Effectiveness of Resistance to Maize Dwarf Mosaic and Maize Chlorotic Dwarf Viruses in Maize

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ABSTRACT

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Progeny of a 13-parent diallel cross of resistant (R) and susceptible (S) inbred lines of maize (*Zea mays*) were evaluated for resistance to maize dwarf mosaic virus (MDMV) and maize chlorotic dwarf virus (MCDV) during 2 yr of testing. Inbreds with similar resistance did not necessarily impart equal levels of resistance to their hybrids when crossed to susceptible inbreds. Lines Ab28A and Mp412 contributed the greatest amount of maize dwarf mosaic (MDM) resistance to their hybrids, whereas Mp412 and T232 contributed the greatest amount of maize chlorotic dwarf (MCD) resistance to their hybrids. When the disease incidence of MDM or MCD was high (85–90% of susceptible plants diseased), resistance expressed by the R × S crosses was close to the midpoint between the R × R and S × S crosses. However, when the disease incidence was low (35–60% of susceptible plants showing symptoms), the same R × S crosses reacted to the two viruses similar to the R × R crosses. Data on percentage of diseased plants were usually as effective in identifying levels of resistance as was data on disease severity ratings. Regression analysis of data on disease reaction enabled estimation of the amount of reduction in disease incidence and severity as well as the probable gain in yield associated with the replacement of each susceptible inbred parent by a resistant one in a hybrid. Our data indicated a lack of synergistic effect on disease severity in corn between MDMV and MCDV.

Since maize dwarf mosaic (MDM) (14) and maize chlorotic dwarf (MCD) (8) were first described as new virus diseases of maize (*Zea mays* L.) much research has been conducted on these two viral plant diseases. Maize dwarf mosaic virus (MDMV), either as strain A or B, has been reported from virtually every state in the USA that is climatically adapted to the cultivation of maize. Maize chlorotic dwarf virus (MCDV), being primarily dependent on the leafhopper *Graminella nigrifrons* (Forbes) for dissemination (8) and on johnsongrass (*Sorghum halepense* (L.) Pers.) for its survival (7), causes a severe disease of maize in the southern USA. Of the two diseases, MCD is more damaging, but MDM can reduce grain yields in susceptible maize hybrids by as much as 45% (10). In some areas, these diseases have forced farmers to change to resistant hybrids or to discontinue growing maize.

Several studies have been conducted in which diallel crosses were used to obtain information on the nature of resistance to viruses in maize (2–6,15). Analyses of the data revealed that the estimates for general combining ability were much higher than those for specific combining ability.

The present study was designed to evaluate simultaneously the progeny of a sizable diallel cross of maize for reactions to both MDMV and MCDV. We wished to learn whether equally resistant inbred lines contribute equal levels of resistance to their hybrids. Further, we wanted to determine which type of data, percentage of diseased plants (disease incidence) or disease severity rating, is more sensitive in discriminating levels of resistance. Finally, we use our data to determine whether synergism exists between MDMV and MCDV.

MATERIALS AND METHODS

The 13 selected parents and their relative responses to MDMV and MCDV are listed in Table 1. Data for classification of the parents were obtained from various experiments. Of the inbred lines selected as being resistant to MDMV, CI90C and Ab416A were considered to be least resistant. Although in some tests all five inbred lines selected as resistant to MCD had shown a similar level of resistance (9), other tests indicated that we might expect Mp490 and Mo12 to be somewhat less resistant than the other three inbreds.

This study was conducted at Mississippi State, MS, in 1972 and 1973. The 78 F_1 crosses of this diallel were grown in single plots, 20 plants per plot, in three replications. All plants were inoculated with MDMV strain A by using a tractor-mounted artist's airbrush when the plants were in the three- to five-leaf stage. Inoculum was obtained from diseased leaf tissue. Because there is no known method for mechanically inoculating plants with MCDV, we had to rely on leafhoppers for natural infection by this virus.

