Peroxidase Activity as a Biochemical Marker for Resistance of Muskmelon (*Cucumis melo*) to *Pseudoperonospora cubensis*

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ABSTRACT

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Peroxidase activity in uninfected muskmelon plants was used to predict the resistance and susceptibility of 257 plants, including cultivars or breeding lines and crosses of susceptible and resistant plants. When values of peroxidase activity greater than or equal to 30 (changes in absorbance at 470 nm $min^{-1}g^{-1}$ fresh weight of leaf tissue) were used, 100% of the resistant plants were detected, whereas at values of less than 30, 89% of the susceptible plants were detected. When values of greater than or equal to 35 were used, 88% of the resistant plants were detected. After infection, peroxidase activity increased with time in both susceptible and resistant plants. The ratio of activity in infected to uninfected leaves increased over time in the susceptible plants. This ratio, however, was lower and remained unchanged in the resistant plants. Using peroxidase activity as a preliminary marker for resistance of muskmelon to certain races of *Pseudoperonospora cubensis* is suggested in this study.

For many years, the role of oxidative enzymes and of their metabolic products in the defense mechanisms of infected plants has been studied (24). Peroxidase activity in diseased plants and its effects on resistance or susceptibility in many host-pathogen interactions have been studied (1,2,5,8-12,22). The direct role of peroxidase in the defense reaction of plant resistance has been supported by findings of Macko et al (10), Leherer (8), and Lovrekovich et al (9). Peroxidase activity was also associated with induced resistance in cucumber (3,4). However, little attention has been given to this enzyme in resistant plants before infection. Our investigations strongly suggest that peroxidase activity is a biochemical marker, which may or may not be part of the resistance mechanism but which can be used to predict resistance to disease. In studies with 12 tomato and four melon cultivars and breeding lines, a high correlation between peroxidase activity in uninfected tomato or melon and resistance to *Verticillium dahliae* or *Sphaerotheca fuliginea*, respectively, was found (16,17). In the case of melon, enhanced peroxidase activity was manifested in several isozymes (17). A recent reported showed a similar relationship between variation for preinfection peroxidase activity and levels of field resistance or susceptibility to downy mildew (*Bremia lactuca*) in lettuce (*Lactuca sativa*) cultivars,

accessions of *L. serriola*, segregating F_3 populations, and selected F_3 families from a cross between field-resistant and susceptible lettuce cultivars (19). In this report, we present evidence to support the suggestion that peroxidase activity might be used as a preliminary marker for resistance of melon to *Pseudoperonospora cubensis* (Berk. & M. A. Curtis) Rostovzev. A preliminary report has been published (18).

MATERIALS AND METHODS

Plants, pathogen, and inoculation. The following cultivars and breeding lines of muskmelon (*Cucumis melo*), differing in susceptibility to *P. cubensis*, were studied: Noy-Yizra'el, Galia, and Ein Dor, susceptible cultivars; line CKR, susceptible; line 202, highly susceptible; lines 534, 10-155, B39-9, and E132, resistant. In addition, we tested segregating F_1 populations and selected F_2 families from crosses between resistant and susceptible lines. Progenies were from a population that was derived from the breeding of CKR (susceptible line) with the F_1 of the cross 534 × CKR, which represents the backcross (BC) of F_1. The population from the self-breeding of this BC, which represents the F_2 population, was also tested. Plants were grown in 250-ml pots in growth chambers maintained at 20 ± 1 C with 50–60% RH. Illumination was by VHO (very-high-output) Gro Lox (Sylvania, Israel) fluorescent tubes and 40-W incandescent lamps with a 16-h photoperiod at a light intensity of 10,000 lx.

At the two-leaf stage, the plants were inoculated with a local isolate of *P. cubensis*, which was collected at random from the field for each experiment. The results of inoculations represent the possible local isolate(s). We inoculated plants with a sporangial suspension of known concentration by using a quantitative inoculator (21). The inoculum was deposited on a target area of about 4.5 cm^2 at a rate of 1,000 sporangia per square centimeter on the left side of the abaxial surface of the second true leaf. The plants were kept in a Percival Dew Chamber (Boone, Iowa) for 24 h in the dark at 15 C.

