Association of *Rmd*1, a Gene Conditioning Reaction to Maize Dwarf Mosaic Virus, with Genes Conditioning Endosperm Color (*y*1) and Type (*su*2) in Maize

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ABSTRACT

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Factors in maize conditioning resistance to maize dwarf mosaic virus (MDMV) have been shown by others to occur on chromosome 6. Genes conditioning endosperm color (*y*1) and type (*su*2) also occur on chromosome 6. Therefore, maize inbred lines B68, Oh7B, and Pa405 having *Rmd*1, and Va85 probably having *Rmd*1, a gene conditioning resistance to MDMV strain A (MDMV-A), were crossed to the genetic marker stock Ill76, having the *y*1 and *su*2 genes and which is susceptible to MDMV. The crosses were assumed to be of the genotype *Rmd*1*Rmd*1 *Y*1*Y*1*Su*2*Su*2 × *rmd*1*rmd*1*y*1*y*1*su*2*su*2. All characters are monogenic and completely dominant; thus, a 3:1 ratio was expected for each character in the F_2. The expected ratios were not achieved; therefore, the data were analyzed by calculating chi-square values for pairs of characters from contingency tables. For the B68, Oh7B, and Pa405 crosses, chi squares for MDMV reaction and endosperm color (*rmd*1/*y*1) were the largest, indicating closest association of gene loci. Chi squares for reaction and endosperm type (*rmd*1/*su*2), were the smallest, indicating least association of loci. The chi squares for endosperm color and type (*y*1/*su*2) were intermediate. Thus, *rmd*1 is near the *y*1 locus and on the centromere side of it, since it is a greater distance from *su*2 than is *y*1. The cross Va85 × Ill76 produced results inconsistent with the other crosses.

Additional keywords: corn, disease resistance, genetics of virus reaction, linkage.

The maize inbred lines B68, Oh1EP, Oh7B, and Pa405 (the B68 group) were shown to have monogenic dominant resistance to a culture of maize dwarf mosaic virus strain A (MDMV-A). No susceptible segregates appeared among the F_2 of crosses of these lines; thus, one gene, *Rmd*1, is common to these inbred lines (8). In addition, inbred lines Va239, Va53, Va85, and VaOM73 (the Va53 group) were found to have monogenic dominant resistance to MDMV-A, but in several crosses between members of the two groups, susceptible segregates were produced, and the gene *Rmd*1 could not be assigned to the Va53 group (8).

Maize inbred lines have been reported to have up to 10 genes conditioning resistance to MDMV (2). Line Pa405 has been widely studied and reported to have one (3,8), two (3), three (7), and five (10) genes conditioning resistance to MDMV. By using chromosomal translocation stocks to associate resistance genes with chromosome arms, workers have consistently reported that resistance genes occur in the short and long arms of chromosome 6 (2,12,13). In addition, in 1983 at Blacksburg, VA, some white kernels appeared on an ear of hybrid (B68 × Oh7B) × Va50 that had been selfed. All the lines in the pedigree have yellow seed. The seed were sorted into yellow and white classes and planted for observation of reaction to MDMV-A in 1984. Plants from yellow seeds segregated 65 resistant: 1 susceptible; plants from white seed segregated 20 resistant: 15 susceptible plants. Susceptibility was clearly associated with white endosperm, which is usually conditioned by the *y*1 gene located on chromosome 6 (Aycock, Roane and Tolin, *unpublished*). Therefore, a study

was initiated to determine if the gene *Rmd*1 was associated with the *y*1 gene, which occurs 17 units from the end of chromosome 6 (1).

MATERIALS AND METHODS

The MDMV-resistant lines B68, Oh7B, Pa405, and Va85, each having yellow (*Y*1 *Y*1), starchy (*Su*2*Su*2) endosperm were crossed onto a gene marker stock Ill76 having a nonshrivelling sugary (*su*2*su*2), white (*y*1*y*1) endosperm and which produces a mild mosaic reaction (mostly type 7) when inoculated with MDMV-A. Thus, the genotype for three of the crosses studied in F_2 was *Rmd*1*Rmd*1 *Y*1 *Y*1*Su*2*Su*2 × *rmd*1*rmd*1*y*1*y*1*su*2*su*2; this is the reciprocal of the genotype of Ill76 × Va85. The resistant lines had been used in the Virginia maize breeding program for several years and when inoculated with MDMV-A in the one- to three-leaf stage, produced only resistant plants (type 1). Ill76 was obtained from the Maize Genetic Stock Center, Urbana, IL.