Four to 5 wk after inoculation (before MCD symptoms appeared), the plants were rated for severity of MDM symptoms on a scale of 1 to 5: 1 = no symptoms; 2 = mosaic confined to narrow bands on the upper one or two leaves; 3 = mosaic covering entire surface of one or two upper leaves; 4 = mosaic covering the entire surface of three to six of the upper leaves; 5 = mosaic covering entire surface of most of the leaves of the plant.

Three to 4 wk after silking, the same plants were rated for severity of MCD symptoms on a scale of 1 to 6 (MDM symptoms do not interfere with recognition of MCD symptoms): 1 = no symptoms; 2 = chlorotic blotches with some yellowish or reddish discoloration in the upper one or two leaves; 3 = similar symptoms in the upper three to five leaves, with slight shortening of upper internodes; 4 = leaf symptoms in the upper half of the plant and considerable stunting; 5 = symptoms throughout the plant and plant height greatly reduced; 6 = plant stunted by one-half to two-thirds and dead or dying.

From these individual plant ratings we obtained plot means for disease severity rating (total ratings for all plants divided by the total number of plants) and percentage of diseased plants, and these plot means were used in the analysis of the randomized block design experiments. The Newman-Keuls test was used for the separation of the means. The regression of percentage of diseased plants and disease severity ratings on the level of resistance (ie, R×R, R×S, and S×S) was calculated to obtain expected magnitude of change in reaction to MDM and MCD with each level of change in resistance.

RESULTS AND DISCUSSION

A comparison of mean responses of all crosses involving each inbred parent provides information on how much resistance (or susceptibility) a given inbred imparts to its hybrids. If different kinds of data are taken to evaluate response to virus infection, a comparison of the number of statistical groupings should give an indication as to which type of data was the most sensitive for distinguishing levels of resistance.

Disease incidence and disease severity ratings for MDM of all crosses involving each of the 13 parents are presented in Table 2. Inbreds Ab28A and Mp412 seemed to contribute the highest level of resistance to their hybrids. However, this level of resistance was not always significantly different from that contributed by T232 to its crosses. Of the resistant lines, CI90C and Ab416A contributed the least resistance to their crosses. Among the susceptible lines, Mp490 contributed the lowest and SC149 the highest level of susceptibility to their hybrids.

The type of disease data that is most useful may depend on the objectives of a particular study. In 1972, more groupings of significance were obtained from data on percentage of diseased plants (a-i) than from data on disease severity ratings (a-e) (Table 2). The more easily obtained data on disease incidence were at least as good, and probably better, for revealing the genotypes that contributed the most resistance to their hybrids.

TABLE 1. Parents of diallel and their relative response to maize dwarf mosaic virus (MDMV) and maize chlorotic dwarf virus (MCDV)

Parent	Response to: MDMV	MCDV
Mp412	Resistant	Resistant
Tx601	Resistant	Resistant
T232	Resistant	Resistant
Ab28A	Resistant	Susceptible
CI90C	Resistant	Intermediate
Ab416A	Resistant	Intermediate
CI21	Susceptible	Intermediate
Mp490	Susceptible	Resistant
Mo12	Susceptible	Resistant
T226	Susceptible	Susceptible
Mp420	Susceptible	Susceptible
SC149	Susceptible	Susceptible
T216	Susceptible	Susceptible

Although all plants were mechanically inoculated with MDMV in both years, the disease incidence and, to a smaller extent, disease severity were greater in 1972 than in 1973. In 1973, the means for disease incidence, disease severity ratings for all plants in a plot and severity ratings of diseased plants were, respectively, 41, 20, and 10% smaller than in 1972. The difference in the disease severity ratings of diseased plants between the years of high and low disease incidence was only 10% while the difference in disease incidence was 41%; this indicates that, in the case of MDM, there is not a close relationship between disease incidence and disease severity over years.

