Genetics and resistance

Inheritance of leaf rust resistance in the wheat cultivars AC Majestic, AC Splendor, and AC Karma

J.A. Kolmer and J.Q. Liu

Abstract: The wheat cultivars AC Majestic, AC Splendor, and AC Karma were developed and licensed for production in western Canada in the mid-1990s. Leaf rust, caused by *Puccinia triticina*, is an important pathogen of wheat throughout North America. Virulent isolates of *P. triticina* are selected and increase following the release of wheats with specific resistance genes, which eventually reduces the effectiveness of the resistance. Knowledge of the genes that condition leaf rust resistance in wheat makes it easier to add additional resistance genes to breeding germplasm. The objective of this study was to identify the leaf rust resistance genes in these three cultivars. The three cultivars were crossed with the susceptible wheat 'Thatcher', and the F_1 plants were backcrossed to 'Thatcher'. The backcross F_2 (BCF_2) families were tested for segregation of leaf rust resistance in seedling tests with specific *P. triticina* isolates. The BCF_2 families were also tested for segregation of leaf rust resistance as adult plants in a field rust nursery that had been inoculated with a mixture of *P. triticina* virulence phenotypes. 'AC Majestic' was determined to have the seedling resistance gene *Lr16* and the adult plant resistance gene *Lr13*. 'AC Splendor' was determined to have *Lr13*, *Lr16*, and the adult plant resistance gene *Lr34*. 'AC Karma' was determined to have *Lr13*, *Lr16*, and the adult plant resistance gene *LrTb*. All three cultivars had genes *Lr13* and *Lr16*, which reflect a lack of genetic diversity for leaf rust resistance in western Canada spring wheats. The results of the study indicate that additional leaf rust resistance genes need to be crossed into the spring wheat germplasm to provide new cultivars with high levels of leaf rust resistance.

Key words: *Triticum aestivum*, *Puccinia triticina*, specific resistance.

Résumé : Au milieu des années 1990, les cultivars de blé AC Majestic, AC Splendor et AC Karma furent développés et enregistrés pour fin de production dans l'Ouest canadien. La rouille des feuilles, causée par le *Puccinia triticina*, est une importante maladie parasitaire du blé dans toute l'Amérique du Nord. Des isolats virulents de *P. triticina* sont sélectionnés et se multiplient avec la mise en circulation de blés possédant des gènes de résistance spécifique, ce qui réduit éventuellement l'efficacité de la résistance. La connaissance des gènes qui conditionnent la résistance du blé rend plus facile la tâche d'ajouter des gènes de résistance supplémentaires dans les germoplasmes lors de la sélection. L'objectif de la présente étude était d'identifier les gènes de résistance à la rouille dans ces trois cultivars. Les trois cultivars furent croisés avec le blé sensible 'Thatcher', et les plantes F_1 rétrocroisées avec 'Thatcher'. Les familles F_2 issues du rétrocroisement (BCF_2) furent testées pour la ségrégation de la résistance à la rouille des feuilles dans des épreuves sur des semis avec des isolats spécifiques du *P. triticina*. Les familles BCF_2 furent aussi testées pour la ségrégation de la résistance à la rouille des feuilles sur des plantes adultes dans une pépinière extérieure qui avait été inoculée avec un mélange d'isolats de *P. triticina* de différents phénotypes de virulence. Il fut déterminé qu''AC Majestic' possède le gène *Lr16* de la résistance des semis et le gène *Lr13* de la résistance des plantes adultes, qu''AC Splendor' possède les gènes *Lr13*, *Lr16* et le gène *Lr34* de la résistance des plantes adultes et qu''AC Karma' possède les gènes *Lr13*, *Lr16* et le gène *LrTb* de la résistance des plantes adultes. Tous les cultivars possédaient les gènes *Lr13* et *Lr16*, ce qui est le reflet d'un manque de diversité génétique pour la résistance à la rouille des feuilles dans les blés de printemps de l'Ouest canadien. Les résultats de cette étude indiquent que des gènes supplémentaires de résistance à la rouille des feuilles devront être introduits dans le matériel génétique du blé de printemps afin de fournir aux nouveaux cultivars un haut niveau de résistance à la rouille des feuilles.

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Mots clés : *Triticum aestivum*, *Puccinia triticina*, résistance spécifique.