Visual estimation of symptom development. We rated symptom development 2, 6, and 10 days after inoculation by using a color index described previously (15). The color index was as follows: 1, greenish; 2, yellowish; 3, yellow; 4, brown (total necrosis). In addition, the infected area index was also recorded on a scale of 1–4: 1, indicates symptoms on 25% or less of the target area; 4, indicates symptoms over the entire target area. Multiplication of the color index and area index for each leaf yields a value (disease incidence) that describes symptom development.

Detection of peroxidase activity. Two leaf disks, 10 mm in diameter, were removed from both sides adjacent to the infected area of each leaf or from the same area of uninfected leaves. Leaf disks were ground with a mortar and pestle in 1 ml of cold 0.015 M sodium phosphate buffer, pH 6.0. After centrifugation (10,000 *g* for 10 min at 4 C), 50 µl of the supernatant was added to 3 ml of the assay mixture. The mixture consisted of a solution of 15 mM sodium phosphate buffer (pH 6.0), 1 mM H_2O_2, and 0.1 mM *o*-methoxyphenol (guaiacol). The increase in absorbance density at 470 nm was recorded with a model Unicon-810 Kontron Spectrophotometer (Zurich, Switzerland). Enzyme activity was expressed as changes in absorbance per minute per gram fresh weight and was statistically analyzed with Duncan's multiple range test ($P = 0.05$).

TABLE 1. Peroxidase activity in leaves of muskmelon cultivars or genetic lines susceptible or resistant to *Pseudoperonospora cubensis*

Cultivar	Peroxidase activity (× 10^2)[y]
10-155 (R)[z]	41.3 a
534 (R)	39.9 a
B39-g (R)	35.2 ab
E-132 (R)	32.1 b
Galia (S)	17.4 c
Noy-Yizra'el (S)	16.2 c
Ein Dor (S)	5.2 d
202 (HS)	2.9 e

[y] Peroxidase activity expressed as change in absorbance at 470 nm × 10^2 $min^{-1}g^{-1}$ fresh weight. Results are from one typical experiment with 10 plants per treatment. Means are for 10 leaves; values followed by the same letter do not differ significantly ($P = 0.05$) according to Duncan's multiple range test. Peroxidase activities were determined on the uninfected second true leaf.

[z] R, resistant, expressed as small necrotic lesions; S, susceptible, expressed as large typical lesions; HS, highly susceptible, expressed as rapid development of large typical lesions.

RESULTS

Peroxidase activity in leaves of melon plants susceptible or resistant to *P. cubensis*. A relationship between high peroxidase activity in uninfected leaves and resistance of four muskmelon genetic lines to *P. cubensis* was found (Table 1). Resistance in these lines is expressed as small necrotic lesions (1–2 mm in diameter). On the other hand, the lowest peroxidase activity was detected in the highly susceptible line 202. Values of peroxidase activity were intermediate in the susceptible cultivars Galia, Noy-Yizra'el, and Ein Dor.

Peroxidase activity and symptom development of *P. cubensis* in susceptible and resistant melon plants. Symptom development 10 days after inoculation in resistant (534), susceptible (Noy-Yizra'el), and highly susceptible (202) cultivars is shown in Figure 1. Symptom development was more rapid in the highly susceptible plants than in the susceptible cultivar Noy-Yizra'el, whereas only a few circular necrotic lesions, 1–2 mm in diameter, appeared on leaves of the resistant plants. Peroxidase activity was 13 times higher in the first leaves of the uninfected resistant plants than in those of the highly susceptible plants (values of 11.9 and 0.9, respectively) (Table 2). In the second leaves, enzyme activity was 12.2 times higher in the resistant plants than in the highly susceptible ones (values of 41.3 and 3.2, respectively). Values for susceptible plants (Noy-Yizra'el) were intermediate in first and second leaves. Calculation of the ratio of peroxidase activity in the infected leaves to that in uninfected leaves showed that the increment in enzyme activity was four times higher in the susceptible plants than in the resistant ones, 36.4:9.1 for the first leaf and 10.2:2.5 for the second leaf.

