Tentative Identification and Verification of Genes for Leaf Rust Resistance in Wheat Cultivars of South Dakota

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ABSTRACT

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Thirty-three winter and spring wheat cultivars and 26 single-gene wheat leaf rust (*Lr*) lines were inoculated with 21 isolates of *Puccinia recondita* and the resulting infection types were compared to detect the existence of possible resistance genes in the cultivars. To verify the presence or absence of the hypothesized gene, cultivars were crossed to lines containing single putative resistance genes and F_2 populations were inoculated with appropriate *P. recondita* isolates. Some hypothesized genes verified in the cultivars were: *Lr3* in Bennett, Brule, Lancer, Rita, and Rose; *Lr10* in Butte; *Lr1* + *Lr10* in Pavon 76; *Lr2a* + *Lr10* in Len; *Lr3* + *Lr10* in Dawn, Nell, and Wheaton; *Lr1* + *Lr2a* + *Lr10* in A99AR and Challenger; *Lr2a* + *Lr3* + *Lr10* in Alex, Erik, Guard, Marshall, Norak, Norseman, Olaf, and Oslo; *Lr3* + *Lr10* + *Lr24* in Butte 86, Centura, and Sage; *Lr3* + *Lr10* + *Lr26* in Pakistan 81 and Sarhad 83; *Lr1* + *Lr2a* + *Lr3* + *Lr10* in Shield and Punjab 83; and *Lr3* + *Lr10* + *Lr24* + *Lr26* in Siouxland.

Resistance genes for leaf rust control in a wheat cultivar can be tentatively identified or hypothesized by inoculating the cultivar with an array of *Puccinia recondita* Roberge ex Desmaz. f. sp. *tritici* (Eriks. & E. Henn.) D.M. Henderson (*Prt*) isolates and comparing the infection types (IT) with those obtained in isogenic lines.

In cereal rusts, the IT (or reaction) is the property of interaction of host and fungus. Resistance is a property of the host and pathogenicity is a property of the fungus. A low infection type indicates a phenotype with restricted production of urediniospores, whereas a high infection type indicates a phenotype with unrestricted urediniospore production (4). Reaction as a host character and pathogenicity as a parasite character both relate to infection type, which could be low or high (21). The interaction of a resistant host and an avirulent pathogen results in a low infection type, whereas all other interactions result in high infection types.

Essential requirements for inferring resistance genes in wheat cultivars by their reaction to *P. recondita* are: 1) IT data are obtained for a wheat cultivar and a line nearly isogenic for a single *Lr* resistance gene by inoculation with an array of *P. recondita* isolates; 2) the IT data of the wheat cultivar are compared with the IT data of the *Lr* line; 3) to hypothesize the presence of an *Lr* gene in a cultivar, the IT on the wheat cultivar must be lower or equal to the IT on the *Lr* line at standard temperatures, e.g., 20, 25, or 30 C, as some genes are heat-sensitive (4,5,18,19,27); 4) similar low or high IT on the *Lr* line and the cultivar suggests, but does not prove, the existence of that single gene in the cultivar; 5) a lower IT on the cultivar than on the *Lr* line suggests that more than one gene may occur in the cultivar; and 6) a higher IT on the cultivar than on the *Lr* line suggests the gene for rust resistance carried in the *Lr* line is absent from the wheat cultivar.

When the procedures outlined above lead to a hypothesis of a gene, then the hypothesis is tested by crossing the cultivar to an appropriate near-isogenic line and subjecting the F_2 population to traditional genetic analysis. If no susceptibility occurs when the F_2 is inoculated with a race that is avirulent on the single-gene parent, then that gene must be present in the cultivar. Such information has frequently supported the hypotheses generated from IT data (2,6,9,14–17,21,25, 26). These procedures were used to hypothesize and verify genes for leaf rust resistance present in a collection of wheat cultivars grown in South Dakota and in a few cultivars from Pakistan.

Genes for resistance to *P. recondita* identified in wheat cultivars of the north central states and adjoining Canada are mainly the seedling genes *Lr1, Lr2a, Lr3, Lr10, Lr24*, and *Lr26* (6,7,11,15,17,21,26) and genes *Lr12, Lrl3*, and *Lr34* for adult plant resistance either singly or in combination with seedling genes for resistance, for example, *Lr13* + *Lr16* as in cv. Columbus (23), *Lr1* + *Lr13* as in cv. Glenlea (6,19), and *Lr10* + *Lr13* + *Lr34* as in cv. Era (7,22). Perhaps the basis of most durable resistance in leaf rust lies in the use of a combination of one or more effective seedling genes along with some genes for adult plant resistance such as *Lr12* + *Lr13* (8,22). Virulence on the seedling genes *Lr1, Lr2a* and its alleles, *Lr3* and its alleles, and *Lr10* in *P. recondita* collections from north central states has been high and has been increasing on *Lr24* and *Lr26* (11).

The objectives of this study were to: 1) tentatively identify the *Lr* genes in selected wheat cultivars and breeding lines and further verify these hypotheses and 2) demonstrate that comparing IT data is a reliable rapid screening technique for identification of genes for rust resistance. A preliminary report has been published (20).

