Genetic Analysis of Resistance to Leaf Rust in Nine Durum Wheats

R. P. SINGH, E. BECHERE, and O. ABDALLA, International Maize and Wheat Improvement Center (CIMMYT), Lisboa 27, Apdo. Postal 6-641, 06600, Mexico, D.F., Mexico

ABSTRACT

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High-yielding durum wheat (*Triticum turgidum*) cultivars, derived from the CIMMYT (International Maize and Wheat Improvement Center) germ plasm, are grown on approximately 40% of the global durum wheat area. Because of the lack of information on their genes for resistance to leaf rust, crosses in a diallel arrangement (without reciprocals) were made among nine resistant CIMMYT-derived durums and the accession DW7276, which is susceptible to Mexican *Puccinia recondita* f. sp. *tritici* pathotype BBB/BN. Mexican durums were also crossed with the adult-plant resistant land race cultivar Iumillo. Inheritance of resistance was investigated in seedlings and/or adult plants of F_1 hybrids, F_2 populations, and F_3 lines. A common, partially dominant gene confers seedling resistance in Altar 84, Carcomun, Morus, and Totanus. This gene alone does not confer an acceptable level of adult-plant resistance; however, it interacts in an additive manner with two additional partially effective adult-plant genes. Two additive genes also confer adult-plant resistance to Mexicali 75, Yavaros 79, Diver, Kingfisher, and Somorguho. At least one adult-plant gene is common in each resistant parent. However, transgressive segregation in the F_2 and F_3 generations for reduced or increased adult-plant leaf rust severity indicates genetic diversity. CIMMYT durums and worldwide-resistant Iumillo carry common adult-plant resistance, which could be of a durable nature.

High-yielding durum wheat (*Triticum turgidum* L.) cultivars, derived from the CIMMYT (International Maize and Wheat Improvement Center) germ plasm, are grown on approximately 40% of the global durum wheat area (14). Reports on the inheritance of leaf rust (*Puccinia recondita* Roberge ex Desmaz. f. sp. *tritici* (Eriks. & E. Henn.) D.M. Henderson) resistance in durums are rare, and no information is available on CIMMYT-derived durums. Statler (16) reported that two complementary recessive genes conferred seedling leaf rust resistance in the cultivar Leeds. Rashid et al (11) also found one or two recessive genes for seedling resistance in Ramsey, D561, and D6733. In a recent study, Zhang and Knott (17) reported that dominant, recessive, or a combination of dominant and recessive genes conferred seedling resistance in eight diverse durum accessions. The genetic basis of adult-plant resistance was not evaluated in any of the above studies.

The current study was conducted to determine the genetic basis of seedling and/or adult-plant leaf rust resistance in CIMMYT durum wheat germ plasm. A selection of three released cultivars and six breeding lines was used.

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MATERIALS AND METHODS

The nine resistant parents included in the study are listed in Table 1 along with their CIMMYT accession numbers. Mexicali 75, Yavaros 79, and Altar 84 were released for cultivation in Mexico. They are also cultivated in various other countries under different names. The number following the cultivar name indicates the year of release, e.g., Mexicali 75 was released for cultivation during 1975. The other six durums represent a set of high-yielding and leaf rust-resistant breeding lines. Iumillo, a land race cultivar from Spain, was included because it was used in the 1970s in CIMMYT's durum breeding program and carries adult-plant leaf rust resistance that is effective worldwide. The susceptible parent, North Dakota line, accession DW7276, was introduced to CIMMYT from North Dakota.

The *P. r. tritici* pathotype used in all genetic studies was BBB/BN (12) with the following seedling avirulence/virulence formula: *Lr1,2a,2b,2c,(3),3ka,3bg, 9,11,13,14a,15,16,17,18,19,21,24,25,(26), 27+31,29,30,32,33,34/10,12,14b, 20,22a,22b,23,28*. This pathotype was selected because Singh (12) found that it occurred most frequently on durums in Mexico.

