Theor Appl Genet (2001) 102:347–352 © Springer-Verlag 2001

W.J. Raupp · Sukhwinder-Singh
G. L. Brown-Guedira · B. S. Gill

Cytogenetic and molecular mapping of the leaf rust resistance gene *Lr39* in wheat

Received: 19 April 2000 / Accepted: 15 May 2000

Abstract Leaf rust, caused by the fungus *Puccinia triticina* Eriks, is one of the most serious diseases of wheat (*Triticum aestivum* AABBDD, 2n=6x=42) worldwide. Growing resistant cultivars is an efficient and economical method of reducing losses to leaf rust. Here we report a new leaf rust resistance gene, *Lr39,* transferred from *Aegilops tauschii* into common wheat. *Lr39* conditions both seedling and adult plant resistance to the leaf rust pathogen. The inter- and intra-chromosomal mapping of the *Lr39* gene showed that it is different from all previously described *Lr* genes. We used monosomic analysis for the inter-chromosomal mapping and wheat microsatellite markers for the intra-chromosomal mapping. The monosomic and ditelosomic analysis indicated that *Lr39* is independent of the centromere on the short arm of chromosome 2D. Eight microsatellite markers for 2DS were used for linkage analysis on a population of 57 F_2 plants derived from a cross of an *Ae. tauschii*-derived wheat, cv. Wichita line TA4186 (possessing *Lr39*), with Wichita monosomics for the D-genome chromosomes. The microsatellite marker analysis confirmed the location of the gene on 2DS. Three markers were polymorphic and linked to the gene. The closest marker *Xgwm210* mapped 10.7 cM from *Lr39*. The location of *Lr39* near the telomere of 2DS distinguishes it from the *Lr2* and *Lr22* loci, which are located on 2DS proximal to *Xgwm210*.

Keywords *Triticum aestivum* · Disease resistance · Microsatellite markers · Telocentric analysis · *Aegilops tauschii*

Communicated by G. Wenzel

Contribution number 00–93-J from the Agricultural Experiment Station, Kansas State University, Manhattan, Kan., USA

W.J. Raupp · B.S. Gill (✉)
Wheat Genetics Resource Center, Department Plant Pathology,
4307 Throckmorton Plant Sciences Center,
Kansas State University, Manhattan, KS 66506–5502, USA
Fax: +1785-532-5692
e-mail: bsg@ksu.edu

Sukhwinder-Singh
Biotechnology Center, Punjab Agricultural University,
Ludhiana-141004 Punjab, India

G.L. Brown-Guedira
USDA-ARS Department of Agronomy, Kansas State University,
Manhattan, KS 66506–5501, USA

Introduction

Leaf rust, caused by the fungus *Puccinia triticina* Eriks. [syn. *P. recondita* Roberge ex Desmaz. F. sp. *tritici* (Eriks. & E. Henn.)], is a destructive disease in most wheat (*Triticum aestivum* L., 2n=6x=42, AABBDD) growing areas of the world (Roelfs et al. 1992). Yield losses may reach 40% in susceptible cultivars (Knott 1989). Growing resistant cultivars is an efficient and economical method of reducing losses to leaf rust. To date, 50 leaf rust (*Lr*) resistance genes have been identified in wheat and related species (McIntosh 1995). However, the constant search for novel resistance genes is essential in order to cope with the dynamic and rapidly evolving pathogen population.

Frequently utilized resources for new resistance genes include the wild relatives of crop plants and germplasm from the center of diversity of the cultivated species. The wild grass *Aegilops tauschii* Coss. [Syns. *Aegilops squarrosa* L. and *Triticum tauschii* (Coss.) Schmal., 2n =2x=14, DD] provides a large gene pool for new sources of resistance to major wheat pests (Gill et al. 1986). The fact that *Ae. tauschii* is the D-genome donor of bread wheat allows for efficient and rapid transfer of genes into breeding populations (Gill and Raupp 1987). Six leaf rust-resistance genes, *Lr21, Lr41,* and *Lr42* (on 1D), *Lr22a* (on 2D), *Lr32* (on 3D), and *Lr43* (on 7D) have been derived from *Ae. tauschii* (Rowland and Kerber 1974; Raupp et al. 1983; Kerber 1987; Cox et al. 1994; Hussien et al. 1997).