MATERIALS AND METHODS

Seed of spring and winter wheat cultivars was supplied by F. A. Cholick and J. L. Gellner of South Dakota State University, Brookings. Single-gene leaf rust (*Lr*) lines in a cv. Thatcher background were obtained from Glen Statler of North Dakota State University, Fargo. Seed of *Lr* lines in cv. Wichita winter backgrounds and 21 collections of *Prt* from the United States (designated by code by David Long of the Cereal Rust Laboratory, St. Paul, MN) (10) were provided by Lewis E. Browder of Kansas State University, Manhattan. Powdery mildew infections in the greenhouse were avoided by treating seed with 51.3% ethirimol (Milstem), 0.1 ml g^{-1}, mixed with an equal quantity of methylcellulose before planting. The soil mix of peat: sterilized soil:washed sand (2:1:1, w/w, pH 6.5) was fertilized with 5 g per pot of granulated Osmocote (14-14-14, N-P-K) when wheat seedlings were 8–10 days old.

Previously described techniques were followed for increase and multiplication of leaf rust isolates (1). Each isolate of *P. recondita* was increased in isolation on the susceptible cultivar Thatcher in open-topped cylindrical plastic chimneys 12 cm in diameter × 36 cm in height. The isolation cylinders were placed around seedlings growing in 8 × 9 cm diameter clay pots. Inoculum of each rust isolate was collected on aluminum foil, shaken into size 00 gelatin capsules,

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dehydrated for 2 hr by placing on $CaCl_2$ pellets in small glass vials, transferred to glass tubing 4 mm in diameter, and stored in aluminum canisters held at −196 C in liquid nitrogen for future use. A necessary prerequisite for recording correct IT data in this technique is aseptic transfer of inoculum to the glass tubing, accomplished by washing hands with diluted benzalkonium (Zephiran) chloride solution at each transfer and avoiding contamination between isolates.

Tester sets comprising 23 spring and 10 winter wheat cultivars along with seed of *Lr* lines *Lr1, Lr2a, LrB, Lr2c, Lr3, Lr3ka, Lr3b, Lr3c, Lr9, Lr10, Lr11, Lr15, Lr16, Lr17, Lr18, Lr19, Lr21, Lr23, Lr24, Lr25, Lr26, Lr27, Lr28, Lr29, Lr30+T,* and *LrEX* were grown under natural daylight in the greenhouse at 20 ± 2 C by supplementing with 12 hr of fluorescent light at a bench intensity of approximately 400–475 $\mu E \cdot m^{-2} \cdot s^{-1}$. Plants 4–5 days old were drenched with approximately 40 mg L^{-1} of an aqueous solution of the growth retardant maleic acid hydrazide.

Plants were inoculated by mixing 0.5 mg of urediniospores in 5 ml of a light petroleum inoculating oil (Soltrol). Inoculated plants were then lightly sprayed with a 1% aqueous solution of Tween 20, incubated in a dew chamber at 100% RH for 24 hr at 20 C, fan-dried, and placed on the greenhouse benches at 20 ± 2 C for symptom development. Data were recorded 10–12 days later, or after pustules erupted on susceptible Thatcher, following the scale developed by Mains and Jackson for leaf rust (12). Infection types 0–2 were rated resistant, 23 and 32 (often environmentally unstable [4,5,18,19,27]) intermediate, and 3–4 susceptible. A score containing two or more digits (e.g., 12, 23, 0;1) indicated that more than one pustule type occurred on the plants. Such scores are commonly encountered from IT data generated in rust rating systems (5,8,10, 15,25,27). Inoculations were repeated at least two times for each isolate of *Prt*.

Cultivars were subsequently crossed to *Lr* lines carrying the specific genes being tested. Failure of F_2 populations from such crosses to segregate upon inoculation with *Prt* isolates avirulent on those genes verified the presence of the hypothesized gene(s).

RESULTS AND DISCUSSION

Seedling reactions of wheat cultivars and near-isogenic lines *Lr1, Lr2a, Lr2c, Lr3, Lr3ka, Lr9, Lr10, Lr11, Lr16, Lr17, Lr24, Lr26,*, and *Lr30* (10) for reaction to *Prt* isolates are presented in Tables 1–4. Other genes were not evaluated in this study because: 1) no isolate was virulent on *Lr19* or *Lr25*; 2) few were virulent on *Lr11, Lr16, Lr17, Lr18, Lr21,* or*Lr29*; and 3) nearly all were virulent on *Lr15, Lr23, Lr28, Lr30+T,* and *LrEX*. Resistance genes in wheat cultivars Prospect, Sharp, and Stoa could not be hypothesized from the IT data, since no isolate was virulent on them.

