Resistance of Durum Wheats Used as Differential Hosts for Stem Rust

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ABSTRACT

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Durum wheat (*Triticum turgidum*) cultivars (Mindum, Spelmar, Arnautka, Kubanka, Acme, Golden Ball, and Entrelargo de Montijo) used as standard or supplemental differentials for wheat stem rust were studied for resistance to selected pathogen cultures in the seedling stage. The presence of *Sr*9d in Mindum, Spelmar, and Arnautka was verified by using an avirulent race, Pgt-MCC, to inoculate F_1, F_2, and F_3 plants from crosses of these cultivars with the susceptible cultivar Glossy Hugenot. Mindum and Spelmar had an additional incompletely recessive gene for resistance to the race Pgt-QTH, and Arnautka had a dominant gene for resistance to Pgt-GMC. Tests of F_1, F_2, and F_3 plants from crosses of Kubanka and Acme with Glossy Hugenot indicated that, in addition to *Sr*9g (verified by using race Pgt-QBB), both cultivars have a single dominant resistance gene to Pgt-QTH. The F_1 and F_2 seedlings of Glossy Hugenot/Golden Ball indicated that the same or an allelic incompletely dominant gene(s) conditioned resistance of Golden Ball to races Pgt-TPM and Pgt-QBB. However, the low infection type expressed by infection with these two cultures differed. Entrelargo de Montijo had two recessive genes for resistance to Pgt-QTH. Continuous variation to Pgt-MCC in low infection type was found in the F_2. However, about one of 64 of the F_2 plants gave a reaction similar to that of the resistant parent indicating three recessive resistance genes. Resistance to these two races may be conditioned by five genes.

Stem rust (caused by *Puccinia graminis* Pers.:Pers.) is one of the most important diseases worldwide. Stem rust importance is related to its wide distribution, the large numbers of urediniospores produced, the potential for long-distance dispersal of the spores, and the ability of the pathogen to mutate for virulence to previously resistant cultivars, as well as the severe damage caused.

Variations in virulence of the pathogen have been studied for many years. Physiological races of *P. graminis* f. sp. *tritici* Eriks. & E. Henn. are identified by infection types produced on a series of 12 differential cultivars (13), including five durum wheat (*Triticum turgidum* L.) cultivars. It has been postulated that Arnautka, Mindum, and Spelmar carry *Sr*9d and Kubanka and Acme carry *Sr*9g. However, many of the races reported by Stakman et al (13) indicated the presence of additional resistance genes in these cultivars.

This study was conducted with selected cultures to determine the number of stem rust resistance genes in the durum wheat cultivars of the standard and supplemental stem rust differentials and of the supplemental differentials.

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MATERIALS AND METHODS

Resistance to wheat stem rust was studied in the F_1 and segregating generations from crosses between the resistant cultivars Mindum (CI 5296), Spelmar (CI 6236), Arnautka (CI 1493), Kubanka (CI 2094), Acme (CI 5284), Golden Ball (CI 11477), and Entrelargo de Montijo (PI 192847) and the susceptible cultivar Glossy Hugenot. Glossy Hugenot was used as the female parent in all cases. When the susceptible parent is the female, the self-fertilized seed will result in susceptible progeny whereas crossed seed will be resistant, providing an easy check for selfed seed. However, when resistance is recessive, all F_1 plants are susceptible (selfed and crossed seed). Seed of the host lines and rust cultures were from the Cereal Rust Laboratory, St. Paul, MN. The race nomenclature used was developed by Roelfs and Martens (9). Glossy Hugenot was susceptible to all rust cultures used in this study. The races Pgt-MCC, Pgt-QBB, and Pgt-TPM were used to verify the postulated genotypes—*Sr*9d in Mindum, Spelmar, and Arnautka; *Sr*9g in Kubanka and Acme; and *Sr*dp-2 in Golden Ball. Races Pgt-QTH, Pgt-GMC, Pgt-QBB, and Pgt-MCC were used to determine if additional genes were present in the resistant parent. The races used were Pgt-QTH for Mindum, Spelmar, Kubanka, Acme, and Entrelargo de Montijo; Pgt-GMC for Arnautka; Pgt-QBB for Golden Ball; and Pgt-MCC for Entrelargo de Montijo. Cultures were selected based on previous testing (10) (A. P. Roelfs and D. V. McVey, *unpublished data*).