Inoculum source, preparation, and inoculation were described previously and a seven-part scale was diagrammed to show the method of plant classification after anthesis (9). By using this scale, two pairs of phenotypes may be recognized, a) those that are healthy or symptomless (type 1) and those that are infected or symptomatic (reaction types 2–7) and b) those that are resistant (reaction types 1–5) and those that are susceptible (reaction types 6–7). Classification by method b is used in this investigation.

We expected that each of the three characters would provide segregation into 3:1 ratios, in which case we would apply Immer's method for calculating linkage intensities (4). Should one or more characters deviate from the 3:1 ratio, a contingency test would be applied to determine associations by magnitudes of chi-square values (5).

TABLE 1. Response of maize parental lines and their F_1 hybrids to inoculation with MDMV-A

Inbred line or hybrid	Reaction type frequency[a]							*N*
	1	2	3	4	5	6	7	
Line:								
B68	49	...	...	...	...	...	...	49
Oh7B	155	...	...	...	...	...	...	155
Pa405	48	...	...	...	...	...	...	48
Va85	37	...	...	...	...	...	...	37
Ill76	6	...	...	2	...	...	60	68
F_1 hybrid:								
B68 × Ill76	49	...	...	...	...	...	...	49
Oh7B × Ill76	185	...	...	...	...	...	...	185
Ill76 × Oh7B	38	...	...	...	...	...	...	38
Pa405 × Ill76	64	...	...	...	...	...	...	64
Ill76 × Pa405	39	...	...	...	...	...	...	39
Va85 × Ill76	132	3	...	1	...	...	1	137
Ill76 × Va85	45	3	...	...	...	...	...	48

[a]Reaction types: 1 = no symptoms, 2 = narrow streaks in leaves below the ear, 3 = narrow streaks in leaves above the ear, 4 = narrow streaks in leaves above and below the ear, 5 = mottled leaves only below the ear, 6 = mottled leaves only above the ear, 7 = mottled leaves above and below the ear.

In field plots, the parental lines F_1 and F_2 were grown and inoculated with MDMV-A. Seed from self-pollinated ears of F_1 plants were separated into the four phenotypes: yellow starchy, yellow sugary, white starchy, and white sugary. No differentiation in classification was made between light and dark yellow seed. The F_1 and F_2 of families analyzed were grown in 1986 and 1987, respectively. Only flat seeds were planted because it was difficult to separate round seeds into starchy or sugary classes. All flat seeds were sorted into the four classes, counted, and then planted such that each class made a plot in the field.

RESULTS

Infected and symptomless plants were easily identified in the field; individual infected plants were classified into one of the reaction types 2 to 7. Parental and F_1 plant responses to inoculation with MDMV-A are shown in Table 1. A few (9%) plants of Ill76 escaped infection. Among the F_1's shown, only Va85 × Ill76 and its reciprocal produced symptomatic plants, one of which was type 7. Symptomless plants among the various F_1's were selfed to produce the F_2 shown in Table 2. For all crosses, segregation into the seven reaction types was bimodal, and only a few plants were classified into reaction types 2–5. These are considered resistant and are grouped with those of type 1, which had no symptoms. Reaction types 6 and 7 were grouped together. It is assumed that plants in reaction type 6 escaped infection when mechanically inoculated but were later inoculated by aphids; therefore, they were probably susceptible plants with delayed symptom expression. For convenience the two groups are designated resistant and susceptible with probable genotypes of *Rmd*1— and *rmd*1*rmd*1, respectively. In crosses of susceptible inbred line Va50 with the resistant lines, all F_2 progenies segregated into a monogenic ratio (8). In crosses with Ill76, most families segregated with a deficiency of susceptible plants. Only two Oh7B × Ill76 families, 4 and 11, and Va85 × Ill76 families 3 and 5 had an excess of susceptible plants (Table 3). Thus, segregation was not random and the impact of the imbalance was apparent when columns were totaled. In addition, heterogeneity tests produced large chi-square values, indicating families should not be combined. For Oh7B × Ill76, nine of 14 families segregated as expected for reaction to MDMV into a 3:1 ratio.

