceptible (S) plants.

^bPhenotypes of sugary (*su su su*) and starchy (*Su Su Su*, *Su Su su*, or *Su su su*) endosperms of corn.

^cChi-square values of homogeneity between classes resistant and susceptible to MDMV and segregating within plants from sugary and starchy corn endosperms.

TABLE 9. Resistance in corn to maize dwarf mosaic virus (MDMV) strain A for a three-gene model in F₂ and testcross progeny of (sweet corn × Pa405)F₂ and tester × (sweet corn × Pa405)F₁, respectively

Generation/year	Incidence ^a				Model ^b	Chi-square ^c	P
	Observed		Expected				
	R	S	R	S			
(Sweet corn × Pa405)F ₁							
1981	65	3					
1982	19	0					
(Sweet corn × Pa405)F ₂							
1981	78	42	84	36	45R:19S	1.621	0.5–0.1
1982	117	56	122	51	45R:19S	0.596	0.5–0.1
Total	195	98	206	87	45R:19S	1.985	0.5–0.1
Tester × (sweet corn × Pa405)F ₁							
1981	53	69	46	76	3R:5S	1.838	0.5–0.1
1982	43	77	45	75	3R:5S	0.142	0.9–0.5
Total	96	146	91	151	3R:5S	0.468	0.5–0.1

^aNumber of MDMV-resistant (R) and -susceptible (S) plants.

^bThe expected ratio of segregation based on a three-gene model being 45R:19S and 3R:5S for F₂ and testcross progeny, respectively.

^cChi-square value of fit to the expected model.

16% (46/285), and 14% (41/285) resistant to MDMV at 14, 21, 28, and 35 dai, respectively. At 21 dai, the testcross progeny fit a 1R:3S two-complementary gene model for resistance to MDMV (chi-square = 0.339, 1 df, 0.9 > P > 0.5).

Breeding for resistance to MDMV. Selection for resistance to MDMV among selfed progeny of single, three-way, and delayed three-way crosses was generally effective (Table 1). Three F₄ lines, two from the two-way cross 59710 × Pa405 and the other from the two-way cross Banner × Pa405, were 100% MDMV resistant in 1982. In Table 1, the F₃ generation of the three-way crosses are from 43 lines within the 11 crosses shown. Five of these lines were 100% resistant to MDMV, one line from 58359 × (Gold Cup × Pa405)F₁, one from B5695 × (Gold Cup × Pa405)F₁, two from 58323 × (59710 × Pa405)F₁, and one from the cross B5705 × (59710 × Pa405)F₁. The delayed three-way cross from the F₃ of (Gold Cup × Pa405)F₅ × 59829 had 6 of 23 and the F₃ of (Gold Cup × Pa405)F₅ × 59872 had 5 of 19 lines 100% resistant to MDMV. In other crosses, not shown in Table 1, 58422 × (Gold Cup × Pa405)F₂ in 1981 as an F₅ was 70% resistant (129 resistant/183 total) to MDMV and one of the 14 lines was 100% resistant to MDMV (in 1981 as an F₅ and 1982 as an F₆); in 1982 four F₆ lines were resistant to MDMV. IL677a × (Gold Cup × Pa405)F₄ in 1982 had four F₄ lines screened with a summed disease incidence of 79% resistant (44 resistant/56 total), and one of the four lines was 100% resistant to MDMV.

Evaluation of environmental stress on lines resistant to MDMV. Resistance to MDMV in our developed sweet corn lines was less effective in a late planting than in an early planting (Table 2). The late planting was under heavy stress from both the high temperatures and the presence of large populations of aphids carrying MDMV. In late plantings, lines derived from two-way crosses appeared more resistant than lines from three-way crosses.

Evaluation of F₁ hybrids of sweet corn × developed MDMV-resistant lines. The F₁ hybrids of several crosses between our developed MDMV-resistant sweet corn lines and MDMV-susceptible sweet corn lines were highly resistant (Table 3). The

incidence of MDMV in the F₁ hybrid was positively correlated with the incidence of MDMV in the selfed resistant parent ($r = 0.60$, $P = 0.01$).

Indexing for resistance to MDMV by ELISA. During the 1981 experiment, plants resistant to MDMV based on visual symptoms (42–43 dai) were also resistant when tested by ELISA ($r = 0.97$, $P = 0.01$, $n = 955$). Plants randomly rated as susceptible to MDMV by visual symptoms were always rated MDMV-positive by ELISA. All 61 of the Pa405 and 15 of the Oh1EP plants which were resistant by visual symptoms on the flag leaves were MDMV-negative by ELISA.

DISCUSSION

No resistance to MDMV was found in sweet corn, but good sources of resistance were found in dent corn. Based on our tests of a wide range of sweet corn genotypes, sweet corn appears to be susceptible to MDMV. Of the dent corn inbreds tested, Pa405, B68, Oh1EP, and Ga209 were resistant to MDMV.

Evaluation of crosses of dent corn inbreds and sweet × dent corn suggests that even though the four dent corn inbreds may carry genes for resistance to MDMV at the same loci, Pa405 was the best source of resistance. The F₁ cross of sweet × dent sources of resistance to MDMV did show an incidence of MDMV in some progeny. This may be due to incomplete penetrance, presence of modifier gene(s), incomplete dominance, or a genotype × environment interaction. Pa405 contributed much more MDMV resistance to the F₁ hybrid in sweet × dent crosses than did B68, Oh1EP, or Ga209, even though all four appeared to be good sources of resistance to MDMV when evaluated as inbreds. Although they carry similar genes for resistance to MDMV, the genes in Pa405 appear more completely dominant than those in B68, Oh1EP, or Ga209.