Sixteen to 20 seeds of the F_1, F_2, and F_3 generations were planted in 6-cm-diameter pots containing vermiculite and placed in the greenhouse (23 ± 3 C). Parents were included as checks in all tests. When the first leaf was fully developed, about 7 days after planting, each line was inoculated with one race. Urediniospores, increased earlier and stored in an ultra-low temperature freezer, were suspended in a light, odorless, nonphytotoxic oil (12) (2–3 mg of spores in 0.5–0.6 ml of oil for six pots) and sprayed from approximately 50 cm to plants on a rotating turntable. Seedlings were then placed in a dew chamber at 18 C for 18–20 hr, the last 3 hr under VHO cool-white fluorescent lights (100 $\mu E \cdot^{-2} \cdot s^{-1}$). During the light period, the temperature rose gradually to 30 C and dew slowly evaporated. The plants were then transferred to either to the greenhouse (18 ± 2 C) or, in summer, to a growth chamber (16–18 C) supplemented with fluorescent light (200 $\mu E \cdot m^{-2} \cdot s^{-1}$). Water-soluble fertilizer (23-19-17, N-P-K) was added after each inoculation. Infection types, based on lesion characteristics, were recorded 13–15 days after inoculation (8). Infection types used are given in Table 1. After observing the host reaction to the first race, plants were labeled, the infected leaves were removed by clipping, and the seedlings were placed in the dew chamber for 3 hr to germinate loose urediniospores. The plants were then transferred to the greenhouse or growth chamber to kill germlings before infection occurred. The next day, the same regime was followed to inoculate the secondary leaf with a second race.

To obtain seed for the next generation, seedlings were transplanted into 15-cm-diameter pots containing sterilized soil. The plants were fertilized and watered as needed through maturity.

RESULTS

Glossy Hugenot/Mindum. Mindum was characterized by X– and 21C infection types with Pgt-QTH and Pgt-MCC, respectively, whereas Glossy Hugenot was characterized by susceptible infection type 4. Infection types on F_1 plants from the crosses of Glossy Hugenot and Mindum were 3+4 and 2C with races Pgt-QTH and Pgt-MCC, respectively (Table 2). Although the pustules with Pgt-QTH were large, they were smaller than those on the susceptible parent. The F_1 data suggested that the resistance of

Mindum to Pgt-QTH was recessive, whereas resistance to Pgt-MCC was dominant. However, the F_1 plants were neither as susceptible as Glossy Hugenot to Pgt-QTH, nor as resistant as Mindum to Pgt-MCC, indicating that neither the recessiveness nor the dominance was complete.

In the F_2, the 108 plants tested with Pgt-QTH segregated into 44 resistant (infection type X) and 64 susceptible (infection type 4) (Table 2). The 37 of the F_2 plants that were resistant to Pgt-QTH were tested with Pgt-MCC and gave 1:2:1 resistant/intermediate/susceptible ratio ($P = 0.05$) for infection types 21C, 2C, and 4, respectively, indicating the resistance was attributable to one gene that was independent of the gene(s) detected with Pgt-QTH.

Seeds of the 10 F_2 plants that were susceptible to Pgt-MCC were planted to obtain F_3 families to be used to isolate single-gene lines for resistance to Pgt-QTH. The number of seeds obtained from the F_2 plants was inadequate for critical testing; however, some families segregated, indicating that some of the F_2 plants classified as resistant to Pgt-QTH had been misclassified. Because the actual number of resistant plants must have been less than 44, resistance to Pgt-QTH was probably attributable to a single resistance gene.

Glossy Hugenot/Spelmar. Spelmar was characterized by infection type 21C for race Pgt-MCC, whereas Glossy Hugenot was susceptible (Table 2). The infection types on the F_1 plants were 4 for Pgt-QTH and 22+C for Pgt-MCC (Table 2), indicating that the resistance of Spelmar is recessive to Pgt-QTH and dominant to Pgt-MCC. In the F_2, 48 of 184 plants were resistant (infection type X) and 136 were susceptible to Pgt-QTH. This fits a 1:3 resistant/susceptible ratio ($P = 0.50$–0.80) for segregation of a single recessive gene. Forty-two F_2 plants resistant to Pgt-QTH were also tested with Pgt-MCC. The segregation fit a 3:1 resistant/susceptible ratio ($P = 0.80$–0.95). Thus, a dominant gene independent of the Pgt-QTH resistance gene conditions resistance of Spelmar to race Pgt-MCC.

