Inheritance of Leaf Rust Resistance in the CIMMYT Wheat Weebill 1

Julia X. Zhang, Ravi P. Singh, James A. Kolmer,
Julio Huerta-Espino, Yue Jin, and James A. Anderson*

ABSTRACT

The CIMMYT spring wheat Weebill 1 has near-immune levels of adult plant resistance (APR) to leaf rust caused by *Puccinia triticina* Eriks. To determine the genetic basis of resistance in seedlings and adult plants Weebill 1 was crossed with two susceptible parents Jupateco 73S and 'Thatcher'. Advanced $F_{4:5}$, $F_{4:6}$, and $F_{5:7}$ recombinant inbred line (RIL) populations from Jupateco 73S/Weebill 1 and BC_1F_2 populations from Thatcher/Weebill 1 were derived. The $F_{5:7}$ RILs and BC_1F_2 families were tested as seedlings with five races of *P. triticina*. The F_1 and $F_{4:5}$, $F_{4:6}$, and $F_{5:7}$ RILs of Jupateco 73S/Weebill 1 were evaluated in plots in Mexico and St. Paul. The Jupateco 73S/Weebill 1 RILs and Thatcher*2/Weebill 1 F_2 families segregated for *Lr14b*, an unknown seedling leaf rust resistance gene derived from Weebill 1 in both crosses, and *Lr17a* derived from Jupateco 73S in the RIL population. *Lr17a* was mapped to the distal end of chromosome 2AS and was linked to microsatellite maker *Xgwm636* at a distance of 4.0 cM. The seedling genes did not condition effective resistance in the field plots with races used in the field trials. The segregation ratio in the RILs and F_2 families indicated the presence of three to four APR genes in Weebill 1. One of the APR genes was linked to the seedling gene *Lr14b* on chromosome 7BL and reduced leaf rust by 47% in St. Paul and 31% in Mexico. Based on the haplotypes of DNA markers, we do not believe that any of the APR genes is *Lr34*.

J.X. Zhang and J.A. Anderson, Dep. of Agronomy and Plant Genetics, Univ. of Minnesota, St. Paul, MN 55108; R.P. Singh, International Maize and Wheat Improvement Center (CIMMYT), Apdo Postal 6-641, 06600, Mexico D.F., Mexico; J.A. Kolmer and Y. Jin, USDA-ARS, Cereal Disease Laboratory, St. Paul, MN 55108; J. Huerta-Espino, Campo Experimental Valle de Mexico, INIFAP, Apdo. Postal 10, Chapingo, 56230 Edo de Mexico, Mexico. Received 17 Dec. 2007. *Corresponding author (ander319@umn.edu).

Abbreviations: APR, adult plant resistance; IT, infection types; PCR, polymerase chain reaction; QTL, quantitative trait loci; RIL, recombinant inbred lines.

Leaf rust or brown rust, caused by *Puccinia triticina* Eriks., is the most common wheat disease worldwide (Samborski, 1985). Resistance genes have been routinely used in wheat cultivars as a cost-effective means to control leaf rust (Singh and Rajaram, 1991; Singh, 1993; Kolmer, 2003; Oelke and Kolmer, 2004). Most leaf rust resistance genes confer effective seedling resistance, are race specific, and lose their effectiveness when new virulent races emerge or increase. Durable leaf rust resistance is mainly expressed in adult plants, and is usually not associated with genes conferring a hypersensitive response (McIntosh, 1992). Two race non-specific adult plant resistance (APR) genes, *Lr34* and *Lr46*, have provided durable leaf rust resistance (Samborski, 1985; Dyck, 1987; Singh et al., 1998). Introduction of additional sources of non-specific adult plant resistance, as found in the CIMMYT germplasm (Singh et al., 2000), may complement and enhance leaf rust resistance in U.S. wheats (Kolmer et al., 2007a). Knowledge of the identity and effectiveness of the seedling and adult plant leaf rust resistance genes in the CIMMYT germplasm in U.S. environments is essential for

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677 S. Segoe Rd., Madison, WI 53711 USA

the incorporation of new durable resistance genes into U.S. breeding programs and maintenance of a diversity of resistance genes in wheat cultivars.

The seedling resistance gene *Lr17a* (Singh et al., 2001) was an important component of resistance of a number of wheat cultivars in Australia, CIMMYT, the Indian Subcontinent, South America, UK (McIntosh et al., 1995), and the hard red winter wheat region of the United States (Kolmer, 2005). In the United States, a significant increase of races that were virulent to the widely grown winter wheat cultivar Jagger that has *Lr17a* occurred in the *P. triticina* population starting in 1996 (Kolmer et al., 2006; Long et al., 1998). *Lr17a* was located on wheat chromosome 2AS by monosomic analysis (Dyck and Kerber, 1977). Although now ineffective against the predominant races in North America, *Lr17a* is present in some U.S. hard red winter wheat germplasm (J.A. Kolmer, unpublished data, 2007) that were derived from crosses with Jagger. Molecular markers linked to *Lr17a* may facilitate the identification of *Lr17a* in breeding germplasm, especially if the germplasm is related by descent.

Weebill 1, a CIMMYT wheat breeding line derived from the cross Babax/4/Bobwhite/Crow//Bucbuc/Pavon 76/3/Veery#10/5/Babax is highly resistant to leaf rust in Mexico and St. Paul, Minnesota. The adult plant resistance in Weebill 1 is not associated with seedling resistance or hypersensitive response. Weebill 1 may contain *Lr46* due to having Pavon 76 in its pedigree, but not *Lr34* on the basis of the absence of the leaf tip necrosis phenotype. Therefore, we suspect that additional, unknown APR genes are responsible for Weebill 1's high level of leaf rust resistance. This study was conducted to (i) determine the genetic basis of seedling and adult plant resistance in Weebill 1, (ii) determine the correlation of adult plant resistance in Mexico and St. Paul environments, and (iii) identify DNA markers linked to *Lr17a* segregating in one of the crosses used in this study.

