

Diversity for Resistance to Leaf Rust in *Triticum aestivum*

SHIWANI and R. G. SAINI, Department of Genetics, Punjab Agricultural University, Ludhiana, India 141004

ABSTRACT

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Multipathotype tests were conducted on 37 selected Indian and international cultivars of wheat (*Triticum aestivum*) against leaf rust (*Puccinia recondita* f. sp. *tritici*) race 77 and its three pathotypes: 77A, 77-1, and 77-2. On the basis of infection types at seedling and adult-plant stages, these cultivars could be classified into 22 distinct groups. These groups seem to carry diverse, undescribed adult-plant resistance (APR) genes. Some of these APR genes exhibit race specificity and can be identified using appropriate races at different developmental stages. Gene *Lr10* is postulated in 10 wheats. Cultivars Girija, HD2135, HD2270, HI977, HUW234, Hybrid 65, and UP262 appear to possess *Lr23*. A resistance gene similar to that in TcLr3ka is suggested to confer APR in CPAN1676. Cultivar Tobarì 66 seems to have *Lr34* and *LrT3*. Because a majority of cultivars were resistant to pathotype 77A and/or 77-1+77-2 in field tests, some may be potential sources of effective and diverse APR factors which, in combination with each other or with known *Lr* genes, may impart durable resistance to leaf rust.

Race 77 and its variants are predominant components of *Puccinia recondita* Rob. ex Desm. f. sp. *tritici* in the Indian subcontinent (17). All known leaf-rust resistance (*Lr*) genes from bread wheat (*Triticum aestivum* L.), except *Lr3ka*, *Lr14b*, and *Lr34*, are ineffective against these pathotypes (24,26,27). In different parts of the world, race 77 is highly variable (M. Paradies, F. Tommasi, and A. Siniscalco, unpublished) and can even infect wheats carrying alien genes such as *Lr26* from *Secale cereale* L. (18). Collaborative efforts at the international level (9,25; R. A. McIntosh, unpublished) suggest that resistance to leaf rust in most wheat cultivars now in production in the world is primarily conferred by adult-plant resistance (APR) genes. Some leaf-rust resistance genes, such as *Lr12*, *Lr13*, *Lr22a*, *Lr22b*, and *Lr34*, have been described as APR genes against various races of the pathogen (2,4,12). The Indian cultivars, however, carry *Lr1*, *Lr3*, *Lr10*, *Lr13*, *Lr17*, *Lr23*, *Lr26*, and *Lr34* (9,10,28). All of these genes except *Lr34* are ineffective against pathotypes 77-1 and/or 77-2. It appears that resistance in the majority of Indian cultivars is due either to *Lr34* or to other undescribed APR genes (9; A. K. Gupta and R. G. Saini, unpublished). Some of these APR genes can be differentiated using variants of race 77. The investigations reported here provide evidence for the diversity of previously undescribed effective APR factors in selected Indian and international cultivars.

MATERIALS AND METHODS

Twenty wheat lines with known *Lr* genes and 28 Indian and nine interna-

tional cultivars (Romany, CSP44, Frontana, Nainari 60, Pavon 76, Oxley, Tobarì 66, Manitou, and Spica) selected for leaf-rust resistance on the basis of glasshouse and field tests conducted from 1974 to 1987, were tested against pathotypes 77, 77A, 77-1, and 77-2 at seedling and adult-plant stages. The wheat land race Agra Local was used as a susceptible check. (The seeds of cultivars are available from the second author, R. G. Saini; R. A. McIntosh, University of Sydney, Australia; and R. P. Singh, Centro Internacional de Mejoramiento de Maiz y Trigo [CIMMYT], Mexico.)

Seven-day-old seedlings of each cultivar were inoculated using a urediospore-talc mixture (inoculum concentration of six to eight spores per 100× microscopic field). Inoculated seedlings were incubated in a dark, humid chamber overnight at 20 ± 1 C, then transferred to artificially illuminated growth chambers maintained at 20 ± 1 C. Eight to 10 seedlings of each wheat line were tested with the four pathotypes in two replications.

For adult-plant tests, three flag leaves from each of two plants per line were inoculated and incubated as described for seedling tests, then transferred to glasshouses at about 25 C. Tests were performed twice for each genotype. Fourteen days after inoculation, infection types (ITs) on the first leaf of seedlings and the flag leaf of adult plants were recorded according to the scale published by Stakman et al (31).