The mechanism for durable resistance to leaf rust is poorly understood, but durability appears to be enhanced when genes are combined. For example, the combination

of *Lr16* and *Lr13* (Long et al. 1993; Samborski and Dyck 1982) or *Lr9* and *Lr24* (Long et al. 1994; McVey and Long 1993; Roelfs et al. 1992) are reported to provide reliable control. Accumulating major genes for resistance in a single genotype by conventional breeding may be laborious and time-consuming when one or more of the genes are effective against all known isolates of the pathogen. The identification of molecular markers closely linked to resistance genes can facilitate the pyramiding of major genes into a single cultivar.

We report here the mapping of the leaf rust resistance gene *Lr39* to chromosome 2DS and confirm that it is a unique resistance gene.

Materials and methods

The *T. aestivum* line TA4186 containing the gene *Lr39* is in the genetic background of the winter wheat cultivar Wichita (pedigree: TA1675/2*Wichita). The *Ae. tauschii* accession TA1675 is from the Mezetli Sount Khakardakek mountain range in Turkmenistan. Monosomic stocks of Wichita and ditelosomic stocks of Chinese Spring wheat were used for chromosome and chromosome-arm mapping of the gene, respectively. All cytogenetic stocks, germplasm lines, and *Ae. tauschii* accessions used in the experiments are maintained by the Wheat Genetics Resource Center, Department of Plant Pathology, Throckmorton Plant Sciences Center, Kansas State University, Manhattan. Screening for resistance to leaf rust and the methodology of embryo rescue were previously described (Gill et al. 1986; Gill and Raupp 1987).

For monosomic analysis, crosses of the resistant line (TA4186) were made with the seven D-genome monosomic lines of Wichita, which are susceptible to leaf rust. Monosomic F_1 plants (2n = 41) were identified cytologically and self-pollinated to produce an F_2 population. The technique used for somatic chromosome counts was that of Endo and Gill (1984). Sixty F_2 plants from each monosomic family were screened for leaf rust resistance at the seedling stage under greenhouse conditions. The plants were moved to a field nursery and re-evaluated as adults under natural infestation. The chi-square test was used to test goodness-of-fit to the expected segregation ratio of 3 resistant : 1 susceptible.

For chromosome arm mapping of *Lr39*, crosses were made with the Chinese Spring ditelosomic lines Dt2DS and Dt2DL. Ditelosomic chromosome lines are not available in cv. Wichita, but both Wichita and Chinese Spring are highly susceptible as seedlings to leaf rust. The F_1 plants were self-pollinated and 80 F_2 plants from two different F_1s were analyzed for chromosome constitution and leaf rust reaction. The chi-square test was used to test for independence of *Lr39* and the centromere.

Leaf rust screening

Genotypes included in the phenotypic and genetic investigations of the resistant line having *Lr39* included isolines of the wheat cv. Thatcher (TC) carrying leaf rust resistance genes located on chromosome 2DS of wheat, *Lr2a* (TC), *Lr2b* (TC), *Lr2c* (TC), *Lr15* (TC), and *Lr22a* (TC). Also included were lines having resistance genes previously transferred from *Ae. taushcii*, *Lr21* (TC), *Lr32* (TC), *Lr41* (KS89WGRC10), *Lr42* (KS91WGRC11), and *Lr43* (KS92WGRC16). The wheat cultivars Wichita, Century, and TAM 107 were included as checks. Seedlings were inoculated at the two-leaf stage with a series of *P. triticina* cultures, PRTUS3 (avirulence/virulence formula 1, 2a, 2b, 2c, 2d, 3b, 3c, 9, 11, 16, 17, 19, 24 / 3a, 10, 18), PRTUS7 (2a, 2b, 2c, 2d, 9, 11, 16, 17, 19, 24/1, 3a, 10), PRTUS19 (1, 2a, 2b, 2c, 2d, 9, 11, 16, 19/3a, 3b, 3c, 10, 15), PRTUS25 (2a, 2b, 2c, 2d, 9, 16, 17, 18, 19/1, 3a, 10, 24), MCDL (2a, 2c, 9, 11, 16, 17, 18, 24, 26 / 1, 3a, 3ka, 10, 11, 30), KDBL (1, 3ka, 9, 11, 16, 17, 18, 26, 30 / 2a, 2c, 3a, 10, 24), and PNMQ (2a, 11, 16, 17, 26 / 1, 2c, 3a, 3ka, 9, 10, 18, 24, 30). Infection types of seedlings were scored according to Roelfs et al. (1992). Leaf rust reactions of adult plants were recorded as either no visible infection or susceptible.

