Partial Resistance of Sugary Enhancer Sweet Corn Genotypes to Two Isolates of the Sugarcane Mosaic Subgroup of Potyviruses

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ABSTRACT

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Sweet corn genotypes containing the sugary enhancer (*se*) allele expressed moderate levels of resistance to maize dwarf mosaic virus (MDMV), a member of the sugarcane mosaic subgroup, under natural infection in the field in Israel. Resistance was identified both in homozygous (*sese*) and heterozygous (*Sese*) genotypes. Most (*sese*) genotypes developed MDMV symptoms when they were mechanically inoculated in the greenhouse. The presence of the virus was verified by ELISA analysis. Plants containing known genes for resistance did not show MDMV symptoms under natural or mechanical inoculation. Two isolates of the sugarcane mosaic virus subgroup of potyviruses, differing in virulence on sweet corn genotypes, were identified. The results show that several *se* inbred lines contain factors contributing to moderate field resistance to maize potyviruses, but it is not clear whether these factors are pleiotropic or are associated with the *se* gene. The mechanism of the resistance exhibited in conjunction with the *se* is not yet understood.

Maize dwarf mosaic virus (MDMV) and other members of the sugarcane mosaic subgroup of potyviruses (27,28) infect maize. They cause potentially one of the most damaging diseases of sweet corn (*Zea mays* L.). Reductions in sweet corn yield result from undeveloped kernels in the basal quarter of the ear, reduced weight and size of ears, and barrenness of plants (1,3,16,17,20,24,29). These viruses have been reported from the United States (20), Europe (30), Asia (7), and Australia (21). Strains have been differentiated serologically (12,28) and by host range (9,31). In Israel, two strains of MDMV have been identified on corn and johnsongrass (1). One strain, designated M-C, induces mosaic in some common sorghum cultivars; the other, designated M-D, is responsible for the appearance of red lesions and systemic necrosis on the same cultivars. We have recently classified one of the Israeli types as johnsongrass mosaic virus. Since the taxonomy of potyviruses infecting corn had recently been reevaluated and the viruses grouped into a subgroup of four viruses (33), the classification of maize potyviruses isolated in Israel followed the new classification.

Resistance in corn to the sugarcane subgroup of potyviruses may result from several different mechanisms. Resistance in dent corn has often been identified by a reduced incidence of symptoms in plants infected with MDMV, either naturally or by mechanical inoculation. Corn that is resistant to the disease is not necessarily resistant to infection by MDMV. Several reports indicate that replication of MDMV was not inhibited in MDMV-inoculated leaves of disease-resistant genotypes, compared with those of susceptible genotypes, but movement of MDMV was restricted in the resistant plants (10,11,32). In other instances, concentrations of MDMV in systemically infected resistant hybrids were found to be lower than in susceptible hybrids (2,8). Several researchers have also identified various sources of disease resistance, in which development of symptoms was delayed (i.e., the incubation period was lengthened), possibly because of slower rates of replication of MDMV (2,8,13, 26). Most inheritance studies have indicated that disease resistance is controlled by a few major genes or by modifier or minor genes (11,18,23,25). However, estimates of the number of genes controlling resistance and interpretations of the gene action varied according to which inbreds were evaluated, the methods of assessing disease, environmental factors, and whether natural infection or controlled inoculation was used. Several sweet corn mutations have been tested for resistance to MDMV. Preliminary observations in our field nurseries have shown that a number of genotypes containing the *se* allele, which is a modifier of the sugary (*su*) locus, were less infected than others when exposed to natural inoculation in the field (data not shown). The objectives of our research were to 1) evaluate the resistance of *Sese* and *sese* genotypes to MDMV potyviruses under natural inoculation in the field, and 2) identify, by controlled mechanical inoculation and enzyme-linked immunosorbent assay (ELISA) analysis, the nature of resistance identified in the field.

MATERIALS AND METHODS

Several genotypes from the original *se* inbreds released by the University of Illinois (6,22), were initially screened for resistance to MDMV. Other inbreds such as M62228, IL793a, and IL796b represented inbreds into which resistance to MDMV has been incorporated from Pa405 (5,15,23). Additional resistant and susceptible *Se* and *se* genotypes were developed at Newe Ya'ar Research Center and evaluated as inbreds and in test cross combinations.