Field evaluations were carried out against pathotype 77A and a mixture of pathotypes 77-1 and 77-2 during wheat seasons 1988-89 and 1990-91, respectively. Each year, two replicates of the material were planted in 2-m paired rows placed 50 cm apart with 15-20 seeds per row. After every 20 rows of experimental

material, Agra Local was planted as an infector row. The rust epidemic was created by repeated inoculations of the infector rows and of the experimental material with urediospores of leaf rust suspended in water (2.0 mg/ml). Terminal disease severity on the flag leaves of adult plants was recorded following the modified Cobb scale (19).

Because the Indian leaf-rust pathotypes are not named according to the North American system of nomenclature (12), avirulence or virulence of the pathotypes used for this study are described. Race 77 is virulent on seedlings of lines with known *Lr* genes from *T. aestivum*, except those carrying *Lr10*, *Lr27+Lr31*, and alien genes *Lr9*, *Lr19*, *Lr21*, *Lr24*, *Lr25*, *Lr26*, and *Lr28*. However, it shows avirulence on adult wheat plants carrying *Lr12*, *Lr22a*, *Lr23*, *Lr33*, and *Lr34*. Unlike 77, pathotype 77A is virulent on *Lr10*; but it remains avirulent on adult plants of wheats possessing *Lr3ka*, *Lr12*, *Lr14b*, *Lr22a*, *Lr23*, *Lr26*, *Lr33*, and *Lr34*. With the exception of *Lr23*, pathotype 77-1, too, is virulent on seedlings of lines with known *Lr* genes from *T. aestivum*. It extends its virulence to the alien gene *Lr26* from *S. cereale*. *Lr3ka*, *Lr14b*, *Lr16*, *Lr20*, *Lr22a*, and *Lr33* are effective against this pathotype only at adult-plant stage. Avirulence of 77-2 is limited to alien genes *Lr9*, *Lr19*, *Lr24*, *Lr25*, *Lr26*, *Lr28*, and *Lr29*, and to adult-wheat plants carrying *Lr3ka*, *Lr14b*, *Lr16*, *Lr21*, *Lr22a*, *Lr33*, and *Lr34*. Virulence against *Lr18* is not available in any of the four pathotypes used for this study. Because this gene is not expected in any of the wheats tested, avirulence of race 77 and its variants on *Lr18* would presumably not influence the interpretations of our results.

RESULTS AND DISCUSSION

On the basis of infection patterns against race 77 and its three variants at two developmental stages, the 37 Indian and international cultivars could be classified into 22 groups (Table 1). Because the infection patterns of only four of these groups (IV, X, XIX, and XX) corresponded to those of testers with known *Lr* genes, namely TcLr22a, PrLr3ka, RL6050, line 896, and TcLr3ka, the resistance of cultivars in other groups seems to be conferred by unknown genes. Many researchers have shown that IT data obtained from cultivars inoculated with pathotypes carrying diverse avirulence/virulence gene combinations can be reliably used for gene identification (1,3,14,15,21). More-

Table 1. Seedling and adult-plant reactions^a on wheats with known or unknown leaf-rust resistance genes against race 77 and its three variants

