RESEARCH

Inheritance of Resistance to the New Race of Powdery Mildew in Watermelon

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ABSTRACT

Watermelon [*Citrullus lanatus* (Thunb.) Matsum. & Nakai] production in the United States has, in the past few years, incurred significant losses to races 1W and 2WU.S. powdery mildew (*Podosphaera xanthii*) infection. We report the mode of inheritance, gene action, and heritability of race 2WU.S. resistance in two populations derived from a cross involving the resistant genotype PI 189225 and the susceptible 'Charleston Gray' and PI 269677. Parents, F_1, F_2, BC_1P_1, and BC_1P_2 plants were inoculated and evaluated for leaf and stem resistance in two replicated greenhouse experiments. Segregation patterns revealed that only leaf resistance rating in Charleston Gray × PI 189225 fit the model for single gene inheritance. Generation mean analysis established only additive gene action for leaf resistance while for stem resistance, additive, dominance, and epistatic effects were important. Narrow-sense heritability estimates were higher for stem (0.81) than for leaf (0.58) resistance. Lack of dominance and epistatic effects combined with high heritability indicated high probability of success in selecting for leaf resistance in early generations. Stem resistance had a higher additive effect, lower dominance, and moderate heritability, but progress toward resistance should be possible. In population PI 269677 × PI 189225, epistatic effects combined with low heritability (0.20) and presence of duplicate epistasis may result in slower progress from selection.

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Abbreviations: 2F, 2 France; 2S, 2 Salinas; h^2, narrow-sense heritability; R, resistant; S, susceptible.

The Cucurbitaceae includes important crop species such as melon (*Cucumis melo* L.), cucumber (*Cucumis sativus* L.), pumpkin (*Cucurbita* L. spp.), squash (*Cucurbita* spp.), gourd (*Lagenaria* Ser. spp., *Luffa* Mill. spp., and *Cucurbita* spp.), and watermelon. Powdery mildew is an important disease of cucurbits that is caused by three fungi, *Podosphaera xanthii* (Castagne) Braun & Shishkoff (syn. *Sphaerotheca fuliginea* auct. p.p.), *Golovinomyces cucurbitacearum* (D.C.) V.P. Heluta (syn. *Erysiphe cichoracearum* auct. p.p.), and *Golovinomyces rotini* (syn. *Erysiphe cichoracearum* auct. p.p.) (Vakalounakis and Klironomou, 1995, 2001). In the past, watermelon was considered to be resistant to powdery mildew (Robinson and Provvidenti, 1975) with few and isolated cases reported in Israel (Cohen and Eyal, 1988) and in the Czech Republic (Kristkova and Lebeda, 2000). However, in the past decade, powdery mildew has been reported on watermelon in the United States and in many parts of the world. The causative agent of the recent outbreaks of powdery mildew in the United States appears to be an aggressive isolate of *P. xanthii*.

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Podosphaera xanthii occurs in physiological races that are identified on differential melon genotypes. So far, there have been 22 races reported of *P. xanthii* that were identified using 22 melon genotypes as well as the identification of 28 putative races that include eight variants of race 1 and six variants of race 2 that were previously unknown on melon cultivars (McCreight, 2006). Although watermelon *P. xanthii* race differential genotypes have not yet been identified, reports are available pointing to the occurrence of cross-infectivity of *P. xanthii* from melon and cucumber cultigens to watermelon (Cohen et al., 2000). In the United States, *P. xanthii* race 2WU.S. appears to cause more losses in watermelon (Davis et al., 2007; Tetteh, 2008) and is different from race 2WF (Zhang et al., 2011)

In a screening study for resistance to powdery mildew race 1W using the U.S. watermelon germplasm collection, Davis et al. (2007) reported that eight (all wild-type) of the 1573 accessions exhibited high levels of resistance while all the cultivated species showed susceptibility. In a similar study on powdery mildew race 2WU.S., all cultivated species and many wild-types showed high susceptibility to *P. xanthii* while some of the wild-types exhibited intermediate resistance (Tetteh et al., 2010). Some accessions with resistance to *P. xanthii* race 1W were susceptible to race 2WU.S. and vice versa, indicating that resistance to these two races was independent.