Crosses were made among the CIMMYT durums in a diallel arrangement without reciprocals. All CIMMYT durums were also crossed with Iumillo and the susceptible parent DW7276. Inheritance studies were based on F_1, F_2, and individual F_2-plant-derived F_3 lines. F_1 plants were evaluated only as adult plants in the field.

Between 95 and 130 F_2 seedlings and 80 individual F_2-plant-derived F_3 lines from the crosses of DW7276 with Altar 84, Carcomun, Morus, and Totanus were classified in the seedling stage for their infection types. From 16 to 20 seedlings of each of 50 F_3 lines from intercrosses of the above four resistant durums were also evaluated. Seedlings (8–9 days old) of the parents, F_2, and F_3 lines were inoculated by spraying urediospores suspended in the lightweight mineral oil Soltrol 170 at a concentration of approximately 2–3 mg of urediospores per milliliter, placed in a dew chamber overnight at 18–20 C, and transferred to a greenhouse maintained at 18–22 C. The rust-reaction data were recorded approximately 10 days after inoculation and were based on a 0–4 scale described by Stakman et al (15).

Field evaluations of parents, F_1 plants, and F_2 populations were carried out at Ciudad Obregon in northwestern Mexico during the 1988–89 crop season, and parents and F_3 lines were evaluated during 1989–90 season. Approximately 100 F_2 plants from each cross, space planted (15–20 cm between plants) in paired rows of 11 m, were evaluated as adult plants in the field. Eighty F_3 lines in all crosses involving DW7276, Iumillo, and Kingfisher, and 50 lines in all other crosses, were also evaluated for their adult-plant field responses. Between 40 and 60 plants of each F_3 line were used in the test. 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. Rows of the two parents were planted at the beginning of each F_3 population, and DW7276 was included every

25 rows as a susceptible check.

The leaf rust epidemic was created by inoculating spreader rows of DW7276 planted at 20-row intervals. The visual estimations of adult-plant leaf rust severities were based on the modified Cobb scale (10). The host response to infection was scored as follows: R = resistant, with miniature uredia surrounded by necrotic tissue; MR = moderately resistant, with smaller to moderate-sized uredia surrounded by necrotic or chlorotic tissue; MS = moderately susceptible, with moderate-sized uredia and no necrotic or chlorotic tissue; and S = susceptible, with large uredia and no necrotic or chlorotic tissue. Flag leaves of parents, F_1s, and other segregating populations were evaluated for leaf rust when the plots of susceptible check DW7276 displayed a response between 80S and 100S. In F_2 populations, individual plants were classified; while for each F_3 line the range of severity (the most resistant to the most susceptible plant) was recorded. Chi-square analyses were carried out to test the distribution of observed F_2 and F_3 phenotypic frequencies with those expected for each cross involving DW7276.

RESULTS

Seedling studies. Table 1 gives the seedling infection types (ITs) displayed by each parent when tested with *P. r. tritici* pathotype BBB/BN. Only four parents (Altar 84, Carcomun, Morus, and Totanus) displayed low reactions (IT 12). IT 4 was recorded for DW7276, and the remaining parents displayed IT 3.

F_2 populations from the crosses of DW7276 with Altar 84, Carcomun, Morus, and Totanus segregated for seedlings with ITs 12, 2+3C, and 4 in a ratio of 1:2:1 (Table 2), indicating that a single gene confers seedling resistance. Moreover, the resistance was intermediate when this gene occurred in a heterozygous condition. The distribution of F_3 lines in each cross was also in accordance with a monogenic segregation ratio (Table 2). All 50 F_3 lines obtained from intercrosses of these four seedling-resistant parents were homozygous for IT 12 (*unpublished*), indicating that the same gene confers resistance in each parent.

Adult-plant studies. Table 1 gives the adult-plant severity and reaction of parents for two seasons. DW7276 displayed high severity and reaction (100S) during both seasons. Responses of other parents ranged from tMRMS to 40MRMS.