Molecular analysis

Total genomic DNA was isolated (Riede and Anderson 1996) from 15–20 progeny plants from each of the 57 F_2 monosomic families (except 2D) segregating for resistance to leaf rust. Eight microsatellite primer pairs (GWM102, GWM210, GWM249, GWM296, GWM301, GWM455, GWM484, and GWM515) known to amplify fragments that map physically and/or genetically on the short arm of chromosome 2D of wheat (Roder et al. 1998) were used for linkage mapping. These markers were evaluated for polymorphism between the leaf rust resistant germplasm (TA4186) and Wichita. The *Ae. taushii* accession TA1675, which is the donor of *Lr39*, was also included in the analysis.

The polymerase chain reaction assays (PCR) were carried out in 25-μl volumes in an MJ thermocycler (Watertown, Mass., USA) as previously described (Roder et al. 1998) with minor modifications. The reaction mixture contained 250 n*M* of each primer, 0.2 m*M* of each dNTP, 1.5 m*M* $MgCl_2$, 1 U *Taq* polymerase, and 50 ng of template DNA. Standard amplification conditions were 3 min at 94°C, 35 cycles of 1 min at 94°C, 1 min at 50°, 55°, or 60°C (as reported for the individual microsatellite by Roder et al. 1998), and 2 min at 72°C, followed by a final extension step at 72°C for 10 min. Nonpolymorphic reaction products were digested with 5 U of *Dra*I, *Hha*I, *Sca*I, and *Nha*I (Promega, Madison, Wis.) per reaction mixture according to the manufacturer instructions. Products were separated on a 2.3% Metaphor agrose gel in 1× Tris borate buffer. Gels were stained with ethidium bromide, visualized with UV light, and photographed.

Linkage analysis was performed using the MAPMAKER computer program, version 3.0 (Lander et al. 1987) using an LOD >3.0 and the Kosambi mapping function (Kosambi 1944).

Results

Chromosome location

Monosomic analysis can be used to locate genes to specific chromosomes (Morris and Sears 1967). If the gene is not located on a monosomic chromosome, F_2 plants will segregate in a disomic ratio. However, if the gene is located on a monosomic chromosome, the segregation of F_2 plants will deviate significantly from disomic inheritance. Segregation for *Lr39* in the F_2 progeny of an *Lr39*-containing wheat line (TA4186) crossed with the D-genome monosomic lines of Wichita wheat is shown in Table 1. Except for the cross with monosomic 2D, all of the F_2 populations segregated in 3 resistant : 1 susceptible ratios, confirming *Lr39* to be a single dominant gene conferring resistance to leaf rust. Segregation clearly deviated from a 3:1 ratio in the cross with monosomic 2D (Table 1), indicating that *Lr39* is located on chromosome 2D.

Telocentric mapping

Once the gene was located on chromosome 2D, telocentric gene mapping was used to map the gene to its respective chromosome arm. The line containing *Lr39* was crossed to the 2DS and 2DL ditelosomic lines.

Table 1 Segregation ratios of F_2 seedlings and adult plants derived from crosses between Wichita monosomic lines and TA4186 (*Lr39*) when tested with *P. triticina* culture PRTUS6

Monosomic chromosome	Number of seedlings		χ^2 (3:1)	Number of adult plants		χ^2 (3:1)
	Resistant	Susceptible		Resistant	Susceptible	
1D	42	14	0.00	43	12	0.29
2D	55	1	16.09[a]	52	0	17.30[a]
3D	44	15	0.00	42	15	0.05
4D	39	12	0.05	37	7	1.93
5D	38	16	0.61	37	15	0.41
6D	39	19	1.87	38	19	2.11
7D	38	17	1.03	42	10	0.92
Total (excluding 2D)	240	93	1.52	239	78	0.03

[a] Significantly different from zero at 0.01 level of probability

Table 2 Segregation of the *Lr39* gene in F_2 plants of monotelodisomic 2DS and 2DL hybrids

Somatic chromosome number	Number of plants			
	Resistant		Susceptible	
	2DS	2DL	2DS	2DL
2n = 40+tt	5	0	4	17
2n = 41+t	33	28	11	3
2n = 42	31	41	10	0
2n = 42+t	0	2	1	0
2n = 43	1	1	0	0
Total	70	72	26	20

