Seedling and Slow Rusting Resistance to Leaf Rust in Chinese Wheat Cultivars

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ABSTRACT

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Identification of resistance genes is important for developing leaf rust resistant wheat (*Triticum aestivum*) cultivars. A total of 102 Chinese winter wheat cultivars and advanced lines were inoculated with 24 pathotypes of *Puccinia triticina* for postulation of leaf rust resistance genes effective at the seedling stage. These genotypes were also planted in the field for characterization of slow rusting responses to leaf rust in the 2006–07 and 2007–08 cropping seasons. Fourteen leaf rust resistance genes—*Lr1*, *Lr2a*, *Lr3bg*, *Lr3ka*, *Lr14a*, *Lr16*, *Lr17a*, *Lr18*, *Lr20*, *Lr23*, *Lr24*, *Lr26*, *Lr34*, and *LrZH84*—either singly or in combinations, were postulated in 65 genotypes, whereas known resistance genes were not identified in the other 37 accessions. Resistance gene *Lr26* was present in 44 accessions. Genes *Lr14a* and *Lr34* were each detected in seven entries. *Lr1* and *Lr3ka* were each found in six cultivars, and five lines possessed *Lr16*, *Lr17a* and *Lr18* were each identified in four lines. Three cultivars were postulated to possess *Lr3bg*. Genes *Lr20*, *Lr24*, and *LrZH84* were each present in two cultivars. Each of the genes *Lr2a* and *Lr23* may exist in one line. Fourteen genotypes showed slow leaf rusting resistance in two cropping seasons.

Leaf rust, caused by *Puccinia triticina* Eriks., is one of the most important and widespread diseases of common wheat (*Triticum aestivum* L.) worldwide. It is adapted to a wide range of environments, occurs wherever wheat is grown, and can cause significant yield and economic losses (38). In China, destructive epidemics of leaf rust occurred in 1969, 1973, 1975, and 1979 (4). During the past decade, leaf rust has periodically caused destructive yield losses in the major wheat production regions, particularly in North China and the Yellow and Huai valleys (42). Resistant cultivars are the most efficient and environmentally friendly method for reducing damage caused by leaf rust (25).

Genetic interactions between wheat and *P. triticina* involve gene-for-gene relationships (27). Gene postulations assume gene-

for-gene specificities in hypothesizing probable resistance genes present in host genotypes (23). The presence of a specific resistance gene in a host line can be postulated from response arrays of pathogen cultures with known avirulence and virulence characteristics. Many researchers have used this approach to identify leaf rust resistance genes (*Lr*) in various sets of wheat lines. For example, Statler (37) postulated *Lr1*, *Lr2a*, *Lr2c*, *Lr10*, *Lr17a*, and *Lr18* in a group of 25 hard red spring wheat genotypes. McVey (19) identified genes *Lr1*, *Lr3*, *Lr10*, *Lr16*, *Lr24*, and *Lr26* in 86 winter wheat cultivars from 26 countries using 15 *P. triticina* races. Unidentified resistance genes were also present in some cultivars. McVey and Long (20) postulated 14 resistance genes, *Lr1*, *Lr2a*, *Lr3*, *Lr3ka*, *Lr9*, *Lr10*, *Lr11*, *Lr14a*, *Lr16*, *Lr17a*, *Lr18*, *Lr24*, *Lr26*, and *Lr30*, in 30 cultivars, and 56 hard red winter wheat lines from 9 breeding programs using 17 isolates of *P. triticina* with known avirulence or virulence to 16 *Lr* genes. Fourteen genes, *Lr1*, *Lr3*, *Lr3bg*, *Lr10*, *Lr13*, *Lr14a*, *Lr16*, *Lr17a*, *Lr19*, *Lr23*, *Lr26*, *Lr27* + *Lr31*, and *Lr34*, were identified among 76 Mexican wheat cultivars

(30,35). Resistance genes were also postulated in selected soft red winter wheat (11,38) and hard red spring wheat cultivars (22) from the United States, and 36 wheat cultivars from Ethiopia and Germany (21). Singh et al. (31) screened 61 spring and 102 facultative and winter wheat cultivars from China with 14 *P. triticina* races and postulated 9 seedling resistance genes, *Lr1*, *Lr3*, *Lr3bg*, *Lr10*, *Lr13*, *Lr14a*, *Lr16*, *Lr23*, and *Lr26*, in some of the cultivars. However, limited information is available with respect to possible leaf rust resistance genes in current commercial wheat cultivars and advanced lines in China. Therefore, characterization of leaf rust resistance genes in current widely grown Chinese wheat cultivars would be extremely useful for breeding new resistant cultivars and for gene deployment schemes using Chinese wheat germplasm.

To date, 61 leaf rust resistance genes have been cataloged in wheat (18). Most of them confer hypersensitive reactions and interact with the pathogen in a gene-for-gene fashion (7). The effectiveness of such genes is often absent or short-lived due to the appearance of pathotypes with corresponding alleles for virulence (10). The pyramiding of several resistance genes in a single cultivar is considered important since their combined effects confer a wider spectrum of resistance (26) and perhaps extends the period of effectiveness. Currently, only a few designated leaf rust resistance genes, such as *Lr9*, *Lr19*, *Lr24*, and *Lr38*, are effective against prevalent Chinese *P. triticina* races (39). Hence, it is very important to search for new resistance genes to cope with the rapidly evolving pathogen population.

Adult-plant resistance (APR) of the slow rusting type is considered more durable than seedling resistance (36) or major gene APR. Slow rusting is characterized by slow disease development in the field despite a high infection type (33), and involves a longer latent period, a low infection frequency, smaller uredial size and reduced duration of sporulation, and less

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spore production (2). Of the 61 leaf rust resistance genes cataloged, *Lr34* and *Lr46* are assumed to be slow rusting genes (32,34). Dyck and Samborski (6) found slow rusting resistance gene *Lr34* in the Brazilian wheat cultivar Frontana. Dyck (5) located *Lr34* on chromosome 7D. Singh (29) and McIntosh (17) reported that *Lr34* is genetically associated with gene *Yr18*, conferring slow rusting resistance to stripe rust. Both genes are also linked with gene *Ltn* for leaf tip necrosis in adult plants, a gene that can often be used as a morphological marker for *Lr34* and *Yr18* (28). Krattinger et al. (12) showed the *Lr34* protein resembled ABC (ATP-binding cassette) transporters of a pleiotropic drug resistance subfamily.

Lr34 confers a moderate level of leaf rust resistance when present alone; however, combinations of *Lr34* with two to four additional slow rusting genes resulted in high resistance in most environments (33). In addition, Singh et al. (34) identified the gene *Lr46* for slow leaf rusting and located it on chromosome 1B of cultivar Pavon 76. This gene has remained effective since 1976. Lillemo et al. (15) reported that *Lr46* was closely linked to the slow stripe rusting gene *Yr29* and powdery mildew resistance gene *Pm39*. The frequent breakdown of leaf rust resistant cultivars has forced wheat breeders to focus on the development of cultivars with durable resistance based on slow rusting genes. Chen et al. (3) screened

7 wheat cultivars with slow rusting resistance to leaf rust in 37 Chinese wheat cultivars based on latent period, epidemic rate, area under disease progress curve (AUDPC), infection type (IT), final disease rating, and accumulation temperature of latent period by the time of pustule eruption up to 50%. Although slow rusting resistance and major genes have been used for durable control of leaf rust, very little information is available on either type of resistance in most current Chinese wheat cultivars.