Peroxidase activity before infection was significantly higher on all dates in the resistant plants (534) than in the susceptible ones (Noy-Yizra'el) (Fig. 2A). After infection, peroxidase activity increased with time in susceptible and resistant plants and was higher on all dates compared with the uninfected controls. Enzyme

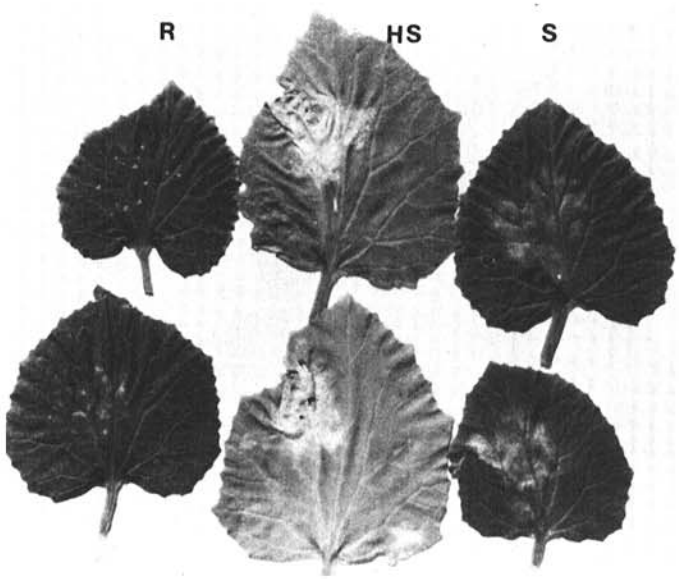

Fig. 1. Symptom development on melon resistant line 534 (R), susceptible cultivar Noy-Yizra'el (S), and highly susceptible line 202 (HS) 10 days after inoculation with *Pseudoperonospora cubensis*.

TABLE 2. Peroxidase activity in leaves of resistant, susceptible, and highly susceptible muskmelon cultivars before and 10 days after inoculation with *Pseudoperonospora cubensis*

Cultivar	Peroxidase activity ($\times 10^2$)[y]				
	Uninfected		Infected	Ratio	
	First leaf	Second leaf after 10 days	Second leaf 10 days after inoculation	Infected	Uninfected
534 (R)[z]	11.9 a	41.3 a	106.3 a	9.1	2.5
Noy-Yizra'el (S)	3.8 b	18.8 b	99.9 a	26.3	5.3
202 (HS)	0.9 b	3.2 c	32.8 b	36.4	10.2

[y] Peroxidase activity expressed as change in absorbance at 470 nm $\times 10^2$ $min^{-1}g^{-1}$ fresh weight. Results are from one typical experiment with 10 plants per treatment. The experiment was performed three times. Means are for 10 leaves; values followed by the same letter do not differ significantly ($P = 0.05$) according to Duncan's multiple range test. Peroxidase activities were determined on the uninfected first true leaf and on the infected second leaf, 10 days after challenge with the fungus. Peroxidase values for the uninfected second leaf are from another set of plants grown alongside the ones described, and the assays were made 10 days after the assays on the first uninfected leaf.
[z] R, resistant; S, susceptible; HS, highly susceptible.

