Genetics of Resistance to *Fusarium oxysporum* f. sp. *melonis* Races 0, 1, and 2 in Muskmelon Line MR-1

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ABSTRACT

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In artificial inoculation studies, muskmelon (*Cucumis melo*) breeding line MR-1 was resistant to races 0, 1, and 2; but not 1,2y or 1,2w of *Fusarium oxysporum* f. sp. *melonis*. Segregation ratios for F_1, F_2, and BC_1 populations of crosses between resistant MR-1 and susceptible Topmark indicated that resistance to races 1 and 2 of Fusarium wilt is conferred by single dominant genes and that resistance to race 0 is also conferred by a single dominant gene. Linkage tests indicated that the genes for resistance to race 1 and race 2 assort independently. Allelism tests showed that the single dominant genes in MR-1 that confer resistance to races 0 and 2 and races 0 and 1 are the same genes or alleles of Fom-1 in differential cultivar Doublon and Fom-2 in differential line CM 17-187, respectively.

Fusarium wilt, incited by *Fusarium oxysporum* Schlechtend. ex Fr. f. sp. *melonis* Snyd. & Hans., is an important disease of muskmelon, *Cucumis melo* L., in the United States and other areas of the world (6). Risser, et al (5) designated races 0, 1, 2, and 1,2 based on the resistance genes that are overcome by variants of the pathogen. Race 1,2 was further divided into 1,2y, a yellowing strain, and 1,2w, a wilting strain. Race 0 incites disease only on those muskmelon genotypes that lack any genes for resistance to *F. o. melonis* (e.g., Topmark). Thus far, any gene that has been found to confer resistance to any other race also confers resistance to race 0. The single dominant gene Fom-1, found in the cultivar Doublon, confers resistance to race 0 and to race 2 of *F. o. melonis* (4). The single dominant gene Fom-2, found in line CM 17-187, confers resistance to races 0 and 1 (5). A second single dominant gene Fom-3, in Perlita-FR, has also been described as conferring resistance to races 0 and 2 (9). No genes have been identified in muskmelon that confer resistance to 1,2y or 1,2w.

Breeding line MR-1 is an inbred line that was derived from *C. melo* PI 124111 (7). It was released as a source of high levels of nonspecific resistance to downy (*Pseudoperonospora cubensis*) and powdery (*Sphaerotheca fuliginea*) mildews. Subsequent to the release of MR-1, we described resistance to races 0, 1, and 2 of *F. o. melonis* in this line (10). Cohen, et al (1) also described resistance to races 0, 1, and 2 of *F. o. melonis* in a breeding line that they derived from this same PI.

This paper reports the reaction of line MR-1 to *F. o. melonis* races 0, 1, 2, and 1,2; the mode of inheritance of resistance to races 0, 1, and 2 in MR-1; and the genetic relationship of *F. o. melonis* resistance in MR-1 to other sources of resistance in muskmelon.

MATERIALS AND METHODS

To determine the mode of inheritance of *F. o. melonis* resistance in MR-1, standard crossing techniques (8) were used between this line and the cultivar Topmark (TM), which is susceptible to races 0, 1, 2, and 1,2 of *F. o. melonis*. To identify alleles for resistance, a second series of crosses was made between MR-1 and both the *F. o. melonis* races 0 and 2 resistant cultivar Doublon and the *F. o. melonis* races 0 and 1 resistant line CM 17-187.

All isolates of *F. o. melonis* used in these studies were obtained from Thomas Gordon, University of California, Berkeley. Races are classified according to the nomenclature of Risser, et al (5). Inoculum of each race consisted of a mixture of macroconidia and microconidia prepared from potato dextrose agar cultures grown for 7–10 days at 20–24 C under continuous illumination. Resistance of MR-1 to races 0, 1, 2, and 1,2y and 1,2w was tested at inocula concentrations of 0.025×10^6, 0.050×10^6, 0.10×10^6, 0.50×10^6, and 1.0×10^6. Because it gave excellent separation of resistant and susceptible phenotypes in a previous study (9) and is the inoculum concentration commonly used by plant breeders in Fusarium wilt resistance selection programs, an inoculum concentration of 0.20×10^6 was used in the inheritance studies.

