New Genes for Leaf Rust Resistance in CIMMYT Durum Wheats

S. A. Herrera-Foessel, Dept. of Ecology and Crop Production Sciences, Swedish University of Agricultural Sciences (SLU), Box 7043, S 750 07 Uppsala, Sweden; **R. P. Singh**, International Maize and Wheat Improvement Center (CIMMYT), Apdo. Postal 6-641, 06600 México, D.F., México; **J. Huerta-Espino**, Campo Experimental Valle de México INIFAP, Apdo. Postal 10, 56230, Chapingo, Edo de México, México; and **J. Yuen** and **A. Djurle**, Dept. of Ecology and Crop Production Sciences, Swedish University of Agricultural Sciences (SLU), Box 7043, S 750 07 Uppsala, Sweden

ABSTRACT

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Leaf rust, caused by *Puccinia triticina*, has become an important disease of durum wheat (*Triticum turgidum*) in Mexico since the detection in 2001 of BBG/BN, a new race virulent on all common cultivars and on more than 80% of CIMMYT's durum wheat collection. We investigated the genetic basis and diversity of resistance in nine durum genotypes that are highly resistant to the new race. These resistant durums were crossed with the susceptible cv. Atil C2000 and intercrossed in a half diallel arrangement. Five diverse sources of resistance were identified by evaluating parents, F₁, F₂, and F₃ populations in greenhouse and/or field trials under artificial epidemics of race BBG/BN. The same pair of partially dominant complementary genes determined resistance in Jupare C2001, Hualita, and Pohowera. Somateria and Llaleta INIA shared the same dominant resistance gene, whereas a partially dominant gene conferred resistance in two sister lines, Guayacan 2 and Guayacan INIA. A different partially dominant gene present in Storlom was linked in repulsion to another partially dominant gene in Camayo. These diverse resistance genes can be used effectively to control leaf rust, preferably by deploying them in combinations.

Additional keywords: brown rust, genetic analysis, inheritance study, *Puccinia recondita* f. sp. *tritici*, *Triticum turgidum* var. *durum*

Durum wheat (*Triticum turgidum* L. var. *durum*) is grown on approximately 17 million hectares worldwide. Leaf rust caused by *Puccinia triticina* Eriks. is an important disease that causes significant durum production losses. In Mexico, durum wheat remained highly resistant to leaf rust until 2001, when a new race, designated BBG/BN, was detected (23). Over 80% of the entire CIMMYT durum wheat collection and the most popular Mexican cultivar, Altar C84, which had remained resistant for 16 years, proved susceptible to the new race. Altar C84 and several other breeding lines carried the same partially dominant seedling resistance gene that conferred resistance to race BBB/BN, prevalent on durum wheat in Mexico during the 1980s and 1990s (22). These cultivars also carried one or two additional minor genes for slow rusting resistance in adult plants. The gene that conferred seedling resistance to race BBB/BN in Altar

C84 and other CIMMYT durums remains undesignated. The leaf rust epidemics on durum wheat during 2001, 2002, and 2003, caused by the new race BBG/BN, resulted in estimated losses of about US\$32 million to Mexican farmers (23).

Although durum wheat showed high susceptibility to the new race in Mexico, bread wheat cultivars in neighboring fields were not affected. Previous reports have revealed differences in virulence specificity of leaf rust races isolated from durum and bread wheat. In 1988 and 1989, Singh (20) studied the pathogenic variation of leaf rust in wheat-growing areas of Mexico and found that race BBB/BN predominated in durum wheat collections, while races TCB/TD and TBD/TM predominated on bread wheat. Huerta-Espino and Roelfs (5) compared leaf rust collections taken globally from durum and bread wheats and reported that races isolated from durum wheat differed in virulence from those collected from bread wheat. The leaf rust isolates collected from durum wheat were avirulent to most of the near-isogenic Thatcher lines used as differentials, suggesting that these lines may not be the most useful in differentiating the durum leaf rust races. Recently, Ordonez et al. (11) also indicated a high degree of avirulence for known leaf rust resistance genes

in leaf rust populations collected in France, Spain, Ethiopia, the United States, Mexico, Chile, and Argentina. Furthermore, their results revealed a high degree of similarity in avirulence–virulence characteristics of races from Europe, South and North America, and Mexico.