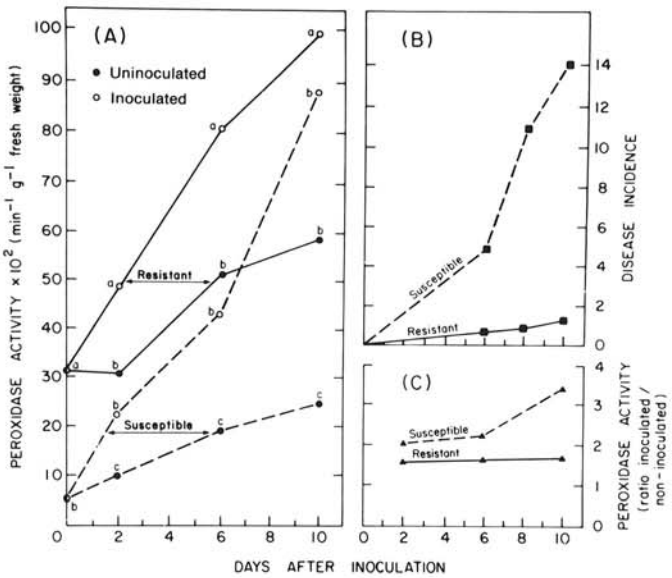

Fig. 2. The relationship between peroxidase activity and symptom development of *Pseudoperonospora cubensis* in inoculated susceptible and resistant melon plants. Resistant line 534: ●—●, uninoculated; ○—○, inoculated. Susceptible cultivar Noy-Yizra'el: ●---●, uninoculated; ○---○, inoculated. Results are from one representative experiment with 10 plants per treatment. The experiment was performed three times. Values followed by the same letter for each date do not differ significantly ($P = 0.05$) by Duncan's multiple range test. **A,** Peroxidase activity is the change in absorbance at 470 nm $\times 10^2$ ($min^{-1}g^{-1}$ fresh weight). **B,** Disease incidence is the color index × infected area index (see text). **C,** Peroxidase activity ratio of infected plants to uninfected plants.

activity in the susceptible plants was positively correlated with disease incidence as shown in Figure 2B. The ratio of enzyme activity in infected to uninfected leaves increased over time in the susceptible plants (Fig. 2C). This ratio, however, remained lower and almost unchanged in the resistant plants, in which disease incidence was very low. The same trend was found in three repeated experiments, in which we used *P. cubensis* isolates from different fields.

Peroxidase activity and resistance to *P. cubensis* in melon populations from crosses of resistant and susceptible parents. Peroxidase activity in populations and individuals within populations from crosses of resistant (534, group A) and susceptible (CKR, group B) parents, their backcross (BC) (group C), and three families from self-breeding of this BC progeny, which produced the F_2 population (groups D, E, F), are presented in Table 3 and Figure 3. On the level of populations, results show that peroxidase activity in the resistant parent was significantly higher ($P = 0.05$) than in the susceptible parent and the BC of F_2 (34.5, 17.6, and 23.1, respectively). Furthermore, a relationship

TABLE 3. Relationship between peroxidase activity and resistance of muskmelon populations to *Pseudoperonospora cubensis* in resistant parent, susceptible parent, or in progenies from their crosses

Tested population[y]	Peroxidase activity[z] ($\times 10^2$)
Group A P1 534 (R)	34.5 a
Group B P2 CKR (S)	17.6 d
Group C BC F_1	23.1 c
Group D F_2 BCa	19.0 cd
Group E F_2 BCb	27.7 b
Group F F_2 BCc	35.2 a

[y] R, resistant; S, susceptible. A, parent 1, resistant line 534; B, parent 2, susceptible line CKR; C, backcross (BC) of F_1 of the cross 534 × CKR with CKR; D,E,F, three families from selfing of the backcross group C and considered F_2 population.
[z] Peroxidase activity expressed as changes in absorbance at 470 nm × 10^2 $min^{-1}g^{-1}$ fresh weight. Means for 38–50 individuals within a group; total number of tested plants is 257. Values followed by the same letter do not differ significantly ($P = 0.05$) according to Duncan's multiple range test.

between high peroxidase activity and the resistance of the tested individuals in each population was found and is demonstrated in Figure 3. In addition, the distribution range of peroxidase activity in the F_2 families (groups D, E, F), as shown in Figure 3, was higher than in the parental population (groups A and B). The ability to predict the resistance or susceptibility of melon plants to *P. cubensis* according to peroxidase activity and the resistance reaction of individuals in these populations is presented in Tables 4 and 5. All resistant plants (groups A, E, F) were predicted to be resistant when the limit value of peroxidase activity was 30. In groups B, C, and D, which only contain susceptible plants, none of the plants was predicted to be resistant. When the limit value of peroxidase activity was 35, none of the susceptible plants was predicted to be resistant, except for three plants in group D and one in group E. At peroxidase activity values of 30, 100% of the resistant plants in groups A, E, and F were predicted to be resistant, and in the same groups 73%, 86%, and 83% of the susceptible plants were predicted to be susceptible (Table 5). When the values of peroxidase activity were less than 35, 100%, 97%, and 100% of the susceptible plants in groups A, E, and F, respectively, were predicted to be susceptible. The reliability of predicting resistance in these groups was 74%, 100%, and 92%, respectively.

