Genetics and Nature of Resistance to Race 2 of *Sphaerotheca fuliginea* in *Cucumis melo* PI 124111

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ABSTRACT

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The inheritance of resistance to race 2 of *Sphaerotheca fuliginea* in *Cucumis melo* PI 124111 was studied in crosses with the susceptible cultivar Ananas Yokneam under greenhouse conditions. F_1 was intermediate based on gross appearance, but in terms of spore germination, colonies per cotyledon, and conidia per cotyledon was more like the resistant parent. When mildewed plants were classified susceptible and mildew-free plants were classified resistant, the F_2 progenies segregated 3 susceptible:1 resistant. Progenies from the backcross of the F_1 with the resistant parent segregated 1 susceptible:1 resistant, and those from the backcross of the F_1 with the susceptible parent were susceptible. We concluded that resistance to race 2 is conferred by an incompletely dominant gene. Resistance of PI 124111 to powdery mildew was attributed to reduced conidial germination of *S. fuliginea* on the leaf surface, reduced colony formation, and reduced sporulation in comparison to the susceptible parent, Ananas Yokneam.

Additional key words: genetics, muskmelon.

Powdery mildew is a devastating disease in muskmelon throughout the world (9). In Israel, frequent sprays with fungicides are required to combat the disease, especially when race 2 of the pathogen occurs, against which no resistant commercial cultivars are available (8). Powdery mildew in Israel is incited by *Sphaerotheca fuliginea* (Schlect. & Fr.) Poll., which was confirmed by Cohen and Eyal, who reported the occurrence of cleisthotecia in 1983 (4).

Early greenhouse and field screening tests showed that *Cucumis melo* L. PI 124111 was highly resistant to downy mildew, to powdery mildew races 1 and 2 in Israel, and to the three known races, 1, 2, and 3, in the United States (5). American cultivars resistant to powdery mildew are known to have genes from PI 124111 (1,2,7,9).

The objectives of this study were to evaluate the resistance of PI 124111 to race 2 of *S. fuliginea* and to study the inheritance of resistance of PI 124111 in crosses with the susceptible commercial cultivar Ananas Yokneam (AY).

MATERIALS AND METHODS

Germ plasm. PI 124111 was obtained from G. Sowell, Jr. (USDA, Southern Regional Plant Introduction Station, Experiment, GA) and was stabilized for powdery mildew resistance by self-pollinating plants selected for powdery mildew resistance for five generations (5). Seed of the commercial cultivar Ananas Yokneam was purchased from Hazera Seed Company (Israel).

Crosses. Crosses were made in the greenhouse. When Ananas Yokneam was used as a female parent, perfect flowers were emasculated. With PI 124111, which is monoaceious, no such procedure was undertaken. The following crosses were made (first for maternal parent): AY × PI F_1; PI × AY F_1; (AY × PI) F_2; (PI ×AY) F_2; (AY×PI)×PI BC_R; (PI×AY)×PI BC_R; PI×(AY×PI) BC_R; PI×(PI×AY) BC_R; (AY×PI)×AY BC_S; AY×(AY×PI) BC_S; (PI×AY)×AY BC_S; AY×(PI×AY) BC_S. Reciprocal crosses were included to test if cytoplasmic factors are involved in resistance to powdery mildew (3).

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Inoculation and evaluation of fungal development. Fungal culture of *S. fuliginea* race 2 was maintained on AY plants by repeated inoculations in a growth chamber at 20 C. Inoculations and disease evaluation were made in the winter of 1983–1984 and in the summer of 1984. Field observations were made in the summer of 1984. Plants were grown in 0.45 kg of air-dried soil mixture (sand:peat:vermiculite, 1:1:1) in 0.5 L pots, one plant per pot. Plants were fertilized once a week with 1% N:P:K fertilizer. Temperature in the greenhouse in the winter ranged between 19–28 C and in summer between 20–38 C. Plants inoculated at either the cotyledonary stage or at the two- to three-leaf stage. Inoculations were done by blowing air of our own breath on infected plants bearing freshly produced conidia over the plants to be inoculated. Inoculated plants were transferred to growth chambers at 25 C (12 hr light/day, illuminated at an intensity of about 120 $\mu E \cdot m^{-2} \cdot s^{-1}$). Disease development on parents and F_1 plants was recorded on cotyledons, leaves, hypocotyls, and stems 7–8 days after inoculation. At this stage, discrete colonies were formed. On cotyledons, the number of colonies and the number of conidia per cotyledon were recorded. On true leaves, numbers of colonies and conidia per unit leaf area were recorded. In some cases, the intensity of fungal growth on leaves was assessed visually. A 0–5 arbitrary scale (0 = no visual fungal development, 5 = leaf fully covered with coalescing colonies) was used. On stems, a 0–3 visual scale was used.