Compared with bread wheat, little is known regarding leaf rust resistance in durum wheat. Of the 50 designated resistance genes in wheat, only two, *Lr14a* and *Lr23*, originated from tetraploid wheat. The acreage in developing countries that is sown to CIMMYT-derived durum wheats (i.e., those with at least one CIMMYT parent) accounts for a major part of the total durum area (13). Increased knowledge of the genetic basis of resistance that is effective against the new Mexican race (BBG/BN) is of high importance to enhance the genetic diversity of resistance in CIMMYT germ plasm and future durum wheat cultivars. Following the detection of the BBG/BN race in Mexico, sources of resistance were identified after screening thousands of germ plasm lines from the CIMMYT durum wheat-breeding program.

The objective of our study was to determine the genetic basis and genetic diversity of resistance in nine durum wheat genotypes that are resistant to Mexican *P. triticina* race BBG/BN.

MATERIALS AND METHODS

The nine resistant durum wheat parents included in the study were Jupare C2001, Hualita, Pohowera, Somateria, Llaleta INIA, Camayo, Storlom, Guayacan 2, and Guayacan INIA. The susceptible durum wheat parent was Atil C2000. Pedigrees and selection history of each of the durum wheats are listed in Table 1. Jupare C2001, released in 2001, is the most commonly grown Mexican cultivar. Both Llaleta INIA and Guayacan INIA were released in Chile in 1997 (14,15). Other parents are advanced CIMMYT breeding lines. Atil C2000, the susceptible parent, was released for cultivation in Mexico in 2000 but proved susceptible to race BBG/BN.

The resistant parents were crossed with the susceptible Atil C2000 and also intercrossed in a half-diallel arrangement, i.e., in all possible combinations without the reciprocals. Space-sown F₁ plants were harvested individually to obtain F₂ prog-

Corresponding author: S. A. Herrera-Foessel
E-mail: sybil.herrera@evp.slu.se

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eny. For each susceptible × resistant cross, approximately 98 F₃ lines were obtained by harvesting space-sown individual F₂ plants derived from two different F₁ plants. Genetic analysis was based on the leaf rust response data for parents, F₁ plants, F₂ populations, and F₃ families, and was conducted in the field at CIMMYT's research station in El Batán, Mexico, during 2003. The parents and the F₁ of the resistant × susceptible crosses were also evaluated in the greenhouse for infection type responses at both seedling and adult plant stages.

The *P. tritricina* race BBG/BN used in this study has the following avirulence–virulence formula (23): *Lr1,2a,2b,2c,3,3bg,3ka,9,12,13,14a,15,16,17,18,19,21,24,25,26,27+31,28,29,30,32,34,35,36,37/10,11,14b,20,23,33*.

In greenhouse trials, the parents and F₁ plants from susceptible × resistant crosses were inoculated at the seedling (two-leaf stage) and adult plant stages (seven-leaf stage) by spraying urediniospores suspended in Soltrol 170, a light mineral oil, at a concentration of 2 to 3 mg/ml. Plants were placed in a dew chamber overnight to ensure spore germination and completion of the infection process, and then transferred to a greenhouse kept at 18 to 25°C. Infection types displayed by the leaves were recorded about 10 days after inoculation according to a 0-to-4 scale (17).

