Resistance to Maize Dwarf Mosaic Virus, Severity of Symptoms, Titer of Virus, and Yield of Sweet Corn

J. K. PATAKY, Associate Professor, J. F. MURPHY, Former Graduate Research Assistant, and CLEORA J. D'ARCY, Associate Professor, Department of Plant Pathology, University of Illinois, Urbana 61801

ABSTRACT

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Nineteen sweet corn hybrids were evaluated in field experiments for symptoms of maize dwarf mosaic (MDM), titer of maize dwarf mosaic virus (MDMV), and yield. Weak associations were observed between yield of sweet corn and titer of MDMV (r = ns to −0.79), yield and symptoms of MDM (r = −0.43 to −0.84), and titer of MDMV and symptoms of MDM (r = 0.66 to 0.92). All associations were influenced strongly by MDMV-resistant hybrids. Titer, symptoms, and yield were not associated among susceptible hybrids. Three types of resistance to MDMV were observed. Terminator and 87-5134 had resistance in which all plants remained asymptomatic and titer of MDMV in the youngest, fully expanded leaves did not differ from that in uninoculated plants. Plants of Seneca 258 segregated for symptom development. Titer of asymptomatic plants of Seneca 258 did not differ from that of uninoculated plants. Titer of symptomatic plants of Seneca 258 was lower than that of the most susceptible hybrid. Sundance and Wintergreen had partial resistance in which titer of MDMV and ratings of MDM symptoms were lower than those of the most susceptible hybrids but higher than those of uninoculated plants.

Maize dwarf mosaic (MDM), caused by maize dwarf mosaic virus (MDMV), is potentially one of the most damaging diseases of sweet corn (*Zea mays* L.) in the continental United States. MDM is endemic to the southern states and the Ohio River Valley, where johnsongrass (*Sorghum halepense* (L.) Pers.) is found. Severe epidemics of MDM in regions where johnsongrass does not occur have been associated with the immigration of viruliferous vectors (23,24,32). A severe epidemic of MDM on sweet corn in Minnesota in 1977, which caused estimated losses of $2.5 million in raw product and $10 million in processed product, is believed to have been caused by long-range transport of MDMV by aphids (31). Reductions in yield of sweet corn are greatest among crops planted late in the growing season and result from undeveloped kernels in the basal quarter of the ear, reduced weight and size of ears, and barrenness of plants (1,3,7,13,14,24,25). Application of oil to sweet corn plants reduced the transmission of MDMV by aphids; however, incidence of MDM was not reduced sufficiently by oil sprays to significantly improve marketable yield (6,26). Thus, disease resistance or tolerance appears to be the most feasible control.

Present address of second author: University of Kentucky, Department of Plant Pathology, Lexington 40546.

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Resistance in corn to MDMV may result from different mechanisms. Resistance in dent corn often has been identified by a lower incidence of plants infected with MDMV either naturally or by inoculation. Nevertheless, corn that is resistant to MDMV is not immune to infection. Tu and Ford (31), Jones and Tolin (8), and Lei and Agrios (10) reported that replication of MDMV was not inhibited in leaves of resistant genotypes that were inoculated with MDMV when compared with susceptible genotypes, but movement of MDMV was restricted in resistant plants. Thus, symptomless plants (10,31) or leaves with occasional longitudinal bands of chlorotic tissue (8) were observed because systemic infection was repressed by this type of resistance. In other instances, concentrations of MDMV in systemically infected resistant hybrids have been lower than in susceptible hybrids (2,9). Several researchers also have identified various sources of resistance to MDMV in which development of symptoms was delayed (i.e., incubation period was lengthened), possibly because of slower rates of replication of MDMV (2,9,21,27). Most inheritance studies have indicated that resistance to MDMV was controlled by a few major genes and/or by modifier or minor genes (10,15,17,19). However, estimates of the number of genes controlling resistance and gene action varied according to inbreds evaluated, methods of assessing MDM, environments, and natural infection vs. inoculation.