The following illustrates how we used IT data in Tables 1–4 to hypothesize resistance genotypes. A hypothesis was formulated on the presence of genes *Lr3* and *Lr10* for resistance in the wheat cultivar Wheaton. Based on comparison of IT data for Wheaton (Table 1) with line *Lr10* (Table 4), gene *Lr10* was identified in Wheaton. The fact that Wheaton was not susceptible to any isolate avirulent on *Lr10*, for example, *Prt* isolates SCD, TBD, and TBB, is the evidence that Wheaton does indeed contain *Lr10*. The susceptible reaction of Wheaton to isolates TCC-10, KBB-10, and TBK-10 as well as to several others (Table 1) that were also virulent on *Lr10* (Table 4) provided support for the existence of *Lr10* in Wheaton. Furthermore, comparison of the reaction of Wheaton with *Lr10* reveals several points of disagreement, i.e., Wheaton was resistant to isolates BBB-10, TBC-10, SCD, and TBJ-10 (Table 1), but these were virulent on *Lr10* (Table 4). This indicates that if Wheaton has *Lr10*, it must have another gene. This must be *Lr3*, since isolates BBB-10 and SCD of *Prt* were also avirulent on *Lr3*. A susceptible reaction on Wheaton when chal-

Table 1. Seedling reactions of spring wheat cultivars to *Puccinia recondita* in South Dakota

	Cultivar[b]																		
Prt code[a]	A9	AL	AP	BU	B86	CH	ER	GU	LE	MA	NRK	NRS	OL	OS	PR	SH	SHI	ST	WH
TCC-10	4[c]	;1	4	4	;1	4	21	4	4	4	4	4	4	;1	;	;1	4	;	4
BBB-10	;	;	;	32	;1	;	;	;	0;	;	;	;	;	;	;	;	;	;	;
TBC-10	;	;1	12	3	;1	12	;1	;	;	;	;1	;	;	;	;	;	;1	;	;1
KBB-10	;	;1	;	4	;	;	;	4	4	;	;1	4	;1	;1	;	;	;	;	4
SCD	;	;1	;1	;12	;	;	0;	;	;1	;1	0;	;1	;1	;1	;	;12	;1	;	;1
TBK-10	4	;1	4	3	;1	4	;1	32	23	;1	0;	;	;1	;	;	;1	;1	;	4
MBB-10	;	;	21	4	;1	;	;	;	1	12	;12	;	;12	23	;1	21	;12	;	;12
TBD	;12	;1	;1	;12	;1	;1	;12	;1	;12	;12	;12	;12	;12	0;	;	;1	;12	0;	;12
SBD-10	4	;	32	4	;1	32	;1	;1	4	;1	;1	;	;1	;	;	;	;	;	;1
KFM-10	;	32	;	4	12	;	23	4	4	4	4	4	4	4	;	;1	;	;	4
TBB	;	;1	;1	;1	;1	12	;	;	;	0;	;1	;	;1	;1	;	;12	;1	;	;1
KDB-10	;	12	;	3	21	;	21	4	4	3	3	3	3	32	;	;	;	;1	4
TBJ-10	4	;1	4	4	;	4	;	3	12	;12	4	;1	;	4	;	;1	;1	;	32
PLR-10	;1	;	;	32	;	;12	;1	;	;1	;1	;12	;	;1	;1	;	;	;	;	32
CDM-10	;	;	;	4	4	;	;	;	;	;	;1	;	;	;12	;	;	;	;	4
TDB-10	4	;	4	3	;12	3	;	;	;	;	3	;	;	0;	;	;1	;1	0;	4
TCT-10	4	12	32	4	;	3	4	4	;12	32	21	;1	;1	3	;	;1	;12	;	4
TDR-10	4	;	4	4	4	3	;1	;	23	;1	4	;	;	3	;	;1	4	12	4
TFT-10	4	;	4	4	4	4	;	4	;1	;	32	;	;1	32	;	12	4	23	4
TBR-10	4	12	4	3	;	3	4	3	12	3	3	21	3	4	;	1	4	0;	;12
CBB-10	;	;	;	3	;	0;	0;	;	;	;	;	;	;	0;	;	0;	;	0;	0;
Probable *Lr* genes	*1 2a 10*	*2a 3 10*	*1 2a 10*	*10*	*3 10 24*	*1 2a 10*	*2a 3 10*	*2a 3 10*	*2a 10*	*2a 3 10*	*2a 3 10*	*2a 3 10*	*2a 3 10*	*2a 3 10*	?	?	*1 2a 3 10*	?	*3 10*

[a]Long and Kolmer (10).

[b]A9 = A99AR, AL = Alex, AP = Apex 83, BU = Butte, B86 = Butte 86, CH = Challenger, ER = Erik, GU = Guard, LE = Len, MA = Marshall, NRK = Norak, NRS = Norseman, OL = Olaf, OS = Oslo, PR = Prospect, SH = Sharp, SHI = Shield, ST = Stoa, WH = Wheaton.

[c]Infection type based on leaf rust scale (12), where 0 = no visible signs, ; = no uredinia but hypersensitive necrotic or chlorotic flecks, 1 = small pustule in necrotic area, 2 = moderate-sized uredinium in necrotic or chlorotic spot, 3 = uredinia often with chlorotic borders, 4 = large pustules and no chlorosis or necrosis. Two or more digits = more than one infection type, ? = *Lr* genes not identified.

lenged by isolate KBB-10 avirulent on *Lr1, Lr9, Lr16, Lr24, Lr26, Lr3ka, Lr11*, and *Lr17* was evidence that Wheaton probably does not contain any of these genes. Furthermore, since Wheaton gave an IT of 4 against isolate CDM-10 (Table 1), which was avirulent on *Lr2a* and *Lr2c*, it probably does not carry these genes either.

