Inheritance of Leaf Rust Resistance in Wheat Cultivars Grandin and CDC Teal

J. Q. Liu and J. A. Kolmer, Agriculture and Agri-Food Canada, Cereal Research Centre, 195 Dafoe Road, Winnipeg, MB, Canada R3T 2M9

ABSTRACT

Liu, J. Q., and Kolmer, J. A. 1997. Inheritance of leaf rust resistance in wheat cultivars Grandin and CDC Teal. Plant Dis. 81:505-508.

The hard red spring wheat cultivars Grandin and CDC Teal were genetically examined to determine the number and identity of the leaf rust resistance genes present in both wheats. The two cultivars were crossed with the leaf rust susceptible cultivar Thatcher, and the F_1 plants were backcrossed to Thatcher. Fifty-four and 80 BC_1F_1 plants derived respectively from Grandin and CDC Teal were selfed to produce BC_1F_2 families. The BC_1F_2 families were tested as seedlings with isolates of *Puccinia recondita* f. sp. *tritici* that differed for virulence to specific leaf rust resistance genes. The BC_1F_2 families were also tested in the adult-plant stage in field rust nursery tests. Segregation of BC_1F_2 families in the seedling tests indicated that Grandin had resistance genes *Lr2a*, *Lr3*, and *Lr10*, and was heterogeneous for *Lr16*. CDC Teal was shown to have the seedling leaf rust gene *Lr1*. In field rust nursery tests, both Grandin and CDC Teal were shown to have adult-plant resistance genes *Lr13* and *Lr34*. Additional leaf rust resistance genes that condition effective field resistance should be incorporated into hard red spring wheat cultivars to diversify the leaf rust resistance in this wheat class.

Leaf rust of wheat (*Triticum aestivum* L.), caused by *Puccinia recondita* Roberge ex Desmaz. f. sp. *tritici* Eriks. & E. Henn., occurs in North America nearly everywhere wheat is grown (10). Yield losses due to leaf rust disease on wheat cultivars can vary from 5 to 15% (18) or more, depending on the level of resistance and stage of crop development when initial infection occurs. Genetic resistance is the most economical and effective means of reducing yield losses to this disease. Resistance to *P. recondita* f. sp. *tritici* in some Canadian spring wheats has been determined to be conditioned by one or more adult-plant resistance genes, such as *Lr13* and *Lr34*, in addition to seedling resistance genes (1,10,19). The leaf rust fungus exists in many physiologic forms, and changes in virulence phenotype frequencies in *P. recondita* f. sp. *tritici* populations often occur after the introduction of new specific resistance genes in host cultivars (8). To control this disease through genetic resistance, plant breeders periodically need to add new resistance genes to their breeding materials. Knowledge of the identity of the leaf rust resistance genes in released cultivars and germ plasm is essential for the incorporation of new effective resistance

genes into breeding programs and maintenance of a diversity of resistance genes in commonly grown cultivars. The hard red spring wheats recently released in the northern Great Plains of Canada and the United States are generally resistant to *P. recondita* f. sp. *tritici*. However, the number and identity of the resistance genes in some recently released cultivars are unknown. The objective of this study was to identify genes for leaf rust resistance in hard red spring wheat cultivars Grandin and CDC Teal.

MATERIALS AND METHODS

Grandin, which was derived from the cross Len//Butte * 2//ND507/ND593, was released by the Agricultural Experiment Station at North Dakota State University. Grandin has been one of the most popular spring wheat cultivars grown in North Dakota. CDC Teal was jointly developed by the Department of Crop Science and Plant Ecology and the Crop Development Centre, University of Saskatchewan. CDC Teal, selected from a three-way cross BW514/Benito/BW38 (BW514 = Nainari 60/Huelquen; BW38 = Sonora 64/Tezanos Pinto Precos/Neepawa) is an early-maturing spring wheat best adapted to the black soil zone of western Canada (7).