When commercial sweet corn hybrids have been evaluated for reactions to MDMV, most have been susceptible, although some have been identified as tolerant to MDMV and a few have been resistant. Mikel et al (15) reported that 510 sweet corn genotypes screened for resistance to MDMV were equally susceptible on the basis of 100% incidence of MDMV-infected plants 4–6 days after inoculation. However, some hybrids, i.e., Cherokee, Golden Gleam, Silver Queen, Sundance, and Wintergreen, were classified as tolerant to MDMV because infection failed to affect yield (13). Similarly, Arny et al (3) classified Bellringer, Cherokee, Golden Gleam, and Quicksilver as tolerant to MDMV because of good development of ears despite infection by MDMV. They did not observe symptoms of MDM on Earliking and Seneca 60 and observed only a few diseased plants among Golden Beauty, Seneca Star, and Sundance. Anzola et al (1) examined the incidence of MDMV-infected plants among sweet corn hybrids and found none that were immune to infection by MDMV, although Bellringer was cited as most resistant, with only 25% of inoculated plants becoming systemically infected. Anzola et al (2) also identified a sweet corn hybrid, Cr288 × Cr290, in which incidence of MDM was lower, development of symptoms was delayed, and titer of MDMV was lower than in susceptible hybrids. Straub (24) evaluated resistance to MDMV among sweet corn hybrids based on the ratio of yield from infected plants to the yield from uninfected plants. He observed that incidence of MDM was not a reliable criterion for evaluating resistance when yield was the basis of comparison. Likewise, during several years of evaluations, such as in 1987, Dale et al (5) identified sweet corn hybrids that performed well in plots exposed to natural epidemics of MDM and maize chlorotic dwarf (MCD). Thus, the tendency to evaluate the reactions of sweet corn hybrids to MDMV based on incidence of infected plants and yield has resulted in some hybrids being classified as tolerant or resistant, with those terms sometimes being interchanged.

Tolerance was defined by Schafer (18) as the capacity of a cultivar to sustain less loss of yield or quality relative to disease severity or pathogen development than other cultivars. In other words, tolerance is the ability of a genotype to endure infection and perform well in spite of that infection, assuming that tolerant genotypes are subjected to equal levels of infection as other genotypes. Genotypes that perform well because of lower levels of infection are resistant or partially resistant rather than tolerant. Schafer noted that tolerance often becomes synonymous with resistance for viral diseases if titer and symptom development are not considered.

Bellringer, Cherokee, Golden Gleam, Quicksilver, Sundance, Wintergreen, and other sweet corn hybrids have been classified as tolerant to MDMV based on lower reductions in yield and better quality of ears in spite of 100% incidence of MDMV-infected plants. However, 100% incidence may not truly reflect the degree of MDMV infection if replication of MDMV differs among infected genotypes. In such cases, titer and symptoms of MDMV may be better indicators of levels of infection and may differentiate between tolerant and partially resistant genotypes.

The objectives of this study were to determine if differences among reductions in yield of sweet corn hybrids infected with MDMV were associated with titer of MDMV as measured by enzyme-linked immunosorbent assay (ELISA) and to assess associations among symptoms of MDM, titer of MDMV, and reductions in yield.

Table 1. Correlations among assessments of titers of maize dwarf mosaic virus in six sweet corn hybrids evaluated four times in 1985

	21 June	2 July	16 July	1 Aug.
21 June	···	0.85[y]	0.92	0.97
2 July	0.59[z]	···	0.90	0.88
16 July	0.63	0.60	···	0.92
1 Aug.	0.38	0.83	0.76	···

[y] Correlation coefficients above the diagonal are for all data, including uninoculated treatments.
[z] Correlation coefficients below the diagonal are for inoculated treatments only.