One hundred and two widely grown Chinese wheat cultivars and advanced lines from 12 provinces in the major wheat production regions were investigated in this study. The objectives were to postulate

Table 1. Pedigrees, origins, and likely presence or absence of the 1B.1R wheat-rye chromosomal translocation and the *Lr34* leaf rust resistance gene based on molecular markers of 102 Chinese wheat genotypes

Line no.	Genotype	Origin	Pedigree	1B.1R ^a	<i>Lr34</i> ^b
1	Han 4599	Hebei	Han 4032/85Zhong47	+	—
2	Han 5316	Hebei	Han 7808/CA 8059//85Zhong47	+	—
3	Aikang 58	Henan	Zhoumai 11 // Wenmai 6/Zhengzhou 8960	+	—
4	Xinmai 208	Henan	Yumai 18/Jimai 5418	+	—
5	Zhoumai 16	Henan	Zhou 9/Zhou 8425B	+	—
6	Zhoumai 18	Henan	Zhou 9/Neixiang 185	+	—
7	(95)18	Shaanxi	843380/81170-1-2-1	+	—
8	Lantian 14	Gansu	Qingshan 895/Zhongliang 17	+	—
9	Lantian 9	Gansu	Xifeng 16/76-89-13	+	—
10	Chuanyu 19	Sichuan	Chuanyu 5/Mo 460//Mianyang 26	+	—
11	N1621-19-4	Sichuan	Mianyang 26/Yiyuan 2	+	—
12	Jing 035-1	Yunnan	/ ^c	+	—
13	Zhoumai 12	Henan	Zhou 8425A/SWD73295	+	—
14	5R608	Beijing	R1//Xuezao/D164	+	—
15	5R610	Beijing	6521-89630278/ K3— ABE//A121	+	—
16	Henong 326	Hebei	84(252)/86(298)	+	—
17	Shi 4185	Hebei	Tal/Zhi 8094//Yumai 2/3/Jimai 26	+	—
18	Lankao 906-4	Henan	84-184/ Yumai 2//90 Selection	+	—
19	Jinan 16	Shandong	Tal Shannongfu 63/AimengniuV	+	—
20	Shaan 715	Shaanxi	Shaan 354/Yanmai 8911	+	—
21	Tian 95HF2	Gansu	Selected from <i>Tal</i> wheat F ₂ recurrent selection population	+	—
22	Huaimai 18	Jiangsu	Zhengzhou 891/Yan 1604	+	—
23	Bi 2002-2	Guizhou	8513-1624/Ji 1002	+	—
24	99-0502	Sichuan	911/MY86-51	+	—
25	Mian 2000-36	Sichuan	Mian92-8/Mian88-304//Guinong 19-4	+	—
26	N711	Sichuan	92-4/Mianyang 4	+	—
27	Yumai 47	Henan	Yumai 2/Baiquan 3199	—	—
28	Yannong 19	Shandong	Yan 1933/Shaan 82-29	—	—
29	Lumai 21	Shandong	Lumai 13/Yumai 2	—	—
30	Emai 14	Hubei	Fan 6/Yanda 72-629	—	—
31	Guizhou 98-18	Guizhou	Sumai 3/C39//Qing 30	+	—
32	Zhengmai 9023	Henan	(Xiaoyan 6/Xinong 65//8323-3/8443)/Shaan 213	—	—
33	5R615	Beijing	D221/891162(Agent)	+	—
34	5R616	Beijing	BL 7Y*2/Agent	—	—
35	Shaannong 981	Shaanxi	Derived from Shaanyou 225 (Xiaoyan 6/NS2761)	—	—
36	Een 1	Hubei	Lovrin 10/761//Sumai 3	+	—
37	Xinmai 19	Henan	C5/Xinxiang 3577//Xinmai 9	—	—
38	Xinong 1043	Shaanxi	Changwu 131/Y 8402	—	—
39	An 96-8	Anhui	L9288022-21/Xingnong 5	—	—
40	58749	Sichuan	SW 3243/35050//21530	+	—
41	Xinong 1163-4	Shaanxi	84Jia79/Xinong 1376	+	—
42	93Xia032-1	Sichuan	93-38-1/93-35	+	—
43	Y 1496-15	Sichuan	94-2/Mianyang 4	+	—
44	Tian 9470	Gansu	Tian 817/Lantian 6	+	—
45	W7	Sichuan	Durum/Xianyang large spike//W7268	—	—
46	LB 0458	Sichuan	Mianyang 90-310/M180	—	—
47	SW 8588	Sichuan	Milan's/SW 5193	—	—
48	Lankaoaizao 8	Henan	84(184)/90 Selection	+	—
49	01-DH689	Sichuan	94-D.H-375/Mianyang 26	+	—

(continued on next page)

^a + = presence of 1BL.1RS, — = presence of normal 1BL.1BS, determined by the method of Zhang et al. (40).

^b + = presence of *Lr34*, — = absence of *Lr34*, according to STS marker cslV34 (12).

^c / = Unknown.

genes conferring seedling resistance and to assess the likelihood of slow rusting resistance in adult plants grown in the field.

MATERIALS AND METHODS

Wheat germplasm and *P. tritricina* pathotypes. The 102 winter wheat cultivars and advanced lines were from major breeding programs across the autumn-sown wheat regions of China, including the provinces of Beijing, Hebei, Henan, Shandong, Shanxi, Shaanxi, Gansu, Anhui, Hubei, Jiangsu, Guizhou, Sichuan, and Yunnan (Table 1). The lines were tested for seedling reaction to 24 *P. tritricina* pathotypes in the greenhouse and for slow leaf rusting resistance in the field. CIMMYT

line Saar with typical slow leaf rusting resistance (15,40) and highly susceptible line Zhengzhou 5389 were used as slow rusting and susceptible controls, respectively. A set of 35 differential lines, mostly near-isogenic lines in the background of Thatcher with known leaf rust resistance genes, were included in the seedling tests, and the ITs displayed by them were used as a basis for postulating resistance genes in the Chinese lines (Tables 2 and 3). The differential lines were kindly provided by the USDA-ARS Cereal Disease Laboratory, University of Minnesota, St Paul, USA. The 24 pathotypes were designated following the coding system of Long and Kolmer (16), with addition of the fourth

letter for the reactions to the fourth set of differentials (http://www.ars.usda.gov/SP2/UserFiles/ad_hoc/36400500Cerealarusts/pt_nomen.pdf). Four Thatcher isogenic lines with genes *Lr1*, *Lr2a*, *Lr2c*, and *Lr3* were the first set of differentials; with genes *Lr9*, *Lr16*, *Lr24*, and *Lr26* were the second set of differentials; with genes *Lr3ka*, *Lr11*, *Lr17a*, and *Lr30* were the third set of differentials; and with genes *LrB*, *Lr10*, *Lr14a*, and *Lr18* were the fourth set of differentials.

Seedling testing. The seedling tests for the 102 cultivars and lines were conducted in 2007 and repeated in 2008, using 24 pathotypes (Table 3), by the method described by Singh et al. (31) with minor

Table 1. (continued from previous page)