In a telocentirc analysis, the non-critical chromosome arm is identified by the absence of the gene in question in plants with 40 + tt chromosomes. In that case, no recombination occurs between the telochromosome and the homologous arm of the normal chromosome carrying the resistance gene. Thus, all plants with two telochromosomes are susceptible (Table 2). In the critical cross, resistant plants with 40 + tt and 41 + t chromosomes are expected. The number of 40 + tt plants is low because telochromosomes are transmitted at a low frequency in pollen when competing with the entire homologous chromosome (Sears 1954). Plants with 42 chromosomes are also expected to segregate for reaction. If the gene is completely linked to the centromere, then assignment of the gene to a chromosome arm by telosomic analysis is not possible. The presence of 40 + tt resistant plants in the progeny of the cross with the 2DS ditelosomic indicated that *Lr39* is on the short arm of chromosome 2D (Table 2). The resistance gene segregated independently of the centromere ($X^2_{independence}$=0.13; P >0.99).

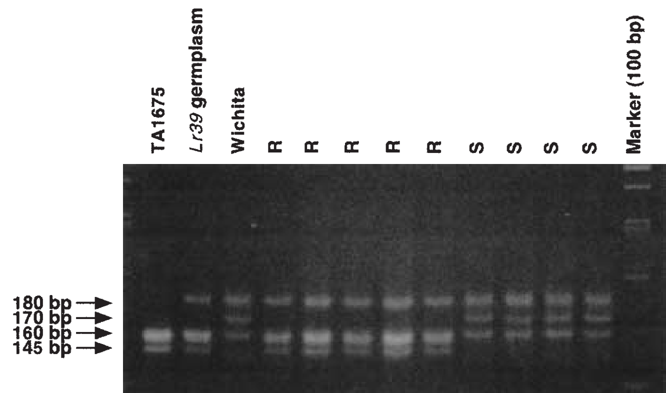

Fig. 1 Gel electrophoresis pattern revealed using microsatellite GWM296. TA1675 *Ae. tauschii* accession donor for *Lr39* gene, Wichita recurrent parent susceptible to leaf rust, R resistant derivatives the carrying *Lr39* gene, and S susceptible derivatives without the *Lr39* gene

Lr39 gene-tagging

Eight microsatellite primer pairs specific to the short arm of homeologous group 2 chromosomes (GWM102, GWM210, GWM249, GWM296, GWM301, GWM455, GWM484, and GWM515) were used to test for polymorphism between the resistant germplasm and Wichita. Of the tested primers, those detecting loci *Xgwm210* and *Xgwm296* were polymorphic. The microsatellite primer pair GWM296 amplified a polymorphic pattern displaying a DNA fragment (145 bp) specific to the resistant germplasm (Fig. 1). The band was also present in *Ae. tauschii* TA1675, the source of *Lr39* but absent in the susceptible parent Wichita (Fig. 1). Primer pair GWM210 also amplified a polymorphic DNA band of 190 bp in the resistant line but not in the susceptible line. The microsatellite GWM455 amplified non-polymorphic DNA fragments. The PCR products amplified by

Table 3 Infection types produced on seedling and adult plants of parental and control lines inoculated with *Puccinia triticina* culture PRTUS6

Line	Growth stage	
	Seedling[a]	Adult plant
Ae. tauschii (TA1675)	;	No symptom
Wichita	4	Susceptible
Chinese Spring	4	Susceptible
TA4186	2X	No symptom

[a] The seedling infection types are: ; = no uredinia but small hypersensitive necrotic or chlorotic flecks present, 2 = small to medium uredinia surrounded by necrosis or chlorosis, 4 = large uredinia without chlorosis, X = heterogeneous (random distribution of variable-sized uredinia on a single leaf)

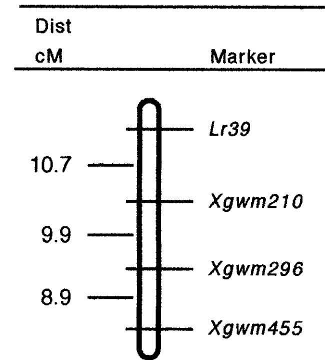

Fig. 2 The position of *Lr39* on the genetic linkage map of wheat chromosome 2DS

Table 4 Seedling infection type (IT)[a] response of germplasm containing known *Lr* genes derived from *Aegilops tauschii* when inoculated with a series of *Puccinia triticina* cultures