Table 3 summarizes the F_1, F_2, and F_3 results of intercrosses of the nine resistant parents and of the parents with Iumillo. The leaf rust severity of F_1 plants in each combination was either similar to or slightly greater than the response of parents showing higher disease levels. Although transgressive segregation occurred in F_2 and F_3, disease levels higher than 40% were not observed. In Table 3, we have presented only the range of disease severity for each F_2 population. Similarly, F_3 lines are grouped based on disease severity of plants with the highest response within each line. The overall results indicate that all parents carry at least one common gene, and that variability occurs at other loci. Because crosses with Iumillo also failed to segregate for highly susceptible (80–100% severity) plants, we concluded that CIMMYT durums and Iumillo share some common genes for adult-plant resistance.

Table 4 presents F_1 and F_2 results for crosses of CIMMYT durums with adult-plant susceptible DW7276. F_1 reaction for the crosses ranged between 40MS and 60MS, indicating that resistance was intermediate. Segregation occurred in each cross, and plants in F_2 populations had diverse responses. In Table 4, we present the frequency of plants as resistant-intermediate (disease severity from t to 60%) and susceptible (disease severity from 80% to 100%). Chi-square analysis on observed frequencies of the two categories indicates that Mexicali 75 possibly carries one partially dominant gene for resistance. Results for other crosses indicate that the resistant parents possibly carry one partially dominant gene and one or two additional recessive genes.

We evaluated 80 F_3 lines from each cross to obtain a clearer estimation of segregating resistance genes (Table 5). Based on the leaf rust severity range, F_3 lines were grouped in four classes as explained in Table 5. Chi-square analysis on the observed distribution of F_3 lines

Table 1. *Triticum turgidum* parents, accession number (DW = durum wheat accessions at CIMMYT), seedling infection type with *Puccinia recondita* f. sp. *tritici* pathotype BBB/BN, and adult-plant ratings during two seasons with the same pathotype

Parent	Accession number	Seedling infection type[a]	Adult-plant rating[b] 1988–89	1989–90
Mexicali 75	DW2158	3	30MRMS	40MRMS
Yavaros 79	DW2159	3	10MRMS	20MRMS
Altar 84	DW2885	12	tMRMS	tMRMS
Carcomun	DW2902	12	tMRMS	tMRMS
Diver	DW5036	3	5MRMS	10MRMS
Kingfisher	DW6823	3	5MRMS	10MRMS
Morus	DW5544	12	tMRMS	tMRMS
Somorguho	DW3014	3	5MRMS	10MRMS
Totanus	DW6822	12	tMRMS	tMRMS
Iumillo	...	3	tMRMS	tMRMS
North Dakota line	DW7276	4	100S	100S

[a]On a 0–4 scale (15), where 12 = small uredia surrounded by necrosis, and small to medium uredia surrounded by green islands occurring on the same leaf; 3 = medium uredia without chlorosis or necrosis; and 4 = large uredia without chlorosis or necrosis.
[b]Includes two components: disease severity based on modified Cobb scale (10), where t = trace, 5 = 5% ... 100 = 100%; and host reaction, where MRMS = moderately resistant to moderately susceptible and S = susceptible.

Table 2. Seedling classification and χ^2 analysis of F_2 populations and F_3 lines from crosses of susceptible DW7276 with four resistant parents inoculated with *Puccinia recondita* f. sp. *tritici* pathotype BBB/BN

Resistant parent	F_2: Number of seedlings of each IT[a]: 12	2+3C	4	$\chi^2$1:2:1 and p values	F_3: Number of lines of each IT[a]: Homozygous IT 12	Segregating IT 12, 2+3C, 4	Homozygous IT 4	$\chi^2$1:2:1 and p values
Altar 84	38	58	33	1.69, $P>0.3$	18	42	20	0.30, $P>0.7$
Carcomun	27	52	25	0.08, $P>0.9$	24	40	16	1.60, $P>0.3$
Morus	31	69	30	0.51, $P>0.7$	22	32	26	3.60, $P>0.1$
Totanus	27	43	25	0.94, $P>0.5$	17	42	21	0.60, $P>0.5$
Total	123	222	113	0.87, $P>0.5$	81	156	83	0.22, $P>0.7$