We were not only interested in how much resistance a line contributed to its hybrids when crossed with many lines of different genetic background, but also in the line's performance when crossed with other lines of like and unlike classification. These comparisons, which were made by using the 1972 data, are

TABLE 2. Average response of all possible crosses for each of the 13 parental maize inbreds of the diallel to inoculation with maize dwarf mosaic virus in 2 yr of testing

Common parent	Percentage of diseased plants[y] 1972	1973	Disease severity rating[y] All plants 1972	All plants 1973	Diseased plants 1972	Diseased plants 1973
Resistant						
Mp412	37 h[z]	18 e	1.66 e	1.37 d	2.78	3.06
Tx601	47 g	26 de	2.21 d	1.59 cd	3.57	3.27
T232	39 h	31 cd	1.80 e	1.61 cd	3.05	2.97
Ab28A	27 i	23 de	1.50 e	1.52 cd	2.85	3.26
CI90C	50 fg	23 de	2.38 d	1.52 cd	3.76	3.26
Ab416A	52 fg	31 cd	2.32 d	1.65 c	3.54	3.10
Susceptible						
CI21	82 ab	39 bc	3.58 b	1.98 b	4.15	3.51
Mp490	59 ef	39 bc	2.94 c	2.06 b	4.29	3.72
Mo12	70 cd	41 b	2.81 c	2.00 b	3.59	3.44
T226	71 cd	36 bc	3.03 c	1.95 b	3.86	3.64
Mp420	76 bc	45 ab	3.45 b	2.13 b	4.22	3.51
SC149	89 a	53 a	3.93 a	2.39 a	4.29	3.62
T216	64 de	51 a	3.10 c	2.35 a	4.28	3.65
Mean	59	35	2.67	1.86	3.71	3.39

[y]Mean value of 12 crosses.
[z]Means within a column not followed by the same letter differ significantly $P = 0.05$.

TABLE 3. Response of maize inbreds in crosses with resistant or susceptible inbreds to inoculation with maize dwarf mosaic virus in 1972

Common parent	Crossed with: Resistant parents: Percentage of diseased plants	Resistant parents: Disease severity ratings: All plants	Resistant parents: Disease severity ratings: Diseased plants	Susceptible parents: Percentage of diseased plants	Susceptible parents: Disease severity ratings: All plants	Susceptible parents: Disease severity ratings: Diseased plants
Resistant						
Mp412	13 a[z]	1.21 b	2.62	55 b	1.98 b	2.78
Tx601	28 a	1.44 ab	2.57	61 ab	2.76 a	3.89
T232	15 a	1.24 ab	2.60	57 ab	2.19 b	3.09
Ab28A	16 a	1.35 ab	3.19	36 c	1.61 c	2.69
CI90C	23 a	1.50 a	3.17	70 ab	3.01 a	3.87
Ab416A	24 a	1.38 ab	2.58	72 a	2.99 a	3.76
Mean	20	1.35	2.78	58	2.42	3.35
Susceptible						
CI21	73 ab	2.91 b	3.62	93 a	4.26 a	4.51
Mp490	28 d	1.52 d	2.86	90 a	4.35 a	4.72
Mo12	50 c	1.97 c	2.94	90 a	3.65 ab	3.94
T226	64 bc	2.53 b	3.39	79 b	3.53 b	4.20
Np420	60 bc	2.68 b	3.80	92 a	4.21 a	4.49
SC149	85 a	3.49 a	3.93	94 a	4.37 a	4.59
T216	47 c	1.86 cd	2.83	93 a	4.33 a	4.58
Mean	58	2.42	3.34	90	4.10	4.43

[z]Means within a group and in a column not followed by the same letter differ significantly, $P = 0.05$.

presented in Table 3. There was little difference in disease reaction among the resistant lines when crossed with other resistant lines, but the superiority of Ab28A in transmitting resistance to its hybrids was evident when comparisons were made of resistant lines crossed with susceptible lines.