Endosperm color conditioned by the *y*1 gene is well known and should segregate into a 3:1 ratio. In the crosses B68 × Ill76, and Ill76 × Va85 both excesses and deficiencies of recessives (white endosperm) were observed (Table 3). In the crosses Oh7B × Ill76 and Pa405 × Ill76, there was usually an excess of white kernels. Heterogeneity tests again indicated that families were not combinable. The character endosperm type conditioned by the gene *su*2 requires great care for classification and is more subject to misclassification of kernels than is the character endosperm color. Endosperm type seemed to segregate more randomly than either reaction to MDMV or endosperm color (Table 3); however, since two of the three characters did not segregate satisfactorily into 3:1 ratios, the data were deemed unsatisfactory for calculating map distances. It may be seen from the regrouping of the data according to phenotype (Table 4) that the percentage of susceptible plants associated with white endosperm (*y*1*y*1) was much greater than that associated with yellow endosperm (*Y*1).

TABLE 2. Frequency in seven reaction types of F_2 plants of four maize dwarf mosaic virus-resistant maize inbred lines crossed to Ill76, a susceptible inbred marker gene stock for endosperm color and type

Cross	F_2 plant reaction type frequency[a]							*N*	Ratio 1–5:6–7	Actual ratio
	1	2	3	4	5	6	7			
B68 × Ill76	1,572	0	0	0	0	59	265	1,896	1,572:324	4.8:1
Oh7B × Ill76	2,028	0	0	4	0	107	415	2,547	2,028:519	3.9:1
Pa405 × Ill76	269	2	0	0	0	4	33	308	217:37	7.3:1
Ill76 × Va85	682	3	0	1	0	48	106	840	686:154	4.4:1

[a]Reaction types: 1 = no symptoms, 2 = narrow streaks in leaves below the ear, 3 = narrow streaks in leaves above the ear, 4 = narrow streaks in leaves above and below the ear, 5 = mottled leaves only below the ear, 6 = mottled leaves only above the ear, 7 = mottled leaves above and below the ear.

TABLE 3. Frequency distribution into phenotypic classes of F_2 plants in families of four maize dwarf mosaic virus (MDMV)-resistant maize inbred lines crossed to Ill76 and probabilities (P) for fits to 3:1 ratios for three characters