Material	Pathotype and plant growth stage at inoculation ^b								Field scores ^c	
	77		77A		77-1		77-2		1988-89 (77A)	1990-91 (77-1+77-2)
	SS	APS	SS	APS	SS	APS	SS	APS		
Lines with known leaf-rust resistance genes										
PrLr3ka ^d	3+	1+	33+	;1+2	33+	X	3+	33+	20MR	40MR
TcLr3ka ^d	3+	3+	3	3	3+	X	33+	3	10S	20S
TcLr10	;	;	33+	33+	33+	33+	3+	3+	80S	80S
PrLr12	3+	;1	3+	3	33+	33+	33+	33+	40MR	40MR
TcLr12	3+	3+	33+	33+	33+	33+	3+	33+	50S	50S
TcLr13	3+	33+	3	3	33+	33+	3+	33+	60S	70S
TcLr14b	3+	3	33+	;1	33+	33+	3+	X	40MR	20MR
TcLr22a	3+	1+2	33+	0;	33+	X	33+	X	10S	TS
Thatcher (Lr22b)	3	3	3	3	33+	3+	33+	33+	70S	70S
TcLr23	3	1+2	3	X-	X	;1	33+	3+	40MR	80S
Pakistan 81/Condor-47 ^e (Lr26)	-	-	33+	;	33+	33+	;	;	-	90S
Pakistan 81/Condor-117 ^e (Lr26)	-	-	33+	;	33+	33+	;	;	-	80S
RL6057 (Lr33)	3	2+	X	3	3+	X	33+	X	10MR	40S
RL6058 (Lr34)	33+	0;	3	3	3+	33+	33+	3	10S	TS
RL6059 (Lr33+Lr34)	;	0;	0;	;1	3+	;	33+	X	10S	TS
Line 897 (Lr34)	3+	3	3+	3	33+	33+	33+	3	5MR	20MR
Line 896 (LrT3)	3	33+	3	X-	3+	33+	33+	3	10MS	60S
RL6050 (Lr34+LrT3)	33+	33+	3	;C	3+	33+	33+	3	10MS	TS
Line 920 (Lr34)	33+	33+	3	3	3+	33+	33+	3	20S	60S
Line 922 (LrT3)	33+	3	3	3	3+	33+	33+	3+	20S	60S
Indian and international cultivars										
I	R-	R	R	R	R	R	R	R ^f		
Romany	;1-N	;	1+2-	;	;1+2-	;	;1	;	20S	5MR
II	R	R	R	R	R	R	S	R		
Girija	;	;	;	0;	1+2-	;	33+	;1+	5MR	10S
III	S	R	R	R	S	R	S	R		
CSP44	3+	;	1+2-	;1	3+	;	3	;	10MR	5MR
IV	S	R	S	R	S	R	S	R		
WG138	3+	X	3	;1-	33+	;1-	33+	X+	0	0
VL404	3	;	3	;	3+	X	33+	0;	0	0
HP1209	3	;1-	3	;1	3+	;1	33+	0;	TR	TS
Frontana	3	;	3	;C	33+	;1	33+	X-	10S	30S

(continued on next page)

^a Data from growth chamber and glasshouse evaluations: 0 = no uredia or other macroscopic signs of infection; ; = no uredia but leaves covered with necrotic or chlorotic flecks; 1 = pinhead uredia often surrounded by necrosis; 2 = small to medium uredia with yellowish halo at the back of leaf; X = variable-sized uredia distributed randomly on single leaf; 3 = sporulating uredia that may be associated with chlorosis or rarely necrosis; + = uredia somewhat larger than normal for the infection type; - = uredia somewhat smaller than normal for the infection type; C = more chlorosis than normal for the infection type; and N = more necrosis than normal for the infection type.

^b SS = Seedling stage; APS = adult plant stage.

^c Data from field evaluations: 0 = immune; TR = traces of resistant type uredia; TS = traces of susceptible type uredia; MR = moderately resistant; MS = moderately susceptible; and S = susceptible.

^d Pr = Prelude; Tc = Thatcher. Background cultivars carrying host gene *Lr3ka*.

^e Single-seed descent lines (F₇).

^f R = Resistant; S = Susceptible. Roman numerals indicate groups.

Table 1. (continued from preceding page)

