

Inheritance of Resistance to Powdery Mildew Race 2 in *Citrullus lanatus* var. *lanatus*

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Abstract. Information on the mode of inheritance of powdery mildew resistance in watermelon is important for designing a breeding strategy for the development of new cultivars. Resistance in the watermelon accession PI 270545 was investigated by generation means analysis by crossing it with susceptible PI 267677. The analyses showed involvement of two genes, a recessive resistance gene, *pmr-1*, and a dominant gene for moderate resistance, *Pmr-2*. Resistance to powdery mildew in the leaf had a large dominance effect and a heritability of 71%. The additive-dominance model was inadequate in explaining variation in leaf resistance as revealed by the joint scaling test. However, nonallelic interactions could not be detected by the nonweighted six-parameter scaling test. For stem resistance, the additive-dominance model was adequate, and inheritance was controlled mainly by additive effects. A high narrow-sense heritability of 79% suggested that selection for stem resistance in early generations would be effective.

Powdery mildew in watermelon [*Citrullus lanatus* (Thumb.) Matsum. and Nakai] caused by the fungus *Podosphaera xanthii* race 2W has in recent years become a concern among growers as well as plant breeders in United States (Davis et al., 2001; McGrath, 2001), China (Feng, 1996; Zhang et al., 2011), and other parts of the world (McGrath, 2001; Tomason and Gibson, 2006). The disease causes significant yield loss as well as decreased fruit quality (McGrath and Thomas, 1996) through mycelial coverage of the leaves, leaf necrosis, and premature death of the plant (Davis et al., 2001). Powdery mildew of watermelon occurs throughout the southeastern United States, extending north to New York as well as into western states (Davis et al., 2005).

Development of genetic resistance is an important objective in watermelon breeding programs. Screening of the U.S. watermelon germplasm collection identified high resistance in several wild accessions of *C. lanatus* var. *citroides* (Davis et al., 2007; Tetteh et al., 2010), but none of the accessions in the primary gene pool. However, one accession of *C. lanatus* var. *lanatus*, PI 270545, originating from Sudan was found to have intermediate resistance (Tetteh et al., 2010). Resistance in this accession was characterized by few mycelium on leaf and stem, and affected plants survived to fruit production stage (Tetteh et al., 2010).

To help breed cultivars resistant to powdery mildew, it is important to understand the inheritance and gene action. Tetteh et al. (2013) evaluated the gene action of leaf and stem resistance in the watermelon accession, PI 189225, and established that mainly additive gene action controlled leaf resistance, whereas for stem resistance, additive, dominance, and epistatic gene actions were significant. There are several reports on inheritance of resistance to *P. xanthii* in melon (*Cucumis melo* L.). Most agree that there are several genes controlling resistance (Epinat et al., 1993; Kenigsbuch and Cohen, 1992; McCreight, 2003; McCreight et al., 1987; Pitrat et al., 1998). Perchepped et al. (2005) working with quantitative trait loci (QTL) revealed that powdery mildew resistance in melon was under the control of major gene effects and

digenic epistasis. Inheritance of powdery mildew resistance in watermelon was investigated by generation means analysis by Tetteh et al. (2013). Studies have demonstrated a close correspondence between generation mean analysis and QTL mapping (Jung et al., 1994; Perchepped et al., 2005).

Estimation of genetic effects in different crosses should inform the breeding strategy for development of resistant cultivars. Although additive and dominance models can be determined with the scaling tests in generation means analysis, the identification of non-allelic interactions requires more powerful tests such as the joint scaling test (Mather, 1949) or QTL analysis (Perchepped et al., 2005). In most cases, the variation unaccounted for by a major gene is provided by digenic epistasis.

A major deficiency of generation means is in nondetection of additive effects resulting from dispersion of alleles with similar effects between parents and internal cancellation of dominance effects exhibited in opposite directions at different loci (Crow and Kimura, 1970). Saudhu and Nittal (1988) studied two *Gossypium arboreum* crosses and reported the absence of nonallelic interaction in the six-parameter model, whereas the joint scaling test predicted the presence of epistasis for yield of seed cotton per plant (Iqbal and Nadeem, 2003).