Grandin and CDC Teal were used as pollen parents and crossed with the leaf rust susceptible cultivar Thatcher (Tc). F_1 plants were used as pollen parents and crossed with Tc. Backcross F_2 (BC_1F_2) families were evaluated for seedling resistance in the greenhouse with selected virulence phenotypes of *P. recondita* f. sp. *tritici* (13). BC_1F_2 families of both crosses, parents, and Thatcher backcross lines near-

isogenic for wheat leaf rust resistance genes were seeded in clumps in fiber flats filled with a sand-peat-soil mix or in a greenhouse bed. Plants were grown at $20 \pm 2^\circ\text{C}$ with 8 h of supplemental fluorescent light ($276 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) per day. Nine to 10 days after seeding, the primary leaves were inoculated by atomizing urediniospores suspended in Dustrol (Ciba-Geigy, Mississauga, ON, Canada) light mineral oil. Inoculated plants were incubated at 100% RH for 16 h at 20°C . Fifteen to 20 seedlings of each BC_1F_2 family were tested with each isolate of *P. recondita* f. sp. *tritici* used. Infection types (IT) on primary leaves were rated 12 days after inoculation using a scale of 0 to 4 (13,20). Infection types of 0 to 2^+ were considered resistant, and IT of 3 to 4 were considered susceptible. The BC_1F_2 families were classified as either segregating or homozygous susceptible. Goodness of fit to segregation ratios in BC_1F_2 families from each cross was determined using chi-square tests (21).

To evaluate adult-plant resistance, approximately 50 seeds of each BC_1F_2 family were planted in 2-m rows in a field rust nursery on 30 May 1995. Susceptible spreader rows were inoculated with a mixture of *P. recondita* f. sp. *tritici* phenotypes prevalent in the eastern prairie regions of Canada (10,12). Grandin, CDC Teal, Thatcher, and 41 Thatcher near-isogenic lines were also evaluated for leaf rust severity and response in the field nursery. Rust ratings were recorded on 29 July in the early milk stage (Growth Stage 73-74) (22) when the susceptible check Thatcher had a severity (16) and response (20) rating of 70% susceptible (70 S). To further determine the identity of the adult-plant resistance genes in Grandin and CDC Teal, single plants with leaf rust ratings characteristic of single-gene lines RL4031 (Tc*Lr13*), RL6058 (Tc*Lr34*), or RL6114 (Tc*Lr13+34*) were selected from the BC_1F_2 families which were homozygous susceptible in the seedling tests to all phenotypes. The selected BC_1F_2 plants with adult-plant resistance were harvested individually, and $BC_1F_{2:3}$ plants were grown in the greenhouse. $BC_1F_{3:4}$ lines derived from single $BC_1F_{2:3}$ plants were evaluated for adult-plant leaf rust resistance in the greenhouse and in the field. In the greenhouse test, flag and penultimate (F-1) leaves were inoculated with *P. recondita* f. sp. *tritici* phenotype BBB, which is avirulent to adult plants with *Lr13*, and with phenotype MBR, which is virulent to *Lr13*. In the 1996 field rust nursery, $BC_1F_{3:4}$ lines

Corresponding author: J. A. Kolmer
E-mail: jkolmer@em.agr.ca

Accepted for publication 3 February 1997.

Publication no. D-1997-0310-06R

This article is in the public domain and not copyrightable. It may be freely reprinted with customary crediting of the source. The American Phytopathological Society, 1997.

with adult-plant resistance derived from Tc * 2/Grandin and Tc * 2/CDC Teal were compared for leaf rust severity and response with the lines TcLr13, TcLr34, and TcLr13 + Lr34.

