Genetics of Leaf Rust Resistance in the Soft Red Winter Wheat 'Caldwell'

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ABSTRACT

The soft red winter wheat (*Triticum aestivum* L.) 'Caldwell' has effective resistance to leaf rust caused by *Puccinia triticina.* To determine the genetic basis of this resistance, Caldwell was crossed with the leaf rust–susceptible spring wheat 'Thatcher', and the F_1 plants were backcrossed to Thatcher to obtain backcross (BC) F_2 (BC_1F_2) families. In the seedlings, the BC_1F_2 families segregated for a single gene to *P. triticina* race SBDG, which is likely *Lr14a* based on tests with BC_1F_3 lines. In field tests, the BC_1F_2 families segregated for a single gene for adult plant resistance that was independent of the seedling resistance. BC_1F_2 adult plants were inoculated in greenhouse tests with *P. triticina* races BBBD and THBJ, and resistant plants were selected and advanced by single-seed descent to produce BC_1F_4 lines. In greenhouse tests, adult plants of some of the BC_1F_4 lines had the same low and high infection type (IT) to different *P. triticina* races as the Thatcher isoline with *Lr12*. Other BC_1F_4 plants had intermediate IT to the *P. triticina* race THBJ. The BC_1F_4 plants with the intermediate ITs were selected and tested as BC_1F_5 adult plants in greenhouse tests and as $BC_1F_{4:6}$ lines in field plot tests at two locations. Caldwell likely has the seedling resistance *Lr14a,* the adult plant gene *Lr12*, and an uncharacterized adult plant resistance gene that conditions an intermediate level of effective resistance in field plots.

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Abbreviations: BC, backcross; IT, infection type; MR, moderately resistant; MS, moderately susceptible; R, resistant; S, susceptible.

Leaf rust, caused by *Puccinia triticina* Eriks., is the most common rust disease of wheat (*Triticum aestivum* L.) in the United States and worldwide (Roelfs et al., 1992). Leaf rust has the potential to overwinter throughout much of the soft red winter wheat region of the southern and eastern United States (Roelfs, 1989). Along the Gulf Coast, leaf rust infections can be seen usually by February and can reach high severity levels in March and April. In the spring, leaf rust infections on wheat move progressively north along the Atlantic seaboard and through the mid-South. By early May, leaf rust is prevalent in North Carolina and Virginia. In Ohio, the leading state for soft red winter wheat production, leaf rust infections reach maximal levels in June.

Losses in wheat due to leaf rust can be substantial. Caldwell et al. (1934) showed that different winter wheat cultivars that varied from highly resistant to susceptible suffered losses of 15 to 28% due to leaf rust. In 1938 leaf rust caused an estimated loss of 25 to 30% in hard red winter wheat in Oklahoma (Chester, 1939). Losses in Kansas in 2007 due to leaf rust were estimated to be 14% (Appel et al., 2007). Khan et al. (1997) developed a yield loss model for southern soft red winter wheats that predicted a 1% yield loss for every 1% increase in rust severity at the milky-ripe stage of grain development. Everts et al. (2001) determined that leaf rust affected the softness parameter and may reduce flour yield of soft red winter wheats.

Stable leaf rust resistance in the soft red winter wheat cultivars has been difficult to obtain because *P. triticina* is highly variable for

Published in Crop Sci. 49:1187–1192 (2009).
doi: 10.2135/cropsci2008.10.0598

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virulence to race specific leaf rust resistance genes in wheat and responds quickly to the selection pressure imposed by resistant cultivars. The early soft red winter wheat cultivars Mediterranean (CI 11489) and Hussar (CI 4843) have leaf rust resistance genes *Lr3* and *Lr11,* respectively (Soliman et al., 1964). Because these cultivars were used in the development of soft red wheat cultivars, both *Lr3* and *Lr11* are likely present in a number of current soft red winter wheats; however, these genes no longer provide effective leaf rust resistance because races of leaf rust with virulence to both genes are very common. *Lr9* from the wild wheat relative *Aegilops umbellulata* was first used in soft red winter wheat cultivars in 1967, and within a few years leaf rust races with virulence to *Lr9* were detected (Shaner et al., 1972), limiting the effectiveness of this gene. Similarly, *Lr26* on the wheat rye 1B/1R translocation is present in a number of soft red winter wheats (Kolmer, 2003), and leaf rust races with virulence to this gene are common in the soft red winter wheat region (Kolmer et al., 2008a). *Lr18* derived from *T. timopheevi* is also present in some soft red winter wheats, and races with virulence to this gene, while not very common, have been detected in the southern and eastern United States.

