Inheritance of Resistance to Pathotypes QCC and MCC of *Puccinia graminis* f. sp. *tritici* in Barley Line Q21861 and Temperature Effects on the Expression of Resistance

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ABSTRACT

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Barley line Q21861 is one of several accessions that possess resistance to pathotypes QCC and MCC of *Puccinia graminis* f. sp. *tritici*. Crosses were made between Q21861 and several barley cultivars to study the inheritance of resistance to pathotypes QCC and MCC. Progeny evaluations indicated that resistance to pathotype QCC in Q21861 was conferred by a recessive gene that conditioned low infection types at low incubation temperatures (18–20 C). This gene was ineffective against pathotype QCC at incubation temperatures greater than 27 C. Resistance to pathotype MCC in Q21861 was controlled by two genes, one dominant and one recessive, that segregated independently. The dominant gene is allelic to *Rpg*1, and the recessive gene identified is the same one conferring resistance to pathotype QCC. This recessive gene is not allelic with *Rpg*2 based on an allelism test. It is unlikely allelic with *Rpg*3 based on reaction to pathotype QCC at the seedling stage, a recessive inheritance pattern, and temperature sensitivity. The locus and allele symbols *Rpg*4 and *rpg*4d, respectively, are suggested for the recessive gene in Q21861.

A pathotype (designated Pgt-QCC) of the wheat stem rust pathogen (*Puccinia graminis* Pers.:Pers. f. sp. *tritici* Eriks. & E. Henn.) virulent for the *Rpg*1 gene in barley (*Hordeum vulgare* L.) was recently detected in the North American stem rust population (3,6). The establishment of this pathotype threatens barley production because *Rpg*1 is the only major stem rust resistance gene that has been bred into commercial barley cultivars of the northern Great Plains (9). Several sources of resistance to pathotype QCC have been identified in barley (2). Q21861, a line originally derived from CIMMYT (International Maize and Wheat Improvement Center, Mexico City, Mexico) and obtained from Australia, possesses one of the highest levels of resistance to pathotype QCC at both the seedling and adult plant stages of development (2). This line also possesses resistance to Pgt-MCC, a pathotype that has proven useful for detecting *Rpg*1 at the seedling stage (10). This study was conducted to elucidate the genetic basis of resistance to pathotypes QCC and MCC of *P. g. tritici* in Q21861. Information obtained from this study may facilitate the efficient transfer of resistance from Q21861 into advanced breeding lines.

MATERIALS AND METHODS

Crosses were made between line Q21861 and several cultivars. Line Q21861 was used as the female parent in a cross with Hietpas 5 (CI 7124) and as the male parent in crosses with Morex (CI 15773), Robust (PI 476976), and Steptoe (CI 15229). Hietpas 5 (source of resistance gene *Rpg*2) is resistant to pathotype QCC at the adult plant stage and susceptible at the seedling stage (2). Morex and Robust possess *Rpg*1 and are resistant to pathotype MCC of *P. g. tritici* at both the seedling and adult plant stages. In contrast, Steptoe is susceptible to pathotype MCC at both growth stages. Morex, Robust, and Steptoe are susceptible to pathotype QCC at both the seedling and adult plant stages of growth. F_1 plants from crosses were grown in a greenhouse to produce seeds for the F_2 generation. Each F_2 population was derived from a single F_1 plant. The offspring of a single F_2 plant was designated as an $F_{2:3}$ (an F_2 family in the F_3 generation). F_1, F_2, and $F_{2:3}$ plants from Morex × Q21861 and Steptoe × Q21861 crosses were evaluated for reaction to pathotypes MCC and QCC at the seedling stage in the greenhouse. A reciprocal cross between Morex and Q21861 also was made and evaluated for reaction to pathotype MCC. F_1 and F_2 plants of Q21861 × Hietpas 5, Robust × Q21861, and Steptoe × Q21861 crosses were evaluated for reaction to pathotype QCC at the adult plant stage in the field.