[a]Infection types (ITs) are based on a 0–4 scale (15), where 12 = small uredia surrounded by necrosis, and small to medium uredia surrounded by green islands; 2+3C = medium to large uredia surrounded by green islands or chlorotic tissues; and 4 = large uredia without chlorosis or necrosis.

indicates that two genes, in an additive manner, confer leaf rust resistance in Mexicali 75, Yavaros 79, Diver, Kingfisher, and Somorguho. The F_3 line distribution for crosses of DW7276 with Altar 84, Carcomun, Morus, and Totanus is in accordance with the segregation of three additive genes. The additive effect of the genes is supported by the fact that F_3 lines homozygous for parental-type resistance or susceptibility occur in low frequencies. No attempt was made to analyze the distribution of F_2 plants or F_3 lines based on the reaction type, because reaction types appeared to be fairly randomly distributed by severity (*unpublished*).

To evaluate the effectiveness of the gene that confers a seedling IT 12 in Altar 84, Carcomun, Morus, and Totanus, we present in Table 6 the highest adult-plant severity range of F_3 lines that are homozygous in seedlings for IT 12. Adult-plant leaf rust severity ranged from a trace to 60%, indicating that the seedling gene does not confer adequate levels of adult-plant resistance on its own. Because all six F_3 lines, which happened to be homozygous for the parental-type adult plant resistance (Table 6), were also homozygous for the seedling gene, we postulate that this gene is also involved in the additive interaction observed for adult-plant resistance. Altar 84, Carcomun, Morus, and Totanus displayed the highest levels of adult-plant resistance.

DISCUSSION

A single, partially dominant gene confers seedling resistance to pathotype BBB/BN of *P. r. tritici* in four CIMMYT durums, namely, Altar 84, Carcomun, Morus, and Totanus. The usefulness of this gene by itself is questionable, because up to 60% leaf rust severity was observed on F_3 segregates homozygous for this gene. Mexicali 75, Yavaros 79, Diver, Kingfisher, and Somorguho are susceptible as seedlings but have effective adult-plant resistance. In each case, this resistance is due to the interaction of two additive genes. Similarly, Altar 84, Carcomun, Morus, and Totanus carry two additive adult-plant effective genes together with the gene that is effective at the seedling stage. Because only limited segregation occurred in intercrosses of CIMMYT durums, they must carry at least one common adult-plant resistance gene. However, the occurrence of limited segregation indicates a certain degree of variability for adult-plant genes around the above common gene(s) in CIMMYT durum germ plasm. Pyramiding of these genes is possible and has resulted in enhanced resistance levels.

Table 3. F_1 severity, F_2 severity range, and classification of adult-plant disease severity (only highest response range presented) of F_3 lines in the crosses of resistant parents tested with *Puccinia recondita* f. sp. *tritici* pathotype BBB/BN