The Purdue Agricultural Experiment Station released the soft red winter wheat cultivar Caldwell (CI 17897) in 1981 (Patterson et al., 1982). The pedigree of Caldwell is 'Benhur' (CI 14054) sib*2/'Siete Cerros' (PI 338921). The pedigree of the Benhur sib line includes the soft red winter wheats 'Knox 62' (CI 13701), 'Vigo' (CI 12220), 'Trumbull' (CI 5657), and 'Hussar', a Purdue breeding line, and the spring wheats 'Hope' (CI 8178) and 'Kenya Farmer' (PI 187165). Siete Cerros is a CIMMYT cultivar. Caldwell was noted to have adult plant field resistance to leaf rust and was widely grown from 1981 to 1985 (Schafer, 1993). The leaf rust resistance in Caldwell has remained effective since release. In 2000 in plots in North Carolina, Caldwell was highly resistant to leaf rust (Kolmer, 2003). Caldwell was chosen for this study because it has had durable resistance to leaf rust and the genetic basis of its leaf rust resistance is not known. The objective of this study was to determine the number and identity of the leaf rust resistance genes in Caldwell.

MATERIALS AND METHODS

Seed of Caldwell was planted in 15-cm-diam. pots that were filled with steamed topsoil and placed on a greenhouse bench with a mixture of fluorescent and incandescent lighting. After 10 d when the plants were at the two-leaf stage, the pots were placed in a growth chamber with incandescent lighting at 10°C for 2 mo of vernalization. After this period, the pots were placed in a growth cabinet with fluorescent and incandescent lighting with a 16-h daylength at 18°C. Pots with seed of the leaf rust susceptible spring wheat cultivar Thatcher (CI 1003) were placed in the growth cabinet 1 wk before the Caldwell plants were removed from the vernalization chamber; and also at the same time, when the Caldwell plants were placed in the growth cabinet. The Thatcher and Caldwell plants were treated with Nutricot 13–13–13 N–P–K (Plantco Inc., Branpton, ON). At heading the Thatcher plants were emasculated and pollen shedding anthers from Caldwell were used to pollinate the Thatcher female parents. The F_1 seed was harvested and then planted and vernalized for 4 wk and backcrossed as the male parent to Thatcher. Approximately 80 BC_1F_1 seeds were obtained. The BC_1F_1 seed was planted in a greenhouse in 15-cm-diam. pots and selfed to obtain BC_1F_2 families.

Ten seeds of Caldwell were planted in individual 3.5-cm^2 plastic pots that were filled with vermiculite (Sunshine Strong-Lite Medium Verniculite Premium Grade, JR Johnson Horticultural Supplies, St. Paul, MN) and placed on a plastic tray. After 8 d when the primary leaves had fully expanded, each pot of seedlings was inoculated separately with *P. triticina* races BBBD (isolate designation: Race 1), THBJ (588-1), MCDS (520-1), MBRJ (6-2B), MFBJ (94 Can), KFBJ (64-1), MJBJ (406-1), and SBDG (Race 9). The four-letter race designation of the isolates is derived from the avirulent–virulent infection types (IT) to 20 Thatcher lines with single genes for leaf rust resistance as described in the *P. triticina* virulence nomenclature system (Long and Kolmer, 1989) and in recent virulence surveys of *P. triticina* (Kolmer et al., 2008a). Fifteen to 20 seeds of each BC_1F_2 family were planted in a 3.5-cm^2 plastic pot and inoculated when the primary leaves were fully expanded with race SBDG. For seedling inoculations, rust urediniospores were mixed with Soltol 170 oil (Phillips Petroleum, Borger, OK) and then spray inoculated onto plants using the equipment and methods previously described (Roelfs et al., 1992). After inoculation seedling plants were allowed to dry for 1 h and then placed in a mist chamber overnight at 18°C and 100% relative humidity. The seedlings were placed on a greenhouse bench after incubation. Seedlings were fertilized with a 20–20–20 N–P–K solution immediately after inoculation and at 14 d after planting. The ITs on the primary leaves of individual plants were read at 10 to 12 d after inoculation. The ITs were classified using a 0 to 4 scale (Long and Kolmer, 1989). Infection types, 0 (no visible sign of infection), ";" (hypersensitive flecks), 1 (small uredinia surrounded by necrosis) and 2 (small-moderate size uredinia surrounded by chlorosis) were considered as low (resistant); and IT from 3 (moderate size uredinia without necrosis or chlorosis) to 4 (large uredinia) were considered as high (susceptible). Mixtures of ITs or mesothetic responses, were indicated by listing the most common IT first, followed by the less common ITs. Larger and smaller uredinia were indicated by "+" and "−," respectively. BC_1F_2 families that had only susceptible seedlings were considered as homozygous susceptible, and families that had both resistant and susceptible plants were considered as segregating. The ratio of segregating to homozygous susceptible families was used to estimate the number of segregating resistance genes. A χ^2 test (Steel and Torrie, 1980) was used to determine if the observed ratio significantly deviated from the expected ratio.

