Inheritance and Allelism of Genes for Resistance to Races 1 and 2 of *Sphaerotheca fuliginea* in Muskmelon

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ABSTRACT

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Crosses between *Cucumis melo* var. *reticulatus* lines PI 124111F, PI 124112, and PMR 6, which are resistant to powdery mildew, and Ananas-Yokneam, the universal susceptible line, were made. Crosses between each pair of the resistant lines were also made. Parents and F_1, F_2, BC_S, BC_R, and TC progeny plants were inoculated with either race 1 or 2 of the powdery mildew pathogen, *Sphaerotheca fuliginea*, in growth chambers. Segregation ratios between resistant, moderately resistant, and susceptible offspring were determined. According to the ratios obtained, PI 124112 contained two genes, the dominant gene *Pm-5* and the partially dominant gene *Pm-4*, that conferred resistance to races 1 and 2, respectively. Resistance to races 1 and 2 in PI 124111F was conferred by the dominant gene *Pm-3* and the partially dominant gene *Pm-6*, respectively, and resistance in PMR 6 was conferred by the dominant gene *Pm-1* and the partially dominant gene *Pm-2* (plus modifier), respectively. None of these resistant host genotypes carry common genes for resistance to *S. fuliginea*.

Additional keywords: breeding for resistance, genetics, germ plasm

Powdery mildew is a devastating disease of cucurbits worldwide (14). Two fungi are known to be the principal causal agents of the disease: *Sphaerotheca fuliginea* (Schlechtend.:Fr.) Pollacci and *Erysiphe cichoracearum* DC. (1,14). Only *S. fuliginea* occurs on muskmelons in Israel (Y. Cohen, *unpublished data*). Races 1, 2, and 3 of *S. fuliginea* have been reported (15). In Israel, race 1 is predominant early in the season (4), whereas race 2 is predominant later in the season (Y. Cohen, *unpublished data*).

Breeding cantaloupes for resistance to powdery mildew was initiated by Jagger and Scott in the early 1930s (14). Three major sources of resistance genes were reported: PI 78374, from which PMR 45 containing *Pm-1*, a single dominant gene effective against race 1 (14), and PMR 5, PMR 6, and PMR 7 each containing a single partially dominant gene effective against race 2 were derived (2); PI 124111, from which PI 124111F (9,10) and MR1 (16) each containing both *Pm-3*, a single dominant gene effective against race 1, and *Pm-6*, a single partially dominant gene effective against race 2, were derived; and PI 124112, from which Seminole containing *Pm-4*, a partially dominant gene, and *Pm-5*, a dominant gene, were derived (7,8,14). McCreight et al described a new recessive gene effective against race 1 and six new genes effective against race 2 (11). Harwood and Markarian (7,8) studied the inheritance of resistance to powdery mildew in *Cucumis melo* PI 124111 and Seminole, which was derived from PI 124112. They proposed that Seminole, in which the "level of resistance was much lower" than that of PMR 5 or PI 124111 (8), carried the genes *Pm-4* and *Pm-5*. They stated that *Pm-5* was not allelic with *Pm-1* from PMR 45, and they designated *Pm-5* for race 1 resistance. Sitterly (14), citing Harwood and Markarian (8), stated that *Pm-4* from Seminole was partially resistant, and *Pm-5* from Seminole was completely dominant (without mentioning against which race). Other gene lists of *C. melo* (12,13) also lack clarity on gene designations for Seminole. Because Seminole was not homozygous for resistance (it segregated 80% resistant/ 20% moderately resistant) to powdery mildew (8), genetic studies should be conducted with the original source, PI 124112.

The purposes of this study were to examine the mode of inheritance of resistance to powdery mildew in PI 124112 when crossed with the universal susceptible Ananas-Yokneam; to examine the allelic relationships among the resistance genes in PI 124112 and PI 124111F; and to determine whether the resistance genes in either PI 124112 or PI 124111F were allelic with the resistance genes in PMR 6. We report on the genes for resistance to races 1 and 2 of *S. fuliginea* in PI 124112 and on the lack of commonality between these genes and the resistance genes of either PI 124111F or PMR 6.