Genes for resistance to *Prt* were hypothesized in widely grown wheat cultivars of South Dakota (Tables 1 and 3) and four spring wheat cultivars grown in Pakistan (Table 2). Information on the presence of genes previously identified in these cultivars or as suggested from an inspection of donor parents in the pedigree of such cultivars was also helpful in interpretation of results (Tables 5 and 6).

Wheat cultivars with a single gene were Bennett, Brule, Lancer, Rita, and Rose with *Lr3* and Butte and Wheaton with *Lr10*. Cultivars with two genes were Pavon 76 with *Lr1* + *Lr10*; Len with *Lr2a* + *Lr10*; and Dawn, Nell, and Wheaton with *Lr3* + *Lr10*. Cultivars with three genes were A99AR, Apex 83, and Challenger with *Lr1* + *Lr2a* + *Lr10*; Alex, Erik, Guard, Marshall, Norak, Norseman, Olaf, and Oslo with *Lr2a* + *Lr3* + *Lr10*; Butte 86, Centura, and Sage with *Lr3* + *Lr10* + *Lr24*; and Pakistan 81 and Sarhad 83 with *Lr3* + *Lr10* + *Lr26*. Genes *Lr1* + *Lr2a* + *Lr3* + *Lr10* were tentatively identified in Shield and Punjab 83, and genes *Lr3* + *Lr10* + *Lr24* + *Lr26* were hypothesized in Siouxland.

Winter wheat cultivars grown in South Dakota, i.e, Bennett, Brule, Lancer, Rita, and Rose, carried a common seedling gene, *Lr3* (Table 3). Browder (3) reported *Lr3* from Pawnee, Ponca, Warrior, and Mediterranean, used in parentage of most of these cultivars (Table 6). Modawi et al (17) also identified *Lr3* from Bennett, and our results support this.

We hypothesized *Lr10* from spring wheat cultivars Butte and Wheaton (Table 1). This gene was previously postulated in Butte (3,21,26) and in Wheaton (15). Era was used as a parent in Wheaton (Table 5), from which *Lr10* was reported (7,13). Our data also support these findings, that *Lr10* is indeed present in Butte and Wheaton. Parents Crim and Bui-gallo could be donors for *Lr3* in Wheaton (Table 5). Singh and Rajaram (25) postulated *Lr1* and *Lr10* from Pavon 76. We also hypothesize the presence of *Lr1* and *Lr10* in this cultivar and support their findings. We found *Lr2a* and *Lr10* in Len (Table 1). Parents Lee, Justin, and Mida were used in the pedigree of Len (Table 5) and are probable carriers of *Lr2a* and *Lr10*. Our hypotheses on the presence of these two genes in Len also support data of McVey (15) and Statler (26).

We tentatively identified *Lr3* and *Lr10* in winter wheat cultivars Dawn and Nell (Table 3). In Nell, *Lr3* probably came from donor parent Scout, a carrier of *Lr3* (Table 6) (17). *Lr3* was also donated by parents Warrior and Mediterranean (Table 6) in the pedigree of Dawn (3,13). Dawn also has Parker, a carrier of *Lr10*, according to McIntosh (13), in its pedigree.

The hypotheses that spring wheat cultivar A99AR, released by Weathermaster in 1982, carried genes *Lr1* + *Lr2a* + *Lr10* is supported by the fact that parents Zaragoza and Glenlea, which contain *Lr1* (6,13,19,25), were used in the A99AR cross (Table 5). Several CIMMYT cultivars, including Zaragoza and Glenlea, have also been reported to carry *Lr10* (13,22,25). We hypothesized *Lr1* + *Lr2a* + *Lr10* in Challenger, released by Western Plant Breeders in 1983 (Table 5); information is lacking on the origin of the Challenger cross. We also hypothesized that Apex 83, believed to be a male sterile recombinant line and released by Seedtech in 1983, carried *Lr1*

Table 2. Seedling reactions of CIMMYT[a] wheat cultivars to *Puccinia recondita* in Pakistan

	Cultivar[c]			
Prt code[b]	PAK	PAV	PU	SA
TCC-10	4[d]	4	4	4
BBB-10	;	;	;	;1
TBC-10	;1	;	;	;1
KBB-10	;12	;	;	;
SCD	;1	0;	0;	0;
TBK-10	;1	4	;	;
MBB-10	;	3	;	;
TBD	;12	;1	;12	;12
SBD-10	;1	3	;1	;1
KFM-10	23	;	;	4
TBB	;1	;12	;	;
KDB-10	;	;	;	12
TBJ-10	;1	4	;12	;1
PLR-10	;	3	;	;
CDM-10	;12	;	;	;
TDB-10	;1	3	;1	;1
TCT-10	4	3	4	4
TDR-10	;1	3	0;	;12
TFT-10	3	3	3	3
TBR-10	;12	23	23	;12
CBB-10	;12	;	;	;12
Lr genes identified	*3* *10* *26*	*1* *10*	*1* *2a* *3* *10*	*3* *10* *26*

[a]Centro Internacional de Mejoramiento de Maiz y Trigo, Mexico City.
[b]Long and Kolmer (10).
[c]PAK = Pakistan 81, PAV = Pavon 76, PU = Punjab 83, SA = Sarhad 83.
[d]Infection type based on leaf rust scale (12), where 0 = no visible signs, ; = no uredinia but hypersensitive necrotic or chlorotic flecks, 1 = small pustule in necrotic area, 2 = moderate-sized uredinium in necrotic or chlorotic spot, 3 = uredinia often with chlorotic borders, 4 = large pustules and no chlorosis or necrosis. Two or more digits = more than one infection type.

