Inheritance of Adult Plant Leaf Rust Resistance in the Brazilian Wheat Cultivar Toropi

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ABSTRACT

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Adult plant resistance to leaf rust in the Brazilian wheat cultivar Toropi (*Triticum aestivum*) was studied in crosses with the susceptible cultivar IAC 13. Cvs. Toropi and IAC 13 are susceptible at the seedling stage to race LCG-RS of *Puccinia triticina* Erikss., and to all other known Brazilian leaf-rust races. Thus, the resistance observed in Toropi in the field was due to adult plant-resistance genes. In the greenhouse at the adult plant stage, resistance segregated in a 7:9 ratio for two complementary recessive genes. Additionally, two recessive genes for leaf-tip necrosis were identified in the greenhouse environment. Necrosis was expressed when the two homozygous recessive genes occurred together in the F₂, independently of the response to leaf rust. The resistance and leaf-necrosis genes differ from those previously reported in wheat. Segregation for leaf-rust resistance in the field at Passo Fundo, Brazil, fit a 1:3 ratio for a single recessive gene. With a different pathogen race, and in crosses of cvs. Toropi and ThatcherLr34, two recessive genes and a dominant gene for resistance were detected in the field in Mexico. The dominant gene was likely *Lr34* from cv. ThatcherLr34 and the two recessive genes were likely those detected in the greenhouse adult plants tests at Passo Fundo.

Additional keywords: adult plant resistance, bread wheat, durable resistance, partial resistance, *Puccinia recondita* f. sp. *tritici*

The resistance of wheat cultivars (*Triticum aestivum* L.) to leaf rust (*Puccinia triticina* Erikss.; 1) was traditionally based on genes effective throughout the plant's developmental cycle. Many of these resistances were quickly overcome by the pathogen. The need for durable resistance has been recently emphasized. The focus has been on the resistance genes expressed at the adult plant stage, theoretically reducing the selection pressure for pathogen virulence.

The mechanism of durable resistance is unknown. The inheritance of durable re-

sistance has often been considered complex, with each host gene having little effect. Wheat cultivars with the most durable leaf-rust resistance worldwide have been those with adult plant resistance. However, the genetic nature of adult plant resistance to leaf rust has been found to be oligogenic. Most durable resistance to leaf rust is conditioned by a combination of a few genes, principally in combinations that include the adult plant resistance genes *Lr13* and *Lr34* (11). Many cultivars with these resistances originated in Argentina, Brazil, and Uruguay. It is suspected that at least a part of the resistance in these cultivars is in common. Many cultivars share some of the resistance of Frontana, a Brazilian cultivar which has been a source of durable leaf rust resistance. Cv. Frontana possesses *Lr13* plus a modifier or modifiers (9), *Lr34* and *LrT3* (5,8), and other genes (5,12,13,15). Toropi, another Brazilian cultivar, has been more resistant than Frontana in Brazil, indicating genetic differences between these cultivars (2).

This work describes genetic studies of F₂ progenies from reciprocal crosses between cvs. Toropi and IAC 13 and Toropi and ThatcherLr34 to determine the number of genes involved in adult plant resistance to leaf rust and determine if they are unique.

MATERIALS AND METHODS

Cv. Toropi (Frontana 1971.37/Quaderna A/Petiblanco 8) was crossed with cv. IAC 13-Lorena (Ciano 67/IAS 51) to determine the number of its genes for effective adult plant leaf-rust resistance. These bread wheat cultivars both are adapted to the climate at Passo Fundo, Brazil. Both cultivars are susceptible at the seedling stage to race LCG-RS used in this study and to all other known Brazilian races of *Puccinia triticina*. Under field conditions, cv. Toropi has an adult plant resistance, and cv. IAC 13-Lorena is susceptible (2). Seeds of the cultivars were obtained from the Active Germ Plasm Bank of the Brazilian Corporation for Agriculture and Livestock Research (EMBRAPA). *Lr34* is the only adult plant resistance gene (naturally occurring in *Triticum aestivum*) currently known to be even partially effective in Brazil. To test for its presence, Toropi was crossed with the near isogenic line ThatcherLr34, RL 6058 (Thatcher*6/PI 58548), originally received from the Research Station, Agriculture Canada, Winnipeg.