MATERIALS AND METHODS

Germ plasm. The resistant monoecious parent PI 124112 was originally obtained from G. Sowell Jr., Experiment, Georgia, in 1979. It passed seven generations of selfing and selection for resistance to races 1 and 2 of *S. fuliginea* as well as to downy mildew caused by *Pseudoperonospora cubensis*. PI 124111F (monoecious, resistant to both races 1 and 2 of *S. fuliginea* [3,5]) was from our germ plasm stock. PMR 6 (andromonoecious, resistant to both races 1 and 2 of *S. fuliginea*) was obtained from C. E. Thomas, Charleston, South Carolina. PMR 45 (andromonoecious, resistant to race 1, susceptible to race 2) was obtained from Petoseed, Saticoy, California. Ananas-Yokneam (AY) (andromonoecious, susceptible to both races) was purchased from Hazera Seed Company, Haifa, Israel.

Crosses. Crosses were made in the greenhouse. In some cases, reciprocal crosses also were made. The following crosses were made (the maternal parent is listed first): AY × PI 124112, PI 124112 × AY, PI 124112 × PMR 45, PI 124112 × PMR 6, PI 124112 × PI 124111F, PI 124111F × PMR 6, AY × PMR 6, and PMR 6 × AY. For each cross, F_2 and a backcross (BC) to either parent were produced. In some cases, a testcross (TC)

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progeny (with AY) also was made.

Fungal cultures. A culture of *S. fuliginea* race 1 was maintained on *C. melo* 'Ananas-Yokneam' by repeated inoculations in a growth chamber at 20 C. A culture of *S. fuliginea* race 2 on *C. melo* PMR 45 (susceptible to race 2, resistant to race 1) was similarly maintained in a different growth chamber. 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 (1987–1989).

Inoculation and evaluation of resistance. Test plants were inoculated at the two-leaf stage (about 3 wk after sowing). Inoculation was made by shaking mildewed plants (AY 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 was recorded 10 days after inoculation. The following scale was used: resistant plants, no apparent fungal development; moderately resistant plants, one to 19 fungal colonies per leaf; and susceptible plants, 20 or more fungal colonies per leaf. At least three populations per cross were tested. For comparison, parents and F_1 plants were included in each inoculation test. Segregation ratios of F_2, BC, and TC populations were tested with chi-square tests for goodness-of-fit to theoretical ratios.

RESULTS AND DISCUSSION

PI 124112 × AY. Reciprocal F_1 families from this cross showed resistance to race 1 of *S. fuliginea* similar to that of the resistant parent PI 124112, which indicates that inheritance of resistance to race 1 was dominant (Table 1). The identical reaction in the reciprocal F_1 families 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 generation (Table 1). A segregation ratio of one resistant/one susceptible was obtained in plants of the backcross of F_1 to the susceptible parent AY. Progeny of the backcross of F_1 to the resistant parent PI 124112 were all resistant (Table 1). Thus, the backcross data support a monogenic dominance of inheritance of resistance to race 1 of *S. fuliginea.* We propose the symbol *Pm-5* for this gene, in accordance with nomenculture rules and previous studies (12–14).

In PI 124112, resistance to race 2 of the fungus was conferred by a partially dominant gene. The reciprocal F_1 families were moderately resistant, and the F_2 pedigree segregated one resistant/two moderately resistant/one susceptible (Table 1). Segregation ratios in the backcross families also supported partially dominant, monogenic inheritance of resistance to race 2 in PI 124112. Progeny of the backcross to the susceptible parent segregated one susceptible/one moderately resistant, and progeny of the backcross to the resistant parent segregated one resistant/one moderately resistant. We propose the symbol *Pm-4* for the partially dominant gene effective against race 2 in PI 124112 (12–14).

PI 124112 × PI 124111F. We reported previously (9,10) that PI 124111F carries a single dominant gene, *Pm-3*, effective against race 1 of *S. fuliginea* and a single partially dominant gene, *Pm-6*, effective against race 2. The F_1 plants of the cross PI 124112 × PI 124111F were all resistant to race 1 (Table 2). The F_2 progeny plants segregated 15 resistant/one susceptible to race 1. This indicates that *Pm-5*, the gene conferring resistance to race 1 in PI 124112, is not allelic with the gene *Pm-3*, which confers resistance to race 1 in PI 124111F. Data in Table 2 further support this model, because the backcross progenies to either parent were all resistant, whereas the testcross progeny plants segregated three resistant/one susceptible.