In the seedling tests, parental lines, F_1's, and F_2 populations were grown in plastic cones (one plant per cone), and $F_{2:3}$ families were grown in clay pots (15–40 plants per family per pot) containing a 3:1 mixture of peat moss and perlite. Plants were grown in a greenhouse at a mean temperature of 23 C with 12 h of supplemental lighting (230–270 μE m^{-2} s^{-1} supplied by 1,000-W sodium vapor bulbs) prior to inoculation. Seedlings were inoculated with pathotype QCC (culture QCC-2) or MCC (culture A-5) 7–8 days after planting, when the primary leaves were fully expanded. Urediniospores were suspended in a light-weight mineral oil at a concentration of 6.0 mg of spores per milliliter of oil and applied on seedlings at an approximate rate of 2 μl of oil per plant. After inoculation, plants were placed in a chamber in which the humidity was maintained near saturation for 16 h at 21 C in the dark. Then, the plants were exposed to light (160–230 μE m^{-2} s^{-1}) and allowed to dry for 4 h to complete

the infection period. After the infection period, plants were placed in a greenhouse or growth chamber for incubation.

Most F_2 populations were tested at a mean incubation temperature of 22 C with fluctuations of three degrees (22 ± 3 C). $F_{2:3}$ families from the Steptoe × Q21861 cross were tested at a low-temperature (21 ± 2 C) and high-temperature (28 ± 2 C) regime. $F_{2:3}$ families of the Morex × Q21861 cross were tested at the low-temperature regime. Evaluations of the parental materials were always conducted at the time of progeny evaluations. Seedling infection types were determined on primary leaves after 12–13 days of incubation in the greenhouse or growth chambers. In classifying seedling infection types, plants exhibiting infection types of 2^{3-} or higher were considered susceptible, and those exhibiting infection types 0, 0;, 1, 2, or combinations thereof were considered resistant according to the system of Stakman et al (8), as modified for barley by Steffenson et al (10). Replicated F_2 populations were evaluated for crosses with Morex, Robust, and Steptoe.

F_2 populations of crosses of Q21861 with Hietpas 5, Robust, and Steptoe were evaluated for their reaction to pathotype QCC in a stem rust nursery at Fargo, ND, in 1992. F_2's were space-planted with a four-row cone planter, with F_2 plants in the middle two rows and susceptible spreader plants in the outer two rows.

TABLE 1. Seedling infection types of barley line Q21861, and cultivars Hietpas 5, Morex, Robust, and Steptoe to pathotypes Pgt-QCC and -MCC of *Puccinia graminis* f. sp. *tritici* at two incubation temperatures (21 and 28 C) in the greenhouse and adult plant infection respones (IRs) and terminal disease severity (TDS) to pathotype QCC in the field

	Seedling infection type[a]				Adult plant reaction to pathotype QCC	
	Pgt-QCC		Pgt-MCC			
Genotype	21 C	28 C	21 C	28 C	IR[b]	TDS[c]
Q21861	0;	3^{3+}	0;1	0;	R–MR	1.0
Hietpas 5	2^{3-}	3^{3-}	3^{3-}	3^{3-}	MS–S	2.0
Morex	$3^{-}2$	3^{3+}	0;1	0;1	S	28.5
Robust	2^{3-}	$3^{-}3$	0;1	0;1	S	33.3
Steptoe	3^{3+}	3^{3+}	3^{3+}	3^{3+}	S	35.0

[a] Infection types are based on the 0–4 scale of Stakman et al (8) as modified for barley by Steffenson et al (10): types 0, 0;, 1, and 2 are considered indicative of host resistance, and types 2^{3-}, 3, and 4 are indicative of susceptibility.

[b] IRs are based on the rating scale of Stubbs et al (11): R = resistant, MR = moderately resistant, MS = moderately susceptible, and S = susceptible.

[c] The mean TDSs are given in percentages.