Although race identification is important for the development of resistant cultivars, it can be obscured by factors that affect plant responses such as humidity, light intensity, plant age, and nutritional status of the plant (Cohen et al., 2004). Shade increases the severity of powdery mildew on partially resistant or susceptible squash (*Cucurbita pepo* L.) plants (Leibovich et al., 1996) making it useful for identifying resistant individuals. However, some resistant cultivars exhibit susceptibility when environmental conditions are changed. In studies where large numbers of cultigens are screened for resistance to a particular race of powdery mildew, it is important to use standardized environmental conditions in greenhouses and growth chambers as well as a fixed age of plant growth to ensure reliable results.

Powdery mildew on watermelon appears as chlorotic spots on leaves with or without white mycelial or conidial development. The disease causes moderate to severe damage to the foliage and leads to reduction of fruit yield and quality (Davis et al., 2001; McGrath, 2001). In recent years, there have been significant losses to powdery mildew race 2WU.S. (Davis et al., 2001). Powdery mildew can be controlled using fungicides, but such control adds expense to crop production. A more economical and environmentally safe means of disease control is to use resistant cultivars. Currently, no powdery mildew resistant watermelon cultivars are available.

In watermelon, resistance to powdery mildew is expressed as absence of powdery mildew colonies on leaf or stem and few chlorotic spots on the leaves. One of the resistant accessions identified by Tetteh et al. (2010) is PI 189225 [*C. lanatus* var. *citroides* (L. H. Bailey) Mansf.], with resistance characterized by few chlorotic spots on leaves and absence of mycelia on the stem. The objective for watermelon breeders is to develop powdery mildew resistant cultivars using efficient selection methods. Davis et al. (2002) reported multigenic inheritance of resistance in PI 525088 to powdery mildew race 1W. For genetic improvement of the crop, the breeding method to be adopted depends mainly on the mode of inheritance and the nature of gene action involved in the expression of a quantitative trait. While it is relatively simple to breed improved cultivars for traits controlled by single genes having large effect, it is more difficult to breed for traits controlled by many genes, especially when epistasis is present. The presence of epistasis can be detected by analysis of generation means. Such scaling tests measure both the gene effects and the type of epistasis, whether it is complementary or duplicate.

The objective of this research was to study the genetic control of resistance to powdery mildew race 2WU.S. in watermelon PI 189225 using Charleston Gray and PI 269677 as susceptible parents and to evaluate the relationship between leaf and stem resistance.

MATERIALS AND METHODS

Plant Material and Inoculation

Two populations of watermelon, each segregating for resistance to powdery mildew race 2WU.S., were derived from crosses of the resistant parent with each of the two susceptible parents. Accessions used as parents were inbred for two generations before crossing to produce lines uniform for powdery mildew resistance. Resistant PI 189225 (P_2) was crossed to susceptible Charleston Gray (P_1) to form one population and to susceptible PI 269677 (P_1) to form the second population. From these, crosses were made to generate six generations encompassing F_1, F_2, BC_1P_1 (the first backcross to P_1), and BC_1P_2 (the first backcross to P_2) generations for the inheritance study and generation means analysis.

Plant Introduction 269677 was originally collected as cultivar Excel from Belize. It was the only accession of 590 *C. lanatus* var. *lanatus* tested that was susceptible to powdery mildew (Robinson and Provvidenti, 1975). High susceptibility to *P. xanthii* in PI 269677 was found to be controlled by the single recessive gene *pm* (Robinson et al., 1975). Charleston Gray (number 51-27) was developed by Andrus (1955) at the Southeastern Vegetable Breeding Lab, Charleston, SC, in 1954 with the following pedigree: (((Africa 8 × 'Iowa Belle') × 'Garrison') × Garrison) × ('Hawkesbury' × 'Leesburg') × Garrison. 'Charleston Gray No. 133' was released in 1961 by Stevenson in India as a selection from Charleston Gray having improved resistance to Fusarium wilt and a thinner rind while retaining resistance to anthracnose and sunburn.

Experiment Design

In 2008, two sets of P_1, P_2, F_1, F_2, BC_1P_1, and BC_1P_2 belonging to each population were planted in the greenhouse at the Department of Horticultural Science, North Carolina State University, Raleigh, NC, in a randomized complete block design with two replications in two separate experiments. Because the nonsegregating generations were homogeneous, fewer plants were required for analysis while for the heterogeneous segregating generations greater number of plants were studied. This was done to compensate for the greater variability in error variance associated with segregating populations (Hallauer and Miranda, 1988).

