Genetics of Leaf Rust Resistance in Canadian Spring Wheats AC Domain and AC Taber

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ABSTRACT

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The hard red spring wheat cultivar AC Domain and the Canada Prairie Spring wheat AC Taber have recently been licensed and released in western Canada and are resistant to leaf rust caused by *Puccinia recondita* f. sp. *tritici*. To determine the genetic basis of this resistance, the two cultivars were crossed with the leaf rust susceptible wheat Thatcher (Tc), and F_1 plants were backcrossed to Thatcher. F_2 families from Tc*2/AC Domain and AC Taber/Tc*2 were tested with isolates of *P. recondita* f. sp. *tritici* as seedlings in the greenhouse and as adults in the field rust nursery. Segregation of BC_1F_2 families indicated that AC Domain had seedling resistance genes *Lr10* and *Lr16*, and the adult plant gene *Lr34*. AC Domain was also hypothesized to have the adult plant gene *Lr12* based on infection types with *P. recondita* f. sp. *tritici* isolates that differed for virulence to *Lr12*. The effective field leaf rust resistance of AC Domain was conditioned by *Lr16* and *Lr34*. Segregation of BC_1F_2 families and infection types of BC_1F_3-derived BC_1F_4 plants indicated that AC Taber had *Lr14a* for seedling resistance, the adult plant gene *Lr13*, plus an additional uncharacterized adult plant resistance gene currently designated as *LrTb*.

Additional keywords: specific resistance, *Triticum aestivum*

Leaf rust of wheat (*Triticum aestivum* L.), caused by *Puccinia recondita* Roberge ex Desmaz. f. sp. *tritici* Eriks & E. Henn, is found in North America almost wherever wheat is grown (8,15). Leaf rust resistant wheat cultivars for the eastern Canadian prairies of Manitoba and Saskatchewan have been released by the Agriculture and Agri-Food Canada Cereal Research Centre in Winnipeg since 1937, when the cultivar Renown with leaf rust gene *Lr14a* was released (6). Following the release of Renown, phenotypes of *P. recondita* f. sp. *tritici* with virulence to *Lr14a* were selected, and within 5 years the resistance conditioned by *Lr14a* was no longer effective (6). When other cultivars such as Lee (1950) with *Lr10* and Selkirk (1953) with *Lr10, Lr14a,* and *Lr16* followed, the resistance of *Lr10* and *Lr16* was also rendered ineffective by selective changes in the *P. recondita* f. sp. *tritici* population (6). In 1965, the cultivar Manitou, with quality and agronomic characteristics of Thatcher and leaf rust resistance derived from Frontana, was licensed for release. Manitou was the first wheat released by the Cereal Research Centre that had the adult plant leaf rust resistance gene *Lr13* (8). This gene is best expressed in the adult plant stage and cannot be detected in the seedling stage in greenhouse tests with *P. recondita* f. sp. *tritici* isolates from Canada. The Thatcher derivatives Neepawa (1969), Napayo (1972), and Katepwa (1982), all with *Lr13*, were the predominant wheat cultivars in the eastern prairie region from the late 1960s to the mid-1990s. Resistance conditioned by *Lr13* was highly effective when first deployed in Manitou, but leaf rust phenotypes with virulence to *Lr13* appeared within a few years. In the past few years, cultivars with *Lr13* had high levels of leaf rust infection, although cultivars with this gene only were more resistant than susceptible cultivars such as Thatcher or Canthatch (10). The Neepawa backcross derivative Columbus has *Lr16* in addition to *Lr13*, and has been highly resistant since its release in 1980. Other Neepawa derivatives with combinations of leaf rust genes were released by the Cereal Research Centre: Roblin (1986) with *Lr1, Lr10, Lr13,* and *Lr34*; Pasqua (1990) with *Lr11, Lr13, Lr14b, Lr30,* and *Lr34*; AC Minto (1991) with *Lr11, Lr13,* and *Lr22a*; and AC Cora (1994) with *Lr13* and *Lr21* (8). These cultivars with combinations of effective seedling and adult plant leaf rust genes have all been resistant since their release.