Plants from the original seed stocks were increased and designated by number. Spikes of the parental and F₁ plants were bagged to avoid cross-pollination. F₂ populations were used for genetic analysis. Adult plant leaf-rust reaction of F₂ progenies, F₁, and parental plants from the resistant-susceptible (R-S) crosses was determined in the greenhouse and in the field at EMBRAPA, Passo Fundo, and from the R × R crosses, with R. P. Singh's participation in the field rust evaluation, at the International Maize and Wheat Improvement Center (CIMMYT), Ciudad Obregon, Mexico.

Seeds planted at Passo Fundo were treated with Iprodione + Thiram. Five plants per pot were grown in the greenhouse. The entirely expanded flag leaf of the main culm was inoculated (1.5 mg of spores/1 ml of mineral oil, Soltrol) using an atomizer after spike emergence and before anthesis. After inoculation, the plants were kept overnight in a high-humidity compartment in the greenhouse. Powdery mildew (*Blumeria graminis tritici*) was controlled by Ethirimol, 280 g a.i./liter (three sprays of 3 ml/liter), and insects with Permetrina, 500 g a.i./liter (three sprays of 1 ml/liter) applied on the leaves in the greenhouse experiments. In

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the field, the blocks consisted of 10-m rows 10 cm apart, with 1 m between blocks. The experiment was surrounded by a 1-m border of leaf rust-susceptible wheat.

Race LCG-RS was used in the greenhouse tests and field tests at Passo Fundo, and race TCB/TD was used at Ciudad Obregon. The nomenclature of the races is in accordance with Long and Kolmer (10), including local supplemental differentials. The avirulence-virulence formulas for LCG-RS and TCB/TD are, respectively, *Lr* 2a, 2c, 3, 3ka, 9, 16, 17, 18, 19, 20, 21, 24, (30)/1, 10, (11), 14a, 14b, 23, 26 (parentheses indicate a variable reaction), and *Lr* 3ka, 9, 10, 11, 16, 17, 19, 21, 24, 25, 27 + 31, 29, 30, 32, 33 / 1, 2a, 2b, 2c, 3, 3bg, 13, 14a, 14b, 15, 18, 20, 23, 26, 28.

In the greenhouse at Passo Fundo, plants were evaluated approximately 2 weeks after the flag leaves were inoculated. Lesion size was estimated on a scale of 1 through 9 with the aid of diagrams, where sizes 1, 2, 4, and 8 corresponded to lesion areas of 0.5, 1.0, 2.0, and 4.0 mm², respectively. In the field at Passo Fundo, susceptible borders 1 m wide were inoculated on 13 August and 3, 15, and 21 September. The experimental plants were also inoculated on the last three dates when the flag leaf had not yet emerged. Rust reaction was evaluated daily (except for six leaves) on flag leaves between 28 September and 31 October. Rust reaction at Ciudad Obregon was evaluated on flag leaves from heading to flowering, and for cvs. Thatcher and ThatcherLr34 on the same date at the late boot stage. Thatcher is day-length sensitive and thereby is later in maturity than the insensitive Brazilian lines and cultivars. *Lr34* provides a high level at resistance at this location.

RESULTS

Greenhouse tests. The area of the leaf affected by the disease (pustule plus associated chlorosis and necrosis) was determined. The mean area affected by the rust on the parent cultivars, F₁, and F₂ progenies is shown in Table 1. Segregation of the F₂ population from the Toropi 7/IAC 13-12 cross indicated two recessive genes in cv. Toropi for adult plant resistance to race LCG-RS under greenhouse conditions. Of 1,574 F₂ plants classified for percentage of leaf area with pustules and chlorosis or necrosis, 684 plants were as resistant as cv. Toropi 7, fitting a 7:9 ratio (Table 2). However, if chlorosis and necrosis were ignored and only the sporulating area considered, the two-recessive-gene hypothesis was not accepted at a 0.05 level of significance.

The same plants were classified for host response according to pustule size. Plants were considered susceptible if the mean pustule size was ≥ 2.1 . The value 2.1 was the mean value (3.1) for pustule size of cv. IAC 13-12 plants (S parent) less one standard deviation (0.954). The total number of

other plants (mean pustule size ≤ 2.0) was 402, fitting a 1 recessive gene ratio (expected ratio = 1:3; probability = 0.70 to 0.50). The nonstandard division between susceptible and resistant plants (susceptible mean minus one standard deviation) was needed because of the variation in response of the individual parental plants.