RESULTS

Grandin. Grandin had very low IT of 0; to isolates avirulent to TcLr2a (Table 1). Grandin also had low IT of ;1 to ;12⁻ to isolates avirulent to Lr10 or Lr3. Grandin was heterogeneous for IT (;1/3⁺) to *P. recondita* f. sp. *tritici* phenotypes that were virulent to Lr2a. Plants of Grandin susceptible as seedlings to leaf rust phenotypes virulent to Lr2a were crossed with Thatcher to develop the BC₁F₂ families. The Tc * 2/Grandin families segregated to fit a three-gene (7 segregating :1 homozygous susceptible) ratio when inoculated in the seedling stage with the widely avirulent *P. recondita* f. sp. *tritici* phenotype BBB (Table 2). The individual BC₁F₂ families had the same IT to phenotypes CGB and MBR, and the segregation fitted an expected 1:1 ratio, which indicated a single gene for resistance. This gene, which conditioned an IT 0₁, was one of the three genes conferring resistance to BBB since all BC₁F₂ families segregating for resistance to CGB and MBR also segregated for IT 0₁ with BBB. This gene appeared to be Lr2a because resistant seedlings in segregating families had the characteristic IT of RL6016 (TcLr2a). When the same BC₁F₂ families were tested with NBB, a phenotype also avirulent to Lr2a, the segregation gave a good fit to a 3:1 ratio, which indicated the presence of a gene for resistance in addition to Lr2a. The BC₁F₂ families segregated in a 1:3 ratio when inoculated with leaf rust phenotype SBD, which is avirulent to Lr3 and virulent to Lr2a and Lr10. This indicated that Grandin has Lr3 and possibly a second gene that suppresses the expression of Lr3 in a Thatcher background. All of the BC₁F₂ families that segregated for resistance to

phenotype SBD also segregated to phenotype NBB, which is also avirulent to RL6002 (TcLr3). The BC₁F₂ families segregated to fit a 1:1 ratio when tested with phenotype TBB, which was virulent to both Lr2a and Lr3. This gene must be Lr10 since the segregating families also segregated with phenotype BBB, and phenotypes BBB and TBB are both avirulent on RL6004 (TcLr10) (Table 1). This was further indicated by contingency table tests, as the segregation of BC₁F₂ families to phenotype TBB was independent of phenotypes CGB and MBR ($\chi^2 = 0.235$, $P = 0.95$ to 0.75).

Grandin was heterogeneous for seedling resistance to phenotypes TBG and KBJ (Table 1), which are avirulent to Lr16 and virulent to Lr2a, Lr3, and Lr10. Plants resistant to TBG were selected from Grandin and crossed with Thatcher and RL6005 (TcLr16). Two F₂ families derived from both crosses were evaluated for seedling resistance with phenotype TBG. The

segregation of F₂ plants from the cross of Thatcher with resistant selections of Grandin gave a good fit to a ratio of 3 resistant : 1 susceptible in both families, while F₂ families from the cross of TcLr16 with the resistant selections of Grandin were homozygous resistant (Table 3). These results indicated that Grandin is heterogeneous for Lr16.

When challenged with a mixture of *P. recondita* f. sp. *tritici* phenotypes in the field rust nursery, the Tc * 2/Grandin families segregated to fit 3:1 and 7:1 ratios, which indicated that Grandin had at least two genes that conditioned field resistance (Table 2). This resistance must be due to adult-plant resistance genes; the lines TcLr2a, TcLr3, and TcLr10 had a leaf rust severity and response rating of 70 to 90% susceptible (Table 1). The near-isogenic line RL4031 (TcLr13) had a field leaf rust reaction of moderately resistant to moderately susceptible with large necrotic flecks and moderate to large uredinia with chloro-

Table 2. Segregation for leaf rust resistance in greenhouse and field tests in backcross F₂ families of Thatcher * 2/Grandin and Thatcher * 2/CDC Teal