Each set consisted of 10 plants of each parent, 10 plants of F_1, 100 plants of F_2, and 30 plants of each BC_1. Pooled over sets, a total of 20 plants for each parent, 11 to 14 plants of the F_1, 130 to 159 plants of the F_2, 53 to 55 plants of BC_1P_1, and 51 to 56 plants of BC_1P_2 were evaluated for powdery mildew leaf and stem resistance (not all seeds produced useable plants).

Plants were grown in 100 mm pots containing 4P Fafard soilless mix (Conrad Fafard Incorporated) and placed on greenhouse benches with a 16 h photoperiod and light intensity of 200 μmol $m^{-2}s^{-1}$ at 20 to 26°C day and 13 to 19°C night. To verify the race of *P. xanthii* race 2, 10 melon differentials were included in the experiment. These were 'Edisto 47', Iran H, MR-1, WMR 29, PI 124112, PI 313970, PI 414723, 'Topmark', 'PMR 45', and 'PMR 5'. Disease reaction of each of the differentials were recorded and compared to a similar study on race 2 Salinas (2S), race 2 France (2F), and race 2U.S. reported by McCreight (2003, 2006) and Pitrat et al. (1998).

Inoculum Production and Seedling Inoculation

Podosphaera xanthii race 2WU.S. inoculum originating from infected commercial watermelon plants in South Carolina was maintained in the greenhouse on PMR 45 melon and 'Gray Zucchini' squash (*Cucurbita pepo*) plants, seeds of which were supplied by Seminis Vegetable Seeds (Woodland, CA). At the first true leaf stage, seedlings were mechanically inoculated with a spore suspension containing 4×10^4 conidia mL^{-1} at 1 wk intervals for 3 wk. Seedlings were maintained under plastic shading at 100% humidity for the first 7 d after each inoculation and subsequently at normal greenhouse conditions of 37 to 70% relative humidity and temperature of 24 to 38°C (night to day).

Disease Assessment

Individual plants were rated for disease severity on leaf and stem at 30 d after first inoculation by using a 0 to 9 scale developed by Tetteh (2008). For leaf resistance rating, 0 represents no symptoms, 1 represents faint yellow specks on leaves, 2 represents chlorotic lesions on leaves, 3 represents chlorotic lesions covering 20% of leaves, 4 represents yellow chlorotic lesions on leaves turned to brown necrotic areas, 5 represented two to three healthy colonies of mycelium on leaves, 6 represents less than 20% mycelium coverage on leaves, 7 represents 20 to 50% mycelium coverage on leaves, 8 represents 50 to 70% mycelium coverage with large necrotic areas, and 9 represents all leaves fully covered with powdery mycelium or plant dead. For stem resistance rating, 0 represents no symptoms, 1 represents first appearance of necrotic spots on stem, 2 represents two to three necrotic spots on the stem, 3 represents necrotic spots covering less than 10% of stem, 4 represents first sign of active mycelium sporulation on stem, 5 represents two to three healthy colonies of mycelium on stem, 6 represents less than 20% mycelium coverage on stem, 7 represents 20 to 50% mycelium coverage on stem, 8 represents 50 to 70% mycelium coverage with large necrotic areas, and 9 represents whole stem fully covered with powdery mycelium or plant dead. Individual plants in each generation were classified into resistant, intermediate, or susceptible: resistant if leaf and stem rating was 0 to 2, intermediate if 3 to 5, and susceptible if 6 to 9.

Statistical and Genetic Analysis

Segregation patterns of resistance were initially fitted to major gene models and goodness of fit was tested using chi square (Srb et al., 1965). Fitting of the major gene model was attempted using the reaction of the resistant F_2 plants and the backcross to the susceptible parent. A rating of 0 to 2 was considered a resistant reaction. In crosses where analysis of data based on the major gene model was inconclusive, generation means analysis was performed. Means, variances, and standard errors of the generations were calculated. Because the various generation means were not estimated with equal precision, for example, standard error of F_1 is about twice that of F_2 in Charleston Gray × PI 189225 cross, the generation means were weighted by the square of the standard errors and subjected to weighted least squares regression of the simple and joint scaling test of Mather and Jinks (1971), which uses the following equation, $Y = m + a_1d + a_2h + a_3i + a_4j + a_5l$, with the assumption that generation means depend only on additive and dominance gene effects and linear relationship among the means (Kearsey and Pooni, 1996; Singh and Chaudry, 1985; Mather, 1949). In this equation, Y is the mean of a given generation, m is the midpoint, d is the pooled additive effect, h is the pooled dominance effect, i is the additive × additive effect, j is the additive × dominance effect, l is the dominance × dominance effect, and a_1 to a_5 are the coefficients of the genetic effects in the equation (Mather and Jinks, 1971; Carson and Hooker, 1981).