Evaluation of the field resistance of inbred lines was conducted at Newe Ya'ar Research Center in 1991 and 1992, and at Eden Experiment Station, in the Jordan Valley, in 1992. Fifteen genotypes at Newe Ya'ar were arranged in a completely randomized block design, comprising four replicates, 2.2-m rows, seven plants per meter. The same genotypes were arranged in a completely randomized design at Eden Experiment Station, with replicate number and plot size as above. Progeny of five *se* inbred lines crossed with susceptible *Se* inbreds were evaluated at Newe Ya'ar in 1992, using the same experimental design as described above for Newe Ya'ar. High natural disease incidence prevails in those regions in the spring every year that enable effective screening for resistance. Disease incidence (plants showing symptoms) was evaluated before silking. Leaf samples from the 1992 Newe Ya'ar inbreds field trial were collected for ELISA analysis at silking, after evaluation of disease symptoms.

Thirteen inbred lines and crosses, which differed in resistance to potyviruses under conditions of natural infection in the field, were selected for mechanical inoculation in the greenhouse at Volcani Center, Bet Dagan. At the three-leaf stage, the plants were mechanically inoculated by rubbing them with Carborundum mixed with extracts of infected leaves (20,24). Evaluation of symptoms and sampling of leaves for ELISA analysis was done 3 wk after inoculation (1 wk after the appearance of symptoms). Leaves exhibiting typical MDMV disease symp-

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toms were ground in 2 volumes (w/v) of 0.05 M phosphate buffer (pH 7.0). Values of A_{405} did not exceed 0.200 in extracts from both healthy control and infected seedlings before symptom expression. Therefore, an A_{405} value of 0.200 was considered as background and was subtracted from all values. Antigen-coated-plate (ACP) ELISA was used in all the described experiments (4).

Rabbit antibodies against the two potyvirus isolates from Israel, which were classified as maize dwarf mosaic and johnsongrass mosaic (R. Salomon, *unpublished*), were prepared. These antisera did not cross react in reciprocal tests in either immunoblot or ELISA procedures when early bleedings were used (4,12). Each plate contained two samples from healthy seedlings and two of both virus isolates from infected cv. Jubilee plants, as negative and positive controls, respectively. Goat anti-rabbit IgG alkaline phosphatase conjugate was purchased from BioMakor (Kiryat Weizman 76326, Rehovot, Israel).

Plates (Coster, Cambridge, MA) with wells of 100-µl volume were used. Color development (A_{405}) was recorded within 30-45 min on an automatic ELISA reader (BioTeck model EL310, Burlington VT).

Table 1. Maize dwarf mosaic virus (MDMV) disease incidence in maize genotypes under natural infection in the field

Genotype	Genetic background	Disease incidence[z] (%)
IL793a	(*se*)	0.0 a
IL796b	(*se*)	0.0 a
M62228	(*se*)	0.0 a
M6222H	(*se*)	0.0 a
IL772aJ99b	(*se*)	0.0 a
IL677a	(*se*)	0.9 b
IL775a	(*se*)	4.6 b
IL775aJ35	(*se*)	8.0 b
IL772a	(*se*)	11.2 b
J99b	(*Se*)	22.7 bc
IL451b	(*se*)	29.3 bc
IL451b	(*Se*)	30.9 bc
IL774c	(*se*)	30.9 bc
J95	(*Se*)	45.0 c
J106a	(*Se*)	46.0 c

[z] Results summarize trials at Newe Ya'ar 1991 and 1992 and at Eden 1992, analyzed by Duncan's multiple range test at $P = 0.05$. Results based on symptom expression. Fifty-four plants were evaluated for each genotype in each location.

Table 2. Resistance to Maize dwarf mosaic virus (MDMV) in crosses of resistant × susceptible inbreds under natural infection in the field, Newe Ya'ar 1992

Cross	Disease incidence[z] (%)
IL793a(*se*) × J95(*Se*)	0 a
IL796b(*se*) × J106a(*Se*)	0 a
M62228(*se*) × J99b(*Se*)	3.2 a
IL775a(*se*) × J106a(*Se*)	17.6 ab
IL775a(*se*) × J95(*Se*)	20.6 abc
IL774c(*se*) × J99b(*Se*)	22.5 abc
Jubilee	36.3 c

[z] Symptom evaluation done at silking; 80 plants evaluated for each cross. Numbers followed by different letters are significantly different at $P = 0.05$, by Duncan's multiple range test.

RESULTS

Several inbreds containing the *se* allele, which is a modifier of the *su* locus, showed moderate resistance to MDMV in repeated trials under exposure to natural inoculation in the field. The presence of MDMV was confirmed serologically by ELISA in all the trials. There was variation in disease incidence, which was up to 100% in some susceptible lines, and in the degree of resistance expressed in *se* genotypes that did not contain any of the alleles known to confer resistance to MDMV. Inbreds IL772a and IL775a had consistently lower levels of disease incidence than did susceptible inbreds (Table 1). Genotypes containing known alleles for resistance to MDMV, such as M62228, IL793a, and IL796b, did not show any symptoms in most trials. The inbred IL451b(se), like its isoline IL451b(Se), had an intermediate level of disease incidence, very similar to that of susceptible *Se* inbreds. Additionally, IL774c seemed to have higher disease incidence than did some of the other *se* lines.