Table 2. Titers of maize dwarf mosaic virus (MDMV) and yields of six sweet corn hybrids infected by MDMV in 1985

Hybrid	ELISA absorbance[v]	Grouped with lowest[w]	Grouped with highest[x]	Yield (%)[y] Weight	Yield (%)[y] Number
Aztec	0.723 a[z]	1	4	70 b	18 b
Seneca Sentry	0.690 ab	1	4	82 ab	44 ab
Cherokee	0.663 ab	1	4	81 ab	71 a
Gold Cup	0.637 b	3	4	81 ab	45 ab
Wintergreen	0.630 b	3	2	85 a	91 a
Sundance	0.530 c	4	0	86 ab	55 ab

[v] Mean of assessments on four dates. Absorbance for uninoculated plants averaged 0.125.
[w] Number of dates (of four) for which absorbance at 405 nm was not significantly different from the lowest value of hybrids that were infected by MDMV, based on Waller-Duncan BLSD comparisons.
[x] Number of dates (of four) for which absorbance at 405 nm was not significantly lower than the highest value of hybrids that were infected by MDMV, based on Waller-Duncan BLSD comparisons.
[y] Yield as a percentage of (MDMV-infected plants/uninoculated, healthy plants) for each hybrid. Weight is based on total weight of ears per plot; number is based on number of marketable ears per plot.
[z] Values in a column followed by the same letter are not different according to Waller-Duncan multiple comparison test.

MATERIALS AND METHODS

Field experiments were done at the University of Illinois Pomology Research Farm, Urbana, in 1985 and at the Agronomy/Plant Pathology Research Farm, Champaign, in 1986 and 1987. The experimental design was a split plot with main plots arranged in a randomized complete block with four replications. Hybrids were planted in main plots and MDM treatments (inoculated and uninoculated) were applied to subplots. Experimental units were four-row plots spaced 76 cm apart with 15 plants per row. Seeds were planted 22 May 1985, 15 May 1986, and 15 May 1987.

Nineteen sweet corn hybrids were evaluated. In 1985, six hybrids, which differed in maturity, were selected on the basis of reactions to MDMV. Sundance, Wintergreen, and Cherokee have been classified as tolerant, and Aztec, Seneca Scout, and Gold Cup as susceptible, to MDMV (13). Aztec and Sundance reach maturity for fresh market in about 68 days, Gold Cup and Cherokee mature in about 78 days, and Wintergreen and Seneca Scout mature in about 80 days. Nine additional hybrids were evaluated in 1986, and four other hybrids were included in 1987.

Plants at the three- to four-leaf stage were inoculated with a mixture of MDMV-A and MDMV-B in 1985 and with MDMV-A in 1986 and 1987. Inocula were prepared by adding leaves of corn infected with MDMV to 0.05 M chilled sodium phosphate buffer (pH 7), 1 g of leaves per 4 ml of buffer, and grinding for 1 min in a blender. The homogenate was filtered through several layers of cheescloth and Miracloth. Carborundum was added to the inoculum at 15 g/L. Whorls of plants were inoculated mechanically with an artist's airbrush operated at an air pressure of 4.9 kg/cm on 7 June 1985, 2 June 1986, and 8 June 1987.

Incidence of plants that displayed symptoms of infection by MDMV was recorded 10 days after inoculation and at weekly intervals thereafter. In 1986 and 1987, each plot was rated for symptoms of MDM on a 0–3 scale, where 0 = no symptoms apparent; 1 = faint mosaic symptoms apparent on some but not all leaves; 2 = obvious mosaic on some but not all leaves, differences between chlorotic and nonchlorotic tissues moderately intense; and 3 = intense mosaic on most of the surface area of all leaves.

Titer of MDMV was measured on 21 June, 2 and 16 July, and 1 August 1985; 28 June and 11 July 1986; and 23 June and 7 and 23 July 1987, using a double-antibody sandwich ELISA. We use the term "titer" to represent the relative amount of MDMV antigen as detected by the ELISA procedure. In 1985, 12 and four plants were sampled in each plot of inoculated and uninoculated treatments, respectively. In 1986 and 1987, sample sizes were five and three plants per plot of inoculated and uninoculated treatments, respectively. Each year, five 6-mm leaf disks were collected per plant from the youngest leaf that was fully expanded from the whorl. The sample of five leaf disks from each plant was placed immediately into a well of a microtiter plate that contained 200 μl of phosphate-buffered saline (16). Microtiter plates were shaken overnight at 100 rpm on a rotary shaker at 4 C. Coating of microtiter plates with MDMV-A immunoglobulin (0.5 μg/ml) and addition of conjugate (diluted 1:500) and substrate were as described by Clark and Adams (4). The absorbance of each sample at 405 nm was read on a Bio-Tek ELISA plate reader.

