Resistance to Stripe Rust in Five Durum Wheat Cultivars

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ABSTRACT

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Durum wheat (*Triticum turgidum*) cultivars developed by the International Maize and Wheat Improvement Center (CIMMYT) are currently grown on more than 8 million hectares worldwide. Because of the lack of information on the genetic basis of resistance to stripe rust (caused by *Puccinia striiformis*), crosses in a diallel arrangement (without reciprocals) were made among five worldwide resistant cultivars and the susceptible cultivar Local Red. Inheritance of resistance was investigated in seedling and adult plant growth stages of F_2 populations, and F_3 lines. The low seedling infection type of each resistant cultivar, namely Kroub 76, Chonta Inia, Sna 3, Syros, and Arena, was based on the additive action of the same two genes. Each of these genes conferred intermediate infection types when present alone. The field resistance of the cultivars was based on the additive action of the two genes identified in the seedlings and one additional, partially effective adult resistance gene. Segregation for plants with stripe rust severities higher than that of the parents in intercrosses of resistant cultivars indicated that some genetic diversity exists for adult genes. The resistance of these cultivars may prove to be long-lasting, since it results from the combined action of at least three genes.

Durum wheat (*Triticum turgidum* L.) is grown on approximately 17 million hectares (2), mostly in the Middle East, North Africa, the Indian subcontinent, and Mediterranean Europe. Other areas include parts of Ethiopia, Argentina, Chile, Mexico, the United States, and Canada. Stripe rust (caused by *Puccinia striiformis* Westend.) is an important disease that can cause significant losses to durum production in cool and humid regions (23,24). Frequent stripe rust epidemics have been reported in Iran (4), Yemen, Egypt, and Turkey (23). Although a few cultivars in India are known to be resistant to the disease, the area under durum wheat cultivation may have greatly diminished, partly because most cultivars are highly susceptible (24). Durum wheat germ plasm has been evaluated for stripe rust resistance in various countries, and resistant sources have been reported in land races from Israel (26) and Jordan (13). Mamluk (23) tested 216 durum cultivars in the field and found that 32% were resistant. We have observed a wide range of seedling and adult resistance to stripe rust in cultivars from various countries (H. Ma, R. P. Singh, and O. Abdalla, *unpublished*). Multilocal testing of advanced breeding lines is an integral part of the durum wheat

improvement program at the International Maize and Wheat Improvement Center (CIMMYT). Such evaluation exposes germ plasm to a wide array of races of *P. striiformis* and aids in the identification of parents with worldwide resistance. Results of the international screening nurseries indicate that the level of resistance to stripe rust for CIMMYT durum germ plasm has increased in recent years; this improved resistance is believed to be due to the accumulation of several resistance genes (1). However, information on the inheritance and genetic diversity of stripe rust resistance in durum wheats is limited, and almost nonexistent for CIMMYT durums that are grown on a large area worldwide. Macer (22) identified major gene *Yr7*, which confers seedling resistance in the land race Iumillo. However, this gene is not effective against *P. striiformis* races present in Mexico and most other countries (15). Minor genes with additive effects have also been reported in durums (18). *Triticum dicoccoides*, an ancestor of cultivated durum wheat, possesses useful stripe rust resistance that is controlled by major (8,11), minor (8,30), or temperature-sensitive genes (9,10).

The objectives of the current study were to determine (i) the genetic basis of stripe rust resistance in seedlings and adult plants of five worldwide resistant durum wheat cultivars, and (ii) the relationship of the genes involved in the resistance of these cultivars.

MATERIALS AND METHODS

The five resistant durum wheat cultivars included in the study were Kroub 76,

Chonta Inia, Sna 3, Syros, and Arena (Table 1). Kroub 76, Chonta Inia, Sna 3, and Syros originated from CIMMYT's durum wheat breeding program and have been released in different countries. The pedigree of the Italian cultivar Arena is not known; however, it may also be of CIMMYT origin. The five resistant parents have also shown high levels of stripe rust resistance when tested internationally in CIMMYT's International Durum Screening Nurseries for several years (5-7).