Line/isolate	PRTUS19	MCDL	PRTUS7	PRTUS25	PRTUS3	KDBL	PNMQ
*Lr*2a (TC)	;	;	0;	3	3	4	3
*Lr*2b (TC)	;	;	;1 C	0	1 C	4	3
*Lr*2c (TC)	;	;	1 C	4	;	4	3
*Lr*15 (TC)	4	4	4	4	4	4	4
*Lr*22a (TC)	4	4	4	4	4	4	4
*Lr*22b (TC)	4	4	4	4	4	4	NG
*Lr*21 (TC)	;1 C	2 C	;1 C	1 C	;1 C	1 C	;
*Lr*32 (TC)	1 C	2 C	;1 C	1 C	3 C	3+	;1
WGRC10 (*Lr*41)	0;	0;	0;	0	0	NG	4
WGRC11 (*Lr*42)	2 C	;1 C	0;	2 C	;C	3+	;1
WGRC16 (*Lr*43)	0	;	0	0	0;	;1 C	NG
TA 4186 (*Lr*39)	0	1 C	01 C	0	;	2X	4
Wichita	4	4	4	4	4	4	4
Century (*Lr*24)	4	1 C	;	4	;1 C	NG	3

[a] The seedling infection types are: 0 =no uredinia or other microscopic sign of infection, ; = no uredinia but small hypersensitive necrotic or chlorotic flecks present, 1 = small uredinia surrounded by necrosis, 2 = small to medium uredinia surrounded by necrosis or chlorosis, 3 = medium uredinia with or without chlorosis, 4 = large uredinia without chlorosis, X = heterogeneous (random distribution of variable-sized uredinia on a single leaf), C = more chlorosis than normal for the IT, + = uredinia somewhat larger than normal for the IT, NG = seeds not germinated

GWM455 were digested with five restriction enzymes, *Dra*I, *Msp*I, *Hha*I, *Nia*II, and *Sca*I. The enzyme *Hha*I produced a polymorphic DNA fragment of 180 bp that was present in the resistant line and the *Ae. tauschii* parental line but absent in the susceptible parent Wichita.

The three polymorphic microsatellites were previously placed on the distal portion of the short arm of group 2 chromosomes both by physical and genetic mapping (Roder et al. 1998). *Xgwm296a* and *Xgwm455* were physically mapped to the distal half of chromosome 2DS. The locus *Xgwm296b* was physically mapped on the distal 22% of 2AS and *Xgwm210* was the most distal locus mapped on 2DS by Roder et al. (1998). The remaining five microsatellite markers tested in our study had been previously mapped toward the centromere of 2DS and detected no polymorphism between the germplasm and Wichita, indicating that the *Ae. tauschii*-derived segment transferred to TA4186 may represent only a small portion of chromosome 2DS.

The polymorphic fragments were scored on a population segregating for the *Lr39* gene to find a marker closely linked to the gene. The linkage map of *Lr39* and three polymorphic 2DS markers is given in Fig. 2. Linkage analysis confirmed the results of the monosomic and ditelosomic analyses. The closest locus to *Lr39* was *Xgwm210*, which mapped 10.7 cM from it. Our data placed *Lr39* distal to *Xgwm210,* indicating that the gene is situated near the telomere of chromosome 2DS. Our unpublished results on the mapping of *Lr2* and *Lr22,* indicated that there is no polymorphism at the *Xgwm210* locus between the wheat variety Thatcher and isogenic lines possessing *Lr2a*, *Lr2b*, and *Lr22a*. Fragments polymorphic between the *Lr2a* (TC), *Lr2b* (TC), and *Lr22a* (TC) isolines and the recurrent parent were amplified by the primer pair GWM455. Our data (and that of Roder et al. 1998) locates *Xgwm455* proximal to *Xgwm210*. This suggests that *Lr2* and *Lr22* are also proximal to *Xgwm210* and are therefore different from *Lr39*.

Disease specificity

When inoculated with *P. triticina* culture PRTUS6 at the seedling stage, TA1675 displayed a lower infection type than the hexaploid resistant germplasm (Table 3). However, no leaf rust was observed when adult plants of the resistant germplasm were exposed to natural infections in the field.