Ears were harvested approximately 21 days after midsilk based on maturity of plants in uninoculated plots. Because of differences in maturity among hybrids, harvest dates ranged from 5 to 15 August 1985, from 11 to 28 July 1986, and from 20 July to 3 August 1987. Ten plants were harvested in 1985 and 20 plants in 1986 and 1987 from the middle two rows of each plot. Weight of ears without husks, diameter and length of ears, the number of marketable ears, and the number of undeveloped kernels in the basal quarter of the ear were recorded. Within hybrids, yield and characteristics of ears were expressed as a percentage of healthy (uninoculated) control plants. Data were analyzed by ANOVA, and hybrids were compared by Waller-Duncan Bayesian least significance (BLSD) values. Yield variables were plotted on assessments of titer and ratings of symptoms and analyzed by ordinary least squares regressions. Correlations among ratings of symptoms, assessments of titer, and yield were compared.

RESULTS

Titer of MDMV and symptoms of MDM. Incidence of inoculated plants that showed symptoms of MDM infection was 100% 10 days after inoculation except for three hybrids: Seneca 258, Terminator, and 87-5134. Approximately 15 and 30% of the inoculated Seneca 258 plants showed symptoms of MDMV infection in 1986 and 1987, respectively. None of the Terminator or 87-5134 plants were symptomatic in the 1987 trial. Plants with symptoms of MDM were found occasionally in uninoculated plots and removed.

ELISA absorbance varied among assessment dates, but grouping of the six hybrids in 1985 was relatively consistent. Correlation coefficients among the four assessments of MDMV titer in 1985 ranged from 0.85 to 0.97 when uninoculated controls were included (Table 1). When correlations were based on inoculated hybrids only, coefficients ranged from 0.38 to 0.83 (Table 1). The higher correlation coefficients due to the influence of the uninfected plants were misrepresentative of the relationships among assessments of titer in infected plants. Likewise, ANOVAs and mean separation tests that included uninoculated treatments did not accurately reflect differences among hybrids that

Table 3. Titers of maize dwarf mosaic virus (MDMV), ratings of MDM symptoms, and yields of 15 sweet corn hybrids infected by MDMV in 1986

Hybrid	ELISA absorbance[x]	Rating[y]	Yield (%)[z]	
			Weight	Number
Jubilee	1.049	2.7	82	79
Sweetie 82	0.977	2.0	90	80
Silver Queen	0.879	2.7	78	85
Sugar Loaf	0.866	2.0	88	78
NK199	0.849	2.7	71	40
Seneca Paleface	0.806	3.0	62	14
Ivory and Gold	0.771	2.5	78	64
Aztec	0.766	2.1	88	83
Gold Cup	0.758	2.5	80	69
Miracle	0.734	2.2	80	55
Wintergreen	0.714	1.7	82	67
Florida Staysweet	0.640	1.7	77	78
Seneca 258	0.596	1.3	94	78
Cherokee	0.569	2.1	86	78
Sundance	0.369	1.4	94	77
BLSD $k = 100$	0.273	1.15	12.3	24.2

[x] Mean of assessments on two dates. Absorbance for uninoculated plants averaged 0.145.
[y] Rating on a 0–3 scale. Mean of assessments on two dates.
[z] Yield as a percentage of (MDMV-infected plants/uninoculated, healthy plants) for each hybrid. Weight is based on total weight of ears per plot; number is based on number of marketable ears per plot.