Phenotype	Gene detected	Number of families ^a		Expected ratio	<i>P</i> ^b
		Seg.	Susc.		
Thatcher * 2/Grandin					
BBB	<i>Lr2a, Lr3, Lr10</i>	44	10	7:1	0.50-0.25
CGB, MBR	<i>Lr2a</i>	31	23	1:1	0.50-0.25
NBB	<i>Lr2a, Lr3</i>	35	19	3:1	0.25-0.10
SBD	<i>Lr3</i>	14	40	1:1	<0.01
				1:3	0.99-0.97
TBB	<i>Lr10</i>	30	24	1:1	0.50-0.25
Field ^c	<i>Lr13, Lr34</i>	45	9	7:1	0.50-0.25
				3:1	0.25-0.10
Thatcher * 2/CDC Teal					
BBB, KBJ	<i>Lr1</i>	39	40	1:1	0.95-0.90
MFM	...	0	79	1:1	<0.001
Field	<i>Lr13, Lr34</i>	66	14	7:1	0.25-0.10
				3:1	0.25-0.10

^a Seg. = segregating for resistant and susceptible plants; Susc. = homozygous susceptible.

^b *P* = probability of χ^2 value.

^c A mixture of *Puccinia recondita* f. sp. *tritici* phenotypes was used to initiate a rust epidemic (10,12).

Table 1. Seedling infection types^a and adult-plant field reactions^b to *Puccinia recondita* f. sp. *tritici* in the wheat cultivars Grandin, CDC Teal, Thatcher, and Thatcher backcross lines near-isogenic for leaf rust resistance genes

Cultivar/ <i>Lr</i> line	<i>P. recondita</i> f. sp. <i>tritici</i> phenotype									Field rust severity and response
	BBB	CGB	KBJ	MFM	MBR	NBB	SBD	TBG	TBB	
Grandin	0;	0;	;1/33 ⁺	0;	0;	;12 ⁻	;1 ⁻	;1/33 ⁺	;1	TR
CDC Teal	0;	0;	0;	;12	;12	;1	;1	;1	;1 ⁻	TR
Thatcher	3+4	3+4	3+4	3+4	3+4	3+4	3+4	3+4	3+4	70-90 S
Tc <i>Lr</i> 1 RL6003	;1	;1	;1	33 ⁺	3 ⁺	3 ⁺	3+4	3 ⁺	3+4	70-90 S
Tc <i>Lr</i> 2a RL6016	0;	0;	3 ⁺	0;	0;	;12	3+4	3 ⁺	33 ⁺	70-90 S
Tc <i>Lr</i> 3 RL6002	;1 ⁻	33 ⁺	33 ⁺	3 ⁺	33 ⁺	;1	;1	3 ⁺	3+4	70-90 S
Tc <i>Lr</i> 10 RL6004	;1	3 ⁺	3 ⁺	33 ⁺	3+4	3 ⁺	3+4	3 ⁺	;11 ⁺	70-90 S
Tc <i>Lr</i> 13 RL4031	22+3C	2+3C	33 ⁺	233 ⁺	33 ⁺	3c	2+33 ⁺	3+4	33 ⁺	50 MRMS
Tc <i>Lr</i> 16 RL6005	;12 ⁻	33 ⁺	;12 ⁻	;12 ⁻	12	;12 ⁻	;12 ⁻	;12 ⁻	;12	50 MRMS
Tc <i>Lr</i> 34 RL6058	23 ⁺	;23	;23 ⁺	;23 ⁺	33 ⁺	23 ⁺	33 ^c	22-/3	2-3	10 M
Tc <i>Lr</i> 13+34 RL6114	23 ⁺	;23 ⁺	;23 ⁺	;23 ⁺	;22 ⁺	23 ⁺	3c3	33 ⁺	3c3	5 M

^a Infection types on primary leaves were rated 12 days after inoculation on a scale of 0 to 4 (13). The + and - symbols denote more or less sporulation, respectively; c indicates uredinia surrounded with chlorosis; / indicates the wheat line was heterogeneous for the indicated infection types.