The significance of the joint scaling test, as tested by chi square, provided evidence of nonallelic interactions. Therefore, the extended genetic effects were estimated by the six-parameter model of Jinks and Jones (1958). To examine the adequacy of the additive and additive–dominance genetic models, the data were subjected to tests of normality and measurement of correlation between generation means and variances. An assessment of the data showed that generation means and variances were not correlated (results not shown). Narrow-sense heritability (h^2) was performed on a single-plant basis as

$$h^2 = \left[2(\sigma^2_{F_2}) - (\sigma^2_{BC_1P_1} + \sigma^2_{BC_1P_2})\right] / \sigma^2_{F_2},$$

in which $\sigma^2_{F_2}$ is the variance among F_2 plants of the single-cross population and $\sigma^2_{BC_1P_1}$ and $\sigma^2_{BC_1P_2}$ are the variances among plants from the backcrosses of $F_1 \times P_1$ and $F_1 \times P_2$ (Warner, 1952). The numerator of the equation is the additive genetic variance while the denominator $\sigma^2_{F_2}$ represents the phenotypic variance among

Table 1. Mean disease reactions and summary reactions of 10 melon *Podosphaera xanthii* race differentials in response to inoculation with three isolates of *P. xanthii* and their comparison with a fourth isolate from South Carolina (designated race 2WU.S).

	Race 2S in 2001†		Race 2U.S. in 2003		Race 2F in 2004		Race 2SC in 2006‡	
Cultigen	Mean disease rating	Reaction	Mean disease rating	Reaction	Mean disease rating	Reaction	Mean disease rating	Reaction
Iran H	8.6§	S	7.1§	S¶	8.8§	S¶	7.9	S
Topmark	8.4§	S	6.9§	S¶	9.0§	S¶	7.9	S
PMR 45	8.4§	S	6.4§	S¶	8.5§	S¶	6.9	S
PMR 5	2.7§	R	1.3§	R¶	1.0§	R¶	0.6	R
WMR 29	7.0§	S	6.4§	H¶	7.7§	H¶	0.4	R
Edisto 47	7.7§	S	5.5§	S¶	3.4§	R¶	1.1	R
PI 414723	3.3§	R	4.1§	S¶	1.5§	R¶	7.7	S
MR-1	1.1§	R	1.4§	R¶	1.1§	R¶	0.1	R
PI 124112	1.1§	R	1.1§	R¶	1.0§	R¶	1.8	R
PI 313970	2.1§	R	1.7§	R#	1.0§	R#	3.0	R

†S, susceptible; H, heterogeneous; R, resistant; 2F, 2 France; 2S, 2 Salinas. Reactions of three *P. xanthii* isolates were based on previous reports: race 2S was collected from Salinas, CA; race 2U.S was observed in a greenhouse test in Riverside, CA, in 2003 (McCreight et al., 1987; Pitrat et al., 1998).

‡*Podosphaera xanthii* isolate collected from infected fields in South Carolina. The 2006 study was carried out in North Carolina State University, Raleigh, NC.

§McCreight (2006).

¶Pitrat et al. (1998).

#McCreight (2003).

plants. A standard error for heritability h^2 was derived as the square root of

$$\sigma^2(h^2) = 2\{[(\sigma^2_{BC_1P_1} + \sigma^2_{BC_1P_2})^2 / df_{F_2}] + [(\sigma^2_{BC_1P_1})^2/(df_{BC_1P_1})] \setminus + [(\sigma^2_{BC_1P_2})^2 / (df_{BC_1P_2})]\} / (\sigma^2_{F_2})^2$$

