Genetic Analysis of Resistance to Stem Rust in Ten Durum Wheats

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ABSTRACT

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Durum wheat (*Triticum turgidum* L.) cultivars derived from CIMMYT (International Maize and Wheat Improvement Center) germplasm are currently grown on more than 8 million ha worldwide. Because negligible information is available on their genes for resistance to stem rust, crosses in a diallel arrangement (without reciprocals) were made among nine resistant CIMMYT-derived durums, and Kingfisher, which was susceptible to one Mexican pathotype of *Puccinia graminis* f. sp. *tritici*. Parents, F_1 plants, F_2 populations, and F_3 lines were evaluated as seedlings in the greenhouse with two pathotypes and in the field with one pathotype. Cultivar Yavaros 79 possibly carried *Sr9e* and *Sr12*, which were also present in Mexicali 75, Diver, Somorguho, and Morus together with an unidentified gene, *SrC*, and in Altar 84, Carcomun, Totanus, and Woodrail together with *SrD*. Kingfisher and eight other durums (except Woodrail) also possessed gene *SrE*, which conferred resistance to pathotype RTR, but not to GFC. Genes *Sr9e* and *SrD* conferred immune and high levels of adult plant resistance, respectively; *Sr12* conferred only moderate levels of resistance, and *SrC* was ineffective under field conditions despite its effectiveness at the seedling stage to the same pathotypes. Because resistance was based on few genes, immediate measures are being undertaken to increase genetic diversity in CIMMYT germplasm.

Durum wheat (*Triticum turgidum* L.) is currently grown on more than 21 million ha worldwide (15). High-yielding cultivars, derived from the CIMMYT germplasm, occupy approximately 40% of this area. Although the stem rust disease (caused by *Puccinia graminis* Pers. f. sp. *tritici* Eriks & E. Henn.) is one of the most important wheat diseases worldwide, there is only limited information about the genetic basis of resistance to stem rust in durum wheats. This is despite the fact that durable resistance to stem rust in bread wheats (*T. aestivum* L.) based on the '*Sr2* gene complex' was transferred from emmer cultivar Yaroslav by McFadden (3,6,7,10,11). Similarly, stem rust resistance from Khapli emmer (*T. dicoccum* L.) resulted in useful, resistant bread wheats (1,4). Also, five durum wheats and two emmers were widely used as differentials for characterization of pathogenic variation in *P. g. tritici* (16). Recently, Bolat and Roelfs (2) identified and isolated several genes present in these differentials.

The current study was conducted to assess the degree of genetic variability for stem rust resistance in CIMMYT durum wheat germplasm using a selection of three released cultivars and six breeding lines.

MATERIALS AND METHODS

Of the nine resistant durum cultivars included in the study, Mexicali 75 (CIMMYT accession DW2158), Yavaros 79 (DW2159), and Altar 84 (DW2885) were released for cultivation in Mexico and various other countries (under different names). The number following the name indicates the year of release, e.g., Mexicali 75 was released for cultivation during 1975. The other six durums represent a set of recent high-yielding and stem rust-resistant breeding lines. These were Carcomun (DW2902), Diver (DW5036), Somorguho (DW3014), Morus (DW5544), Totanus (DW6822), and Woodrail (DW5509). The susceptible parent was Kingfisher (DW6823).

The two Mexican-derived *P. g. tritici* pathotypes used in genetic studies were GFC and RTR. The pathotypes' nomenclature is based on that described by Roelfs and Martens (12). The avirulence/virulence formulae are GFC: *Sr5,6,7a,7b,8b,9b,9e,10,11,12,13,14,22,23,24,25,26,27,29,30,31,32,33,35,36/8a,9a,9d,9f,9g,15,17,21,28,34* and RTR: *Sr7a,9e,10,12,13,14,22,23,24,25,26,27,29,30,31,32,33,35/5,6,7b,8a,8b,9a,9b,9d,9f,9g,11,15,17,21,28,34,36*. These two pathotypes were selected because Singh (unpublished data) found that GFC occurred most frequently on durums and because RTR possesses the widest virulence range among pathotypes present in Mexico (13). Seedlings of the parents were also evaluated with four additional pathotypes, MCC, QFC, RKQ, and RTQ. Avirulence/virulence formulae of these pathotypes are described in Singh (13).