F_2 plants resistant to Pgt-QTH and susceptible to Pgt-MCC were planted to check for homozygosity. All 140 plants from the six families were resistant to Pgt-QTH and susceptible to Pgt-MCC. Seeds from six F_3 families derived from two homozygous resistant plants were saved as single-gene (with Pgt-QTH) lines.

Glossy Hugenot/Entrelargo de Montijo. The F_1 from the crosses Glossy Hugenot and Entrelargo de Montijo, the F_2 generation, and parents were tested with the culture Pgt-QTH (Table 2). Entrelargo de Montijo was resistant (infection type X−) and Glossy Hugenot was susceptible. F_1 plants were susceptible (infection type 4), indicating that the resistance of Entrelargo de Montijo to race Pgt-QTH is recessive.

In the F_2, 93 of 129 plants were susceptible, 25 had infection type XX+, and 11 had an infection type 12−X− (Table 2). The data fit a 12:3:1 susceptible/moderately resistant/resistant ratio ($P = 0.50$–0.80), indicating that resistance of Entrelargo de Montijo was controlled by

Table 1. Description of infection types used[a]

Host response	Class[b]	Infection type[c]	Severity	Symptoms
Immune	R	0	Low	No uredinia or other macroscopic sign of infection
Nearly immune	R	;	Low	No uredinia but hypersensitive necrotic or chlorotic flecks of varying size present
Very resistant	R	1	Low	Small uredinia surrounded by necrosis
Moderately resistant	R	2	Low	Small to medium uredinia often surrounded by chlorosis or necrosis; green island may be surrounded by chlorotic or necrotic border
Heterogeneous	M	X	Low	Random distribution of variable-sized uredinia on single leaf with a pure culture
Heterogeneous	M	Y	Low	Ordered distribution of variable-sized uredinia, with larger uredinia at leaf tip
Heterogeneous	M	Z	Low	Ordered distribution of variable-sized uredinia, with larger uredinia at leaf base
Moderately susceptible	S	3	Low	Medium-sized uredinia that may be associated with chlorosis or rarely necrosis
Susceptible	S	4	High	Large uredinia without chlorosis or necrosis

[a] After Roelfs (8).
[b] R = Resistant, M = mesothetic, S = susceptible.
[c] The infection types are often refined by modifying characters as follows: uredinia at the lower size limit for the infection type (=); uredinia somewhat smaller than normal for the infection type (−); uredinia somewhat larger than normal for the infection type (+); uredinia at the upper size limit for the infection type (++); more chlorosis than normal for the infection type (C); and more necrosis than normal for the infection type (N). Discrete infection types on a single leaf when infected with a single biotype are separated by a comma (e.g., 4,; or 2+, 2+ or 1,3C). A range of variation between infection types is recorded by indicating the range, with the most prevalent infection type listed first (e.g., 23 or ;1C or 31N).

Table 2. Infection types of parents, F_1, and F_2 plants of durum cultivars Glossy Hugenot crossed with Mindum, Spelmar, and Entrelargo de Montijo and inoculated with *Puccinia graminis* f. sp. *tritici*

	Race Pgt-QTH		Race Pgt-MCC	
Host	Number	Infection type[a]	Number	Infection type[a]
Glossy Hugenot (GH)	10	4	10	4
Mindum (Md)	10	X−	10	21C
Spelmar (Spl)	10	X	10	21C
Entrelargo de Montijo (EdM)	10	X−	10	X−
F_1 plants (GH/Md)	5	3+4	9	2C
F_2 plants (GH/Md)	44[b]	X−X++	7[c]	21C
	64	4	20	2C
			10	4
F_1 plants (GH/Spl)	6	4	9	22+C
F_2 plants (GH/Spl)	136[d]	4	31[e]	21C, 22+C
	48	X	11	4
F_1 plants (GH/EdM)	11	4	0	
F_2 plants (GH/EdM)	93[f]	4	232[g]	4
	25	XX+	15	XX+
	11	12−X−	3	X−