In the field plot tests, 50 seeds of each genotype were planted in 2-m rows spaced 30 cm apart, perpendicular to rows of a mixture of wheat cultivars Thatcher, 'Morocco' (PI 278386), 'Max' (CI 15093), and 'Little Club' (CI 4066) that are susceptible to leaf rust. The spreader rows and BC_1F_2 families of Thatcher/Caldwell were inoculated in St. Paul, MN, with a mixture of isolates MJBJ, THBJ, MCRK, TNRJ, and TDBG in 2005. In 2008 the spreader rows and the Thatcher*2/Caldwell F_6 lines in St. Paul and Crookston, MN, were inoculated with races MCDS, TDBG, MFPS, THBJ,

and TNRJ. The adult plants were rated for leaf rust severity using the modified Cobb scale (Peterson et al., 1948). Leaf rust response in the adult plants was rated as previously described (Roelfs et al., 1992). The field plots were rated for leaf rust when the susceptible cultivar Thatcher had a leaf rust severity of 70 to 80% with a susceptible (S, large uredinia without chlorosis) response (70–80 S).

For greenhouse-based evaluation of adult plants, four seeds of each genotype were planted in a 15-cm pot and grown in a greenhouse at 18 to 25°C with a 16-h light period. Flag leaves of adult plants were inoculated in the same manner as in the seedling tests with a mixture of urediniospores and oil. Infection types were read 14 d after inoculation using the same IT scale as for the seedling tests.

RESULTS

Seedlings of Caldwell when tested with *P. triticina* isolates BBBD, THBJ, MCDS, MBRJ, TNRJ, MFBJ, KFBJ, and MJBJ had high IT of 3 to 3^+ and had a mesothetic IT of 3^+; (large uredinia with flecks) to isolate SBDG. Isolate BBBD is avirulent to most of the leaf rust resistance genes that are effective in seedling plants; however, it had high IT of 3^+ to the Thatcher line with *Lr14a* and IT 2^+ to the Thatcher line with *Lr23*. Isolate SBDG has low IT of ;23 to *Lr14a* and ; (fleck) to *Lr23*. When tested with isolate SBDG, seedlings of the 79 BC_1F_2 families of Thatcher/Caldwell segregated in a 1:1 ratio ($P = 0.74$) (Table 1) for families that segregated for resistant and susceptible plants and for families that were homozygous susceptible indicating that a single gene conditioned resistance. The resistant seedlings had IT of 3^+; to isolate SBDG. In field plots at St. Paul in 2005, the BC_1F_2 families also segregated in a 1:1 ratio ($P = 0.58$) for families that were segregating for resistant and susceptible plants and for families that were homozygous susceptible. In the field test, the resistant plants in the segregating families had leaf rust severity and response of 20 to 50 MRMS (MR = moderately resistant, medium to large uredinia surrounded by necrosis; MS = moderately susceptible, medium to large uredinia surrounded by chlorosis), and susceptible plants had severity and response of 60 to 80 S. The resistant plants were easily distinguished from susceptible plants based on the fewer uredinia, and the abundant necrosis and chlorosis surrounding the uredinia. The BC_1F_2 families segregated independently in a 1:1:1:1 ratio ($P = 0.32$) for seedling and adult plant field leaf rust resistance, indicating that two different genes conditioned resistance (Table 1).