The Pa405 three-gene model was confirmed by resistance to MDMV segregation of both F₂ and testcross progeny over 3 yr of testing. Inheritance of resistance of sweet × B68 F₂ and testcross progeny fit a three-complementary gene model. As with Pa405, the MDMV resistance of B68 segregated independently of the sugary/starchy alleles. Thus, no linkage of resistance to MDMV and the starchy locus exists, simplifying the transfer of resistance from dent to sugary corn.

When ratings of the incidence of MDMV prior to anthesis were evaluated, simpler genetic models fit the segregation of the progeny. Most of the Pa405 data fit a one-gene model at 28 dai. The B68 F₂ and testcross progeny fit a two-gene model at 21 dai. An additional gene was necessary for either source to impart complete resistance at anthesis. If breakdown of resistance to MDMV occurs after anthesis, we could not detect any such breakdown 1–2 wk after anthesis when tested by ELISA.

In comparisons of early (12 May) and late (14 July) plantings in 1982, breakdown of resistance to MDMV was observed in the late planting. This may have been due to the stressful environment of the late planting, which may require an additional modifier(s) to supplement the three-gene model for resistance to MDMV. These additional alleles would not have been fixed because these lines

TABLE 10. Resistance to maize dwarf mosaic virus (MDMV) strains A and B in corn F₂ progeny (sweet corn × B68) for a three-gene model of 27 resistant:37 susceptible

Cross ^a	Incidence ^b				Chi-square ^c	P
	Observed		Expected			
	R	S	R	S		
Gold Cup × B68	44	51	40	55	0.663	0.5–0.1
Banner × B68	33	40	31	42	0.272	0.9–0.5
Golden Gleam × B68	45	49	40	54	1.244	0.5–0.1
59710 × B68	34	51	36	49	0.166	0.9–0.5
Total	156	191	146	201	1.091	0.5–0.1

^aSegregates of F₂ progeny from MDMV-susceptible sweet corn × B68 (MDMV-resistant). Presented are field data from 1982.

^bNumber of MDMV-resistant (R) and -susceptible (S) plants.

^cChi-square value of fit to the expected 27 resistant:37 susceptible ratio with one degree of freedom.

TABLE 11. Resistance to maize dwarf mosaic virus (MDMV) strains A and B in corn testcross progeny (tester × [sweet corn × B68]F₁) for a three-gene model of 1 resistant:7 susceptible

Testcross ^a	Incidence ^b				Chi-square ^c	P
	Observed		Expected			
	R	S	R	S		
Tester × (Gold Cup × B68)F ₁	13	71	11	73	0.580	0.5–0.1
Tester × (Banner × B68)F ₁	10	56	8	58	0.424	0.9–0.5
Tester × (Golden Gleam × B68)F ₁	7	67	9	65	0.625	0.5–0.1
Tester × (59710 × B68)F ₁	11	50	8	53	1.702	0.5–0.1
Total	41	244	36	249	0.925	0.5–0.1

^aTestcross progeny are from resistant F₁ plants derived from MDMV-susceptible sweet corn × B68 (MDMV-resistant) testcrossed to MDMV-susceptible sweet corn. Presented are field data from 1982.

^bNumber of MDMV-resistant (R) and -susceptible (S) plants.

^cChi-square value of fit to the expected 1 resistant:7 susceptible ratio with one degree of freedom.

were selected for resistance to MDMV for several generations under normal stress environments (earlier plantings).

We were able to obtain sweet corn lines highly resistant to MDMV from two-way, three-way, and delayed three-way crosses. Several of these lines have been recently released as germ plasm resistant to MDMV (6). When we selected for both resistance to MDMV and sweet corn quality, we found that plants resistant to MDMV in segregating populations could be selected before anthesis and used in controlled pollinations. When observed several weeks after anthesis little additional breakdown of resistance to MDMV was observed in these selected plants. Our ELISA test after anthesis on visually selected plants resistant to MDMV confirmed this. Sweet corn quality was better in progeny from three-way and delayed three-way crosses that had an additional "backcross" to sweet corn. Early generation testing of these lines by crossing them to sweet corn lines susceptible to MDMV and evaluating the incidence of MDMV in the F₁ hybrid showed that satisfactory MDMV resistance has been obtained in several of the lines, even though many were selected at an early generation of inbreeding and may still have been segregating for resistance to MDMV. Our experimental hybrids, of which all derived resistance to MDMV from Pa405, performed better than the resistant commercial F₁ sweet corn hybrids tested, all of which derived resistance to MDMV from B68.

Several breeding methods can be utilized for incorporating resistance to MDMV into sweet corn. Backcrossing into selected elite inbreds should result in incorporation of resistance to MDMV. Continuous backcrossing without selfing between backcrosses should be possible since resistance to MDMV appears to be largely dominant. For line development, it would be possible to self and select from specifically synthesized populations. These populations could be assembled from two-way, three-way, and four-way crosses of a resistant source(s) and several sweet corn genotypes. Selection should be for both resistance to MDMV and

sweet corn quality. Based on our results, Pa405 appears to be the best source of resistance to MDMV for such populations.

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