Characterization of Leaf Rust Resistance in Hard Red Spring Wheat Cultivars

L. M. Oelke and **J. A. Kolmer,** Department of Plant Pathology, University of Minnesota, and United States Department of Agriculture–Agricultural Research Services Cereal Disease Laboratory, St. Paul MN, 55108

ABSTRACT

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Leaf rust, caused by *Puccinia triticina* Eriks., is the most common disease of wheat (*Triticum aestivum* L.) in the United States and worldwide. The objective of this study was to characterize seedling and adult plant leaf rust resistance in hard red spring wheat cultivars grown in Minnesota, North Dakota, and South Dakota, and postulate the identity of the seedling leaf rust resistance genes in the cultivars. Twenty-six cultivars, near-isogenic lines of Thatcher wheat that differ for single leaf rust resistance genes, and three wheat cultivars with known leaf rust resistance genes, were tested with 11 different isolates of leaf rust collected from the United States and Canada. The leaf rust infection types produced on seedling plants of the cultivars in greenhouse tests were compared with the infection types produced by the same isolates on the Thatcher near-isogenic lines to postulate which seedling leaf rust resistance genes were present. Seedling leaf rust resistance genes *Lr1*, *Lr2a*, *Lr10*, *Lr16*, *Lr21,* and *Lr24* were postulated to be present in spring wheat cultivars. Seedling genes *Lr3*, *Lr14a,* and *Lr23* likely were present in some cultivars but could not be clearly identified in this study. Most of the cultivars had some level of adult plant leaf rust resistance, most likely due to *Lr34*. Cultivars that had seedling resistance genes *Lr1, Lr2a, Lr10,* or *Lr16* had poor to intermediate levels of leaf rust resistance in field plots. Cultivars with combinations of seedling resistance genes *Lr16* and *Lr24* with additional adult plant resistance were highly resistant to leaf rust.

Additional keywords: specific resistance

Leaf rust, caused by *Puccinia triticina* Eriks., is the most common disease of wheat (*Triticum aestivum* L.) worldwide. The most widely used and economical method for controlling leaf rust is the use of resistant cultivars. Resistance to leaf rust in wheat often is determined by adult plant resistance genes in combination with seedling resistance genes (4,11,12). Many different virulence phenotypes or races of *P. triticina* are found annually in the United States (14). Wheat cultivars often are leaf rust resistant when initially released, but can be rendered susceptible due to selection and increase of virulent leaf rust races. Genes that condition effective resistance to the current leaf rust population need to be added to wheat breeding programs in order to maintain high levels of leaf rust resistance.

Genetic studies have been conducted on spring wheat cultivars to determine the number and identity of genes that condition leaf rust resistance (3,6,13,15). The resistant cultivars are crossed with a susceptible parent, and F_3 or backcross F_2 families are tested with different leaf rust races to determine the number and identity of segregating resistance genes. However, genetic analysis requires time and resources to grow multiple generations of plants and test the segregating families for rust resistance.

Gene postulation of leaf rust resistance genes can be used to determine the seedling resistance genes that may be present in a large group of wheat germplasm (27,29). Gene postulation uses gene-for-gene specificity to hypothesize which leaf rust resistance genes may be present in the cultivars tested (8,21). Resistance to wheat leaf rust can be characterized by a hypersensitive response or a chlorotic response with reduced size of uredinia. Low infection types or resistant responses occur only when a wheat line has a gene which conditions resistance to leaf rust races with the corresponding avirulence gene. Resistance genes are postulated based on the infection types of the cultivars to a series of leaf rust isolates that differ for virulence to the specific leaf rust resistance genes. Gene postulation originally was developed by Loegering et al. (16) and Browder (1). Gene postulation studies previously were conducted with hard red spring wheat cultivars that were grown in Minnesota, North Dakota, and South Dakota in the 1980s and early 1990s (19,23,24).

The objective of this study was to characterize the leaf rust resistance in hard red spring wheat cultivars that have been grown in Minnesota, North Dakota, and South Dakota since 2000. The leaf rust resistance genes in these more recent cultivars have not yet been identified.

MATERIALS AND METHODS

The hard red spring wheat cultivars tested for leaf rust resistance were selected from the Minnesota Agricultural Experiment Station 2001 variety trials. The cultivars and their pedigrees, if available, are listed in Table 1. The pedigree information was collected from various sources, including research publications, the Germplasm Resource Information Network database and the United States Department of Agriculture–Cereal Disease Laboratory database. The cv. Thatcher plus 18 near-isogenic lines of Thatcher with single resistance genes (Table 2), 26 hard red spring wheat cultivars from the variety trials (Table 3), and the cvs. Era, Glenlea, and Roblin that have known seedling and adult plant *Lr* genes (Tables 1 and 3) were tested for seedling resistance.

In the seedling tests, six to eight seed of each cultivar were planted in 3.5-cm^2 pots in vermiculite (Sunshine Strong-Lite Medium Vermiculite Premium Grade; JR Johnson Horticultural Supplies, St. Paul, MN) in clumps spaced at the four corners of the square pot, with four cultivars per pot and six pots per tray. Seedlings were watered daily, fertilized at emergence with 20-20-20 NPK soluble fertilizer (Spectrum Group, St. Louis), and grown for 8 days in a greenhouse at temperatures of 18 to 22°C with 16 h of supplemental metal halide light. The seedlings were inoculated at 8 days after planting, at full emergence of primary leaves.

Isolates of *P. triticina* used in seedling test were collected from wheat in the United States and Canada. The isolates were selected based on either importance in leaf rust populations in the United States or for low infection types to specific *Lr* genes found in spring wheat. Isolates used for the greenhouse seedling test were THBJ 99 ND 588, TNRJ 99 VA 67-2, TLGF 00 SC 218, TDBJ 82 MN 01, SBDG 59 CAN 01, MJBJ 97 NE 406, MFBJ 94 CAN 01, MCDS 00 SD 520, MBRK 97 CAN 253-3, MBRJ 99 ND 16-2B, and KFBJ 97 CAN 64-1 (Table 2). The four-letter code indicated the virulence combination as designated by Long and Kolmer (17); the two-digit number indicated year of collection, followed by state abbreviation, or CAN if originally collected in Canada; and isolate number.