Table 4. Titers of maize dwarf mosaic virus (MDMV), ratings of MDM symptoms, and yield of 18 sweet corn hybrids infected by MDMV in 1987

Hybrid	ELISA absorbance[x]	Rating[y]	Yield (%)[z]	
			Weight	Number
Jubilee	1.418	2.9	80	77
Apache	1.408	2.9	71	72
Sweetie 82	1.303	2.8	83	85
NK199	1.234	3.0	60	16
Florida Staysweet	1.218	3.0	68	35
Gold Cup	1.182	2.5	68	79
Sugar Loaf	1.105	2.5	70	79
Cherokee	1.093	2.4	77	64
Seneca Paleface	1.093	2.9	65	34
Ivory and Gold	1.032	3.0	71	32
Silver Queen	0.949	2.6	72	40
Miracle	0.936	2.9	81	73
Summer Sweet 7200	0.924	2.9	69	50
Wintergreen	0.923	2.4	82	47
Sundance	0.826	1.6	85	86
Seneca 258	0.331	0.5	88	90
Terminator	0.185	0	96	98
87-5134	0.156	0	100	100
BLSD $k = 100$	0.284	0.21	14.4	24.2

[x] Mean of assessments on three dates. Absorbance for uninoculated plants averaged 0.172.
[y] Rating on a 0–3 scale. Mean of assessments on three dates.
[z] Yield as a percentage of (MDMV-infected plants/uninoculated, healthy plants) for each hybrid. Weight is based on total weight of ears per plot; number is based on number of marketable ears per plot.

were inoculated. Therefore, all comparisons were made among inoculated plants.

Sundance had the lowest titer in 1985 based on the mean of the four assessments. On all assessments, Sundance was grouped with the hybrid that had the lowest value of absorbance and was never grouped with the hybrid that had the highest value (Table 2). Aztec, Seneca Sentry, Cherokee, and Gold Cup always were grouped with the hybrid that had the highest value. Gold Cup also was grouped on three assessments with the hybrid that had the lowest value. Wintergreen was grouped with the hybrid that had the highest value on two

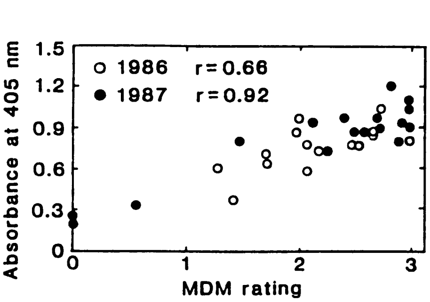

Fig. 1. Associations between titer of MDMV as determined by double-antibody sandwich ELISA (405 nm) and ratings of MDM symptoms on a 0–3 scale for sweet corn hybrids evaluated in 1986 and 1987.

assessments and with the hybrid that had the lowest value on three assessments. Thus, comparisons based on the means of the four assessments were representative of responses of hybrids, although ranking of hybrids was not consistent among the four assessments.

When additional hybrids were evaluated in 1986 and 1987, some hybrids, such as Jubilee, Sweetie 82, and NK199, consistently had high absorbance values (Tables 3 and 4). Other hybrids, such as Sundance and Seneca 258, were grouped consistently with hybrids having low absorbance values (Tables 3 and 4). Some hybrids, however, responded inconsistently over years, e.g., Florida Staysweet had a low titer in 1986 and a high titer in 1987, and Cherokee had a high absorbance value in 1985 and 1987 and a low value in 1986. Two hybrids, Terminator and 87-5134, had absorbance values that did not differ significantly from those of uninoculated controls (Table 4). Seneca 258 also had low absorbance values based on the mean of all plants sampled, but values for symptomatic Seneca 258 plants were similar to those for Sundance, and values for asymptomatic Seneca 258 plants did not differ from those for uninoculated plants.