RESULTS AND DISCUSSION

The identity of the *P. xanthii* isolate collected from powdery mildew infected watermelon fields in South Carolina was investigated by means of 10 melon *P. xanthii* race differential genotypes. Testing of the South Carolina isolate was done in 2006 and was compared side by side with the expected disease reaction of *P. xanthii* race 2S, race 2U.S., and race 2F provided by McCreight (2006), which caused less damage to watermelon than the new isolate. The reaction of the South Carolina population was found to differ from the reaction of race 2U.S. and race 2F by the reaction of WMR 29, PI 414723, and Edisto 47 to the four isolates. While race 2U.S. and race 2F showed a heterogeneous reaction to WMR 29 in 2003 and 2004, in the 2006 evaluation, WMR 29 was highly resistant to the South Carolina isolate. Edisto 47 was susceptible to race 2S and race 2U.S. but showed resistance to race 2F and an even higher resistance to the South Carolina isolate. In these respects, it appeared that the South Carolina isolate was similar to race 2F. However, reaction of PI 414723 to the four isolates confirmed that the South Carolina isolate was a different race. Plant Introduction 414723 demonstrated high susceptibility to the South Carolina isolate (Table 1), a high level of resistance to race 2F, and moderate susceptibility to race 2U.S. and race 2S. The reactions of the remaining differentials to the three isolates were identical.

The reaction of the South Carolina isolate to WMR 29, PI 414723, and Edisto 47 was unexpected since it had already been reported that race 2U.S. was prevalent in the southeastern United States. The South Carolina isolate therefore appears to be a variant of race 2U.S., which is more aggressive in its reaction to PI 414723 and is capable of infecting previously resistant watermelon cultivars. Further testing of this isolate on watermelon cultivars showed that it can infect PI 269677, Charleston Gray, and 'Navajo Sweet', which were previously resistant to the Robinson powdery mildew reported in 1975 (Robinson and Provvidenti, 1975). This new variant of *P. xanthii* race 2 was previously described by Davis et al. (2007) as race 2WU.S to differentiate it from the earlier race 2U.S.

A single dominant gene Mendelian ratio, 3 resistant (R):1 susceptible (S) in F_2 progeny was found to be the best fit and was further confirmed by 1R:1S ratio as best fit for backcross to susceptible parent (Table 2). This result suggests that powdery mildew leaf resistance in this cross is controlled by a single dominant gene. For stem resistance of Charleston Gray × PI 189225 and for both leaf and stem resistance of PI 269677 × PI 189225, no major gene model could adequately describe the inheritance of powdery mildew resistance (Table 2). However, a modified digenic model of 15:1 based on epistasis and modifiers in stem resistance of the cross Charleston Gray × PI 189225 could not be entirely discarded.

In the generation means analysis for leaf and stem ratings, effects due to sets and generations × sets were not significant in both crosses, indicating the absence of environmental variation for these traits (Table 3). This was expected since both sets were grown in the same greenhouse and were subjected to the same environmental factors.

Table 2. Disease reactions exhibited by parents, F_1, F_2, and backcross generations in response to inoculation with cucurbit powdery mildew race 2WU.S isolate in a greenhouse study in Raleigh, NC.

Population	Number of plants with disease reaction†					Probability of calculated χ^2 for F_2 genetic model						
						Charleston Gray × PI 189225						
Leaf resistance	Total	0–2	3–5	6–7	8–9	3:1	9:6:1	12:3:1	9:3:4	9:7	15:1	13:3
P_1 (Charleston Gray)	20	0	0	16	4	–	–	–	–	–	–	–
P_2 (PI 189225)	20	20	0	0	0	–	–	–	–	–	–	–
F_1	12	3	9	0	0	–	–	–	–	–	–	–
F_2	130	57	39	31	3	0.76	<0.01	<0.01	<0.01	<0.01	<0.01	0.03
BC_1P_1	53	5	22	20	6	0.89	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
BC_1P_2	56	32	19	5	0	–	–	–	–	–	–	–
Stem resistance												
P_1 (Charleston Gray)	20	0	19	1	0	–	–	–	–	–	–	–
P_2 (PI 189225)	20	20	0	0	0	–	–	–	–	–	–	–
F_1	12	5	7	0	0	–	–	–	–	–	–	–
F_2	130	70	57	1	2	<0.01	0.09	<0.01	<0.01	<0.01	0.06	<0.01
BC_1P_1	53	6	37	8	2	<0.01	<0.01	<0.01	<0.01	<0.01	0.30	0.30
BC_1P_2	56	45	11	0	0	–	–	–	–	–	–	–
						PI 269677 × PI 189225						
Leaf resistance	Total	0–2	3–5	6–7	8–9	3:1	9:6:1	12:3:1	9:3:4	9:7	15:1	13:3
P_1 (PI 269677)	20	0	0	0	20	–	–	–	–	–	–	–
P_2 (PI 189225)	20	19	1	0	0	–	–	–	–	–	–	–
F_1	14	1	12	1	0	–	–	–	–	–	–	–
F_2	159	53	53	27	26	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
BC_1P_1	55	5	8	11	31	<0.01	<0.01	<0.01	<0.01	0.82	<0.01	<0.01
BC_1P_2	51	25	21	5	0	–	–	–	–	–	–	–
Stem resistance												
P_1 (PI 269677)	20	0	0	14	6	–	–	–	–	–	–	–
P_2 (PI 189225)	20	20	0	0	0	–	–	–	–	–	–	–
F_1	14	10	4	0	0	–	–	–	–	–	–	–
F_2	159	73	67	15	4	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.03
BC_1P_1	55	5	24	18	8	0.68	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
BC_1P_2	51	38	13	0	0	–	–	–	–	–	–	–