The *P. striiformis* race used in all studies was 14E14 (16), which is virulent to stripe rust resistance genes *Yr2*, 3, 6, 7, and A. Race 14E14 is the predominant race in the highlands of Mexico, where the studies were conducted. Vacuum-dried (32) urediniospores of this race are stored at CIMMYT. Fresh inoculum obtained by multiplying urediniospores on the susceptible cultivar Morocco was used in the study.

Crosses were made among resistant durums in a diallel arrangement without reciprocals. Resistant durums were also crossed with the susceptible female parent Local Red. Inheritance studies were based on F_2 populations, and individual F_2 -plant-derived F_3 lines were obtained from two or three individual F_1 plants. Disease data for F_1 plants are not available because they were grown during the off-season.

Between 188 and 338 F_2 seedlings, as well as 115 and 180 individual F_2 -plant-derived F_3 lines, from crosses of Local Red with five resistant parents, were classified at the seedling stage for their infection types. Individual F_3 family size consisted of 30 to 40 seedlings. Between 108 and 253 F_2 seedlings from each intercross involving resistant parents were also evaluated. Nine-day-old seedlings of the parents, F_2 , and F_3 lines, were inoculated by spraying urediniospores suspended in Sol-trol 170, a lightweight mineral oil, at a concentration of approximately 4 to 5 mg/ml. After inoculation, plants were placed in a dew chamber for 18 h at 10 to 14°C and then transferred to the greenhouse under 16-h light and 8-h dark photoperiod and 15 to 20°C temperature. Inoculation was repeated 3 days later to avoid any escape. Infection type (IT) data based on a 0 to 9 scale (20) were recorded approximately 3 weeks after inoculation.

For susceptible $\times$ resistant crosses, frequencies of the F_2 seedlings rated as resistant (IT 0 to 3, no visible symptoms to necrotic and/or chlorotic blotches or stripes with trace sporulation) and intermediate

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(IT 4 to 6, necrotic and/or chlorotic blotches or stripes with light to moderate sporulation) were pooled for the chi-square analyses. The susceptible group included all seedlings rated as IT 7 to 9 (slightly necrotic and/or chlorotic blotches or stripes with abundant sporulation to abundantly sporulating blotches or stripes with no chlorosis or necrosis). The F_3 lines were grouped into three categories, namely, homozygous parental type resistant (all seedlings with ITs within the range of the resistant parent), segregating-intermediate (ITs of the seedlings ranging from resistant to intermediate, resistant to susceptible, intermediate to susceptible, or homozygous intermediate), and homozygous parental type susceptible (all seedlings with ITs within the range of the susceptible parent). Chi-square analyses were carried out to test the distribution of observed F_2 and F_3 phenotypic frequencies against those expected for a two-gene segregation model.

Field evaluations of parents and F_2 populations from the resistant $\times$ resistant crosses were conducted at CIMMYT's research station near Toluca, Mexico State, during the 1994 crop season. Approximately 150 F_2 seeds from each cross were planted 20 cm apart in three 75-cm-wide paired row plots of 5-m length. Spreader rows of cultivar Morocco were sown down the middle of the 1-m pathway on both sides of the plots. Ninety F_3 lines from

each of the resistant $\times$ resistant crosses and between 115 to 180 lines from the susceptible $\times$ resistant crosses were grown at INIFAP's (National Forestry, Agriculture and Livestock Research Institute) research station near Celaya (Guanajuato State) during the 1994-95 season. Approximately 60 seeds of each F_3 line were sown in 75-cm-wide paired row plots of 1-m length with 20-cm row spacing and a 50-cm pathway between plots. Rows of the two parents were planted at the beginning of each F_3 population. The stripe rust epidemic was initiated approximately 1 month after sowing by inoculating spreader rows of Morocco planted on one side of the plots in the pathway. Both field sites, namely Toluca and Celaya, are located in the highlands and have a favorable environment for stripe rust development. Disease severity of each F_2 plant was rated following the Modified Cobb Scale (27) when plants of the susceptible check Local Red displayed 80 to 100% severity. Severity range for each F_3 line was recorded twice; first when the susceptible parent Local Red had 80 to 100% severity and approximately 2 weeks later when stripe rust had dried out the leaves of Local Red. Previous studies at CIMMYT (39) showed that the timing of the first rating is critical for identifying plants or lines that are similar in susceptibility level to the susceptible parent; whereas the second rating

time is critical for identifying plants or lines that are similar in resistance level to the resistant parent. On the basis of the two data sets, F_3 lines from the susceptible $\times$ resistant crosses were grouped into three categories as described earlier for seedling studies. Chi-square analyses were again carried out.