DISCUSSION

The use of biochemical markers for resistance may expedite breeding programs by reducing the number of field trials. The main criteria for practical use of such markers are reliability in predicting resistance and ease in handling the assay.

Enhanced peroxidase activity very often is associated with resistance phenomena such as lignin production (3,20), phenylalanine

TABLE 4. Ability to predict the resistance and susceptibility of melon plants to downy mildew (*Pseudoperonospora cubensis*) according to peroxidase activity

Group[x]	Total no. of plants	No. of resistant plants[y]	No. of susceptible plants	No. of resistant or susceptible plants predicted from peroxidase values[z]			
				≥30 Resistant	<30 Susceptible	≥35 Resistant	<35 Susceptible
A	42	27	15	27	11	20	15
B	38	0	38	0	38	0	38
C	39	0	39	0	39	0	39
D	47	0	47	0	43	0	44
E	41	12	29	12	25	12	28
F	50	26	24	26	20	24	24
Total	257	65	192	65	176	56	188

[x]A, parent 1, resistant line 534; B, parent 2, susceptible line CKR; C, backcross (BC) of F_1 of the cross 534 × CKR with CKR; D,E,F, three families from selfing of the backcross group C and considered F_2 population.
[y]Resistance or susceptibility was determined by disease incidence index after inoculation in growth chambers (see text).
[z]Change in absorbance at 470 nm × 10^2 $min^{-1}g^{-1}$ fresh weight of leaf tissue (see Fig. 3).

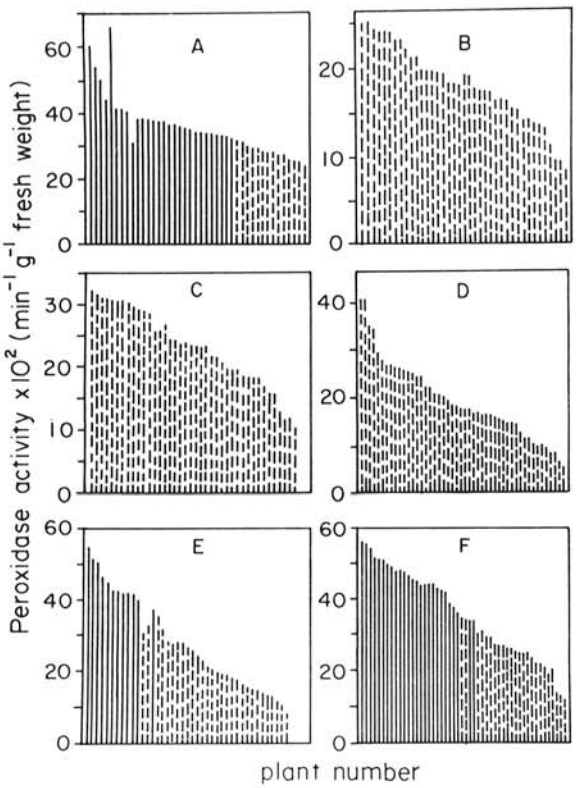

Fig. 3. The relationship between peroxidase activity and resistance of individual muskmelon plants to *Pseudoperonospora cubensis* in resistant parent, susceptible parent, and in progenies from their crosses. Resistant plants are represented by the dotted lines, and susceptible plants are represented by the solid lines. **A,** Parent 1, resistant line 534; **B,** parent 2, susceptible line CKR; **C,** backcross (BC), population from crossing F_1 (534 × CKR) with CKR; **D,E,F,** three families from self-breeding of the above cross and considered as F_2 populations. Peroxidase activities (change in absorbance at 470 nm × 100 $min^{-1}g^{-1}$ fresh weight) are for individual plants, and they are the mean of the activities obtained from two leaf disks from the second true leaf. The third leaf of each individual plant was inoculated and evaluated as resistant or susceptible as described in text.