Ratings of MDM symptoms and absorbance values were weakly correlated (Fig. 1). Correlation coefficients were 0.66 and 0.92 in 1986 and 1987, respectively. When the three hybrids that had asymptomatic plants in inoculated treatments were removed from the 1987 data, however, the correlation coefficient was 0.51. Thus, symptoms of MDM and titer of MDMV were associated but the relationship was not particularly strong unless resistant hybrids were included. Symptomatic plants of Seneca 258 and Sundance consistently had less severe symptoms and lower ratings than many of the other hybrids (Tables 3 and 4). Ratings of MDM symptoms on Wintergreen also were lower than those of some of the other hybrids.

Yield, titer, and ratings. In 1985, yield, expressed as a percentage of (MDV-infected plants/uninoculated, healthy plants), was significantly higher for Wintergreen than for Aztec (Table 2). Yield of MDMV-infected Wintergreen was 95 and 91% of that of uninoculated Wintergreen, based on weight of ears and number of marketable ears, respectively; yield of MDMV-infected Aztec was 70 and 18% of that of its uninoculated control, respectively. Titer of MDMV was significantly higher in Aztec than in Wintergreen. On the basis of number of marketable ears, Cherokee also performed better than Aztec in 1985, although absorbance values did not differ significantly.

Titer of MDMV was not related to either measurement of yield in 1986 (Figs. 2 and 3). Except for Florida Staysweet, however, hybrids that were grouped statistically by absorbance values with Sundance (which had the lowest absorbance value) also were grouped with the hybrids that had the highest yield (Table 3). In 1987, there was a weak relationship among titer and yield (r values of −0.79 and −0.51 for ear weight and number of ears, respectively), although this association was due primarily to the performance of Seneca 258, Terminator, and 87-5134 (Figs. 2 and 3). Yield of these resistant hybrids was not adversely affected by inoculation with MDMV. Yield of Sundance, which also had a lower titer of MDMV, did not differ significantly from the hybrids that yielded best.

Ratings of MDM symptoms and yield were associated weakly. Correlation coefficients ranged from −0.43 to −0.84 and were higher for ratings and yield based on weight of ears than for ratings and yield based on number of marketable ears (Figs. 2 and 3). Higher correlation coefficients in 1987 were due to the performance of Seneca 258, Terminator, and 87-5134. Yield of hybrids with MDM ratings below 2 did not differ significantly from the highest yield except for Florida Staysweet in 1986 (Tables 3 and 4).

None of the hybrids with a high titer of MDMV and severe symptoms yielded

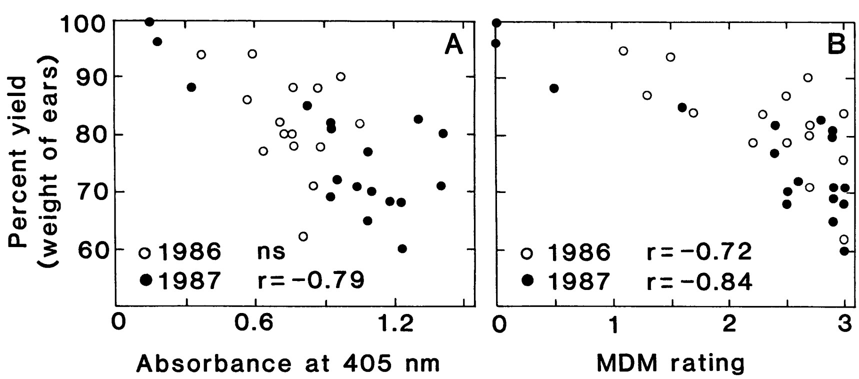

Fig. 2. Associations between yield of sweet corn hybrids based on ear weight as a percentage of (MDMV-infected plants/uninoculated, healthy plants) and **(A)** titer of MDMV as determined by double-antibody sandwich ELISA (405 nm) and **(B)** rating of MDM symptoms on a 0–3 scale.