Table 3. Seedling reactions of winter wheat cultivars to *Puccinia recondita* in South Dakota

	Cultivar[b]									
Prt code[a]	BE	BR	CE	DA	LA	NE	RI	RO	SA	SI
TCC-10	4[c]	4	;1	23	4	4	4	4	;1	;1
BBB-10	;1	;1	;1	;1	;1	;1	;1	;1	;1	;
TBC-10	3	3	;	;1	4	;1	4	3	;1	;
KBB-10	4	;12	;	3	4	4	4	4	;	;
SCD	;1	;1	;	;1	;1	;1	;1	;1	;	;
TBK-10	4	4	;1	23	4	23	4	4	;1	;1
MBB-10	4	4	;	4	4	4	3	4	;	;
TBD	3	3	;1	;1	23	;12	23	23	;1	;1
SBD-10	;1	0;	;	;	;	;	;1	;	;	;
KFM-10	4	4	;1	4	4	4	4	4	;	;
TBB	4	4	;1	;12	4	;12	4	3	;	;
KDB-10	4	3	;	3	3	3	3	3	;	;
TBJ-10	4	3	;1	3	4	4	4	4	;1	;1
PLR-10	4	4	;1	4	4	4	4	4	4	;
CDM-10	4	4	4	4	4	4	4	4	4	;12
TDB-10	3	3	3	4	4	3	3	3	3	;
TCT-10	4	4	;	3	4	4	4	4	;	;
TDR-10	4	4	3	4	4	4	4	4	3	;1
TFT-10	4	4	4	4	4	4	4	4	4	4
TBR-10	4	4	;1	4	4	4	4	4	;1	;
CBB-10	4	3	;1	3	4	4	4	4	;1	;
Lr genes identified	*3*	*3*	*3* *10* *24*	*3* *10*	*3*	*3* *10*	*3*	*3*	*3* *10* *24*	*3* *10* *24* *26*

[a]Long and Kolmer (10).
[b]BE = Bennett, BR = Brule, CE = Centura, DA = Dawn, LA = Lancer, NE = Nell, RI = Rita, RO = Rose, SA = Sage, SI = Siouxland.
[c]Infection type based on leaf rust scale (12), where 0 = no visible signs, ; = no uredinia but hypersensitive necrotic or chlorotic flecks, 1 = small pustule in necrotic area, 2 = moderate-sized uredinium in necrotic or chlorotic spot, 3 = uredinia often with chlorotic borders, 4 = large pustules and no chlorosis or necrosis. Two or more digits = more than one infection type.

Table 4. Seedling reactions of *Lr* (isogenic) lines to *Puccinia recondita*

	Set A[b]					Set B				Set C			
***Prt* code**[a]	***1***	***2a***	***2c***	***3***	***10***	***9***	***16***	***24***	***26***	***3ka***	***11***	***17***	***30***
TCC-10	4[c]	4	4	4	4	;	;1	;1	4	2	23	23	4
BBB-10	;	;1	;1	;1	4	;	23	;1	12	;12	23	23	13
TBC-10	4	4	4	4	4	;	;	;1	;12	21	21	21	4
KBB-10	0;	4	4	4	4	;	12	;1	;12	21	21	23	4
SCD	4	4	4	;1	;12	0;	0;	;	4	1	21	4	;1
TBK-10	4	4	4	4	4	;1	21	;1	;1	21	4	4	4
MBB-10	4	12	21	4	4	;	23	;	;	21	2	2	12
TBD	4	4	4	4	;12	;	12	;1	21	21	21	4	21
SBD-10	4	4	4	;1	4	;	;12	;1	2	;1	21	4	21
KFM-10	;	4	4	4	4	;	12	4	4	4	21	21	4
TBB	4	4	4	4	12	;	12	;1	;12	12	12	12	21
KDB-10	;	4	4	4	4	;	;1	4	12	21	21	12	21
TBJ-10	4	4	4	4	4	;	12	;1	;1	12	4	4	21
PLR-10	4	;12	4	4	4	4	21	;1	;1	4	4	21	4
CDM-10	;	;12	12	4	4	;	12	4	;12	4	23	21	4
TDM-10	4	4	4	4	4	;	23	4	;12	12	12	12	23
TCT-10	4	4	4	4	4	;	12	;	4	4	4	4	4
TDR-10	4	4	4	4	4	;	23	4	;12	4	32	12	4
TFT-10	4	4	4	4	4	;1	23	4	4	4	4	4	4
TBR-10	4	4	4	4	4	;	23	;1	;12	4	4	23	4
CBB-10	;	;	;	4	4	;	;1	;1	;12	1	1	1	12

[a] Long and Kolmer (10).
[b] Sets A, B, and C are leaf rust differentials used in *Prt* race nomenclature (10).
[c] Infection type based on leaf rust scale (12), where 0 = no visible signs, ; = no uredinia but hypersensitive necrotic or chlorotic flecks, 1 = small pustule in necrotic area, 2 = moderate-sized uredinium in necrotic or chlorotic spot, 3 = uredinia often with chlorotic borders, 4 = large pustules and no chlorosis or necrosis. Two or more digits = more than one infection type.