Crosses were made in a diallel arrangement without the reciprocals. The inheritance studies were based on F_1, F_2, and individual F_2 plants derived F_3 lines. F_1 plants and approximately 100 plants of each F_2 were evaluated only in the adult plant stage in the field with pathotype GFC. Eighty F_3 lines in crosses involving Kingfisher, and 50 lines in all other crosses, were classified for their seedling reactions with pathotypes GFC and RTR, and for their adult plant field response with pathotype GFC. Between 40 and 60 plants of each F_3 line were used in each test. Seedlings (8–9 days old) of the parents and F_3 lines were inoculated by spraying urediospores suspended in a lightweight mineral oil (Soltrol 170), placed in a dew chamber overnight at 18–20 C, and then transferred to a greenhouse. Unless otherwise mentioned, the greenhouse temperature was maintained at 18–20 C. The rust reaction data were recorded approximately 2 wk after inoculation and were based on a 0–4 scale described by Stakman et al (16).

The field evaluations were carried out at Ciudad Obregon in northwestern Mexico. The plots of parents, F_1 plants and F_3 lines consisted of two 1-m rows seeded 20 cm apart with 70 cm between plots. F_2 plants were space planted (15–20 cm between plants) in paired rows of 11 m. The stem rust epiphytotic was created by inoculating spreader rows of Kingfisher planted at 20-row intervals. The adult plant stem rust responses were based on the modified Cobb scale (9).

The F_3 seedling and adult plant data in the crosses involving Kingfisher were used in deriving the genotypes of the parental F_2 plants. Chi-square analyses were carried out to test the distribution of observed F_2 genotypic frequencies with those expected for each cross.

RESULTS

Except for Kingfisher, the nine resistant durums displayed a fleck (;) infection type (IT) with all six *P. g. tritici* pathotypes,

indicating the possibility that all nine durums possess the same gene(s) for resistance to all pathotypes. The adult plants of these durums displayed a response of 0 when tested in the field with pathotype GFC. Kingfisher displayed a high seedling IT with pathotype GFC and a mesothetic IT (X) with the other five pathotypes. The adult plants of Kingfisher were highly susceptible.

The adult F_1 plants derived from all crosses, including those with Kingfisher, displayed a zero response when tested with pathotype GFC, indicating that resistance was fully dominant. All F_2 adult plants derived from the intercrosses of the nine resistant parents were resistant in the field with a response of 0. Moreover, the 50 F_3 lines in each cross displayed IT ; in the seedling stage with both pathotypes GFC and RTR, and displayed a 0 adult plant response with pathotype GFC. The homozygous status of the seedling for IT ; and the adult plant reaction of 0 confirmed that all nine resistant durums probably possessed a gene in common. Furthermore, this gene conferred a very high degree of resistance upon both seedlings and adult plants.

TABLE 1. Classification of the F_2 population for adult plant reaction, seedling, and adult plant responses of the F_3 progenies, postulated genotypes of the F_2 plants with genotypic frequencies in the cross Kingfisher/Yavaros 79, when tested with *Puccinia graminis* f. sp. *tritici* pathotype GFC

F_2 adult plant reaction[a]	F_3 progeny response		Genotype of F_2 plant	F_2 genotypic frequency[c]
	Seedling[b]	Adult plant[c]		
0	;&2-	0	AA--	19
0	;&2-/X-	0/40M	AaBB	15
0	;&2-/X-/3	0/40M/80S	AaBb	19
0	;/3	0/80S	Aabb	10
20–60M	X-	40M	aaBB	5
20–60M	X-/3	40M/80S	aaBb	8
80–100S	3	80S	aabb	4
			$\chi^2$4:2:4:2:1:2:1 (6 df)	3.2
			P value	>0.5

[a]Adult plant disease estimation is based on modified Cobb scale (9) and has two components: disease severity and infection type (IT); e.g., 0 = no disease; 20 = 20% severity; etc.; R-MR = resistant to moderately resistant IT; M = moderately resistant to moderately susceptible IT; S = susceptible IT.

[b]Seedling ITs are based on Stakman et al (16), where ; = no uredia, but hypersensitive necrotic or chlorotic flecks of varying size present; 2 = small to medium uredia usually in green islands surrounded by a decidedly chlorotic or necrotic border; X = random distribution of variable-sized uredia on single leaf with a pure culture; 3 = medium-sized uredia with rare chlorosis but no necrosis; - = uredia somewhat smaller than normal for the IT; + = uredia somewhat larger than normal for the IT.