The field trial was grown on 0.75-m-wide raised beds with paired rows 0.2 m apart. Approximately 60 seeds of parents and F₃ lines were sown as 0.8-m-long paired rows with 0.4-m alleys. Twelve F₁ plants were space-sown 10 to 15 cm apart in plots of the same size, and 50 to 100 F₂ plants derived from three different F₁ plants were space-sown on three pairs of rows 5 m in length. This F₂ planting arrangement allowed us to evaluate 150 to 300 F₂ plants per cross. Spreaders of susceptible Atil C2000 were planted around the field and as hills in the middle of the pathway on one side of each plot. To initiate the disease epidemic, spreaders were inoculated on 18 June (about a month after planting) and 25 June 2003, using a hand-held sprayer containing urediniospores suspended in Soltrol 170. Rust severity and host response to infection were recorded

for the parents five times at weekly intervals starting on 15 July, when the flag leaves of Atil C2000 were fully expanded. Disease data for the F₁, F₂, and F₃ were recorded between 29 July and 2 August, the last date being when the susceptible parent Atil C2000 displayed a 100S response. Percent rust severity on flag leaves of parent, F₁, and F₂ plants was estimated using the modified Cobb scale (12). Host response to infection was recorded according to Roelfs et al. (17). Although some variation in percent severity was noted in a few crosses, for simplicity each F₃ line was classified as homozygous resistant (HR), segregating (Seg), or homozygous susceptible (HS) based on reaction and severity. The comparison between the observed phenotypic distributions of segregating populations (in the F₂ and F₃ generations) and the expected ratio was performed by chi-squared (χ^2) tests.

RESULTS

Responses of the parents. Of the parents, only Atil C2000 displayed susceptible infection type responses in the green-

house as seedling and as adult plant (Table 2). Five of the nine resistant parents displayed mesothetic infection types X–, X, or X+ at the seedling stage. However, when evaluated as adult plants, the infection types of the parents were generally lower, except for Camayo, which displayed infection type 1+ as seedling and 3C as adult plant. Storlom, the most resistant parent, displayed infection types ; at the seedling stage and 0; at the adult plant stage. In adult plant, the infection type for Jupare C2001 and Pohowera was ;1–, which was similar to infection type ;1 displayed by Guayacan 2 and Guayacan INIA. Both Hualita and Somateria displayed infection type X–, which was similar to infection type X displayed by Llaret INIA. Seedling and adult plant infection type data thus indicated phenotypic diversity among parents.

In the field trial, the nine resistant parents showed high levels of resistance. When Atil C2000 displayed 100% severity, five parents (Jupare C2001, Hualita, Pohowera, Somateria, and Storlom) were immune to leaf rust; Llaret INIA, Guay-

Table 2. Greenhouse and field responses of parents and F₁ plants from the crosses of susceptible parent Atil C2000 with nine resistant parents when inoculated with *Puccinia tritricina* race BBG/BN

Parent	Parental response			F ₁ response	
	Greenhouse ^a		Field ^b	Greenhouse ^a	
	Seedling	Adult		Adult	Field ^b
Resistant					
Jupare C2001	X–	;1–	0	3+	30M
Hualita	X–	X–	0	3+	5MR
Pohowera	X	;1–	0	3+	5MR
Somateria	X+	X–	0	X+3	0
Llaret INIA	3C	X	1R-MR	X+3	1R-MR
Camayo	1+	3C	5-10R	3C	50M
Storlom	;	0;	0	;	20M
Guayacan 2	X	;1	1R-MR	X	50MS
Guayacan INIA	;1	;1	1R-MR	3C3	60MS
Susceptible					
Atil C2000	3+	3+	100S	3+	100S

^a Infection types are based on a 0-to-4 scale (17), where 0 = no uredinia or other macroscopic signs of infection, ; = no uredinia, but hypersensitive necrotic or chlorotic flecks of varying sizes present, 1 = small uredinia surrounded by necrosis, 2 = small to medium uredinia surrounded by green islands, X = random distribution of variable-sized uredinia on single leaf with a pure culture, 3 and 4 = medium and large uredinia, respectively, without chlorosis or necrosis, + and – = uredinia somewhat larger and smaller, respectively, than normal for infection type, C = more chlorosis than normal for the infection type. More than one designation represents a range of infection types.

^b Field disease ratings have two components: disease severity and host response to infection. Severity follows the modified Cobb scale (12), and host response to infection are R = resistant, MR = moderately resistant, MS = moderately susceptible, M = MR-MS, and S = susceptible (17).