MATERIALS AND METHODS

Plant Materials

The wheat line Weebill 1 was crossed as a male parent with the CIMMYT-derived spring wheat line Jupateco 73S and the U.S. spring wheat cultivar Thatcher. Jupateco 73S is a leaf rust susceptible (non-*Lr34*) reselection from the Mexican spring wheat cultivar Jupateco 73 (Singh, 1992) and was postulated to have *Lr17a* (Singh and Rajaram, 1991; Zhang et al., 2007). Thatcher has been used as a standard leaf rust susceptible check in leaf rust research in the U.S. and Canada. The F_1 plants of Thatcher/Weebill 1 were backcrossed to Thatcher and BC_1F_2 families were derived. The F_1, $F_{4:5}$, $F_{4:6}$, and $F_{5:7}$ recombinant inbred lines (RILs) of Jupateco 73S/Weebill 1 (developed by single seed descent) and BC_1F_2 families of Thatcher/Weebill 1 were used in the field studies. The $F_{5:7}$ RILs of Jupateco 73S/Weebill 1 and BC_1F_2 families of Thatcher*2/Weebill 1 were also used in the seedling greenhouse experiments. The $F_{5:7}$ RILs of Jupateco 73S/Weebill 1 were used for identifying microsatellite markers linked to the seedling resistance gene *Lr17a*. Thirty-four spring wheat cultivars and lines from a wide range of geographic regions of the world were tested with different leaf rust races to postulate the presence of *Lr17a* and were analyzed with the DNA makers linked to *Lr17a* in Jupateco 73S/Weebill 1.

Studies of Seedling Resistance Genes in Weebill 1

Twelve races of *P. triticina* were used to determine the seedling infection types (IT) of Weebill 1 and Jupateco 73S (Table 1). The isolates of these races were collected from wheat in the United States and Canada, and were designated for virulence phenotype following the four-letter code system of Long and Kolmer (Long and Kolmer, 1989; Kolmer et al., 2006). Race BBBD (isolate designation: Race 1), MCDS (00 SD 520), and TLGF (00 SC 218) were used for testing 129 $F_{5:7}$ RILs of Jupateco 73S/Weebill 1 and 60 BC_1F_2 families of Thatcher*2/Weebill 1. After selection for lines that did not contain *Lr17a* (based on high IT to BBBD and TLGF), a subset of 11 RILs resistant to MCDS, 10 BC_1F_2 families of Thatcher*2/Weebill 1 segregating for MCDS, and six BC_1F_2 families susceptible to MCDS were selected for further testing with races TGBG (04 MN 485) and TCTD (03 VA 190). Weebill 1, Jupateco 73S, Thatcher, and 18 near-isogenic lines of Thatcher with different leaf rust resistance genes were included in the tests.

The RILs were planted in 3.5 cm^2 square plastic pots in vermiculite in clumps at each corner of the pot as described by Oelke and Kolmer (2004). The BC_1F_2 seed was space planted with 12 to 15 seeds/family/pot. The plants were grown on a greenhouse bench at 18 to 22°C with 16 h of supplemental light.

Table 1. Seedling infection types† of wheat lines Thatcher, Weebill 1, Jupateco 73S and three Thatcher near- isogenic (Tc) lines to 12 races of *Puccinia triticina*.

Wheat Lines	BBBD	KFBJ	MCDS	MCRK	MHDS	MJBJ	SDBG	TCTD	TGBG	THBJ	TLGF	TNRJ
Thatcher	3+	3+	3+	3+	3+	3+	3+	3+	3+	3+	3+	3+
Weebill 1	3+	3	;	3+	33+	33+	33+	0;	X	33+	3+	3+
Jupateco 73S	0;	0;1	3+	23	3	;12	3+	3+	X	;2+	;1	;2
Tc*Lr17a* RL6008 (Tc*Lr17a*)	;2–	;2	3	23	3+	;2+	33+	3	;22+	2	;1	;2
Tc*Lr14b* RL6006 (Tc*Lr14b*)	3+	3+	;	3	3	3+	3+	;	3+	3+	…‡	3
TcLr1 RL6003 (Tc*Lr1*)	;	;	33+	33+	3+	3+	3+	3+	X,3+§	3+	3+	3+
RL6013 (Tc*Lr14a*)	3+	3	3+	3+	3+	3+	X	3	;12	3+	3+	3+

†Infection types as described in Long and Kolmer (1989).

‡Data not available.

§',' indicating that the wheat line was heterogeneous for reaction to the test race; the predominant plant type was given first.

Eight days after planting, urediniospores of the individual races suspended in Soltrol 170 oil (Phillips Petroleum Co. Borger, TX) were spray-inoculated onto the fully expanded primary leaves. The inoculated plants were air-dried for 30 min, then incubated in a mist chamber for 16 to 24 h at 18°C and 100% relative humidity. The plants were moved back to the greenhouse for further incubation.

About 10 to 12 d after inoculation, the IT of each line was recorded following a 0–4 scale (Long and Kolmer, 1989). ITs of 0 to 2^+ including X (mesothetic) indicated host resistance to the race and were classified as low, whereas ITs of 3 to 4 indicated host susceptibility to the race and were classified as high. ITs combining different numbers and symbols indicated a range of ITs present on the same leaf. The RILs with plants that had only low ITs were classified as homozygous resistant, RILs and BC_1F_2 families with only high ITs were classified as homozygous susceptible, and RILs and BC_1F_2 families that had plants with low and high ITs were classified as segregating. The numbers of homozygous resistant, homozygous susceptible and segregating RILs were used in determining the numbers of seedling genes that conditioned resistance to each race. The frequencies of homozygous susceptible and segregating BC_1F_2 families were used to determine the number of effective resistance genes in Weebill 1. The probable genes in each RIL and BC_1F_2 were postulated by comparing the ITs of the Thatcher near-isogenic lines that have individual leaf rust resistance genes. Chi-square-analyses were performed to test the goodness of fit of the observed ratios with those expected for the hypothesized number of resistance genes.

Microsatellite Marker Tagging of Leaf Rust Resistance Gene *Lr17a* and Postulation of Presence or Absence of *Lr34* in Weebill 1

Microsatellite markers mapped to wheat chromosome 2AS (Röder et al., 1998; Somers et al., 2004; Song et al., 2005) were used to screen Jupateco 73S and Weebill 1 for polymorphism. The polymorphic markers were assayed on the $F_{5:7}$ RILs. DNA was extracted from leaf segments of five random plants of each RIL and parents following the protocol described by Liu et al. (2006). Polymerase chain reaction (PCR) assays were performed in 10 μL reaction volumes, each containing 3 μL genomic DNA (30–45 ng). After an initial denaturing step for 3 min at 94°C, 35 cycles were performed with 1 min at 94°C, 2 min at the annealing temperature of the individual primer pairs, followed by a final extension step of 10 min at 72°C. PCR products were separated by polyacrylamide gels containing 32% (v/v) formamide (Litt et al., 1993). The gels were visualized by silver staining (Bassam et al., 1991). Linkage analysis was performed using MAPMAKER for Macintosh v. 2.0 (Lander et al., 1987) at LOD 3.0.