Cross and F_1 family no.	Phenotypic classes[a]									Segregation for characters					
										Reaction		Endosperm color		Endosperm type	
	RYSu	RYsu	RySu	Rysu	rYSu	rYsu	rySu	rysu	N	R:r	P for 3:1	Y:y	P for 3:1	Su:su	P for 3:1
B68 × Ill76															
1	88	30	5	9	4	1	21	8	166	132:34	>0.1	123:43	>0.7	118:48	>0.2
2	218	21	25	5	13	2	21	6	311	269:42	<0.01	254:57	<0.01	277:34	<0.01
3	140	23	3	12	6	2	3	8	197	178:19	<0.01	171:26	<0.01	152:45	>0.3
4	187	42	7	27	24	4	24	26	341	263:78	>0.8	257:84	>0.8	242:99	>0.05
5	202	21	13	17	5	3	20	24	305	253:52	<0.01	231:74	>0.1	240:65	>0.1
6	200	50	35	12	22	1	12	18	350	297:53	<0.01	273:77	>0.1	269:81	>0.3
7	111	38	14	17	3	1	22	20	226	180:46	>0.1	153:73	<0.02	150:76	<0.01
Total	1,146	225	102	99	77	14	123	110	1,896	1,572:324	<0.01	1,462:434	<0.05	1,448:448	>0.1
Oh7B × Ill76															
1	95	25	24	10	13	2	15	12	196	154:42	>0.2	135:61	<0.05	147:49	>0.99
2	123	38	26	39	7	3	9	7	252	226:26	<0.01	171:81	<0.01	165:87	>0.01
3	68	13	13	5	1	0	12	4	116	99:17	<0.02	82:34	>0.2	94:22	>0.1
4	70	15	14	10	7	0	16	17	149	109:40	>0.5	92:57	<0.01	107:42	>0.3
5	121	18	38	13	3	3	19	26	241	190:51	>0.1	145:96	<0.01	181:60	>0.95
6	72	23	12	17	9	1	17	9	160	124:36	>0.3	105:55	<0.01	110:50	>0.05
7	70	15	25	11	8	1	18	9	157	121:36	>0.5	94:63	<0.01	121:36	>0.5
8	81	22	19	7	6	1	17	13	166	129:37	>0.3	110:56	<0.01	123:43	>0.7
9	94	29	4	10	12	1	11	17	178	137:41	>0.5	136:42	>0.5	121:57	<0.05
10	106	23	15	32	20	13	23	13	245	176:69	>0.2	162:83	<0.01	164:81	<0.01
11	92	25	15	14	7	0	8	9	170	146:24	<0.01	124:46	>0.5	122:48	>0.3
12	93	25	17	19	8	1	19	19	201	154:47	>0.5	127:74	<0.01	137:64	<0.05
13	88	8	8	15	4	2	8	8	141	119:22	<0.01	102:39	>0.3	108:33	>0.5
14	79	18	26	21	3	0	15	13	175	144:31	<0.05	100:75	<0.01	123:52	<0.1
Total	1,252	297	256	223	108	28	207	176	2,547	2,028:519	<0.01	1,685:862	<0.01	1,823:724	<0.01
Pa405 × Ill76															
1	62	16	13	8	0	0	4	2	105	99:6	<0.01	78:27	>0.2	79:26	>0.95
2	120	5	34	13	14	0	12	5	203	172:31	<0.01	139:64	<0.05	180:23	<0.01
Total	182	21	47	21	14	0	16	7	308	271:37	<0.01	217:91	>0.05	259:49	<0.01
Ill76 × Va75															
1	100	26	27	28	18	0	3	4	206	181:25	<0.01	144:62	>0.05	148:58	>0.2
2	89	23	18	26	7	4	7	2	176	156:20	<0.01	123:53	>0.1	121:55	>0.05
3	118	15	13	14	23	8	18	14	223	160:63	>0.2	164:59	>0.5	172:51	>0.3
4	86	4	12	6	3	3	1	0	115	108:7	<0.01	96:19	<0.05	102:13	<0.01
5	57	9	8	7	30	0	5	4	120	81:39	>0.05	96:24	>0.2	100:20	<0.05
Total	450	77	78	81	81	15	34	24	840	686:154	<0.01	623:217	>0.5	643:197	>0.3

[a]R, r = resistant and susceptible to MDMV-A conditioned by the genes *Rmd*1 and *rmd*1; Y, y = yellow and white endosperm conditioned by the genes *Y*1 and *y*1; Su, su = starchy and sugary endosperm conditioned by the genes *Su*2 and *su*2.

TABLE 4. The percentages of susceptible (*rmd*l) plants of each seed phenotype in F_2 of crosses of four inbred lines with the white (*y*l*y*l) sugary (*su*2*su*2) marker gene stock, Ill76

Cross	Phenotype of seed planted[a]	Total no. plants	Number susceptible plants	Percent susceptible plants	Percent susceptible plants of each seed phenotype
B68 × Ill76	Y_Su_	1,223	77	6.30	6.22 Y_
	Y_susu	239	14	5.86	53.68 yy
	yySu_	225	123	54.67	13.81 Su_
	yysusu	209	110	52.63	27.68 susu
Oh7B × Ill76	Y_Su_	1,360	108	7.94	8.07 Y_
	Y_susu	325	28	8.62	44.43 yy
	yySu_	463	207	44.71	17.28 Su_
	yysusu	399	176	41.11	28.18 susu
Pa405 × Ill76	Y_Su_	196	14	7.14	6.45 Y_
	Y_susu	21	0	0.00	25.27 yy
	yySu_	63	16	25.40	11.58 Su_
	yysusu	28	7	25.00	14.29 susu
Ill76 × Va85	Y_Su_	531	81	15.25	15.41 Y_
	Y_susu	92	15	16.30	26.73 yy
	yySu_	112	34	30.36	17.88 Su_
	yysusu	105	24	22.86	19.79 susu

[a]For brevity the symbols Y, y, Su, and su are substituted for *Y*1, *y*l, *Su*2, and *su*2, respectively.