TABLE 5. Percentage of reliability in predicting resistance and susceptibility of melon plants to downy mildew (*Pseudoperonospora cubensis*) according to peroxidase activity

Group[x]	Peroxidase activity/plant reaction[y]			
	≥30 Resistant	<30 Susceptible	≥35 Resistant	<35 Susceptible
A	100	73	74	100
B	...[z]	100	...	100
C	...	100	...	100
D	...	92	...	94
E	100	86	100	97
F	100	83	92	100
Total	100	89	88	99

[x]A, parent 1, resistant line 534; B, parent 2, susceptible line CKR; C, backcross (BC) of F_1 of the cross 534 × CKR with CKR; D,E,F, three families from selfing of the backcross group C and considered F_2 population.
[y]Values in table represent percentage of the total tested plants (257). Based on absorbance at 470 nm $min^{-1}g^{-1}$ fresh weight of leaf tissue (see Fig. 3).
[z]No resistant plants in these groups, and none was predicted by the peroxidase value.

ammonia lyase activity, and phenol accumulation (13,14,23). In this study, peroxidase activity was investigated in a model system, common in breeding programs, consisting of resistant and susceptible parents, their F_1 populations, and selected segregated F_2 families. Our results show that peroxidase activity was associated with resistance, and its activity positively correlates with the various levels of resistance or susceptibility of melon plants before infection with *P. cubensis* (Figs 1–3; Tables 1–5). After infection with *P. cubensis*, peroxidase activity increased with time in susceptible and resistant plants regardless of the source of the pathogen isolate (Fig. 2). The ratio of enzyme activity in infected to uninfected leaves also increased with time in the susceptible plants. This ratio remains lower and almost unchanged in the resistant plants. It seems, therefore, that susceptible plants have enhanced peroxidase activity after infection, but enhancement occurs too late to prevent development of the disease. Kuć and co-workers observed that the longer the pathogen suppresses or avoids recognition by the host, the more likely the pathogen will not be restricted (6,7). The speed and magnitude for activation of the defense mechanism(s) appear to be critical for the expression of resistance (6,7).

Environmental and physiological factors affect peroxidase activity, and our experiments were conducted under very controlled conditions. However, we suggest by the results shown in Figures 1–3 and Tables 1–4 that peroxidase activity in uninfected plants can be used as a marker for resistance under such conditions. Without considering the complicated, nuclear inheritance of resistance to *P. cubensis*, we investigated peroxidase activity and its distribution in populations from crosses of resistant and susceptible lines. We obtained such crosses from one resistant line to produce a reasonable number of segregating populations for this study. Our results demonstrate a clear relationship between high peroxidase activity in uninfected plants and the resistance of individuals in each population (Fig. 3; Tables 4,5). Among all the tested individuals, 100% of the resistant plants were predicted according to peroxidase values of 30 (Table 5). The percentage of predictability of susceptibility in this case was also

high and ranged from 73 to 100%. At a peroxidase value of less than 35, 94–100% of the susceptible plants were predicted, and at greater than or equal to 35, 94–100% of the resistant plants were predicted. In practical terms, our results mean that a primary selection to eliminate susceptible families (group D in this case) can be made at an early stage. Only individuals with high peroxidase activity among the favorable families (groups E and F) would be retained for inoculation. Our data show that peroxidase activity under controlled conditions correlates to resistance, although it may or may not be part of the resistance mechanism. The data presented are similar to data reported recently, in which a correlation between high peroxidase activity and field resistance or susceptibility of six lettuce cultivars (*L. sativa* and accessions of *L. serriola*) was shown (19). The results support the contention that peroxidase activity can be used as a marker for resistance and susceptibility in uninfected resistant plants at early stages of plant development and thereby decrease the time necessary for the development of resistant plants by breeding.

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