This F₂ population was classified at the adult plant stage in the greenhouse for the presence of leaf-tip necrosis, such as that conditioned by gene *Ltn* (known to be associated with *Lr34*). Among the 1,574 plants, 114 were necrotic (Table 3). Neither cv. Toropi nor cv. IAC 13 expressed necrosis, and necrosis was not associated with the F₂ resistance genotypes; thus, the necrosis expressed was not due to the previously described gene *Ltn*. The segregation ratio indicated that the necrosis was expressed when two homozygous recessive genes occurred together in the F₂ (1 necrotic to 15 normal plants; probability = 0.20 to 0.10; Table 3).

Field tests. Segregation for leaf-rust resistance in F₂ populations from cvs. Toropi 6/IAC 13-2 and IAC 13-12/Toropi 6 segre-

gated 1:3 for resistance in reciprocal crosses, which indicated a single recessive gene in Toropi (Table 4). The populations were heavily infected with LCG-RS, the same race used in the greenhouse tests. The hypothesis of a recessive gene in cv. Toropi conditioning adult plant resistance in the field in Brazil was accepted when the severity was estimated by either total lesion (sporulating area plus chlorotic or necrotic areas, or both) or by only the sporulating area.

The testing for *Lr34* in cv. Toropi was done in Mexico, using an artificial infection of race TCB/TD in the field. F₂ populations from crosses involving cvs. Toropi and ThatcherLr34 segregated fitting the ratio of 55:9 (R:S) plants (Table 5), indicating resistance conditioned by two recessive and a dominant gene. In the Toropi 7/IAC 13-12 cross, either of two allele pairs of recessive genes in the homozygous condition resulted in expression of resistance. The dominant gene detected in Toropi/ThatcherLr34 was likely *Lr34* from the ThatcherLr34 parent. The recessive genes would then be from Toropi and

Table 1. Percent severity of race LCG-RS, *Puccinia triticina*, on adult plants of wheat cultivars Toropi (resistant), IAC 13 (susceptible), with the F₁ and F₂ progenies in the greenhouse at Passo Fundo, Brazil

Hosts	No. of plants	Area with pustules (%) ^a		
		Minimum	Mean	Maximum
Toropi 7	13	<1	2	6
IAC 13-12	13	3	18	32
F ₁	14	5	18	44
F ₂	1,574	<1	10	42

^a Percent of the area with pustules plus chlorosis or necrosis or both.

Table 2. Segregation for adult plant resistance (percent of leaf area with pustules plus chlorosis or necrosis or both) of the F₂ population of wheat cultivar Toropi 7/IAC 13-12 cross, to race LCG-RS of *Puccinia triticina* based on severity in greenhouse tests at Passo Fundo, Brazil

Resistant ^a	No. of plants		Expected ratio	Probability ^b
	All others			
684	890		7:9	0.90–0.70

^a Resistance includes all plants as resistant as Toropi 7 (0 to 6% severity).

^b Probability values greater than 0.05 indicate a nonsignificant value of χ^2 -square.

Table 3. Segregation for leaf tip necrosis on adult plants of F₂ population of the wheat cultivar Toropi 7/IAC 13-12 cross in the greenhouse at Passo Fundo, Brazil

Leaf-tip necrosis	No. of plants		Expected ratio	Probability ^a
	Normal tips			
114	1460		1:15	0.20–0.10

^a Probability values greater than 0.05 indicate a nonsignificant value of χ^2 -square.

Table 4. Segregation for adult plant resistance to race LCG-RS of *Puccinia triticina* of F₂ populations of the reciprocal cross of wheat cultivars Toropi/IAC 13 and IAC 13/Toropi, based on severity in the field at Passo Fundo, Brazil

Cross	No. of plants		Expected ratio	Probability ^b
	Resistant ^a	All others		
Toropi 6/IAC13-2	230	789	1:3	0.10–0.50
IAC13-12/Toropi 6	217	710	1:3	0.30–0.20

^a Resistance includes all plants as resistant as Toropi 6 (0 to 20% severity).

^b Probability values greater than 0.05 indicate a nonsignificant value of χ^2 -square.

could be the pair detected in the greenhouse adult plant test in Brazil. Only one of these genes was detected in the field in Brazil.