[a] See Table 1.
[b] Chi-square test of F_2 for 1:3 was significant ($P < 0.05$).
[c] Chi-square test of F_2 for 1:2:1 was nonsignificant ($P = 0.50$–0.80).
[d] Chi-square test of F_2 for 1:3 was nonsignificant ($P = 0.50$–0.80).
[e] Chi-square test of F_2 for 3:1 was nonsignificant ($P = 0.80$–0.95).
[f] Chi-square test for 12:3:1 in F_2 was nonsignificant ($P = 0.50$–0.80).
[g] Chi-square test for 60:3:1 in F_2 was nonsignificant ($P = 0.50$–0.80).

two recessive genes. These two genes conditioned a reaction similar to the reaction of Entrelargo de Montijo. One of these genes may condition moderate resistance, but the other had no recognizable independent effect.

The F_2 plants tested with Pgt-QTH and some additional F_2 plants were tested with Pgt-MCC. The results were unclear (Table 2). Two hundred and thirty-two of the 250 plants were susceptible, 15 were moderately susceptible (infection type XX+), and three plants had an infection type X−, similar to Entrelargo de Montijo. These data fit a 60:3:1 susceptible/moderately susceptible/resistant ratio ($P = 0.50$–0.80), indicating that Entrelargo de Montijo may have three recessive genes conditioning resistance to culture Pgt-MCC and that, singly, none of the genes has a recognizable effect. The combination of two of the genes conditioned infection type XX+, but the third gene did not have an observable effect in combination with either of the others. There may be no genes in common conditioning resistance to these two races in Entrelargo de Montijo because with the F_2, plants resistant to race Pgt-QTH segregated when inoculated with Pgt-MCC.

Glossy Hugenot/Arnautka. The F_1 progeny of the cross Glossy Hugenot/Arnautka gave an infection type 22+ to Pgt-MCC; Pgt-GMC was not tested. Arnautka had an infection type 12− to Pgt-MCC and ;1 to Pgt-GMC, whereas Glossy Hugenot was susceptible (Table 3).

Because of poor infection, the test of the F_2 population was inadequate to determine genetic ratios. Eighteen F_3 families were infected with culture Pgt-MCC, but the classification of infection types was not clear cut. However, all plants in four families were resistant and all plants in five families were susceptible. The remaining nine families segregated (Table 3). Several families had an intermediate-high infection type (X++ to 4−) and were included in the susceptible class. In addition, these F_3 plants were tested at the boot stage with the culture Pgt-GMC, which is avirulent on Arnautka but virulent on *Sr*9d. Five of the 20 families were homozygous resistant, 11 segregated (3:1 resistant/susceptible ratio) ($P = 0.80$–0.95), and four families were susceptible. Arnautka has a single gene for resistance to Pgt-GMC. The resistance gene detected with Pgt-GMC was independent of the gene detected with Pgt-MCC. Eight lines resistant to Pgt-MCC and susceptible to Pgt-GMC and seven lines resistant to Pgt-GMC and susceptible to Pgt-MCC were saved as potential single-gene lines.

Glossy Hugenot/Kubanka. Kubanka and seven F_1 plants from the cross Glossy Hugenot/Kubanka were tested with the race Pgt-QBB and gave 2 and 2+ infection types, respectively (Table 4). Kubanka gave an X to Pgt-QTH. In the F_2 tested to QBB, 48 plants segregated into resistant and susceptible phenotypes, but because of difficulty in clearly differentiating a range of intermediate infection types, a good fit to a genotypic ratio was not obtained. In the F_3, nine of the 15 resistant F_2 families did not segregate, indicating that nine of 48 F_2 plants were homozygous resistant, which fits a 1:3 homozygous resistant/heterozygous resistant and susceptible ratio ($P = 0.25$–0.50). Thus, a dominant gene provides the resistance of Kubanka to race Pgt-QBB.