^b Field reactions to a mixture of *P. recondita* f. sp. *tritici* phenotypes in the 1995 field rust nursery. Percent rust severity ranging from TR (trace) to 100% on individual plants, where R = resistance (flecks and small uredinia with necrosis), M = mixed infections (small and moderate-sized uredinia), MR = moderately resistant (large necrotic flecks and large uredinia), MS = moderately susceptible (moderate to large uredinia with chlorosis), and S = susceptible (large uredinia).

sis (Table 4). The same field leaf rust reaction was observed in BC₁F_{3,4} line 79 derived from a single BC₁F₂ plant selection (Table 4). The second adult-plant resistance gene could be *Lr34*, since lines 71 and 73 had field leaf rust reactions identical to Tc*Lr34* (Table 4) and also showed leaf tip necrosis, a condition often associated with this gene (2). In the greenhouse tests, line 79 was resistant to phenotype BBB and susceptible to MBR, which indicated that line 79 had *Lr13*. Lines 71 and 73 produced intermediate IT to both phenotypes, which indicated that these lines lack *Lr13* but may carry *Lr34*. Line 98 had resistance equal to RL6114 (Tc*Lr13* + *34*) in the field test and had low IT to BBB and intermediate IT to MBR, which indicated the presence of *Lr13* and *Lr34*.

CDC Teal. CDC Teal had seedling IT 0; to isolates avirulent to *Lr1*, and IT of ;1⁻ to ;12 to isolates virulent to *Lr1* (Table 1). The Tc * 2/CDC Teal families were tested with leaf rust phenotypes BBB, KBJ, and MFM. The BC₁F₂ families segregated for a 1:1 ratio with BBB and KBJ, which are avirulent to *Lr1* (Table 2). All BC₁F₂ families were homozygous susceptible when tested with phenotype MFM, which is virulent to *Lr1*. These results indicated that CDC Teal had *Lr1*. Selected BC₁F₂ families were further tested with an additional 10 *P. recondita* f. sp. *tritici* phenotypes, but no seedling genes other than *Lr1* were identified (data not presented).

Segregation of the Tc * 2/CDC Teal families for field resistance gave a good fit to both 7:1 and 3:1 ratios, which indicated that at least two genes conditioned adult-plant resistance (Table 2). The segregating BC₁F₂ families from this cross had plants with rust reactions very similar to Tc*Lr13*, Tc*Lr34*, and Tc*Lr13* + *34*, which indicated that CDC Teal could have both *Lr13* and *Lr34*. The identity of adult-plant resistance genes in CDC Teal was further determined by evaluating BC₁F_{3,4} lines derived from single BC₁F_{2,3} plant selections as adult-plants in the greenhouse and in the 1996 field rust nursery (Table 4). BC₁F₄ lines 265 and 270 had IT ;1 to phenotype BBB and IT 3⁺4 to MBR in the greenhouse test and had the same field leaf rust resistance as Tc*Lr13*, which indicated the presence of *Lr13* in these lines. Line 250 had intermediate IT to both phenotypes BBB and MBR in the greenhouse test and had the same field leaf rust reaction as Tc*Lr34*, which indicated the presence of *Lr34*. Line 304 had IT ;1 to phenotype BBB and IT 23 to MBR in the greenhouse test, and had a similar field leaf rust reaction to Tc*Lr13* + *34*, which indicated that line 304 had both *Lr13* and *Lr34*.

DISCUSSION

Grandin was determined to have seedling resistance genes *Lr2a*, *Lr3*, and *Lr10*, and was heterogeneous for *Lr16*. The Canadian spring wheat cultivar Columbus

was also initially heterogeneous for *Lr16* (19). *Lr10* was determined to be present in Len and Butte, which are in the pedigree of Grandin, and *Lr2a* was shown to be in Len (15). This cultivar was selected from a single F₄ plant (T. F. Townley-Smith, *personal communication*) that may have been heterozygous for *Lr16*. Genes *Lr2a*, *Lr3*, and *Lr10* are common in hard red spring wheats, but do not currently condition effective resistance to *P. recondita* f. sp. *tritici*. Frequency of virulence on *Lr2a*, *Lr3*, and *Lr10* in North American *P. recondita* f. sp. *tritici* populations has been high (10). The widespread use of cultivars with these seedling genes has selected *P. recondita* f. sp. *tritici* phenotypes with virulence to these genes (8). Grandin has been used as a parent in Canadian and U.S. wheat breeding programs.