Table 1. Pedigrees and selection histories of the *Triticum turgidum* parents included in the study

Parent	Cross	Selection history ^a
Jupare C2001	Stinkpot//Altar 84/Alondra	CD91Y636-1Y-040M-030Y-1M-0Y-0B-1Y-0B
Hualita	Rascon_21/Longshanks	CDWS91M377-9M-030Y-030M-1Y-0M
Pohowera	Chen/Altar84//Hui/Tub/3/CMH82A.1062/Rissa	CD90226-501M-503YRC-502B-0Y
Somateria	Srn_1/6/Fgo/Dom//Nach/5/Altar84/4/Garza/Afn//Cra/3/Ggovz394/7/Eudo	CD89529-040PAP-030Y-040M-2Y-0PAP-1Y-0B
Llaret INIA	(D67.54.4 ^a .9A//Jori 'S' × Rosner Durum 119-200-4Y) Sahel 77	CD 64399-4p-2p-3p
Camayo	Eth-Lrbr A1-133/3*Altar 84	CDSP91B931-A-1H-030Y-030M-3Y-0M-1Y-0B
Storlom	Sitella/3 Musk_4	CD91Y1719-B-11Y-040M-030Y-2M-1Y-0B
Guayacan 2	Altar 84/Stint//Silver_45	CD80545-A-1Y-030YRC-040M-2YRC-0PAP
Guayacan INIA	Altar 84/Stint//Silver	CD80545-A-1Y-030YRC-049M-3YRC-0PAP
Atil C2000	Sooty_9/Rascon_37	CD91B1938-6M-030Y-030M-4Y-0M-0B-1Y-0B

^a Consists of the cross number and selection identification in different segregating generations.

acan 2, and Guayacan INIA had trace (1%) severity with resistant or moderately resistant reactions; and Camayo displayed 5 to 10% rust with a resistant reaction (Table 2).

Responses of F₁ plants of susceptible × resistant crosses. In the greenhouse tests, the F₁ adult plants produced by crossing Atil C2000 with Jupare C2001, Hualita, and Pohowera, respectively, displayed susceptible infection type 3+, indicating that the resistance was recessive (Table 2). The infection types of F₁ plants produced by crossing Atil C2000 with Camayo and Storlom, respectively, were very similar to the infection types of their respective parents, indicating that the resistance was dominant. In contrast, the infection types displayed by F₁ plants of the remaining four crosses were higher than those displayed by the respective parents, but not compatible, indicating the partially dominant nature of the resistance.

In the field trial, responses of F₁ plants ranged from 0 to 60MS compared with the 100S response of the susceptible parent Atil C2000, indicating that resistance was either dominant or partially dominant (Table 2). Field results were thus different from greenhouse results for several crosses. Only Somateria and Llareta INIA

displayed F₁ responses similar to those of the resistant parents, indicating that the resistance was dominant. Rust severities and reactions of the F₁ plants of the remaining seven crosses were higher than those of their respective resistant parents, indicating that the resistance was partially dominant.

F₂ and F₃ segregation in susceptible × resistant crosses. The F₂ populations from crosses of susceptible Atil C2000 with resistant Jupare C2001, Hualita, Pohowera, Guayacan 2, and Guayacan INIA, respectively, had a greater number of susceptible plants than expected for segregation of a single dominant or partially dominant resistance gene (Table 3). The frequencies of resistant and susceptible plants in the crosses involving Jupare C2001, Pohowera, Guayacan 2, and Guayacan INIA as resistant parents conformed to a 9:7 ratio ($P \geq 0.05$), which is as expected for the segregation of two dominant–partially dominant complementary genes. In the cross with Hualita as the resistant parent, the segregation conformed to a 7:9 ratio, indicating the presence of two recessive genes. Distributions of homozygous resistant (HR), segregating (Seg), and homozygous susceptible (HS) F₃ lines in Jupare C2001 and Pohowera crosses were in ac-

cordance with a 1:8:7 ratio, further supporting the hypothesis that two complementary genes conferred resistance. Also, the F₃ lines in the cross involving Hualita were distributed in accordance with a 1:8:7 ratio, indicating the presence of two complementary genes. The F₃ distributions for crosses involving Guayacan 2 and Guayacan INIA showed a better fit with a 1:2:1 ratio, which is as expected for segregation of a single resistance gene, although the P value in the χ^2 test for the latter cross was only 0.02.