Conidial germination. At 24–48 hr after inoculation, 1-cm leaf disks were taken from inoculated plants, stained in boiling 0.1% trypan blue in lactophenol for 2 min and clarified in 5% chloralhydrate for 48 hr. Disks were mounted in 50% glycerol and microscopically examined for conidial germination.

Evaluation of resistance in F_2 and BC populations. The F_2 and BC progenies were evaluated for resistance in plants at the two- to three-leaf stage. Mildew-free plants, with no apparent fungal development, were considered resistant. Plants with either minor or luxuriant fungal development were considered susceptible. This classification was used to overcome any difference in plant response due to nonuniformity in inoculation. PMR 6, PMR 45 (11), PI 124111, and AY were included in these inoculation tests as indicator plants.

TABLE 1. Germination, colony formation, and sporulation of *Sphaerotheca fuliginea* on cotyledons of *Cucumis melo* cultivars Ananas Yokneam, PI 124111 and their reciprocal F_1 hybrids

Entry	Germination (%)[a]	Colonies cotyledon[b]	Conidia/cotyledon $\times 10^3$ (%)[b]
Ananas Yokneam (=AY)	60 a[c]	15.0 a	82.5 a (100)
AY × PI	50 b	3.4 b	16.0 b (19.4)
PI × AY	35 c	3.3 b	15.0 b (18.2)
PI 124111 (=PI)	29 d	1.1 c	2.7 c (3)

[a]Germinating with three germ tubes per conidium, counted 48 hr after inoculation.
[b]Seven days after inoculation.
[c]Different letters following figures in columns indicate significant differences at 5% level (Duncan's multiple range test). Ten plants per entry.

TABLE 2. Germination, colony formation, and sporulation of *Sphaerotheca fuliginea* on true leaves of *Cucumis melo* cultivars Ananas Yokneam, PI 124111, and their reciprocal F_1 hybrids

Entry	Germination (%)[b]	Colonies/ cm^2	Conidia/ cm^2	Conidia/ colony
	Experiment 1, winter 1983-1984[a]			
Ananas Yokneam (=AY)	66 a[c]	9.6 a	25.6 a	2,672
AY × PI	55 b	2.1 b	1.8 b	833
PI × AY	45 b	3.2 b	2.6 b	800
PI 124111 (=PI)	6 c	0 c	0 c	0
	Experiment 2, summer 1984[d]			
Ananas Yokneam	63 a	4.1 a	23.0 a	5,609
AY × PI	...	3.0 b	10.6 b	3,533
PI × AY	...	3.0 b	9.9 b	3,300
PI 124111	12 b	0 c	0 c	0

[a]Leaf 2 of two-leaf plants.
[b]Germinating with three germ tubes per conidium counted 48 hr after inoculation on leaf 1 of three-leaf plants.
[c]Different letters following figures in columns indicate significant differences at 5% level (Duncan's multiple range test). Ten plants per entry.
[d]Leaf 2 of three-leaf plants.

Statistical analyses. Significance ($P = 0.05$) of differences in fungal growth on parents and hybrids (10 plants per entry) were determined using Duncan's multiple range test for each category of fungal growth. Segregation ratios of F_2 and BC populations were tested for good fit to theoretical ratios with chi-square tests. Population sizes of F_2 and BC progenies ranged between 150–181 and 73–153 plants, respectively.