Corresponding author: J. A. Kolmer
E-mail: jkolmer@umn.edu

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The primary leaves of the seedlings were inoculated by spraying a suspension of approximately 20 to 30 µg of urediniospores mixed in 350 µl of Soltrol 170 oil (Phillips Petroleum Co., Borger, TX). Inoculated plants were allowed to air dry for 60 min. The inoculated plants then were moved to a dew chamber and held at approximately 18°C and 100% relative humidity (RH). After 24 h of incubation, the plants were allowed to air dry for 60 min. The seedling plants were fertilized with 20-20-20 NPK soluble fertilizer after the dew chamber incubation period. All plants were placed in a greenhouse at 18 to 22°C with 16 h of supplemental light and watered daily.

Seedling test infection types were evaluated at 12 days after inoculation. The infection types were classified using a 0-to-4 scale developed by Long and Kolmer (17), where 0 = no hypersensitive flecks, necrosis, or uredinia; 0; = faint hypersensitive flecks; ; = distinct hypersensitive flecks; 1 = small uredinia surrounded by distinct necrosis; 2 = small uredinia surrounded by distinct chlorosis; 3 = moderate size uredinia without chlorosis; 4 = very large ured-

Table 1. Pedigrees of spring wheat cultivars tested for leaf rust resistance

Cultivar	Pedigree
2375	Olaf // Era / Squamux 168 / Cis / ND487 // Lark
Alsen	Grandin // Grandin / Glupro // Sumai 3 / Wheaton // Grandin / ND688
Amazon	Not available
Aurora	Not available
BacUp	Nyu-Bay // 2375 // Marshall
Dandy	Not available
Ember	SD3078 / Grandin
Forge	Butte 86 // Sharp/Guard
Gunner	Not available
Hanna	N93-2424 / AC Domain
HJ98	W8814 / Norak
Ingot	Butte / SD3004 / Dalen
Ivan	MN74103 / Success / 3 / Brule Mesa mother line // Bergen
Keystone	Lars / Sharpshooter
Knudson	Karl / Krona / 3 / Bergen // Erik / MN73167
Marshall	Waldron / Era
McKenzie	Columbus / Amidon
McVey	Ning 8331 / MN81136 / Vance // MN89068
Mercury	Not available
Norm	MN73167 / MN81070
Norpro	Norseman / Pr2369 // Dalen
Oxen	SDY366A / SDZ004A
Parshall	Keene / ND674
Reeder	IAS20*4 / H567.71 // Stoa / 3 / ND674
Russ	SD8052 / SD2971
Verde	MN7663 / SBY354A
Era	Thatcher / Supreza // Frontana / 3 / Kenya 58 / Newthatch/7 / Frontana / 6/Frontana / Thatcher // Pembina / 5 / Frontana / Thatcher / 2/Mida / Kenya 117A / 3 / Norin 10 / Brevor // unknown line / 4/Kenya 58 / Newthatch / 2 / Lee
Glenlea	Pembina*2 / Bage // CB 100
Roblin	Manitou / Tobari 66 / 2 / CT615 / Neepawa

Table 2. Seedling infection types of Thatcher near-isogenic lines inoculated with 11 isolates of the leaf rust fungus *Puccinia triticina* used in this study in 2002 and 2003[a]

	Isolates[b]										
Thatcher line, *Lr* gene	**THBJ 99 ND 588**	**TNRJ 99 VA 67-2**	**TLGF 00 SC 218**	**TDBJ 82 MN 01**	**SBDG 59 CAN 01**	**MJBJ 97 NE 406**	**MFBJ 94 CAN 01**	**MCDS 00 SD 520**	**MBRK 97 CAN 253-3**	**MBRJ 99 ND 16-2B**	**KFBJ 97 CAN 64-1**
RL 6003 *Lr1*	33+	33+	3+	33–	33+	3	33+	3+	33–	3	;1
RL 6016 *Lr2a*	33+	3	33–	33–	3	0;	0;	;	0	;	3
RL 6047 *Lr2c*	33+	33–	33–	33–	33–	0;	;1–	;	;	;1–	3
RL 6002 *Lr3*	33+	33–	3+	33+	0;	3+	3+	3	33+	3+	33+
RL 6010 *Lr9*	;	33+	3+	0	0;	;	0;	;	;	;	0;
RL 6005 *Lr16*	33+	11+	1	1	;1	3	11–	22–	11+	22–	22–
RL 6064 *Lr24*	;	33–	0;	33–	;	3	3	;	0;	;	33+
RL 6078 *Lr26*	33+	11+	;1–	;1	;1	;1–	3+	3	33–	;1	3
RL 6007 *Lr3ka*	22–	3+	22–	22+	22–	;22–	2	2	3+	33+	2–
RL 6053 *Lr11*	22–	33+	33–	22+	2	;2	2+	2	33+	3	22–
RL 6008 *Lr17*	2+	11+	11–	2;	33+	;22–	2+	3	22–	;1	2–
RL 6049 *Lr30*	2–	33+	11–	2–	;2–	;22–	2	2-	33–	3	1
RL 6051 *LrB*	2+	22+	22+	22+	1+	2+	2	3+	22+	2	2+
RL 6004 *Lr10*	3–	33+	0;	3+	3	3+	3	3+	3	3	33+
RL 6013 *Lr14a*	33–	3+	33+	3+	;2–	3+	3+	3+	33+	3	3+
RL 6009 *Lr18*	;11–	11–	33+	11–	2-	22–	11–	;1–	33+	;1–	11–
RL 6012 *Lr23*	;2–3+	;2-3+	3+	3+	;	;22+	3+	;1	3+	2–3+	3+
RL 6058 Lr34	3+	3+	3	33+	33+	3+	3	3	3+	33+	3+

[a] Seedling infection types: 0 = immune response, no sign of infection; ; = hypersensitive chlorotic or necrotic flecks; 1 = small uredinia surrounded by necrosis; 2 = small uredinia surrounded by chlorosis; 3 = moderate size uredinia without necrosis or chlorosis; 4 = large uredinia without necrosis or chlorosis; + = uredinia larger than normal; – = uredinia smaller than normal. A range of infection types is indicated by more than one infection type, with the predominant type listed first.