Parents and F_1's were planted by hand. Cultivar Robust was used as a spreader row for pathotype QCC in the nursery and was planted 14 days prior to the seeding date of F_2 plants to increase the inoculum level. Natural stem rust infections on Robust spreader plants were tentatively identified as pathotype QCC based on the diagnostic low infection phenotype expressed on the wheat cultivar McNair 701 (2). These tentative identifications were confirmed on the wheat stem rust differentials of Roelfs and Martens (7). To augment the level of rust infection, urediniospores were collected from Robust spreader plants in the nursery and suspended in a light-weight mineral oil. F_2 plants were inoculated with the urediniospore suspension using a sprayer when the majority of F_2 plants were between the late-boot and early-heading stages of development. Infection responses of F_2 plants were assessed using the scale of Stubbs et al (11) at the stages from soft to hard dough. The mean terminal disease severity on parents was based on four observations, and each observation consisted of an average disease-severity estimate from 20 to 30 tillers in a 1.8-m row.

The chi-square method was used to test the hypotheses of independent segregation for various genetic ratios in the F_2 and $F_{2:3}$ generations. Variance homogeneity among replicated F_2 populations of the same cross was tested using chi-square statistics provided by the FREQ procedure in SAS (SAS User's Guide: Statistics, V5, SAS Institute, Cary, NC). The observed frequencies of phenotypic classes were cross-tabulated to obtain a two-way table ($m \times n$), in which m = number of phenotypic classes and n = number of replicated F_2 populations. Data from replicated F_2 populations were pooled when the chi-square statistic was not significant.

RESULTS

Interaction of pathotype, host genotype, and incubation temperature. Table 1 summarizes the reactions of parental genotypes to pathotypes QCC and MCC. Seedlings of Q21861 exhibited a low infection type (0;) to pathotype QCC when incubated at 21 C, and high infection types (3 to 3^+) when incubated at 28 C. The reaction of Q21861 seedlings to pathotype MCC was not affected by incubation temperature; low infection types (0; to 1) were observed at both low and high incubation temperatures. Morex exhibited low infection types (0; to 1) to pathotype MCC and high infection types (3^-2 to 3^+) to pathotype QCC at both incubation temperatures. Robust exhibited reactions similar to Morex, except for the slightly lower infection types at low incubation temperature. Hietpas 5 and Steptoe exhibited high infection

TABLE 2. Infection type (IT) of F_1 plants and segregation in F_2 populations and $F_{2:3}$ families to pathotype Pgt-QCC of *Puccinia graminis* f. sp. *tritici* at the seedling and adult plant stages

Cross	Mean incubation temperature (C)	F_1 IT[a]	Number of F_2 plants		Expected ratio	χ^2	Probability ($>\chi^2$)
			Resistant	Susceptible			
Morex × Q21861[b]	22	3^-2	185	512	1:3	0.88	0.347
Steptoe × Q21861[b]	22	3^-3	144	502	1:3	2.53	0.112
Steptoe × Q21861	28	3^3-	0	480	...[c]		
			Number of $F_{2:3}$ families				
			Homozygous resistant	Segregating	Homozygous susceptible		
Morex × Q21861	21	17	29	25	1:2:1	4.18	0.124
Steptoe × Q21861	21	18	36	17	1:2:1	0.04	0.980
Steptoe × Q21861	28	0	0	41	...		
			Number of F_2 plants[d]				
			Resistant	Susceptible			
Robust × Q21861		113	234		1:3	10.59	0.001
Steptoe × Q21861		139	315		1:3	7.64	0.006
Q21861 × Hietpas 5		381	42		13:3	21.60	<0.001

[a] Table 1 gives IT classifications.

[b] Pooled data from two F_2 populations after variance homogeneity test.

[c] No segregation.

[d] From field experiments.

types (23^- to 3^+) to both pathotypes at low and high incubation temperatures.

At the adult plant stage in the field, Q21861 exhibited low infection responses (R [resistant] to MR [moderately resistant]) and low disease severity (1.0%) to pathotype QCC (Table 1). This adult plant reaction corresponded closely with the seedling reaction at the low incubation temperature. Hietpas 5 exhibited high infection types at the seedling stage and low disease severity at the adult plant stage. High infection responses and disease severity were observed on Morex, Robust, and Steptoe in the field. This response was indicative of their susceptibility to pathotype QCC at the adult plant stage and agreed with their seedling reaction.