If linkage is not a factor, a similar percentage of susceptible plants should be associated with each seed phenotype. A predominance of susceptible plants associated with white, sugary endosperm (*y*1*y*1*su*2*su*2) is expected in the coupling phase if linkage is a factor. The predominant percentage of susceptible plants associated with white (*y*1*y*1) and to lesser extent with sugary endosperm (*su*2*su*2) suggests that *rmd*1 is closely linked with *y*1*y*1 and may also be distantly linked with *su*2*su*2 (Table 4). Therefore, chi squares were calculated from contingency tables to provide some indication of the relative degree of association of genes conditioning pairs of characters (Table 5).

Although as previously stated, the data for the various families in each cross were heterogeneous and should not be combined, contingency chi squares calculated from the total resulted in the same trends as those calculated from individual families; therefore, only the contingency chi squares for the totals are shown (Table 5). When B68, Oh7B, and Pa405 were the resistant parents, largest chi squares were calculated for the MDMV reaction-endosperm color interaction. The larger the chi-square value, the closer the genes. For all four crosses, chi squares for the MDMV reaction-endosperm types were the smallest, indicating the farthest spacing or possibly independence of genes. Because the magnitude of chi square is indicative of the degree of association, a gene order on the chromosome can be derived. It appears from the B68, Oh7B, and Pa405 data that the order is:

$$\text{——— } rmd1 \text{———} \underset{17}{y1} \text{———} \underset{57}{su2} \text{———}$$

Because the *y*1 locus is near the centromere, it is not clear whether *rmd*1 is in the long arm with *y*1 and *su*2 or in the short arm. Thus, the diagram may be:

$$\text{(a) } \underset{0}{\text{———}} rmd1 \overset{\text{cent.}}{\text{———}} \underset{17}{y1} \text{———} \underset{57}{su2} \text{———}$$

or:

$$\text{(b) } \underset{0}{\overset{\text{cent.}}{\text{———}}} rmd1 \text{———} \underset{17}{y1} \text{———} \underset{57}{su2} \text{———}$$

The data from Ill76 × Va85 would place the *rmd*1 gene near the end of the short arm or on the long arm terminal to *su*2 (Table 5). Since the map distance between *y*1 and *su*2 is 40 units (1), the largest chi square would place *y*1 and *su*2 close together and *rmd*1 and *su*2 farther apart. These data indicate that *rmd*1 is at the end of the short arm near map distance 0 and certainly the centromere would be between *rmd*1 and *y*1. Since *Rmd*1 was not definitely assigned to Va85 (8), it may have a different gene conditioning resistance on chromosome 6. Diagram b seems to be the most logical solution for three of the four crosses.

Although the families in the four crosses were heterogenous, the recombination percentages were calculated for comparison from the totals by using Immer's formula (4) for characters segregating in a 3:1 ratio (Table 6). For endosperm color and type, a recombination percentage near 30 was calculated for all four crosses. This is 10% less than the published value (1). The largest recombination percentage was calculated for reaction and endosperm type. The values were consistently large for all four crosses. For B68, Oh7B, and Pa405, the recombination percentages for reaction and endosperm color were smallest. The value for Va85 again suggests that this inbred may have a gene other than *Rmd*1. For three inbreds, the recombination data support that of the contingency chi-square method and indicate the gene order is as in the foregoing diagrams. If *rmd*1 is on the centromere side of *y*1, as both contingency chi squares and recombination percentages indicate, *rmd*1 distance exceeding 17 units is not feasible since *y*1 is reported to be only 17 units from the end of the short arm. Therefore, only a gene order can be determined by calculating recombination percentages.