Thirty-five spring wheat cultivars and lines were evaluated for seedling ITs to races BBBD, THBJ (99 ND 588–1), MCDS, TNRJ (04 TX 46), MHDS (03 OH 237), MJBJ (97 NE 406), and MFBJ (94 CAN). The presence or absence of *Lr17a* in a line was determined by comparison with the IT assay of the Thatcher near-isogenic line with *Lr17a*. Leaf rust inoculation and IT designations were the same as previously described. The 35 wheat lines were also analyzed with the microsatellite markers linked to *Lr17a* in Jupateco 73S.

A sequence-tagged site DNA marker *csLV34* developed by Lagudah et al. (2006) was used to screen for *Lr34* in Weebill 1. This marker is 0.4 cM from *Lr34* and was diagnostic of the *Lr34* gene in wheat cultivars from different parts of the world. Jupateco 73S, Thatcher, and RL 6058 (*Lr34*) were included as checks. DNA extraction and PCR reaction were the same as the *Lr17a* tagging study.

Adult-Plant Field Studies

Field evaluations to determine the genetic basis of adult plant resistance were conducted at Ciudad Obregon, Sonora, Mexico; El Batan, State of Mexico, Mexico; and St. Paul, MN, during 2003 to 2006. The crop season at Ciudad Obregon is from late November to early April, whereas at El Batan it is mid May to early October. At St. Paul, wheat is grown from April to August.

In Mexico, each plot consisted of two 1-m rows, 20 cm apart, on the top of 80-cm-wide raised beds with 0.5-m alleys between beds. The field plots at St. Paul were 2-m long single-row plots with 20 cm between plots and 2-m alleys. In the experiments with RILs, each plot was planted with approximately 100 seeds. In Mexico, the spreader rows of the highly susceptible cultivar Morocco were planted as hills on one side of the plots in the middle of the pathway and as long rows around the experimental block at the same time as the experimental plots. In St. Paul, spreader rows of highly susceptible wheat cultivars Thatcher, Morocco, and LMPG-6 were planted perpendicular to the research plots one week before the experimental plots.

In the 2002–2003 crop season, the F_1 and 140 $F_{4:5}$ RILs of Jupateco 73S/Weebill 1 were planted at Ciudad Obregon. The F_1 was space planted in two plots with 20 seeds/plot. Weebill 1 and Jupateco 73S were planted at the beginning, middle, and end of the $F_{4:5}$ lines as standard checks. The $F_{4:6}$ RILs were grown in St. Paul and Ciudad Obregon in 2004. The $F_{5:7}$ RILs were evaluated in Mexico in 2005 and 2006 and St. Paul, MN in 2005. In 2005, the RILs were evaluated at Ciudad Obregon, and in 2006 at El Batan. The F_4-derived RILs were planted with one replication/environment. Experimental design for $F_{5:7}$ RILs was a randomized complete block with two replications in the two Mexican environments and one replication in the 2005 St. Paul field.

Leaf rust epidemics in each environment (one environment = 1 yr/location) were initiated by artificial inoculations of susceptible spreader rows. A Mexican leaf rust race, MCJ/SP (Singh, 1991) with avirulence/virulence formula *Lr2a, 2b, 2c, 3ka, 9, 16, 19, 21, 24, 25, 28, 29, 30, 32, 33, 34/1, 3, 3bg, 10, 11, 12, 13,14a, 14b, 15, 17a, 18, 20, 22b, 23, 26, 27+31* was used in all field studies in Mexico. Both Jupateco 73S and Weebill 1 had high ITs to this race at the seedling stage. The spreader rows were inoculated with urediniospores suspended in a lightweight mineral oil once a day for three consecutive days four weeks after planting in El Batan, and six weeks after planting in Ciudad Obregon. The spreader rows of St. Paul experiments were inoculated with a mixture of races THBJ, MCDS, and MBRJ. Races THBJ and MCDS are common in the current *P. triticina* population in the U.S. (Kolmer et al., 2005), and MBRJ was common in the 1990s (Long et al., 1998).

Average leaf rust severity of each plot was based on the modified Cobb scale (Peterson et al., 1948). The $F_{4:5}$, $F_{4:6}$, and $F_{5:7}$ RILs of Jupateco 73S/Weebill 1 were classified into three categories for χ^2 analyses, (i) homozygous susceptible = lines with severity responses similar to the susceptible parent Jupateco 73S (95–100% leaf rust severity), (ii) homozygous resistant = lines with severity responses similar to the resistant parent (0–1% leaf rust severity), (iii) others = lines homozygous for leaf rust severities higher than the resistant parent or segregating for low/intermediate and high severities. The BC_1F_2 of Thatcher/Weebill 1 were classified into two categories, (i) homozygous susceptible = lines with severities similar to susceptible parent Thatcher (>60% leaf rust severity), (ii) other = lines segregating for low and high severities. The goodness of fit of observed-to-expected phenotypic groups of RILs or BC_1F_2 families was determined by χ^2 tests. Pearson correlation coefficients of leaf rust severity of F_4-derived and $F_{5:7}$ lines were estimated using the mean leaf rust severities of each line in each environment. To test the effectiveness of the seedling genes across environments, a Student's *t* test was conducted between lines of different seedling gene combinations using the means of each $F_{5:7}$ RIL in each environment.

RESULTS

Genes for Seedling Resistance to Leaf Rust

The ITs of the parents and three Thatcher near-isogenic lines to the 12 *P. triticina* races are listed in Table 1. Jupateco 73S had low ITs to races BBBD, KFBJ, MCRK, MJBJ, TGBG, THBJ, TLGF, and TNRJ and high ITs to MCDS, MHDS, SDBG, and TCTD. The high and low IT pattern of Jupateco 73S to those races was the same as the near-isogenic Thatcher line (RL6008) with *Lr17a*, confirming that *Lr17a* was probably present in Jupateco 73S. Weebill 1 had low IT of ; (fleck) to races MCDS, and TCTD, and high ITs to the other nine races. The near-isogenic Thatcher line (RL6006) with gene *Lr14b* gave low IT to MCDS and TCTD, and high IT to the other races, suggesting that *Lr14b* was probably present in Weebill 1. The Thatcher line with *Lr1* (RL6003) and Weebill 1 gave IT X to TGBG. However, the IT X to TGBG in Weebill 1 was not due to *Lr1* gene because RL6003 gave a low IT; to BBBD and KFBJ. A second gene, different from *Lr1* in RL6003, conditioned the IT X to TGBG (Kolmer et al., 2006) and might also be present in Weebill 1.

Table 2. Segregation of leaf rust reaction in seedling plants of $F_{5:7}$ recombinant inbred lines (RIL) of Jupateco 73S/Weebill 1 and BC_1F_2 families of Thatcher*2/Weebill 1.

