Independent Inheritance of Resistance to Race 1 and Race 2 of *Sphaerotheca fuliginea* in Muskmelon

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ABSTRACT

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Gynoecious *Cucumis melo* WI 998, susceptible to powdery mildew, was stabilized for gynoecy and crossed with *C. melo* PI 124111F, a monoecious breeding line resistant to races 1 and 2 of *Sphaerotheca fuliginea*. F_1 plants (all monoecious) were resistant to race 1 and moderately resistant to race 2. F_2 plants (one of 16 gynoecious) segregated three resistant:one susceptible to race 1, and one resistant:two moderately resistant:one susceptible to race 2. The backcross progeny of F_1 to the susceptible parent (WI 998) segregated one resistant:one susceptible to race 1, and one moderately resistant:one susceptible to race 2. The backcross progeny to the resistant parent (PI 124111F) were all resistant to race 1 and segregated one resistant:one moderately resistant to race 2. The data support a monogenic, dominant inheritance of resistance *Pm*3 against race 1 and a monogenic, partially dominant inheritance of resistance against race 2. The symbol *Pm*6 is assigned to the latter gene. The two genes for resistance were not linked and no cytoplasmic (maternal) factors or modifier genes were involved in their inheritance.

Additional keywords: breeding for resistance, cucurbits, F_1 hybrids, genetics, germ plasm, gynoecious muskmelon, resistance genes

Seed production of F_1 hybrids of muskmelons (*Cucumis melo* L.) requires manual emasculation and hand pollination of hermaphrodite flowers, which make seed a costly product. By using a gynoecious parent in F_1 hybrid production, seed price may be greatly reduced because emasculation is not needed and pollination is carried out by bees. When a gynoecious plant is used as a parent it is desirable to incorporate into it genes for disease resistance.

In the present study, an attempt was made to elucidate the mode of inheritance of powdery mildew resistance in a cross between the monoecious *C. melo* PI 124111F, which carries multiple disease (including Fusarium wilt) and race resistances (3), and the gynoecious *C. melo* WI 998 (10), with the objective of producing a gynoecious breeding line resistant to powdery mildew. A preliminary report on this study was published (7).

MATERIALS AND METHODS

Germ plasm. The resistant, monoecious parent PI 124111F was derived from PI 124111 after seven generations of selfing and selection (3). PI 124111F is homozygous for resistance to races 1 and 2 of *Sphaerotheca fuliginea* (Schlecht. ex Fr.) Poll., which incite powdery mildew in cucurbits in Israel (3). The parent WI 998, susceptible to powdery mildew, was a gift from C. E. Petersen (University of Wisconsin, Madison). It segregated gynoecious:gynomonoecious. Homozygosity for gynoecy was achieved in WI 998 after four generations of selfing and selection, using the methods described by Kenigsbuch and Cohen (6).

Crosses. Crosses were made in the greenhouse. Because WI 998 was gynoecious and PI 124111F was monoecious, no emasculation was required when the former line served as a female parent. For reciprocal crosses (WI 998 serves as a pollen donor), perfect flowers were induced in the gynoecious parent by silver nitrate in the method described before (6). A single plant from the two crosses, WI 998 × PI 124111F (F_1) and PI 124111F × WI 998 (E_1), was propagated by cuttings and used for the production of the F_2 and the E_2 progenies, respectively, and for the backcrosses to the resistant parent (BC_r) and to the susceptible parent (BC_s). The following crosses were made (first for maternal parent, with WI = WI 998 and PI = PI 124111F): WI × PI, F_1; PI × WI, E_1; (WI × PI), F_2; (PI × WI), E_2; (WI × PI) × WI, BC_s; (PI × WI) × WI, BC_s; (WI × PI) × PI, BC_r; and (PI × WI) × PI, BC_r.

Fungal cultures. A culture of *S. fuliginea* race 1 was maintained on *C. melo* 'Ananas-Yokneam' (Hazera Seed Corp., Haifa, Israel) by repeated inoculations in a growth chamber at 20 C. A culture of *S. fuliginea* race 2 was similarly maintained on *C. melo* 'PMR 45' (Petoseed, Saticoy, CA, susceptible to race 2 and resistant to race 1). Purity of cultures was periodically tested by inoculation of Ananas-Yokneam, PMR 45, and PMR 6 (resistant to races 1 and 2, susceptible to race 3). No culture contaminations were detected during the research period (1985–1987).