AC Domain, licensed for release in western Canada in 1993, is a leaf rust resistant, early-maturing, lodging resistant, high-quality bread wheat well adapted to Manitoba. AC Domain was selected from BW83/ND585 (BW83 = ND499/RL4137; ND585 = Butte*3//Waldron/RL4205). AC Domain is the first wheat cultivar released by the Cereal Research Centre since 1969 that has a diverse parentage and does not have Neepawa as a major component of its pedigree.

AC Taber is a Canada Prairie Spring (CPS) wheat, which was developed by the Semi-Arid Prairie wheat breeding project at the Agriculture and Agri-Food Canada Research Centre at Swift Current, Saskatchewan (5). AC Taber was selected from the cross of HY320*2/BW553 (HY320 = Tobari 66/Romany; BW553 = Red Bobs*2/PI 78383//8*Neepawa). AC Taber has a yield potential similar to Biggar (HY320) but has higher protein content and better milling quality. AC Taber also has better resistance to prevalent phenotypes of *P. recondita* f. sp. *tritici* and common bunt (*Tilletia caries*) than does Biggar. The objective of this study was to determine the number and identity of leaf rust resistance genes in both AC Domain and AC Taber.

MATERIALS AND METHODS

AC Domain was used as the pollen parent and crossed with the leaf rust susceptible cultivar Thatcher (Tc). F_1 plants were used as pollen parents and crossed with Tc. For the crosses with AC Taber, Thatcher was used as the pollen parent since AC Taber and other CPS wheats shed pollen poorly. 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* (11). 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-Giegy Canada Ltd., Mississauga, ON) 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

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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 (11). Infection types 0 to 2^+ were considered resistant, and IT 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 (20).

To evaluate adult plant resistance, approximately 50 seeds of each BC_1F_2 family were planted in 2-m rows in the 1995 field rust nursery. Susceptible spreader rows were inoculated with a mixture of *P. recondita* f. sp. *tritici* phenotypes (MBR, MDR, MFM, and TDG) prevalent in the eastern prairie regions of Canada in 1994 (9). AC Domain, AC Taber, Thatcher, and 41 near-isogenic Thatcher lines were also evaluated for leaf rust severity and response in the field nursery. Rust ratings were recorded in the early milk stage when the susceptible check Thatcher had a severity (13) and response (19) rating of 70 to 90% susceptible (70-90 S). To further determine the identity of the adult-plant resistance genes in AC Domain and AC Taber, single plants with different leaf rust resistant responses were selected from the BC_1F_2 families which were homozygous susceptible in the seedling stage to all leaf rust phenotypes tested. 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/AC Domain and AC Taber/Tc*2 were compared for leaf rust severity and response with Thatcher backcross lines RL4031 (Tc*Lr13*) and RL6058 (Tc*Lr34*).

RESULTS

AC Domain. AC Domain had a low IT of ; to ;1 to all *P. recondita* f. sp. *tritici* isolates listed in Table 1 that had low IT on RL6005 (Tc*Lr16*), and IT ;23 to phenotype CGB, which is virulent to Tc*Lr16*. The Tc*2/AC Domain F_2 families segregated to fit a two-gene ratio (3 segregating :1 homozygous susceptible) when inoculated as seedlings with *P. recondita* f. sp. *tritici* phenotypes BBB and TBB, which are both avirulent to *Lr10* and *Lr16* (Table 2). When tested with phenotype SBD, which is virulent to *Lr10* and avirulent to *Lr16*, the same BC_1F_2 families segregated to fit a single-gene ratio (1:1). Since the families that segregated with phenotype SBD also segregated with phenotypes BBB and TBB, one of the two genes conferring resistance to BBB and TBB must also confer resistance to SBD. All BC_1F_2 families were homozygous susceptible when tested with phenotype CGB, which is virulent to both *Lr10* and *Lr16*. These results indicated that AC Domain has two seedling genes for leaf rust resistance; one is *Lr10*, which conditioned resistance to BBB and TBB, and the other is *Lr16*, which conditioned resistance to phenotypes BBB, TBB, and SBD.