Line no.	Genotype	Origin	Pedigree	1B.1R ^a	Lr34 ^b
50	Chuannong 17	Sichuan	91S-23/A302	+	–
51	Mian 2000-13	Sichuan	Mianyang 01821/90Zhong165//Guinong 19-4	+	–
52	Chuannong 19	Sichuan	Qian 1104A/R935	–	–
53	Qinnong 151	Shaanxi	Zhengzi R84019-0-7-5/Xinong 1376	+	–
54	351-15	Sichuan	Mian 99-310/GansuM180	–	–
55	Neixiang 991	Henan	87C27/Zhengzhou 84115// Yumai 13	+	–
56	LB 0288	Sichuan	Mianyang 90-310/M180	–	–
57	Zhou 8425B	Henan	Guangmai 74/Lianfeng 1//Predgornayi 2/3/Annong 7959	+	–
58	Zhoumai 11	Henan	Zhou 8425B/Yumai 17	+	–
59	01-018	Sichuan	Chuannong 21/89-8//89-107	+	+
60	R 97	Sichuan	Mianyang 92-8/91S-5-7	+	+
61	Lantian 12	Gansu	Qingnong 4/Xiannong 4	–	+
62	Libellula	Gansu	Tevere/Giuliani//San Pastore (Italy)	–	+
63	Strampelli	Gansu	Introduced from Italy	–	+
64	99422	Sichuan	Mian 87-19/R1301	–	+
65	Chinese Spring	Sichuan	Landrace	–	+
66	3S587	Beijing	Bai//108/Flaminio-IDO2229/3/BT 881	–	–
67	5R631	Beijing	93/Yantsr	–	–
68	Zhongyou 9507	Beijing	Reselection of Zhongyou 8	–	–
69	Henong 822	Hebei	88S522/92	–	–
70	Luohan 2	Henan	Luoyang 78 (111) ai/Jinmai 33	–	–
71	Pingyuan 50	Henan	Landrace	–	–
72	Xinmai 16	Henan	Yumai 13/Neixiang 82C6// Yumai 2	–	–
73	Xinmai 9	Henan	Baiquan 3047-3/Neixiang 82C6	–	–
74	Yumai 49	Henan	Bainong 791//Wenxuan 1/Zhengzhou 761/3/Yumai 2	–	–
75	Yannong 9	Shandong	Derived from Bima 1	–	–
76	Zimai 12	Shandong	917065/910292	–	–
77	N95175	Shaanxi	92R/Yuancai 142//Xiaoyan 6	–	–
78	Shaan 512	Shaanxi	Shaanmai 150/Shaan 354	–	–
79	Xiaoyan 926	Shaanxi	Derived from Xiaoyan 6	–	–
80	Xinong 8925-13	Shaanxi	Xiaoyan 168/Zhi 763	–	–
81	96-22-2-3	Gansu	Cappelle Desprez/935	–	–
82	Lantian 17	Gansu	92R137/Lantian 6	–	–
83	Zhongliang X9610	Gansu	92R178/92R178//Chuanjian 134	–	–
84	Yangmai 158	Jiangsu	Yangmai 4/ST1472/506	–	–
85	Fengmai 24	Yunnan	Yunmai 36/Mo 965	–	–
86	4S589	Beijing	Yanda 1817/we1//Tuyou/3/Jing 411*3	–	–
87	4S615	Beijing	T601/Jing 411*3	–	–
88	Nongda 189	Beijing	Lv7you/Yanshi 9//Changfeng 1/H. w y1775/3/Ji 82-4255	–	–
89	Henong 215	Hebei	Anyang 10/Aifeng 1//Beijing 8/3/Lovrin 10/4/HH/5/Orofen	–	–
90	Xinmai 11	Henan	Zhou 8826/Xinxiang 3577	–	–
91	Xinmai 13	Henan	Yuanyuanchangbai//C5/Xinxiang 3577	–	–
92	Yanzhan 1	Henan	89(35)-14/Yumai 18	–	–
93	Yanzhan 4110	Henan	C39/Xibei 78(6)9-2//FR 81-3/Aizao 781-4/3/Aizao 781-4	–	–
94	Yumai 18	Henan	Zhengzhou 761/Yanshi 4	–	–
95	Zhoumai 19	Henan	Zhoumai 13/Shaanyou 225//PH82-2	–	–
96	Mingxian 169	Shanxi	Landrace	–	–
97	Shaanmai 139	Shaanxi	Xiaoyan 22/6//Triticum dicoccoides AS846//Shaanmai 8003/Shaanmai 8007/F ₃ /3/Shaan 229/4/AizaofengJF ₃ /5/N9134	–	–
98	94t-133	Gansu	Hybrid 46/Xiannong 4//Tao 157	–	–
99	Zhongliang 98702	Gansu	Zhongliang 21/92R137	–	–
100	Annong 98005	Anhui	Aizao 781/Wansu 8802	–	–
101	Yangfu 2	Jiangsu	Yangmai 158/101-90	–	–
102	Chuannong 21	Sichuan	91S-23/Qianhui 3	–	–

modifications. Forty cultivars or lines, with six to eight seeds each, were sown in a plastic growth chamber (35 × 24 cm). Zhengzhou 5389 was included as the susceptible control. Seedling inoculations were performed by brushing urediniospores from sporulating susceptible seedlings onto test seedlings when the first leaves were fully expanded. Inoculated seedlings were subsequently placed in plastic-covered cages and incubated at 18°C and 100% relative humidity (RH) for 24 h. They were then transferred to a growth chamber maintained with 12 h light/12 h darkness at 18 to 20°C with 70% RH. ITs were scored 10 to 14 days after inoculation according to the 0 to 4 Stakman scale as modified by Roelfs et al. (26). In addition to the genes detected based on reaction patterns to different phenotypes, *Lr26*, *Lr34*, and *LrZH84* were also confirmed by molecular markers.

Identification of *Lr26* and *Lr34*. To determine the presence of the 1BL.1RS translocation carrying *Lr26*, two molecular markers, one with a specific sequence from the *ω-secalin* rye gene generating a 1,076-bp fragment in genotypes with the 1BL.1RS translocation, and the other

from the wheat *Glu-B3* gene generating a 636-bp fragment amplified in genotypes without the 1BL.1RS translocation, were used to assay the 102 cultivars and lines following the procedure developed by Zhang et al. (41) with minor modifications. The slow rusting resistance gene *Lr34* was identified using the STS marker *csLV34* as described by Lagudah et al. (13) (Table 1).

Field testing. The 104 cultivars and lines, including Saar and Zhengzhou 5389, were planted in a randomized complete block design with three replicates in Baoding, Hebei Province, in the 2006–07 and 2007–08 cropping seasons. Fifty seeds of each line were sown in a single-row plot with 1.5-m length and 30 cm between rows. Spreader rows of Zhengzhou 5389 were planted perpendicular and adjacent to the test rows. Leaf rust epidemics were initiated by spraying aqueous suspensions of urediniospores of *P. tritricina* pathotype THTT, to which a few drops of Tween 20 (0.03%) were added, onto the spreader rows at the tillering stage. Disease severities were assessed three times at weekly intervals with the first scoring 4 weeks after inoculation using the modified Cobb

scale (24), and ITs were scored using a 0 to 4 scale (26). The disease severity data were used to calculate AUDPC based on the method described by Broers et al. (1). AUDPC was calculated as:

$$\text{AUDPC} = \sum_{i=1}^n [(X_i + X_{i+1})/2](T_{i+1} - T_i)$$

where T_i = number of days after inoculation and X_i = disease severity. The relative AUDPC (rAUDPC) value for each wheat genotype in each cropping season was calculated as the percentage of the AUDPC value of the susceptible check (Zhengzhou 5389). The maximum disease severity (MDS, %) was recorded for each genotype in each cropping season as percentage of leaf area infected when the susceptible check displayed its MDS.

Statistical analysis. The SAS software was used for analysis of variance (ANOVA) and for determining least standard deviations (LSDs) for comparing the rAUDPC and MDS values among the wheat genotypes. Cultivars and lines that were seedling-susceptible to THTT and had lower or nonsignificantly higher values of MDS and AUDPC than those of

Table 2. Seedling infection types^a on 35 wheat lines with known leaf rust resistance genes when tested with 24 pathotypes of *Puccinia tritricina* collected from China