Seedling BC_1F_2 plants were selected on the basis of low IT to isolate SBDG and grown to maturity to obtain BC_1F_3 lines for further seedling tests. Fifteen BC_1F_3 lines derived from different BC_1F_2 families were tested with three *P. triticina* isolates that varied for IT on Thatcher lines with genes *Lr14a* and *Lr23*. Nine of the BC_1F_3 lines had low IT of ;23 to isolates SBDG and PBLQ and high IT of 3^+ to isolate MHDS, which was identical to the Thatcher line with *Lr14a* (Table 2). The Thatcher line with *Lr23* had low IT of ; to isolates MHDS and SBDG and high IT of 3 to PBLQ. The remaining six lines had high IT of 3^+ to the three isolates. The result suggested that the seedling resistance to SBDG in Caldwell is most likely due to *Lr14a*.

Table 1. Segregation of 'Thatcher'*2/'Caldwell' F_2 wheat families for leaf rust resistance in seedlings to isolate SBDG and in adult plant field experiments.

Field	SBDG		Total
	Segregating	Homozygous Susceptible	
Segregating	24	18	42
Homozygous susceptible	17	20	37
Total	41	38	

In a greenhouse test, eight adult plants from each of 13 BC_1F_2 families of Thatcher/Caldwell were tested for IT to isolate BBBD, which has low IT on plants with *Lr12* and *Lr13* that are optimally expressed in adult plants. To isolate BBBD, the adult plant ITs ranged from ; to $;2^+$ to 3^+. Eight adult plants from each of seven families were tested with isolate THBJ that has high IT on plants with *Lr12* and *Lr13*. To THBJ the ITs ranged from $;22^+$ to 3^+. BC_1F_2 plants that had low IT to isolate BBBD and THBJ were selected, and the seed was harvested. A single BC_1F_3 seed from each selected BC_1F_2 plant was grown out to maturity and the seed harvested. Four plants from each of 12 BC_1F_4 lines were tested as adult plants with isolates BBBD, TCTD (190), MCRK (267), and THBJ. These four isolates differ for virulence and avirulence to genes *Lr12* and *Lr13*. Results for 11 lines are presented in Table 3. Three lines had low IT to isolates BBBD and MCRK that were similar or identical to the low ITs the Tc line with *Lr12* had to the same isolates. The Thatcher line with *Lr13* had low IT to BBBD

Table 2. Seedling leaf rust infection types† of nine 'Thatcher'*2/'Caldwell' F_3 wheat lines and near-isogenic lines of 'Thatcher' wheat with leaf rust resistance genes to three isolates of *Puccinia triticina*.

Line	Infection type isolate			Gene
	MHDS	SBDG	PBLQ	
Thatcher*2/Caldwell F3				
14	3^+	;23	;23	*Lr14a*
15	3^+	;23	;23	*Lr14a*
16	3^+	;23	;23	*Lr14a*
18	3^+	;23	;23	*Lr14a*
31	3^+	;23	;23	*Lr14a*
33	3^+	;23	;23	*Lr14a*
35	3^+	;23	;23	*Lr14a*
36	3^+	;23	;23	*Lr14a*
43	3^+	;23	;23	*Lr14a*
Thatcher	3^+	3^+	3^+	
Thatcher*Lr14a* RL6013	3^+	;23	;23	
Thatcher*Lr23* RL6012	;	;	3	

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

Table 3. Adult plant infection types† of 'Thatcher'*2/'Caldwell' F_4 wheat lines and isogenic lines of 'Thatcher' wheat with leaf rust resistance genes to four isolates of *Puccinia triticina*.

Line	Infection type isolate				Gene
	BBBD	TCTD	MCRK	THBJ	
Thatcher*2/Caldwell F4					
14-1	;2$^-$	3$^+$	22$^+$	3$^+$	*Lr12*
22-1	;12$^-$	3$^+$	22$^+$	3$^+$	*Lr12*
20-3	;1	22$^+$	2	3$^+$	*Lr12*
11-1	22$^+$ – 3$^+$	3$^+$	3$^+$	2	APR‡
4-2	;2$^-$ 22$^+$	23$^-$ 3$^+$	22$^+$	23	APR
21-1	3$^+$	3$^+$	3$^+$	2$^+$	APR
25-1				23	APR
24-1				2$^+$	APR
9-3				0; – ;2 – 23	APR
20-2				;22$^+$	APR
15-2				;22$^+$	APR
Thatcher	3$^+$	3$^+$	3+	3$^+$	
Thatcher*Lr12* RL6011	;1	3$^+$	;22+	3$^+$	
Thatcher*Lr13* RL4031	;1	;2$^-$	3+	3$^+$	
Thatcher*Lr34* RL6058	2	2$^-$	2$^-$	0;2$^-$	