The number of statistical groups within a particular type of cross obtained by the Newman-Kuels method was essentially the same when the analysis was conducted with either disease severity ratings or percentage of plants showing MDM symptoms. This indicated that both types of data were equally effective for identifying the levels of resistance contributed by the parental lines to their hybrids within these groups.

It was expected that data on disease severity ratings would detect smaller differences in disease reaction among corn genotypes than would data on disease incidence when differences in disease incidence were relatively small (eg, 6–10%) and differences in disease severity in diseased plants were relatively large (eg, 2.0–2.5 disease severity grades) or a positive correlation between disease incidence and disease severity existed. In 1972, the average disease severity index of diseased plants and the average disease incidence for the R × R crosses were 2.78 and 20% compared to 4.43 and 90% for the S × S crosses (Table 3). This positive correlation between disease severity and disease incidence suggested that if comparisons were made among individual hybrids (individual hybrid means were not presented), the data on disease severity ratings should give more statistical groupings than the data on disease incidence. This was found to be true because means for disease severity ratings among the 78 hybrids were separated into 19 statistical groupings (a through s), while the means for disease incidence were separated into only 14 such groupings (a through n). Thus for MDM, disease severity ratings were more sensitive than percentages of diseased plants in distinguishing levels of resistance among all individual

TABLE 4. Average reaction of all possible crosses for each of the 13 parental inbreds of the diallel to natural inoculation with maize chlorotic dwarf virus in 2 yr

Common parent	Percentage diseased plants[y]		Disease severity rating[y]			
			All plants		Diseased plants	
	1972	1973	1972	1973	1972	1973
Resistant						
Mp412	8 d[z]	18 f	1.17 e	1.28 e	3.13	2.56
Tx601	14 cd	31 e	1.28 de	1.45 e	3.00	2.45
T232	14 cd	21 f	1.26 de	1.31 e	2.86	2.48
Mp490	15 cd	35 e	1.34 de	1.66 d	3.27	2.89
Mo12	18 bc	37 e	1.33 de	1.70 d	2.83	2.89
Intermediate						
CI21	20 bc	54 cd	1.42 de	2.12 bc	3.10	3.07
CI90C	18 bc	47 d	1.42 de	1.72 d	3.33	2.53
Ab416A	18 bc	53 cd	1.38 de	1.71 d	3.11	2.34
Susceptible						
Ab28A	23 bc	56 bc	1.50 cd	1.89 cd	3.17	2.59
T226	40 a	63 b	1.86 b	2.22 b	3.15	2.94
Mp420	45 a	77 a	2.05 a	2.51 a	3.33	2.96
SC149	20 bc	60 bc	1.47 cde	2.03 bc	3.35	2.72
T216	27 b	71 a	1.65 c	2.23 b	3.41	2.73
Mean	22	48	1.47	1.83	3.16	2.70

[y]Mean value of 12 crosses.
[z]Means within a column not followed by the same letter differ significantly, $P = 0.05$.

TABLE 5. Reaction of crosses of maize with different levels of resistance to natural inoculation with maize chlorotic dwarf virus in 1973

Type of cross[a]	No. of crosses	(%) Diseased plants	Disease severity rating	
			All plants	Diseased plants
R × R	10	8	1.09	2.16
R × I	15	25	1.37	2.45
R × S	25	46	1.85	2.79
I × I	3	47	1.86	2.81
I × S	15	79	2.83	3.31
S × S	10	89	3.48	3.80

[a]R, S, and I denote resistant, susceptible, and intermediate, respectively.