Tester	<i>Lr</i> gene	Infection types to <i>Puccinia tritricina</i> pathotypes																							
		PH	FC	FC	PC	TC	PG	FG	FK	PC	FB	FH	PH	FH	PG	PC	TC	PH	FH	FH	PH	TH	FC	PC	
		QT	QR	ST	BT	GT	SN	SQ	QT	HS	HT	ST	SS	GS	TS	TT	JT	HT	ST	HQ	TR	JT	TT	TT	GR
RL 6003	<i>Lr1</i>	3	0	0	3	3	4	;	2	3	2	2	3	0	0	3	3	3	0	0	3	4	;	3	
RL 6016	<i>Lr2a</i>	1	1	;	1	3	1+	1+	2	1	2	1	3	0	1	1	2	3	;	0	0	2	4	;	;
RL 6019	<i>Lr2b</i>	3	4	3	4	3	4	3	3	3	3	3	3	3	3	3	3	3	3	3	3	4	4	3	
RL 6047	<i>Lr2c</i>	3	3	3	4	3	3C	4	3	3	3	3	3	3	4	3	3	3	3	3	3	4	4	3	
RL 6002	<i>Lr3</i>	3	4	3	3	3	4	4	3	3	3	4	3	3	3	3	3	3	3	3	3	4	4	3	
RL 6042	<i>Lr3bg</i>	3	3	3	3	3	4	4	3	3	3	3	3	3	3	3	3	2	2	3	2	3	3	4	3
RL 6007	<i>Lr3ka</i>	3	3	3	1	;	4	4	3	2	2	3	3	2	3	3	0	0	3	0	3	2	3	3	2
RL 6010	<i>Lr9</i>	0	;	0	0	0	0	0	0	0	;	0	0	0	0	0	0	0	0	0	0	0	0	;	0
RL 6004	<i>Lr10</i>	3	3	3	3	3	2+,3-	4	3	3	3	3	3	3	3	3	3	3	3	3	3	3	4	3	
RL 6053	<i>Lr11</i>	3	3	3	12	3	3	3+	3	3	3	3	3	3	3	3	3	3	3	3	3	3	4	3	
RL 6013	<i>Lr14a</i>	3	3	3	4	3	3C	2	3	3	3	3	3	3	3	3	3	3	2	2	3	3	4	2	
RL 6052	<i>Lr15</i>	0	0	;	1	2	4	1+	2	3	1	1	3	;	1	3	;	1,2	1	2	2	1	1	3	
RL 6005	<i>Lr16</i>	3	1	1	1+	2	3	4	3	2	2	3	3	3	3	3	2	2	3	3	4	3	4	2	
RL 6008	<i>Lr17a</i>	2	2	3	;	2	3	3+	2	1	1	3	3	2	3	3	3	1	3	1	3	3	3	2	
RL 6009	<i>Lr18</i>	3	3	3	3	3	2	1	3	2	3	3	2	2	2	3	3	3	2	3	3	3	4	3	
RL 6040	<i>Lr19</i>	0	;	;	0	;	0	;	0	0	0	0	0	0	;	1	0	2	0	0	0	;	0	;	
RL 6092	<i>Lr20</i>	3	3	1	0	1	3	4	;	3	0	3	0	0	0	0	3	3	2	3	3	3	3	3	
RL 6043	<i>Lr21</i>	0	1	3	2	2	3	3	2	2	3	3	12	2	3	2	2	3	3	2	3	3	3	2	
RL 6012	<i>Lr23</i>	;	;	3	1	2	2+	4	1	1	;	3	;	12	1	4	4	4	3	2	0	;	3	3-	
RL 6064	<i>Lr24</i>	0	0	;	0	;	;	;	;	;	;	;	0	0	0	;	;	0	0	;	0	;	;	;	
RL 6084	<i>Lr25</i>	3	4	3	4	3	4	4	3	3	3	3	3	3	3	3	3	3	3	3	3	3	4	3	
RL 6078	<i>Lr26</i>	3	3	3	3	4	1+	0	3	3	;	3	3	3	3	2+	3	3	3	3	3	3-	3	4	
RL 6079	<i>Lr28</i>	0	0	;	0	0	0	;	3	;	2	0	0	3	0	0	;	0	;	;	3	0	0	0	
RL 6080	<i>Lr29</i>	3	3	3	2	3	;	4	;	;	;	3	3	3	3	3	1	2	3	3	3	2	3	3	
RL 6049	<i>Lr30</i>	0	;	;	1	1	1	2	3	3	;	2	2	3	3	0	2	3	2	3	3	2	3	2	
RL 5497	<i>Lr32</i>	;	;	;	1	1	2+,3-	4	12	1	;	0	12	1	1	1+	1	1	2	;	3	0	2	3	
RL 6057	<i>Lr33</i>	3	3	3	3	3	4	4	3	4	3	4	3	4	3	3	4	4	4	3	3	3	3	3	
E84018	<i>Lr36</i>	3	1	1	;	;	2	2+	0	2	1	;	;	1	0	;	2	1	1	2	0	;	3	;	
RL 6097	<i>Lr38</i>	0	0	;	0	0	1	1	;	0	0	;	;	0	0	0	0	0	;	0	0	0	;	;	
KS86	<i>Lr39</i>	3	3	;	2	2	1	1	2	2	2	1	1	2	2	2	2	2	3	3	3	2	;	1	
NGRC02																									
KS91	<i>Lr42</i>	0	0	;	0	12	1	1	;	12	2	2	2	2	2	2	3	2	;	3	0	0	1	0	
WGRC11																									
RL 6147	<i>Lr44</i>	3C	2	3	3	3	1+	3	12	2	2	2	2	2	2	2	1+	1	2	3	1	3	3	2	
RL 6144	<i>Lr45</i>	3	3	;	2	1	;	1	3	;	3	3	3	3	3	1	0	2	2	3	3	0	;	0	
TeLr50	<i>Lr50</i>	0	0	;	;	;	4	4	;	2	;	1	;	0	;	3	;	0	;	0	0	1	3	2	
RL 6051	<i>LrB</i>	4	3	3	3	3	4	4	3	3	4	3	3	3	3	3	3	3	3	3	3	3	4	3	

^a According to the 0–4 Stakman scale as modified by Roelfs et al. (26).

the slow rusting check in field trials were considered to be slow rusting genotypes.

RESULTS

Resistance genes identified from seedling reactions or molecular markers.

Variation in ITs conferred by known *Lr* genes in differential lines, inoculated with 24 *P. tritici* pathotypes (Table 2), provided an ability to postulate 24 resistance genes (*Lr1*, *Lr2a*, *Lr3*, *Lr3bg*, *Lr3ka*, *Lr11*, *Lr14a*, *Lr15*, *Lr16*, *Lr17a*, *Lr18*, *Lr20*, *Lr21*, *Lr23*, *Lr26*, *Lr28*, *Lr29*, *Lr30*, *Lr32*, *Lr36*, *Lr39*, *Lr42*, *Lr44*, and *Lr50*). Resistance genes *Lr9*, *Lr19*, *Lr24*, and *Lr38* conferred low ITs with all pathotypes. Postulation of genes *Lr2b*, *Lr2c*, *Lr3*, *Lr10*, *Lr25*, *Lr33*, and *LrB* was not possible because high ITs were recorded with all pathotypes.

Fourteen resistance genes (*Lr1*, *Lr2a*, *Lr3bg*, *Lr3ka*, *Lr14a*, *Lr16*, *Lr17a*, *Lr18*, *Lr20*, *Lr23*, *Lr24*, *Lr26*, *Lr34*, and *LrZH84*), either singly or in combinations, were postulated to be present in 65 genotypes, whereas 37 accessions carried undetectable or unknown resistance genes (Table 3).

Forty-four entries contained *Lr26*; 12 displayed low ITs with four *Lr26*-avirulent pathotypes (P6, P7, P10, and P15) and high reactions with the remaining 20 pathotypes, showing the same response pattern as that of RL 6078 carrying *Lr26*. Thirty-one lines were postulated to possess *Lr26* plus other known or unknown *Lr* genes according to their low reactions with certain *Lr26*-virulent pathotypes (Tables 2 and 3). All entries postulated to have *Lr26* were also confirmed using markers for the presence or absence of the 1BL.1RS translocation (Tables 1 and 3). Three lines (L13 = Zhoumai 12, L26 = N711, and L60 = R97) displayed high ITs to all or some of the four *Lr26*-avirulent pathotypes, but were positive for the presence of 1BL.1RS translocation using the markers. The high ITs with *Lr26*-avirulent pathotypes might be due to an inhibitor of *Lr26* or to the presence of a 1RS translocated chromosome not possessing a leaf rust resistance gene. Seven lines might carry *Lr1*, showing low ITs to 10 pathotypes avirulent to *Lr1*. Two cultivars (L27 = Yumai 47, and L28 = Yannong 19) are likely to carry gene *Lr1* alone because they displayed only low ITs with 10 pathotypes avirulent to *Lr1*. Guizhou 98-18 (L31) carried *Lr1*, *Lr26*, and the other unidentified genes based on its reaction patterns. Another three cultivars (L29 = Lumai 21, L30 = Emai 14, and L55 = Neixiang 991) were postulated to have *Lr1* and other resistance genes.