Inoculation and evaluation of resistance in progenies. Test plants were inoculated at the two-leaf stage (about 3 wk after sowing). Inoculation was made by shaking mildewed plants (Ananas-Yokneam for race 1 and PMR 45 for race 2) over the test plants in walk-in growth chambers maintained at 23 C (50–70% relative humidity) with a 12-hr photoperiod (120 $\mu E \cdot m^{-2} \cdot s^{-1}$. Disease records were taken 10 days after inoculation using the following scale: resistant plants with no apparent fungal development; moderately resistant plants with one to 19 fungal colonies per leaf; and susceptible plants with 20 or more fungal colonies per leaf. At least three populations per cross were tested with each fungal race. A combined value for each cross is given. Parents and F_1 plants were included in each inoculation test for comparison purposes. Segregation ratios of F_2 and BC populations were tested for good fit to theoretical ratios with chi-square tests. E_1 and E_2 were assigned to reciprocal crosses of F_1 and F_2, respectively.

RESULTS

The F_1 (WI 998 × PI 124111F) and the reciprocal E_1 (PI 124111F × WI 998) plants (all monoecious) exhibited resistance to race 1 of *S. fuliginea* similar to that of the resistant parent PI 124111F, indicating that inheritance of resistance against race 1 was dominant (Table 1). The similarity of resistance of F_1 and E_1 plants indicated that no cytoplasmic (maternal) factors were involved in expression of resistance to race 1. Dominance was further supported by segregation of three resistant:one susceptible in the F_2 and E_2 generations (Table 1). In these populations, one of 16 of the plants were gynoecious. A segregation ratio of one resistant:one susceptible was obtained in plants of the backcrosses of F_1 or E_1 to the susceptible parent WI 998. Progeny of the backcrosses of F_1 or E_1 to the resistant parent PI 124111F were all resistant. Thus, the backcross data further supported a monogenic dominance of inheritance to race 1 of *S. fuliginea*.

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Data presented in Table 2 indicate that resistance in PI 124111F to race 2 of the fungus was conferred by a partly dominant gene. The F_1 and E_1 plants were moderately resistant and the F_2 and E_2 pedigrees segregated one resistant:two moderately resistant:one susceptible. Segregation ratios in the backcross populations also supported a partially dominant, monogenic inheritance of resistance against race 2. Progenies of the backcrosses (F_1 and E_1) to the susceptible parent segregated one susceptible:one moderately resistant, and those to the resistant parent segregated one resistant: one moderately resistant.

The relationship between the two genes was tested in 291 plants of the F_2 generation, of which 221 plants exhibited resistance to race 1. These 221 plants (resistant to race 1) were grown for another 2 wk to allow for two to three new leaves to develop, and were inoculated with race 2. A segregation ratio of one resistant:two moderately resistant:one susceptible (chi-square = 0.076, $P = 0.95$) was obtained indicating that resistance to race 2 is not linked to resistance to race 1. Among the resistant plants, three were gynoecious. They were propagated by cuttings, treated with silver nitrate, and selfed. F_3 plants were gynoecious and exhibited resistance to both races 1 and 2 of *S. fuliginea*.

DISCUSSION

The major finding of this study was that PI 124111F contains two independent genes for resistance against *S. fuliginea*: a dominant gene that confers resistance against race 1 of the fungus and a partially dominant gene that confers resistance against race 2. Kenigsbuch and Cohen (6) had previously shown that gynoecism in WI 998 is conferred by two recessive genes in a cross with the monoecious PI 124111F. Indeed, a few gynoecious plants resistant to powdery mildew (race 1 and race 2) were selected in this study. These plants will serve for the production of a new breeding line for breeders' use.

Harwood and Markarian (5) reported, with partially supporting data, that PI 124111 carries a dominant gene, *Pm*3, for resistance against race 1 of powdery mildew. They showed that *Pm*3 was different from *Pm*1, a dominant gene in PMR 45 that confers resistance against race 1. Resistance in PMR 45 was derived from PI 78374 from India (13).