DISCUSSION

The parental cvs. Toropi and IAC 13 were susceptible as seedlings to leaf rust, indicating that resistance detected in Toropi in the greenhouse is strictly of the adult plant type. Cultivars without seedling genes for resistance were chosen to study to simplify the analysis and to avoid interactions between seedling and adult plant resistance genes. Of the adult plant resistance genes previously described in *T. aestivum* (i.e., *Lr12*, *Lr22b*, *Lr13*, and *Lr34*), only *Lr34* currently has any effect in Brazil, and even it is often inadequate. Toropi is more resistant than the cultivars with *Lr34* in Brazil. The known adult plant resistance genes are generally inherited as a dominant trait (3,6,8,9) except for *Lr22b* in cv. Thatcher. Genes *Lr13* and *Lr34* can be recessive under certain conditions (8,9). *Lr34* is partially dominant in Mexico, where leaf-tip necrosis conditioned by the gene *Ltn* is observed in the F_1 generation. Strong genetic association or pleiotropism exists between *Lr34* and *Ltn* (14). The data obtained in Mexico indicated that the F_2 populations from crosses between cv. Toropi and the near isogenic line ThatcherLr34 segregated for susceptibility. This is strong evidence that either *Lr34* is absent from Toropi (if present the entire F_2 would have been homozygous resistant) or, if *Lr34* is in Toropi, it must have been translocated to another chromosome region (7). We cannot rule out this possibility; however, the leaf-tip necrosis detected in the Toropi/IAC 13 cross was due to two recessive genes and was not *Ltn*, known to be a single dominant gene, and tightly linked or pleiotropic to *Lr34* (7,14). Recent studies (4) have placed Toropi resistance on chromosome 1A and 4D where other adult plant resistance

genes in *T. aestivum* are not known to occur.

Adult plant tests in the greenhouse (Table 1) clearly showed that resistance was recessive, because the mean leaf-rust severity and the range of severities observed in the F_1 were essentially equal to the mean and range of the susceptible parent. Thus, resistance is not mainly due to additive effects. Furthermore, the resistance must be rather simply inherited, because over 40% of the F_2 population showed a high level of resistance (Table 2), whereas the F_1 plants were essentially equal to the mean and range of the susceptible parent. The ratio of "all others" to resistant plants best fits a 7:9 ratio, indicating that recessive alleles at either of two independent loci confer resistance.

When host response was measured as sporulation area rather than the total area of pustules and the chlorotic or necrotic area around them, the second gene was not seen. Then F_2 segregation fitted a 1:3 R:S ratio, but only if susceptibility was defined as having pustule sizes equal to or larger than the mean size of those on the susceptible parent less one standard deviation. It is possible that adult plant resistance, expressed as reduction in pustule size, was due to only one of the genes in cv. Toropi. F_2 progeny advanced to the F_6 show that resistant plants maintained their resistance (50 of 54 plant progenies) while susceptible selections segregated for resistance, thus confirming the recessive nature of the resistance.

In the field at Passo Fundo, segregation for resistance fit the 1:3 rather than a 7:9 ratio. The parental cultivars of the F_2 progenies were the same in the field and in the greenhouse, although different plant selections were used. These selections responded identically in all tests. The detection of only a single gene might be due to many causes. In the field, multiple pathogen cycles result in infections at different host growth stages and in infections

in different environments. Inoculum levels in later infection periods are, in part, related to the success of earlier infections on the same plant. In the field, the plants were artificially and naturally inoculated several times, resulting in infection of the entire plant. In this experiment, the interference of natural inoculum was minimal. In the greenhouse, inoculum density was controlled and uniform, environmental conditions were consistent, and inoculum was applied to the flag leaf of the main culm approximately 2 weeks before making the disease evaluation.

Leaf-rust resistance is often expressed to a greater degree in the field than in the greenhouse, contrary to our experience. Adult plants with gene *Lr34* may, under field conditions, be sufficiently resistant to mask the interacting effects of a second gene, but presence of both genes was necessary for the highest level of adult plant resistance in greenhouse tests (8).

In Mexico, the progenies were evaluated with race TCB/TD, which is virulent to *Lr12*, *13*, and *22b* and avirulent to *Lr34*. Cvs. Toropi and ThatcherLr34 were R and Thatcher was 80 to 100 S (80 to 100% of leaf area covered by susceptible pustules). The F_2 segregation ratio indicated two recessive genes and one dominant gene conditioned the resistance in progeny of Toropi/ThatcherLr34 (Table 5, $P = 0.70$ to 0.50 and 0.90 to 0.70; and, considering the four populations [118:35 R:S, $P = 0.70$ to 0.50]). The resistance of cv. ThatcherLr34 is due to *Lr34*, so this is doubtless the dominant gene detected in the Toropi/ThatcherLr34 progeny. The recessive genes were likely those detected in Toropi in the greenhouse at Passo Fundo. In the field in Mexico and greenhouse in Passo Fundo, the number of F_2 plants rated as resistant as Toropi corresponded to those homozygous for either or both of the two recessive genes for resistance. The data from Mexico support two recessive genes in Toropi, but does not rule out a single