When the progenies of the cross PI 124112 × PI 124111F were inoculated with race 2 of the fungus, all F_1 plants were resistant (Table 2). This indicated that the single partially dominant genes of the parents (*Pm-4* in PI 124112 and *Pm-6* in PI 124111F) were complementary. The F_2 population segregated 11 resistant/five susceptible to race 2, indicating an independent inheritance of these two partially dominant genes (Table 2). This assumption was further supported by the observation that the offspring from backcrosses with either parent segregated three resistant/one susceptible, whereas the TC offspring segregated one resistant/three susceptible (Table 2).

PI 124112 × PMR 45. PMR 45 carries a single dominant gene, *Pm-1*, effective against race 1 (12–14). It is susceptible to race 2 but not as susceptible as AY. We therefore compared the reaction to

Table 1. Segregation for resistance to powdery mildew caused by race 1 or race 2 of *Sphaerotheca fuliginea* in muskmelon in crosses of the resistant PI 124112 and the susceptible Ananas-Yokneam (AY)

		Race 1					Race 2					
		Number of plants					Number of plants					
Pedigree	Generation	Resistant	Susceptible	Expected ratio	χ^2	*P*	Resistant	Moderately resistant	Susceptible	Expected ratio	χ^2	*P*
PI 124112	P_1	84	0	...	...	...	67	0	0	...	...	...
AY	P_2	0	88	...	...	...	0	0	73	...	...	...
PI 124112 × AY	F_1	146	0	...	...	...	0	77	0	...	...	...
AY × PI 124112	F_1	148	0	...	...	...	0	71	0	...	...	...
PI 124112 × AY	F_2	431	148	3:1	0.097	0.76	133	275	139	1:2:1	0.148	0.93
F_1 × PI 124112	BC_R	173	0	...	...	...	75	82	0	1:1	0.312	0.59
F_1 × AY	BC_S	163	167	1:1	0.048	0.83	0	75	84	1:1	0.509	0.48

Table 2. Segregation for resistance to powdery mildew caused by race 1 or race 2 of *Sphaerotheca fuliginea* in muskmelon in crosses of the resistant PI 124112 and PI 124111F

		Race 1					Race 2				
		Number of plants					Number of plants				
Pedigree	Generation	Resistant	Susceptible	Expected ratio	χ^2	*P*	Resistant	Susceptible	Expected ratio	χ^2	*P*
PI 124112	P_1	58	0	...	...	...	80	0	...	...	...
PI 124111F	P_2	41	0	...	...	...	60	0	...	...	...
PI 124112 × PI 124111F	F_1	52	0	...	...	...	94	0	...	...	...
PI 124112 × PI 124111F	F_2	194	15	15:1	0.31	0.60	329	159	11:5	0.403	0.53
F_1 × PI 124112	BC	42	0	...	...	...	95	32	3:1	0.003	0.96
F_1 × PI 124111F	BC	45	0	...	...	...	89	28	3:1	0.071	0.79
F_1 × Ananas-Yokneam	TC	98	29	3:1	0.32	0.59	51	155	1:3	0.006	0.94

race 2 of the offspring derived from the cross PI 124112 × PMR 45 to that of the parents. A reaction resembling that of PMR 45 was considered susceptible. The F$_1$ plants of this cross were all susceptible to race 2 (Table 3). F$_2$ plants segregated one resistant/three susceptible, suggesting a single resistance gene in PI 124112. The BC progeny of the resistant parent segregated one resistant/one susceptible, whereas the BC of the susceptible parent were all susceptible (Table 3).

AY × PMR 6. PMR 6 carries the single dominant gene, *Pm-1*, effective against race 1 and a single partially dominant gene, *Pm-2*, effective against race 2. *Pm-2* interacts with a modifier gene (2). When the progenies of AY × PMR 6 were inoculated with race 2, reciprocal families were moderately resistant (Table 4), which indicated partial inheritance of resistance to race 2 in PMR 6. The F$_2$ plants segregated three resistant/nine moderately resistant/four susceptible. This shift towards susceptibility compared with the expected ratio of 1:2:1, typical for a single partially dominant gene, indicated a modifier gene in the expression of resistance in PMR 6. The BC data confirmed inheritance of a single partially dominant gene for resistance to race 2 in PMR 6. The BC progeny to the resistant parent segregated one resistant/one moderately resistant, and that to the susceptible parent segregated one moderately resistant/one susceptible (Table 4).