PI 124111 is known to carry genes for resistance against races 1, 2, and 3 of *S. fuliginea* (3–5,8,9,11–13) and is in the pedigree of American cultivars such as Campo, Jacumba, and Perlita (5). However, no clear data are available as to the mode of inheritance of these resistances nor to possible linkages between resistances in this line. The present study provides conclusive evidence for the presence of *Pm* 3, a dominant pair of genes effective against race 1, in PI 124111F, thus confirming the preliminary observation made by Harwood and Markarian (5). The monogenic resistance in PI 124111F against race 2 reported here is different from *Pm*2. In PMR 5 and PMR 6, *Pm*2 is a partially dominant gene that, in combination with *Pm*1, confers resistance against race 2 (1,9,11). PMR 5 and PMR 6 were derived also from PI 78374 and possibly PI 79376 (5,13) with no evidence for PI 124111 in their pedigree. In line 36486 (P_3) of Bohn and Whitaker (1), which contains PI 124111 in its pedigree, *Pm*2 acts together with two to three additional modifier genes (1).

PI 124112 (from which Seminole was derived) was reported to carry *Pm*4 (partly dominant) and *Pm*5, which confer resistance against race 1 of *S. fuliginea* (4). These genes have no allelic relationships with *Pm*1 from PMR 45 (4). We therefore suggest that PI 124111F (which was selected from PI 124111 after seven generations of selfing) has a partially dominant gene, *Pm*6, against race 2 of *S. fuliginea*. Our previous study (2) supports this conclusion. That study was conducted with the highly susceptible parent Ananas-Yokneam, on which the pathogen produced two to six times more spores per unit leaf area compared with WI 998 (*data not shown*). The present study clearly showed that *Pm*6 is not linked to *Pm*3. PI 124111 and PI 124112 are known to be resistant also to race 3 of *S. fuliginea* (9). The gene(s) conferring these resistances have not yet been studied or assigned.

Table 1. Segregation for powdery mildew resistance caused by race 1 of *Sphaerotheca fuliginea* in muskmelon

Pedigree	Generation	Number of plants		Expected ratio	χ^2	*P*
		Resistant	Susceptible			
WI 998	P_1	0	47	0:1		
PI 124111F	P_2	46	0	1:0		
WI 998 × PI 124111F	F_1	85	0	1:0		
PI 124111F × WI 998	E_1	80	0	1:0		
WI 998 × PI 124111F	F_2	278	84	3:1	0.615	0.30
PI 124111F × WI 998	E_2	280	98	3:1	0.172	0.80
	F_2 total	558	182	3:1	0.065	0.80
F_1 × WI 998	BC_s	41	40	1:1	0.012	0.95
E_1 × WI 998	BC_s	54	55	1:1	0.009	0.95
	BC_s total	95	95	1:1	0	0.995
F_1 × PI 124111F	BC_r	101	0	1:0		
E_1 × PI 124111F	BC_r	82	0	1:0		
	BC_r total	183	0	1:0		

Table 2. Segregation for powdery mildew resistance caused by race 2 of *Sphaerotheca fuliginea* in muskmelon

Pedigree	Generation	Number of plants			Expected ratio	χ^2	*P*
		Resistant	Moderately resistant	Susceptible			
WI 998	P_1	0	0	78			
PI 124111F	P_2	64	0	0			
WI 998 × PI 124111F	F_1	0	120	0			
PI 124111F × WI 998	E_1	0	113	0			
WI 998 × PI 124111F	F_2	86	178	85	1:2:1	0.146	0.90
PI 124111F × WI 998	E_2	90	187	97	1:2:1	0.262	0.80
	F_2 total	176	365	182	1:2:1	0.160	0.90
F_1 × WI 998	BC_s	0	45	45	0:1:1	0	0.99
E_1 × WI 998	BC_s	0	69	73	0:1:1	0.113	0.70
	BC_s total	0	114	118	0:1:1	0.068	0.80
F_1 × PI 124111F	BC_r	47	46	0	1:1:0	0.011	0.95
E_1 × PI 124111F	BC_r	70	78	0	1:1:0	0.43	0.50
	BC_r total	117	124	0	1:1:0	0.203	0.70

C. melo 92417, PI 414723, and WMR 29 were recently reported to carry six new genes for resistance against race 2 (9). Progeny 92417 has also a recessive gene against race 1 that is nonallelic to *Pm*1. Allelic and linkage relationships of these new genes with the previously known genes for powdery mildew resistance are unknown (9).

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