The same BC_1F_2 families segregated to fit a 3:1 ratio as adult plants in the field rust nursery, which indicated that AC Domain had two genes that conditioned field resistance to *P. recondita* f. sp. *tritici*. Of the two seedling resistance genes identified in this cultivar, only *Lr16* conferred some resistance to *P. recondita* f. sp. *tritici* in the field. Tc*Lr16* had a leaf rust severity and response of 50% moderately resistant to moderately susceptible (50 MRMS) in the rust nursery (Table 1). RL6004 (Tc*Lr10*) had a leaf rust reaction of 70-90 S, the same rating as Thatcher. All Tc*2/AC Domain F_2 families that segregated for resistance to phenotype SBD also segregated for resistance as adults in the field rust nursery, which indicated that *Lr16* conditioned effective field resistance. Of the Tc*2/AC Domain F_2 families that were homozygous susceptible to SBD as seedlings, 15 segregated for adult plant resistance in the rust nursery test, and 16 were homozygous susceptible. The 1:1 ratio indicated the presence of a single effective adult plant resistance gene in AC Domain. This adult plant resistance gene should be *Lr34* since all $BC_1F_{3:4}$ lines derived from single BC_1F_2 plant selections had field leaf rust reactions identical to those of Tc*Lr34* (Table 3) and also showed leaf tip necrosis, a condition often associated with this gene (2). In the greenhouse tests, these lines produced an intermediate IT 23 to both phenotypes BBB and MBR, which was the same IT as for Tc*Lr34*.

Adult plants of AC Domain, Thatcher, RL6011 (Tc*Lr12*), Tc*Lr16*, and Tc*Lr34* were tested with leaf rust isolates that produced IT 3^+ to Tc*Lr16* in the seedling stage. Adult plants of AC Domain had very low IT 0; and ; to isolates MJB 34-1 and MJB 76-2, which had very low IT ; and ;1^- on adult plants of Tc*Lr12* and had intermediate to high IT 2^+3^+ on adult plants of Tc*Lr16* (Table 4). AC Domain had intermediate to high IT of 2^+3^+ to isolate TJB 77-2, which had high IT 3^+4 on Tc*Lr12* and intermediate to high IT 2^+3^+ on Tc*Lr16*. Both AC Domain and Tc*Lr12* had intermediate IT 22^-c when inoculated with isolate TJB 50-1 (Table 4). The adult plant IT indicated that AC Domain probably has *Lr12* in addition to *Lr34* for adult plant resistance. However, *Lr12* did not confer effective field resistance in the Tc*2/AC Domain F_2 families, since Tc*Lr12* was as susceptible as Thatcher in the 1995 field test (Table 4).

AC Taber. AC Taber had seedling IT ;12 to 2^+ to all isolates tested except isolate TBJ, which produced IT ; (Table 1). When tested with isolate TBJ, which is avirulent to *Lr14a*, the AC Taber/Tc*2 F_2 families segregated to fit a 1:1 ratio, which indicated a single gene for resistance. The resistant plants in segregating BC_1F_2 fami-

Table 1. Seedling infection types[a] and adult plant field reactions[b] to *Puccinia recondita* f. sp. *tritici* in wheat cultivars AC Domain, AC Taber, and Thatcher backcross lines near-isogenic for leaf rust resistance genes

Cultivar/*Lr* line	*P. recondita* f. sp. *tritici* phenotype							Field rust severity and response
	BBB	CGB	MFM	MBR	SBD	TBJ	TBB	
AC Domain	;1	;23	;1	;1	;1	;$1^=$	;	TR
AC Taber	;12^+	22^+	22^+	2^+	;12	;	;2^+	TR
Thatcher	3^+4	3^+4	3^+4	3^+4	3^+4	3^+4	3^+4	70-90 S
Tc*Lr10* RL6004	;1	3^+	33^+	3^+4	3^+4	;1	;11^+	70-90 S
Tc*Lr13* RL4031	22^+3c	2^+3c	233^+	33^+	2^+33^+	…	33^+	50 MRMS
Tc*Lr14a* RL6013	3^+4	3^+4	3^+4	3^+4	;1^+	;12^-	3^+4	70-90 S
Tc*Lr16* RL6005	;12^-	3	;1	12	;12^-	2^-	;12	50 MRMS
Tc*Lr34* RL6058	23^+	;23	;23^+	33^+	33c	…	23^+	10 M

[a] Infection types on primary leaves were rated 12 days after inoculation on a scale of 0 to 4 (11). The + and – symbols denote more or less sporulation, respectively; c indicates uredinia surrounded by chlorosis.