Introduction

Leaf rust of wheat, caused by *Puccinia triticina* Eriks., is the most common and widespread pathogen of wheat in North America. In the Canadian prairie provinces of Manitoba and Saskatchewan, leaf rust infections can usually be found on spring wheat by mid-July, when the wheat is at heading stage. Leaf rust severity in wheat is directly related to the effectiveness of the rust resistance genes in the cultivars. Leaf rust resistance genes, such as *Lr1*, *Lr3*, and *Lr10*, are common in the spring wheat germplasm (Kolmer 1994, 1996) yet do not condition any effective resistance, since *P. triticina* phenotypes with virulence to these genes are very common (Kolmer 1999a, 2001). The widespread cultivation of wheat cultivars with specific leaf rust resistance genes almost always results in an increase of *P. triticina* phenotypes with virulence to the resistance genes. Virulences to genes *Lr3ka*, *Lr11*, and *Lr17* increased rapidly in the Great Plains of the United States and Canada after winter wheat cultivars with these genes were widely grown (Kolmer 1999b). The genetic diversity of virulence in *P. triticina* populations and the rate at which leaf rust virulence phenotypes can increase has greatly complicated efforts to develop wheat cultivars that have long-lasting, or durable, resistance to leaf rust.

In wheats bred in western Canada, the leaf rust resistance genes *Lr13* and *Lr34*, which condition resistance mainly at the adult plant stage, have the longest history of effectiveness. Gene *Lr13* has been in many cultivars since the mid-1960s, when the cultivar Manitou was released (Samborski 1985). Initially cultivars with *Lr13* had a very high level of resistance; however, within a few years, *P. triticina* isolates with virulence to this gene began to increase, which reduced the effectiveness of the resistance. Cultivars with only *Lr13* have had intermediate levels of leaf rust resistance since the early 1980s (Kolmer et al. 1991). Gene *Lr34* was first used in spring wheat in the United States in the cultivar Chris in the mid-1960s (Samborski 1985). In Canada, the cultivars Glenlea (Dyck et al. 1985) and Roblin (Dyck 1993) were among the first wheats to have *Lr34*. Gene *Lr34* has conditioned a useful level of partial resistance to leaf rust since it was first selected in the North American spring wheat germplasm (Kolmer et al. 1991).

Genetic diversity for effective leaf rust resistance is currently the only practical method of maintaining acceptable levels of rust resistance in commonly grown wheat cultivars. Selection for virulence in *P. triticina* populations is less likely to affect the resistance of a number of wheat cultivars if the cultivars differ for effective leaf rust resistance genes. Genetic uniformity of resistance genes can result in different wheat cultivars being vulnerable to the increase and spread of a few *P. triticina* phenotypes with virulence to the common resistance genes. The results from genetic analysis of leaf rust resistance in wheat cultivars can be used to help diversify leaf rust resistance in breeding programs, by providing information on the identity of the leaf rust resistance genes in commonly grown cultivars. The objectives of this study were to identify the leaf rust resistance genes in the wheat cultivars AC Majestic, AC Splendor, and AC Karma, which were released in the mid-1990s in western Canada.

Materials and methods

'AC Majestic' and 'AC Splendor' were released in 1995 and 1996, respectively, by the Cereal Research Centre of Agriculture and Agri-Food Canada in Winnipeg, Manitoba. Both cultivars have high bread making quality with excellent resistance to wheat stem rust. The pedigree of 'AC Majestic' is 'Columbus *2' // 'Saric 70' / 'Neepawa' / 3 / 'Columbus *5' // 'Saric 70' / 'Neepawa'. The pedigree of 'AC Splendor' is 'Laura' / 'RL 4596' // 'Roblin' / 'BW 107'. 'AC Karma' is a Canada Prairie Spring Wheat and was developed and released in 1994 by the Semiarid Prairie Agricultural Research Centre, Agriculture and Agri-Food Canada, in Swift Current, Saskatchewan. (DePauw et al. 1997). 'AC Karma' has high grain yield and is also resistant to stem rust, common bunt, and loose smut. The pedigree of 'AC Karma' is 'HY320 *5' / 'BW553' // 'HY358' / 3 / 'HY358' / '7915-QX76B2'.