Given the lack of genetic information on powdery mildew resistance in the primary gene pool of watermelon, a generation means analysis was carried out to determine inheritance, gene action, and heritability of resistance in PI 270545. Information on these parameters would be useful for designing an efficient breeding strategy for watermelon powdery mildew resistance.

Materials and Methods

Plant material. A single population of watermelon segregating for resistance to powdery mildew race 2W-U.S. was derived from a cross between the susceptible P₁ (PI 269677) and resistant P₂ (PI 270545). The parents were inbred for two generations before crossing to produce plants uniform for powdery mildew resistance. From this, crosses were made to create a total of six generations, F₁, F₂, BC₁P₁ (the first backcross to P₁), and BC₁P₂ (the first backcross to P₂) for a study of inheritance of resistance.

Experimental design. Seeds of inbred powdery mildew-resistant PI 270545 and -susceptible PI 269677, together with their F₁, reciprocal F₁, F₂ (generated by self-pollination of the F₁), and backcross generations were produced in 2007 to 2008 in greenhouses at the Department of Horticultural Science, North Carolina State University, Raleigh, NC. Seeds were planted in two sets, each consisting of 10 plants of each parent, 10 plants of F₁, 10 plants of F₁ reciprocal, 100 plants of F₂, and 30 plants of each BC₁. Pooled over sets, a total of 20 plants for each parent, 17 plants of F₁, 19 of F₁ reciprocal, 190 plants of the F₂, and 59 plants each of BC₁P₁ and BC₁P₂ were evaluated for powdery

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mildew leaf and stem resistance, accounting for missing plants.

Seeds were planted in 100-mm pots containing 4P Fafard soilless mix (Conrad Fafard Incorporated, Agawam, MA) and arranged on greenhouse benches. Conditions of growth in the greenhouse were 16-h photoperiod, light intensity of 200 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, and 20 to 26 °C day and 13 to 19 °C night air temperature.

Inoculum production and seedling inoculation. Seedlings were inoculated three times at weekly intervals, starting at the first true leaf stage. A spore suspension of *Podospheera xanthii* race 2W-U.S. (4×10^4 conidia/mL) was sprayed over the plants until runoff. The suspension was prepared from inoculum isolated from infected commercial watermelon fields in South Carolina over the surface. After each inoculation, seedlings were maintained under plastic shading at 100% humidity for 7 d 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 a 0 to 9 scale on leaves and stems at 21 and 30 d after first inoculation. For leaf resistance rating, 0 = no symptoms; 1 = faint yellow speck on leaves; 2 = chlorotic lesions on leaves; 3 = chlorotic lesions covering 20% of leaves; 4 = yellow chlorotic lesions on leaves turned to brown necrotic areas; 5 = two to three healthy colonies of mycelium on leaves; 6 = less than 20% mycelium coverage on leaves; 7 = 20% to 50% mycelium coverage on leaves; 8 = 50% to 70% mycelium coverage with large necrotic areas; 9 = all leaves fully covered with powdery mycelium or plant dead. For stem resistance rating, 0 = no symptoms; 1 = first appearance of necrotic spots on stem; 2 = two to three necrotic spots on the stem; 3 = necrotic spots covering less than 10% of stem; 4 = first sign of active mycelium sporulation on stem; 5 = two to three healthy colonies of mycelium on stem; 6 = less than 20% mycelium coverage on stem; 7 = 20% to 50% mycelium coverage on stem; 8 = 50% to 70% mycelium coverage with large necrotic areas; 9 = entire stem fully covered with powdery mycelium or plant dead. On the basis of resistance levels of parental genotypes, plants were classified into two groups. In Group 1, plants having leaf and stem resistance ratings of 0 to 2 were classified as resistant, whereas ratings of 3 to 9 were classified as susceptible. Classification in Group 2 was based on ratings of 0 to 2 as resistant, 3 to 5 as moderately resistant, and 6 to 9 as susceptible.