[b] Isolate designations: four-letter code indicates virulence combination on 16 differential lines of Thatcher wheat (17); two-digit numbers indicate year of isolate collection; followed by state of collection or CAN if isolate originated in Canada, and isolate number.

inia without chlorosis. Designations of "+" indicated larger than normal uredinia and "–" indicated smaller than normal uredinia. All isolate–cultivar combinations were tested at least twice to confirm infection type. The infection type responses to the *P. triticina* isolates were used to determine the gene postulations of the cultivars.

Wheat cultivars were evaluated for adult plant resistance in greenhouse tests using isolates that produced high infection types on the cultivars in the seedling tests. Some cultivars were resistant to all isolates in the seedling tests. These cultivars were tested with isolates that produced intermediate or low infection types on the cultivars in the seedling tests. Twenty-six cultivars, four Thatcher near-isogenic lines (Thatcher, RL 6001 *Lr12*, RL 4031 *Lr13*, and RL 6058 *Lr34*), and Era, Glenlea, and Roblin, were tested for adult plant resistance (Table 4). Four seeds of each cultivar were planted in 15-cm pots for the adult test. The plants were watered daily, fertilized with osmocote 14-14-14, and grown under greenhouse conditions at approximately 20°C and 16 h of supplemental light. Approximately 3 to 4 weeks after planting, the plants were trimmed to three tillers. The adult plants were inoculated at the flag leaf stage at anthesis. The flag leaves were inoculated by spraying a suspension of urediniospores in Soltrol 170. Inoculated plants were allowed to air dry for 60 min. The inoculated plants then were moved to a dew chamber and held at approximately 18°C and 100% RH. After 24 h of incubation, the plants were allowed to air dry again for 60 min and then grown for 14 days in the greenhouse at 18 to 22°C with 16 h of supplemental light.

The wheat cultivars were evaluated for field leaf rust resistance at two locations in 2002 and one location in 2003. The cultivars and Thatcher near-isogenic lines (RL 6003 *Lr1*, RL 6016 *Lr2a*, RL 6047 *Lr2c*, RL 6002 *Lr3*, RL 6005 *Lr16*, RL 6064 *Lr24*, RL 6004 *Lr10*, RL 6013 *Lr14a*, RL 6043 *Lr21*, RL6012 *Lr23*, Thatcher, RL 6001 *Lr12*, RL 4031 *Lr13*, and RL 6058 *Lr34*, RL 6122-2 *Lr1* and *Lr13*, RL 6108-1 *Lr1* and *Lr34*, RL 6109-1 *Lr2a* and *Lr34*, RL 6110-1 *Lr3* and *Lr34*, RL 6114 *Lr13* and *Lr34*, RL 6128-1 *Lr16* and *Lr13*, RL 6115-1 *Lr16* and *Lr34*, RL 6131-1 *Lr21* and *Lr13*, RL 6118-2 *Lr21* and *Lr34*, and RL 6132 *Lr24* and *Lr13*) were assessed for field leaf rust resistance (Table 5). The cultivars and near-isogenic lines were planted in field plots at St. Paul, MN and Fargo, ND in late April 2002. In 2003, the St. Paul field was planted in mid-April. Each cultivar and near-isogenic line was planted in approximately 3-m rows, 30 cm apart, and 40 to 50 seed were planted per plot. Spreader rows of the susceptible cv. Max were planted perpendicular at the St. Paul plots and were inoculated in early June with isolates THBJ 99 ND 588, MCDS 00 SD 520, and MBRJ 99 ND 16-2B. The isolates were chosen because THBJ and MCDS are prevalent in the current rust population and MBRJ was common in the mid-1990s. For the St. Paul field inoculations, a mixture of the three isolates in Soltrol 170 oil was sprayed on the spreader rows in early to mid-June using a backpack sprayer. The Fargo plots were infected with the naturally occurring leaf rust population.

The severity and response rating for the adult plant field resistance was based on the modified Cobb scale (22). The host infection response was rated as R = resistant, very small uredinia with necrosis; MR = moderately resistant, small to moderate uredinia with necrosis; MS = moderately susceptible, small to moderate uredinia with chlorosis; and S = susceptible, large uredinia without necrosis or chlorosis. The

Table 3. Seedling infection types of hard red spring wheat cultivars with 11 isolates of the leaf rust fungus *Puccinia triticina* used in this study in 2002 and 2003[a]