'AC Majestic', 'AC Splendor', and 'AC Karma' were used as pollen parents and crossed with the leaf rust susceptible cultivar Thatcher (Tc). The F_1 plants were used as pollen parents and backcrossed with Tc. BCF_1 plants were selfed to obtain BCF_2 families. 'AC Majestic', 'AC Splendor', 'AC Karma', and the BCF_2 families were evaluated for seedling resistance in greenhouse tests with selected isolates of *P. triticina*. Fifteen to 20 seedlings of each BCF_2 family were tested with each isolate of *P. triticina*. Plants for the seedling tests were seeded in clumps in 25 × 30 cm fibre flats filled with a sand–peat–soil mix. Plants were grown at 20 ± 2°C in a greenhouse with 8 h of supplemental fluorescent light per day. Nine to 10 days after seeding, the primary leaves were inoculated by atomizing a suspension of urediniospores in a nonphytotoxic light mineral oil. Inoculated plants were incubated at 100% RH for 16 h at 20°C. Infection types on primary leaves were rated 12 days after inoculation using a scale of 0–4 (Long and Kolmer 1989). Infection types of 0–2^+ were considered resistant, and infection types of 3 or 4 were susceptible. The BCF_2 families were classified as either segregating or homozygous susceptible. Goodness of fit to segregation ratios in BCF_2 families was determined using χ^2 tests (Sokal and Rohlf 1981).

To evaluate adult plant resistance, approximately 50 seeds of each BCF_2 family were planted in 2-m rows in a field rust nursery. Susceptible spreader rows of wheat were inoculated with a mixture of *P. triticina* virulence phenotypes prevalent in the eastern prairie region of Canada in 1997 and 1998 (Kolmer 1999a, 2001). 'AC Majestic', 'AC Splendor', 'AC Karma', and 'Thatcher' lines that are nearly isogenic for leaf rust resistance were evaluated for leaf rust severity and response in the field nursery. Rust ratings were recorded at the early milk stage (Zadoks growth stage 73–

74) when the susceptible check 'Thatcher' had a severity and response rating of 80–90% susceptible (80–90 S).

Results

'AC Majestic', 'AC Splendor', and 'AC Karma', and the 'Thatcher' line with *Lr16* (Tc*Lr16* -RL 6005) had low infection types of ;1 (flecks with small pustules surrounded by necrosis), ;(fleck), ;1, and ;1$^-$, respectively, to isolate BBB (three letter hexadecimal code for *P. triticina* virulence phenotypes; Long and Kolmer 1989) (Table 1). The 'Thatcher' line with *Lr13* (Tc*Lr13* RL 4031) expressed very little seedling resistance to isolate BBB with an infection type of 33$^+$c and had a high infection type of 3$^+$ to isolate TDB. The 'Thatcher' line with *Lr34* (RL 6058) expressed some resistance to isolates BBB and TDB with infection type of 23. 'AC Majestic', 'AC Splendor', 'AC Karma', and Tc*Lr16* had infection types of 22$^=$, 22$^-$, 2$^+$3, and 22$^+$, respectively, to isolate TDB (Table 1). The leaf rust susceptible cultivar Thatcher had infection type of 3$^+$ to both isolates BBB and TDB.

Forty F_2 families of 'Thatcher *2' / 'AC Majestic' segregated for infection types ;1$^-$ to 3$^+$ in seedling tests with isolate BBB (Table 2), and 39 families were homozygous for susceptible plants with infection types of 3 to 3$^+$, which indicated that a single gene controlled resistance to isolate BBB. With isolate TDB, the same 40 families segregated for resistance, and the same 39 families were homozygous susceptible. The infection type in the segregating families ranged from 2 to 3$^+$ and in the susceptible families from 3 to 3$^+$. Since the 'Thatcher' line with *Lr16* had a ;1$^-$ infection type to isolate BBB and a 22$^+$ infection type to isolate TDB the single gene in 'AC Majestic' that conditioned seedling resistance to both virulence phenotypes was most likely *Lr16*. In the field test, 57 F_2 families of 'Thatcher *2' / 'AC Majestic' segregated for resistant and susceptible plants, and there were 22 families that were homozygous susceptible. The number of segregating and homozygous susceptible families fit a 3:1 ratio, which indicated that two genes conditioned resistance to the field mixture of *P. triticina* isolates. All of the 40 families that segregated for seedling resistance to isolates BBB and TDB also segregated for field resistance. Of the 39 families that were homozygous susceptible to isolates BBB and TDB, 17 segregated for adult plant resistance in the field test (Table 3). These families all had rust response and severity ratings of 10 MR MS to 60 MS, which was similar to the response conditioned by the adult plant resistance gene *Lr13* (Table 1). Twenty-two of the seedling susceptible families were also homozygous susceptible as adults in the field tests. The ratio of 17 segregating to 22 homozygous susceptible families fit a 1:1 ratio ($\chi^2 = 0.64$), which indicated that a single gene, most likely *Lr13*, conditioned adult plant resistance in 'AC Majestic'.