Statistical analysis. Generation means and variances were calculated. Variances for the two parents and reciprocal F_1 were examined for correlation (data not shown). Correlation of variance with mean indicated a need for transformation of the data. A \log_{10} transformation was applied but this did not reduce the correlation. A nonsignificant test of homogeneity of F_1 and F_{1r} variance demonstrated no maternal effect; hence, the two generations were pooled. Chi square was used to test the goodness of fit of the observed ratio of

segregation to expected ratio in the F_2 and backcross progenies. Analysis of variance was performed with generations as fixed effects and blocks (sets) as random effects. Phenotypic correlation between leaf and stem resistance was calculated. Data for each generation were pooled over replicates within each block. Generation means analysis was conducted on plot means by the ABC scaling test and the joint scaling test based on additive-dominance model (Cavalli, 1952; Mather and Jinks, 1971) in which the generations were subjected to a weighted least squares regression based on the equation:

$$Y = m + a_1d + a_2h + a_3i + a_4j + a_5l$$

and a nonweighted scaling test based on the six-parameter model (Mather and Jinks, 1971). 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 \times additive effect, j is the additive \times dominance effect, l is the dominance \times dominance effect, and a_1 to a_5 are the coefficients of the genetic effects in the equation (Carson and Hooker, 1981; Mather and Jinks, 1971). The significance of the joint scaling test, as tested by χ^2 , provided evidence of non-allelic interactions.

Narrow-sense heritability was calculated as

$$h^2 = (2V_{F_2} - [V_{BC1P_1} + V_{BC2}]) / V_{F_2}$$

where V_{F_2} = variance among F_2 plants of the single-cross population; and V_{BC1P_1} and V_{BC1P_2} are variances among plants from the backcrosses of $F_1 \times P_1$ and $F_1 \times P_2$ (Warner, 1952). A SE of heritability h^2 was derived as the square root of

$$V(h^2) = 2\{[(V_{BC1P_1} + V_{BC1P_2})^2 / df_{F_2}] + [(V_{BC1P_1})^2 / (df_{BC1P_1})] + [(V_{BC1P_2})^2 / (df_{BC1P_2})]\} / (V_{F_2})^2$$

Results and Discussion

Faint specks of mycelium were observed 14 d after inoculation. On Day 21, disease development was poor with few patches of mycelium on few plants of the susceptible genotypes. On Day 30, major differences in

disease scores for resistant, intermediate resistant, and susceptible plants were evident. Hence, disease ratings on Day 30 were used for all analyses. All plants of PI 270545 demonstrated resistance to moderate resistance with none showing absence of disease. The reaction of PI 269677 to *P. xanthii* was highly susceptible.

Table 1 shows the reactions of watermelon accessions to powdery mildew. For leaf rating, all plants of the resistant genotype were consistently rated between 1 and 3. None of the plants showed absence of disease. Of 20 plants, 25% scored 1, 55% scored 2, and 20% had a rating of 3, corresponding to 16 resistant and four moderately resistant plants. For stem resistance, 40% scored 0, 35% scored 1, 20% scored 2, and 5% scored 3, corresponding to 19 resistant and one moderately resistant plant. Thus, PI 270545 was between resistant and moderately resistant. All F_1 plants were susceptible (Table 1) and F_1 mean was greater than the midparent indicating dominance of the allele for susceptibility. Robinson et al. (1975) had earlier reported that high susceptibility to *P. xanthii* in PI 269677 was controlled by the single recessive gene, *pm*. The new and more virulent *P. xanthii* races on watermelon recently appear to exhibit different mode of inheritance.

For leaf rating in the F_2 progenies, there were 29 highly resistant, 40 moderately resistant, and 121 susceptible plants. A χ^2 goodness-of-fit test on all three-category expected segregation ratios gave probability values < 0.01 . However, the combination of moderately resistant with susceptible individuals fitted a 3:13 segregation ratio (Table 1) that was supported by a corresponding backcross segregation ratio of 1:3. The apparent model for this ratio was two genes with one recessive for high resistance and the other dominant for moderate resistance. The cumulative effect of the two genes in the F_2 produced some highly resistant and some moderately resistant plants. Similar inheritance was observed for stem rating, in which the F_2 gave a good fit for 3:13 model (χ^2_1 of 0.39, $P = 0.53$) supported by a backcross to the resistant parent of 1:3 (χ^2_1 of 4.75; $P = 0.03$). This provided further evidence that two independent genes, one recessive and one dominant,

Table 1. Reactions of watermelon plants inoculated with powdery mildew race 2W-U.S isolate.