Inheritance of resistance to pathotype QCC. Seedling infection types of F_1 plants and segregation in F_2 populations and $F_{2:3}$ families to pathotype QCC are given in Table 2. Crosses of Q21861 with Robust and Hietpas 5 were not tested at the seedling stage. F_1 plants exhibited infection types similar to Morex and Steptoe, suggesting that resistance to pathotype QCC is recessive in line Q21861. At low incubation temperature, segregation of F_2 plants in the two crosses Morex × Q21861 and Steptoe × Q21861 fit a 1:3 ratio of resistant/susceptible, indicating that a single recessive gene confers resistance at the seedling stage. The results of evaluations of $F_{2:3}$ families at low incubation temperature were in agreement with the F_2 data. Segregation of $F_{2:3}$ families fit an expected ratio of 1:2:1 for homozygous resistant/segregating/homozygous susceptible. One F_2 population and 41 $F_{2:3}$ families from the Steptoe × Q21861 cross were evaluated at high incubation temperature (28 C). No segregation was observed in these experiments (Table 2). All plants exhibited susceptible reaction types, indicating that the resistance gene to pathotype QCC in Q21861 is ineffective at high incubation temperature.

Segregation for resistance and susceptibility at the adult plant stage in the field in crosses Robust × Q21861 and Steptoe × Q21861 deviated from the one-recessive-gene model because the number of resistant plants was larger than expected. Segregation for susceptibility occurred in the Q21861 × Hietpas 5 cross, indicating that the recessive gene locus in Q21861 is different from the *Rpg*2 locus in Hietpas 5. The segregation ratio in the Q21861 × Hietpas 5 cross, however, did not fit the expected ratio of independent segregation of one dominant and one recessive gene, due to the excessive number of resistant plants.

Inheritance of resistance to pathotype MCC. Segregation in F_2 populations of the cross Steptoe × Q21861 at low incubation temperature suggested that possibly two genes are involved in conferring resistance to pathotype MCC in Q21861, and at least one of the two genes is dominant (Table 3). At low incubation temperature (21 C), the $F_{2:3}$ segregation fit a 7:8:1 ratio for homozygous resistant/segregating/homozygous susceptible families. This segregation ratio suggested that two independently segregating genes, one dominant and the other recessive, confer resistance to pathotype MCC in Q21861. At the high incubation temperature (28 C), the recessive gene for resistance to pathotype MCC was apparently rendered ineffective, because the F_2 and $F_{2:3}$ segregation fit a ratio of a single dominant gene. Ten of the 120 $F_{2:3}$ families were homozygous resistant at low incubation temperature but homozygous susceptible at high incubation temperature. These families presumably possess only the recessive resistance gene that is ineffective at the high incubation temperature. Results from allelism tests with F_2 populations of crosses Morex × Q21861, Q21861 × Morex, and Robust × Q21861 suggested that Q21861 possesses the *Rpg*1 allele (Table 3); thus, the dominant gene detected in the Steptoe × Q21861 cross was *Rpg*1.

Relationship between genes conferring resistance to pathotypes QCC and MCC. Results from evaluations of the same $F_{2:3}$ families to pathotypes QCC and MCC at low incubation temperature (21 C) are given in Table 4. All $F_{2:3}$ families homozygous resistant to pathotype QCC also were homozygous resistant to pathotype MCC. This indicates that the same recessive gene conferred resistance to both QCC and MCC. Therefore, two genes, *Rpg*1 and a recessive gene, segregated in the test to pathotype MCC in the Steptoe × Q21861 cross. The expected frequencies of the nine phenotypic classes in Table 4 were derived based on independent segregation of these two genes. The observed frequencies of phenotypic classes fit the expected ratio for the segregation of two genes to pathotypes QCC and MCC. The absence of three classes in the $F_{2:3}$ families, $HR_{QCC}SE_{MCC}$ (homozygous resistant to QCC and segregating to MCC), $HR_{QCC}HS_{MCC}$ (homozygous resistant to QCC and homozygous susceptible to MCC) and $SE_{QCC}HS_{MCC}$ (segregating to QCC and homozygous susceptible to MCC), confirmed that the recessive gene conferred resistance to both pathotypes QCC and MCC.