Cross	F_1 severity[a]	F_2 severity range[a]	Number of F_3 lines with plants of greatest severity[a]					
			t	5	10	20	30	40
Mexicali 75/Yavaros 79	30	5–40	...	2	16	16	13	3
Mexicali 75/Altar 84	20	t–30	5	5	6	15	11	8
Mexicali 75/Carcomun	40	t–20	4	3	12	12	17	2
Mexicali 75/Diver	30	5–40	...	1	3	23	17	6
Mexicali 75/Kingfisher	40	10–30	...	...	13	23	30	14
Mexicali 75/Morus	20	t–30	5	8	8	21	5	3
Mexicali 75/Somorguho	40	5–30	...	3	7	12	9	19
Mexicali 75/Totanus	20	t–20	3	10	12	15	8	2
Yavaros 79/Altar 84	10	t–20	18	9	20	3	...	...
Yavaros 79/Carcomun	10	t–10	30	10	2	8	...	...
Yavaros 79/Diver	20	5–15	5	16	6	23	...	...
Yavaros 79/Kingfisher	15	t–15	20	30	22	8	...	...
Yavaros 79/Morus	10	t–10	23	16	11	...	...	...
Yavaros 79/Somorguho	10	t–10	11	29	10	...	...	...
Yavaros 79/Totanus	15	t–10	14	10	17	9	...	...
Altar 84/Carcomun	5	t–5	23	11	16	...	...	...
Altar 84/Diver	10	t–10	10	18	14	8	...	...
Altar 84/Kingfisher	10	t–10	17	16	27	20	...	...
Altar 84/Morus	5	t–5	40	2	8	...	...	...
Altar 84/Somorguho	5	t–5	17	18	15	...	...	...
Altar 84/Totanus	5	t–5	31	9	10	...	...	...
Carcomun/Diver	5	t–5	11	23	16	...	...	...
Carcomun/Kingfisher	10	t–10	37	18	18	7	...	...
Carcomun/Morus	5	t–10	11	29	5	5	...	...
Carcomun/Somorguho	15	t–10	25	15	8	2	...	...
Carcomun/Totanus	10	t–10	20	14	13	3	...	...
Diver/Kingfisher	10	t–10	10	32	21	17	...	...
Diver/Morus	10	t–5	14	26	5	5	...	...
Diver/Somorguho	15	t–5	15	22	8	5	...	...
Diver/Totanus	15	t–10	11	14	19	6	...	...
Kingfisher/Morus	20	t–10	52	16	12	...	...	...
Kingfisher/Somorguho	20	t–10	8	30	27	15	...	...
Kingfisher/Totanus	15	t–10	16	28	23	13	...	...
Morus/Somorguho	20	t–10	8	14	8	20	...	...
Morus/Totanus	10	t–10	9	13	23	5	...	...
Somorguho/Totanus	15	t–10	15	10	12	13	...	...
Iumillo/Mexicali 75	20	t–30	19	18	13	15	15	...
Iumillo/Yavaros 79	10	t–10	33	22	19	6	...	...
Iumillo/Altar 84	5	t–5	72	8	...	...	...	...
Iumillo/Carcomun	5	t–5	73	7	...	...	...	...
Iumillo/Diver	10	t–5	52	18	10	...	...	...
Iumillo/Kingfisher	10	t–5	42	25	13	...	...	...
Iumillo/Morus	5	t–5	78	2	...	...	...	...
Iumillo/Somorguho	10	t–5	40	30	10	...	...	...
Iumillo/Totanus	5	t–5	70	6	4	...	...	...

[a]Based on modified Cobb scale (10), where t = trace, 5 = 5% ... 100 = 100%.

Table 4. F_1 adult-plant response, classification, and χ^2 analysis of F_2 adult plants in crosses of susceptible DW7276 with the resistant parents tested with *Puccinia recondita* f. sp. *tritici* pathotype BBB/BN during 1988–89

Resistant parent	F_1 response	Number of F_2 plants[a]		χ^2 and *P* value for ratio		
		Resistant-intermediate	Susceptible	3:1[b]	13:3[c]	55:9[d]
Mexicali 75	60MS[e]	69	29	1.10, $P > 0.25$	7.56, $P < 0.01$	...
Yavaros 79	60MS	101	21	3.95, $P > 0.03$	0.19, $P > 0.50$	1.00, $P > 0.25$
Altar 84	40MS	103	21	4.30, $P > 0.03$	0.27, $P > 0.50$	0.85, $P > 0.25$
Carcomun	40MS	80	12	7.01, $P < 0.01$	1.97, $P > 0.10$	0.08, $P > 0.75$
Diver	50MS	80	18	2.30, $P > 0.10$	0.01, $P > 0.90$	1.50, $P > 0.10$
Kingfisher	50MS	102	14	10.4, $P < 0.01$	3.40, $P > 0.05$	0.38, $P > 0.50$
Morus	40MS	84	16	4.32, $P > 0.03$	0.50, $P > 0.25$	0.31, $P > 0.50$
Somorguho	60MS	74	21	0.42, $P > 0.05$	0.70, $P > 0.25$	5.08, $P > 0.01$
Totanus	40MS	74	12	5.60, $P > 0.01$	1.30, $P > 0.25$	0.00, $P > 0.99$