†Disease reactions of 0 to 2 were considered resistant, 3 to 5 intermediate, and 6 to 9 susceptible. The corresponding ratios tested s for BC_1P_1 genetic model are given as 1:1, 1:2:1, 2:1:1, 1:1:2, 1:3, 3:1, and 3:1.

Table 3. Mean squares for powdery mildew race 2WU.S. leaf and stem resistance of generation mean analysis for two families from crosses of the resistant PI 189225 with susceptible Charleston Gray and PI 269677.

		Generation means by family			
		Charleston Gray × PI 189225		PI 269677 × PI 189225	
Source	df	Leaf	Stem	Leaf	Stem
Set (S)	1	0.29 NS†	0.43 NS	0.99 NS	0.86 NS
Replication	2	0.03	0.03	0.27	0.29
Generation (G)	5	21.46**	11.90**	35.87**	31.06**
G × S	5	0.37NS	0.18 NS	0.53 NS	0.92 NS
Error	10	0.19	0.16	0.54	0.41

**Significant at the 0.01 probability level.

†NS, not significant.

Highly significant ($P < 0.01$) differences were observed among generations for both traits and crosses. Variation among generations was greater in leaf resistance than in stem resistance in both crosses. The greatest variation was observed in PI 269677 × PI 189225, as expected since they were more divergent than Charleston Gray × PI 189225 (Table 2). In both crosses, PI 189225 was highly resistant for leaf and stem ratings while Charleston Gray was moderately susceptible and PI 269677 was highly susceptible to powdery mildew. In both populations, the stem showed greater resistance to powdery mildew than the leaf (Table 3). Leaf and stem resistance of the F_1 plants in both crosses showed either high or intermediate resistance with none being susceptible indicating dominance of the genes controlling resistance to powdery mildew in PI 189225 (Table 2). The F_2 population means were significantly different ($P < 0.05$) from the resistant parent mean in both crosses and for both leaf and stem ratings. There was no difference between the F_2 and F_1 population means for both leaf and stem ratings, with overall resistance rating in the intermediate range (Table 4). The means of BC_1P_1 and BC_1P_2 were significantly different ($P < 0.05$) for both families, with the BC_1P_1 population means approaching the means of the susceptible parent while the BC_1P_2 population mean values approached the means of the resistant parent. In both crosses, the BC_1P_2

Table 4. Mean, ranges, and standard errors for leaf and stem powdery mildew race 2WU.S. resistance reactions for parents, F_1, F_2, and backcross generations of resistant (PI 189225) and susceptible (Charleston Gray and PI 269677) watermelon crosses.

	Leaf rating			Stem rating		
Generation	Mean	Range	SE	Mean	Range	SE
	Charleston Gray × PI 189225					
P_1	6.9 e†	6–8	0.16	4.8 d	4.5–6.3	0.12
P_2	0.3 a	0–1	0.10	0.1a	0–0.45	0.04
F_1	3.4 c	1–5	0.38	2.5 c	0.9–4.5	0.35
F_2	3.4 c	0–9	0.20	2.4 c	0–9	0.17
BC_1P_1	5.3 d	2–9	0.28	4.5 d	0.9–9	0.24
BC_1P_2	2.3 b	0–6	0.25	1.3 b	0–4.5	0.15
LSD (5%)	0.63			0.56		
	PI 269677 × PI 189225					
P_1	8.95 e	8–9	0.08	7.52 e	6.3–9	0.20
P_2	0.4 a	0–1	0.175	0.14 a	0–0.45	0.05
F_1	4.0 c	0–6	0.27	2.36 c	0.45–4.5	0.27
F_2	4.201c	0–9	0.21	2.87 c	0–9	0.17
BC_1P_1	6.93 d	2–9	0.31	5.52 d	0.9–9	0.30
BC_1P_2	2.63 b	0–7	0.38	1.37 b	0–5	0.31
LSD (5%)	1.03			0.90		

†Values within columns followed by the same letter are not different according $LSD_{0.05}$.