The inbreds IL772a(*se*) and IL775a(*se*) were crossed with *Se* inbred lines to create F_1s that have undergone pedigree selection for improved agronomic traits and presence of the *se* gene. The new inbred lines, IL772aJ99b and IL775aJ35, that have been developed without selection for resistance, have shown consistent resistance to maize potyviruses (Table 1). In order to test the type and level of resistance, several crosses with susceptible inbred lines were created. Crosses with the inbreds IL793a, IL796b, and M62228, which had genes for resistance that have been introgressed from Pa405, had the highest levels of resistance, with very few plants having MDMV symptoms (Table 2). The crosses of IL775a and IL774c (the latter considered a less resistant inbred) with susceptible inbreds had an intermediate disease incidence, even though only one parent in each cross contributed a moderate level of resistance. Cultivar Jubilee, a susceptible (*suSe*) commercial hybrid, had the highest level of disease incidence (Table 2).

Resistance of inbred lines and crosses was also evaluated in the greenhouse by mechanical inoculation with two potyvirus isolates (Table 3). The isolate from Lehavot Haviva (MDMV) was generally more virulent than the isolate from Sheluhot (JGMV). Results in two trials were consistent. The ELISA values of A_{405} confirmed the virus presence in the leaves of mechanically inoculated genotypes (Table 3) that had moderate resistance to the disease in the field (Table 1).

Partial resistance to MDMV has been defined as lack of symptoms, in spite of the presence of propagating virus in the plant (10). Therefore, inbred lines showing field resistance were analyzed by ELISA to determine whether such plants were resistant to MDMV infection or merely symptomless. Virus was identified in *Se* inbreds that had disease symptoms and in IL772a(se), which was completely free of symptoms in the field at Newe Ya'ar. Inbred IL772a(*se*) showed the highest A_{405} ELISA value of eight genotypes in this test (Table 4). Line IL775a(*se*), which was also symptomless, did not contain detectable amounts of the virus. Tests with specific antibodies showed that only MDMV was present in these plants. The IL772aJ99E4(*se*) and IL775aJ120(*se*) genotypes, developed from crosses with IL772a(*se*) and IL775a(*se*), were both symptomless.

DISCUSSION

Introgression of resistance to leaf diseases is one of the major goals in breeding sweet corn. Resistance to several leaf

Table 3. Disease incidence and ELISA readings of sweet corn seedlings, following mechanical inoculation in the greenhouse

Genotype	Genetic background	JGMV incidence[y]	ELISA[z] A_{405}	MDMV incidence[y]	ELISA[z] A_{405}
IL796b	(*se*)	0/11	0.00	0/10	0.00
IL793a	(*se*)	0/12	0.00	0/13	0.00
M62228	(*se*)	2/10	0.172	2/10	0.550
IL772a	(*se*)	5/9	0.552	6/9	0.623
IL772aJ99	(*se*)	0/5	0.00	0/6	0.00
IL775a	(*se*)	3/7	0.701	5/8	0.658
IL767b	(*se*)	6/13	0.385	12/13	0.605
J92b	(*se*)	1/6	0.217	5/7	0.600
IL744a	(*se*)	0/12	0.00	10/13	0.536
J95	(*Se*)	4/15	0.653	6/15	0.710
J68	(*Se*)	5/5	0.335	6/6	0.798
IL793a × J95	(*se* × *Se*)	0/12	0.00	0/13	0.00
IL775a × J95	(*se* × *Se*)	11/15	0.371	15/18	0.595
Jubilee	(*Se*)	10/14	0.488	10/14	0.475

[y] Number of plants showing symptoms/number of plants inoculated.
[z] Values are average of infected plants showing $A_{405} > 0.200$.

diseases is often required, but difficult to achieve in a single genotype. The type and level of resistance required to ensure minimum economic damage must also be considered. Genotypes such as IL793a, IL796b, and M62228, which contain genes for resistance introgressed from Pa405 (5,15), were resistant to MDMV and JGMV and were without any symptoms when exposed to natural infection in the field or mechanical inoculation in the greenhouse (Tables 1, 3). Several inbred lines had lower disease incidence than the susceptible genotypes J95*Se* and J106*Se*, under natural infection in the field (Table 1). These inbred lines, however, developed typical symptoms when they were mechanically inoculated in the greenhouse. The moderate level of resistance expressed in the field in inbreds IL677a, IL772a, IL775a and some of their derivatives, and to a lesser extent in IL774c, was consistent. Moreover, this resistance was also expressed in crosses of these inbred lines with susceptible lines (Table 2). These results raised two questions: What is the nature of the field resistance, and what is the best procedure for identification and selection of resistant genotypes?