		Isolates[b]										
Cultivar	*Lr* genes postulated	THBJ 99 ND 588	TNRJ 99 VA 67-2	TLGF 00 SC 218	TDBJ 82 MN 01	SBDG 59 CAN 01	MJBJ 97 NE 406	MFBJ 94 CAN 01	MCDS 00 SD 520	MBRK 97 CAN 253-3	MBRJ 99 ND 16-2B	KFBJ 97 CAN 64-1
2375	*Lr1*[c]	3	2	33–	2	0;	2+3	22+	33+	;2	3	;
Alsen	*Lr2a*, *Lr10*	3+	33-/;1	;1	33–/;2–	;1–	0;	0;	0;	0;	;	3
Amazon	*Lr1*, *Lr10*	3+	3+	;1–	3+	3+	33+	33+	2–	3+	3+	;1
Aurora	*Lr16*	3	;1	;	1+	;1–	33+	;1–	;1	2–	22–	;1–
BacUp	*Lr1*, *Lr10*	3+	3+	;	33+	3+	33+	3	3+	3+	3+	0;
Dandy	*Lr24*	;	23	;	3	0;	22–	11–	0;	0;	;	22–
Ember	*Lr2a, Lr16*	33+	;1	;	11+	;1	;1	1–	;1	22–	;1	11–
Forge	*Lr2a, Lr16*	2+3	;1	;1–	1	;1–	0;	;1–	;1–	11–	;1	11–
Gunner	*Lr2a*[c]	3	3+	3	33+	;1–	;	0	0;	0	;	2+3
Hanna	*Lr16*	2	2	0;	1	0;	;2–	;1	;1–	1+	2	;1–
HJ98	*Lr10*[c]	3	3+	;1	3	;1–	3+	3+	;	3+	3+	3+
Ingot	*Lr16*	3+	;1	0;	1+	;1	2+3	0;	;1–	1+	;1	11–
Ivan	*Lr24*	;1–	2	0;	22+	;	;2+	11+	;	0	;	1+
Keystone	*Lr16*	23	;1	0;	11+	0;	;2+	1–	;1	1+	;1	0;
Knudson	*Lr16*	2	;1–	0;	11+	0;	;2–	0;	;1–	;1	;1–	1
Marshall	*Lr2a*, *Lr10*[c]	3+	3+	0;	33+	;1–	;	0;	;	;	;	3
McKenzie	*Lr21*	;	0;	;	;	;1–	;	0;	;	0;	;	;
McVey	*Lr16*	33+	;2	;1	11+	;1	33+	;1	22+	2	22+	11–
Mercury	*Lr16*	22+	;1	0;	1	;1–	33+	;1–	;1–	;1	;1–	;1–
Norm	*Lr16*	2+3	;1–	0;	1+	0	;1–	;1–	;1	;1	;1	;1–
NorPro	*Lr2a*, *Lr16*	3+	;1	0	1;	;	;	0	;	0	0;	0;
Oxen	*Lr1*, *Lr2a*, *Lr10*[c]	3+	3+	;1+	33+	1–;	;	0;	;	;	;	0;
Parshall	*Lr16*	3+	1–	;2–	11–	0;	;2	;1	;1–	11+	;1	11–
Reeder	*Lr2a*, *Lr16*	3+	;1	;	11+	0;	;	0;	;	;	;	11+
Russ	*Lr2a*, *Lr10*[c]	3	3	0;	33–	0;	;	0;	0;	0	;	;2
Verde	*Lr16*	3+	0;	;	0;	0;	;2+3	0;	;1	;1–	;1	0;
Era	*Lr10*	3+	3+	0;	33+	33+	3+	3/;2	3+	3+	3+	33+
Glenlea	*Lr1*	3+	3+	;22+	33+	3+	3+	3+	;1	3+	;	0;
Roblin	*Lr1*, *Lr10*	3+	3+	0;	33+	3+	33+	33+	3	3+	3+	;

[a] Seedling infection types: 0 = immune response, no sign of infection; ; = hypersensitive chlorotic or necrotic flecks; 1 = small uredinia surrounded by necrosis; 2 = small uredinia surrounded by chlorosis; 3 = moderate size uredinia without necrosis or chlorosis; 4 = large uredinia without necrosis or chlorosis; + = uredinia larger than normal; – = uredinia smaller than normal. A range of infection types is indicated by more than one infection type, with the predominant type listed first.

[b] Isolate designations: four-letter code indicates virulence combination on 16 differential lines of Thatcher wheat (17); two-digit numbers indicate year of isolate collection; followed by state of collection or CAN if isolate originated in Canada, and isolate number.

[c] An additional gene, either *Lr3*, *Lr14a,* or *Lr23*.

St. Paul plots were scored in mid-July 2002 and 2003, and the Fargo plot was scored in late July 2002. Leaf rust severity and resistance responses were recorded when the susceptible cv. Thatcher had leaf rust severity of at least 80% in mid-July.

RESULTS

Seedling resistance. The infection types of the 11 *P. triticina* isolates to 18 Thatcher near-isogenic lines are listed in Table 2, for comparison with the cultivar infection types in Table 3. The Thatcher line with *Lr23* varied for low and high infection type to isolates THBJ, TNRJ, and MBRJ. This gene previously has been noted to be very temperature sensitive (2,18). The seedling infection types of the *P. triticina* isolates to the hard red spring wheat cultivars are listed in Table 3. The infection types of the cultivars and the Thatcher near-isogenic lines to the different *P. triticina* isolates determined the gene postulations. For example, Gunner had low infection type of 0; to ;1$^-$ to isolates MJBJ, MFBJ, MCDS, MBRJ, and MBRK, which are all avirulent to *Lr2a* (Table 2). Gunner had high infection types of 2$^+$3 to 3$^+$ to isolates THBJ, TNRJ, TLGF, TDBJ, and KFBJ, which are all virulent to *Lr2a*. On this basis, Gunner was postulated to have *Lr2a*. Gunner also had a low infection type of ;1 to isolate SBDG. Isolate SBDG had low infection types to *Lr3*, *Lr14a,* and *Lr23* and was virulent to *Lr2a* (Table 2); therefore, Gunner was postulated to have one of these three genes. With the isolates used in this study, it was not possible to differentiate between resistance conditioned by genes *Lr3, Lr14a*, or *Lr23*. The final seedling gene postulation for Gunner was *Lr2a* and either *Lr3*, *Lr14a*, or *Lr23*.