Seeds of plants to be assayed for disease reaction were treated with 5% calcium hypochlorite solution for 5 min and placed in autoclaved vermiculite (seedling pots). After about 10 days, plants in the cotyledon to first-true-leaf stage were removed from the seedling pots. The roots were washed in tap water, pruned to about 2.5 cm, and dipped for 1 min in the inoculum suspension. Inoculated seedlings were transplanted into cell-type (cell volume 55 ml) plastic growing trays (one plant per cell) filled with a sterilized potting mix of peat and vermiculite (1:1) and placed in a glasshouse at 20–27 C. Roots of control plants were pruned and dipped in tap water only.

Plants were examined at 2- to 3-day intervals. Symptoms first appeared 10–14 days after inoculation and the number of infected plants as evidenced by stunting, wilting, or death was recorded. However, by the final assessment at 28 days postinoculation, the population under test fell into two classes. Plants were either dead or free of wilt symptoms. Dead plants were classified as susceptible and those that were free of symptoms were classified as resistant. At the end of a test, selected resistant plants were transplanted into 10-L pots and grown to maturity for either self- or cross-pollinations.

The standard differential cultivars Doublon, CM 17-187, and Charentais T (4,5,9), as well as TM and MR-1, were included in each test to monitor for any changes in pathogen virulence or race.

RESULTS AND DISCUSSION

Reaction of MR-1 to races 0, 1, 2, and 1,2. Twenty-six seedlings of MR-1 and 10 seedlings of the standard differential cultivars Charentais T, Doublon, and CM 17-187 were inoculated with the races of *F. o. melonis* over the range of inoculum concentrations. Line MR-1 was resistant to races 0, 1, and 2 at the highest inoculum concentration tested (1.0×10^6) and susceptible to 1,2y and 1,2w at the lowest concentration tested (0.025×10^6). Charentais T was susceptible to all races at all inoculum concentrations tested. Doublon and CM 17-187 were resistant to races 0 and 2 and races 0 and 1, respectively, and susceptible to all other races at all inoculum concentrations.

Inheritance of resistance to races 1 and 2. Crosses between MR-1 and TM produced F_1 families that were resistant to both races 1 and 2 (Table 1). The F_2 segregation indicated simple inheritance (3:1) of disease reaction to race 1 and race 2 with resistance to each race controlled by a single dominant gene. To verify the pattern of resistance to races 1 and 2, the F_1 was backcrossed to susceptible TM. The BC_1 families of this cross gave a 1:1 ratio of resistant to susceptible plants. The F_1 backcrossed to resistant MR-1 resulted in homogeneous resistant families. The segregation data in the backcross families clearly support the one-gene hypothesis.

Inheritance of resistance to race 0. Crosses between MR-1 and TM produced plants that were all resistant to race 0 (Table 2). The results obtained in the F_2 populations indicate a ratio of approximately 15 resistant to 1 susceptible. The BC_1 (MR-1 × TM) × TM families segregated in a 3:1 ratio of resistant to susceptible plants. The F_1 × MR-1 families were all resistant. These data indicate that each of two dominant genes confers resistance to race 0 in MR-1.

Allelism tests. The F_2 families from the crosses between MR-1 with a dominant gene for resistance to race 1, and CM 17-187, reported to have the dominant gene Fom-2 for resistance to race 1, and the cross (MR-1 × CM 17-187) × TM were all resistant to race 1 (191 resistant:0 susceptible). If resistance to race 1 in MR-1 and CM 17-187 was conferred by two nonallelic dominant genes, then the F_2 families would have been expected to segregate in a ratio of 15 resistant:1 susceptible. Backcross families (MR-1 × CM 17-187) × TM and (CM 17-187 × MR-1) × TM were also homogeneous resistant (85 resistant:0 susceptible and 98 resistant:0 susceptible, respectively). A ratio of three resistant:1 susceptible would have been expected if resistance in MR-1 and CM 17-187 was conferred by two nonallelic dominant genes. These results indicate that the dominant gene in MR-1 that confers resistance to race 1 is allelic to the gene Fom-2 in CM 17-187.