Thirty-eight of the F_2 families of 'Thatcher *2' / 'AC Splendor' segregated for infection types ;1 to 3$^+$ in seedling tests with isolate BBB (Table 2), and 35 families were homozygous susceptible with infection types 3 to 3$^+$. The 1:1 ratio of segregating to homozygous susceptible families indicated that a single gene conditioned resistance to isolate BBB. The 38 families that segregated for resistance to isolate BBB also segregated for resistance to isolate TDB with infection types of 2 to 3$^+$. Thirty-five families were homozygous susceptible to isolate TDB. Since the 'Thatcher' line with *Lr16* had a ;1$^-$ infection type to isolate BBB and a 22$^+$ infection type to isolate TDB the single gene in 'AC Splendor' that conditioned seedling resistance to both races was most likely *Lr16*. In the field test, 59 of the BCF_2 families segregated for resistant and susceptible plants, and 14 families were homozygous susceptible. This segregation fits either a 3:1 or 7:1 ratio, which indicated that at least two genes, and possibly three genes in 'AC Splendor' conditioned field resistance. Of the 35 BCF_2 families that were seedling susceptible to isolates BBB and TDB, 11 had rust response and severity of 80 MR MS in the field test, which was similar to the 'Thatcher' line with *Lr13* (Table 3). Ten BCF_2 families had rust response and severity of 10–50 M, which was similar to the rust response of the 'Thatcher' line with *Lr34* in the field tests. If 'AC Splendor' has two genes for resistance that are expressed in the adult plant stage, then the ratio of segregating to homozygous susceptible families among the 35 families that were homozygous susceptible as seedlings would be expected to fit a 3:1 ratio. In the 35 seedling susceptible BCF_2 families, there were 21 families that segregated for resistance and 14 homozygous susceptible families that did not fit a 3:1 ratio ($\chi^2 = 4.18$). However, 11 of the segregating BCF_2 families had a resistance response that was similar to the response conditioned by *Lr13*, and 10 families had a resistance response similar to *Lr34*. If *Lr13* and *Lr34* conditioned the adult plant resistance; therefore, it would be expected that one quarter of the families would segregate for both genes, one quarter would have only *Lr13*, one quarter would have only *Lr34*, and one quarter would be susceptible. Some of the 11 and 10 BCF_2 families that had rust responses similar to *Lr13* and *Lr34*, respectively, probably also had the other adult plant resistance gene. It was not possible to classify families that had both genes, as opposed to families that segregated for only a single gene.

Thirty-eight of the F_2 families of 'Thatcher *2' / 'AC Karma' segregated for infection types ;1 to 3$^+$ in seedling tests with isolate BBB (Table 2), and 36 families were ho-

Table 1. Seedling infection types to isolates of *Puccinia triticina* and field responses to leaf rust of wheat cultivars AC Majestic, AC Splendor, and AC Karma, and Thatcher wheat lines with *Lr13*, *Lr16*, and *Lr34*.

Cultivar	Isolate		Field[a]
	BBB	TDB	
AC Majestic	;1	22$^=$	5 R – 30 MR
AC Splendor	;	22$^-$	TR – 5 R
AC Karma	;1	2$^+$3	5 R – 30 MR
Thatcher: *Lr13*	33$^+$c	3$^+$	80 MR MS
Thatcher: *Lr34*	23	23	20–50 M
Thatcher: *Lr16*	;1$^-$	22$^+$	40–60 MS
Thatcher	3$^+$	3$^+$	90 S

Note: Infection types are according to Long and Kolmer (1989).
[a]TR, trace level of uredinia; R, small necrotic uredinia with flecks; MR, uredinia with necrosis; MS, uredinia with chlorosis; M, mixture of small and large uredinia; S, large uredinia without necrosis or chlorosis.