Seven lines were postulated to contain *Lr14a*; they gave low or intermediate reactions to five *Lr14a* avirulent pathotypes (P6, P7, P19, P20, and P24). *Lr14a* was present in combination with *Lr26* in four lines (L41 = Xinong 1163-4, L42 = 93Xia032-1, L43 = Y 1496-15, and L44 =

Tian 9470). The other three lines (L45 = W7, L46 = LB 0458, and L47 = SW 8588) might carry *Lr14a* and other unknown or known genes.

Lr34 was postulated in seven lines with the molecular marker *csLv34* (13), and these lines also showed symptoms of leaf tip necrosis (*Ltn*) at the adult stage. Two lines (L59 = 01-018, and L60 = R97) carried *Lr34* in addition to *Lr26*.

Lr3ka was postulated in combination with other known *Lr* genes in six lines according to their low reactions to nine *Lr3ka*-avirulent pathotypes and some *Lr3ka*-virulent pathotypes.

Gene *Lr16* may be present in five lines, showing low ITs with the 10 pathotypes that were avirulent on the *Lr16* NIL (Tables 2 and 3). *Lr16* was present in combination with *Lr3ka* in Shaannong 981 (L35) because low ITs were observed in seedlings inoculated with 10 *Lr16*-avirulent pathotypes and three *Lr3ka*-avirulent pathotypes (P13, P19, and P21). Een 1 (L36) carried *Lr16* in addition to *Lr3ka* and *Lr26* according to its low reactions to all pathotypes avirulent to the three genes. Another three lines (L32 = Zhengmai 9023, L40 = 58749, and L56 = LB 0288) may carry *Lr16* and other known or unidentified genes.

Lr17a and *Lr18* were each found in four lines. The four lines carrying *Lr17a* displayed low ITs to 11 *Lr17a*-avirulent pathotypes. *Lr17a* and *Lr3ka* were present in An 96-8 (L39), and *Lr17a* was postulated in combination with *Lr3ka*, *Lr16*, and *Lr26* in line 58749 (L40). Xinmai 19 (L37) and Xinong 1043 (L38) may contain *Lr17a* and other unknown genes. *Lr18* was postulated in combination with *Lr26* in four lines (L48 = Lankaoizao 8, L49 = 01-DH689, L50 = Chuannong 17, and L51 = Mian 2000-13) based on low ITs with four *Lr26*-avirulent pathotypes (P6, P7, P10, and P15) and intermediate ITs with five *Lr18*-avirulent pathotypes (P9, P12-P14, and P19).

Three lines displayed intermediate or low ITs to three pathotypes (P17, P18, and P20) lacking virulence for *Lr3bg*, indicating that they contain *Lr3bg*. *Lr3bg* was postulated in combination with *Lr26* in Qinnong 151 (L53) and in combination with *Lr2a* in 351-15 (L54). Chuannong 19 (L52) was postulated to have *Lr3bg* and other unidentified genes.

Lr20 was detected in Neixiang 991 (L55) in combination with *Lr1*, and LB 0288 (L56) carried known *Lr* genes additional to *Lr20*. 5R615 (L33) and 5R616 (L34) showed high levels of resistance to all 24 pathotypes and may contain *Lr24* because the two lines were derived from Agent, a known *Lr24* carrier (Table 1). 5R615 also possessed *Lr26*, as it had the 1BL.1RS translocation detected with molecular markers. *LrZH84* was present in combination with *Lr26* in Zhou 8425B (L57). According to Zhao et al. (42), Zhou

8425B contains gene *LrZH84*. Zhoumai 11 (L58) is a derivative of Zhou 8425B and had a reaction pattern similar to that of Zhou 8425B, indicating that it may also carry *LrZH84*.

Line 351-15 (L54) displayed low ITs with all 21 pathotypes avirulent to *Lr2a* and an intermediate IT to P17 (TCHT) which is avirulent for *Lr3bg*, indicating that *Lr2a* is present in combination with *Lr3bg* in this line. *Lr23* was present in combination with *Lr16* and *Lr20* in LB 0288 (L91), displaying low ITs with pathotypes lacking virulence for *Lr16*, *Lr20*, and *Lr23*.

Eighteen genotypes (L85-L102) showed high ITs with all pathotypes, indicating that they do not have any resistance gene corresponding to an avirulence gene present in any of the pathotypes. The reactions of 18 cultivars and lines (L66 and L68-L84) were not consistent with the response of any known resistance gene or predicted response of any gene combination.

5R631 (L67) conferred resistance to all pathotypes tested, indicating that it carries one or more unidentified resistance genes.

Slow rusting resistance in field tests. Highly significant differences were found for wheat genotypes and environments (years) for rAUDPC and MDS in the field trials (Table 4). The genotype-environment interaction was also significant, but its effect on variation was much less than the genotypic differences.

The MDS value of the susceptible check, Zhengzhou 5389, was 100 and 85%, respectively, in the 2006-07 and 2007-08 cropping seasons (Table 5), indicating that the disease developed well in both seasons. The MDS value of the slow rusting check, Saar, was 18 and 12%, respectively, and its rAUDPC was 15% in both seasons (Table 5).

Twelve entries, including 5R608 (L14), 5R610 (L15), Tian 95HF2 (L21), Bi 2002-2 (L23), Guizhou 98-18 (L31), 5R615 (L33), 5R616 (L34), Xinong 1163-4 (L41), LB0288 (L56) Zhou 8425B (L57), Zhoumai 11 (L58), and 5R631 (L67), were highly resistant to pathotype THTT at both the seedling and adult stages. Fifteen genotypes exhibiting high ITs at the seedling stage showed slow leaf rusting resistance in the field to the same pathotype in both seasons (Table 5). The correlations of MDS and relative AUDPC between the two cropping seasons were 0.77 and 0.74 ($N = 104$ and $P = 0.01$), respectively, indicating highly consistent results for slow rusting resistance. The correlation between relative AUDPC and MDS at the two locations varied from 0.96 to 0.99 ($N = 104$ and $P = 0.01$), indicating that MDS was a reliable indicator of AUDPC (14).

DISCUSSION

Seedling tests for leaf rust response. Yuan et al. (39) postulated 10 known

Table 3. Seedling infection types^a of 102 wheat cultivars and lines when tested with 24 pathotypes of *Puccinia triticina* collected from China