PI 124112 × PMR 6. The F$_1$ plants of these two resistant parents were all resistant to race 1. F$_2$ plants segregated at a ratio of 15 resistant/one susceptible, indicating that the resistance genes in both parents (*Pm-1* in PMR 6 and *Pm-5* in PI 124112) are not allelic (Table 5). The backcross progenies to either parent were all resistant due to the dominance of both genes, whereas the TC plants segregated three resistant/one susceptible (Table 5). This further supports the nonallelic relationship between the resistance genes of the parents.

When these families were inoculated with race 2, the F$_1$ plants were all resistant (Table 5). F$_2$ families segregated 244 resistant/132 susceptible (43:21) instead of 259 resistant plants and 117 susceptible plants as expected for the segregation of two independently in-

Table 3. Segregation for resistance to powdery mildew caused by race 2 of *Sphaerotheca fuliginea* in muskmelon in the cross of the resistant PI 124112 and the susceptible PMR 45

		Number of plants				
Pedigree	Generation	Resistant	Susceptible	Expected ratio	χ^2	P
PI 124112	P$_1$	40	0	...	...	...
PMR 45	P$_2$	0	38	...	...	...
PI 124112 × PMR 45	F$_1$	0	52	...	...	...
PI 124112 × PMR 45	F$_2$	65	184	1:3	0.162	0.69
F$_1$ × PI 124112	BC$_R$	69	73	1:1	0.113	0.74
F$_1$ × PMR 45	BC$_S$	0	151	...	...	...

Table 4. Segregation for resistance to powdery mildew caused by race 2 of *Sphaerotheca fuliginea* in muskmelon in the cross of the resistant PMR 6 and the susceptible Ananas-Yokneam (AY)

		Number of plants					
Pedigree	Generation	Resistant	Moderately Resistant	Susceptible	Expected ratio	χ^2	P
PMR 6	P$_1$	55	0	0	...	...	...
AY	P$_2$	0	0	55	...	...	...
PMR 6 × AY	F$_1$	0	68	0	...	...	...
AY × PMR 6	F$_1$	0	56	0	...	...	...
PMR 6 × AY	F$_2$	126	385	151	3:9:4	1.726	0.43
					1:2:1	19.5	<0.001
F$_1$ × PMR 6	BC$_R$	39	46	0	1:1	0.576	0.46
F$_1$ × AY	BC$_S$	0	61	64	1:1	0.072	0.79

Table 5. Segregation for resistance to powdery mildew caused by race 1 or race 2 of *Sphaerotheca fuliginea* in muskmelon in crosses of the resistant PI 124112 and PMR 6

		Race 1					Race 2				
		Number of plants					Number of plants				
Pedigree	Generation	Resistant	Susceptible	Expected ratio	χ^2	P	Resistant	Susceptible	Expected ratio	χ^2	P
PI 124112	P$_1$	66	0	...	...	...	28	0	...	...	...
PMR 6	P$_2$	66	0	...	...	...	37	0	...	...	...
PI 124112 × PMR 6	F$_1$	110	0	...	...	...	58	0	...	...	...
PI 124112 × PMR 6	F$_2$	475	36	15:1	0.551	0.47	244	132	43:21	0.899	0.30
									11:5	2.600	0.11
F$_1$ × PI 124112	BC	49	0	...	...	...	86	32	3:1	0.282	0.50
F$_1$ × PMR 6	BC	52	0	...	...	...	92	36	3:1	0.666	0.30
F$_1$ × Ananas-Yokneam	TC	226	77	3:1	0.028	0.88	34	104	1:3	0.009	0.90

Table 6. Segregation for resistance to powdery mildew caused by race 1 or race 2 of *Sphaerotheca fuliginea* in muskmelon in crosses of the resistant PI 124111F and PMR 6

		Race 1					Race 2				
		Number of plants					Number of plants				
Pedigree	Generation	Resistant	Susceptible	Expected ratio	χ^2	P	Resistant	Susceptible	Expected ratio	χ^2	P
PI 124111F	P$_1$	20	0	...	...	...	72	0	...	...	...
PMR 6	P$_2$	18	0	...	...	...	72	0	...	...	...
PI 124111F × PMR 6	F$_1$	48	0	...	...	...	97	0	...	...	...
PI 124111F × PMR 6	F$_2$	286	24	15:1	0.178	0.28	304	157	43:21	0.324	0.58
									11:5	1.680	0.20
F$_1$ × PI 124111F × AY[a]	BC	52	0	...	...	...	69	29	3:1	1.102	0.30
F$_1$ × PMR 6	BC	51	0	...	...	...	131	49	3:1	0.474	0.49
F$_1$ × AY	TC	139	52	3:1	0.504	0.48	36	125	1:3	0.598	0.45

[a] Ananas-Yokneam.