Material	Pathotype and plant growth stage at inoculation ^b								Field scores ^c	
	77		77A		77-1		77-2		1988-89 (77A)	1990-91 (77-1+77-2)
	SS	APS	SS	APS	SS	APS	SS	APS		
V	R	R	R	R	R	R	S	S		
H1977	;1=	;	;	;	X-	;	3+	3+	TR	5S
UP262	;1N	;1	;1-	0;	;	;	33+	3	5MR	TR
HD2270	;1=	;	1	;1+	;	;1	3+	33+	TR	60S
VI	R	R	S	R	R	R	S	S		
Hybrid 65	;1=	0;	3	;	X	0	3+	3+	40S	70S
HD2135	;1N	1+	3	;	X++	;	33+	3	5MR	20MS
VII	R	R	R	R	S	R	S	S		
Nainari 60	;1=	;	;1	;C	33+	0;	33+	33+	TR	10S
VIII	R	R	S	S	R	R	S	R		
HUW37	;1N	;1=	3+	33+	;1	;1	33+	0;	TR	10S
IX	S	S	S	R	S	R	R	R		
CPAN1796	33+	3	3	;1-	33+	;	1+2-	0;	0	TR
X	S	R	S	R	S	R	S	S		
HD2204	3	;1+	3	;1-	33+	;	3	3	TR	40S
HW517	33+	X	3	;	33+	X-	33+	33+	5MR	10MS
XI	S	S	S	R	S	R	S	R		
CPAN1235	33+	33+	3	;1-	3	;	3	0	0	5MR
XII	R	R	R	R	S	S	S	S		
HD2281	;1=	;1	;1=	;1=	33+	3+	3+	33+	TS	80S
XIII	R	R	S	R	S	S	S	S		
HD2285	1+2-	;	3	;	33+	3+	3+	33+	10S	80S
Pavon 76	;1	;	3	;	3+	3	3+	3	5S	5S
HD2278	;1=	;	3	;	3	3	3+	3	TS	60S
XIV	S	S	R	R	S	R	S	S		
UP215	33+	3	1+2-	;1-	3+	X+	3	3	10S	20S
XV	S	S	S	R	R	R	S	S		
HUW234	33+	3	3	;1	;	;	3	3	20MR	90S
XVI	S	R	S	S	S	S	S	R		
VL616	3+	X	33+	3	3+	3	33+	;1+	5S	20MR
XVII	S	R	S	S	S	R	S	S		
Oxley	3+	1+2	33+	3	3+	X-	3	33+	10S	5S
XVIII	R	R	S	S	S	S	S	S		
IWP72	;1-	;1	3	3	3+	3	3+	3	10S	5S
WL2265	;1N	0;	3	33+	3+	33+	33+	3+	30S	60S
HD2329	;1-	;	3	3	3	3	33+	33+	20S	50S
HD2009	;1=	;	33+	3	3+	3	3	33+	40S	30S
XIX	S	S	S	R	S	S	S	S		
Tobari 66	3	33+	33+	;1	3+	3	33+	3	20S	30S
XX	S	S	S	S	S	R	S	S		
CPAN1676	33+	3	3	3	3+	X	3	3	0	5MR
XXI	S	S	S	S	S	S	S	R		
Manitou	33+	33+	33+	3	3+	33+	33+	;1+	TS	5S
XXII	S	S	S	S	S	S	S	S		
WH147	33+	3	3	33+	3+	3+	3+	3+	80S	40S
HS208	3	3	3	3	3+	33+	33+	33+	60S	80S
Spica	3+	3+	3+	3+	3+	3+	33+	3+	80S	80S
WL711	3+	3+	33+	33+	3+	3+	3+	3+	80S	90S
Susceptible check										
Agra Local	3+	3+	3+	3+	3+	33+	33+	3+	90S	90S

over, in most cases the hypotheses derived were shown to be valid by conventional genetic analyses (14,16). Using a similar approach, we have postulated *Lr* genes and an undescribed resistance gene(s) in some of the cultivars under study (Table 2).

The line with host gene *Lr10* was resistant to race 77 and susceptible to pathotype 77A at seedling and adult-plant stages under the defined test conditions (Table 1). *Lr10* is effective against pathotypes with corresponding avirulence at 20 C (6). Therefore, on the basis of ITs against 77 and 77A, cultivars Hybrid 65, HD2135 (group VI), HUW37 (group VIII), HD2285, Pavon 76, HD2278 (group XIII), IWP72, WL2265, HD2329, and HD2009 (group XVIII) appear to carry *Lr10* (Tables 1 and 2). Also, on the basis of tests with Mexican pathotypes, *Lr10* is predicated in Hybrid 65, HD2135, IWP72, HD2329, HD2009 (28), and Pavon 76 (29). Cultivar Gabo, one of the parents of Hybrid 65 and WL2265, carries *Lr10* (13) and may be the source of this gene in the latter two cultivars. Because the isogenic line TcLr10 was susceptible in the field, *Lr10* did not contribute to field resistance of the wheats proposed to carry this gene. Present observations along with earlier reports (26) explain the ineffectiveness of *Lr10* in India.

The genes *Lr23* and *Lr26* confer APR to pathotype 77A (Table 1). Therefore, field resistance shown by many wheats during 1988–89 may be due to either of these genes. Pathotype 77-1 is virulent on *Lr26* and avirulent on *Lr23* at seedling as well as adult-plant stages, and pathotype 77-2 is virulent on *Lr23* and avirulent on *Lr26*. To eliminate the resistance imparted by *Lr23* or *Lr26*, a mixture of pathotypes 77-1 and 77-2 was used for field tests during 1990–91. Therefore, the cultivars maintaining resistance during both test years would have either *Lr34* or an undescribed APR gene(s).