Leaf rust race & generation	Gene detected	Lines†			χ^2-value‡	*P* value‡
		Res.	Sus.	Seg.		
BBBD						
$F_{5:7}$	*Lr17a*	57	61	6	0.56	0.76
TLGF						
$F_{5:7}$	*Lr17a*	57	57	4	1.65	0.44
MCDS						
$F_{5:7}$	*Lr14b*	50	66	13	5.03	0.07
BC_1F_2	*Lr14b*		29	31	0.07	0.80
TGBG						
$F_{5:7}$§	*Unknown*	4	7	0		
BC_1F_2¶	*Unknown*		4	6		
BC_1F_2#	*Unknown*		3	3		

†Res. = Resistant to the race; Sus. = Susceptible to the race; Seg. = segregating for resistant and susceptible plants.

‡The postulated ratios wereas 0.4688:0.4688:0.0625 in $F_{5:7}$ RILs, and 1:1 in BC_1F_2 families.

§A subset of RILs without *Lr17a* and resistant to MCDS and TCTD.

¶A subset of BC_1F_2 that were segregating for MCDS and TCTD.

#A subset of BC_1F_2 homozygous that were susceptible to MCDS and TCTD.

In the seedling test with races BBBD and TLGF, the Jupateco 73S/Weebill 1 $F_{5:7}$ RILs segregated for resistant, susceptible, and segregating lines in numbers that fit 0.4688:0.4688:0.0625 ratios expected for segregation of a single resistance gene in an F_5-derived population (Table 2). The BC_1F_2 families of the Thatcher*2/Weebill 1 population were all homozygous susceptible to BBBD and TLGF. All RILs tested with both races gave the same responses, indicating that the same gene, *Lr17a* from Jupateco 73S, conditioned resistance to both races in the RILs.

The Jupateco 73S/Weebill 1 $F_{5:7}$ RILs segregated to race MCDS for resistant, susceptible, and segregating lines in proportions conforming to an expected monogenic ratio. The BC_1F_2 of Thatcher*2/Weebill 1 had segregating and susceptible families in accordance with a 1:1 ratio expected for a single gene segregation. The segregation ratios of the RILs and BC_1F_2 families suggested that one gene in Weebill 1 conditioned resistance to race MCDS. A subset of 11 $F_{5:7}$ RILs without *Lr17a*, but with low IT 0; to MCDS, also displayed low IT 0; to race TCTD in the seedling experiments. In Thatcher*2/Weebill 1 BC_1F_2 families, a subset of 10 families segregating to MCDS ITs 0; and 3^+ also segregated for TCTD. A subset of six BC_1F_2 families susceptible to MCDS was also susceptible to TCTD. The co-segregation of the subsets of $F_{5:7}$ RILs and BC_1F_2 families to MCDS and TCTD indicated that resistance to MCDS and TCTD in Weebill 1 was due to the same seedling resistance gene. As *Lr14b* had low IT (;) to MCDS and TCTD, and high ITs to the other 10 races, the resistance gene in Weebill 1 was postulated to be *Lr14b*.

The 11 $F_{5:7}$ RILs, resistant to races MCDS and TCTD and postulated to have *Lr14b*, segregated to race TGBG (Table 2). The subset of 10 BC_1F_2 families segregating for MCDS and six BC_1F_2 families susceptible to MCDS segregated to race TGBG. The random segregation to TGBG of the $F_{5:7}$ and BC_1F_2 families resistant to races MCDS and TCTD, and BC_1F_2 families susceptible to MCDS indicated that resistance to MCDS in Weebill 1 was independent of resistance to TGBG. Resistance to TGBG in Weebill 1 can be attributed to a gene that conditioned low IT to TGBG and high IT to the other 11 races. Because none of the known leaf rust resistance genes from common wheat had such a narrow resistance spectrum, the resistance in

Weebill 1 to TGBG was most likely due to an unknown leaf rust resistance gene that might also be present in some plants of the Thatcher line with *Lr1*.

Table 3 lists ITs of a subset of Jupateco 73S/Weebill 1 RILs with individual seedling resistance genes. RILs 100 and 158 were postulated to have *Lr14b* because they had high ITs to races BBBD, TLGF, TGBG, and low ITs to races MCDS and TCTD. RILs 104 and 106 carried *Lr17a* because of their low ITs to BBBD and TLGF, and high IT to MCDS. RILs 121 and 157 likely possessed a combination of *Lr14b* and *Lr17a* because they had low ITs to BBBD, TLGF, and MCDS. RIL 150 and 128 likely possessed *Lr14b* and the unknown gene from Weebill 1 because they had ; to 0; ITs to MCDS and TCTD and X IT to TGBG. We could not postulate the presence or absence of the unknown seedling resistance gene in lines with *Lr17a* because those lines were not included in the study with TGBG.

Adult Plant Resistance

Expression of adult plant resistance in various environments

Marker *csLV34* produced an allele of about 155 bp in the Thatcher line with *Lr34*, and an alternative allele of about 250 bp in Weebill 1, Thatcher, and Jupateco 73S suggesting that Weebill 1 most likely does not have the *Lr34* gene. In addition, Weebill 1 does not show the leaf tip necrosis characteristic of other materials carrying *Lr34*. Jupateco 73S had 100 S leaf rust severity and response in contrast to 0 to 1 MSS for Weebill 1 in all environments. The correlations of leaf rust severity for Jupateco 73S/Weebill 1 RILs for 2003 and 2004 were moderately high (r = 0.75) and very high (r = 0.93) for 2005 and 2006 (Table 4). The correlations (r = 0.61–0.66) between the St. Paul and Mexican locations were also moderately high (Table 4).

Number of adult plant resistance genes in Weebill 1

The frequency distribution of mean leaf rust severities of F_4-derived ($F_{4:5}$ and $F_{4:6}$) RILs and $F_{5:7}$ RILs are shown in Fig. 1. The severity distribution was continuous, suggesting quantitative inheritance of adult plant resistance in Weebill 1. The F_1 plants had leaf rust severities of 60 to 70% and moderately susceptible-susceptible responses. The mean leaf rust severities of $F_{4:5}$ and $F_{4:6}$ RILs evaluated in 2003 and 2004, respectively were 54 and 42%. The $F_{4:5}$ and $F_{4:6}$ were considered to be the same genotypes. The high mean leaf rust severity in 2003 was probably due to the higher than normal temperature in the rust development period in Obregon in 2003. In Mexico, the average temperature during rust development period (Feb. 1–Mar. 15 in Obregon, July 1–Aug. 15 in El Batan) is about 16°C with average daily maximum temperature of 25°C and minimum temperature of 9°C. In 2003, six days in the period from March 1 to March 15 had maximum daily temperatures above 30°C. In such hot weather leaf-rust-infected leaves became necrotic in a short period of time and moderately susceptible plants tend to resemble plants with high terminal disease severity. The projected F_1 severity in 2004, when adjusted according to the ratio of mean leaf rust severity in 2003 and mean leaf rust severity in 2004, would be 54%. Thus, the F_1 data indicated lack of dominance of the APR genes in Weebill 1.