Tc * 2/Grandin families did not segregate in a single-gene ratio for *Lr3* as expected when tested with phenotype SBD. *Lr3* must be present in the segregating families, because SBD is virulent to *Lr2a* and *Lr10*. A second gene in Grandin may suppress the expression of *Lr3* in a Thatcher background. A gene in the culti-

var Prelude inhibited the resistance of *Lr3* to some *P. recondita* f. sp. *tritici* phenotypes (6). A gene in Thatcher inhibits the expression of *Lr23* to leaf rust isolates from Canada (14).

The effective leaf rust resistance in Grandin was conditioned by adult-plant resistance genes *Lr13* and *Lr34*. BC₁F_{3,4} lines with *Lr13* and *Lr34* singly and together were selected from Tc * 2/Grandin F₂ families. In the field rust nursery, line 79 had leaf rust severity and response identical to Tc*Lr13*. Inoculation of adult plants of line 79 in the greenhouse with phenotype BBB should have produced IT ;1, which is the characteristic IT of Tc*Lr13* to phenotype BBB. However, a slightly higher IT (2) was produced, possibly due to the influence of environmental factors or segregating background effects.

CDC Teal was shown to have adult-plant resistance genes *Lr13* and *Lr34*, and the seedling gene *Lr1*. The cultivar Neepawa, which is in the pedigree of CDC Teal, also has *Lr13* (11). CDC Teal also has very clear leaf-tip necrosis, a condition often associated with the presence of *Lr34* (2). CDC Teal had a seedling IT ;12 to *P.*

Table 3. Segregation for seedling resistance to phenotype TBG of *Puccinia recondita* f. sp. *tritici* in F₂ families from crosses of Grandin resistant to phenotype TBG with Thatcher and the near-isogenic line RL6005 (Tc*Lr16*)

Cross	F ₂ family	Number of plants ^a		Expected ratio	P ^b
		Res.	Susc.		
Thatcher/Grandin	1	140	48	3:1	0.95-0.90
	2	147	41	3:1	0.50-0.25
Tc <i>Lr16</i> RL6005/Grandin	1	193	0	3:1	<0.001
	2	198	0	3:1	<0.001

^a Res. = resistant; Susc. = susceptible.

^b P = probability of χ^2 value.

Table 4. Adult-plant greenhouse infection types and field reactions to *Puccinia recondita* f. sp. *tritici* in BC₁F_{3,4} lines selected from Thatcher * 2/Grandin and Thatcher * 2/CDC Teal, and Thatcher near-isogenic lines with the adult-plant resistance genes *Lr13* and/or *Lr34*

Line	Gene detected	Greenhouse ^a		Field rust severity and response ^b
		BBB	MBR	
Thatcher * 2/Grandin ^c				
Line 79	<i>Lr13</i>	2 ⁻	3 ⁺ 4	60 MRMS
Line 71	<i>Lr34</i>	;23	2 ⁺ 3	10-20 M
Line 73	<i>Lr34</i>	;23	23	TR-5 M
Line 98	<i>Lr13, Lr34</i>	0;1	22 [±]	TR
Thatcher * 2/CDC Teal				
Line 265	<i>Lr13</i>	;1	3 ⁺ 4	40 MRMS
Line 270	<i>Lr13</i>	;1	3 ⁺ 4	40 MRMS
Line 250	<i>Lr34</i>	22 ⁺	22 [±] 3	5-20 M
Line 304	<i>Lr13, Lr34</i>	;1	23	TR
Thatcher		3 ⁺ 4	3 ⁺ 4	90 S
Tc <i>Lr13</i> RL4031		;1	3 ⁺ 4	40-60 MRMS
Tc <i>Lr34</i> RL6058		;12	;23	10 M
Tc <i>Lr13+34</i> RL6114		0;	;23	5-10 M

^a Infection types on flag and F-1 leaves were rated 12 to 14 days after inoculation on a scale of 0 to 4 (13). The + and - symbols denote more or less sporulation, respectively.