DISCUSSION

The data from this study suggest that the interaction between the host genotypes and rust pathotypes in the barley-stem rust pathosystem is mediated by environment, specifically incubation temperature. The effects of incubation temperature on the expression of resistance to pathotype QCC were obvious in Q21861, but not in the other genotype-pathotype combinations (Table 1). Evaluations of the same $F_{2:3}$ families at low and high incubation temperatures indicated that the genetic basis for this interaction is due to the temperature sensitivity of the resistance gene in Q21861 (Table 2). Much genetic information on the relationship between genes for resistance to pathotypes QCC and MCC in line Q21861 was obtained by evaluating the same $F_{2:3}$ families with the two pathotypes (Table 3). This method enabled us to characterize the reaction of the recessive gene in Q21861 to both pathotypes QCC and MCC and its relationship with *Rpg*1. Evaluation of a doubled haploid population (Q21861 × SM89010) to

TABLE 3. Infection type (ITs) of F_1 plants and segregation in F_2 populations and $F_{2:3}$ families to pathotype Pgt-MCC of *Puccinia graminis* f. sp. *tritici* at the seedling stage

Cross	Mean incubation temperature (C)	F_1 IT[a]	Number of F_2 plants		Expected ratio	χ^2	Probability ($>\chi^2$)
			Resistant	Susceptible			
Steptoe × Q21861[b]	22	0;	708	86	13:3	32.68	<0.001
Steptoe × Q21861	28	0;1	381	110	3:1	1.77	0.184
Morex × Q21861	22	0;1	418	0	...[c]		
Q21861 × Morex	22	0;1	228	0	...		
Robust × Q21861[b]	25	0;	844	0	...		
			Number of $F_{2:3}$ families				
			Homozygous resistant	Segregating	Homozygous susceptible		
Steptoe × Q21861	21		58	54	8	7:8:1	1.21	0.546
Steptoe × Q21861	28		29	60	31	1:2:1	0.07	0.966

[a] Table 1 gives IT classifications.
[b] Pooled data from two F_2 populations after variance homogeneity test.
[c] No segregation.

TABLE 4. Relationship between genes for resistance to pathotypes Pgt-QCC and -MCC of *Puccinia graminis* f. sp. *tritici* based on seedling reactions of the same $F_{2:3}$ families from a Steptoe × Q21861 cross at low incubation temperature (21 C)

$F_{2:3}$ reaction[a]	Observed frequency	Expected frequency
$HR_{QCC}HR_{MCC}$	14	17.5
$HR_{QCC}SE_{MCC}$	0	0
$HR_{QCC}HS_{MCC}$	0	0
$SE_{QCC}HR_{MCC}$	13	8.8
$SE_{QCC}SE_{MCC}$	20	26.3
$SE_{QCC}HS_{MCC}$	0	0
$HS_{QCC}HR_{MCC}$	7	4.4
$HS_{QCC}SE_{MCC}$	10	8.8
$HS_{QCC}HS_{MCC}$	6	4.4
Total	70	

$\chi^2_{(8)} = 6.61$, $P(>\chi^2) = 0.579$ for the nine class segregations to pathotypes QCC and MCC

$\chi^2_{1:2:1} = 2.54$, $P(>\chi^2) = 0.281$ for segregation to pathotype QCC: $\Sigma(HR_{QCC}):\Sigma(SE_{QCC}):\Sigma(HS_{QCC})$[b]

$\chi^2_{7:8:1} = 1.69$, $P(>\chi^2) = 0.430$ for segregation to pathotype MCC: $\Sigma(HR_{MCC}):\Sigma(SE_{MCC}):\Sigma(HS_{MCC})$[b]

[a] $F_{2:3}$ reactions were HR = homozygous resistant, SE = segregating, and HS = homozygous susceptible. The subscripts denote the corresponding pathotypes tested.