The infection types of the remaining cultivars to the 11 *P. triticina* isolates were analyzed in a similar manner to postulate which seedling resistance genes were present. Cv. 2375 was determined to have *Lr1,* because it had a ; (fleck) infection type to isolate KFBJ, which is avirulent to *Lr1* (Table 2). Because 2375 had a 0; infection type to isolate SBDG, either *Lr3, Lr14a,* or *Lr23* (Table 2) also was present. An additional resistance gene must be present in 2375 because it also had low infection types of ;2 to 22$^+$ to isolates TNRJ, TDBJ, MBRK, and MFBJ. Alsen, Marshall, and Russ were postulated to have *Lr2a* and *Lr10,* because all had low infection types to isolates avirulent to *Lr2a* and had a low infection type to isolate TLGF, which is avirulent to *Lr10* (Table 2). Alsen and Marshall had low infection types to SBDG, which indicated that both also could have either *Lr3, Lr14,* or *Lr23*. Alsen was heterogeneous for low and high infection type to isolates TNRJ and TDBJ, which indicated that Alsen was a mixture that varied for an additional resistance gene. Russ had a low infection type of ;2 to KFBJ, which was too high to be conditioned by *Lr1* (Table 2). An additional resistance gene may be in Russ. Amazon, BacUp, and Roblin were postulated to have *Lr1* and *Lr10*, because all had low infection types to isolates KFBJ and TLGF. Amazon also had low infection type of 2$^-$ to isolate MCDS, which indicated that this cultivar may have an additional resistance gene or genes. Glenlea had an infection type of 0; to KFBJ, which indicated that *Lr1* was present. An additional resistance gene must be present because isolates TLGF, MCDS, and MBRJ, had low infection types of ; to ;22$^+$ to Glenlea. Dandy had infection types of 22$^-$ to 3 to isolates TNRJ, TDBJ, MJBJ, and KFBJ, which are all virulent to *Lr24* (Table 2). Dandy had very low infection types to all other isolates; therefore, it was postulated to have *Lr24*. The cultivar Ivan had infection types of ;2$^+$, 2, and 22$^+$ to isolates MJBJ, TNRJ, and TDBJ, which are all virulent to *Lr24* (Table 2). Ivan was postulated to have *Lr24* and likely has an additional gene.

HJ98 and Era were postulated to have *Lr10*, because both had a low infection type to TLGF. HJ98 also had a low infection type to isolate SBDG, which indicated that either *Lr3, Lr14a,* or *Lr23* was present. The low infection type of ; (fleck) to isolate MCDS indicated that HJ98 had an additional resistance gene. Era was heterogeneous for high and low infection types to isolate MFBJ. Oxen was postulated to have *Lr1, Lr2a,* and *Lr10* because it had low infection types to all isolates avirulent to *Lr2a*, and had low infection types to KFBJ and TLGF. Oxen also had a low infection type to SBDG, which indicated that either *Lr3, Lr14a,* or *Lr23* was present.

Cvs. Aurora, Hanna, Ingot, Keystone, Knudson, McVey, Mercury, Parshall, and Verde had infection types of 2 to 3$^+$ to isolates THBJ and MJBJ and low infection types of ; to ;1 to all other isolates (Table 3). THBJ and MJBJ were the only isolates virulent to *Lr16* used in this study (Table 2); therefore, the infection types indicated that these cultivars have *Lr16*. Norm had an infection type of 2$^+$3 to THBJ and ;1$^-$ to MJBJ, which indicated that Norm has *Lr16* plus another resistance gene. Cvs. Ember, Forge, Norpro, and Reeder had infection types of 2$^+$3 to 3$^+$ to isolate THBJ only,

Table 4. Adult plant infection types of hard red spring wheat cultivars to isolates of the leaf rust fungus *Puccinia triticina*

Cultivars	Postulated *Lr* genes	Isolate[a]	Infection type[b]	Isolate[a]	Infection type[b]
2375	*Lr1*	THBJ	;23 vf	MCDS	;23 f
Alsen	*Lr2a, Lr10*	THBJ	;23 vf	TNRJ	0;
Amazon	*Lr1, Lr10*	THBJ	23$^+$	TNRJ	;23 vf
Aurora	*Lr16*	THBJ	23$^+$	MBRJ	;1$^-$
BacUp	*Lr1, Lr10*	THBJ	;23 f	MCDS	;23 f
Dandy	*Lr24*	TDBJ	;12$^-$	TNRJ	;
Ember	*Lr2a, Lr16*	THBJ	;12$^-$	MBRK	;2$^-$ vf
Forge	*Lr2a, Lr16*	THBJ	;12$^-$	MCDS	;2
Gunner	*Lr2a*	THBJ	;2	TNRJ	;
Hanna	*Lr16*	THBJ	;2$^-$ vf	MCDS	;2$^-$ vf
HJ98	*Lr10*	THBJ	23$^+$	MBRJ	;2 vf
Ingot	*Lr16*	THBJ	23$^+$	MBRK	;
Ivan	*Lr24*	TDBJ	;1	TNRJ	;
Keystone	*Lr16*	THBJ	23 f	MCDS	;2$^-$3$^-$ vf
Knudson	*Lr16*	THBJ	0;	TDBJ	0;
Marshall	*Lr2a, Lr10*	THBJ	23$^+$	TNRJ	23$^+$
McKenzie	*Lr21*	THBJ	0;	MCDS	;2 f
McVey	*Lr16*	THBJ	;23 f	MCDS	;23 vf
Mercury	*Lr16*	THBJ	23 f	MCDS	0;
Norm	*Lr16*	THBJ	;1	MCDS	;2$^-$ vf
Norpro	*Lr2a, Lr16*	THBJ	;2$^-$ vf	MCDS	;2$^-$ vf
Oxen	*Lr1, Lr2a, Lr10*	THBJ	;23 f	TNRJ	;
Parshall	*Lr16*	THBJ	;2 vf	MCDS	0;
Reeder	*Lr2a, Lr16*	THBJ	;23 f	MCDS	0;
Russ	*Lr2a, Lr10*	THBJ	0;	TDBJ	0;
Verde	*Lr16*	THBJ	0;	MCDS	;1$^-$ vf
Era	*Lr1, Lr13, Lr34*	THBJ	23	MCDS	23 f
Glenlea	*Lr1, Lr34*	THBJ	;23 f	MCDS	;3 vf
Roblin	*Lr1, Lr10, Lr13, Lr34*	THBJ	;23 f	MCDS	23 f
Thatcher	…	THBJ	3$^+$	MCDS	3$^+$
RL 6001	*Lr12*	THBJ	3$^+$	MCDS	3$^+$
RL 4031	*Lr13*	THBJ	3$^+$	MCDS	3$^+$
RL 6058	*Lr34*	THBJ	23 f	MCDS	23 f

[a] Isolate designations: four-letter code indicates virulence combination on 16 differential lines of Thatcher wheat (17).