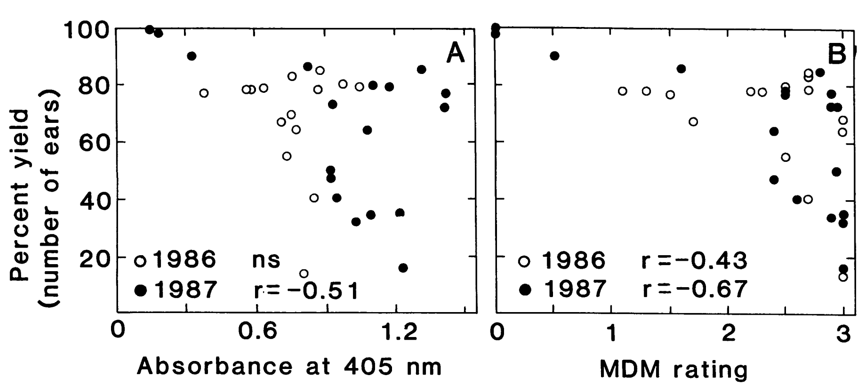

Fig. 3. Associations between yield of sweet corn hybrids based on number of marketable ears as a percentage of (MDMV-infected plants/uninoculated, healthy plants) and **(A)** titer of MDMV as determined by double-antibody sandwich ELISA (405 nm) and **(B)** rating of MDM symptoms on a 0–3 scale.

as well as the best hybrid based on all four assessments of yield (weight of ears and number of marketable ears in 1986 and 1987). However, yields of three hybrids that had a high titer—Jubilee, Sweetie 82, and Sugar Loaf—did not differ significantly from the best yield for three of the four assessments, even though yields of these three hybrids were 4–23% lower than the highest yield (Tables 3 and 4). In 1987, yield based on weight of ears was less for these three hybrids than for the MDMV-resistant hybrid, 87-5134 (Table 4).

DISCUSSION

Yield of sweet corn, titer of MDMV, and symptoms of MDM were associated only weakly for the sweet corn hybrids evaluated in this study. Yield of hybrids that had a low titer of MDMV and mild symptoms usually did not differ significantly from the highest yield. However, yield of many hybrids with high titer and severe symptoms also did not differ significantly from the highest yield. The relationship between yield and MDM ratings was slightly less variable than the relationship between yield and titer of MDMV, although both relationships were greatly influenced by MDMV-resistant hybrids that were asymptomatic. Titer, symptoms, and yield were not associated among the susceptible hybrids.

The lack of close relationships between yield and titer of MDMV and yield and MDM symptoms may have been due, in part, to the inability of our sampling and rating procedures to detect differences among the susceptible hybrids or to the susceptibility of the hybrids evaluated in these trials. Our sampling procedure for estimating titer was based on the findings of Tu and Ford (28–30) and Shukla and Joshi (22) in which titer of MDMV reached a maximum shortly after leaves became fully expanded and each successive new leaf had a lower concentration of MDMV. Although our sampling procedure and ELISA allowed for the separation of symptomatic hybrids with the highest and lowest concentrations of MDMV (i.e., Jubilee and Sundance), most of the hybrids were grouped in overlapping categories and did not differ significantly from one another. Most of the hybrids in this trial appeared to be relatively susceptible to MDMV, which did not provide an appropriate sampling of hybrids with low and moderate titers, such as Sundance and Wintergreen. Likewise, ratings of MDM symptoms tended to be grouped between 2 and 3, with few hybrids between 0 and 2. We are unaware, however, of other sweet corn hybrids that have low or moderate titer or mild MDM symptoms. Such genotypes not only would be useful to these studies but could also be of substantial value in production of sweet corn in areas where MDM is a recurring problem.

Three types of resistant reactions to MDMV were observed among the 19 sweet corn hybrids evaluated in this study. Hybrids were observed that displayed asymptomatic resistance to MDMV, that segregated for resistance to MDMV, and for which MDMV titers and MDM symptom ratings were lower than those for susceptible hybrids but higher than those for uninoculated plants.

