

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 F₁ plants were backcrossed to Thatcher. F₂ 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 BC₁F₂ 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 BC₁F₂ families and infection types of BC₁F₃-derived BC₁F₄ 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 = Tobar 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). F₁ 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 F₂ (BC₁F₂) families were evaluated for seedling resistance in the greenhouse with selected virulence phenotypes of *P. recondita* f. sp. *tritici* (11). 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-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 BC₁F₂ 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 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 (20).

To evaluate adult plant resistance, approximately 50 seeds of each BC₁F₂ 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 BC₁F₂ families which were homozygous susceptible in the seedling stage to all leaf rust phenotypes tested. The selected BC₁F₂ plants with adult plant resistance were harvested individually, and BC₁F_{2:3} plants were grown in the greenhouse. BC₁F_{3:4} lines derived from single BC₁F_{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, BC₁F_{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 F₂ 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 BC₁F₂ 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 BC₁F₂ 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 BC₁F₂ 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 F₂ 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 F₂ 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 BC₁F_{3:4} lines derived from single BC₁F₂ 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 F₂ 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 F₂ families segregated to fit a 1:1 ratio, which indicated a single gene for resistance. The resistant plants in segregating BC₁F₂ 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/ <i>Lr</i> line	<i>P. recondita</i> f. sp. <i>tritici</i> phenotype							Field rust severity and response
	BBB	CGB	MFM	MBR	SBD	TBJ	TBB	
AC Domain	;1	;23	;1	;1	;1	;1 ⁼	;	TR
AC Taber	;122 ⁺	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 <i>Lr10</i> RL6004	;1	3 ⁺	33 ⁺	3 ⁺ 4	3 ⁺ 4	;1	;11 ⁺	70-90 S
Tc <i>Lr13</i> RL4031	22 ⁺ 3 ^c	2 ⁺ 3 ^c	233 ⁺	33 ⁺	2 ⁺ 33 ⁺	...	33 ⁺	50 MRMS
Tc <i>Lr14a</i> RL6013	3 ⁺ 4	3 ⁺ 4	3 ⁺ 4	3 ⁺ 4	;1 ⁺	;12 ⁻	3 ⁺ 4	70-90 S
Tc <i>Lr16</i> RL6005	;12 ⁻	3	;1	12	;12 ⁻	2 ⁻	;12	50 MRMS
Tc <i>Lr34</i> RL6058	23 ⁺	;23	;23 ⁺	33 ⁺	33 ^c	...	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 (TcLr14a). All AC Taber/Tc*2 F₂ 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 F₂ 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 TcLr14a had a leaf rust rating as high as Thatcher (70-90 S) (Table 1). The single gene line RL4031 (TcLr13) 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 BC₁F_{3;4} line 409, derived from a single BC₁F₂ 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. BC₁F_{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 TcLr34 had an intermediate-high IT ;23 to isolate CGB in the seedling tests; however, the BC₁F₂ 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 BC₁F₂ families.

Of the four genes identified in AC Domain, only Lr16 and Lr34 contributed significantly to effective leaf rust field resistance in the BC₁F₂ 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 F₂ families of Thatcher*2/AC Domain and AC Taber/Thatcher*2

Phenotype	Gene detected	Number of families ^a			P ^b
		Seg.	Susc.	Ratio	
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 χ^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 BCF₄ lines selected from Thatcher*2/AC Domain and AC Taber/Thatcher*2, and Thatcher backcross lines near-isogenic for leaf rust resistance genes

Line	Gene detected	Phenotype		Field rust severity and response
		BBB	MBR	
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 ⁺	12	30 R
Thatcher		3 ⁺ 4	3 ⁺ 4	90 S
TcLr13 RL4031		;1	3 ⁺ 4	40-60 MRMS
TcLr16 RL6005		40 MS
TcLr34 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 BC₁F_{3;4} lines were derived from single BC₁F₂ 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

Cultivar/Lr line	Phenotypes				Field rust severity and response
	TJB 50-1	TJB 77-2	MJB 34-1	MJB 76-2	
AC Domain	22 ^{-c}	2 ⁺ 3 ⁺	;	0;	TR
Thatcher	3 ⁺	4	4	3 ⁺	90 S
TcLr12 RL6011	22 ⁺	3 ⁺ 4	;1 ⁻	;	90 S
TcLr16 RL6005	22 ⁺	2 ⁺ 3 ⁺	2 ⁺ 3	2 ⁺ 3 ⁺	50 MS
TcLr34 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 *TcLr12*, *TcLr13*, and *TcLr34* to confirm that the resistance is conditioned by a previously uncharacterized adult plant gene.

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