DISCUSSION

The fact that none of the characters segregated into monogenic ratios was unexpected. Endosperm color conditioned by *y*1 and endosperm type conditioned by *su*2 on chromosome 6 are well known (1). Reaction to MDMV conditioned by *rmd*1 was shown to be monogenic (8), but a monogenic ratio was not obtained in most families (Tables 2 and 3). Therefore, map distances for the three characters could not be properly calculated from formulas. However, for comparison, the distances obtained by applying

TABLE 5. Chi squares calculated from contingency tables for pairs of characters[a]

Cross (maize lines)	N	Character pairs: Reaction and endosperm color χ^2	P	Reaction and endospoerm type χ^2	P	Endosperm color and type χ^2	P
B68 × Ill76	1,896	532.08	<0.01	46.43	<0.01	187.64	<0.01
Oh7B × Ill76	2,547	464.68	<0.01	37.93	<0.01	204.33	<0.01
Pa405 × Ill76	308	21.49	<0.01	0.84	<0.3	21.32	<0.01
Ill76 × Va85	840	13.77	<0.01	0.37	<0.5	101.33	<0.01

[a] *P* values less than 0.05 indicate that the characters are not inherited independently. Largest chi-square values indicate greatest degree of association and shortest map distances; smallest indicate greatest distances.

TABLE 6. Recombination percentages obtained for pairs of characters in coupling from Immer's formula for total number of individuals in each cross[a]

Cross (maize lines)	Character pairs: Reaction and endosperm color	Reaction and endosperm type	Endosperm color and type
B68 × Ill76	17.67± 9.60	38.16 ± 0.02	29.85 ± 0.03
Oh7B × Ill76	23.17 ± 0.96	57.27 ± 1.36	33.04 ± 1.19
Pa405 × Ill76	29.50 ± 3.20	46.63 ± 4.11	31.40 ± 3.31
Ill76 × Va85	40.46 ± 2.30	48.24 ± 2.54	28.42 ± 1.90

[a] The application of formulas to determine recombination in this case is predicated on having an acceptable fit to the 3:1 ratio for each pair of characters. Since the 3:1 ratios were not achieved, these calculations are presented for comparison with our contingency chi squares. The data above merely confirm the gene order derived by our contingency method in Table 5.

Immer's formula (4) were consistent with magnitudes of chi squares obtained from contingency tables (Tables 5 and 6). It is more important to discuss the relative positions of genes than to discuss reasons for failure of the characters to segregate monogenically. The genes *y*1 and *su*2 are reported to be 40 map units apart (1); when chi squares were calculated from contingency tables, the *y*1*su*2 chi squares were consistently intermediate to the *rmd*1*y*1 and *rmd*1*su*2 values for the B68, Oh7B, and Pa405 crosses. These results indicate that *rmd*1 is near and in a distal position relative to *y*1 from *su*2; therefore, *rmd*1 is nearer to the centromere on the long arm or on the short arm. It was shown from studies with translocation stocks to determine the number of genes conditioning reaction to MDMV, that the genes have been consistently associated with both the short and long arms of chromosome 6 (2,12,13). If, as indicated by our results *rmd*1 is near the centromere, it is not surprising that in studies using translocation stocks, gene loci were reported on both arms. Since Va85 gave results inconsistent with those of B68, Oh7B, and Pa405, some credence is given to the fact that the B68 group and Va53 group, of which Va85 is a member, may have different *Rmd* genes (8).

Recent preliminary reports are in agreement with the results reported here. Scott found endosperm color and reaction to MDMV to be closely associated (11). Using restriction fragment length polymorphism (RFLP) analysis of inbred line Pa405, McMullin has located resistance gene(s) in a region near the centromere of chromosome 6, six to eight recombination units toward the centromere from *y*1 (6; McMullin, *personal communication*). This agrees well with our map b. It is quite significant that the two diverse approaches, RFLP analysis and contingency chi square, produced results in such close agreement.

Note added in proof: The paper by M. D. McMullen and R. Louie, "The linkage of molecular markers to a gene controlling the symptom response in maize to maize dwarf mosaic virus", was recently published in Molecular Plant – Microbe Interactions 2:309-314, 1989. It is the basis for the abstract cited below (6). They assign the gene symbol *Mdml* to resistance in Pa405. *Rmd*1 from our work is synonym of *Mdml.*

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