[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, with 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).

lies had IT identical to the Thatcher backcross line RL6013 (Tc*Lr14a*). All AC Taber/Tc*2 F_2 families were homozygous susceptible when tested with phenotypes BBB and MFM, which are virulent to *Lr14a* (Table 2). The seedling segregation data indicated that AC Taber has *Lr14a.*

When challenged with a mixture of *P. recondita* f. sp. *tritici* phenotypes in the field rust nursery, the AC Taber/Tc*2 F_2 families segregated to fit a 3:1 ratio, which indicated that AC Taber had two effective genes for field leaf rust resistance. This resistance must be due to adult plant resistance genes, since line Tc*Lr14a* had a leaf rust rating as high as Thatcher (70-90 S) (Table 1). The single gene line RL4031 (Tc*Lr13*) had a field leaf rust reaction of 40 to 60% moderately resistant to moderately susceptible with large necrotic flecks and moderate to large uredinia with chlorosis (40-60 MRMS) (Table 3). The same field leaf rust reaction was observed in $BC_1F_{3:4}$ line 409, derived from a single BC_1F_2 plant selection (Table 3). In the greenhouse tests of adult plants, this line had low IT ;12 to phenotype BBB and high IT 33^+ to MBR, which indicated that line 409 had *Lr13*. AC Taber also had a second gene that conditioned adult plant resistance. $BC_1F_{3:4}$ lines 381 and 412 had a field leaf rust reaction of flecks and small uredinia with chlorosis, which was distinct from the adult plant resistance conditioned by *Lr13* or *Lr34*. In greenhouse adult plant tests, lines 381 and 412 had a high IT of 33^+ to leaf rust phenotype BBB and low IT of $;1^-$ to 2 to phenotype MBR (Table 3), which indicated that these lines lack *Lr13* but may have an uncharacterized adult plant gene for leaf rust resistance. The second adult plant resistance gene in AC Taber is temporarily designated as *LrTb*.

DISCUSSION

It was determined that AC Domain had two genes for seedling resistance, *Lr10* and *Lr16,* and probably two genes for adult plant resistance, *Lr12* and *Lr34*. *Lr10* was determined to be present in Butte and Waldron (12), which are in the pedigree of AC Domain. *Lr16* is present in a number of Canadian and U.S. hard red spring wheats and interacts with *Lr13* and *Lr34* for improved levels of resistance (4,16). *Lr12* is present in Exchange (3), which is in the background of AC Domain, and is also in the Neepawa derivative Benito (J. A. Kolmer, *unpublished*). *Lr34* may have been introduced into North American wheats from several different sources, as this gene has been found in many wheats worldwide (1,2,14). *Lr34* is currently one of the most important genes for leaf rust resistance in the Canadian and U.S. spring wheats (8).

AC Domain and Tc*Lr34* had an intermediate-high IT ;23 to isolate CGB in the seedling tests; however, the BC_1F_2 families derived from AC Domain all had high IT 3^+4 to phenotype CBG. The small amount of seedling resistance previously shown by *Lr34* to phenotype CGB was not reliably expressed in the BC_1F_2 families.

Of the four genes identified in AC Domain, only *Lr16* and *Lr34* contributed significantly to effective leaf rust field resistance in the BC_1F_2 families (8). The *P. recondita* f. sp. *tritici* population in Manitoba has high frequencies of phenotypes with virulence to genes *Lr10* and *Lr12,* such that these genes no longer condition effective resistance. AC Domain is the first wheat cultivar released by the Cereal Research Centre since Manitou in 1965 that

Table 2. Segregation for resistance to *Puccinia recondita* f. sp. *tritici* in the greenhouse and field rust nursery in backcross F_2 families of Thatcher*2/AC Domain and AC Taber/Thatcher*2

		Number of families[a]			
Phenotype	**Gene detected**	**Seg.**	**Susc.**	**Ratio**	***P*[b]**
Thatcher*2/AC Domain					
BBB, TBB	*Lr10, Lr16*	53	20	3 : 1	0.75 to 0.50
SBD	*Lr16*	42	31	1 : 1	0.50 to 0.25
CGB	…	0	73	1 : 1	<0.001
Field[c]	*Lr16, Lr34*	57	16	3 : 1	0.75 to 0.50
AC Taber/Thatcher*2					
TBJ	*Lr14a*	38	29	1 : 1	0.50 to 0.25
BBB, MFM	…	0	67	1 : 1	<0.001
Field[c]	*Lr13, LrTb*	54	23	3 : 1	0.25 to 0.10

[a] Seg. = segregating for resistant and susceptible plants; susc. = homozygous susceptible.
[b] *P* = probability of x^2 value.
[c] A mixture of *P. recondita* f. sp. *tritici* phenotypes was used to initiate a rust epidemic (9).