Previous experiments with resistant sweet corn genotypes indicated that there were no immune plants (2,23). Pataky et al (20) found weak associations between sweet corn yield and titer of MDMV or symptoms in susceptible hybrids. Yield was positively correlated with symptomless plants of resistant and partially resistant (tolerant) genotypes. The general procedure to determine resistance to MDMV is evaluation of plants that have been mechanically inoculated by rubbing their leaves with a mixture of the virus and Carborundum (20). Inoculation by this mechanism circumvents transfer of the virus by its vector, the aphid, so that the virus is inserted directly into the plant tissue. In the field, where vectors are involved, resistance can also be achieved by preventing transmission. The moderate resistance observed in a group of *se* genotypes following natural inoculation in the field (Table 1) was completely overcome by mechanical inoculation (Table 3). We assume that the resistance observed in the field is related to inhibition of transmission by vectors. Such phenomenona may be related to environmental impact on symptom expression, aphid populations and preferences, virus strains, and timing of all the above. Mechanical barriers, repellence, and preference are the main mechanisms associated with resistance to insects (10); which of those may be involved in the present case is not clear.

Introgression of moderate polygenic resistance into elite germ plasm is quite complicated. However, the use of genetic material that contains polygenic resistance in its background may be very helpful, especially if there is resistance to several pathogens. The original *se* inbred IL677a, which was moderately resistant to MDMV in the field (Table 1), has been reported to be susceptible when mechanically inoculated (5,15). This inbred was considered susceptible to northern leaf blight caused by *Exserohilum turcicum* (Pass.) K.J. Leonard & E.G. Suggs. A later report indicated that IL677a and some of its pedigree have partial resistance to northern leaf blight and Stewart's wilt (14) and partial resistance to common rust (19). It seems that inbreds with IL677a in their pedigree have factors contributing to partial resistance to several leaf diseases. Reaction of these genotypes to infection may vary with location, environment, and pathogen. This partial resistance is apparently very effective in delaying the appearance and spread of symptoms in the field. It is particularly important in sweet corn, where delayed buildup of the disease prevents most of the economic damage.

Natural infection by potyviruses in the field should be used for selection of resistant genotypes only when disease pressure is high. In cases of partial resistance, selection under natural infection or by mechanical inoculation may be misleading. Evaluation of symptoms and virus titer after mechanical inoculation may lead to elimination of field-resistant genotypes. Furthermore, field-resistant types may include plants that were not infected and those that are symptomless but supporting high levels of virus replication (Table 4). Therefore, selection of field-resistant lines cannot be based only on symptoms but must be accompanied by a method to detect the virus, such as ELISA.

The mode of action and number of genes involved in partial resistance of sweet corn to mosaic diseases is not known. The various levels of resistance in different genotypes carrying the *se* gene, including heterozygosity of the *se* locus in crosses with *Se* inbreds, indicate that more than one gene is involved. We do not know whether the resistance is a QTL, linked to the *se* locus, or a pleiotropic effect of the *se* allele. Our future investigations will be directed at elucidating the mode of action of the partial resistance identified in some *se* genotypes. In order to investigate the type of resistance further it is proposed that evaluation of selected resistant genotypes under natural infection should include the additional experimental procedure of placing viruliferous aphids on the leaves under controlled conditions.

Table 4. ELISA readings (A_{405}) of sweet corn genotypes evaluated for resistance in the field (Newe Ya'ar 1992)

Genotype	Genetic background	MDMV incidence[y] (%)	ELISA[z] (A_{405})	Plants sampled for ELISA
J68	(*Se*)	92	0.266	8
J95E1	(*Se*)	73	0.228	15
J92bE1	(*se*)	25	0.072	8
IL772a	(*se*)	0	0.270	11
IL772aJ99E4	(*se*)	0	0.137	7
IL775a	(*se*)	0	0.019	12
IL775aJ120	(*se*)	0	0.085	7
IL796b	(*se*)	0	0.031	9

[y] Evaluation of disease symptoms of 50 plants for each genotype.
[z] Leaves sampled for ELISA analysis at silking, 2 days after evaluation of symptoms. Values are average of infected plants in each genotype showing $A_{405} > 0.200$.

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