Table 5. Parent and progenies of reciprocal crosses of wheat cultivars Toropi-Thatcher *Lr34* evaluated for adult plant resistance in the field inoculated with race TCB/TD of *Puccinia triticina* at Ciudad Obregon, Mexico

Host	Generation	No. of plants per class		Expected ratio	Probability ^c
		Trace MS-S ^a	All others ^b		
Toropi 6	Parent	All	0	...	...
Thatcher <i>Lr34</i> -4	Parent	All	0	...	...
Toropi 6/Tc <i>Lr34</i> -4	F_1	All	0	...	...
Toropi 6/Tc <i>Lr34</i> -4	F_2	44	9	55:9	0.70-0.50
Tc <i>Lr34</i> -4/Toropi 6	F_1	All	0	...	...
Tc <i>Lr34</i> -4/Toropi 6	F_2	54	11	55:9	0.70-0.50
Toropi 6A	Parent	All	0	...	...
Thatcher <i>Lr34</i> -7	Parent	All	0	...	...
Toropi 6A/Tc <i>Lr34</i> -7	F_1	All	0	...	...
Toropi 6A/Tc <i>Lr34</i> -7	F_2	40	8	55:9	0.90-0.70
Tc <i>Lr34</i> -7/Toropi 6A	F_1	All	0	...	...
Tc <i>Lr34</i> -7/Toropi 6A	F_2	50	7	55:9	0.90-0.70
Thatcher	Check	0	all	...	...

^a Trace MS-S = trace severity of moderately susceptible to susceptible lesions.

^b All others = 10 to 100% severity of moderately susceptible to susceptible lesions.

^c Probability values higher than 0.05 indicate nonsignificant values of χ^2 -square.

recessive resistance gene. If a single gene for resistance in Toropi had been expressed in Mexico, as in the field at Passo Fundo, the F₂ populations would have segregated 13:3 R:S (one recessive and one dominant gene). This hypothesis is accepted with 0.90 to 0.70 probability, except for one population (50:7 R:S, $P = 0.30$ to 0.20) or the combined four populations (188:35 R:S, $P = 0.30$ to 0.20).

Leaf-tip necrosis was expressed in the greenhouse at Passo Fundo when two homozygous recessive genes occurred together in the F₂, on both rust-resistant and susceptible plants. However, leaf-tip necrosis was not expressed by cvs. Toropi, IAC 13, or their F₁ progenies in these tests. The absence of necrosis in Toropi and IAC 13 plants indicates that both cultivars must possess one of the complementary recessive necrosis gene pairs necessary for necrosis to be expressed in the F₂ progeny. Cvs. Era, Frontana, ThatcherLr34, ThatcherLr34+LrT3, and ThatcherLr13+Lr34 all expressed the typical *Lr34* resistance response and *Ltn* leaf-tip necrosis. Since *Lr34* and *Ltn* are linked or pleiotropic, *Ltn* was not the necrosis gene detected in the Toropi 7/IAC 13-12 progenies.

Brazilian cultivars with resistance derived from Toropi usually have Toropi as the female parent. However, no significant differences in resistance were found between reciprocal F₂ populations in the field at Passo Fundo (Table 4). Although a monogenic recessive ratio fit both of the reciprocal populations when Toropi was the male parent, the ratio fit better.

Due to the effectiveness of the resistance of cv. Toropi in Brazil, it was considered that a combination of *Lr13* and *34* might be involved. However, the results indicate that this is unlikely.

Cv. Toropi varied in expression to leaf-rust infection. The resistance response varied from plants without sporulation to

plants with 20% of the flag leaf infected. The infection type included both fully susceptible and a range of resistant lesions mixed on the same flag leaf, much like *Lr34*. In spite of susceptible lesions, the area of leaf tissue affected was much reduced, as was the total number of lesions when compared to susceptible checks. The Toropi reaction permitting some pathogen growth and reproduction is a form of incomplete resistance (slow rusting).

The variation in the resistance response made it difficult to classify the segregating populations. Nevertheless, the data support the conclusion that two genes likely condition this resistance. Durability of the adult plant Toropi resistance, previously undescribed, lends confidence that further research to isolate and characterize these genes will contribute to achieving long-term resistance. Combinations of Toropi resistance with *Lr34* should be possible and could provide for increased durability in leaf-rust resistance.

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