RESULTS

In all inoculation tests, PMR 45 was susceptible, whereas PMR 6 was resistant. Significant differences were recorded in conidial germination between AY and PI at the cotyledon stage (Table 1). At 48 hr, germination on PI was half that of AY. Germination on F_1 reciprocal hybrids was intermediate and significantly different from either parent (Table 1). Colony formation and sporulation of the pathogen was evident but very much reduced on PI when compared with AY cotyledons (Table 1). The F_1 reciprocal hybrid plants allowed intermediate fungal growth, but it was significantly different from that of either parent (Table 1). Conidial germination on leaf 1 (of three-leaf plants) was reduced severely in PI at 48 hr compared with AY (Table 2), with intermediate germination observed on the F_1 reciprocal hybrids (Table 2). The percentages of conidia germinating with three germ tubes per conidium at 48 hr were 63, 52, and 44 in leaves 1, 2, and 3 of AY, respectively, in comparison with 12, 31, and 31 in corresponding leaves of PI. Colony formation and sporulation of *S. fuliginea* on leaf 2 (of two- to three-leaf plants) is also given in Table 2. Whereas luxuriant fungal development was recorded on AY, none was observed on PI. F_1 reciprocal hybrid plants showed moderate fungal growth, significantly different from either parent. In most cases, no significant difference was detected between the reciprocal F_1 hybrids.

Disease development on leaves and stems of two- to three-leaf plants is given in Table 3. In leaves and stems of PI, no disease was apparent, whereas a heavy leaf and stem coverage with fungal structures was observed in AY. Reaction of F_1 plants was intermediate in leaf 2 and leaf 3, but resistant (Table 3, experiment 2) in leaf 1. Under field conditions, AY plants suffered a heavy powdery mildew attack and set no fruits, whereas PI was mildew-

TABLE 3. Powdery mildew development on leaves (0–5 visual scale) and stems (0–3 visual scale) of two- to three-leaf plants of *Cucumis melo* cultivars Ananas Yokneam, PI 124111, and their reciprocal F_1 hybrids

	Experiment 1, winter 1983-1984			Experiment 2, summer 1984			
Entry	Leaf 1	Leaf 2	Stem	Leaf 1	Leaf 2	Leaf 3	Stem
Ananas Yokneam (=AY)	5.0 a[a]	4.0 a	2.8 a	5.0 a	5.0 a	4.0 a	3.0 a
AY × PI	0.5 b	2.0 b	2.1 b	0 b	1.8 b	1.0 b	2.0 b
PI × AY	0.3 b	2.3 b	2.6 b	0 b	1.7 b	1.0 b	2.0 b
PI 124111 (=PI)	0 c	0 c	0 c	0 b	0 c	0 c	0 c

[a]Different letters following figures in columns indicate significant differences at 5% level (Duncan's multiple range test). Ten plants per entry.

TABLE 4. Powdery mildew resistance segregation in two- to three-leaf *Cucumis melo* plants grown in the greenhouse, summer 1984

		Plants (no.)					
Cross[a]	Generation	Total	Resistant[b]	Susceptible[c]	Ratio	X^2	*P*
AY × PI	F_2	150	35	115	1:3	0.2222	0.5–0.7
PI × AY	F_2	181	40	141	1:3	0.4061	0.5–0.7
PI × (PI × AY)	BC_R	153	72	81	1:1	0.5294	0.2–0.5
PI × (AY × PI)	BC_R	124	56	68	1:1	1.161	0.2–0.5
(PI × AY) × PI	BC_R	73	32	41	1:1	1.110	0.2–0.5
(AY × PI) × PI	BC_R	90	30	60	1:1	10.0	0.01–0.001
AY × (AY × PI)	BC_S	120	0	120	...	...	...
AY × (PI × AY)	BC_S	82	0	82	...	...	...
(AY × PI) × AY	BC_S	103	0	103	...	...	...
(PI × AY) × AY	BC_S	77	0	77	...	...	...

[a]Parent on the left was female; parent on the right was the male.
[b]No mycelium observed by the naked eye.
[c]Mildewed to various degrees.

free throughout the season (June–September) and set fruits.

The F_2 populations segregated 3 mildewed:1 mildew-free (Table 4). Mildew-bearing plants exhibited various degrees of disease development, whereas mildew-free plants showed no fungal development. All backcrosses to the resistant parent (BC_R) yielded offspring that segregated 1:1 mildewed:mildew-free, except one that did so at a ratio of 2:1 (Table 4). All backcrosses to the susceptible parent (BC_S) yielded offspring, all of which became mildewed upon inoculation. It is noteworthy that F_2 families of the cross between the cultivar Hemed (another susceptible domestic cultivar) and PI 124111, similarly segregated 126 mildewed:41 mildew-free in Hemed × PI, and 121:37 in PI × Hemed.