Table 5. *Lr* genes suggested from inspection of parentages of spring wheat cultivars

Cultivar	Origin[a]	Year of release	Parentages	Donor parents of *Lr* genes[b]	References
A99AR	WM	1982	Glenlea/Zaragoza	Glenlea, *Lr1*	6,13,19,25
				Zaragoza, *Lr10*	13,25
Alex (CI 17910)	ND	1981	ND 500 = SD 507/ND 496 ND 496 (= Olaf 'S'/Wald. /Justin)	Olaf/Waldron, *Lr2a* + *Lr10*	3,13,21,26
Apex 83	ST	1983	Male ster. recomb. sel.	Not known	. . .
Butte	ND	1977	ND 480/Polk/Wisc. 261	Justin, *Lr10*	21,26
Butte 86	ND	1986	Butte*2/3/ND 551//	Butte, *Lr10*	3,13,15,26
			Butte*/ND 507	Agent, *Lr24*	2,3
Challenger	WPB	1983	Not known	Not known	. . .
Erik (PI 476849)	NAPB	1982	Kitt//Waldron/Era	Kitt, *Lr3* + *Lr10*	21
				Waldron, *Lr2a* + *Lr10*	3,21,26
				Era, *Lr10*	3,7,21,26
Guard	SD	1983	Eureka/Dawn	Dawn, *Lr3* + *Lr10*	17
				Era and Parker, *Lr10*	3,13,17
				Dawn, *Lr3* from Mediterranean,	3,13,17
				Lr10 from Parker	13,17
Len	ND	1979	Lee, Justin, Mida	Justin, *Lr10*	13,21
				Len, *Lr2a* + *Lr10*	15,26
Marshall	MN	1982	MN 70170 R = Era (CI 13986) /Waldron (CI 13958)	Era/Waldron, *Lr2a* + *Lr10*	3,13,15,26
Norak	RH	1984	Era × Tobari × Cno × Protor	Era, *Lr2a* + *Lr10*	3,7,15,20,21
Norseman	NAPB	1984	HS 78-1139 (Comp. X)	Not known	. . .
Olaf	ND	1973	Justin*/3/ND 259/ Conley/5/Waldron Conley/ND 122/4/Justin	Justin/Waldron, *Lr2a* + *Lr10*	3,13,15,17,26
Oslo (CI 17901)	NAPB	1981	Son. 64/Yaq 50E/Guahatole	Not known	. . .
Prospect (PI 491568)	SD	1988	Butte/Co 53427//WS 1809	Butte/1809, *Lr10* ?	3,15,26
				Co 53427, ?	
Sharp	SD	1990	=SD 2980 Butte//MN 7125	Butte, *Lr10* ?	3,15,26
				MN 7125, ?	
Shield (PI 491570)	SD	1987	Coteau/Dawn	Coteau, *Lr10*	26
				Dawn, *Lr3* + *Lr10*	3,13,15
Stoa	ND	1984	ND 527/Coteau sib/Era	Could be *Lr1* + *Lr10* + *Lr2a* + ?	3,13,15,26
				/3/Inia/4/Cno/Elgan/Son. 64	
Wheaton (PI 469271)	MN	1983	Crim/2*Era//Bui-gallo	Era, *Lr10*	3,13,15,26

[a] WM = Weathermaster, ND = North Dakota, ST = Seedtech, WPB = Western Plant Breeders, NAPB = North American Plant Breeders, SD = South Dakota, MN = Minnesota, RH = Rohm & Haas.
[b] ? = *Lr* genes not identified.

Table 6. *Lr* genes suggested from inspection of parentages of CIMMYT[a] and winter wheat cultivars