Lr23 is operative at higher temperatures (6). It confers APR to pathotype 77A and provides resistance against 77-1 effective throughout the plant life,

but succumbs to the virulence of 77-2. On the basis of ITs against pathotypes 77A, 77-1, and 77-2, cultivars Girija (group II), HI977, UP262, HD2270 (group V), Hybrid 65, HD2135 (group VI), and HUW234 (group XV) appear to possess *Lr23* (Tables 1 and 2). Tests on Girija, HI977, UP262, HD2270, Hybrid 65, and HD2135 using Mexican pathotypes (28), and on HUW234 with Australian leaf-rust isolates (R. G. Saini, unpublished), clearly suggest the presence of *Lr23* in these Indian cultivars. Hybrid 65 may have inherited *Lr23*, like *Lr10*, from Gabo (13). Because Girija, HI977, UP262, and HD2135 were resistant to the mixture of pathotypes 77-1 and 77-2 in field tests (Table 1), each of these wheats is expected to carry, apart from *Lr23*, one or more resistance genes, which may be effective against all three pathotypes of race 77. This additional resistance in Girija could be differentiated with pathotype 77-2, as adult plants of this cultivar were resistant to it. The resistant ITs against 77 and 77A on seedlings and adult plants of HD2270 (group V) may be due to an additional gene ineffective against pathotype 77-1 or 77-2 under field conditions. Although the field scores of HD2281 (group XII), HD2285, HD2278 (group XIII), and WL2265 (group XVIII) suggest the presence of *Lr23* in these cultivars, the susceptible ITs against pathotype 77-1 on seedlings and adult plants rule out such a possibility (Table 1). We think that the resistance of these four wheats during 1988–89 was due to an undescribed resistance gene(s) effective only against pathotype 77A. In group XIII, Pavon 76 was resistant during both test years, indicating the presence of a resistance factor(s) effective against pathotypes 77-1 and 77-2, in addition to a factor(s) similar to that hypothesized in HD2285 and HD2278.

The resistance of Romany (group I) to all four pathotypes at seedling and adult-plant stages (Table 1) may be due to a combination of several genes. The similarity in infection patterns and field scores between the cultivars WG138, VL404, HP1209, and Frontana (group IV), and the single gene line TcLr22a, suggests the presence of *Lr22a* in these four wheats. Because *Lr22a* was derived from *Aegilops squarrosa* L. (7,23), which does not appear in the pedigrees of WG138, VL404, HP1209, and Frontana, its presence in these wheats is unlikely. However, the possibility that *Lr22a* was incorporated into bread wheat during its evolution cannot be ruled out. Singh and Gupta (28) proposed that a gene effective at low temperature probably confers field resistance to HP1209 against Mexican pathotypes of leaf rust. Penjamo 62, one of the parents of HP1209, also possesses a resistance gene operative at low temperature (29). Hence, this gene from Penjamo 62 might have been transferred

into HP1209. Furthermore, Frontana, which carries *Lr34* (8,30), is involved in the parentage of VL404, also postulated to carry *Lr34* (28). Thus, cultivars HP1209 and VL404, though exhibiting similar infection patterns in the present study, may carry different resistance genes. An allelic test between the two wheats also revealed dissimilarities in their resistance (Shiwani and R. G. Saini, unpublished).

HD2204 and HW517 (group X) developed ITs similar to those of the single-gene line PrLr3ka, and reactions on CPAN1676 (group XX) corresponded to the infection pattern of isogenic line TcLr3ka (Table 1). Although single-gene lines for gene *Lr3ka* in Prelude and Thatcher backgrounds were resistant in field tests during 1988–89 and 1990–91, these lines did not show similar ITs against either race 77 or pathotype 77A. Gene *Lr3ka*, originally identified from cultivar Klein Aniversario (11), has remained effective under field conditions against Indian leaf-rust races. Cultivar Prelude, a susceptible parent for developing isogenic lines, shows field resistance against highly virulent Indian races (R. G. Saini, unpublished). It is, therefore, not possible to indicate whether the resistance of HD2204 and HW517 is due to *Lr3ka* or to a gene with phenotypic effects similar to those of Prelude resistance. However, a gene similar to that in TcLr3ka may be imparting APR to CPAN1676 against the three pathotypes of race 77. There are indications of additional resistance in TcLr3ka against pathotypes 77A+77-1 (R. G. Saini, unpublished). Browder (2) also proposed such a possibility for near-isogenic lines with *Lr3* alleles. Though the ITs on HD2204, HW517, and isogenic line PrLr3ka were similar, different disease severities on HD2204 and HW517 during 1990–91 indicate the presence of distinct APR factors in the two cultivars.