Table 2. Segregation of leaf rust resistance in backcross F_2 families of cv. Thatcher wheat crossed with 'AC Majestic', 'AC Splendor', and 'AC Karma' in seedling and field tests.

	No. of families (infection types)			
Puccinia triticina isolate	Segregating	Susceptible	Expected ratio	χ^2
'Thatcher *2' / 'AC Majestic'				
Seedling				
BBB	40 (;1–3$^+$)	39 (3–3$^+$)	1:1	0.013
TDB	40 (2–3$^+$)	39 (3–3$^+$)	1:1	0.013
Field mixture	57	22	3:1	0.341
'Thatcher *2' / 'AC Splendor'				
Seedling				
BBB	38 (;1–3$^+$)	35 (3–3$^+$)	1:1	0.123
TDB	38 (2–3$^+$)	35 (3–3$^+$)	1:1	0.123
Field mixture	59	14	3:1	1.318
			7:1	2.976
'Thatcher *2' / 'AC Karma'				
Seedling				
BBB	38 (;1–3$^+$)	36 (3–3$^+$)	1:1	0.054
TDB	38 (2–3$^+$)	36 (3–3$^+$)	1:1	0.054
Field mixture	64	10	7:1	0.068

mozygous susceptible with infection types 3 to 3$^+$. The 1:1 ratio of segregating to homozygous susceptible families indicated that a single gene conditioned resistance to isolate BBB. The 38 families that segregated for resistance to isolate BBB also segregated for resistance to isolate TDB, with infection types of 2 to 3$^+$. Thirty-six families were homozygous susceptible to isolate TDB. Since the 'Thatcher' line with *Lr16* had a ;1$^-$ infection type to isolate BBB and a 22$^+$ infection type to isolate TDB, the single gene in 'AC Karma' that conditioned seedling resistance to both races was most likely *Lr16*. In the field test, 64 BCF_2 families segregated for resistant and susceptible plants, and 10 were homozygous susceptible, fitting a 7:1 ratio, which indicates that three genes in 'AC Karma' conditioned resistance in the field. The 38 BCF_2 families that were seedling resistant all expressed resistance similar to the 'Thatcher' line with *Lr16* in the field tests. Of the 36 BCF_2 families that were seedling susceptible, 15 had rust response and severity of 10 MR MS – 60 MS in the field test, which was similar to the response conditioned by the 'Thatcher' line with *Lr13*. Eleven of the seedling susceptible BCF_2 families had a rust response and severity of 50–60 MS, which was similar to the resistance conditioned by a gene tentatively designated as *LrTb*, which was previously described in the wheat cutivars Biggar (Kolmer 1994) and AC Taber (Liu and Kolmer 1997). Gene *LrTb* conditions a resistant response in adult plants that is distinct from either *Lr13* or *Lr34*. Twenty-six of the BCF_2 families that were seedling susceptible, segregated in the field for resistant and susceptible plants, and 10 were homozygous susceptible, fitting a 3:1 ratio (χ^2 = 0.148), which indicated that two genes conditioned adult plant resistance in 'AC Karma'. It was not possible to distinguish between BCF_2 families that segregated for both *Lr13* and *LrTb*, compared with families that segregated for only *Lr13* or *LrTb*.

Table 3. Adult plant rust resistance and response of seedling susceptible backcross F_2 families of cv. Thatcher crossed with 'AC Majestic', 'AC Splendor', and 'AC Karma', as assessed in rust nursery field tests.

Cross	No. of F_2 families	Rust severity and response[a]	Postulated gene
'Thatcher *2' / 'AC Majestic'	17	10 MR MS – 60 MS	*Lr13*
	22	80–90 S	—
'Thatcher *2' / 'AC Splendor'	11	80 MR S	*Lr13*
	10	10–50 M	*Lr34*
	14	90 S	—
'Thatcher *2' / 'AC Karma'	15	10 MR MS – 60 MS	*Lr13*
	11	50–60 MS	*LrTb*
	10	80–90 S	—

[a]See Table 1 for rust response codes.