The F₂ populations originating from crosses involving Atil C2000 as the susceptible parent and Somateria, Llareta INIA, Camayo, and Storlom as the resistant parents segregated according to a 3:1 ratio ($P \geq 0.05$), indicating that a single dominant gene conferred resistance (Table 3). Distributions of F₃ lines in each cross were also in agreement with F₂ results; however, for the Somateria cross, the P value in the χ^2 test was 0.02 due to a higher number of segregating F₃ lines.

Intercrosses among resistant parents. All F₁ plants from the resistant × resistant crosses were resistant in the field trial (Table 4). Only five of the 36 intercrosses displayed rust severities higher than 0%. This indicated that F₁ plants usually fol-

Table 3. Frequencies of resistant and susceptible F₂ plants; and distributions of homozygous resistant, segregating, and homozygous susceptible F₃ families in crosses of susceptible parent Atil C2000 with nine resistant *Triticum turgidum* parents when tested in the field with *Puccinia triticina* race BBG/BN

Resistant parent	Number of F ₂ plants				Number of F ₃ lines				
	R ^a	S ^b	Exp. ratio	P value for χ^2	HR ^c	Seg ^d	HS ^e	Exp. ratio	P value for χ^2
Jupare C2001	124	100	9:7	0.79	5	45	48	1:8:7	0.56
Hualita	72	123	7:9	0.05	9	37	31	1:8:7	0.14
Pohowera	139	115	9:7	0.62	5	49	42	1:8:7	0.91
Somateria	148	55	3:1	0.49	15	62	21	1:2:1	0.02
Llareta INIA	170	52	3:1	0.59	25	48	25	1:2:1	0.98
Camayo	128	41	3:1	0.82	20	48	30	1:2:1	0.35
Storlom	207	62	3:1	0.46	32	41	19	1:2:1	0.09
Guayacan 2	136	105	9:7	0.95	13	51	24	1:2:1	0.08
Guayacan INIA	125	99	9:7	0.89	33	51	14	1:2:1	0.02

^a Resistant.

^b Susceptible.

^c Homozygous resistant.

^d Segregating.

^e Homozygous susceptible.

Table 4. Reactions of F₁ plants for intercrosses among parents (right diagonal) and frequencies of resistant–susceptible F₂ plants (left diagonal) when evaluated in the field with *Puccinia triticina* race BBG/BN

Number of F ₂ plants	F ₁ reaction ^a								
	Jupare C2001	Hualita	Pohowera	Somateria	Llareta INIA	Camayo	Storlom	Guayacan 2	Guayacan INIA
Jupare C2001		0	0	0	0	0	0	0	0
Hualita	205/0		0	0	0	0	0	0	1MR
Pohowera	210/0	206/0		0	0	0	0	0	0
Somateria	136/29	204/28	243/23		0	0	0	0	0
Llareta INIA	177/6	209/14	206/12	248/0		0	0	0	0
Camayo	139/20	209/20	234/12	187/35	178/27		0	40MR	50MR
Storlom	167/17	224/15	150/11	183/10	202/20	198/0 ^b		15MR	10MR
Guayacan 2	190/32	204/30	140/19	196/35	144/25	206/27	218/34		0
Guayacan INIA	152/35	187/33	206/22	169/41	160/32	223/40	211/44	195/0	

^a Field disease ratings have two components: disease severity and host response to infection. Severity follows the modified Cobb scale (12), and host response to infection are R = resistant, MR = moderately resistant, MS = moderately susceptible, and S = susceptible (17).