Plants of two hybrids, Terminator and 87-5134, were asymptomatic and displayed resistance similar to that reported for the dent corn inbred, Pa405, which has been introgressed into sweet corn germ plasm (12). Since incidence of symptomatic plants was 0% and titers of MDMV in the youngest, fully expanded leaves of Terminator and 87-5134 did not differ from those of uninoculated plants, the resistance in these hybrids appeared to be complete. Nevertheless, we cannot determine whether MDMV replication and/or translocation was inhibited because we did not sample leaves that had been inoculated. Previous work (8,10,31) indicated that MDMV replicated in inoculated leaves of asymptomatic plants.

Plants of Seneca 258 segregated for resistance. Approximately 85 and 70% of the Seneca 258 plants were asymptomatic and had titers that did not differ from those of uninoculated plants in 1986 and 1987, respectively. In the uninoculated plots, plants of Seneca 258 were uniform for all traits that we observed, i.e., plant height, maturity, length and width of ears, rows of kernels, etc. Thus, plants of Seneca 258 appeared to be homogeneous and the variable reaction of Seneca 258 in inoculated plots did not appear to be due to a mixture of seed or to self-pollination of seed-parent plants in seed production fields. Also, the variable reaction of Seneca 258 could not be attributed to "escapes," because inoculation resulted in 100% incidence of MDMV-infected plants among susceptible genotypes. Louie (11) has reported variability in expression of resistance to MDMV among homogeneous inbreds in spite of inoculation protocols that included multiple inoculations and rubs. Scott and Rosenkranz (20) observed variable reactions to MDMV in the three corn inbreds that they reported were not conditioned by genetic variability within the inbreds. They proposed that the variability in reaction to MDMV could have been due to the physiology or the microenvironment of individual plants. If the variable reaction was due to seedlings of a resistant inbred at first being physiologically susceptible, but becoming progessively more resistant with maturity, as Scott and Rosenkranz speculated, then this type of resistance appears to be different from that of Terminator and 87-5134.

Symptomatic plants of Sundance and Seneca 258 had titers of MDMV and ratings of MDM symptoms that were significantly lower than those of the hybrids with the highest values and ratings. Wintergreen also had ratings of MDM symptoms and titers that were lower than those of the hybrid with the highest values but did not differ from those of most of the other hybrids. Apparently, titer of MDMV was lower in Sundance, Seneca 258, and Wintergreen and the subsequent expression of mosaic symptoms was less severe. However, the development of symptoms was not delayed by this type of resistance, as all plants of Sundance and Wintergreen were symptomatic 10 days after inoculation. Other reports of resistance to MDMV in which concentration of MDMV was lower have been associated with a delay in the development of symptoms (2,9,21).

Sundance and Wintergreen have been classified as tolerant to MDMV (13) on the basis of incidence of infected plants and yield. On the basis of our results, we prefer to classify Sundance and Wintergreen as partially resistant to MDMV in order to stress that the concentration of the virus (i.e., replication and/or translocation of MDMV) was reduced in these genotypes, and these reactions did not fit Schafer's (18) or our definitions of tolerance. In addition, we speculate that this type of resistance is similar to the "rate-reducing" resistance (i.e, "slow-rusting," "slow-mildewing") observed for many fungal pathogens. Consequently, one would expect yield to be affected less for MDMV-infected hybrids that are partially resistant than for infected hybrids that are susceptible to MDMV because of a lower level of disease in the partially resistant genotypes.

In evaluating strategies of breeding for disease resistance, "rate-reducing" or partial resistance often is considered to be durable because it frequently is controlled by many genes in the host and thus is less likely to be "overcome" by genotypes of the pathogen that have specific virulence. However, selection for partial resistance in segregating populations often is more difficult than selection for resistance that results in distinct reactions, because partial resistance does not result in easily recognized, qualitatively different reactions. Selection for partial resistance to MDMV also would be difficult because symptoms of MDMV are difficult to assess and assessment of titer of MDMV is labor-intensive. Nevertheless, partial resistance to MDMV may be more durable than the resistance of Pa405, Terminator, and 87-5134. Differences in the durability of the various types of resistance to MDMV and inheritance of resistance to MDMV need to be examined further.

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