Line no. ^b	Lr gene	Infection types to <i>Puccinia triticina</i> pathotypes																							
		PH QT	FC QR	FC ST	PC BT	TC GT	PG SN	FG SQ	FK QT	PC HS	FB HT	FH ST	PH SS	FH GS	FH TS	PG TT	PC JT	TC HT	PH ST	FH HQ	FH TR	PH JT	TH TT	FC TT	PC GR
1	Lr26	3C	4	4	4	4	1+	;1	4	4	;1	3	3	4	4	1+	4	4	4	4	4	4	4	4	4
2	Lr26	3C	4	4	3C	4	1+	;1	4	4	;1	3	3	4	4	1+	4	4	4	4	4	4	4	4	4
3	Lr26	3C	3+	4	3+	4	2	;	4	3	1	4	3	4	4	1	4	3	4	4	4	4	4	4	4
4	Lr26	3	4	3	3	4	2	;1	4	3+	0	4	4	4	3	1+,2	4	4	4	3	3	4	4	4	4
5	Lr26	3	4	4	3	4	1+	;1	4	3	;	3	4	4	4	12	4	4	4	4	4	4	4	4	4
6	Lr26	3C	4	4	3C	4	1+	;1	4	3	0	4	3	4	3	1+	4	4	4	3+	3	4	4	4	4
7	Lr26	3	3+	3+	3	3+	1+	;	4	3	;	3	3	4	3	2	4	4	3	4	4	4	4	4	4
8	Lr26	3	3+	4	4	4	1+	;	4	3	;1	3	3	4	4	12	4	4	4	4	4	4	4	4	4
9	Lr26	3	4	4	4	4	;1	0	3	3	0	4	3	4	4	2	4	4	4	4	4	4	4	4	4
10	Lr26	3	3	4	3	4	1	;	3	3	;	3	3+	3	3	1	4	4	3	3+	4	4	3-	4	4
11	Lr26	3	4	4	3	4	1+	;	4	3	2	3	4	4	4	2	4	4	4	4	4	4	4	4	4
12	Lr26	3	4	4	3+	4	1+	;	4	3	0;	3	3	4	3	2	3	4	4	4	4	4	4	4	4
13	Lr26 ^c	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4
14	Lr26 ^d +	0	0	0	0	0	;	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15	Lr26 ^d +	;	;	;	;	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
16	Lr26+	2+	3+	2+,3C	22+	2	1+	;	4	2+,3-	1	3	3	3	4	1+	4	4	3	4	4	3	3	4	4
17	Lr26+	2	0	0	0	0	0	0;	0	3	0;	3	3	0	3	0	3	3	3	2	0	3	3	3	3
18	Lr26+	3	3C	2	2	2	;1	0	4	2	0	3	3	3	4	;1	3	4	2	4	4	2+,3-	3	3	4
19	Lr26+	3	3	3	3	4	1	;1	;2	2	0;	2	3	;0	2	2	2	3	3	3	4	4	3	3	0
20	Lr26+	2	3	3	3	3	1+	1	3	3	0	3	3	2	3	2	3	3	3	3	3	3	3	3	3
21	Lr26 ^d +	2	0	;	0;	;1	;	;	;	0;	;	;	0	0	0	0	0;	;2	;	0;	0;	0;	;	0;	0;
22	Lr26+	0;	0	3	2	3-	1+	;1	3	3	0;	3	3	2	3	2	3	3	3	3	3	3	3	3	3
23	Lr26 ^d +	0;	;	;	0;	0	;	;	0	0;	;1	;	;	0	0	0	0;	0;	;	0	3	0	;	0	;2
24	Lr26+	2	3	3	2+	3	1+	1	3	3	2	3	2	3	0	3	3	3	3	3	3	3	3	3	2
25	Lr26+	2	;2	3	;1	;2	1+	1+	;2	2	2	2	2	1	3	2	3	3	3	2	2	;2	3	3	3
26	Lr26 ^c +	1	3	2	2	3	3+	3	;1	12	0;	2	3	1	;1	3	;	3	3	2	2	2	3	4	3
27	Lr1	3	;	1+	3	3	4	;	1	3	;	;	4	;	1	4	3	4	3	;	1+	4	4	1	3
28	Lr1	3	0;	0	3	3	3	1	0;	3	;	0	3	0	;	3	3	3	3	0;	;	3	4	;	3
29	Lr1+	;	0	0	3	3	4	1	0;	;	0	0	3	0	;	3	3	3	;	0	0	4	;	3	3
30	Lr1+	3	;	;	0	3	1+	;1	;	0	0	0	3	0	0	;	3	3	;	0;	0	3	3	0	3
31	Lr1, Lr26+	;2	;	;	;	;1	1	;1	;1	;	;1	;	1;	;	1	0	0;	2	;	;	0;	0;	;1	;	3
32	Lr16+	2	0	2	;1	1+	4	3	2	2	2	2	3	2	1	2	2	2;	12	3	2	3-	2	1	1
33	Lr26 ^d , Lr24	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
34	Lr24	0	;	0	0	0	;	0	0	0	0	0	0	0	0;	0	0	0	0	;	0	0;	0	0	0
35	Lr3ka, Lr16+	3	2	1	2	;2	3	3	2	;1	;2	2	2	2	1	0	;1	2	2;	;1	3	2+	4	2	2
36	Lr26, Lr16, Lr3ka +	3	1	2	2	1+	1+	1	2	2	;	2	2	0	3	1	0;	1+	2	2	3	2	4	2	2
37	Lr17a+	;2	1	1	1	1+,2	3	3C	2	2	2	3	3	2	2	1;	3	2	3	2	2	3	3	3	2
38	Lr17a+	2	0	1	2	2	4	4	2	2	2	3	3	2	2	3	3	;	2	1	3	2	3	2	1
39	Lr3ka, Lr17a	2	2+	2	2+	2	3+	3+	2	2	2	3	3	2	1	2	2	2	3	1	2	1+	3	3	2
40	Lr26, Lr3ka, Lr16, Lr17a+	2	2	2	2	2	;	1	2	2	0;	2	3	2	2	;	2	2	3	2	3	2	3	2	1+
41	Lr26, Lr14a+	;	0;	3	0;	0	1	;1	0;	;	0	;	;	0	;	0	;1	;	;	0	2	;	;	;	2
42	Lr26, Lr14a+	2	3	3	2	2	1	1	2	2	;	3	2	1	2	0	2	3	;2	;1	2	3	3	3-	1
43	Lr26, Lr14a+	;2	0;	3	;2	;2	;	;	2	0	0;	3	1	;	1	0	2	3	;	0;	0	3	3	3	0;
44	Lr26, Lr14a+	;	0;	;	;1	;2	1	1	2	1	;2	3	1	1	;	;	;2	3	3	;2	0	;2	3	3-	2
45	Lr3ka, Lr14a+	;2	2	3	;1	;1	;	1	2	0	;	;	1	0	;	;	0;	;	;	0	2	0;2	4	;	1
46	Lr14a+	3	0;2	0	3	3	;	;	0	0	3	0	;1	0	0	3	0	2+	3	0	0	0	3	;	;
47	Lr14a+	3	;0	;	0	3	;	;	0	0	0	;	1	2	3	0	0	3	;	0;	0	3	4	0	;

(continued on next page)

^a According to the 0–4 Stakman scale as modified by Roelfs et al. (26).^b Line numbers correspond to those in Table 1 and are arranged in groups according to postulated *Lr* genes.^c Postulation of 1BL.IRS was based on molecular markers. These lines were susceptible to all or some of four *Lr26*-avirulent pathotypes.^d Postulation of 1BL.IRS was based on molecular markers. These lines were resistant to all or most of pathotypes.^e Postulation of *Lr34* was based on molecular markers. These lines also showed symptoms of leaf tip necrosis (*Ltn*) and lower disease severity at the adult-plant stage.