Table 5. Estimates of gene effects for powdery mildew race 2WU.S. leaf and stem resistance for PI 189225 families.

	Family			
	Charleston Gray × PI 189225		PI 269677 × PI 189225	
Gene effect	Leaf	Stem	Leaf	Stem
	Three-parameter model†			
m	3.57**	2.40**	4.69**	3.84**
d	−3.31**	−2.38**	−4.27**	−3.71**
h	0.02 NS‡	0.11 NS	−0.57*	−1.46*
χ^2	2.43	10.44	4.02	5.61
P	0.6	0.01	0.3	0.15
	Six-parameter model§			
m	3.46**	2.35**	4.20**	2.87**
d	2.99**	3.19**	4.29**	4.15*
h	1.06 NS	2.07*	1.63 NS	0.83 NS
i	1.22 NS	−2.03**	2.30 NS	2.29*
j	−0.33 NS	0.83**	0.02 NS	0.46*
l	−2.99 NS	−3.49*	−4.06*	−3.68*

*Significant at the 0.05 probability level. Significant estimates based on *t* test calculated from the standard errors.

**Significant at the 0.01 probability level. Significant estimates based on *t* test calculated from the standard errors.

†*m*, midpoint; *d*, pooled additive effect; *h*, pooled dominance effect.

‡NS, not significant.

§*i*, additive × additive effect; *j*, additive × dominance effect; *l*, dominance × dominance effect.

means were lower ($P < 0.05$) and therefore more resistant than the F_1 and F_2 means (Table 4).

As observed by Kearsey and Pooni (1996), we identified individual F_2 and BC_1 plants having powdery mildew ratings lower than the resistant parent or their F_1 mean (transgressive segregation) in both crosses. For example, in Charleston Gray × PI 189225, 12 and 53% of F_2 individuals exhibited stronger leaf and stem resistance than the means of P_2 and F_1, respectively. Also, the BC_1P_1 of that cross produced 24% transgressive segregants for leaf resistance and 11% for stem resistance. The BC_1P_2 generation contained 16% transgressive segregants in both leaf and stem ratings.

A joint scaling test was used to test the fitness of the three-parameter model (mean, additive, and dominance effects) in explaining the variability observed among the progeny from both crosses. In Charleston Gray × PI 189225, the three-parameter generation mean analysis model satisfactorily explained the genetic differences for powdery mildew resistance in only leaf resistance but this model was inadequate for stem resistance (Table 5). In Charleston Gray × PI 189225, estimates of additive genetic effects were highly significant and negative for both leaf and stem resistance, ranging between −2.38 and −4.27 (Table 5), and dominance effects were not significant. The significant and negative additive gene action was in the direction of the resistant parent. For leaf resistance, a test of goodness of fit of the additive–dominance model for this cross produced a chi square of 2.436 (3 df and probability 0.6). The additive–dominance model therefore was adequate for leaf rating. In contrast, chi square goodness of fit test showed that the additive–dominance model was inadequate for stem resistance. An extension of the model to include nonallelic interactions was performed using the six-parameter model (Table 5).

The nonsignificance of the epistatic interaction parameters in the six-parameter test for leaf resistance of Charleston Gray × PI 189225 further confirmed that the simple additive–dominance model was adequate in explaining the variation in leaf resistance, agreeing with the conclusions from the joint scaling test. The lack of dominance and epistatic effects in this cross indicated that there would be a high probability of success in selecting for resistance to powdery mildew in early generations using symptom ratings. For stem resistance, an epistatic digenic interaction was important in explaining the variation since the six-parameter tests were significant (Table 5). Both additive and dominance effects were significant for stem rating with the additive component being greater in magnitude than its corresponding dominance component. Therefore, powdery mildew resistance in watermelon was predominantly under additive genetic control. Since additive effects were equally important as nonadditive effects for stem resistance, breeding progress might be slower than for leaf resistance.

Epistatic interactions represented by additive × additive and additive × dominance interaction were important in explaining variation associated with stem resistance in Charleston Gray × PI 189225. The significant and positive additive × additive gene action suggested homozygous loci in Charleston Gray × PI 189225 stem resistance

and combined with a significant and positive additive × dominance interaction suggested a reducing effect in the expression of powdery mildew resistance in this cross (Hakizimana et al., 2004).