An abnormally high frequency of susceptible lines was observed in 2003 (Table 5). Only six of the 23 $F_{4:5}$ RILs scored as susceptible in 2003 were susceptible in 2004, and the others had rust severities of 50 to 90% in 2004.

Table 3. Seedling infection types and field leaf rust severities of eight $F_{5:7}$ recombinant inbred lines (RILs) of Jupateco 73S/Weebill 1 and two Thatcher near-isogenic lines tested with leaf rust resistance to five races of *Puccinia triticina*.

	Races					Field environment			
						Obregon	El Batan	St. Paul	
Lines	BBBD	TLGF	MCDS	TCTD	TGBG	2005	2006	2005	Seedling genes
	Infection type†					Leaf rust severity			
Thatcher	33+	3	33+	3+	33+	…‡	…	70	
RL6013 (*Lr14b*)	3+	…	;	;	3+	…	…	70	
RL6008 (*Lr17a*)	;2–	;1	3+	3	X	…	…	20–70	
RIL#100	3	3	0;	0;	3+	5	10	15	*Lr14b*
RIL#158	3	3	0;	0;	3+	10	5	20	*Lr14b*
RIL#104	0;	0;	33+	…	…	100	90	100	*Lr17a*§
RIL#106	;1	;2	33+	…	…	100	75	100	*Lr17a*§
RIL#121	;1	0;	0;	…	…	95	75	100	*Lr14b*, *Lr17a*§
RIL#155	;	0;	0;	…	…	60	85	70	*Lr14b*, *Lr17a*§
RIL#150	33+	33+	0;	0;	X	23	20	30	*Lr14b,* unknown
RIL#128	3+	3	0;	;	X	95	90	60	*Lr14b,* unknown

†Infection types follow a 0–4 scale as described in Long and Kolmer (1989).

‡Data not available.

§The unknown gene in the RIL cannot be postulated because the line was not tested with race TGBG.

Apparently 17 lines had gene(s) that did not confer effective resistance in 2003 under high disease pressure. A chi-square test was done on the $F_{4:5}$ RIL data using the ratio of the number of lines phenotypically similar to Weebill 1, susceptible lines and the lines with some resistance. The segregation of the F_4-derived RILs conformed to a postulated four-gene segregation ratio in both Mexico and St. Paul. In Mexico, the segregation ratio for the $F_{5:7}$ RILs fitted a three- and four-gene segregation model with a higher probability for a four genes than for three genes in El Batan (Table 5). In St. Paul, the segregation of resistant lines, susceptible lines, and lines with some resistance among the $F_{5:7}$ lines fitted both three-gene and four-gene models with equal probability. In St. Paul, the ratio of susceptible and segregating F_2 families of Thatcher*2/Weebill 1 fitted a four-gene model ($P = 0.34$) better than three-gene model ($P = 0.24$). Thus the segregation ratios in both Jupateco 73S/Weebill 1 RILs and Thatcher*2/Weebill 1 BC_1F_2 families, in seven environment/generation combinations, suggested that Weebill 1 has three or four APR genes.

Table 4. Correlation coefficients for leaf rust severities of F_4-derived ($F_{4:5}$ and $F_{4:6}$) and $F_{5:7}$ recombinant inbred lines (RILs) of Jupateco 73S/Weebill 1 RILs with and without *Lr14b* tested in different environments.

Generation and environment	Genotype	Mexico	
		Obregon 2003	Obregon 2004
F_4-derived†			
St. Paul 2004	All RILs	0.70	0.65
Obregon 2003	All RILs		0.75
F_5-derived‡		Obregon 2005	El Batan 2006
St. Paul 2005	All RILs	0.66	0.61
	+Lr14b	0.59	0.58
	– Lr14b	0.66	0.60
Obregon 2005	All RILs		0.93
	+Lr14b		0.94
	–Lr14b		0.90

†The data of 2003 were collected from $F_{4:5}$ RILs, the 2004 data were collected from $F_{4:6}$ RILs.

‡Using leaf rust severities of two replications in Mexico and one replication in St. Paul.

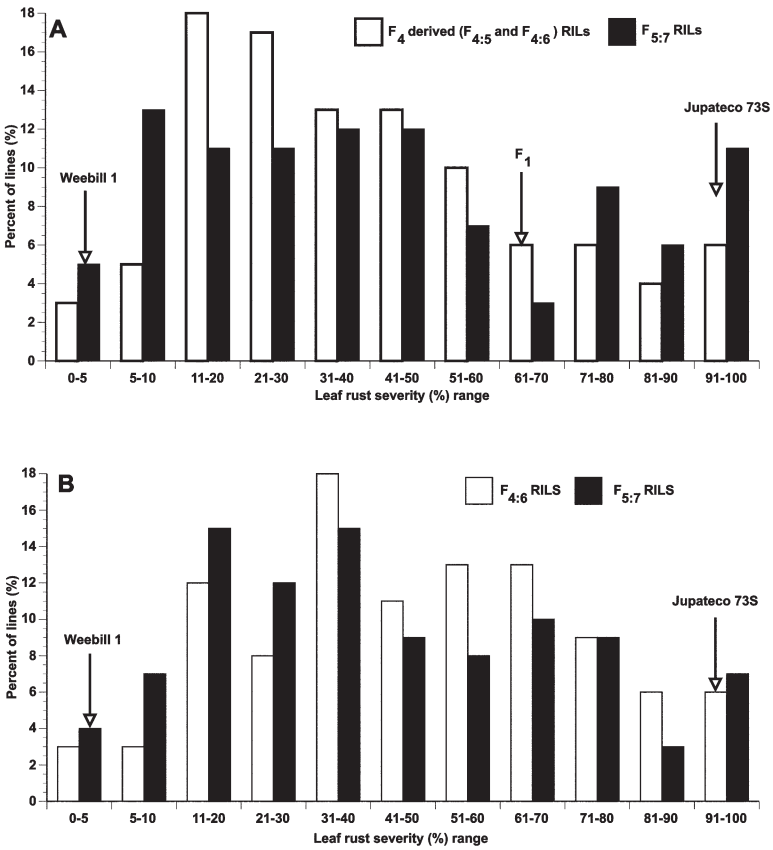

Figure 1. Frequency distributions of leaf rust severities of F_4- ($F_{4:5}$ and $F_{4:6}$) and F_5-($F_{5:7}$) derived recombinant inbred lines (RILs) of Jupateco 73S/Weebill 1 evaluated in Mexico (A) and St. Paul (B). F_1 data was collected in Ciudad Obregon in 2003. Data of F_4-derived RILs planted in Mexico were based on means of $F_{4:5}$ in 2003 and $F_{4:6}$ in 2004 in Ciudad Obregon. Data of $F_{5:7}$ RILs in Mexico were based on means of Ciudad Obregon in 2005 and El Batan in 2006 with two replications in each year. Data from St. Paul were collected in 2005 with one replication.