Table 7. Proposed genetic designations for resistance factors in genotypes of *Cucumis melo* effective against race 1 and race 2 of the powdery mildew fungus *Sphaerotheca fuliginea*

	Gene designation	
Host genotype	**Race 1**	**Race 2**
Ananas-Yokneam	—	—
PMR 45	*Pm-1*, dominant	—
PMR 6	*Pm-1*, dominant	*Pm-2*, partially dominant + a dominant modifier gene
PI 124111F	*Pm-3*, dominant	*Pm-6*, partially dominant
PI 124112	*Pm-5*, dominant	*Pm-4*, partially dominant

herited partially dominant genes for resistance (11:5). This shift towards susceptibility probably resulted from the absence of the modifier gene of PMR 6 in some of the segregants. The BC pedigrees to either parent segregated three resistant/one susceptible, whereas the TC segregated one resistant/three susceptible (Table 5).

PI 124111F × PMR 6. F_1 plants were all resistant to race 1. F_2 plants segregated 15 resistant/one susceptible to race 1 (Table 6), which indicated that *Pm-1* (conferring resistance to race 1 in PMR 6) and *Pm-3* (conferring resistance to race 1 in PI 124111F) are nonallelic. The BC progenies were all resistant, whereas the TC plants segregated three resistant/one susceptible (Table 6). This further supports that *Pm-1* and *Pm-3* are nonallelic.

Inoculation of these progenies with race 2 revealed that the F_1 plants were all resistant, whereas F_2 plants segregated 304 resistant/157 susceptible (Table 6) (43:21) instead of 317:144 as would be expected for the segregation of two independently inherited partially dominant genes for resistance (11:5). This shift towards susceptibility to race 2 in the F_2 progeny resulted from the absence of the modifier gene of PMR 6 in some of the segregants. The BC progenies to either parent segregated three resistant/one susceptible as expected, whereas the TC progeny segregated one resistant/three susceptible (Table 6).

Using our data (Tables 1–6), we propose the following. PI 124112 carries a single dominant gene effective against race 1 of *S. fuliginea* and a single partially dominant gene effective against race 2. The symbols assigned to these genes should be *Pm-5* and *Pm-4*, for race 1 and race 2 resistance genes, respectively. This proposition is in accordance with Sitterly (14) but adds the race-gene relationship. The resistance gene, *Pm-5*, effective against race 1 in PI 124112 is not allelic with the resistance gene, *Pm-1*, of PMR 45 or PMR 6, nor with *Pm-3* of PI 124111F. *Pm-4*, the partially dominant resistance gene effective against race 2 in PI 124112, is not allelic with *Pm-2*, the partial resistance gene effective against race 2 in PMR 6, nor with *Pm-6*, the partially dominant resistance gene effective against race 2 in PI 124111F. PI 124111F carries a single dominant gene, *Pm-3*, effective against race 1 and a single partially dominant gene, *Pm-6*, effective against race 2 (10). *Pm-3* is not allelic with *Pm-1* in PMR 6, and *Pm-6*, effective against race 2, is not allelic with *Pm-2* in PMR 6. PMR 6 carries a dominant modifier gene that interacts with the partially dominant *Pm-2*, which is effective against race 2. This modifier may be *Pm-1* (effective against race 1) or another unknown gene. PI 124112 and PI 124111F each carry a partially dominant gene effective against race 2, which does not show any interaction with their respective genes effective against race 1. This indicates that the shifts in the segregation ratios in PMR 6 pedigrees do not necessarily have any relationship to *Pm-1*. Table 7 summarizes the genetic designations we propose for the genes with resistance to *S. fuliginea* in the genotypes of *C. melo* studied.

Different genes for resistance may induce similar structural responses in leaves inoculated with *S. fuliginea*. The structural responses of PMR 6, PI 124111F, and PI 124112 to powdery mildew races 1 and 2 are very similar and involve the accumulation of callose and lignin in the infected cells (6). PMR 6 is unique in that noninfected cells adjacent to the infected cells accumulated callose and lignin.

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