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

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ABSTRACT

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 F1 plants were backcrossed to Thatcher. Fifty-four and 80 BC1F1 plants derived respectively from Grandin and CDC Teal were selfed to produce BC1F2 families. The BC1F2 families were tested as seedlings with isolates of Puccinia recondita f. sp. tritici that differed for virulence to specific leaf rust resistance genes. The BC1F2 families were also tested in the adult-plant stage in field rust nursery tests. Segregation of BC1F2 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.

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/Butito/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 crossed with the leaf rust susceptible cultivar Thatcher (Tc). F1 plants were used as pollen parents and crossed with the leaf rust susceptible cultivar Thatcher (Tc). F1 plants were used as pollen parents and crossed with Tc. Backcross F2 (BC2F2) families were evaluated for seedling resistance in the greenhouse with selected virulence phenotypes of P. recondita f. sp. tritici (13). BC1F2 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 µE·m–2·s–1) per day. Nine to 10 days after seeding, the primary leaves were inoculated by atomizing urediniospores suspended in Dustrol (Ciba-Geigy, Missis- sauga, ON, Canada) light mineral oil. Inoculated plants were incubated at 100% RH for 16 h at 20°C. Fifteen to 20 seedlings of each BC1F2 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 BC1F2 families were classified as either segregating or homozygous susceptible. Goodness of fit to segregation ratios in BC1F2 families from each cross was determined using chi-square tests (21).

To evaluate adult-plant resistance, approximately 50 seeds of each BC1F2 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 (TcLr13), RL6058 (TcLr34), or RL6114 (TcLr13+34) were selected from the BC1F2 families which were homozygous susceptible in the seedling tests to all phenotypes. The selected BC1F2 plants with adult-plant resistance were harvested individually, and BC1F2 plants were grown in the greenhouse. BC1F3 lines derived from single BC1F2 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 MBB, which is virulent to Lr13. In the 1996 field rust nursery, BC1F3 lines...
with adult-plant resistance derived from Tc * 2/Grandin and Tc * 2/CDC Teal were response with the lines TcLm13, TcLm34, and TcLm13 + Lr34.

RESULTS

Grandin. Grandin had very low IT of 0; to isolates avirulent to TcLm2a (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 BC1 families. The Tc * 2/Grandin families segregated to fit a three-gene (7 segregating +1 homogenous susceptible) ratio when inoculated in the seedling stage with the widely virulent P. recondita f. sp. tritici phenotype BBB (Table 2). The individual BC2 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 of 0, was one of the three genes conferring resistance to BBB since all BC2 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 (TcLm2a). When the same BC2 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 BC2 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 BC2 families that segregated for resistance to phenotype SBD also segregated to phenotype NBB, which is also avirulent to RL6002 (TcLm3). The BC2 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 (TcLm10) (Table 1). This was further indicated by contingency table tests, as the segregation of BC2 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 (TcLm16). 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 TcLm16 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 TcLm2a, TcLm3, and TcLm10 had a leaf rust severity and response rating of 70 to 90% susceptible (Table 1). The near-isogenic line RL4031 (TcLm13) had a field leaf rust reaction of moderately resistant to moderately susceptible with large necrotic flecks and moderate to large uredinia with chloro-

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### Table 1. Segregation for leaf rust resistance in greenhouse and field tests in backcross F2 families of Thatcher * 2/Grandin and Thatcher * 2/CDC Teal

<table>
<thead>
<tr>
<th>Phenotype</th>
<th>Gene detected</th>
<th>Number of families</th>
<th>Expected ratio</th>
<th>$p^b$</th>
</tr>
</thead>
<tbody>
<tr>
<td>TcLm13 RL6003</td>
<td>Lr1</td>
<td>34</td>
<td>3:1 0.25-0.10</td>
<td>0.99-0.97</td>
</tr>
<tr>
<td>TcLm2a RL6006</td>
<td>Lr2a</td>
<td>3</td>
<td>1:1 0.50-0.25</td>
<td>0.99-0.97</td>
</tr>
<tr>
<td>TcLm3 RL6002</td>
<td>Lr2a</td>
<td>31</td>
<td>1:1 0.50-0.25</td>
<td>0.99-0.97</td>
</tr>
<tr>
<td>TcLm10 RL6004</td>
<td>Lr3</td>
<td>14</td>
<td>1:1 &lt;0.01</td>
<td>0.99-0.97</td>
</tr>
<tr>
<td>TcLm13 RL4031</td>
<td>Lr10</td>
<td>30</td>
<td>1:1 0.50-0.25</td>
<td>0.99-0.97</td>
</tr>
</tbody>
</table>

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

<table>
<thead>
<tr>
<th>Phenotype</th>
<th>Gene detected</th>
<th>Number of families</th>
<th>Expected ratio</th>
<th>$p^b$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Thatcher * 2/Grandin</td>
<td>Lr2a, Lr3, Lr10</td>
<td>44/10 7:1</td>
<td>0.50-0.25</td>
<td>0.99-0.97</td>
</tr>
<tr>
<td>CGB, MBR</td>
<td>Lr2a</td>
<td>31/23 1:1</td>
<td>0.50-0.25</td>
<td>0.99-0.97</td>
</tr>
<tr>
<td>NBB</td>
<td>Lr2a, Lr3</td>
<td>35/19 3:1</td>
<td>0.25-0.10</td>
<td>0.99-0.97</td>
</tr>
<tr>
<td>SBD</td>
<td>Lr3</td>
<td>14/40 1:1</td>
<td>&lt;0.01</td>
<td>0.99-0.97</td>
</tr>
<tr>
<td>TBB</td>
<td>Lr10</td>
<td>30/24 1:1</td>
<td>0.50-0.25</td>
<td>0.99-0.97</td>
</tr>
<tr>
<td>Field</td>
<td>Lr13, Lr34</td>
<td>45/9 7:1</td>
<td>0.50-0.25</td>
<td>0.99-0.97</td>
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### Table 3. Field rust severity and response rating of BC F2 families of Thatcher * 2/Grandin and Thatcher * 2/CDC Teal