[b] Seedling infection types: 0 = immune response, no sign of infection; ; = hypersensitive chlorotic or necrotic flecks; 1 = small uredinia surrounded by necrosis; 2 = small uredinia surrounded by chlorosis; 3 = moderate size uredinia without necrosis or chlorosis; 4 = large uredinia without necrosis or chlorosis; + = uredinia larger than normal; – = uredinia smaller than normal. A range of infection types is indicated by more than one infection type, with the predominant type listed first; f = fewer pustules and vf = very few pustules.

which indicated that genes *Lr2a* and *Lr16* were present. Isolate MJBJ had low infection types to Ember, Forge, Norpro, and Reeder because it is avirulent to *Lr2a* (Table 2).

McKenzie had a low infection of 0; to ;1$^-$ to all isolates. All of the isolates had a low infection to RL 6043 *Lr21* (*data not shown*), a parent of Amidon, which in turn is a parent of McKenzie. McKenzie likely has *Lr21*.

Adult plant and field resistance. All cultivars except Dandy and Ivan were tested for adult plant infection type with isolate THBJ and a second isolate that varied for different cultivars (Table 4). THBJ had an infection type of 3$^+$ with many uredinia on adult plants of the susceptible control Thatcher, and also to the Thatcher lines with the adult plant resistance genes *Lr12* and *Lr13*. THBJ had an infection type of 23, with fewer uredinia on the Thatcher line with the adult plant resistance gene *Lr34*. None of the cultivars had as high an infection type as Thatcher to isolate THBJ. Cvs. McKenzie, Knudson, Norm, Russ, and Verde had very low infection types of 0; to ;1 to THBJ. Cvs. Ember, Forge, Gunner, Hanna, Norpro, and Parshall had low infection types of ;12$^-$ to ;2. Cvs. Reeder, McVey, Oxen, 2375, Alsen, BacUp, and Glenlea had an infection type of ;23 with few uredinia, which was similar to the infection of the Thatcher line with *Lr34*. Cvs. Amazon, Aurora, HJ98, Ingot, Keystone, Marshall, Mercury, Era, and Roblin had infection type of 23$^+$, which also was similar to the Thatcher line with *Lr34*. Cvs. Dandy and Ivan had infection types of ;12$^-$ and ;1, respectively, to TDBJ.

The cultivars also were tested with MCDS, TNRJ, MBRJ, MBRK, or TDBJ for the second isolate in the adult plant tests. Forge, Hanna, McKenzie, Norm, and Norpro had infection types of ;2$^-$ to ;2 to MCDS. Cvs. 2375, BacUp, Keystone, McVey, Glenlea, and Roblin had infection types of ;23, with few uredinia, to MCDS, which was similar to the infection type of the Thatcher line with *Lr34*. Alsen, Dandy, Gunner, Ivan, and Oxen had 0; to ; (fleck) infection types to isolate TNRJ. Amazon and Marshall had infection types of ;23 and 23$^+$, respectively to TNRJ. Aurora and HJ98 had infection types of ;1$^-$ and ;2$^-$, respectively, to isolate MBRJ. Cvs. Ember and Ingot had infection types of ;2$^-$ and ; (fleck), respectively, to isolate MBRK.

Cvs. Dandy, Ivan, Knudson, McKenzie, and Norm were highly resistant, with leaf rust severity and response readings of 0 to 5 MR in all three of the field tests in 2002 and 2003 (Table 5). Alsen also had good resistance, with severity and response of 5 MR to 10 MR MS. Cv. Ingot was moderately susceptible in all three tests, with leaf rust severities and responses of 30 to 60 MS. The other cultivars all had an intermediate level of resistance, with severity and response readings between 5 MR to 50 MR MS at one or more of the three locations.

Thatcher was rated as 80 S at the three locations. The Thatcher lines with *Lr1, Lr3, Lr10, Lr12,* and *Lr14a,* were highly susceptible, with severities and responses of 40 to 80 S at all three locations. The Thatcher lines with *Lr2a* and *Lr2c* were at 80 S in St. Paul in 2002, but were only 20 S at St. Paul in 2003. The Thatcher lines with *Lr3ka* and *Lr11* were 60 S and 70 S, respectively, in 2002, and were 10 to 20 MR and 20 MR MS, respectively, in St. Paul in 2003. The Thatcher lines with pairs of genes *Lr13, Lr24; Lr21, Lr34;* and *Lr13, Lr21* had low severity and response ratings of 0 to 10 MR at St. Paul in 2002 and 2003. The other Thatcher lines with combinations of seedling genes and either *Lr13* or *Lr34* had severities and responses of 10 to 70 MR MS in both years at St. Paul.

Table 5. Leaf rust severity and resistance response of hard red spring wheat cultivars and Thatcher near-isogenic lines in field plots in St. Paul, MN and Fargo, ND in 2002 and 2003[a]