In group XVIII, cultivars IWP72 and HD2009 maintained field resistance against all three pathotypes. During 1990–91, disease severity on WL2265 and HD2329 increased to 60S and 50S, respectively (Table 1). These observations suggest that genes imparting resistance to IWP72 and HD2009 are different than those in WL2265 and HD2329. Although the four cultivars developed susceptible ITs against three pathotypes of race 77 at both developmental stages, low disease scores on these latter wheats during 1988–89, and on IWP72 and HD2009 during 1990–91, suggest their resistances to be nonhypersensitive. Cultivars VL616 and Oxley (groups XVI and XVII, respectively) also carried nonhypersensitive APR against 77A. The available literature supports nonhypersensitive responses of HD2009 and HD2329 against pathotype 77A (9).

Cultivar Tobar 66 in group XIX showed ITs similar to those of line 896

Table 2. Postulated *Lr* genes in some Indian and international cultivars

Cultivar(s)	Postulated <i>Lr</i> gene(s)
Girija, HI977, UP262, HD2270	23, + ^a
Hybrid 65	10, 23
HD2135	10, 23, +
HUW37, HD2285, Pavon 76, HD2278, IWP72, WL2265, HD2329, HD2009	10, +
HUW234	23
Tobar 66	34, T3

^a + Indicates additional undescribed resistance factor(s) that may or may not be similar in any two cultivars.

and RL6050 against race 77 and its three pathotypes (Table 1). RL6050 and Tobar 66 were resistant under field conditions during both test seasons, while line 896 was susceptible to the mixture of pathotypes 77-1 and 77-2. This difference in disease scores indicates the presence of at least two resistance genes among these three wheats. Line 896 and RL6050, derivatives from cultivar Terenzio, carry *LrT3* and two complementary genes *Lr34+LrT3*, respectively (4,8). The resistance of line 896 to pathotype 77A was due to *LrT3*, but this gene was ineffective against pathotypes 77-1 and 77-2. *Lr34* confers resistance in an epidemic of pathotypes 77A and 77-1 (27). Thus, the field resistance of RL6050 during 1990-91 was apparently due to *Lr34*. Because RL6050 and Tobar 66 had similar infection patterns and disease severities, the latter seems to carry *Lr34+LrT3*.

Cultivars in group XXII were susceptible to race 77 and its variants at both developmental stages and in the field, except for WH147, which showed a disease score of 40S during 1990-91. Thus, WH147 has an APR gene that can be identified by using pathotypes 77A and 77-1 or 77-2.

As the known *Lr* genes in the 37 cultivars tested are ineffective against variants of race 77, resistance in the majority of these wheats is probably due to undescribed APR factors. In addition to *Lr23*, cultivars Girija, HI977, UP262, and HD2135 appear to carry an APR gene(s) conferring field resistance against the three pathotypes of race 77 (for summary see Table 2). An additional resistance gene(s) in HD2281, HD2285, HD2278, WL2265, and HD2329 is effective only against pathotype 77A. Cultivar CPAN1676 seems to possess a resistance gene similar to that in TcLr3ka. The differential resistance of some cultivars to 77A or 77-1+77-2, and of other cultivars to all three pathotypes, suggests that APR factors in these wheats are genetically diverse. Because none of the cultivars studied has an alien parent in its pedigree, these unidentified resistance factors appear to have originated from hexaploid wheats. In breeding programs, it is easier to use hexaploid wheats than aliens as a source of resistance genes. Briefly, the experiments on 37 cultivars against four pathotypes at two developmental stages revealed additional APR genes. If tests are conducted on more cultivars at different developmental stages against a wide spectrum of pathotypes, more undescribed APR genes may be detected.

Lr34 is a widely distributed gene (5,22). Frontana, which possesses *Lr34* (8,30), is the ultimate source of leaf-rust resistance for many Indian wheats. It is therefore likely that some of the cultivars used in this study carry *Lr34*. However,

the testers for *Lr34*—RL6058 and line 897—show additional resistance against pathotypes 77A, 77-1, and 77-2 (27; Shiwani and R. G. Saini, unpublished), making identification of *Lr34* in any wheat difficult. Furthermore, the presence of *Lr13* in more than 50% of the resistant wheats in this investigation (9) indicates its possible role in enhancing their levels of resistance (25). *Lr13* in combination with other resistance genes may impart durable resistance to leaf rust (20,22). To achieve this objective of durable resistance, effective and diverse APR factors need to be identified.

As suggested by these results, many APR factors are race-specific and can be detected by using appropriate races, both at different developmental stages and under field conditions. Identification of these diverse APR genes through multipathotype tests and systematic genetic analyses may help us synthesize variable combinations of APR genes that will provide durable resistance to leaf rust in the future.

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