[b] The χ^2 values were calculated based on a ratio of 1:2:1 for segregation to QCC, and a ratio of 7:8:1 to MCC for the sum (Σ) of frequencies of classes HR, SE, and HS.

pathotypes QCC and MCC at low and high temperatures confirmed the genetic relationship between the two genes for stem rust resistance in Q21861 (B. J. Steffenson and Y. Jin, *unpublished data*).

From the analysis of segregation for infection response to pathotype QCC in field experiments, the number of resistant F_2 plants was more than expected for the one-recessive-gene model in the Robust × Q21861 and Steptoe × Q21861 crosses. The same was true for the model of one dominant and one recessive gene in the Q21861 × Hietpas 5 cross. A likely explanation for the above deviations is that a number of plants escaped infection in the field. The growth stage of barley is a critical factor in the expression of resistance (i.e., infection responses) at the adult plant stage (A. P. Roelfs, *personal communication*; Y. Jin and B. J. Steffenson, *unpublished data*). Q21861 matures early and exhibits a strong photoperiod response. Segregation for earliness occurred in these crosses; therefore, segregants in growth stages either too early or too late at the time of inoculation might have escaped infection and were rated as resistant. This hypothesis could not be tested because $F_{2:3}$ evaluations were not made from the field materials.

Three genes for resistance to *P. g. tritici* have been reported in barley: *Rpg*1 derived from Chevron (CI 1111) and Peatland (CI 5267) (5), *Rpg*2 derived from Hietpas 5 (CI 7124) (4), and *Rpg*3 derived from PI 382313 (1). Evaluations of F_2 and $F_{2:3}$ plants at the seedling stage in this study indicate that the recessive gene in Q21861 segregates independently from *Rpg*1. Allelism tests of the recessive gene in Q21861 with *Rpg*2 and *Rpg*3 at the seedling stage have not been conducted because the specific combinations of pathotypes and incubation temperatures that would allow the detection of the *Rpg*2 and *Rpg*3 genes at the seedling stage have not been characterized. Hietpas 5 possesses resistance to pathotype QCC at the adult plant stage (Table 1), and the gene conferring resistance is presumably *Rpg*2. Segregation at the adult plant stage in the Q21861 × Hietpas 5 cross indicates that the recessive gene in Q21861 is different from *Rpg*2. At the seedling stage, line PI 382313 exhibited infection types 2^3⁻ to pathotype QCC (Y. Jin and B. J. Steffenson, *unpublished data*) distinctly higher than that of Q21861 at low incubation temperature. Because the gene in Q21861 is recessive and temperature sensitive, it is unlikely to be allelic with *Rpg*3.

The locus *Rpg*4 and the resistant allele *rpg*4d are proposed for the recessive gene in Q21861. In addition to *rpg*4 in Q21861, there is some evidence that another gene may be involved in conferring the low infection types to pathotype QCC. This gene may act as a modifier of *rpg*4. As mentioned previously, Q21861 exhibited a very low infection type of 0; to pathotype QCC when incubated at low temperature. In two F_2 populations classified on the basis of the Q21861 infection type (0;) versus all higher infection types (1 or higher), 14 of 260 F_2 plants in the Morex × Q21861 cross ($\chi^2 = 0.33$, $P = 0.564$) and 15 of 283 F_2 plants in the Steptoe × Q21861 cross ($\chi^2 = 0.44$, $P = 0.509$) exhibited the Q21861 infection type—a good fit of a 1:15 ratio in both populations. A similar pattern also was observed in the segregation of $F_{2:3}$ families of these two crosses. This indicates that a gene with a recessive inheritance pattern for reaction to pathotype QCC is present in Q21861 in addition to *rpg*4. This gene modified *rpg*4, resulting in the Q21861 infection type of 0;. The effect of this gene was not obvious when it was present without *rpg*4.

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