The F_2 was also tested with Pgt-QTH (Table 4). Twenty plants were resistant and eight were susceptible. Although the number of plants evaluated was small, the data fit the 3:1 ratio. In the F_3, the 15 plants most resistant to Pgt-QBB were tested with Pgt-QTH. Five families were resistant, seven segregated, and three were susceptible, indicating a 1:2:1 ratio ($P = 0.50$–0.75). The F_2 and F_3 data indicate a dominant gene conditioned the resistance of Kubanka to Pgt-QTH and that the gene is independent from the gene for resistance to Pgt-QBB. Two F_3 lines resistant to Pgt-QBB and susceptible to Pgt-QTH and five F_3 lines susceptible to Pgt-QBB and resistant to Pgt-QTH were maintained as single-gene lines.

Glossy Hugenot/Acme. Acme and the F_1 plants from the cross Glossy Hugenot/Acme were resistant to the cultures Pgt-QBB and Pgt-QTH (Table 4). Infection types on the F_1 were 2+ and X+, whereas those on Acme were 2 and X to Pgt-QBB and Pgt-QTH, respectively. In the F_2 tested with QBB, 22 plants had an infection type 2, 39 had infection type 2+, and 22 were susceptible (Table 4). The observed distribution fits a 1:2:1 ratio ($P = 0.75$–0.90). Thus, a single gene conditions the resistance of Acme to Pgt-QBB. The F_2 plants were also tested with the culture Pgt-QTH. Twenty-five plants had infection type X, 42 had infection type X+, and 28 were susceptible, a 1:2:1 ratio ($P = 0.50$–0.75). The resistance was independent of resistance to Pgt-QBB. Thus, a second incompletely dominant gene conditioned the resistance of Acme to Pgt-QTH. Two lines having infection type 2 to Pgt-QBB and 4 to Pgt-QTH were selected and saved as single-gene lines.

Glossy Hugenot/Golden Ball. The parents, Glossy Hugenot and Golden Ball, and F_1 progeny were tested with Pgt-TPM and Pgt-QBB (Table 5). Glossy Hugenot was susceptible to both cul-

Table 3. Infection types of parents, F_1, and F_3 families of durum cultivars Glossy Hugenot crossed with Arnautka and inoculated with *Puccinia graminis* f. sp. *tritici*

	Race Pgt-MCC		Race Pgt-GMC	
Host	Number	Infection type[a]	Number	Infection type
Glossy Hugenot	10	4	10	4
Arnautka	10	12−	10	;1
F_1 plants	7	22+	0	
F_3 families	4[b]	Low	5[b]	Low
	9	Segregated	11	Segregated
	5	High	4	High

[a] See Table 1 F_2 tests.
[b] Chi-square test of F_3 for 1:2:1 was nonsignificant ($P = 0.80$–0.95).

Table 4. Infection types of parents, F_1, and F_2 families of durum cultivars Glossy Hugenot crossed with Kubanka and Acme to *Puccinia graminis* f. sp. *tritici*

	Race Pgt-QBB		Race Pgt-QTH	
Host	Number	Infection type	Number	Infection type
Glossy Hugenot (GH)	10	4	10	4
Kubanka (Kub)	10	2	10	X
Acme	10	2	10	X
F_1 plants (GH/Kub)	7	2+	0	
F_2 plants (GH/Kub)	25[a]	Low	20[b]	Low
	23	High	8	High
F_3 families[c] (GH/Kub)	9	Low	5	Low
	6	Segregated	7	Segregated
			3	High
F_1 plants (GH/Acme)	14	2+	18	X+
F_2 plants (GH/Acme)	22[d]	2	25[e]	X
	39	2+	42	X+
	22	4	28	4

[a] Chi-square test of F_2 for 3:1 is significant.
[b] Chi-square test of F_2 for 3:1, and F_3 for 1:2:1 is nonsignificant ($P = 0.50$–0.80).
[c] Resistant F_2 plants to Pgt-QBB were tested as F_3 families.
[d] Chi-square test of F_2 for 1:2:1 was nonsignificant ($P = 0.75$–0.90).
[e] Chi-square test of F_2 for 1:2:1 was nonsignificant ($P = 0.50$–0.75).