Population	PI 269677 \times PI 270545			Probability of calculated χ^2		
	Total	0-1 (R)	2-4 (MR)	5-9 (S)	1:3	3:13
Leaf resistance						
P ₁ (PI 269677)	20	0	0	20	—	—
P ₂ (PI 270545)	20	5	15	0	—	—
F ₁	25	0	0	25	—	—
F ₂	190	29	161		<0.01	0.22
BC ₁ P ₁	54	0	54			
BC ₁ P ₂	59	20	39		0.01	0.11
Stem resistance						
P ₁ (PI 269677)	20	0	0	20	—	—
P ₂ (PI 270545)	20	15	5	0	—	—
F ₁	23	0	0	23	—	—
F ₂	190	39	151		0.15	0.53
BC ₁ P ₁	51	0	51			
BC ₁ P ₂	59	22	37		0.05	0.03

Table 2. Mean squares for powdery mildew race 2W-U.S. leaf and stem resistance of generation mean analysis for the cross PI 269677 × PI 270545.

Source	df	PI 269677 × PI 270545	
		Leaf	Stem
Set (S)	1	0.67 NS	0.59 NS
Repetition (E)	2	0.36	0.17
Generation (G)	5	24.86**	26.98**
G × S	5	1.96 NS	2.69 NS
Error	10	0.99	1.15

**Significant at $P < 0.01$; NS = nonsignificant.

control powdery mildew resistance in PI 270545. Occurrence of epistasis suggests that the dominant allele at one locus could mask the expression of alleles at the second, whereas the recessive allele at the second locus could mask the expression of the alleles at the first. The resistance genes found in PI 270545 were designated *pmr-1* for the recessive gene for high resistance and *Pmr-2* for the dominant gene for moderate resistance.

Analysis of variance (Table 2) revealed significant differences ($P < 0.01$) for both leaf and stem resistance among the generations, indicating the presence of genetic variability for both leaf and stem resistance. Variation was similar for both leaf and stem resistance. This is in contrast to the observation made on watermelon families of the PI 189225 resistant accession in which leaf resistance among the generations was higher than stem resistance (Tetteh et al., 2013). Comparison of means of P_1 and P_2 showed significant differences for both leaf and stem rating (Table 3). Disease development in F_1 and F_2 generations were not significantly different. Both had significantly lower ($P < 0.05$) disease development than the susceptible parent and were less resistant ($P < 0.05$) than the resistant parent (Table 3). These values were higher than the backcross to the resistant parent but lower than the backcross to the susceptible parent. Mean performance of the BC_1P_2 individuals showed more resistance to powdery mildew than the BC_1P_1 . There was a highly significant correlation ($r = 0.99$, $P < 0.0001$) between leaf and stem resistance.

Leaf resistance. In the generation means analysis, although the ABC scaling test (Table 4) was not significant, indicating that a simple additive-dominance model was adequate, the joint scaling test indicated a model that goes beyond additive-dominance for leaf resistance [$\chi^2_{(3)} = 564$; $P < 0.001$]. Therefore, the six-parameter model was required to explain the observed variation. The estimates of mean (m) as well as additive (d) and dominance (h) effects were significant, and the dominance effect was greater than the additive effect (Table 4). The large and negative dominance effect indicated that leaf resistance was predominantly controlled by nonadditive genetic effects with recessive alleles for leaf resistance in PI 270545, hence the lowest positive degree of dominance.

The large dominance effect suggests that selection of resistant plants should be done after self-pollination to identify the resistant recessive genotypes. Recurrent selection can

Table 3. Mean, range, and SE for leaf and stem powdery mildew race 2W-U.S. resistance ratings parents, F_1 , F_2 , and backcross generations of resistant × susceptible watermelons.