TABLE 6. Response of crosses of maize with different levels of disease resistance to two virus diseases and the regression of disease response with resistance level

Type of cross[a]	1972			1973		
	Percentage of diseased plants	Disease severity ratings		Percentage of diseased plants	Disease severity ratings	
		All plants	Diseased plants		All plants	Diseased plants
Maize dwarf mosaic virus						
R × R	20	1.35	2.79	22	1.45	3.02
R × S	58	2.42	3.35	28	1.60	3.10
S × S	90	4.10	4.43	59	2.66	3.79
y-Intercept	−14.00	−0.13	1.88	−0.67	0.69	2.53
Slope	35.00	1.38	0.82	18.50	0.61	0.39
r	1.00	0.99	0.98	0.93	0.92	0.91
Maize chlorotic dwarf virus						
R × R	4	1.08	3.04	8	1.09	2.16
R × I	8	1.16	3.26	25	1.37	2.44
R × S	25	1.49	2.96	46	1.85	2.78
I × I	11	1.19	2.76	47	1.86	2.81
I × S	33	1.74	3.23	79	2.83	3.31
S × S	38	1.95	3.50	89	3.48	3.80
y-Intercept[b]	−3.27	0.86	2.92	−7.80	0.45	1.80
Slope[b]	6.60	0.17	0.06	16.23	0.47	0.31
r[b]	0.87	0.88	0.41	0.98	0.96	0.98
y-Intercept[c]	−11.67	0.64	2.71	−33.33	−0.25	1.27
Slope[c]	17.00	0.44	0.23	40.50	1.20	0.82
r[c]	0.99	1.00	0.79	1.00	0.98	0.99

[a]R, S, and I denote resistant, susceptible, and intermediate, respectively.
[b]Calculated with six levels of hybrid response.
[c]Calculated with three levels (R × R, R × S, and S × S) of hybrid response.

hybrids.

In the case of MCD, inbreds Mp412 and T232 contributed the greatest level of resistance, followed closely by Tx601. Inbred Mp420 contributed the highest level of susceptibility to its hybrids (Table 4). The number of identifiable statistical groupings was about the same whether data on disease incidence or data on disease severity ratings were analyzed.

Of the two years, 1973 had the higher natural infection rate of MCDV. Although the average percentage of diseased plants was 54% lower, the average disease severity rating of diseased plants was 10% higher in 1972 than in 1973. As was found with MDM, there was no close relationship between disease incidence and disease severity for MCD between the two years.

A comparison of crosses within groups in which parental inbreds had been crossed with similarly (eg, R × R) or dissimilarly (eg, R × S) classified lines showed relatively little difference in disease response in 1973 (*unpublished*). Even though differences within groups of crosses were small, differences among groups of crosses were often relatively large (Table 5). Both disease incidence and disease severity for MCD increased as the level of resistance decreased. This positive correlation between disease incidence and severity suggested that if comparisons were made among all 78 hybrids, data on disease severity ratings would classify the hybrids into more statistical groupings than would data on disease incidence. This was not true; both sets of data gave essentially the same number of statistical groupings.

Whether a single value, such as disease severity ratings (total rating of all plants in a plot divided by the total number of plants in a plot), which includes both disease incidence and disease severity, is suitable could be questioned. Obviously, the total ratings of all plants in a plot will be influenced by both disease incidence and disease severity of diseased plants, but not independently. It can be shown that for each unit of change of grade ratings of diseased plants, the disease severity ratings for the plot will change by an amount equal to the percentage of diseased plants expressed as a decimal. Thus, one grade change in diseased plants will change disease severity ratings by 0.1 and 1.0 with a disease incidence of 10 and 100%, respectively. Also, the magnitude of the change of disease severity ratings for each 10% change in disease incidence can be expressed as:

$$\frac{\text{Average disease severity ratings of diseased plants}}{10} - 0.1$$

Thus, a 10% change in disease incidence will change the disease severity ratings by 0.1 and 0.5 of a grade when the disease severity rating of diseased plants is 2.00 and 6.00, respectively.

An outbreak of either MDM or MCD, either locally (eg, near an area of johnsongrass) or more widespread provides the opportunity to collect data on disease incidence, severity, etc. One may know the relative resistance or susceptibility of the hybrids that are being grown, but not how hybrids with different levels of resistance might have performed under those conditions. To obtain some initial estimates of these kinds of information, we calculated linear regression of disease incidence and disease severity ratings on levels of resistance. We had three levels of resistance for MDM and six levels of resistance for MCD. For ease of comparison, we also made the calculations with MCD data for the same three levels of resistance used for MDM; ie, R × R, R × S, and S × S. These data are presented in Table 6.