^b Fully susceptible plants were absent, but plants with higher disease ratings than expected for either parents or their F₁ were present.

lowed the response of the parent with a higher resistance level. Exceptions were F_1 plants from Guayacan INIA $\times$ Hualita, which displayed responses similar to that of the less resistant parent Guayacan INIA instead of the more resistant parent Hualita. For four crosses, Camayo $\times$ Guayacan 2, Camayo $\times$ Guayacan INIA, Guayacan 2 $\times$ Storlom, and Guayacan INIA $\times$ Storlom, the F_1 plants displayed more susceptible responses than those of their respective parents.

The F_2 field segregation data for the intercrosses indicated that several parents carry common resistance genes due to the lack of susceptible plants in their progeny (Table 4). All F_2 plants were immune (0% rust) in intercrosses among Jupare C2001, Hualita, and Pohowera, indicating that they carried the same pair of complementary resistance genes. Similarly, all F_2 plants of the Somateria $\times$ Llaretia INIA cross showed immunity or trace severity with resistant reaction. The Guayacan 2 $\times$ Guayacan INIA cross also failed to segregate. Although segregation was observed in the Camayo $\times$ Storlom cross, completely susceptible progeny were absent in a population of 198 plants, 135 of which displayed a 0-1R response, 43 scored 5-15MR, 9 scored 30M, 7 scored 50M, 1 scored 60 MS, and 3 scored 70 MS. Several susceptible plants were found in the remaining crosses.

DISCUSSION

We have identified five different sources of resistance to *P. tritici* race BBG/BN among nine CIMMYT durum wheat parents included in the study. Resistance in Jupare C2001, Hualita, and Pohowera was controlled by the same two partially dominant complementary genes (source 1), while the resistance in Somateria and Llaretia INIA was determined by the same single dominant gene (source 2). A single partially dominant gene was found to confer resistance in Camayo (source 3) and another partially dominant gene in Storlom (source 4); however, these two genes seem to be closely linked. A different partially dominant gene was present in sister selections Guayacan 2 and Guayacan INIA (source 5).

Hualita displayed infection type X- in adult plant greenhouse tests, which was somewhat higher than the infection type ;1- displayed by Jupare C2001 and Pohowera, belonging to the same source (Table 2). The seedling infection types and field reactions of all three were the same. The variation observed in adult plant greenhouse trials may therefore be due to the effect of genetic background. The F_1 plants from the crosses of these three durums with susceptible parent Atil C2000 were scored as susceptible in the greenhouse, but resistant in the field. It must be noted that F_1 plants involving Jupare C2001 showed higher disease responses in

the field than F_1 plants involving the other two durums. This indicated that the recessive or dominant nature of resistance or the expression of resistance may change depending on test conditions and genetic background. We have repeatedly observed that leaf rust resistance in durum wheat expresses better under field conditions than in seedling or adult plant greenhouse tests. We have also attempted to classify F_2 populations in the greenhouse, but have had difficulty distinguishing plants with slight resistance from those showing susceptibility. The distribution of F_3 lines for Atil C2000 $\times$ Hualita was in accordance with the segregation expected for two dominant complementary genes, despite the fact that the F_2 segregation conformed to a 7:9 ratio for segregation of two recessive genes. However, the presence of two recessive genes cannot be supported because the F_1 plants were resistant in the field.