DISCUSSION

This study showed that PI 124111 is a highly resistant line to powdery mildew incited by race 2 of *S. fuliginea*. Except for a very limited mildew development on cotyledons, no fungal development was detected on this line in the greenhouse on two- to three-leaf plants, nor in the field on fruit-bearing plants. Earlier, we reported that PI 124111 is also resistant to races 1 and 3 of the pathogen (4). Ananas Yokneam, a domestic cultivar of *C. m.* var. *reticulatus*, is extremely susceptible to powdery mildew in Israel. F_1 plants of the cross PI × AY were significantly more resistant than AY, especially in leaf 1 of three-leafed plants, but less resistant than PI, indicating incomplete dominance of the resistant factor(s) in PI 124111. Unlike the cytoplasmic nature of inheritance of resistance to downy mildew in PI 124111 (5), no such cytoplasmic factors were involved in resistance to powdery mildew race 2. The 1:3 mildew-free:mildewed segregation ratio in F_2 and 1:1 in backcrosses to the resistant parent indicate that resistance to race 2 in PI 124111 is conferred by a single, incompletely dominant gene. This conclusion would be valid had we grouped segregates into three (resistant, moderately resistant, susceptible), rather than two (resistant, susceptible) categories.

Our preliminary microscopic examinations of inoculated leaves (*unpublished*) showed that the first germ tube of the pathogen penetrates into the epidermal cells of both AY and PI, but some cells of PI, especially of leaf 1, in contrast to those of AY, undergo rapid necrosis. This necrosis is probably responsible for the partial inhibition of development of germ tubes 2 and 3 in PI.

PI 124111 was collected in Madras, India, in March 1937 (9) and used in the United States as a source for powdery mildew resistance (1,2,6). Bohn's breeding lines P_3 and P_6 contain PI 124111 germ plasm in their pedigrees (1,2). P_3 is in the pedigree of the American cultivars Campo and Jacumba (6) and P_6 is in the pedigree of Perlita (6). Bohn and Whitaker (2) studied the inheritance of resistance to race 2 by crossing PMR 45 (resistant to race 1, susceptible to race 2) with eight race 2 resistant parents (P_2 through P_9). They found that all F_1 hybrids were intermediate-resistant, resembling the resistant parent, rather than the susceptible one. Segregation in F_2 and backcross families indicated a partly dominant gene for resistance, Pm^2.

P_3, the most resistant parent, was exceptional in that it had two modifiers in addition to Pm^2, which were epistatic to Pm^2, but hypostatic to pm^2. Because P_2 to P_8 Bohn's lines had additional sources of resistance to race 2 such as PI 79376 (6), it is impossible to determine if their race 2 resistance was derived solely from PI 124111.

In Michigan, Hardwood and Markarian (6) studied the inheritance of resistance to race 1 of powdery mildew in crosses between PI 124111 and the extremely susceptible parent, Gynoecious. They concluded that PI 124111 contained a single dominant gene for resistance against race 1. This gene was different from Pm^1 of PMR 45, as evidenced by the 3:1 ratio of the testcross of PMR 5 × PI 124111. The symbol Pm^3 was proposed to designate the gene.

Sivakami et al (10) studied the inheritance of resistance to race 2 in India in crosses between Campo (resistant) and PMR 6 and Campo and LSS (a local susceptible variety). Because Campo × PMR 6 did not segregate for resistance in F_2, they concluded that these cultivars share common gene(s) for resistance. Campo × LSS was partially resistant in F_1 and segregated in F_2: 20 resistant, 56 moderately resistant, and 72 susceptible. Sivakami et al concluded that two factors (major loci) with unequal effects condition a high level of resistance in Campo. Campo is a trihybrid between P_3, PMR 45, and PMR 450.

It becomes apparent that PI 124111 contains a single dominant gene, Pm^3, for resistance against race 1 in Michigan (6) and a single incompletely dominant gene for resistance against race 2 in Israel. Breeding lines derived from PI 124111 contain a single, incompletely dominant gene for resistance against race 2 in the United States (2). With our present knowledge we are unable to determine whether resistance to race 2 in Israel is conferred by Pm^2 and/or Pm^3 or by other gene(s).

The multiple-race resistance of PI 124111 to powdery and downy mildews makes it an excellent source for developing resistant breeding lines. Such breeding lines are currently being produced in both the United States and Israel.

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