Generation	Family/trait					
	PI 269677 × PI 270545					
	Leaf rating			Stem rating		
	Mean	Range	SE	Mean	Range	SE
P_1	8.85 d	8–9	0.82	8.15 d	6–9	0.23
P_2	2.00 a	1–5	0.15	1.00 a	1–5	0.14
F_1	5.83 c	1–9	0.43	5.07 c	1–9	0.46
F_2	6.15 c	0–9	0.19	5.30 c	0–9	0.21
BC_1P_1	7.69 d	5–9	0.26	7.01 d	1–9	0.32
BC_1P_2	4.25 b	0–9	0.30	3.54 b	0–9	0.28
LSD (5%)	1.40			1.51		

Values in columns having common alphabets are not significantly different at the 0.05 P level. LSD = least significant difference.

also be useful, because it increases the frequency of resistant alleles for leaf resistance in the population. Failure to detect nonallelic interaction in leaf rating, as inferred from nonsignificance of the epistatic effects (Table 4), may arise from an unequal dispersion of genes with similar effects between the two parents. Judging from the mean value of F_2 , it is likely that genes for powdery mildew susceptibility are not only in the susceptible parent, but also present in the moderately resistant parent. The negative dominance effect in leaf rating indicates that, in PI 270545, the high resistance gene is recessive, whereas the moderate resistance gene is dominant. Significant additive (0.90) and dominance (−4.34) effects explained 7% and 67% of the variation in leaf rating, respectively (Table 4). The remaining variation may be contributed by undetected nonallelic effects. This agrees with the high narrow-sense heritability of 71%, indicating that improvement in leaf resistance can be achieved through selection. Application of QTL mapping analysis may contribute to the detection of epistatic effects in this population. Zalapa et al. (2007) reported detection of digenic epistatic effects in melon architectural traits using QTL analysis.

Stem resistance. In contrast to leaf resistance, nonsignificance of the ABC components was supported by the joint scaling test. The additive-dominance model was adequate in explaining the variation in stem rating [$\chi^2_{(3)} = 1.98$; $P = 0.6$]. Both additive (d) and dominance (h) effects were significant, but the additive effect was negative and considerably larger than the dominance effect, indicating that stem resistance was predominantly controlled by additive effects. Because larger additive effects were important for stem resistance, breeding progress would be faster than for leaf resistance.

The i , j , and l effects were not significant, demonstrating absence of a nonallelic interaction. The contribution of additive and dominance effects was 58% and 15%, respectively. A high heritability (79%) indicates that selection for stem resistance in this population would be effective.

Conclusions

Powdery mildew resistance in watermelon PI 270545 was controlled by a recessive gene for high resistance and a dominant

Table 4. A, B, and C scaling test and estimates of components in a generation means analysis for leaf and stem resistance to powdery mildew in PI 270545 × PI 269677.

Scale	A, B, C scaling test	
	Leaf	Stem
A	0.71 ± 0.62 NS	0.80 ± 0.80 NS
B	0.87 ± 0.88 NS	0.82 ± 0.81 NS
C	2.27 ± 1.23 NS	1.73 ± 1.34 NS
Joint scaling test and genetic components		
m	8.89 ± 0.06*	4.73 ± 0.15*
d	0.46 ± 0.08*	−3.48 ± 0.14*
h	−4.34 ± 0.24*	0.90 ± 0.36*
i	−0.69 ± 1.11 NS	−0.10 ± 1.23 NS
j	−0.08 ± 0.44 NS	−0.01 ± 0.45 NS
l	−0.90 ± 2.02 NS	−1.52 ± 2.19 NS
h^2	0.71 ± 0.16	0.79 ± 0.09

A and B provide evidence of i , j , and l interactions; C = indicates l type interaction; NS = nonsignificant.

*Significant estimates based on t test calculated from the SES.

gene for moderate resistance. Based on generation means analysis, the dominance genetic effect was larger for leaf resistance, whereas the additive genetic effect was larger for stem resistance. The large narrow-sense heritability in PI 269677 × PI 270545 combined with major additive genetic effects suggested that selecting for powdery mildew stem resistance in the segregating population of this cross could be done efficiently using single-plant selection, whereas for leaf resistance, selection in self-pollinated progeny rows would be necessary.

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