A Student's *t* test of the leaf rust severities of $F_{5:7}$ RILs indicated no difference between the means of RILs with and without *Lr17a* across environments ($P > 0.05$), suggesting that *Lr17a* was not effective at the adult stage of the Jupateco 73S/Weebill 1 cross. The mean rust severities in field trials of RILs without *Lr14b* was 60 and 48 to 54% at St. Paul and Mexico, respectively, in contrast with 32 and 35% at St. Paul and Mexico, respectively, for lines with *Lr14b* (Table 6). Therefore, lines with *Lr14b* had 47 and 31% less leaf rust at St. Paul and Mexico, respectively compared to lines without *Lr14b*. The differences were highly significant ($P < 0.01$). Although most RILs with *Lr14b* had some leaf rust resistance in the field, response of RIL121 was 95 S in Obregon, 75 S in El Batan, and 100 S in St. Paul (Table 3). The high leaf rust severity of RIL#121 indicated that an APR gene was most likely linked to the gene *Lr14b*. RIL#121 was most likely a recombinant that had *Lr14b* but lacked the APR gene. It is difficult to determine the exact recombination frequency of the adult plant resistance gene and *Lr14b* because the population segregated for two to three additional APR genes. The Thatcher near-isogenic line with *Lr14b* is susceptible to the race used in Mexico in seedling and adult plants. Among the three races used in St. Paul, MN, only race MCDS is avirulent to *Lr14b*. However, the Thatcher line with *Lr14b* (RL6013) was as susceptible as the standard susceptible check Thatcher (Table 3), indicating that *Lr14b* was not effective at that site. The susceptibility of RL6013 at St. Paul field was most likely due to the high frequency of races virulent to *Lr14b*. *Lr14b* is located on chromosome 7BL and is tightly linked (rather than allelic) to *Lr14a* (Dyck and Samborski, 1970). Based on the rust severity of RL6013 in St. Paul, and its

Table 5. Distribution and χ^2 tests for Jupateco 73S/Weebill 1 $F_{4:5}$, $F_{4:6}$, and $F_{5:7}$ recombinant inbred lines and Thatcher*2/Weebill 1 BC_1F_2 families evaluated for leaf rust reaction in field trials in Mexico and the U.S.

Environment	Generation	No. of lines			Estimated gene number†	χ^2 value	*P* value
		Resistant	Susceptible	Other			
Mexico							
Obregon, 2003	$F_{4:5}$	5	23	112	3	4.2	0.04
					4	0.00	0.96
Obregon, 2004	$F_{4:6}$	4	6	146	3	12.10	0.00
					4	0.54	0.76
Obregon, 2005	$F_{5:7}$	7	13	128	3	5.31	0.07
					4	5.43	0.07
El Batan, 2006	$F_{5:7}$	7	11	128	3	6.15	0.05
					4	2.57	0.28
St. Paul, MN							
2004	$F_{4:6}$	4	5	147	3	13.50	0.00
					4	0.64	0.72
2005	$F_{5:7}$	7	13	128	3	5.43	0.07
					4	5.31	0.07
	BC_1F_2		8	86	3	1.37	0.24
					4	0.82	0.34

†The ratios used in $F_{4:5}$ lines was 0.0827 resistant:0.9163 susceptible and others for three genes, and 0.0366 resistant:0.9634 susceptible and others for four genes. The ratios used for $F_{4:6}$ lines were 0.0827 resistant:0.0827 susceptible:0.8346 others for three genes, and 0.0366 resistant:0.0366 susceptible:0.9268 others for four genes. The ratios used in $F_{5:7}$ lines were 0.101 resistant:0.101 susceptible:0.798 other for three genes, and 0.0473 resistant:0.0473 susceptible:0.9054 other for four genes. The ratios used in the BCF2 lines were 1 susceptible:7 other for three genes, and 1 susceptible:15 other for four genes.

IT and severity to the race used in Mexico, we concluded that an APR gene linked to *Lr14b* in chromosome 7BL was present in Weebill 1. The APR gene linked to *Lr14b* explained a much larger proportion of the variance of leaf rust severity in St. Paul (25%, Table 6) than in Mexico (5–8%). The correlation coefficient for environments using RILs with *Lr14b* and lines without *Lr14b* were similar to the correlation coefficients using data for all RILs (Table 4), suggesting that the adult plant resistance gene linked to *Lr14b* responded similarly to the environment as the other adult plant resistance genes in Weebill 1.

Microsatellite Marker Tagging of *Lr17a*

Resistance gene *Lr17a* in the Jupateco 73S/Weebill 1 cross was mapped to the distal end of chromosome 2AS by linkage analysis. Two markers, *Xgwm636* and *Xbarc124*, were linked to *Lr17a* (Fig. 2). In common wheat, the consensus map shows *Xbarc124* and *Xgwm636* are at 8.0 cM and 11.0 cM from the 2A telomere (Somers et al., 2004). In Jupateco 73S/Weebill, *Xgwm636* was 4.0 cM distal to *Lr17a* gene, and *Xbarc124* was 4.8 cM distal to *Xgwm636*. *Xgwm636* produced a 110 bp PCR amplicon in Jupateco 73S and a 115 bp amplicon in Weebill 1. *Xbarc124* is a dominant marker for *Lr17a* with a 235 bp PCR amplicon in Jupateco 73S and a null allele in Weebill 1. The null allele of Weebill 1 in the 2AS region was valid because *Xbarc124* produced a second amplicon of 280bp in both Weebill 1 and Jupateco 73S.

In seedling tests of the 35 wheat lines listed in Table 7, races BBBD, THBJ, TNRJ, MJBJ, and MFBJ were avirulent to the Thatcher line with *Lr17a* and Jupateco 73S, and MCDS and MHDS were virulent to both. Races BBBD, THBJ, TNRJ, MJBJ, and MFBJ produced low ITs to wheat cultivars Buck Manantial, Klein Lucero, Noroeste 66, Timson, Torim 73, Songlen, Sunkota, and Jagger confirming that those wheat lines were most likely to have *Lr17a*. The cultivars Lerma Rojo 64 and Tanori 71 were heterogeneous for low and high ITs to BBBD, and Tanori 71 was also heterogeneous for low and high ITs to THBJ. All the lines from Mexico, Australia, and Argentina and postulated to have *Lr17a* had the same haplotypes for *Xgwm636* and *Xbarc124* as Jupateco 73S (Table 7). However, RL6008 had the same allele of *Xbarc124* as Jupateco 73S. Among the 22 U.S. wheat lines without

Table 6. Mean leaf rust severity of $F_{5:7}$ RILs with *Lr14b* and without *Lr14b* and correlations of determination (R^2) between *Lr14b* and leaf rust severity in three different environments.

