Inheritance of Resistance to Downy Mildew in a Gynoecious Muskmelon

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ABSTRACT

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The gynoecious, downy mildew-susceptible *Cucumis melo* WI998 was stabilized for gynoecity and crossed with *C. melo* PI 124111F, a monoecious breeding line resistant to pathotype 3 of *Pseudoperonospora cubensis*. F_1 plants (all monoecious) were moderately resistant to downy mildew (reaction types 22 and 23). F_2 plants (1/16 gynoecious) segregated 1 susceptible (reaction type 11):14 moderately resistant (reaction types 12, 13, 22, 23, 24, and 33):1 resistant (reaction types 33 and 34). The backcross progeny of F_1 to the susceptible parent (WI998) segregated 3 susceptible:1 moderately resistant. The backcross progeny to the resistant parent (PI 124111F) segregated 3 moderately resistant:1 resistant. The data support a digenic partially dominant inheritance of resistance against pathotype 3 of *P. cubensis*.

Additional keywords: Cucurbitaceae, genetics, germ plasm, resistance genes

Downy mildew incited by *Pseudoperonospora cubensis* (Berk. & Curt.) Rostov. is a major disease of cucurbits in temperate growing regions of the world (1,7). Five pathotypes—1, 2, 3, 4, and 5—of the fungus were recently delineated by Thomas et al (13) according to their pathogenicity to six genera of the Cucurbitaceae: *Cucumis, Citrullus, Cucurbita, Lagenaria, Momordica,* and *Luffa*. Pathotype 3, which was found to occur in Israel (13), is pathogenic to *Cucumis* only. *Cucumis sativus* L. (cucumber) and *C. melo* var. *reticulatus* Naudin are the major hosts of *P. cubensis* in Israel.

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Recently, a breeding line, PI 124111F, of *C. m.* var. *reticulatus* resistant to downy mildew, powdery mildew, and Fusarium wilt was developed by Cohen and Eyal (4). A closely related breeding line, MR-1, was found to be resistant to pathotypes 4 and 5 in the United States (10).

The purpose of this study was to elucidate the mode of inheritance to downy mildew in crosses between the resistant PI 124111F and the susceptible gynoecious mutant WI998 (8). A gynoecious line was selected as a partner with the aim of developing a gynoecious resistant parent line for the production of F_1 resistant hybrids.

MATERIALS AND METHODS

Germ plasm. The resistant monoecious parent (PI 124111F) was derived from PI 124111 after seven generations of selfing and selection (4). PI 124111F is homozygous for resistance to pathotype 3 of *P. cubensis*, races 1 and 2 of *Sphaerotheca fuliginea* (Schlecht.:Fr.)

Pollacci (causing powdery mildew), and races 0, 1, and 2 of *Fusarium oxysporum* Schlecht.:Fr. f. sp. *melonis* Synd. & Hans. (4). The downy mildew-susceptible parent (WI998) was a gift from P. E. Peterson of the University of Wisconsin, Madison. WI998 segregated gynoecious:gynomonoecious when obtained (8). Homozygosity for gynoecity was obtained in this line after four generations of selfing and selection using silver nitrate and cuttings as described before (6).

Crosses. Crosses were made in the greenhouse. Because WI998 was gynoecious and PI 124111F monoecious, no emasculation was required when the former line served as a female parent. For reciprocal (designated E) crosses (WI998 served 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, WI998 × PI 124111F and PI 124111F × WI998, was propagated by cuttings and used to produce the F_2 and the E_2 progenies, respectively, and for the backcrosses. The following crosses were made (first for maternal parent, with WI = WI998 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.