tures, whereas Golden Ball was characterized by infection type 2− to Pgt-TPM and ;1 to Pgt-QBB. Eight F_1 plants tested with Pgt-TPM gave 22+ infection type and five F_1 plants gave ;1+ to Pgt-QBB (Table 5). In the F_2, 31 plants segregated into three infection type classes; seven were a 2−, 16 a 22+, and eight a 4 to Pgt-TPM. The data fit a 1:2:1 ratio (P = 0.95–0.99), although the number of plants was low. The same plants were tested with Pgt-QBB. Those plants with a resistant reaction to Pgt-TPM were also resistant to Pgt-QBB, and those susceptible were again susceptible. However, infection types of the plants with Pgt-QBB were more distinct (seven plants were 1, 16 were ;1+, and eight were 4). The data indicate that one incompletely dominant gene conditions the resistance of Golden Ball to both races.

Several F_3 families derived from resistant and susceptible F_2 plants were tested with both races but did not segregate. F_3 families derived from the intermediate class F_2 plants segregated in the F_3. Results suggest a single gene conditions resistance in Golden Ball to both Pgt-TPM and Pgt-QBB. Seeds of six homozygous resistant lines were saved as potential single-gene lines.

DISCUSSION

Mindum, Spelmar, Arnautka, Kubanka, and Acme have at least two resistance genes each. Golden Ball may have a single resistance gene to Pgt-TPM and Pgt-QBB. Entrelargo de Montijo may have three to five resistance genes. The detected resistance genes were given tentative designations (Table 6).

The resistance detected in a host depends on the pathogen genotype, inoculum density, the environment, host genotype, and host growth stage. In the present study, the cultures did not vary during the experiment. When infection was inadequate, the test was repeated. To maintain a uniform environment for testing, a greenhouse was used during the winter and a growth chamber in the summer. Besides specific resistance genes in the resistant parent, the total genetic background of both parents used in the cross may affect the reaction of the progeny. The main uncontrolled variable among tests was probably the host growth stage, because two cultures were sequentially used to inoculate the same plants at different growth stages and the test was sometimes repeated if the infection density was inadequate.

It has been postulated that Mindum, Spelmar, and Arnautka each possess a common gene, *Sr*9d, which conditions a ; to a 2 type of infection (6,10). The race Pgt-MCC is avirulent on *Sr*9d, but race Pgt-QTH, used to evaluate Mindum and Spelmar, and race Pgt-GMC, used to evaluate Arnautka, were virulent on *Sr*9d. This helped distinguish *Sr*9d from the other resistance genes. A monogenic ratio was obtained in progenies from Mindum, Spelmar, and Arnautka with Glossy Hugenot in tests with Pgt-MCC. The genes in each cultivar (*Srm*A in Mindum, *Srs*C in Spelmar, and *Sra*rE in Arnautka) are postulated to be *Sr*9d (Table 7). Crosses have not been made between a single-gene line for *Sr*9d and the genes isolated from these three cultivars, as the *Sr*9d lines are hexaploids. A further indication that these genes are probably *Sr*9d is that the infection types of the cultivars and homozygous resistant classes of the F_2 varied between 1 and 2 for Pgt-MCC, typical for *Sr*9d. In the studies of Williams and Miller (16), a single-gene line, *Sr*dm1, was resistant to cultures 111-SS2 and 56-1 and was derived from Mindum. *Sr*dm1 was believed to be *Sr*9d also (A. P. Roelfs, *unpublished data*). One of the two undifferentiated genes that conditioned infection type 0; to 3− to the culture 111-SS2 in Spelmar (15) might be *Sr*9d because the culture used was avirulent on *Sr*9d. A third gene conditioned necrosis around pustules, which is not characteristic of *Sr*9d.

*Sr*dm2 and *Sr*dm3, the single-gene lines derived from Mindum (2), gave infection type X to the culture Pgt-QTH. Infection types produced by *Srm*B and *Srs*D to the same culture were very similar (X− and X, respectively) to the infection types of these two lines. It is likely that one of the *Sr*dm2 and *Sr*dm3, and *Srm*B and *Srs*D are the same genes. However, further testing of the progeny from crosses among them is necessary. The gene *Sra*rF found in Arnautka was different from *Sra*B and *Srs*D because Pgt-QTH was virulent to Arnautka and Pgt-GMC resulted in a ;1 infection type.