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

‡Adult plant resistance.

and TCTD and high IT to MCRK and THBJ. Four plants from each of 25 BC_1F_4 lines were tested with only isolate THBJ. The results for eight lines are presented in Table 3. These lines all had IT 2 to 23 to THBJ. One plant in line 9-3 had IT of 0; (no uredinia with faint flecking) to isolate THBJ. Seed of 19 resistant BC_1F_4 plants was harvested.

Four BC_1F_5 seeds from each harvested BC_1F_4 plant were planted for testing as adult plants to isolate THBJ. The ITs of seven of the BC_1F_5 lines are presented in Table 4. These seven lines varied to THBJ from IT 0; in line 9-3A to IT of 2$^+$ and 3$^+$ in line 21-1A. Line 15-2A had a high IT of 3$^+$ with few uredinia. Seed of all BC_1F_5 plants was harvested and bulked within a line and BC_1F_6 lines were planted in rust nursery plots at Crookston and St. Paul Minnesota, MN, in 2008. The lines in Table 4 had rust severity and response of 10 to 40 MRMS in the field plots. Line 9-3A had the lowest severity and response of 5 resistant (R, small uredinia with necrosis) and 5 MR at the two locations. Thatcher and the Thatcher lines with *Lr12* and *Lr14a* had high rust response and severity of 70 to 80% with a susceptible response. The Thatcher line with the adult plant resistance gene *Lr34* had a rust severity and response of 10 to 20 MS.

DISCUSSION

The results of this study indicate that Caldwell likely has the seedling leaf rust resistance gene *Lr14a*, the adult plant gene *Lr12*, and a second adult plant gene that conditions effective resistance in field plot tests. The resistance response of the Thatcher lines with the unidentified adult plant resistance gene derived from Caldwell had much more necrosis and chlorosis compared with the Thatcher line with *Lr34*. Caldwell did not have the allele associated with *Lr34* (Lagudah et al., 2006; Kolmer et al., 2008b) in tests with the marker *csLV34*. The BC_1F_6 lines with the adult plant resistance from Caldwell varied for IT in greenhouse tests and to a lesser extent for leaf rust severity and response in field tests. Line 9-3A in particular had much lower IT and field severity. Segregation of the BC_1F_2 families indicated only a single gene segregation in the field tests. Genetic modifiers of leaf rust resistance may affect expression of this adult plant resistance.

Gene *Lr12* is present in the cultivar Chinese Spring (CI 14108) (Dyck, 1991), which was used as a parent of the soft red winter cultivar Knox (CI 12798) (Caldwell et al., 1954). Knox 62 was derived from Knox and may be the source of *Lr12* because it is in the pedigree of the Benhur sib line used as a parent of Caldwell. Because many current isolates of *P. triticina* in the southern and eastern United States are virulent to *Lr12* (Kolmer et al., 2003), this gene by itself no longer provides highly effective resistance. Hope (McFadden, 1930) is a possible source of *Lr14a* in Caldwell because it is present in the pedigree of the Benhur sib line. Gene *Lr14a* no longer provides effective resistance because virulence to this gene is now very common. The source of the unidentified adult plant resistance gene in Caldwell is not immediately apparent. Siete Cerros, the other parent of Caldwell, had

Table 4. Adult plant infection types† to *Puccinia triticina* isolate THBJ and field leaf rust severity‡ and response§ of seven Thatcher*2/Caldwell F_4–derived wheat lines and isogenic lines of Thatcher with leaf rust resistance genes tested in greenhouse and in field plots at two locations in Minnesota in 2008.