^b Field reactions to a mixture of *P. recondita* f. sp. *tritici* phenotypes in the 1996 field rust nursery. Percent rust severity ranging from TR (trace) to 100% on individual plants, where R = resistance (flecks and small uredinia with necrosis), M = mixed infections (small and moderate-sized uredinia), MR = moderately resistant (large necrotic flecks and large uredinia), MS = moderately susceptible (moderate to large uredinia with chlorosis), and S = susceptible (large uredinia).

^c The BC₁F_{3,4} lines were derived from the cross of Thatcher with Grandin plants that lack *Lr16*.

recondita f. sp. *tritici* phenotype MFM and other phenotypes that are virulent to *Lr1*. However, this resistance was not expressed in the Tc * 2/CDC Teal families, as all the BC₁F₂ families were homozygous susceptible (IT 3*4) to MFM and other phenotypes virulent to *Lr1*. One possible explanation is that the adult-plant genes *Lr13* and *Lr34* may express some seedling resistance in the CDC Teal background that was lost when the genes were put into a Thatcher background. The effect of cultivar background on the differential expression of *Lr* genes has been previously noted (11).

Genes *Lr13* and *Lr34* are present in both Grandin and CDC Teal. Both genes are also present in Roblin (4) and Pasqua (3). *Lr13* is present in all of the wheats derived from Neepawa (11) and Canada Prairie Spring wheats (9), while *Lr34* is present in Laura (9) and Glenlea (5). Roelfs (17) has indicated that *Lr13* and *Lr34* may be present in many wheats on a worldwide basis and that cultivars with combinations of two or more effective adult-plant or adult and seedling genes have displayed durable rust resistance.

In the North American hard red spring wheats, leaf rust resistance currently relies on the use of only a few effective resistance genes, such as *Lr13*, *Lr16*, and *Lr34*. Gene *Lr13* was first used in the cultivar Manitou released in 1965 (11). Lines with *Lr13* still have effective resistance to leaf rust; plants with this gene produce medium- to large-sized uredinia mixed with necrosis when evaluated in the field plots. However, in years favorable for leaf rust epidemics, cultivars such as Katepwa and Neepawa with only *Lr13* will suffer significant yield losses. Isolates with complete virulence to *Lr13* have increased in recent years in Manitoba and Saskatchewan (J. A. Kolmer, unpublished). Cultivars such as CDC Teal, Roblin, and Columbus, which have more than one effective resis-

tance gene, are more resistant and have had negligible yield losses to leaf rust. Gene *Lr16* has been used in U.S. winter wheat breeding programs, and recent Nebraska winter wheats have *Lr16* (J. A. Kolmer, unpublished). Leaf rust isolates with virulence to *Lr16* were detected in Manitoba in 1995 and 1996. The effectiveness of *Lr16* will be diminished if *Lr16*-virulent *P. recondita* f. sp. *tritici* phenotypes are further selected. Gene *Lr34* currently confers effective resistance to all *P. recondita* f. sp. *tritici* phenotypes in Manitoba and Saskatchewan (J. A. Kolmer, unpublished). However, additional effective resistance genes should be incorporated into hard red spring wheat germ plasm to diversify the leaf rust resistance in this wheat class.

ACKNOWLEDGMENTS

We thank the Western Grain Research Foundation for funding this research and P. Seto-Goh for excellent technical assistance.