Dominance and dominance interaction effects were significant and negative for stem rating, indicating their enhancing effect in the expression of powdery mildew resistance in the stem. We observed that the dominance and dominance × dominance gene effects for stem resistance in Charleston Gray × PI 189225 were in the opposite direction, which are indicative of duplicate-type epistasis between dominant increasing alleles (Mather and Jinks, 1971). This implied that interactions between heterozygous loci were negative while those involving one or more homozygous loci were positive.

In PI 269677 × PI 189225, on the basis of the joint scaling test, both additive and dominance effects were significant ($P < 0.01$) (Table 5), demonstrating their contribution to the inheritance of leaf and stem resistances. Both additive and dominance effects were negative, with the additive genetic effect being close to the overall mean and offering a greater contribution to the inheritance of resistance. The contribution of dominance effect although significant was small compared to the mean. The six-parameter model revealed a nonsignificant dominance effect for both leaf and stem ratings. Although the additive–dominance model was found to be adequate, the six-parameter model showed that nonallelic interactions contributed significantly to the variation, especially for stem rating, while the joint scaling test failed to detect epistatic interaction effects in this cross. This condition may arise when a dispersed pair of genes controls the trait or when the direction of the epistatic interaction terms differs from one pair of interacting genes to another (Mather and Jinks, 1971). In PI 269677 × PI 189225, additive × additive (*i*) interaction was higher in magnitude than additive (*d*) component. The dominance × dominance (*l*) interaction in both leaf and stem resistance of both crosses was larger than the additive × additive (*i*) and additive × dominance (*j*) effects combined.

Epistatic interactions represented by additive × additive and dominance × dominance were important in explaining variation associated with leaf and stem resistance in both crosses except leaf resistance in Charleston Gray × PI 189225. These findings were in agreement with the joint scaling test and revealed nonallelic interactions expressed as additive × additive, additive × dominance, and dominance × dominance. Significant additive gene action along with significant and positive dominance gene action suggested that powdery mildew resistant alleles were contributed by only the resistant parent. Significant and positive additive × additive gene action combined with significant and negative dominance × dominance gene action in PI 269677 × PI 189225 suggested homozygous loci for stem resistance in the resistant parent (PI 189225) and heterozygous loci for stem resistance in the susceptible parent (PI 269677), respectively. Therefore, alleles for resistance to powdery mildew also were present in the susceptible parent. The additive × additive type of gene interaction and duplicate epistasis identified in powdery mildew resistance in both leaf and stem suggest the possibilities of obtaining transgressive segregants in later generations (Sharmila et al., 2007). The significance of additive × dominance effect in stem resistance of both crosses revealed that selection through self-pollination for improvement of stem resistance may not be as rapid as predicted. However, since additive × dominance was not significant in leaf ratings of both crosses and combined with a larger additive effect than dominance, selection under self-pollination will be effective for breeding for powdery mildew resistance in leaf (Farshadfar et al., 2001; Sharifi, 2005). Therefore, both additive and nonadditive gene effects must be exploited to obtain the greatest gain in resistance.

Table 6. Narrow-sense heritability estimates for powdery mildew resistance in watermelon.

Family	Parameter	Heritability
Charleston Gray × PI 189225	Leaf	0.58 ± 0.11
	Stem	0.81 ± 0.07
PI 269677 × PI 189225	Leaf	0.20 ± 0.17
	Stem	0.00 ± 0.12

For both crosses, h^2 ranged from 0.20 to 0.58 for leaf resistance and from 0.00 to 0.81 for stem resistance (Table 6). The moderate to high heritability of leaf and stem resistance found in Charleston Gray × PI 189225 (0.58 and 0.81) suggests that conventional breeding and early selection methods should be effective in improving powdery mildew resistance while the low heritability values plus complex gene action in PI 269677 × PI 189225 suggests that the genes involved will result in slower development of resistant lines.

CONCLUSIONS

Generation mean analysis showed that additive and epistatic effects offer major contributions to the inheritance of powdery mildew resistance in watermelon PI 189225. The contribution of nonadditive genetic effects was more pronounced in stem resistance but small in leaf resistance of both crosses. The large narrow-sense heritability in Charleston Gray × PI 189225 combined with major additive genetic effects suggests that selection for powdery mildew leaf resistance in the segregating population of this cross is expected to show progress in early generations.

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