		2002		2003
Cultivar	**Postulated *Lr* genes**	**St. Paul**	**Fargo**	**St. Paul**
2375	*Lr1*[b]	40 MR MS	5-10 MR MS	30 MR MS
Alsen	*Lr2a, Lr10*	10 MR MS	5 MR	10 MR MS
Amazon	*Lr1, Lr10*	20 MR MS	10-20 MR	40 MR MS
Aurora	*Lr16*	10-20 MR MS	5 MR MS	10 MR MS
BacUp	*Lr1, Lr10*	40 MR MS	10 MS	30 MR MS
Dandy	*Lr24*	5 R	5 MR	0
Ember	*Lr2a, Lr16*	40-60 MR MS	50 MS	20 MR MS
Forge	*Lr2a, Lr16*	40-50 MR MS	30 MS	40 MR MS
Gunner	*Lr2a*[b]	5-20 MR MS	30-40 MS	20-30 MR MS
Hanna	*Lr16*	30-50 MR MS	20 MS	30 MR MS
HJ98	*Lr10*[b]	20 MR MS	10 MR MS	20 MR MS
Ingot	*Lr16*	50-60 MS	30-40 MS	50 MS
Ivan	*Lr24*	0	0	5 R MR
Keystone	*Lr16*	10-20 MR MS	5 MR MS	30 MR MS
Knudson	*Lr16*	5 R	0	0
Marshall	*Lr2a, Lr10*[b]	20 MR MS	10 MR	30 MR MS
McKenzie	*Lr21*	5 R	5 R	0
McVey	*Lr16*	5-10 MR	5 MR MS	30 MR MS
Mercury	*Lr16*	5 R- 20 MR MS	5-10 MR MS	5 MR MS
Norm	*Lr16*	0	0	0
Norpro	*Lr2a, Lr16*	10-20 MR MS	5 MR MS	20 MR MS
Oxen	*Lr1, Lr2a, Lr10*[b]	20 MR MS	20 MS	30 MR MS
Parshall	*Lr16*	20-30 MR MS	20-30 MR MS	30-40 MS
Reeder	*Lr2a, Lr16*	20-30 MS	5-10 MS	10-20 MS
Russ	*Lr2a, Lr10*[b]	10-20 MR MS	20-30 MS	5-10 MR MS
Verde	*Lr16*	10-20 MR MS	5 R	5-20 MR
Era	*Lr10, Lr13, Lr34*	…	5 MR MS	10 MR MS
Glenlea	*Lr1, Lr34*	…	20 MR	10-20 MR
Roblin	*Lr1, Lr10, Lr13, Lr34*	…	10 MR	50 MR
RL 6003	*Lr1*	80 S	…	80 S
RL 6016	*Lr2a*	60 S	…	20 S
RL 6047	*Lr2c*	60 S	…	20 S
RL 6002	*Lr3*	70 S	…	50-70 S
RL 6004	*Lr10*	80 S	…	50-80 S
RL 6001	*Lr12*	80 S	70 S	50 S
RL 4031	*Lr13*	50 MR MS	50 S	50 MR MS
RL 6013	*Lr14a*	80 S	…	50-70 S
RL 6005	*Lr16*	30 MS S	…	60 MS S
RL 6043	*Lr21*	10 MR MS	…	5 MR
RL 6044	*Lr23*	20 MR MS	…	20 MR MS
RL 6064	*Lr24*	10 MR MS	…	10-20 S
RL 6058	*Lr34*	30-50 MR MS	…	40-60 MR MS
RL 6122	*Lr1, Lr13*	20-40 MR MS	…	50 MR MS
RL 6108	*Lr1, Lr34*	30-60 MR MS	…	40-50 MR MS
RL 6109	*Lr2a, Lr34*	50 MR MS	…	10-40 MR MS
RL 6125	*Lr3, Lr13*	50 MR MS	…	50 MR MS
RL 6110	*Lr3, Lr34*	40 MR MS	…	50-70 MR MS
RL 6112	*Lr10, Lr34*	30 MR MS	…	50-70 MR MS
RL 6114	*Lr13, Lr34*	10-20 MR MS	…	30-40 MR MS
RL 6128	*Lr13, Lr16*	50 MR MS	…	30-40 MR MS
RL 6115	*Lr16, Lr34*	20 MR MS	…	20-30 MR MS
RL 6131	*Lr13, Lr21*	10-20 MR	…	0
RL 6118	*Lr21, Lr34*	5 MR	…	0
RL 6132	*Lr13, Lr24*	10 MR	…	5 R
Thatcher	…	80 S	80 S	80 S

[a] Rust response: 0 = no flecks or uredinia, R = small uredinia with necrosis, MR = mixture of small and large uredinia with necrosis, MS = moderate size uredinia with chlorosis, S = large uredinia, without necrosis or chlorosis; … = not tested.

[b] An additional gene is present, either *Lr3, Lr14a,* or *Lr23.*

DISCUSSION

Based on the seedling infection type data, *Lr1*, *Lr2a*, *Lr10*, *Lr16*, *Lr21*, and *Lr24*, were postulated to be present in the hard red spring wheat cultivars grown in Minnesota and the Dakotas. The high levels of field resistance of Dandy, Ivan, Knudson, and Norm likely was due to combinations of seedling resistance genes such as *Lr16* or *Lr24* with at least one adult plant resistance gene. The Thatcher line with *Lr16* had response and severity ratings of 30 MS and 60 MS S in 2002 and 2003, respectively, in St. Paul. Virulence phenotype THBJ with virulence to *Lr16* has been a common phenotype in Minnesota and the Dakotas since 2001 (14), yet *Lr16* still conditions some degree of effective leaf rust resistance. Gene *Lr24* is still highly effective because virulence to this gene is at a very low level in the *P. triticina* population in the upper Midwest (14). Gene *Lr16* has been shown to interact with *Lr34* and *Lr13* to condition lower seedling infection types and higher field resistance than either of the seedling or adult plant genes condition separately (9,26).

Cv. Norm had a ;1 infection type to THBJ in the adult plant test, and had a $2^{+}3$ infection type to this isolate in the seedling tests. Based on these infection types, Norm likely has at least one additional resistance gene. Results from a genetic study have indicated that Norm has *Lr1, Lr10, Lr16, Lr13*, *Lr23*, and *Lr34* (L. M. Oelke, *unpublished data*). Cv. Alsen, postulated to have seedling genes *Lr2a, Lr10,* and either *Lr3, Lr14a,* or *Lr23,* also had good field resistance at all three field locations. Results from a genetic study indicate that Alsen has *Lr2a, Lr10, Lr13, Lr23,* and *Lr34* (L. M Oelke, *unpublished data*). The seedling infection type data in this study indicated that Alsen was heterogeneous for an additional seedling resistance gene, which could be *Lr16*. McKenzie was postulated to have *Lr21* based on pedigree and the low infection types to all the isolates used in this study. McKenzie must also have an adult plant gene because, in the field tests, it had lower rust severity and response compared with the Thatcher line with *Lr21*. The Thatcher line with *Lr21* and *Lr34* had very low leaf rust severity readings in both field tests.