[c]Based on the number of F_3 lines.

Segregation for stem rust reaction occurred in the F_2 generation when Kingfisher was used as one parent. The classification of only 80 randomly harvested F_2 plants are included in Tables 1 through 3 together with the F_3 data to show the good correlation that existed between the F_2 reactions and the behavior of F_3 progenies. The F_2 and F_3 results for the cross Kingfisher/Yavaros 79, when inoculated with pathotype GFC, are summarized in Table 1. This cross segregated in the F_2 generation for adult plants displaying three distinct reactions, viz., 0, 20–60M, and 80–100S. The F_3 lines derived from the F_2 adult plants with 0 reaction, were either homozygous for seedling ITs ranging between ; to 2-, or segregated for these ITs, and ITs X- and 3. Similarly, the adult plants were either homozygous 0 or segregated for this reaction, 40M (the actual range pooled together was 20–60M) and 80S reactions. The F_2 adult plants classified to display 40M reactions gave either homozygous F_3 lines with seedling IT X-, or segregating F_3 lines with ITs X- and 3. The adult plant responses of these lines were either homozygous 40M or segregating with 40M and 80S. The F_2 adult plants with 80–100S reactions gave F_3 lines with homozygous seedling IT 3 and homozygous adult plant reactions of 80S. The genotypes of the F_2 plants were deduced from the response of the F_3 lines assuming that segregation occurred at two loci. Gene *SrA* conferred seedling ITs ; to 2- and adult plant reaction 0, whereas gene *SrB* was responsible for seedling IT X- and variable adult plant response 40M. Moreover, the response conferred by gene *SrA* was epistatic to that conferred by gene *SrB*. The observed genotypic frequency conformed with those expected for segregation at two genetically independent loci (Table 1).

Table 2 gives the classifications of F_2 adult plants for reactions and the F_3 progeny responses for the crosses of Kingfisher with Mexicali 75, Diver, Somorguho, and Morus. All four crosses showed segregation for seedling response conforming with that expected for three genes. Based on the seedling ITs and adult plant reactions, it was evident that genes *SrA* and *SrB* were present in the four resistant wheats. All four wheats carried a third gene, *SrC*, conferring IT 2+ (ranged from ITs 2 to 3C). Gene *SrC* was not effective in adult plants, because F_3 lines homozygous for this gene showed highly susceptible adult plant responses. The χ^2 analysis (Table 2) for individual crosses and on pooled results clearly indicated that segregation for seedling response

TABLE 2. Classification of the F_2 population for adult plant reaction, seedling, and adult plant responses of the F_3 progenies, postulated genotypes of the F_2 plants with genotypic frequencies in crosses involving four durum wheats with Kingfisher, when tested with *Puccinia graminis* f. sp. *tritici* pathotype GFC

F_2 adult plant reaction[a]	F_3 progeny response		Genotype of F_2 plant[a]	F_2 genotypic frequency[b] in crosses of Kingfisher with				
	Seedling[a]	Adult plant[a]		Mexicali 75	Diver	Somorguho	Morus	Total
0	;&2-	0	AA----	16	22	22	15	75
0	;&2-/X-	0/40M	AaBB--	9	7	6	12	34
0	;&2-/X-/2+	0/40M/80S	AaBbCC	4	5	7	8	24
0	;&2-/X-/2+/3	0/40M/80S	AaBbCc	7	11	8	10	36
0	;&2-/X-/3	0/40M/80S	AaBbcc	6	6	3	7	22
0	;&2-/2+	0/80S	AabbCC	2	4	3	2	11
0	;/2+/3	0/80S	AabbCc	4	7	4	3	18
0	;/3	0/80S	Aabbcc	4	1	4	4	13
20–60M	X-	40M	aaBB--	6	3	5	2	16
20–60M	X-/2+	40M/80S	aaBbCC	5	3	4	3	15
20–60M	X-/2+/3	40M/80S	aaBbCc	6	6	5	7	24
20–60M	X-/3	40M/80S	aaBbcc	3	2	5	1	11
80–100S	2+	80S	aabbCC	2	1	1	1	5
80–100S	2+/3	80S	aabbCc	4	2	2	3	11
80–100S	3	80S	aabbcc	2	0	1	2	5
χ^2 16:8:4:8:4:2:4:2:4:2:4:2:1:2:1 (14 df)				8.3	6.6	8.3	10.3	8.1
P value				>0.9	>0.95	>0.9	>0.75	>0.9

[a]See footnotes in Table 1 for details of the seedling and adult plant disease scales.