Table 3. (continued from preceding page)

Line no. ^a	Lr gene	Infection types to <i>Puccinia triticina</i> pathotypes																							
		PH QT	FC QR	FC ST	PC BT	TC GT	PG SN	FG SQ	FK QT	PC HS	FB HT	FH ST	PH SS	FH GS	FH TS	PG TT	PC JT	TC HT	PH ST	FH HQ	FH TR	PH JT	TH TT	FC TT	PC GR
48	<i>Lr26</i> , <i>Lr18+</i>	2	3	3	2+,3-	3-	1+	;	2	1	2	3	2	2	2	2	3	3	2	2	2	3	3	3	3
49	<i>Lr26</i> , <i>Lr18+</i>	2	3	3	;2	3-	1	0;	2	2	0;	3	2	0	1	2+	0	3	2	;2	3	3	3	3	3
50	<i>Lr26</i> , <i>Lr18+</i>	2	0	3	;1	2	1	1	2	2	0	3	1	0	1	2+	2+	3	3	2	3	3-	3	3-	2
51	<i>Lr26</i> , <i>Lr18+</i>	;	3	3	3	3	1	0;	;2	;1	0;	3	2	0	;	0	0;	3	2	;2	3	3	3	3	;1
52	<i>Lr3bg+</i>	;2	0	1	;2	;1	3	3	;2	2	;	2;	3	1	1	1	3	2	;1	;	1	3	3	;	3
53	<i>Lr26</i> , <i>Lr3bg+</i>	3	;2	3	3	2+	1+	1+	3	3	0;	3	2	;2	3	0	3	2	2	1	2	3	3	3	3
54	<i>Lr2a</i> , <i>Lr3bg</i>	;	0	0	0;	3	1	;	;	0	;	0	;	0	0	1	;	2	;	0	0	0	4	0;	0;
55	<i>Lr26</i> , <i>Lr1</i> , <i>Lr20+</i>	3	0	;	;2	3	1	;1	0	0	0	;	0	0	0	0	0;	2	0	0;	0;	0	3	;	3
56	<i>Lr16</i> , <i>Lr20</i> , <i>Lr23+</i>	;	0	0;	0;1	;2	;	;	;	0	0	3	;	0	0	0	0	;	0	0	0	0	0;	;0	1
57	<i>Lr26^d</i> , <i>LrZH84</i>	0	0;	;1	;1	2+	1+	;1	12	1	1	2	2	0;	1	0;2	1	3	;	0;	2	1	2	2	2
58	<i>Lr26^d</i> , <i>LrZH84</i>	;	0	;	;2	2+	;1	1	;1	0	0;	;2	;2	0	;	0	;	;2	;	;	0;	;	;1	;	1
59	<i>Lr26</i> , <i>Lr34^c</i>	;1	;	2	;	2	;	;	4	2	;1	3	3	3	3	;	3	4	3	3	4	4	4	4	4
60	<i>Lr26^c</i> , <i>Lr34^c</i>	3	3	3	3	3	;	;	3	3	;	2	3	2	3	3	3	3	3	3	3	3	3	3	3
61	<i>Lr34^c</i>	3	3	3	4	3	1	3	3	3	3	3	3	3	3	3	3	3	3	;2	3	3	3	3	3
62	<i>Lr34^c</i>	3	2	2	1+2	2	4	4	3	3	3	3	3	3	3	3	3	2	3	2	3	1+2	4	2	2
63	<i>Lr34^c</i>	4	4	4	4	4	4	3	4	4	4	4	4	4	3+	4	4	4	4	4	4	4	4	4	4
64	<i>Lr34^c</i>	;	0;2	;	3	3	3-	;1	3	3	3	;	3	0	3	0	3	3	;	0	0	3	4	0	3
65	<i>Lr34^c</i>	3+	4	3+	3+	;	4	4	4	4	3	4	4	4	4	4	4	4	3+	4	3	4	4	4	4
66	+	2	0	3	2	2	3	2	2	3	3	3	3	3	3	2	3	3	3	2	3	2+	3	2	3
67	+	0	0	0	0	;	0	0	0	0	0	0	0	0	0	0	0	0	;	0	0	0	0	0	0
68	+	3	4	3	4	3	3	3	3	3	3	3	3	3	3	3	3	3	3	2	3	3	4	3	3
69	+	3	2	2	1+2	2	3+	4	2	3	3	3	2	2	3	3	2	2+	3	2	3	1+2	3	2	2
70	+	2	3	3	3	3-	3	3+	2	2	3	3	3	2	2	3	3	3	3	2	3	3	3	3	3
71	+	3	3	3	4	3	3	3	3	3	3	3	3	2	3	3	3	2+	3	3	3	3	4	3	3
72	+	4	4	4	4	4	4	4	4	4	;1	3	3	4	4	4	4	4	3	3	4	4	4	4	4
73	+	1+	4	2+,3-	3	3	4	4	3	4	0	4	3	4	4	4	4	4	3	4	3	4	4	3	4
74	+	3	3	3	3	3	4	;1	3	2	3	3	3	3	3	3	3	3	3	3	3	3	3	4	3
75	+	;	0	0	3	2	3+	;1	;2	;	3	;	3	0	3	1	2	3	2	;	2	2+	3	3	3
76	+	0;	3	3	3	3	4	4	2	3	3	3	3	3	2	3	2	3	3	2	3	3	3	3	3
77	+	3	0	3	2	3-	4	3+	3	3	3	3	3	2	3	0	3	3	2	3	3	2+,3-	3	3-	2
78	+	4	4	3	4	3	4	4	4	4	;	3	4	4	4	4	4	4	3	4	4	4	4	4	4
79	+	3	3	3	4	3	4	4	2	2	3	3	3	2	3	3	3	3	3	2	3	4	4	3	3
80	+	3	3	3	3	3	3+	4	3	0	3	3	3	0	3	3	3	3	3	3	3	2	3	3	3
81	+	;	3	2	2	3	1+	2+	;2	;	2	3	1	3	3	;2	3	3	;2	;	;2	3	4	3	3
82	+	2	2+	3	2	2	3	2	3	3	2	2	3	2	3	1	2	2	3	3	2	2	3	3	2
83	+	3	2	3	1+2	1+	4	4	2	3	3	3	3	3	3	1	3	3	3	3	3	3	3	2	3
84	+	2	0	3	12	1	4	4	2	2	3	3	2+	3	3	3	3	2	3	2	3	3	3	2	2
85	+	0	2	3	;2+	1	4	4	;2	3	2	2	2	2	1+	2	2	2+	3	2	2	2	4	3	2
86	+	3+	3+	3	3+	4	4	4	4	4	3	4	4	3+	3	4	4	3	3	4	3	4	4	3	4
87	+	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4
88	+	4	4	4	4	4	4	4	4	4	3	4	4	4	4	4	4	4	4	4	4	4	4	4	4
89	+	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4
90	+	4	4	4	4	4	4	4	3	4	4	4	3	4	4	4	4	3	3	3+	4	4	4	3	4
91	+	4	4	4	4	4	4	4	4	4	4	3	3	4	3	4	4	4	4	4	4	4	4	4	4
92	+	4	4	3+	4	4	3+	4	3	4	4	4	4	4	4	4	4	4	3	4	3	4	4	4	4
93	+	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4
94	+	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4
95	+	4	4	4	4	4	4	4	4	4	4	3	3	4	4	4	4	4	4	4	4	4	4	4	4
96	+	4	4	4	4	4	4	4	3	4	4	3	4	4	4	4	4	4	4	4	4	4	4	4	4
97	+	4	4	4	4	4	4	4	3+	4	3	4	4	4	3	4	4	4	3	4	3	4	4	4	4
98	+	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4
99	+	3+	4	4	4	4	4	4	3	4	3	4	4	4	3	4	4	3	3	4	3	4	4	4	4
100	+	3	4	4	3	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4
101	+	4	4	4	4	4	4	4	4	4	3	4	4	4	4	4	4	4	4	4	4	4	4	4	4
102	+	3+	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4

genes, *Lr1*, *Lr3*, *Lr3bg*, *Lr9*, *Lr10*, *Lr13*, *Lr16*, *Lr23*, *Lr26*, and *Lr34*, in 47 new wheat cultivars from China using 17 pathotypes of *P. tritici*. Six of them, *Lr1*, *Lr3bg*, *Lr16*, *Lr23*, *Lr26*, and *Lr34*, were also identified in our seedling tests. The postulation of genes *Lr3*, *Lr9*, and *Lr10* was not possible in the present study because high ITs or low ITs were recorded with all pathotypes. *Lr13* was not tested in the seedling tests because the gene is an APR gene.