RESULTS

Seedling studies. Seedlings of all five resistant parents displayed low infection types compared to the susceptible parent Local Red when tested with *P. striiformis* race 14E14 (Table 1). Chonta Inia had the lowest IT range, followed by Kroub 76, Arena, Sna 3, and Syros.

F_2 populations from crosses of Local Red with five resistant parents segregated for seedlings with a range of resistant, intermediate, and susceptible ITs (Table 2). Frequencies of seedlings considered to have some resistance (ITs between 0 and 6) versus those considered to be susceptible (ITs between 7 and 9) were in accordance with a 15:1 ratio for each cross. This ratio is expected for segregation of two partially dominant resistance genes. The distribution of F_3 lines in each cross conformed to a ratio of 1 homozygous parental type resistant to 14 segregating-intermediate to 1 homozygous parental type susceptible, expected for segregation of two genes having additive action. Intermediate ITs were observed when resistance genes were present alone.

F_2 populations obtained from the intercrosses of resistant parents had some seedlings with slightly higher ITs than those of the parents (Table 3). Lack of seedlings with susceptibility (IT 7 to 9) indicated that the resistant parents may carry at least one common gene.

Field studies. The resistant parents showed a high level of resistance in field tests at both locations (Table 1). The maximum disease recorded was 5MR for each resistant parent, compared to 100S for Local Red.

Comparison of seedling and adult reactions of the F_3 lines from crosses of Local Red with the five susceptible parents is given in Table 4. Only a few lines classified as homozygous parental type resistant

Table 1. Durum wheat cultivars, country of release, seedling infection type with *Puccinia striiformis* race 14E14, and adult ratings with the same race at two locations

Parent	Country of release	Seedling infection type ^a	Adult rating ^b	
			Toluca 1994	Celaya 1994-95
Kroub 76	Algeria	1 to 2	5MR	5MR
Chonta Inia	Chile	0 to 2	1MR	5MR
Sna 3	Chile	1 to 3	5MR	5MR
Syros	Greece	1 to 3	5MR	5MR
Arena	Italy	1 to 2	5MR	5MR
Local Red	India	7 to 9	100S	100S

^a Based on a 0 to 9 scale (20), where 0 = no visible symptom, 1 = necrotic and/or chlorotic flecks without sporulation, 2 = necrotic and/or chlorotic blotches or stripes without sporulation, 3 = necrotic and/or chlorotic blotches or stripes with trace sporulation, 7 = necrotic and/or chlorotic blotches or stripes with abundant sporulation, 8 = chlorosis behind the abundantly sporulating area, and 9 = abundant sporulation with no chlorosis or necrosis.

^b Rating includes two components: disease severity based on the Modified Cobb Scale (27), where 1 = 1%, 5 = 5%, up to 100 = 100%; and host response based on scale described by Roelfs et al. (32), where MR = moderately resistant and S = susceptible.

Table 2. Seedling classification and chi-square analysis of F_2 populations and F_3 lines in the crosses of susceptible Local Red with resistant durums inoculated with *Puccinia striiformis* race 14E14

Cross	F ₂				F ₃				
	No. of seedlings ^a		χ ² 15:1, P value	Estimated gene no.	No. of lines ^b			χ ² 1:14:1, P value	Estimated gene no.
	R/Int	S			HPTR	Seg/Int	HPTS		
Local Red × Kroub 76	185	14	0.2, <i>P</i> > 0.50	2	9	94	12	4.5, <i>P</i> > 0.10	2
Local Red × Chonta Inia	174	14	0.2, <i>P</i> > 0.50	2	15	151	14	2.6, <i>P</i> > 0.25	2
Local Red × Sna 3	322	16	1.0, <i>P</i> > 0.25	2	14	152	14	1.9, <i>P</i> > 0.25	2
Local Red × Syros	224	12	0.4, <i>P</i> > 0.50	2	9	99	9	1.3, <i>P</i> > 0.50	2
Local Red × Arena	230	16	0.0, <i>P</i> > 0.99	2	10	154	16	2.5, <i>P</i> > 0.25	2

^a R/Int = resistant-intermediate (IT 0 to 6), S = susceptible (IT 7 to 9).