[a] Resistant-intermediate = severity of 60% or less; susceptible = severity of 80% or more.
[b] Expected for segregation of one dominant gene.
[c] Expected for independent segregation of one dominant gene and one recessive gene.
[d] Expected for independent segregation of one dominant gene and two recessive genes.
[e] MS = moderately susceptible.

Table 5. Adult-plant classification and χ^2 analysis of F_3 lines from the crosses of susceptible DW7276 with nine resistant parents, inoculated with *Puccinia recondita* f. sp. *tritici* pathotype BBB/BN during 1989–90

Resistant parent	Number of F_3 lines				Tested ratio, χ^2, and *P* values	Estimated gene number
	HPTR[a]	HPTS[b]	SEGI[c]	SEGS[d]		
Mexicali 75	9	8	26	37	1:1:6:8 = 5.76, $P > 0.1$	2
Yavaros 79	7	4	34	35	1:1:6:8 = 2.16, $P > 0.5$	2
Altar 84	1	1	47	31	1:1:36:26 = 0.26, $P > 0.9$	3
Carcomun	1	1	50	28	1:1:36:26 = 1.28, $P > 0.5$	3
Diver	4	4	36	36	1:1:6:8 = 2.00, $P > 0.5$	2
Kingfisher	8	5	31	36	1:1:6:8 = 2.23, $P > 0.5$	2
Morus	2	1	40	37	1:1:36:26 = 1.68, $P > 0.5$	3
Somorguho	5	4	31	40	1:1:6:8 = 0.23, $P > 0.9$	2
Totanus	2	1	49	28	1:1:36:26 = 1.48, $P > 0.5$	3

[a] Homozygous for parental-type resistance (homozygous for all resistance alleles).
[b] Homozygous for parental-type susceptibility (homozygous, lacking all resistance alleles).
[c] Either segregating or homozygous for disease levels higher than that of the resistant parent but less than that of the susceptible parent (homozygous for at least one resistance allele).
[d] Segregating with disease levels reaching the susceptible parent's response (heterozygous for at least one locus and homozygous for susceptibility alleles at other loci).

Table 6. Comparison of adult-plant disease severity (only highest response range presented) of F_3 lines, with a homozygous seedling IT 12, from the crosses of DW7276 with four resistant parents

Resistant parent	Number of F_3 lines with plants of highest severity[a]					
	t	10	20	30	40	60
Altar 84	1	1	2	3	5	6
Carcomun	1	2	3	4	6	8
Morus	2	2	3	3	5	7
Totanus	2	1	3	2	4	5

[a] Based on modified Cobb scale (10), where t = trace, 5 = 5% ... 100 = 100%.

For example, five F_3 lines from the cross of Yavaros 79 with Diver displayed only trace leaf rust severity (Table 3), while the two parents displayed 20 and 10% severity (Table 1), respectively.

Some, if not all, adult-plant resistance genes in CIMMYT durum wheat germ plasm can be traced to Iumillo. Iumillo, which is susceptible at the seedling growth stage, displays only trace leaf rust severity in Mexico and is known to be resistant globally. However, the genetic basis of its resistance is unknown. Mexicali 75, Yavaros 79, and Altar 84, released for cultivation during 1975, 1979, and 1984, respectively, have maintained their resistance in Mexico. The resistance of Altar 84 is also very effective worldwide (1,2,4,5).

We believe that the resistance of Altar 84 and several other CIMMYT durums could be of a durable nature because of its long-term effectiveness in Mexico and various other countries, and because two or three additive genes are involved. Most known durable resistances to rust diseases are known to involve a few additive genes (3,6–9,13).

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