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

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ABSTRACT

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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.

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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 ± 2°C with 8 h of supplemental fluorescent light (276 $\mu E \cdot m^{-2} \cdot s^{-1}$) 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 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 Tc*Lr13,* Tc*Lr34,* and Tc*Lr13 + Lr34*.

RESULTS

Grandin. Grandin had very low IT of 0; to isolates avirulent to Tc*Lr2a* (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 BC_1F_2 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 BC_1F_2 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 0;, was one of the three genes conferring resistance to BBB since all BC_1F_2 families segregating for resistance to CGB and MBR also segregated for IT 0; with BBB. This gene appeared to be *Lr2a* because resistant seedlings in segregating families had the characteristic IT of RL6016 (Tc*Lr2a*). When the same BC_1F_2 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 BC_1F_2 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 BC_1F_2 families that segregated for resistance to phenotype SBD also segregated to phenotype NBB, which is also avirulent to RL6002 (Tc*Lr3*). The BC_1F_2 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 (Tc*Lr10*) (Table 1). This was further indicated by contingency table tests, as the segregation of BC_1F_2 families to phenotype TBB was independent of phenotypes CGB and MBR (X^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 (Tc*Lr16*). Two F_2 families derived from both crosses were evaluated for seedling resistance with phenotype TBG. The segregation of F_2 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 F_2 families from the cross of Tc*Lr16* 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 Tc*Lr2a*, Tc*Lr3*, and Tc*Lr10* had a leaf rust severity and response rating of 70 to 90% susceptible (Table 1). The near-isogenic line RL4031 (Tc*Lr13*) 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 F_2 families of Thatcher * 2/Grandin and Thatcher * 2/CDC Teal

Phenotype	Gene detected	Number of families[a] Seg.	Susc.	Expected ratio	P[b]
Thatcher * 2/Grandin					
BBB	*Lr2a, Lr3, Lr10*	44	10	7:1	0.50-0.25
CGB, MBR	*Lr2a*	31	23	1:1	0.50-0.25
NBB	*Lr2a, Lr3*	35	19	3:1	0.25-0.10
SBD	*Lr3*	14	40	1:1	<0.01
				1:3	0.99-0.97
TBB	*Lr10*	30	24	1:1	0.50-0.25
Field[c]	*Lr13, Lr34*	45	9	7:1	0.50-0.25
				3:1	0.25-0.10
Thatcher * 2/CDC Teal					
BBB, KBJ	*Lr1*	39	40	1:1	0.95-0.90
MFM	…	0	79	1:1	<0.001
Field	*Lr13, Lr34*	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/*Lr* line	*P. recondita* f. sp. *tritici* phenotype BBB	CGB	KBJ	MFM	MBR	NBB	SBD	TBG	TBB	Field rust severity and response
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*Lr1* RL6003	;1	;1	;1	33^+	3^+	3^+	3^+4	3^+	3^+4	70-90 S
Tc*Lr2a* RL6016	0;	0;	3^+	0;	0;	;12	3^+4	3^+	33^+	70-90 S
Tc*Lr3* RL6002	;1^-	33^+	33^+	3^+	33^+	;1	;1	3^+	3^+4	70-90 S
Tc*Lr10* RL6004	;1	3^+	3^+	33^+	3^+4	3^+	3^+4	3^+	;11^+	70-90 S
Tc*Lr13* RL4031	22^+3C	2^+3C	33^+	233^+	33^+	3c	2^+33^+	3^+4	33^+	50 MRMS
Tc*Lr16* RL6005	;12^-	33^+	;12^-	;12^-	12	;12^-	;12^-	;12^-	;12	50 MRMS
Tc*Lr34* RL6058	23^+	;23	;23^+	;23^+	33^+	23^+	33^c	$22^-/3$	2^-3	10 M
Tc*Lr13+34* RL6114	23^+	;23^+	;23^+	;23^+	;22^+	23^+	3^c3	33^+	3^c3	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 $BC_1F_{3:4}$ line 79 derived from a single BC_1F_2 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 BC_1F_2 families segregated for a 1:1 ratio with BBB and KBJ, which are avirulent to *Lr1* (Table 2). All BC_1F_2 families were homozygous susceptible when tested with phenotype MFM, which is virulent to *Lr1*. These results indicated that CDC Teal had *Lr1*. Selected BC_1F_2 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 BC_1F_2 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 $BC_1F_{3:4}$ lines derived from single $BC_1F_{2:3}$ plant selections as adult-plants in the greenhouse and in the 1996 field rust nursery (Table 4). BC_1F_4 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 F_4 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 cultivar 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.* $BC_1F_{3:4}$ lines with Lr*13* and *Lr34* singly and together were selected from Tc * 2/Grandin F_2 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 F_2 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] Res.	Number of plants[a] Susc.	Expected ratio	*P*[b]
Thatcher/Grandin	1	140	48	3:1	0.95-0.90
	2	147	41	3:1	0.50-0.25
Tc*Lr16* 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 $BC_1F_{3:4}$ 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] BBB	Greenhouse[a] MBR	Field rust severity and response[b]
Thatcher * 2/Grandin[c]				
Line 79	*Lr13*	2^-	3^+4	60 MRMS
Line 71	*Lr34*	;23	2^+3	10-20 M
Line 73	*Lr34*	;23	23	TR-5 M
Line 98	*Lr13, Lr34*	0;1	$22^\pm$	TR
Thatcher * 2/CDC Teal				
Line 265	*Lr13*	;1	3^+4	40 MRMS
Line 270	*Lr13*	;1	3^+4	40 MRMS
Line 250	*Lr34*	22^+	$22^\pm3$	5-20 M
Line 304	*Lr13, Lr34*	;1	23	TR
Thatcher		3^+4	3^+4	90 S
Tc*Lr13* RL4031		;1	3^+4	40-60 MRMS
Tc*Lr34* RL6058		;12	;23	10 M
Tc*Lr13+34* 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 BC_1 $F_{3:4}$ 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 BC_1F_2 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 resistance 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.

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