^b HPTR = homozygous parental type resistant, ITs of seedlings within the range of the IT of the resistant parent; Seg/Int = segregating-intermediate, ITs of seedlings in a family range from resistant to intermediate, resistant to susceptible, intermediate to susceptible, or homozygous intermediate; HPTS = homozygous parental type susceptible, ITs of seedlings within the range of the IT of the susceptible parent.

(HPTR) as seedlings were HPTR in the field. The remaining lines either segregated for plants with somewhat higher (up to 30MR reaction) disease levels or were homozygous for plants with somewhat higher disease levels. F₃ lines classified as segregating-intermediate (Seg/Int) were also Seg/Int in field tests. F₃ lines classified homozygous parental type susceptible

(HPTS) as seedlings were either HPTS in the field, or segregated, or homozygous for plants with intermediate responses (40 to 60MR). Distribution of F₃ lines in each cross-conformed with the ratio expected for segregation of three independent resistance genes (Table 4). Two of these genes also conferred seedling resistance; whereas an additional gene was involved in adult

resistance. Although this adult resistance gene conferred only moderate resistance when present alone, it must have enhanced the effects of the seedling resistance genes to confer the high levels of adult resistance seen in the cultivars.

The F₂ and F₃ results for intercrosses involving the resistant parents are summarized in Table 5. A few plants in each cross displayed stripe rust severities higher than the parents; however, none were as susceptible as Local Red. This indicated that the resistant parents probably have at least one resistance gene in common. Ninety F₃ lines from each cross were also evaluated to verify F₂ results (Table 5). Although limited segregation was observed in each cross, the highest stripe rust severity for plants in any line was 30% or less. F₃ lines from crosses of Chonta Inia with Sna 3, Syros, or Arena had the least variation for disease severity; the highest severity recorded was 10%. Overall results indicated that at least one or two genes are common in the resistant parents.

Table 3. Distribution of F₂ seedlings by infection types in resistant × resistant crosses infected with *Puccinia striiformis* race 14E14

Cross	No. of F ₂ seedlings with infection type ^a					Total
	0	1	2	3	4	
Kroub 76 × Chonta Inia	15	25	70	36 ^{ab}	5*	151
Kroub 76 × Sna 3	0	20	40	40	8*	108
Kroub 76 × Syros	0	77	121	40	2*	240
Kroub 76 × Arena	0	49	141	43*	4*	237
Chonta Inia × Sna 3	45	62	81	35	14*	251
Chonta Inia × Syros	59	70	91	31	2*	253
Chonta Inia × Arena	11	13	82	91	7*	204
Sna 3 × Syros	0	11	68	131	19*	229
Sna 3 × Arena	0	10	65	127	33*	235
Syros × Arena	0	13	71	42	2*	128

^a Based on a 0 to 9 scale (20), where 0 = no visible symptom, 1 = necrotic and/or chlorotic flecks without sporulation, 2 = necrotic and/or chlorotic blotches or stripes with trace sporulation, 3 = necrotic and/or chlorotic blotches or stripes with trace sporulation, and 4 = necrotic and/or chlorotic blotches or stripes with moderate sporulation.

^b Infection type of the seedlings higher than the parental range.

Table 4. Seedling and field responses of F₃ lines from the crosses of Local Red with the resistant parents when inoculated with *Puccinia striiformis* race 14E14

Response ^a		No. of F ₃ lines when crossed with Local Red				
Seedling	Field	Kroub 76	Chonta Inia	Sna 3	Syros	Arena
HPTR	HPTR	2	3	2	2	3
HPTR	Seg/Int	7	12	12	7	10
HPTR	HPTS	0	0	0	0	0
Seg/Int	HPTR	0	0	0	0	0
Seg/Int	Seg/Int	94	151	152	99	154
Seg/Int	HPTS	0	0	0	0	0
HPTS	HPTR	0	0	0	0	0
HPTS	Seg/Int	8	9	10	6	8
HPTS	HPTS	4	5	4	3	6
Total		115	180	180	117	180
χ ² 1:3:0:0:56:0:3:1		4.96	2.55	1.93	1.65	3.27
P value		>0.75	>0.90	>0.90	0.99	>0.90
Estimated no. of genes		3	3	3	3	3

^a HPTR = homozygous parental type resistant, responses of plants within the range of the resistant parent; Seg/Int = segregating-intermediate, responses of plants within a family range from resistant to intermediate, resistant to susceptible, intermediate to susceptible, or homozygous intermediate; HPTS = responses of plants within the range of the susceptible parent.