In a year of high incidence of MDM when S × S crosses had about 90% diseased plants (ie, 1972) we estimated that each level of resistance would reduce the percentage of diseased plants, disease severity ratings, and ratings of diseased plants by approximately 35, 1.38, and 0.82, respectively (see "slope" in Table 6). In a year such as 1973, when S × S crosses had about 60% diseased plants, a change of approximately half that magnitude would be expected. These kinds of data have some very practical applications. For instance, they can be used to estimate the effectiveness of resistance in preventing yield losses.

A few research workers have determined losses of yield due to MDM (1,10,11). If it is assumed that the average reduction in yield in susceptible plants is 25% (which is a realistic assumption based on experimental evidence), we can calculate the expected losses (percent yield loss for field = percent diseased plants [as a decimal] × percent yield loss per diseased plant [as a decimal]). In a disease environment such as that in 1972, we would conclude that yield reductions for the R × R, R × S, and S × S crosses would be 5, 14.5, and 22.5%, respectively, while in 1973 comparable losses would be 5.5, 7, and 14.8 percent. These estimates do not take into account the probable added advantage of less severe symptoms causing proportionally smaller yield reduction in the more resistant genotypes.

Because the damage to maize from MCD is more severe than that from MDM, the effect of resistance in preventing yield losses can be more dramatic. We showed previously (13) that the average reduction in yield of all MCD×diseased plants was 60%. When disease incidence is high (90% for susceptible hybrids), we would expect yield reductions of 5, 30, and 54% for R × R, R × S, and S × S crosses, respectively.

From time to time the question arises whether there is a synergistic effect between MDMV and MCDV in maize. We attempted to answer this question since many plants were doubly infected. We cannot determine from our data if MCDV affected the severity of infection of MDMV because the symptoms of MDM developed and were recorded before any symptoms of MCD became evident. Our data can be used, however, to determine if infection by MDMV affected the severity of symptom expression of MCD. Of the lines selected for resistance to MCDV, Mp490 and Mo12 are susceptible and Mp412, Tx601, and T232 are resistant to MDMV. If MDMV has a synergistic effect on the expression of MCD symptoms, the disease severity ratings of MCD-disease plants should be significantly higher (reflecting more severe symptoms) for crosses involving Mp490 and Mo12 than for crosses involving Mp412, Tx601, and T232. Our data, shown in Table 4, do not support this assumption. In 1972, the disease severity ratings of MCD-diseased plants for all crosses containing Mp490 and Mo12 averaged 3.05 compared to the average of 3.00 for all crosses containing Mp412, Tx601, and T232. The comparable disease severity ratings of MCD for the two groups of crosses in 1973 were 2.89 and 2.50. These differences in disease severity are not great enough to suggest a synergistic effect between MDMV and MCDV.

Another way to look for synergism is to compare the severity of MCD symptoms in crosses involving inbreds that are susceptible to MCDV but resistant to MDMV with those in crosses involving inbreds that are susceptible to both viruses. In the first category we had only Ab28A, in the second, T226, Mp420, SC149, and T216. The disease severity ratings of 3.17 and 2.59 for MCD-diseased plants of crosses containing Ab28A in 1972 and 1973, respectively, differ only slightly from the comparable average disease severity ratings of 3.31 and 2.83 for crosses involving T226, Mp420, SC149, and T216. And these small differences in the severity of MCD symptoms occurred when the percentage of MDM-diseased plants in crosses containing any one of the four doubly susceptible inbreds was three (in 1972) and two (in 1973) times greater than the percentage of MDM-diseased plants in the Ab28A crosses.

Thus, our data indicate an absence of synergism, as measured by disease severity, between MDMV and MCDV. In a previous study, we also found that the genes for resistance in maize to MDM and MCD were independent (12).

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