During the early 1970s, the 1BL.1RS translocation with *Yr9* and *Lr26* for resistance to stripe rust (*P. striiformis* f. sp. *tritici*) was introduced to Chinese wheat breeding programs through the introduction of wheat germplasm such as Lovrin 10, Lovrin 13, Predgoraia 2, Kavkaz, and Neuzucht (9), leading to a high frequency of *Lr26* in Chinese wheat cultivars and lines. Among 102 wheat lines tested in the present study, *Lr26* was identified in 44 (43.1%). Three lines (L13 = Zhoumai 12, L26 = N711, and L60 = R97) were suscep-

tible to all or some of four *Lr26*-avirulent pathotypes, but had a 1BL.1RS translocation based on the test with molecular markers. This indicated that an inhibitor gene might suppress the expression of *Lr26* in these two lines, or that a 1BL.1RS translocation lacking *Lr26* might be present. Hanušová et al. (8) reported an inhibitor of *Pm8* in certain 1BL.1RS wheat genotypes, but suppression of leaf rust resistance gene *Lr26* has not been reported and therefore needs to be verified.

Lr1 was postulated to be present in seven cultivars and lines. A study by Singh et al. (31) indicated that *Lr1* was present in many Chinese cultivars. *Lr1* in Yumai 47 might be derived from Baiquan 3199, because Bainong 3217 with *Lr1* (31) had the same parent, Funo, as Baiquan 3199, indicating that *Lr1* in Yumai 47 and Bainong 3217 was likely derived from Funo. *Lr1* in Lumai 21 might be derived from Lumai 13 (Table 1), because Baiyoubao carrying *Lr1* (31) was one of the parents of Lumai 13. *Lr1* in Emai 14 was derived from Yanda

72-629, as Emai 14 and Bainong 64 carrying *Lr1* had the same parent Yanda 72-629 (31). *Lr1* in Neixiang 991 might be derived from Bainong 3217 based on its pedigree (Table 1). *Lr16*, detected in five lines, was postulated in En 1, in agreement with the result reported by Singh et al. (31). *Lr16* in Zhengmai 9023 and Shaanong 981 might be derived from Shaan 213 and Xiaoyan 6 (31), respectively, according to their pedigrees (Table 1). Most lines with *Lr1* and *Lr16* were highly susceptible to pathotype THTT at the adult plant stage. Genes *Lr3ka*, *Lr14a*, *Lr17a*, and *Lr18* could be present in some lines (Tables 2 and 3); however, these postulations will require further verification because few avirulent pathotypes were available for testing, and the resistant reactions displayed by the four genes were vulnerable to genetic background of host and environment.

Various lines were widely resistant to many of the pathotypes used in the study, but the resistance could not be attributed to known leaf rust resistance genes. This indicates that new leaf rust resistance genes may be present in some lines. Genetic analyses are now being undertaken on lines with superior leaf rust resistance, and the results of those studies will permit an assessment of the postulations made herein. *Lr1* and an unknown *Lr* gene were identified in Tian 95HF2, and *LrZH84* was detected in Xinong 1163-4 and Guizhou 98-18 using SSR markers (data not shown).

Slow rusting resistance. The 14 genotypes with slow leaf rusting resistance to THTT were tested as seedlings with all 24 *P. tritici* pathotypes. Twelve of them contained *Lr26*; two of those (L59 = 01-018, and L60 = R97) carried *Lr34* based

Table 4. Analysis of variance of relative area under the disease progress curve (rAUDPC) and maximum disease severity (MDS) in 104 wheat cultivars and lines including slow rusting and susceptible checks tested in Baoding in the 2006–07 and 2007–08 cropping seasons

Parameter	Source of variation	df	MS	F value	P
rAUPDC	Cultivar	103	5,710.81	72.00	<0.0001
	Season	1	1,745.76	21.94	<0.0001
	Replication	2	58.71	0.74	0.48
	Cultivar*season	103	1,005.96	12.68	<0.0001
	Cultivar*replication	206	78.24	0.99	0.54
	Error	208	79.34		
MDS	Cultivar	103	5,595.44	112.53	<0.0001
	Season	1	21,443.85	431.27	<0.0001
	Replication	2	52.15	1.05	0.35
	Cultivar*season	103	930.84	18.72	<0.0001
	Cultivar*replication	206	51.73	1.04	0.39
	Error	208	49.72		

Table 5. Infection types (IT)^a in the seedling test with *Puccinia tritici* pathotype THTT, presence and absence of the 1B.1R wheat-rye chromosomal translocation and *Lr34* based on molecular markers, and IT, mean maximum disease severity (MDS), and mean relative area under the disease progress curve (rAUDPC) in field experiments with the same pathotype in Baoding, Hebei in the 2006–07 and 2007–08 growing seasons for wheat genotypes with slow rusting resistance to leaf rust

Genotype (line number)	Seedling IT to THTT	1B.1R and <i>Lr34</i> ^b	2006–07			2007–08		
			IT	MDS (%)	rAUDPC (%)	IT	MDS (%)	rAUDPC (%)
Saar ^c	4	<i>Lr34</i>	4	18	15.11	4	12	15.43
Zhengzhou 5389 ^d	4	–	4	100	100.00	4	85	100.00
(95)18 (L7)	4	1B.1R	3	4	2.22	4	18	20.31
Lantian 9 (L9)	4	1B.1R	3	7	5.89	4	22	25.14
Jing 035-1 (L12)	4	1B.1R	3	7	7.45	3, 4	12	9.71
Lankao 906-4 (L18)	3	1B.1R	3	1	0.66	3, 4	4	3.81
Huaimai 18 (L22)	3	1B.1R	3	7	5.78	4	13	15.43
58749 (L40)	3	1B.1R	3	1	1.29	3	1	1.53
Y 1496-15 (L43)	3	1B.1R	3	1	0.85	3	7	5.67
LB0458 (L46)	3	–	3	1	0.55	2, 3	1	0.95
SW 8588 (L47)	4	–	3	1	0.66	4	1	1.21
Mian 2000-13 (L51)	3	1B.1R	3	3	4.44	4	5	5.21
351-15 (L54)	4	–	3	1	0.67	3	1	0.87
Neixiang 991 (L55)	3	1B.1R	2, 3	1	1.22	2, 3	4	4.37
01-018 (L59)	4	1B.1R, <i>Lr34</i>	4	5	3.64	4	12	11.43
R97 (L60)	3	1B.1R, <i>Lr34</i>	3	2	2.11	4	13	14.29
LSD (<i>P</i> = 0.05)		–		13	15.25		15	14.36

^a According to the 0–4 Stakman scale as modified by Roelfs et al. (26).

^b 1B.1R = presence of 1B.1R, *Lr34* = presence of *Lr34*, – = absence of 1B.1R and *Lr34*.

^c Slow rusting check.

^d Susceptible check.

on molecular marker detection. Four genotypes (L40 = 58749, L43 = Y1496-15, L51 = Mian 2000-13, and L55 = Neixiang 991) had other known leaf rust resistance genes (*Lr1*, *Lr3ka*, *Lr14a*, *Lr16*, *Lr17*, *Lr18*, and *Lr20*), and two (L18 = Lankao 906-4, and L22 = Huaimai 18) likely possessed unidentified genes (Tables 3 and 4). In these genotypes, the seedling resistance gene(s) were overcome by pathotype THTT, and the slow rusting resistances probably resulted from *Lr34* and other minor APR genes. Slow rusting resistance in LB 0458 (L46) may be derived from CIMMYT wheat germplasm (Table 1). Of all the slow leaf rusting cultivars and lines, 10 genotypes displayed slow rusting resistance to stripe rust (14). Slow rusting in these lines to both diseases might be conferred by common genes, as in the examples of *Lr34/Yr18* and *Lr46/Yr29* (15).

Singh et al. (33) reported that acceptable levels of slow rusting are conferred by combinations of minor additive genes. In the present study, we identified six lines with *Lr34*, but only two lines displayed a significant level of slow rusting resistance in the 2 years of field trials, indicating that *Lr34* alone does not provide adequate resistance. However, *Lr34* combined with other minor resistance genes can provide near-immune levels of leaf rust resistance.

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