DISCUSSION

Two resistance genes were involved in the seedling resistance of each of five worldwide resistant durum wheat cultivars when the cultivars were tested with *P. striiformis* race 14E14. These genes appeared to confer an intermediate infection type (IT 4 to 5) when present alone. The combination of these two genes resulted in lower ITs (0 to 3) characteristic of the resistant parents, indicating that the two genes complemented each other (Table 2). This was supported by the fact that only a few (1/16) F₃ lines were as resistant as the resistant parent, and similarly, that the same proportion of lines was as susceptible as the susceptible parent (Table 2). Additive gene action is known for rust resistance genes that confer intermediate seedling infection types (17,33,34,36). Limited segregation in intercrosses of the resistant parents indicated that these durums share common resistance genes. Although the five durum parents have been released in four different countries, they are derived from CIMMYT germ plasm. This explains their limited, or lacking, genetic diversity for seedling re-

Table 5. Field responses of F₂ and F₃ populations in the resistant × resistant crosses when inoculated with *Puccinia striiformis* race 14E14

Cross	F ₂				F ₃						
	Plants in disease severity ^a range			Total	Lines with plants of greatest disease severity ^a						Total
	0 to 5	10 to 15	20 to 40		1	5	10	15	20	30	
Kroub 76 × Chonta Inia	110	2	0	112	6	56	16	6	3	3	90
Kroub 76 × Sna 3	108	2	0	110	11	33	14	14	16	2	90
Kroub 76 × Syros	112	4	0	116	16	42	19	3	9	1	90
Kroub 76 × Arena	112	1	0	113	17	39	20	9	5	0	90
Chonta Inia × Sna 3	124	1	0	125	46	39	5	0	0	0	90
Chonta Inia × Syros	129	3	0	132	76	11	3	0	0	0	90
Chonta Inia × Arena	117	5	0	122	73	13	4	0	0	0	90
Sna 3 × Syros	103	16	6	125	36	38	7	5	4	0	90
Sna 3 × Arena	133	5	4	142	45	27	8	7	3	0	90
Syros × Arena	101	8	3	112	21	37	15	11	6	0	90

^a Disease severities based on Modified Cobb Scale (27), where 0 = 0%, 1 = 1%, 5 = 5%, up to 100 = 100%.

sistance genes. Each cultivar also carries an additional adult resistance gene. At least some genetic diversity was evident in intercrosses of the resistant parents. Adult genes were only partially effective when present alone, but their presence increased the level of adult resistance conferred by seedling genes. Such additive action involving seedling and adult rust resistance genes has been observed in other studies (12,37,38).

Despite the fact that the stripe rust resistance of these durums is currently effective all over the world, the limited genetic diversity for resistance observed in this study may be cause for concern. Earlier studies on resistance to leaf and stem rusts in selected CIMMYT durums indicated a similar situation (36,37). Evaluation of stripe rust resistance of other durums of CIMMYT origin having adequate field resistance showed that several of them were only moderately resistant; whereas others were susceptible as seedlings (21; H. Ma, R. P. Singh, and O. Abdalla, *unpublished*). Our preliminary results (*unpublished*) indicated that such adult resistance is based on additive action of three to five partially effective genes. This kind of adult stripe rust resistance is quite common in hexaploid wheats (3,14,18,19, 25,28,29,35,40). Stripe rust has not yet posed a major threat to CIMMYT-derived durum cultivars. It is possible that most seedling and adult resistance genes in CIMMYT durums are only partially effective. Therefore, selection of high resistance levels in the field would indirectly enhance the accumulation of necessary seedling and adult genes that act additively. Resistances based on combinations of effective genes are likely to be longer lasting than those based on single genes (31).

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