Complementary genes with dominant interaction conditioning rust resistance are not known to occur in durum wheat. In fact, complementary gene interaction determining resistance to the wheat rusts is rare. The only identified and designated complementary leaf rust resistance genes are *Lr27* and *Lr31* (24,25). Gene *Lr31* is either completely linked or the same as *Lr12* (18). Genes *Lr27* and *Lr31*, originally found in bread wheat, have been located on chromosomes 3BS and 4BL, respectively (10,25). The infection type response of bread wheat cultivar Gatcher carrying *Lr27* and *Lr31* is X- and ; when tested at 20 to 23°C and 15 to 18°C, respectively, at the seedling stage with race BBG/BN (23). Since the three durums (Jupare C2001, Hualita, and Pohowera) carrying complementary resistance genes displayed infection types similar to that of Gatcher, at least at higher temperatures, it may be argued that the complementary resistance in durum wheat could involve the same complementary genes present in Gatcher. Gene *Lr27* is closely linked to stem rust resistance gene *Sr2* (24), originally identified in *T. turgidum* var. *dicoccum* (emmer wheat) cv. Yaroslav and later transferred to hexaploid wheat (7). Gene *Sr2*, also associated with pseudo-black chaff and seedling chlorosis, is not known to occur in CIMMYT durum wheat germ plasm. *Lr27* is present but *Sr2* absent in a few hexaploid wheat cultivars: Timgalen (Australia), Jupateco 73S and Opata 85 (Mexico), plus Chinese Spring (Ciano 3B), a chromosome substitution line (8,24). Stem rust resistance gene *Sr12* is located on the same chromosome arm (3BS) as *Lr27* but is genetically independent and common in CIMMYT durum wheat germ plasm (21). Whether the complementary resistance genes in durum are the same as *Lr27* and *Lr31* could be determined either by mapping them onto wheat chromosomes using molecular markers or by developing a

synthetic hexaploid wheat using a susceptible *T. tauschii* accession and then conducting the allelism test with tester lines such as Gatcher.

It should also be pointed out that the segregation of 9 resistant: 7 susceptible in the F_2 , and the distribution of 1HR: 8Seg: 7HS in the F_3 families fit the expected ratios, not only for two complementary genes, but also for a dominant resistance gene together with a recessive suppressor gene. Genes suppressing rust resistance have been reported previously in the wheat rust system. Bai and Knott (2) found evidence of several suppressors of leaf rust resistance in the D-genome of bread wheat. In hexaploid synthetic wheat, Nelson et al. (10) identified a suppressor gene (*SuLr23*) derived from *T. tauschii* on chromosome arm 2DS that suppressed gene *Lr23* located at the orthologous position on chromosome 2BS in durum wheat. Knott (6) found suppressors in the A and B genomes of durum wheat Medea for stem rust resistance genes; Assefa and Fehrman (1) also indicated the presence of genes suppressing leaf rust resistance in the A and/or B genomes of durum wheat.

According to segregation results, Llaretia INIA and Somateria carry the same dominant gene (resistance source 2). The seedling and adult plant responses of these two durums were comparable to those belonging to source 1 (Table 2). Cross Atil C2000 $\times$ Llaretia INIA fit the hypothesis of one dominant gene in the F_3 generation better than did cross Atil C2000 $\times$ Somateria.

Greenhouse infection type responses and field ratings of resistance sources 3 and 4 were quite different. Camayo displayed infection types 1+ at seedling and 3C at adult plant stage, whereas Storlom was highly resistant, with infection types ; at seedling and 0; at adult plant stage. Different temperatures and light conditions could have caused somewhat higher infection types in adult plants of Camayo in the greenhouse, as the tests were not carried out together. In the field, Camayo displayed a 5-10R response, while Storlom showed immunity (Table 2). Although completely susceptible recombinants were not found in the F_2 population from the intercross of these two durums, we infer that the two parents carry different but closely linked resistance genes in repulsion. Assuming that the two resistance genes are not linked, approximately 12 completely susceptible plants (1/16) should have occurred in the F_2 population of the 198 evaluated plants. If a complete repulsion genetic linkage is assumed, the conformation of the F_2 progeny will be 1AAbb: 2 AaBb: 1aaBB. Considering the response of both parents (0% for Storlom and 5-10MR for Camayo) and the response of the F_1 of the intercross (0%), all the plants should then have been resistant, with 75% of them showing no disease and 25% with 5-10MR reactions. This was not