[b]Based on the number of F_3 lines.

TABLE 3. Classification of the F_2 population for adult plant reaction, seedling, and adult plant responses of the F_3 progenies, postulated genotypes of the F_2 plants with genotypic frequencies in crosses involving four additional durum wheats with Kingfisher, when tested with *Puccinia graminis* f. sp. *tritici* pathotype GFC

F_2 adult plant reaction[a]	F_3 progeny response		Genotype of F_2 plant	F_2 genotypic frequency[b] in crosses of Kingfisher with				
	Seedling[a]	Adult plant[a]		Altar 84	Carcomun	Totanus	Woodrail	Total
0	;&2-	0	AA----	18	16	21	19	74
0	;&2-	0/20RMR	AaDD--	12	11	14	8	45
0	;&2-/X-	0/20RMR/40M	AaDdBB	4	7	3	7	21
0	;&2-/X-/3	0/20RMR/40M/80S	AaDdBb	8	8	11	7	34
0	;&2-/3	0/20RMR/80S	AaDdbb	6	7	4	7	24
0	;&2-/X-	0/40M	AaddBB	4	3	2	4	13
0	;&2-/X-/3	0/40M/80S	AaddBb	6	4	3	7	20
0	;&2-/3	0/80S	Aaddbb	2	3	2	2	9
20–30RMR	;&2-	20RMR	aaDD--	4	6	4	3	17
20–30RMR	;&2-/X-	20RMR/40M	aaDdBB	3	4	2	4	13
20–30RMR	;&2-/X-/3	20RMR/40M/80S	aaDdBb	6	5	7	4	22
20–30RMR	;&2-/3	20RMR/80S	aaDdbb	2	3	3	2	10
20–60M	X-	40M	aaddBB	1	0	1	2	4
20–60M	X-/3	40M/80S	aaddBb	2	2	3	1	8
80–100S	3	80S	aaddbb	2	1	0	3	6
χ^2 16:8:4:8:4:2:4:2:4:2:4:2:1:2:1 (14 df)				3.9	5.9	6.4	10.6	6.2
P value				>0.995	>0.95	>0.95	>0.5	>0.95

[a]See footnotes in Table 1 for details of the seedling and adult plant disease scales.
[b]Based on the number of F_3 lines.

TABLE 4. Distribution of seedling infection types displayed by the F_3 lines in the crosses of Kingfisher with nine durums, when tested with *Puccinia graminis* f. sp. *tritici* pathotype RTR

Second parent	Infection types[a] and number of F_3 lines						
	;&2-	;&2-/X	X	;&2-/X/3	;&2-/3	X/3	3
Mexicali 75	16	36	28	0	0	0	0
Yavaros 79	19	44	17	0	0	0	0
Diver	22	41	17	0	0	0	0
Somorguho	22	35	23	0	0	0	0
Morus	15	46	19	0	0	0	0
Altar 84	34	41	5	0	0	0	0
Carcomun	33	44	3	0	0	0	0
Totanus	39	37	4	0	0	0	0
Woodrail	30	27	4	10	7	2	0

[a]See footnotes in Table 1 for details of the infection type scale.

occurred at three independent loci and that the four crosses gave similar results.

Table 3 summarizes the F_2 and F_3 results with pathotypes GFC for the crosses of Kingfisher with Altar 84, Carcomun, Totanus, and Woodrail. Gene *SrA* was present in all four resistant wheats. A second gene, *SrD*, conferring seedling ITs ; to 2-, similar to those conferred by *SrA*, was postulated. Although the seedling responses conferred by genes *SrA* and *SrD* were indistinguishable, an adult plant reaction of approximately 20RMR appeared to be associated with *SrD*, whereas gene *SrA* conferred a 0 reaction. Segregation also occurred for IT X-, which was postulated to be due to the gene *SrB*. The observed distribution of the various genotypes in each cross and when pooled conformed with that expected for the segregation at three independent loci (Table 3).