<table>
<thead>
<tr>
<th>Cultivar/Lr line</th>
<th>BBB</th>
<th>CGB</th>
<th>KBJ</th>
<th>MFM</th>
<th>MBR</th>
<th>NBB</th>
<th>SBD</th>
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<td>0</td>
<td>.12</td>
<td>.1</td>
<td>.1</td>
<td>TR</td>
</tr>
<tr>
<td>CDC Teal</td>
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<td>0</td>
<td>.133 +</td>
<td>0</td>
<td>0</td>
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<td>3' +</td>
<td>3' +</td>
<td>3' +</td>
<td>3' +</td>
<td>3' +</td>
<td>3' +</td>
<td>3' +</td>
<td>70-90 S</td>
</tr>
<tr>
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<td>.1</td>
<td>.3</td>
<td>3'</td>
<td>3' +</td>
<td>3'</td>
<td>3'</td>
<td>3'</td>
<td>70-90 S</td>
</tr>
<tr>
<td>TcLm2a RL6006</td>
<td>0</td>
<td>0</td>
<td>.3</td>
<td>.1</td>
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<td>3' +</td>
<td>3' +</td>
<td>3'</td>
<td>70-90 S</td>
</tr>
<tr>
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<td>.1</td>
<td>.3</td>
<td>3' +</td>
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<td>.1</td>
<td>.1</td>
<td>.1</td>
<td>70-90 S</td>
</tr>
<tr>
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<td>.1</td>
<td>.3</td>
<td>3' +</td>
<td>3' +</td>
<td>3' +</td>
<td>3'</td>
<td>3' +</td>
<td>3'</td>
<td>70-90 S</td>
</tr>
<tr>
<td>TcLm13 RL4031</td>
<td>22' +</td>
<td>22' +</td>
<td>33' +</td>
<td>33' +</td>
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<td>.23</td>
<td>.23</td>
<td>.23</td>
<td>.23</td>
<td>.23</td>
<td>.23</td>
<td>10 M</td>
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<td>TcLm13+4 RL6114</td>
<td>23' +</td>
<td>.23</td>
<td>.23</td>
<td>.23</td>
<td>.23</td>
<td>.23</td>
<td>.23</td>
<td>.23</td>
<td>5 M</td>
</tr>
</tbody>
</table>

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**a** Seg. = segregating for resistant and susceptible plants; Susc. = homozgyous susceptible.

**b** $p = probability of \( \chi^2 \) value.

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

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**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; i indicates the wheat line was heterogeneous for the indicated infection types.**

**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 (large to moderate uredinia with chlorosis), and S = susceptible (large uredinia).**
sis (Table 4). The same field leaf rust reaction was observed in BC_{F_{14}} line 79 derived from a single BC_{F_{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 TcLr34 (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 (TcLr13 + 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 Lrl and IT of 1 to :12 to isolates virulent to Lrl (Table 1). The Tc * 2/CDC Teal families were tested with leaf rust phenotypes BBB, KBJ, and MFM. The BC_{F_{2}} families segregated for a 1:1 ratio with BBB and KBJ, which are avirulent to Lrl (Table 2). All BC_{F_{2}} families were homozygous susceptible when tested with phenotype MFM, which is virulent to Lrl. These results indicated that CDC Teal had Lrl. Selected BC_{F_{2}} families were further tested with an additional 10 P. recondita f. sp. tritici phenotypes, but no seedling genes other than Lrl 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_{F_{2}} families from this cross had plants with rust reactions very similar to TcLr13, TcLr34, and TcLr13 + 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_{F_{2}} lines derived from single BC_{F_{2}} plant selections as adult-plants in the greenhouse and in the 1996 field rust nursery (Table 4). BC_{F_{2}} 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 TcLr13, 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 TcLr34, 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 TcLr13 + 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_{2} 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_{F_{3}} lines with Lr13 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 TcLr13. Inoculation of adult plants of line 79 in the greenhouse with phenotype BBB should have produced IT 1, which is the characteristic IT of TcLr13 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 Lrl. The cultivar Neepawa, which is in the pedigree of CDC Teal, also has Lrl (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. recondita f. sp. tritici.

| Cross | F_{2} family | Number of plants | Expected ratio | P
<table>
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<tr>
<th></th>
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<th></th>
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<tbody>
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<td>Thatcher/Grandin</td>
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<td>140</td>
<td>48</td>
<td>3:1</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>147</td>
<td>41</td>
<td>3:1</td>
</tr>
<tr>
<td>TcLr16 RL6005/Grandin</td>
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<td>193</td>
<td>0</td>
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</tr>
<tr>
<td></td>
<td>2</td>
<td>198</td>
<td>0</td>
<td>3:1</td>
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</tbody>
</table>

* Res. = resistant; Susc. = susceptible.

P = probability of $X^2$ value.

| Line | Gene detected | Greenhouse | Field rust severity and response
<table>
<thead>
<tr>
<th></th>
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<td>Thatcher * 2/Grandin</td>
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<td></td>
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</tr>
<tr>
<td>Line 79</td>
<td>Lr13</td>
<td>+</td>
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<td>TcLr13+34 RL6114</td>
<td>0</td>
<td>23</td>
<td>5-10 M</td>
</tr>
</tbody>
</table>

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).
which have more than one effective resistance, such as CDC Teal, Roblin, and Columbus, in recent years in Manitoba and Saskatchewan. However, 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. 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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