Environment	Mean leaf rust severity (%)		Percentage leaf rust reduction†	R^2
	+Lr14b	*–Lr14b*		
Mexico				
Cidad Obregon, 2005	35	54	35***	0.08
El Batan, 2006	35	48	27**	0.05
St. Paul 2005	32	60	47***	0.25

**Significant at the 0.01 probability level.

***Significant at the 0.001 probability level.

†Difference between mean leaf rust severity of lines with genotype *lr14blr14b* and mean leaf rust severity of lines with genotype *Lr14bLr14b* divided by the mean leaf rust severity of lines with genotype *Lr14bLr14b*.

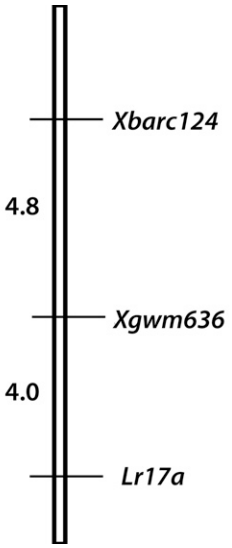

Figure 2. Genetic distance in cM between two simple sequence repeat markers and the leaf rust resistance gene *Lr17a*. The linkage map was constructed using 129 $F_{5:7}$ recombinant inbred lines of Jupateco 73S/Weebill 1. Names of markers and the gene are shown on the right.

Lr17a, the 110 bp amplicon of *Xgwm636* linked to *Lr17a* in Jupateco 73S appeared in 'McVey', and the 235 bp amplicon of *Xbarc124* appeared in 'Oklee' and 'Verde'.

DISCUSSION

Our studies determined that Weebill 1 had seedling leaf rust resistance gene *Lr14b* and an unknown seedling resistance gene. Field trials with races virulent to the two genes indicated that Weebill 1 also carried either three or four additional APR genes. The STS marker *csLV34* that is highly diagnostic of *Lr34* (Lagudah et al., 2006) indicated that Weebill 1 does not have *Lr34*. One of the APR genes, linked to *Lr14b* in chromosome 7BL, had a larger effect in plots at St. Paul than in Mexico. We also mapped the seedling gene *Lr17a* present in Jupateco 73S to the distal region of chromosome 2AS. The *Lr17a* linked microsatellite markers *Xgwm636* and *Xbarc124* were located distal to *Lr17a*.

The effect of *Lr14b* in combination with the adult plant resistance genes could not be determined because we could not postulate the adult plant resistance genes in the RILs. Nelson et al. (1997), Singh and Rajaram (1992) and Zhang et al. (2008) indicated that race specific resistance genes *Lr10, Lr13,* and *Lr23* when ineffective, did not provide any resistance at the adult plant stage. Thus, *Lr14b* most likely did not provide any resistance in combination with other adult plant resistance genes. This hypothesis can only be validated when the adult plant resistance genes can be postulated.

We used a small sample size (a random set of families without *Lr17a*) to study resistance to TGBG, thus we couldn't statistically conclude whether the resistance was due to one gene or interaction of multiple genes. The majority of the seedling leaf rust resistance genes are dominant following the gene-for-gene relationship (Kolmer 1996). Seedling resistance due to two genes was only found in the complementary genes *Lr27* and *Lr31* (Singh and McIntosh, 1984), which is also present in Jupateco 73S (Singh and Rajaram, 1991). The Jupateco 73S/Weebill 1 population segregated for reaction to TGBG, thus the resistance to TGBG in Weebill 1 was not due to *Lr27* and *Lr31*. The segregation ratios of $F_{5:7}$ and BC_1F_2 families were very close to a 1:1 ratio. The unknown seedling resistance in Weebill 1 is probably a singe gene. The unknown seedling resistance gene in Weebill 1 has a very narrow resistance spectrum when tested with a range of races. Of the 12 *P. triticina* races used in seedling studies, this unknown seedling resistance gene conferred resistance only to race TGBG. Race TGBG was first detected in the U.S. in 2002 at a very low frequency (Kolmer et al., 2004); and, since 2004, this race has been detected in the U.S. (Kolmer et al., 2006; Kolmer et al., 2007b). This gene might also be present in 'Little Club', 'Marquis' (Kolmer JA, unpublished data, 2007), and some plants of the Thatcher near isogenic line with *Lr1* (RL6003) (McCallum et al., 2005). The low IT displayed by some plants in RL6003 was a mesothetic IT X. The unknown gene in Weebill 1 also produced a mesothetic IT. Thus, we speculate that the mesothetic IT displayed by Weebill 1 and some plants of RL6003 to leaf rust race TGBG was possibly due to the same unknown leaf rust resistance gene. However, this can only be validated through an allelism test by crossing Weebill 1 with selected plants of RL6003 that have IT X and evaluating the segregating population.

The leaf rust severity of Jupateco 73S/Weebill 1 F_1 plants in the field was above the mid-parent value suggesting lack of dominance of adult plant resistance. In this study, we only tested the F_1 in one environment. Thus, the high severity of the Jupateco 73S/Weebill 1 F_1 could have been caused by above normal temperature in Obregon 2003. However, in a similar study conducted in Obregon 2003, the F_1 severity of Jupateco 73S/Brambling (Brambling was resistant) was only 5% (Zhang et al., 2008). Apparently the adult plant resistance genes in Weebill 1 lack dominance and were different from adult plant resistance genes in Brambling. Weebill 1 was derived from a cross involving 'Pavon 76' in the pedigree. Pavon 76 has the durable adult plant leaf rust resistance gene *Lr46* (Singh et al., 1998). Future studies by quantitative trait loci (QTL) mapping will be able to postulate whether *Lr46* is present in Weebill 1. Another adult plant resistance gene in Weebill 1 was most likely linked to the seedling gene *Lr14b* located on chromosome 7BL. The APR gene on 7BL in Weebill 1 reduced leaf rust by 30% in Mexico and 50% in St. Paul. In a similar study using the $F_{5:7}$ RILs of Jupateco 73S/Brambling, *Lr34* reduced leaf rust by about 90% in Mexico and

Table 7. Infection types of 35 wheat lines to seven *Puccinia triticina* races and allele sizes of two microsatellite markers linked to leaf rust resistance gene *Lr17a*.