There was no segregation in the F_2 (MR-1 × Doublon) when inoculated with race 2, nor in the BC_1 (MR-1 × Doublon) × TM. Doublon has the dominant gene Fom-1 that confers resistance to race 2, and resistance to race 2 in MR-1 is also conferred by a dominant gene. The F_2 (MR-1 × Doublon) and its reciprocal were homogeneous resistant to race 2 (94 resistant:0 susceptible and 98 resistant:0 susceptible, respectively). If

TABLE 1. Segregation in progenies from crosses between resistant (R) muskmelon breeding line MR-1 and susceptible (S) cultivar Topmark after inoculation with race 1 or race 2 of *Fusarium oxysporum* f. sp *melonis*

Parents and crosses	Expected ratio	Observed (no.)[z] R	S	X^2	df	P
Inoculated with race 1						
MR-1 (MR)	All R	42	0	···	···	···
Topmark (TM)	All S	0	46	···	···	···
F_1 MR × TM	All R	49	0	···	···	···
TM × MR	All R	50	0	···	···	···
F_2 MR × TM	3:1	193	62	0.064	1	0.80
TM × MR	3:1	148	41	1.10	1	0.30
F_2 Total	3:1	341	103	0.769	1	0.40
F_2 Homogeneity	···	···	···	0.40	1	0.54
BC_1 (MR × TM) × TM	1:1	46	55	0.802	1	0.39
(TM × MR) × TM	1:1	41	47	0.409	1	0.53
BC_1 × TM Total	3:1	87	102	1.19	1	0.28
BC_1 × TM Homogeneity	···	···	···	0.02	1	0.89
BC_1 (MR × TM) × MR	All R	50	0	···	···	···
(TM × MR) × MR	All R	48	0	···	···	···
Inoculated with race 2						
MR	All R	46	0	···	···	···
TM	All S	0	47	···	···	···
F_1 MR × TM	All R	50	0	···	···	···
TM × MR	All R	48	0	···	···	···
F_2 MR × TM	3:1	178	67	0.719	1	0.41
TM × MR	3:1	139	56	1.437	1	0.24
F_2 Total	3:1	317	123	2.05	1	0.16
F_2 Homogeneity	···	···	···	0.11	1	0.75
BC_1 (MR × TM) × TM	1:1	29	22	0.961	1	0.34
(TM × MR) × TM	1:1	28	20	1.33	1	0.25
BC_1 × TM Total	1:1	57	42	2.27	1	0.14
BC_1 × TM Homogeneity	···	···	···	0.02	1	0.89
BC_1 (MR × TM) × MR	All R	50	0	···	···	···
(TM × MR) × MR	All R	49	0	···	···	···

[z]R = resistant, S = susceptible.

TABLE 2. Segregation in progenies from crosses between resistant (R) breeding line MR-1 and susceptible (S) cultivar Topmark after inoculation with race 0 of *Fusarium oxysporum* f. sp. *melonis*

Parents and crosses	Expected ratio	Observed (no.)[z] R	S	X^2	df	P
MR-1 (MR)	All R	34	0	···	···	···
Topmark (TM)	All S	0	30	···	···	···
F_1 MR × TM	All R	51	0	···	···	···
TM × MR	All R	47	0	···	···	···
F_2 MR × TM	15:1	133	7	0.373	1	0.55
TM × MR	15:1	91	4	0.674	1	0.43
F_2 Total	15:1	224	11	0.988	1	0.33
F_2 Homogeneity	···	···	···	0.602	1	0.45
BC_1 (MR × TM) × TM	3:1	70	31	1.74	1	0.19
(TM × MR) × TM	3:1	72	20	0.522	1	0.48
BC_1 × TM Total	3:1	142	51	0.209	1	0.66
BC_1 × TM Homogeneity	···	···	···	2.059	1	0.16
BC_1 (MR × TM) × MR	All R	48	0	···	···	···
(TM × MR) × MR	All R	50	0	···	···	···

[z]R = resistant, S = susceptible.