the case, since 20 F₂ plants displayed 30M-70MS reactions, indicating that the two genes were not alleles at the same locus. The likelihood of obtaining recombinants with higher responses depends on the recombination frequency (crossing-over) between the two genes. Considering the response of the parents, 0 and 5 to 10%, and the response of the F₁ plants, 0%, we may assume that plants with response 0 to 1% (i.e., a total of 135 plants among the 198) have genotypes AAB₋ and AaB₋. These genotypes, parental and recombinant, cannot be distinguished from each other because they are probably showing the same immune response in the field. Forty-three plants had 5-15MR field response, similar to the reaction of the resistant parent Camayo, and therefore probably belong to genotype aBB. Because F₁ plants from crosses of susceptible parent Atil C2000 with Storlom and Camayo displayed 20M and 50M reactions, respectively, it can be assumed that the nine F₂ plants showing a 30M response and the 11 plants whose response ranged from 50M to 70MS represent genotypes Aabb and aaBb. In a total of 20 plants, genotypes Aabb and aaBb are the only recombinants that can be distinguished. Recombinant aabb was absent, as no totally susceptible plant was found. Since we know that the total number of Aabb, aaBb, and aabb recombinants is 20 plants, it can be assumed that the total number of AAB₋, AABb, and AaBB recombinants is also the same. Thus, the total number of recombinants would be 40 out of 198 evaluated plants. Therefore, the recombination frequency would be approximately 20%. This estimate should be confirmed by studying segregation in the F₃ generation. Only in this way can the different genotypes giving immune leaf rust response in the F₂ generation be distinguished.

Another partially dominant resistance gene was found in the two durums belonging to resistance source 5. Guayacan 2 and Guayacan INIA are sister selections from the same cross and, hence, likely to carry the same resistance gene. This hypothesis is strongly supported by the following: (i) both parents and the F₁ plants from crosses with susceptible parent Atil C2000 displayed similar greenhouse and field reactions (Table 2); (ii) no segregation was observed in the F₂ when the two resistant parents were crossed (Table 4); and (iii) F₁ plants displayed intermediate, but similar, reactions when both parents were crossed with Camayo and Storlom (Table 4). The F₂ segregation for crosses Atil C2000 × Guayacan 2 and Atil C2000 × Guayacan INIA conformed to a 9:7 segregation ratio. The F₃ segregations for both crosses indicated, however, that resistance was due to a single gene, despite the fact that the P value for χ^2 test for the Guayacan INIA cross was only 0.02 (Table 3). The lower P value of this cross is because a smaller

number of F₃ lines scored as HS and an excess of lines scored as HR. This situation could in no way have been caused by the presence of two complementary genes. Because the F₁ plants from these crosses were rated as 50MS and 60MS, it is possible that we misclassified some heterozygous F₂ plants into the susceptible group. When the F₃ segregation data for the two crosses (Atil C2000 × Guayacan 2 and Atil C2000 × Guayacan INIA) were pooled, the χ^2 test for segregation of a single resistance gene gave a P value of 0.30.

Dominant and recessive genes for leaf rust resistance have previously been reported in durum wheat (3,4,9,16,22,26–28). However, only a few of the designated genes were originally derived from durum (*Lr14a* and *Lr23*), and only a few known designated genes have been reported to be present in durum wheat. In addition to *Lr14a*, which is effective against Mexican *P. triticina* race BBG/BN, other effective leaf rust resistance genes reported in durum wheat are *Lr3*, *Lr13* (19), *Lr16* (27), and *Lr17* (27), but further studies are required to confirm if any of these genes are present in the durum wheats included in this study. Nonetheless, it is worth mentioning that some of the present durum wheat lines, such as Jupare C2001, Hualita, and Storlom, are known to have bread wheat in their pedigrees. Further mapping studies will also be required to determine whether the five sources of resistance identified in our study correspond to any previously designated genes or are new genes specifically present in durum wheat.

These resistance genes confer a high level of protection against the new *P. triticina* race BBG/BN that currently predominates in durum wheat growing areas of Mexico and could therefore be used in breeding to enhance genetic diversity. These genes could also be useful to breeding programs in countries where leaf rust races attacking durum wheats have similar virulence specificity. However, to enhance their life span, these genes must be used in combinations. Identification of DNA markers closely linked to each resistance gene could help to locate these genes in the genome, to understand the relationship between leaf rust resistance genes in durum and bread wheat, and to pyramid these genes for long-term control of the disease.

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