Line	Infection type to THBJ	Field plots	
		Crookston	St. Paul
'Thatcher'*2/'Caldwell' F4			
4-2	;22$^+$	20–30 MRMS	30 MRMS
9-3A	0;	5 R	5 MR
11-1A	22$^+$	30–40 MRMS	20–30 MRMS
15-2A	3$^+$ f	10–20 RMR	20 MRMS
20-2A	2$^+$	10–20 RMR	30 MRMS
21-1A	2$^+$ – 3$^+$	20 MRMS	40 MRMS
24-1	;2 – 22$^+$	20–40 MRMS	30 MRMS
Thatcher		70–80 S	80S
Thatcher*Lr12* RL6011		70 S	70 S
Thatcher*Lr14a* RL6013		70 S	70 S
Thatcher*Lr34* RL6058		10–20 MS	20 MS

†Infection types as described in Long and Kolmer (1989) to *P. triticina* race THBJ.

‡Modified Cobb scale (Peterson et al., 1948).

§R = resistant, small uredinia surrounded by necrosis; MR = moderately resistant, medium to large uredinia surrounded by necrosis; MS = moderately susceptible, medium to large uredinia surrounded by chlorosis; S = susceptible, large uredinia without necrosis or chlorosis.

a lower leaf rust score of 60 S in field plot tests in Mexico when compared with the fully susceptible cultivars Inia 66 (PI 338916) and Sonora 64 (CI 13930), which were 100 S (Singh and Rajaram, 1991). The other possibility is that this gene originated in the pedigree of the Benhur sib line. The leaf rust resistance in these cultivars has not been studied.

Genetic studies of leaf rust resistance in soft red winter wheat cultivars have been limited. Shaner and Finney (1980) characterized five winter wheat lines for latent period and uredinia size and number. The soft red winter wheat line CI13227 was determined to have four genes, one with a major effect that conditioned longer latent period (Shaner et al., 1997). Quantitative trait loci derived from CI 13227 that conditioned longer latent period were mapped on chromosomes 2DS, 2B, and 7BL (Xu et al., 2005). The relationship of the adult plant resistance gene derived from Caldwell with the genes in CI 13227 will be resolved only by chromosome mapping of the Caldwell resistance. Adult plant resistance conditioned by genes other than *Lr34* may be present in other soft red winter wheat cultivars. Kolmer (2003) postulated that soft red winter wheat cultivars with ineffective seedling genes such as *Lr1*, *Lr10*, and *Lr11* that still had field leaf rust resistance may have some effective adult plant resistance genes. Caldwell was used as a parent in the northern-eastern soft red winter wheat breeding programs; thus, this adult plant resistance gene may be present in other wheat cultivars.

Lr46 is another adult plant resistance gene that has a leaf rust response somewhat similar to the adult plant gene derived from Caldwell. In greenhouse tests of adult plants and in field plots, the Thatcher lines with *Lr46* derived from 'Pavon 76' (PI 520003) and a selection of 'Lalbahadur' with *Lr46* were less resistant (unpublished data) than the Thatcher lines with the Caldwell adult plant resistance. In a population of recombinant inbred lines derived from the CIMMYT cultivar Brambling, lines that likely had *Lr46* were less resistant in plots at St. Paul than in two Mexican locations (J. X. Zhang and J. A. Kolmer, unpublished data). Using a polymerase chain reaction marker for *Lr46* that was provided courtesy of E. Lagudah (CSIRO, Canberra, Australia) the Thatcher*2/Caldwell F_6 lines did not have the marker allele associated with *Lr46* (unpublished data). Determination of the chromosome location of the resistance gene from Caldwell will clarify if this gene is unique compared to *Lr46*, and also *Lr48* and *Lr49*, which are adult plant resistance genes derived from 'CSP 44' (PI 520360) and 'VL404', respectively (Bansal et al., 2008). Crosses of the resistant BC_1F_6 lines with Thatcher have been made to develop segregating populations to map this resistance gene.

Although not widely grown since the mid-1980s, the cultivar Caldwell has had effective leaf rust resistance since release in 1981. In field plot tests in North Carolina in 2000, Caldwell had a severity and response of 10 R MR and trace-5R at two different locations (Kolmer, 2003). Soft red winter wheat germplasm with highly effective and durable adult plant resistance could easily be developed by combining the adult plant resistance from Caldwell with *Lr34*. It is fitting that the wheat cultivar Caldwell has an adult plant gene that has provided durable resistance to leaf rust. R.M. Caldwell (Schafer, 1993), for whom the cultivar is named, was an early proponent of generalized nonspecific resistance in cereal crops (Caldwell, 1968).

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