Table 3. Adult plant greenhouse infection types[a] and field reactions[b] to *Puccinia recondita* f. sp. *tritici* in BCF_4 lines selected from Thatcher*2/AC Domain and AC Taber/Thatcher*2, and Thatcher backcross lines near-isogenic for leaf rust resistance genes

		Phenotype		Field rust severity
Line	**Gene detected**	**BBB**	**MBR**	**and response**
Thatcher*2/AC Domain[c]				
Line 173	*Lr34*	23	23	10-20 M
Line 182	*Lr34*	23	23	5-20 M
AC Taber/Thatcher*2				
Line 409	*Lr13*	;12	33^+	40-60 MRMS
Line 381	*LrTb*	33^+	12	10 R
Line 412	*LrTb*	33^+	1^-2	30 R
Thatcher		3^+4	3^+4	90 S
Tc*Lr13* RL4031		;1	3^+4	40-60 MRMS
Tc*Lr16* RL6005		…	…	40 MS
Tc*Lr34* RL6058		;12	;23	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 (11). 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, with 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 $BC_1F_{3:4}$ lines were derived from single BC_1F_2 plant selections that were susceptible to phenotype SBD in the seedling test.

Table 4. Adult plant greenhouse infection types[a] and field reactions[b] to *Puccinia recondita* f. sp. *tritici* phenotypes of AC Domain, Thatcher, and Thatcher backcross lines near-isogenic for leaf rust resistance genes

	Phenotypes				Field rust severity
Cultivar/*Lr* line	**TJB 50-1**	**TJB 77-2**	**MJB 34-1**	**MJB 76-2**	**and response**
AC Domain	22^-c	2^+3^+	;	0;	TR
Thatcher	3^+	4	4	3^+	90 S
Tc*Lr12* RL6011	22^+	3^+4	$;1^-$	;	90 S
Tc*Lr16* RL6005	22^+	2^+3^+	2^+3	2^+3^+	50 MS
Tc*Lr34* RL6058	22^-	23	2^-3	23	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 (11). The + and – symbols denote more or less sporulation, respectively.
[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, with 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).

does not have *Lr13*. Due to superior yield, desirable agronomic characteristics, and overall disease resistance, AC Domain may become a commonly used parent in western Canada wheat breeding programs.

AC Taber was determined to have *Lr14a* for seedling resistance and *Lr13* and an additional uncharacterized gene (*LrTb*) for adult plant resistance. As with other CPS wheat cultivars such as Biggar and Genesis (7), CIMMYT (International Maize and Wheat Improvement Centre, Mexico City, Mexico) lines are prominent in the background of AC Taber. Many spring wheats released by CIMMYT have *Lr14a* and *Lr13* (17), and these two genes have also been identified in Biggar and Genesis (7). The effective field leaf rust resistance of AC Taber was conditioned by the adult plant genes *Lr13* and *LrTb*, since *P. recondita* f. sp. *tritici* phenotypes prevalent in the eastern prairie regions of Canada are virulent to *Lr14a* (9). Gene *Lr13* still conditions moderate field resistance to leaf rust, although lines with only this gene have medium- to large-sized uredinia mixed with necrosis in field rust nursery tests.

AC Taber/Tc*2 $F_{3:4}$ lines with *LrTb* singly had field rust reactions that were distinct from *Lr12*, *Lr13*, and *Lr34*, but appeared to be similar to an adult plant gene identified in Biggar (7). Since AC Taber and Biggar have a very similar genetic background (5), it is likely that *LrTb* is the same uncharacterized gene in Biggar. Singh and Rajaram (18) also found that CIMMYT wheats had adult plant resistance genes other than *Lr13* and *Lr34.* Line 412, which was homozygous for *LrTb*, will be crossed and backcrossed to Thatcher to confirm that a single adult plant gene is present, and intercrossed with Tc*Lr12*, Tc*Lr13*, and Tc*Lr34* to confirm that the resistance is conditioned by a previously uncharacterized adult plant gene.

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