Discussion

The results of this study indicated that 'AC Majestic' has leaf rust resistance genes *Lr13* and *Lr16*; 'AC Splendor' has genes *Lr13*, *Lr16*, and *Lr34*; and 'AC Karma' has genes *Lr13*, *Lr16*, and an adult plant gene that is most likely *LrTb*. The presence of *Lr13* and *Lr16* in the three cultivars is indicative of the lack of genetic diversity for effective leaf rust resistance in Canadian spring wheats. The cv. Columbus (*Lr13*, *Lr16*) (Samborski and Dyck 1982) is prominent in the pedigree of 'AC Majestic' and is also in the pedigree of RL 4596, which was used to develop 'AC Splendor'. 'Columbus' has been used as a source of sprouting resistance in western Canadian breeding programs. By crossing with 'Columbus' and selecting for sprouting and leaf rust

resistance, *Lr16* has been incorporated into a number of recent spring wheats in western Canada. The source of *Lr16* in 'AC Karma' is most likely HY358.

The frequency of *P. triticina* isolates with virulence to genes *Lr13* and *Lr16* has increased in recent years in Manitoba and Saskatchewan. A large majority of isolates are now virulent to gene *Lr13*, and virulence to *Lr16* has significantly increased in recent years (Kolmer 1999a, 2001). In the late 1980s and early to middle 1990s, 'Columbus' was highly resistant to leaf rust. As the frequency of isolates with virulence to *Lr13* and *Lr16* increased, the resistance conditioned by these genes has been eroded. AC Barrie is a cultivar that most likely has *Lr13* and *Lr16* and was widely grown in Manitoba and North Dakota in 1999 because of its improved tolerance of head blight disease caused by *Fusarium graminearum* Schw. Leaf rust severities were extremely high on AC Barrie in 1999 because of the prevalence of isolates with virulence to *Lr13* and *Lr16*. Cultivars such as AC Majestic, which have only *Lr13* and *Lr16*, will continue to suffer losses due to leaf rust infections.

Leaf rust resistance gene *Lr34* was determined to be in 'AC Splendor'. The cultivars Laura (Kolmer 1994) and Roblin (Dyck 1993), which are in the pedigree of 'AC Splendor', have *Lr34*. Wheats that have *Lr34* combined with other leaf rust genes (Liu and Kolmer 1997) have better leaf rust resistance than cultivars with only *Lr13* and *Lr16*. In greenhouse tests of adult plants, the resistance of wheat lines with *Lr34* is characterized by fewer and smaller uredinia compared with a susceptible line. The resistance conditioned by *Lr34* is nonspecific, since isolates that are fully virulent to this gene have not yet been detected (Kolmer 1999a, 2001). At times the resistance of wheat lines with *Lr34* can be difficult to detect in field tests, often being classed as susceptible. The underrepresentation of the 'Thatcher *2' / 'AC Splendor' F_2 families in the field tests that segregated for adult plant resistance, was most likely due to the classification as susceptible of families that had *Lr34*. A different adult plant gene, designated as *LrTb*, is probably in 'AC Karma'. This gene has a rust response of moderate to large uredinia with distinct chlorosis, which is different from the resistance conditioned by *Lr13* and *Lr34*. This gene was determined to be in the cultivars Biggar (Kolmer 1994) and AC Taber (Liu and Kolmer 1997), which are highly related to 'AC Karma'. The cv Tobari is most likely the original source of *LrTb*.

The continual selection of *P. triticina* virulence phenotypes by wheats with specific leaf rust resistance genes has eroded the leaf rust resistance of U.S. and Canadian spring wheats in recent years. Genes *Lr13* and *Lr16*, which are very common in Canadian spring wheats, no longer condition high levels of rust resistance. Wheats with *Lr34* combined with *Lr16* have better levels of leaf rust resistance but still can suffer moderate levels of leaf rust infection. Genes that have not yet been widely exploited in breeding programs, such as *Lr21*, *Lr22a*, and *Lr37,* could be backcrossed into adapted germplasm to increase the diversity of effective leaf rust resistant wheat genotypes. However, the widespread use of any of these genes will most likely result in the selection of virulent *P. triticina* phenotypes. The use of genes that condition nonspecific resistance may offer the best chance of stable leaf rust resistance. Adult plant gene *Lr34* conditions an isolate nonspecific resistance and has provided durable resistance to leaf rust in wheats throughout the world (Kolmer 1996). The adult plant gene *Lr46* also conditions an apparently isolate-nonspecific resistance and is in the cv. Pavon 76 (Singh et al. 1998). The development of wheat germplasm with combinations of adult plant genes *Lr34* and *Lr46* may potentially offer the best chance to develop cultivars with high levels of durable leaf rust resistance.

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