Wheat line	Accession number†	Origin	*Lr17a* postulation	*P. triticina* races							Microsatellite marker‡	
				BBBD	THBJ	TNRJ	MJBJ	MFBJ	MCDS	MHDS	*Xgwm636*	*Xbarc124*
Thatcher		USA	Absent	33+	3+	3	33+	3+	3+	33+	86	null
Weebill 1		Mexico	Absent	33+	33+	3+	33+	3	0;	33+	115	null
Jupateco 73S		Mexico	Present	;	0;	;1–	;12	0;	3+	33+	110	235
TcLr17a	RL6008	USA§	Present	;	0	1+2	;12	;1–	33+	3+	86	235
Buck Manantial	PI 344455	Argentina	Present	;	;	;	;	;	2	3+	110	235
Klein Lucero	Citr 14047	Argentina	Present	;	;	;1–	;	;	23	33+	110	235
Noroeste 66	Citr 17391	Mexico	Present	;	;1–	0;	;1–	;12	4	33+	110	235
Timson	PI 404115	Australia	Present	;	;	;1	0;	;12	;	3+	110	235
Torim 73	PI 433769	Mexico	Present	;	;22–	23	;	12	4	3+	110	235
Songlen	PI 442904	Australia	Present	0;	;1–	;1–	;1–	;12	4	3+	110	235
Sunkota	PI 483050	Australia	Present	;1,3+¶	2	;	1+	;1–	4	3+	110	235
Jagger		USA	Present	;	;12	0	0	2	3+	3+	105	null
Lerma Rojo 64	Citr 13929	Mexico	Heterogeneous	;0;,23,3+	22+	22+	;2+	22+	3+	3+	110	235
Tanori 71	Citr 17416	Mexico	Heterogeneous	0;,3+	;12,3+	0;	;1	;12	4	33+	110	235
2375		USA	Absent	0	2+3	33+	3+	33+	4	3+	113	null
Alsen		USA	Absent	0	33+	33+	0;	0;	0	0	113	225
Amigo		USA	Absent	;	;1–,3+	33+	33+	33+	;1	;1–	115	null
BacUp		USA	Absent	3	3+	3	3	3+	3+	3+	113	null
Forge		USA	Absent	12	3	;12	2+	;1–1	;12	3+	113	null
Grandin		USA	Absent	1+	3+	3	0;	0;	0;	0;	113	225
Gunner		USA	Absent	2+	3	3+	0;	;	0;	0;	113	null
Hamer		USA	Absent	0;	33+	;12	2+	;	2+	3+	113	null
HJ98		USA	Absent	3+	3+	3	2+	33+	;123	3	113	null
Ingot		USA	Absent	;	3+	2N	33+	;1–	;12	33+	113	null
Knudson		USA	Absent	0	2	12	3	;1–	;12	;12	113	null
Kulm		USA	Absent	0;	;	2	3+	;1–	;	0;	113	null
Marshall		USA	Absent	0	3+	3+	0;	0;	0;	0	113	null
McVey		USA	Absent	;12	33+	2+	33+	;1	2+	33+	110	null
Mercury		USA	Absent	;	3+	;	3N,33+	;	;12	;2,33+	113	null
Oklee		USA	Absent	0	0	;1–	;	33+	3+	3+	118	235
Oxen		USA	Absent	0;	3+	33+	0;	0;	0;	0;	113	null
Parshall		USA	Absent	;12	3+	2	3+	;1–	;1	3+	83	null
Sharp		USA	Absent	1+	22+	2	3	;	;12	2+3	113	null
Verde		USA	Absent	0	;12	0	3	0;	;1–	2	118	235
Wheaton		USA	Absent	0;	…	3	2+	33+	0	;2+	113	null
PIC#											0.69	0.54
Allele number											7	3

†Lines with accession numbers were provided by the USDA National Small Grains Collection. Seed of the other lines was from the Univ. of Minnesota.

‡Numeric values are the amplicon size in bp for the corresponding marker, and null = null allele.

§The near isogenic line was initially developed in Canada. Thatcher is a U.S. spring wheat. Thus, we refer Thatcher near-isogenic line for *Lr17a* as USA in the context of its origin of genetic background.

¶',' Indicating the wheat line was heterogeneous for reaction to the test race; the predominant plant type was given first.

#Polymorphic information content (PIC) was based on Botstein et al. (1980).

65 to 80% in St. Paul (Zhang et al., 2008). Thus, the 7BL gene in Weebill 1 was less effective than the very widely used APR gene *Lr34*. The *Lr34* gene was more effective in Mexico than St. Paul (Zhang et al., 2008); whereas, the APR gene on 7BL was more effective in St. Paul than in Mexico. Compared to Mexican locations, the rust development period in St. Paul was much shorter and the daily temperature rose at a faster rate. *Lr34* conditions higher resistance at low temperature than at high temperature (Dyck and Samborski, 1982; Singh and Huerta-Espino, 2003). Contrary to *Lr34*, the APR on chromosome 7BL in Weebill 1 appeared to condition better resistance at high temperatures than at low temperatures. This hypothesis is also supported by similar correlation coefficients between

the 2003 and 2004 Mexico nurseries and the Mexico and St. Paul nurseries because the temperature in the 2003 Mexico nursery was abnormally higher than in the 2004 Mexican nurseries. Therefore, slow rusting APR genes may exhibit varying levels of effectiveness depending on environmental conditions.

Adult plant resistance QTLs on 7BL were reported in the CIMMYT spring wheat cultivars Parula (William et al., 1997) and Opata 85 (Nelson et al., 1997; Faris et al., 1999), and a Swiss winter wheat cultivar Forno (Messmer et al., 2000). However, some of these may be different APR genes. Two QTLs, one with larger effect than the other, were identified on 7BL in Forno. The APR QTL on 7BL in Opata 85, which was effective in Ithaca, NY, and not effective in Ciudad Obregon, was in a cluster of defense response genes (Faris et al., 1999). The QTL in Parula was effective in Ciudad Obregon (William et al., 1997). Future studies by QTL mapping are needed to verify if the APR gene on 7BL in Weebill 1 is the same as the previously identified QTL in Forno and Parula.

Microsatellite markers *Xgwm636* and *Xbarc124* tagged *Lr17a* at the terminal region on chromosome 2AS. Our marker data with *Xgwm636* and *Xbarc124* had good agreement with the leaf rust IT data associated with *Lr17* in non-U.S. wheat backgrounds. Results indicated that although markers *Xgwm636* and *Xbarc124* determined the presence or absence of *Lr17a* in Mexican, Australian, and Argentinean wheat lines, they are less likely to be useful if *Lr17a* is present in the U.S. winter wheat backgrounds where Jagger would be a likely donor.

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