Seedlings of F_3 lines from each cross involving Kingfisher were also tested with pathotype RTR (Table 4). The F_3 lines, which were homozygous for ITs ; to 2- with pathotype GFC were also homozygous with pathotype RTR with similar ITs. This indicated that genes *SrA* and *SrD* were also effective against pathotype RTR. In all crosses, except that involving Woodrail, the highest response of individual plants within segregating lines was IT X. Because Kingfisher also displayed IT X, these results indicated that a gene, *SrE*, was present in Mexicali 75, Yavaros 79, Diver, Somorguho, Totanus, Altar 84, Carcomun, and Morus as well as Kingfisher. The cross Kingfisher/Woodrail segregated for ITs ranging to 3, indicating that Woodrail did not carry *SrE* (Table 4).

All F_3 lines segregating with pathotype GFC for ITs X- and 3 (i.e., segregating for only *SrB*) in each cross were also tested at 24–28 C. All seedlings in each line displayed ITs 3C to 3, indicating that gene *SrB* was temperature sensitive and was more effective at lower temperatures.

DISCUSSION

A total of five genes conferring low seedling reactions to *P. g. tritici* were identified in the CIMMYT-derived durums. Based on the seedling IT ; to 2- associated with *SrA*, and the susceptibility of these durums in East Africa (Kenya and Ethiopia), where virulence for *Sr9e* is common (unpublished data of A. P. Roelfs and J. Huerta, USDA Cereal Rust Laboratory, St. Paul, MN), we postulate that gene *SrA* is *Sr9e*, which is known to be very widely distributed in durum wheats (R. A. McIntosh, *personal communication*). This hypothesis could be confirmed either by crossing one of the durum parents with emmer cultivar Vernal, which is known to carry *Sr9e*, or by testing selected F_3 lines from the current crosses with a series of unrelated *P. g. tritici* cultures with known virulence for *Sr9e*. Gene *SrB*, which conferred a mesothetic IT at 18–20 C and high IT at 24–28 C, could be *Sr12*. Gene *Sr12* was transferred to bread wheats from the durum cultivar Marquillo (5) and is known to show temperature sensitivity (5,14). The variation in seedling IT (from ; to 2-) associated with *Sr9e* in the segregating population could be due to the segregation of *SrB* (postulated to be *Sr12*). Unpublished results of R. A. McIntosh (*personal communication*) have shown that *Sr12* can modify the expression of several *Sr9* alleles, including *Sr9e*. Therefore, the hypothesis that all resistant parents carried *Sr9e* and *Sr12* was further strengthened, because parents displayed a consistent fleck IT.

Gene *SrE*, present in Kingfisher, is different from any named gene for stem rust resistance because the high IT response with pathotype GFC and a mesothetic response with other pathotypes does not match with any known gene. The usefulness of this gene, at least in Mexico, is limited, because pathotype GFC is virulent. The usefulness of *SrC* at any location can be questioned as it did not confer detectable levels of adult plant resistance, even when a resistant response to the same pathotype was present in seedlings. Gene *SrD* can be used in Mexico; however, its widespread use could lead to the emergence of a mutant pathotype. Virulence appears to occur for this gene in Ethiopia since Altar 84 is susceptible there (CIMMYT database). The international virulence survey at USDA Cereal Rust Laboratory involves only selected single *Sr* gene lines. Therefore, it was not possible to

visualize what other special virulences occur in East African durum stem rust population.

Although resistance appears to be very effective in Mexico, the results presented above indicate that the limited genetic variability among CIMMYT germplasm-derived durums exposes a degree of genetic vulnerability. All cultivars are protected primarily by two effective genes. One of these genes, *Sr9e*, is known to be ineffective at many locations including the United States. Genetic vulnerability in CIMMYT triticale germplasm was expressed in Australia when a mutation for virulence for gene *Sr27* in an Australian *P. g. tritici* pathotype resulted in susceptibility of over 70% of the entries in the 12th International Triticale Screening Nursery (8).

Measures to enhance the genetic diversity for stem rust resistance in CIMMYT durum germplasm have been initiated. Resistant durum wheats from East Africa (Ethiopia and Kenya) and North Dakota, and old cultivars, such as Iumillo durum and Khapli emmer, are being used as sources of resistance genes for transfer to durum populations. Because of the lack of virulence for genes *SrA* (*Sr9e*) and *SrD* in Mexico, selection for other genes will be difficult. One strategy to incorporate further genes into durum populations will be to shuttle segregating populations between Mexico and sites where Mexican durums are susceptible. Shuttle breeding and genetic monitoring of the promising advanced lines will enhance genetic diversity and thus reduce the genetic vulnerability that is currently evident in durum germplasm.

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