TABLE 3. Segregation in progenies from the cross (MR-1 × Topmark) × Topmark[z] after inoculating successively with races 1 and 2 of *Fusarium oxysporum* f. sp. *melonis*

Parents and crosses	Race	Expected ratio	Observed (no.)[y] R	S	X^2	df	P
First inoculation							
MR-1	1	All R	33	0	...	...	...
	2	All R	26	0	...	...	...
(MR-1 × TM) × TM[z]	1	1:1	103	95	0.323	1	0.58
	2	1:1	82	71	0.791	1	0.39
Second inoculation							
MR-1	2	All R	33	0	...	...	...
	1	All R	26	0	...	...	...
(MR-1 × TM) × TM	2	1:1	60	43[1]	2.80	1	0.096
	1	1:1	48	34	2.39	1	0.13

[y]R = resistant, S = susceptible.
[z]Parent Topmark (TM): susceptible to races 0, 1, and 2 in the first or second inoculation.

resistance in MR-1 and Doublon was conferred by two nonallelic dominant genes, the expected ratio would be 15 resistant to one susceptible. Likewise, if resistance in MR-1 and Doublon was conferred by two nonallelic dominant genes, then (MR-1 × Doublon) × TM and (Doublon × MR-1) × TM families would be expected to segregate 3 resistant:1 susceptible, but they were also homogeneous resistant (51 resistant:0 susceptible and 48 resistant:0 susceptible, respectively). These data indicate that the dominant gene in MR-1 that confers resistance to race 2 is allelic to the gene Fom-1 in Doublon.

Linkage test. A series of crosses were made to determine if the dominant gene that confers resistance to race 1 and the dominant gene that confers resistance to race 2 are linked in MR-1. Linkage was tested by inoculating plants successively with races 1 and 2. Ten-day-old seedlings of the parents and backcross (MR-1 × TM) × TM were inoculated with race 1 (first inoculation) and, 28 days later, the surviving plants (38-day-old) were inoculated with race 2 (second inoculation). The reciprocal of this inoculation was made also (race 2 followed by race 1). A delay of 28 days between successive inoculations tends to minimize the suppression by one race on the action of a second race on the host (2,3). If the genes are tightly linked, the backcross progenies surviving the first inoculation, when inoculated with a second race, would be expected to segregate minimally or not at all. However, segregation for resistance in the backcross progenies following the second inoculation fit a 1:1 ratio (Table 3), indicating that the genes are not linked.

MR-1 is a monoecious muskmelon that is used as a source of high levels of resistance to five pathotypes of downy mildew and three races of powdery mildew (7). The occurrence of both Fom-1 and Fom-2 conferring resistance to races 0, 1, and 2 of Fusarium wilt in this line make it an even more valuable source of disease resistance to muskmelon breeding programs. Knowledge of the presence and inheritance of these resistances should make them more useful to plant breeders.

The genes conferring resistance to race 1 and race 2 of Fusarium wilt in MR-1 appear to be Fom-1 and Fom-2, respectively, or are allelic since they failed to show segregation in allelism tests. The reactions of MR-1 and Doublon to race 2, and MR-1 and CM 17-187 to race 1 in inocula concentration tests were similar: all were resistant at the highest concentration (1.0×10^6). These data suggest that the gene in MR-1 that confers resistance to race 2 and a second gene that confers resistance to race 1 are Fom-1 and Fom-2, respectively. These two genes were shown not to be linked.

Studies are now underway to identify the mode of inheritance of resistance to powdery mildew races 1, 2, and 3 in MR-1 and to investigate the possible linkage between genes for powdery mildew, downy mildew, and Fusarium wilt resistance in this line.

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