Kubanka and Acme each have a common gene, *Sr*9g, which conditions a "2−" to a 2+3−" type of infection depending on the culture used (6). Race Pgt-QBB, used to test progenies of the crosses of Kubanka and Acme with Glossy Hugenot, was avirulent on *Sr*9g, whereas race Pgt-QTH was virulent.

Kubanka and Acme conditioned an infection type 2, whereas the F_1 was 2+ to race Pgt-QBB. F_1 and F_2 data indicated that the incompletely dominant genes *Srk*H in Kubanka and *Sra*j in Acme are probably *Sr*9g because the culture Pgt-QBB was avirulent on this gene.

McIntosh et al (7) suggested that both Kubanka and Acme have other genes for resistance because they responded differently to many races. Acme was found to have three genes for resistance to culture 111-SS2 (2,14); however, the Acme selection used was atypical (3). Kubanka and Acme have gene(s) in addition to *Sr*9g. The F_2 plants from crosses of both Kubanka and Acme with Glossy Hugenot fit a one-gene segregation ratio with Pgt-QTH virulent to *Sr*9g. The infection types of Kubanka, Acme, and homozygous resistant lines obtained with this culture were identical (infection type X). The isolated genes, *Srk*G from Kubanka and *Sra*I from Acme, could be allelic or identical, but the isolated single-gene lines need to be crossed and the progeny tested with Pgt-QTH to determine if they are allelic. If *Srk*G and *Sra*I are identical, a third gene would be neces-

Table 5. Infection types of parents, F_1, and F_2 families of durum cultivars Glossy Hugenot crossed with Golden Ball to *Puccinia graminis* f. sp. *tritici*

	Race Pgt-TPM		Race Pgt-QBB	
Host	Number	Infection type	Number	Infection type
Glossy Hugenot	10	4	10	4
Golden Ball	10	2−	10	;1
F_1 plants	8	22+	5	;1+
F_2 plants	7[a]	2−	7[a]	;1
	16	22+	16	;1+
	8	4	8	4

[a] Chi-square test of F_2 for 1:2:1 was nonsignificant (P = 0.95–0.99).

Table 6. Tentative designations for the stem rust resistance genes found in selected durum cultivars

	Pathogen race Pgt-				
Cultivar	TPM	MCC	QTH	QBB	GMC
Mindum		*Srm*A	*Srm*B		
Spelmar		*Srs*C	*Srs*D		
Arnautka		*Sra*rE			*Sra*rF
Kubanka			*Srk*G	*Srk*H	
Acme			*Sra*I	*Sra*J	
Golden Ball[a]	*Srg*bK1			*Srg*bK2	
Entrelargo de Montijo			*Sre*N	*Sre*L	
		*Sre*O	*Sre*M		
		*Sre*P			

[a] *Srg*bK1 and *Srg*bK2 are either identical or closely linked.

sary to explain the responses observed on Kubanka and Acme to many cultures. Three genes were found in Acme for resistance to race 111 (2).

Golden Ball is resistant to race 15B (4), and the resistance gene was designated as *Sr*d4. PI 94701 has a gene designated *Sr*dp-2 (11) that conditions moderate resistance to cultures 111-SS2 and 15B-SS1. Because Golden Ball and PI 94701 had similar infection types to the same cultures of race 15B, it was assumed that *Sr*d4 and *Sr*dp-2 were the same gene (11). Luig (5) indicated that worldwide data indicates two resistance genes in crosses of Golden Ball. In this study, segregation for one gene was found to cultures Pgt-TPM and Pgt-QBB in Golden Ball. Because the cultures used in the tests were known to be avirulent on *Sr*dp-2 and that the infection type was similar to previous reports (10,11) it was assumed the gene isolated was *Sr*dp-2. The isolated single gene lines should be crossed with Medea Ap9d, which is also used as a source of *Sr*dp-2 (10).