Fungus, inoculation, and evaluation of resistance in progenies. A colony of *P. cubensis* was maintained on *C. melo* var. *reticulatus* 'Ananas-Yokneam' (Hazera Seed Corp., Haifa, Israel) by repeated inoculations in a growth chamber at 20 C. Test plants were grown in the greenhouse (18–26 C) in sandy loam soil in 10-cm-diameter plastic pots (one plant per pot) and inoculated when two fully expanded true leaves had developed (about 3 wk after sowing). Inoculation was done by spraying the adaxial leaf surfaces with a sporangial suspension of *P. cubensis* containing about 10,000 sporangia per milliliter. Inoculated plants were kept in a moisture-saturated atmosphere at 20 C in the dark for about 12 hr, then reexposed to the greenhouse atmosphere. This procedure was repeated on the seventh night to allow for fungal sporulation. Reaction types, as were expressed on the eighth day after inoculation, were used to identify resistance to downy mildew (11; Table 1). Leaf 1 and leaf 2 (from the stem base) were evaluated separately using the 1–4 index of reaction types (RT) described before (11). Assignment of a separate RT to each leaf resulted in a two-digit numerical classification in which the first digit represented the RT for leaf 1 (from the stem base) and the second digit represented the RT for leaf 2. RTs were categorized as follows: 11, susceptible; 12, 13, 22, 23, 24, and 33, moderately resistant; and 34 and 44, resistant. Plants with RT 14 were not detected.

Data analysis. Two populations per pedigree were tested. 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 represent pedigrees of reciprocal crosses of F_1 and F_2, respectively.

RESULTS

The susceptible parent plants were all gynoecious and had a RT index of 11. The resistant parent plants were all monoecious, with about two-thirds showing the highest level of resistance, RT 44, and about one-third showing RT 34 (Fig. 1).

The F_1 (WI998 × PI 124111F) and the reciprocal E_1 (PI 124111F × WI998) plants were all monoecious. They all showed a moderate level of resistance to downy mildew, with 80% showing RT 23 and 20% showing RT 22 (Table 2, Fig. 1).

The moderate level of resistance in F_1 and E_1 plants indicated that resistance in PI 124111F was partially dominant. F_1 plants did not differ from E_1 plants in RTs (Table 2), indicating that no cytoplasmic (maternal) factors were involved in expression of resistance to downy mildew.

F_2 and E_2 plants (1/16 gynoecious) segregated 1 susceptible:14 moderately resistant:1 resistant (Table 2), supporting the hypothesis on two partially dominant genes conferring resistance against downy mildew in PI 124111F. Segregation for reaction types in a population of 1,329 plants of the $F_2 + E_2$ pedigrees is shown in Figure 1. This population contained individuals with RTs 12, 13, 24, and 33, which were not found among the parents or the F_1 or E_1 populations. No linkage was noticed between the gynoecious sex type and resistance to downy mildew.

Progenies of the backcrosses of F_1 or E_1 to the susceptible parent (WI998) segregated 3 susceptible:1 moderately resistant, whereas those of the resistant parent (PI 124111F) segregated 3 moderately resistant:1 resistant (Table 2). Thus, the backcross data further supported a digenic partial dominant inheritance of resistance to *P. cubensis.*

DISCUSSION

The genetic control of resistance in muskmelon to downy mildew has not been fully investigated (1). Ivanoff (5) was the first to approach the problem, showing that the resistant cultivar Smith's Perfect, which originated from the West Indies, had a partial dominance when crossed with the susceptible cultivar Hale's Best. Thomas (9) found that whereas Smith's Perfect was resistant to one pathotype of *P. cubensis*, it was highly susceptible to another pathotype. In Thomas's study (9), PI 124111 showed a high level of resistance to both pathotypes. Cohen (1) examined the resistance of 19 U.S. PI entries under field conditions in Israel. With the heavy epidemics that developed, PI 124111 (India), PI 164323 (India), and PI 165449 (Mexico) showed a considerable amount of resistance. Cohen and Eyal (3) confirmed that a high level of resistance occurs in PI 124112 (India). This PI is in the background of several American cultivars (1), but no information is available on the mode of inheritance of its resistance to downy mildew.

The present study confirms two previous reports (2,12) on the occurrence of two incompletely dominant genes for

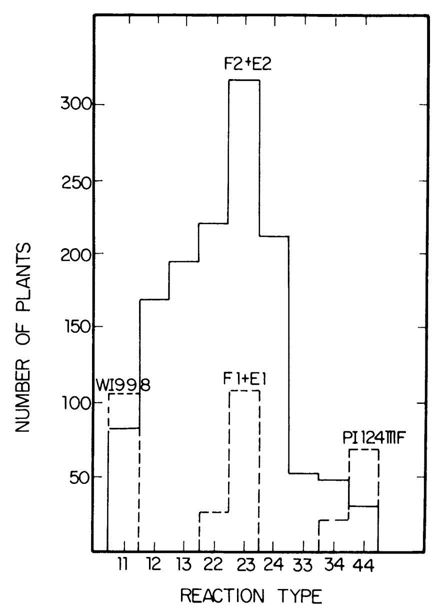

Fig. 1. Segregation of F_1 and F_2 muskmelon populations for reaction type to downy mildew. WI998 = susceptible parent, PI 124111F = resistant parent. The F_2 population consisted of 1,329 plants (F_2 + E_2 populations).