Cultivar	Origin[b]	Year of release	Parentages	Donor parents of *Lr* genes	References
CIMMYT					
Punjab 83	Pakistan	1983	Ore F_1 158/FDL/ Mef"s"/2*Tiba/ Coc. CM 37987	Not known, *Lr1*	13
Pakistan 81	Pakistan	1981	Veery#5 KVZ/Buho "s"//Kal/BB CM3327-F-15M-500Y-0M	Kavkaz, *Lr3* + *Lr10* + *Lr26*	13,18,25
Pavon 76	Pakistan	1976	VCM//CNO"s"/7C/3 /Kal/BB CM8399-D-4M-3Y-1M-1Y-1M-OY	Vicam 71, *Lr1*	13,25
Sarhad 83	Pakistan	1983	=Bob White AU//Kal/BB/3/ Wop"s"CM 33203	Blue Bird, *Lr10* Wop"s"= Kavkaz, *Lr3* + *Lr10*	25 13
Winter wheats					
Bennett	NE	1978	Scout/3/Quivera /Tenmarq/Marquillo/ Oro/4/Homestead	Scout, *Lr3*	17
Brule	NE	1981	NE 68723//NE 68719/Gage	Ponca/Mediterranean, *Lr3*	3,13,17
Centura	NE	1984	Warrior*5/Agent/NE 68457 /3/Centurk 78	Warrior, *Lr3* Agent, *Lr24*	3,17 3,13,17
Dawn	CO	1980	II 21031/Trapper/ CO 652363 (= Warrior/2/ Kenya 58/New Thatch/2* Cheyenne/Tenmark/Medit. Hope/3/Parker)	Warrior/Mediterranean, *Lr3* Parker, *Lr10*	3,13,17 3,15,17
Lancer (CI 13547)	NE	1963	Sel. Turkey-Cheyenne × Hope × Cheyenne	Cheyenne, *Lr3*	17
Nell (CI 17803)	SD	1980	Scout sel./Capitan Capitan = Pawnee/Chey. /3/Pawnee/Ken. 58//Chey.	Parents in Nell cross, *Lr3* Kenya 58, *Lr10*	3,13,15 17
Rita	SD	1980	Ponca; Mediterranean	Both parents, *Lr3*	3,13,15
Rose (CI 17795) = SD 7279	SD	1981	Pawnee; Cheyenne	Pawnee/Cheyenne, *Lr3*	3,13,15
Sage (CI 17277)	KA	1973	Agent/4*Scout	Scout, *Lr3*; Agent, *Lr24*	2,3,13,15
Siouxland (PI 483469)	NE	1984	Warrior*5/Agent//Kavkaz to Warrior*5/Agent	Warrior/Kavkaz, *Lr3*; Agent, *Lr24*; Kavkaz, *Lr26*	3,13,15 3,13,18,25

[a]Centro Internacional de Mejoramiento de Maiz y Trigo, Mexico City.
[b]NE = Nebraska, CO = Colorado, SD = South Dakota, KA = Kansas.

Table 7. Seedling reactions to four *Prt* isolates in F_2 plants of winter wheat cultivars crossed to Wichita lines nearly isogenic for various *Lr* genes

Cross	*Prt* code[a]	F_1 plants	F_2 plants[b] R	F_2 plants[b] S	*Lr* gene verified
Bennett × *Lr3*	BBB-10	16	940	0	*Lr3*
Brule × *Lr3*	BBB-10	10	219	0	*Lr3*
Centura × *Lr3*	BBB-10	18	903	0	*Lr3*
Centura × *Lr24*	TCC-10	15	655	0	*Lr24*
Dawn × *Lr3*	BBB-10	15	638	0	*Lr3*
Lancer × *Lr3*	BBB-10	17	947	0	*Lr3*
Nell × *Lr3*	BBB-10	11	629	0	*Lr3*
Nell × *Lr10*	TBD	13	691	0	*Lr10*
Rita × *Lr3*	BBB-10	14	633	0	*Lr3*
Rose × *Lr3*	BBB-10	19	1,045	0	*Lr3*
Sage × *Lr3*	BBB-10	12	660	0	*Lr3*
Sage × *Lr24*	TCC-10	10	230	0	*Lr24*
Siouxland × *Lr3*	BBB-10	14	644	0	*Lr3*
Siouxland × *Lr24*	TCC-10	16	766	0	*Lr24*
Siouxland × *Lr26*	TBK-10	19	1,088	0	*Lr26*

[a]Long and Kolmer (10).
[b]Resistant and susceptible reactions (12).

+ *Lr2a* + *Lr10*.

The spring wheat cultivars Alex, Erik, Guard, Marshall, Norak, Norseman, Olaf, and Oslo are hypothesized to carry genes in common, i.e., *Lr2a* + *Lr3* + *Lr10* (Table 1). *Lr2a* and *Lr10* have been previously reported in several of the cultivars mentioned above (3,7,15,21,26). Dawn and Eureka in Guard's pedigree probably serve as donors of *Lr3* and *Lr10* (Table 5). Our data support previous reports on the existence of these genes in the above-mentioned cultivars (3,13,15,17,26)). We also hypothesized genes *Lr3* + *Lr10* + *Lr24* in Butte 86, Centura, and Sage (Tables 1 and 3). *Lr10* was probably donated by Butte and *Lr24*, by Agent in Butte 86 (Table 5). Our hypotheses also supported previous information on the occurrence of these genes in Butte 86 (3,13,15,26). The hypothesis of common genes *Lr3, Lr10*, and *Lr24* in Centura and Sage stands verified (3,17).