Low infection types on Entrelargo de Montijo included all types from "0;" to "X" depending on the culture used (5). Luig suggested that Entrelargo de Montijo had a gene conditioning an ;X− infection type with race 126 and a 2 with other cultures. The gene responsible for the infection type 2 was located on chromosome 6A of hexaploid derivatives of Entrelargo de Montijo and Golden Ball. These genes conditioned similar infection types and may be allelic with *Sr*13. This resistance gene, like *Sr*13, tended to be more effective at high temperatures. In the present study, the resistance of Entrelargo de Montijo to the cultures Pgt-QTH and Pgt-MCC was found to be recessive. The genes *Sre*L and *Sre*M, when tested with Pgt-QTH, conditioned resistance when both genes were present. *Sre*L alone conditioned moderate resistance, but the effect of *Sre*M alone was unrecognizable. The results of testing F_2 plants with Pgt-MCC were unclear. Three plants of 250 seemed to be as resistant as Entrelargo de Montijo. The reactions of some other plants varied from infection type "X" to "X++" or were "4−". Plants with infection types X and X+ were classified as resistant, whereas those with X++ or 4− infection type were classified as susceptible. Based on this classification, a three-gene ratio (60:3:1 susceptible/moderately resistant/resistant) fits. The plants that were resistant to Pgt-QTH segregated when tested with Pgt-MCC, indicating that *Sre*L and *Sre*M were different from *Sre*N, *Sre*O, and *Sre*P. Alone, *Sre*N, *Sre*O, and *Sre*P genes had no visible effect. *Sre*N and *Sre*O conditioned moderate resistance when in combination. *Sre*P had no visible effect in combination with either of the other two genes. It should be emphasized that the segregation of F_2 plants to Pgt-MCC was not definitive. The resistance level of Entrelargo de Montijo to Pgt-MCC differed depending on its growth stage and temperature. Because Pgt-MCC inoculation was done after the Pgt-QTH test, the F_2 plants and parents were inoculated as 3-wk-old plants. At that stage, the infection type of Entrelargo de Montijo and resistant plants was X−, whereas the infection types of 7-day-old seedlings of Entrelargo de Montijo were XX+ and X++ in the growth chamber (15–18 C) and in the greenhouse (20 ± 3 C), respectively.

Lines identified as possessing a single gene for resistance were selected from the F_2 or F_3 generation for use in further studies.

Table 7. Genes for stem rust resistance in selected durum cultivars, their temporary designations, and the probable equivalents

Cultivar	Genes	Equivalent	Reference
Acme	*Sr*da1		2
	*Sr*da2	*Sr*9g?	2
	*Sr*da3		2
	*Sr*dmrc1		3
	Gene "0; to 1="		14
	Gene "0; to 1="		14
	Gene "12−"		14
	Gene "2−2"	*Sr*9g	6
	Gene "X"		6
	*Sra*I	*Sr*9g	1
	*Sra*J		1
Arnautka	Dom. gene "0; to 1"	*Sr*9d?	14
	Rec. gene "0; to 1"		14
	Dom. gene "12−"	*Sr*9d?	14
	Gene "2"	*Sr*9d	6
	Gene "X"		6
	*Sra*rE	*Sr*9d	1
	*Sra*rF		1
Entrelargo de Montijo	Gene ";−X−"		4
	Gene "2"		4
	*Sre*L		1
	*Sre*M		1
	*Sre*N		1
	*Sre*O		1
	*Sre*P		1
Golden Ball	*Sr*d4	*Sr*dp-2	4
	*Sr*dp-2		11
	*Sr*dp-2		5
	*Srg*bK1	*Sr*dp-2	1
	*Srg*bK2	*Sr*dp-2	1
Kubanka	1 gene		15
	Gene "2−2"	*Sr*9g	6
	Gene "X"		6
	*Srk*G	*Sr*9g	1
	*Srk*H		1
Mindum	*Sr*dm1	*Sr*9d	3
	*Sr*dm2		3
	*Sr*dm3		3
	Gene "2"	*Sr*9d	6
	Gene "X"		6
	*Srm*A	*Sr*9d	1
	*Srm*B		1
Spelmar	Gene "0; to 3−"	*Sr*9d?	15
	Gene "0; to 3−"	*Sr*9d?	15
	Gene "Necrosis"		15
	Gene "2"	*Sr*9d	6
	Gene "X"		6
	*Srs*C	*Sr*9d	1
	*Srs*D		1

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