LITERATURE CITED

1. Dyck, P. L. 1989. The inheritance of leaf rust resistance in wheat cultivars Kenyon and Buck Manantial. Can. J. Plant Sci. 69:1113-1117.
2. Dyck, P. L. 1991. Genetics of adult-plant rust resistance in 'Chinese Spring' and 'Sturdy' wheats. Crop Sci. 24:309-311.
3. Dyck, P. L. 1993. The inheritance of leaf rust resistance in the wheat cultivar Pasqua. Can. J. Plant Sci. 73:903-906.
4. Dyck, P. L. 1993. Inheritance of leaf rust and stem rust resistance in 'Roblin' wheat. Genome 36:289-293.
5. Dyck, P. L., Samborski, D. J., and Martens, J. W. 1985. Inheritance of resistance to leaf rust and stem rust in the wheat cultivar Glenlea. Can. J. Plant Pathol. 7:351-354.
6. Haggag, M. E. A., and Dyck, P. L. 1973. The inheritance of leaf rust resistance in four common wheat varieties possessing genes at or near the *Lr3* locus. Can. J. Genet. Cytol. 15:127-134.
7. Hughes, G. R., and Hucl, P. 1993. CDC Teal hard red spring wheat. Can. J. Plant Sci. 73:193-197.
8. Kolmer, J. A. 1989. Virulence and race dynamics of *Puccinia recondita* f. sp. *tritici* in Canada during 1956-1987. Phytopathology

79:349-356.

9. Kolmer, J. A. 1994. Genetics of leaf rust resistance in three western Canada spring wheats. Plant Dis. 78:600-602.
10. Kolmer, J. A. 1994. Physiologic specialization of *Puccinia recondita* f. sp. *tritici* in Canada in 1993. Can. J. Plant Pathol. 16:326-328.
11. Kolmer, J. A. 1996. Genetics of resistance to wheat leaf rust. Annu. Rev. Phytopathol. 34:435-455.
12. Kolmer, J. A. 1996. Physiologic specialization of *Puccinia recondita* f. sp. *tritici* in Canada in 1994. Can. J. Plant Pathol. In press.
13. Long, D. L., and Kolmer, J. A. 1989. A North American system of nomenclature for *Puccinia recondita* f. sp. *tritici*. Phytopathology 79:525-529.
14. McIntosh, R. A., and Dyck, P. L. 1972. Cytogenetical studies in wheat. VII. Gene *Lr23* for reaction to *Puccinia recondita* in Gabo and related cultivars. Aust. J. Biol. Sci. 25:765-773.
15. McVey, D. V. 1989. Verification of infection-type data for identification of genes for resistance to leaf rust in some hard red spring wheat. Crop Sci. 29:304-307.
16. Peterson, R. F., Campbell, A. B., and Hannah, A. E. 1948. A diagrammatic scale for estimating rust intensity on leaves and stems of cereals. Can. J. Res. 26(C):496-500.
17. Roelfs, A. P. 1988. Resistance to leaf and stem rusts in wheat. Pages 10-22 in: Breeding Strategies for Resistance to the Rusts of Wheat. N. W. Simmonds and S. Rajaram, eds. CIMMYT, Mexico, D.F.
18. Samborski, D. J. 1985. Wheat leaf rust. Pages 39-59 in: The Cereal Rusts, Vol. 2. A. P. Roelfs and W. R. Bushnell, eds. Academic Press, Orlando, FL.
19. Samborski, D. J., and Dyck, P. L. 1982. Enhancement of resistance to *Puccinia recondita* by interactions of resistance genes in wheat. Can. J. Plant Pathol. 4:152-156.
20. Stakman, E. C., Stewart, D. M., and Loegering, W. Q. 1962. Identification of physiologic races of *Puccinia graminis* var. *tritici*. U.S. Dep. Agric. Agric. Res. Serv. E 6/7.
21. Steel, R., and Torrie, J. 1980. Principles and Procedures of Statistics. McGraw-Hill, New York.
22. Zadoks, J. E., Chang, T. T., and Konzak, C. F. 1974. A decimal code for the growth stages of cereals. Weed Res. 14:415-421.