When a series of *P. triticina* cultures were used to inoculate seedlings differences in infection type were observed on lines having leaf rust resistance genes located on 2DS (*Lr39*, *Lr2a*, *Lr2b*, *Lr2c*, *Lr22a*, and *Lr22b*) and those having resistance genes previously transferred to wheat from *Ae. tauschii* (*Lr21*, *Lr32, Lr41, Lr42,* and *Lr43*) (Table 4). *Lr22a* and *Lr22b* are ineffective at the seedling stage and seedlings of the Thatcher isolines having these genes were susceptible to all of the *P. triticina* cultures tested. High infections types were observed on seedlings of the *Lr2a*, *Lr2b*, and *Lr2c* isolines with two of the seven isolates tested (Table 4). *Lr2b* (TC) was resistant to *P. triticina* cultures PRTUS3 and PRTUS25, whereas *Lr2a* (TC) was susceptible to both cultures. *Lr2c* (TC) gave a high infection type when inoculated with PRTUS25. Low infection types were observed on seedlings of the germplasm having *Lr39* when inoculated with seven leaf rust cultures (Table 4). An intermediate infection type (2X) was observed when the germplasm was inoculated with the KDBL isolate, and a high infection type resulted after inoculation with PMNQ. The latter leaf rust isolate also gave a high infection type on seedlings of KS89WGRC10, which has the *Ae. taushcii*-derived gene *Lr41* located on chromosome 1D (Cox et al. 1994). Seedlings of germplasm having the *Ae. tauschii*-derived genes *Lr21*, *Lr32*, *Lr42*, and *Lr43* were resistant to PNMQ. *Lr39* should be an effective gene for the control of leaf rust when used in combination with other resistance genes.

Discussion

The new leaf rust gene transferred from *Ae. tauschii* to the common wheat cultivar Wichita was designated *Lr39*. Monosomic analysis located the gene on chromosome 2D, and telocentric and molecular mapping placed it on the short arm of 2D. These results confirm the earlier finding of Raupp et al. (1989) and contradict the finding of Cox et al. (1994) who reported that *Lr39* is allelic to *Lr21* and located on chromosome 1D. These anomalous results were recently clarified by molecular mapping studies (Huang 1999). Molecular marker analysis revealed that the rust resistance genes in germplasms KS86WGRC2 (Gill et al. 1988) and KS89WGRC7 (Gill et al. 1991) trace to the same *Ae. tauschii* accession (TA1649) and are allelic to *Lr21* (Huang 1999). Thus, the described pedigree of KS86WGRC2 is incorrect. Line TA4186 is the only source of *Lr39* and was never released as germplasm.

Two genes conferring resistance to leaf rust, *Lr2* and *Lr22*, have been mapped on the short arm of chromosome 2D. Mapping *Lr39* distal to *Xgwm210* near the telomere of 2DS suggests that the gene is at a different location than *Lr2,* because *Lr2* is linked to the centromere (McIntosh et al. 1997). The *Lr22* locus is independent of the centromere (McIntosh 1995). Our unpublished results indicate that both *Lr2* and *Lr22* are proximal to *Xgwm210*. There are at least two alleles at the *Lr22* locus, one of which (*Lr22a*) was transferred to wheat from *Ae. tauschii* (Dyck 1979). Both *Lr22a* and *Lr22b* confer resistance to leaf rust only at the adult plant stage, whereas *Lr39* exhibits both seedling and adult plant resistance. In addition, *Lr22a* was derived from *Ae. tauschii* var. *strangulata*, whereas *Lr39* was from var. *eusquarrosa*. These data support the conclusion that *Lr39* is different from *Lr2* and *Lr22*.

To date, eight different germplasm lines with *Ae. tauschii* as a source of the leaf rust resistance have been produced (Rowland and Kerber 1974; Dyck 1979; Kerber 1987; Gill et al. 1988, 1991; Cox et al. 1994). These lines are from eight different *Ae. tauschii* accessions from diverse geographical areas, and all appear to contain different *Lr* genes. *Ae. tauschii* should continue to represent a rich source of new resistance genes for wheat improvement. *Lr21* and *Lr22a* have been exploited in Canadian cultivars AC Cora and AC Minto, respectively, and *Lr41* in the U.S. cultivar Thunderbolt.

Acknowledgements We thank Duane Wilson for his excellent technical assistance. This research was supported by a special USDA grant to Wheat Genetics Resource Center. The experiments comply with the current laws of the country in which the experiments were performed.

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