Cvs. Aurora, Mercury, Ember, Forge, Keystone, McVey, Norpro, Parshall, Reeder, and Verde, which all were postulated to have *Lr16,* had an intermediate level of MR to MS field resistance. These lines also likely have some additional adult plant resistance genes. In the adult plant test, Aurora, Mercury, McVey, Keystone, and Reeder had infection types to isolate THBJ that were similar to the infection type of the Thatcher line with *Lr34*. Ember, Forge, Norpro, Parshall, and Verde had infection types to THBJ in the adult plant test that were lower than the Thatcher line with *Lr34*. This could be due to the interaction of *Lr34* with *Lr16*, or it also could be due to the presence of *Lr16* singly. Kolmer (10) found that isolates of *P. triticina* that had high infection types to the Thatcher line with *Lr16* in seedling tests often had lower infection types to adult plants of the same line. This makes it difficult to distinguish between the effect of *Lr34* interacting with *Lr16,* or the presence of *Lr16* or *Lr34* singly, in gene postulation studies. Cultivars that have *Lr16* and *Lr34* often have lower seedling infection types to isolates virulent on the Thatcher line with *Lr16*. Ingot, also postulated to have *Lr16*, was moderately susceptible at all locations in the field test and most likely does not have an additional adult plant resistance gene.

Cvs. 2375, Amazon, BacUp, Gunner, HJ98, Marshall, Oxen, and Russ were postulated to have combinations of *Lr1, Lr2a,* and *Lr10.* The cultivars with only *Lr1, Lr2a,* or *Lr10* for seedling resistance genes also must have some effective adult plant resistance genes. Amazon, HJ98, and Marshall had infection type 23^{+} to isolate THBJ in the adult plant tests, which indicated these cultivars probably have *Lr34*. Cvs. 2375, BacUp, and Oxen had lower infection types of ;2 to ;23 to THBJ. These cultivars probably have *Lr34* and may have an additional adult plant resistance gene. Cv. Russ had a 0; infection type to both THBJ and TNRJ in the adult plant tests. Russ must have an additional adult plant resistance gene. All of these cultivars also had intermediate leaf rust severities with MR to MS responses in the field plots at St. Paul. Roblin, with genes *Lr1, Lr10, Lr13*, and *Lr34* (3), had an infection type of 23 to THBJ in the adult plant test, and was 10 MR and 50 MR in Fargo in 2002 and St. Paul in 2003, respectively. Glenlea, with genes *Lr1* and *Lr34*, had a ;23 infection type to THBJ in the adult plant test, and a ;3 infection type to MCDS. Glenlea was 10 to 20 MR in Fargo and St. Paul in 2002 and 2003, respectively. Dyck et al. (6) determined that Glenlea had *Lr34* and an additional adult plant resistance gene.

Genes *Lr3*, *Lr14a,* or *Lr23* likely were present in some cultivars, but could not be differentiated with the isolates used in this study. Gene *Lr14a* originally was derived from the tetraploid Yaroslav emmer (12), which was used as an early stem rust-resistant parent in the hard red spring wheat breeding programs. Gene *Lr23* originally was derived from the durum wheat Gaza (2) and also may be present in hard red spring wheat cultivars (24,30). The older Minnesota cv. Lee was the source of *Lr23* for the Thatcher line with this gene (18). The temperature sensitivity of *Lr23* makes it difficult to consistently score infection types for wheat lines with this resistance gene. The Thatcher line with *Lr23* had effective resistance in the field plot tests in St. Paul in 2002 and 2003. Gene *Lr23* likely contributes some degree of effective resistance in the hard red spring wheat cultivars. Gene *Lr3* originally was derived from winter wheat cultivars (5,20) and is less likely to be present in hard red spring wheat. Nearly all of the *P. triticina* isolates in the United States are virulent to *Lr3* and *Lr14a* (14); therefore, these two genes would not condition any effective leaf rust resistance in cultivars.

It is likely that the cultivars in this study also had other seedling resistance genes, because the limiting factors in any gene postulation study are the virulence combinations of the isolates. For example, only KFBJ was avirulent on *Lr1*. KFBJ also was avirulent on *Lr16*, which made it impossible to distinguish lines that might have *Lr1* and *Lr16*. It also was not possible to clearly identify which cultivars had *Lr34* based on the adult plant infection types and field resistance. The presence of seedling *Lr* genes, especially *Lr16*, confounded some of these results. Genetic analysis of segregating populations remains the best method to determine which seedling and adult plant *Lr* genes are present in wheat germplasm.

Adult plant resistance gene *Lr34*, which likely is present in many of these wheat cultivars, conditions an intermediate level of nonspecific resistance to leaf rust. Isolates of *P. triticina* with complete virulence to adult plants with *Lr34* have not been described (14). However, most isolates are virulent to *Lr13*, which also is likely present in many of these cultivars. Gene *Lr13* has been present in U.S. spring wheat cultivars since cv. Chris was released in the mid-1960s (25) and was highly effective for a number of years. Cv. Era (7), with *Lr10, Lr13,* and *Lr34*, has been used extensively as a parent. In recent years, *Lr13* has lost effectiveness as virulent leaf rust isolates have increased.

This study confirms that the wheat cultivars with the best leaf rust resistance have combinations of effective seedling and adult plant resistance genes. Additional seedling resistance genes should be added to the spring wheat germplasm, because *Lr16, Lr21,* and *Lr24* were the only seedling genes found in these cultivars that conditioned effective field resistance. Other adult resistance genes, such as *Lr46* (28), a slow-rusting adult resistance gene, also should be utilized to enhance leaf rust resistance in the spring wheat cultivars. The genetically variable and dynamic nature of the *P. triticina* population in the United States requires that new leaf rust resistance genes be added to wheat germplasm on a regular basis in order to maintain effective levels of field resistance.

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