Table 1. Reaction type key index for assessing resistance in leaves of muskmelon to downy mildew incited by *Pseudoperonospora cubensis*

Reaction type	Description
1	Susceptible reaction typical of WI998; 10- to 15-mm irregular lesions with profuse sporulation that may extend beyond the apparent margins of the lesions
2	Moderately resistant reactions: type 1 lesions mixed with type 3 lesions
3	Moderately resistant reaction: 3- to 4-mm, irregular to circular chlorotic lesions with water-soaked margins beneath and sparse sporulation
4	Resistant reaction typical of PI 124111F: 1-mm, circular chlorotic lesions with necrotic centers and water-soaked margins beneath and limited or no apparent sporulation

Table 2. Segregation for downy mildew resistance caused by *Pseudoperonospora cubensis* in muskmelon

Pedigree	Generation	Number of plants: Susceptible	Moderately resistant	Resistant	Expected ratio	χ^2	*P*
WI998	P1	107	...	...	...	...	...
PI 124111F	P2	...	...	86	...	...	...
P1 × P2	F_1	...	66	...	...	...	...
P2 × P1	E_1	...	69	...	...	...	...
P1 × P2	F_2	78	1,005	69	1:14:1	0.53	0.70
P2 × P1	E_2	13	153	11	1:14:1	0.37	0.80
F_1 × P1	BC_s	66	24	0	3:1:0	0.13	0.70
E_1 × P1	BC_s	58	22	0	3:1:0	0.257	0.50
F_1 × P2	BC_r	0	59	20	0:3:1	0.004	0.95
E_1 × P2	BC_r	0	52	19	0:3:1	0:117	0.70

resistance to downy mildew (*Pc*-1 and *Pc*-2) in *C. melo* PI 124111. In the study by Cohen et al (2), a fifth generation inbred of PI 124111 was used in crosses with either Ananas-Yokneam or Hemed as susceptible parents. In the study by Thomas et al (12), MR-1 (an F_6 inbred developed from line 90319, which is an F_{10} inbred developed from PI 124111) was used in a cross with Ananas-Yokneam. In both studies (2,12) a 6:9:1 segregation ratio among susceptible, moderately resistant, and resistant plants was found in the F_2 populations. In those studies, the RT phenotypes 11, 12, and 13 were considered susceptible. In the present study, PI 124111F, an F_7 inbred of PI 124111, was used in a cross with the gynoecious WI998 as a susceptible parent. We used the same RT key index we used before (2,12) except that RTs 12 and 13 were classified as moderately resistant and not as susceptible. The segregation ratios in our F_2 + E_2 populations (total of 1,329 plants) had a high fit (chi-square 0.117, $P = 0.90$) to the 1:14:1 model. When plants were grouped to RT categories in the manner described before (2,12), with RTs 12 and 13 added to the susceptible category, a poor fit was obtained to the 6:9:1 model (chi-square 9.6, $P = 0.001$). We therefore suggest that in the cross of PI 124111F with WI998, two incompletely resistant genes with no epistatic relationships confer resistance to pathotype 3 of *P. cubensis*.

We assume that MR-1 (10) and PI 124111F (4), both inbreds of PI 124111, carry the same two genes, *Pc*-1 and *Pc*-2, for resistance to *P. cubensis*. These genes are effective against pathotypes 3 and 4 of *P. cubensis*. Because pathotypes 3 and 4 have a wider host range than pathotypes 1 and 2 (13), we assume that genes *Pc*-1 and *Pc*-2 may be effective also against pathotypes 1 and 2, thus making them highly valuable sources of resistance against downy mildew in muskmelons. The fact that PI 124111F is also resistant to races 1 and 2 of *S. fuliginea* and races 0, 1, and 2 of *F. o.* f. sp. *melonis* makes this breeding line a valuable source for multiple pathogen and race resistances in muskmelons.

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