Spring wheat cultivars from Pakistan via CIMMYT that carried common genes *Lr3* + *Lr10* + *Lr26* were Pakistan 81 (= Veery No. 5, CIMMYT) and Sarhad 83 (= Bob White, CIMMYT). These Veery lines have their origin in Kavkaz and Blue Bird, the common carriers of *Lr3* + *Lr10* + *Lr26* (Table 6). Our hypotheses also supported previous conclusions on the existence of these genes in the CIMMYT lines (3,13,18,25). *Lr1* + *Lr2a* + *Lr3* + *Lr10* were tentatively identified in Shield and Punjab 83 (Tables 1 and 2). Shield is a sister line of Guard and was released by South Dakota State University in 1987, with parents Dawn the donor of *Lr3* and *Lr10* and Coteau the probable donor of *Lr2a* and/or *Lr10* (Table 5) (26).

Finally, the hypotheses of *Lr24* in Siouxland, in addition to *Lr3*, plus *Lr10* and *Lr26* stand verified (Table 3). *Lr3* and *Lr26* in Siouxland were derived from parent Kavkaz, a common carrier of *Lr3* and *Lr26* (13,18,24), used in the pedigree

Table 8. Seedling reactions to five *Prt* isolates in F_2 plants of spring wheat cultivars crossed to Thatcher lines nearly isogenic for various *Lr* genes

Cross	*Prt* code[a]	F_1 plants	F_2 plants[b] R	F_2 plants[b] S	*Lr* gene verified
A99AR × *Lr1*	CBB-10	14	656	0	*Lr1*
Alex × *Lr2a*	BBB-10	10	411	0	*Lr2a*
Alex × *Lr10*	TBD	11	626	0	*Lr10*
Apex 83 × *Lr1*	CBB-10	10	419	0	*Lr1*
Butte × *Lr10*	TBD	11	637	0	*Lr10*
Butte 86 × *Lr10*	TBD	13	733	0	*Lr10*
Butte 86 × *Lr24*	TBC-10	12	630	0	*Lr24*
Challenger × *Lr1*	CBB-10	19	1,007	0	*Lr1*
Erik × *Lr2a*	BBB-10	15	660	0	*Lr2a*
Erik × *Lr10*	TBD	12	627	0	*Lr10*
Guard × *Lr2a*	CDM-10	18	911	0	*Lr2a*
Len × *Lr2a*	BBB-10	7	320	0	*Lr2a*
Len × *Lr10*	TBD	15	678	0	*Lr10*
Marshall × *Lr2a*	BBB-10	16	835	0	*Lr2a*
Marshall × *Lr10*	TBD	8	407	0	*Lr10*
Norak × *Lr10*	TBD	18	1,056	0	*Lr10*
Norseman × *Lr10*	TBD	9	435	0	*Lr10*
Olaf × *Lr2a*	BBB-10	13	487	0	*Lr2a*
Olaf × *Lr10*	TBD	12	675	0	*Lr10*
Oslo × *Lr10*	TBD	11	679	0	*Lr10*
Shield × *Lr2a*	CDM-10	16	830	0	*Lr2a*
Wheaton × *Lr10*	TBD	17	900	0	*Lr10*
CIMMYT lines					
Pakistan 81 × *Lr26*	TBK-10	7	236	0	*Lr26*
Pavon 76 × *Lr1*	CBB-10	12	328	0	*Lr1*
Punjab 83 × *Lr26*	CBB-10	10	413	0	*Lr26*
Sarhad 83 × *Lr26*	TBK-10	7	236	0	*Lr26*

[a]Long and Kolmer (10).
[b]Resistant and susceptible reactions (12).

of Siouxland (Table 6). Long et al (11), on the basis of previous information (13,17,24), also reported *Lr24* and *Lr26* in Siouxland.

In the first phase of our study, *Lr* genes were hypothesized in wheat cultivars on the basis of the IT data in Tables 1–4. Although we hypothesized *Lr3* and *Lr10* from several cultivars, we felt there was a need for more isolates of *Prt* avirulent on these genes to precisely ascertain their explicit expression in the cultivars studied. We felt that under such situations, this technique could create problems by overestimating the number of genes hypothesized. To avoid overestimation, we subsequently verified the existence of many of these genes, including *Lr3* and *Lr10*, because of failure of F_2 populations to segregate from crosses of cultivars with the hypothesized genes to *Lr* lines *Lr1*, *Lr2a*, *Lr3*, *Lr10*, *Lr24*, and *Lr26* after inoculation with appropriate leaf rust isolates. Because of seed increase problems, some cultivars were not crossed with all lines carrying the tentatively identified seedling genes. Data for the crosses that produced enough F_2 plants are presented in Tables 7 and 8.

Seedling genes alone are not the only sources conferring resistance to the cultivars studied. Many of these cultivars have *Lr12*, *Lr13*, *Lr22a*, and *Lr34* conferring adult plant resistance, either singly or in various combinations of seedling and adult plant resistance (6,7,11,13,21,22). Roelfs (22) mentioned that any combination of adult gene(s) listed above, coupled with resistance supplemented by seedling genes, is prone to provide the most durable resistance to wheat leaf rust in the field. Resistance of many U.S. cultivars grown in the north central states and Canada is probably operating under such a control.

The genetic test of confirmation conducted in this study demonstrates that comparing IT data would not only continue to be a reliable tool at wheat breeding centers throughout the world for rapid identification of gene(s) for resistance to rusts but would also facilitate early elimination of ineffective genes, thereby more efficiently providing genetic sources of resistance for disease control.

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