



***Aegilops*-derived specific genes in common wheat and their introgression into Indian bread wheat cultivars**

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(Received: July 2000; Revised: February 2001; Accepted: March 2001)

Abstract

Nine diverse wheat stocks carrying *Aegilops*-derived known genes conditioning resistance to rusts and 39 accessions of *Aegilops*, viz., *Ae. squarrosa* (18), *Ae. speltoides* (17), *Ae. umbellulata* (3) and *Ae. comosa* (1) were evaluated for adult plant resistance to stem rust, leaf rust and stripe rust and seedling resistance to powdery mildew. The study revealed that the genes *Lr9*, *Lr28*, *Lr32*, *Lr37*, *Sr32* and *Yr8* conditioned a high degree of resistance whereas *Lr21*, *Lr22a*, *Sr33*, *Sr38* and *Yr17* conferred moderate resistance. *Aegilops comosa* derived gene *Sr34* was ineffective against stem rust in the Nilgiris. The dominant leaf rust resistance genes *Lr9*, *Lr28*, *Lr32* and *Lr37* were introgressed into 16 bread wheat cultivars through a backcross programme. The improved cultivars carrying *Lr28* were observed to be moderately resistant to powdery mildew (score 2) whereas the backcross derivatives carrying *Lr9* and *Lr37* showed enhanced susceptibility to powdery mildew (score 4) as compared to the recurrent parents (score 3). Accessions of *Ae. speltoides*, a suspected donor of B genome, exhibited a high degree of resistance to rusts and powdery mildew whereas the accessions of *Ae. squarrosa*, the donor of the D genome, were found susceptible to rusts but showed moderate to high degree of seedling resistance to powdery mildew. In general, the accessions of *Ae. umbellulata* and *Ae. comosa* carried high resistance to rusts and powdery mildew although the former showed high susceptibility to stem rust. Five wheat stocks were found to be non-carriers of genes for hybrid necrosis (*nel ne2*) whereas four stocks carried a weak allele for progressive hybrid necrosis

Key words: *Aegilops*, *Puccinia recondita*, resistance, back-cross lines, powdery mildew, hybrid necrosis

Introduction

Wild relatives of wheat including *Aegilops* spp. are rich sources of useful genes, particularly those for disease resistance and have been exploited to develop commercial cultivars carrying resistance to rusts and powdery mildew. A number of resistance genes from several species of *Aegilops* have been transferred into

the genetic background of common wheat [1]. However, alien genetic transfers are often associated with undesirable traits restricting their use in breeding programmes [2]. Nevertheless, they constitute a reservoir of potentially useful genes for disease and pest resistance, desirable agronomic traits and quality characteristics. The present study was carried out to assess the effectiveness of *Aegilops*-derived resistance genes under natural conditions at Wellington, an important 'hot spot' for rusts and other foliar diseases in south India. This communication also reports incorporation of *Aegilops*-derived rust resistance genes, namely, *Lr9*, *Lr28*, *Lr32* and *Lr37* into commercial Indian bread wheat cultivars through a judicious backcross programme. The distribution of genes for hybrid necrosis was also studied in the stocks carrying specific genes for rust resistance.

Materials and Methods

The material used in the present study comprised 10 diverse wheat stocks carrying *Aegilops*-derived specific genes conditioning resistance to stem rust, leaf rust and stripe rust; 16 Indian commercial wheat cultivars which are susceptible to rusts particularly to leaf rust, namely, C 306, HD 2009, HD 2285, HD 2329, HD 2402, HD 2687, HS 240, HUW 234, J 24, Kalyansona, Lok 1, NI 5439, PBW 226, Sonalika, WHI47 and WH 542 and 39 accessions belonging to four species of *Aegilops*, viz., *Ae. squarrosa* (18 accessions), *Ae. speltoides* (17 accessions), *Ae. umbellulata* (3 accessions) and *Aegilops comosa* (one accession). The wheat stocks and commercial wheat cultivars were critically evaluated for 12 seasons, whilst the backcross lines and the accessions of *Aegilops* were tested for four seasons under high levels of natural infection of rust. The rust reactions were recorded by combining severity (percentage leaf area affected) and response (type of reaction) at the adult plant stage. The stocks were also studied for seedling resistance to a sample

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of *Erysiphe graminis* DC. f. sp. *tritici* em. Marchal collected in the Nilgiris.

The seedling inoculations for powdery mildew were carried out as described earlier [3] and the seedlings were scored for resistance on 0 to 4 scale [4]. The wheat stocks were crossed to two *Triticum aestivum* L. testers, C 306 (*Ne1Ne1 ne2ne2*) and Sonalika (*ne1ne1 Ne2Ne2*). The genotypes of the stocks with respect to the genes for necrosis were deduced from the phenotype of the F₁ plants. Since the genes *Lr9*, *Lr28*, *Lr32* and *Lr37* were dominant in nature, the standard backcross method was followed to introgress the specific genes into commercial Indian bread wheat cultivars.

Results and Discussion

Results are summarised in Tables 1, 2 and 3. Table 1 shows that wheat stocks possessing *Aegilops*-derived alien genes viz., *Lr9*, *Lr28*, *Lr32*, *Lr37*, and *Yr8* conditioned high degree of resistance whereas those with genes *Lr21*, *Lr22a*, *Sr33*, *Sr38* and *Yr17* conferred moderate resistance. The *Aegilops comosa* derived gene *Sr34* was ineffective against stem rust. Backcross derivatives carrying the alien resistance genes and their response to rust and powdery mildew are presented in Table 2. It was observed that the chromosome segment carrying *Lr28* from *Ae. speltoides* is associated with moderate resistance to powdery mildew (score 2) whilst the segment carrying the linked genes *Sr38* *Lr37* and *Yr17* (*Ae. ventricosa*) as well as the segment with *Lr9* (*Ae. umbellulata*) were associated with enhanced

susceptibility to powdery mildew in the backcross derivatives (score 4) compared to recurrent parents (score 3). Enhanced susceptibility to powdery mildew is also evident on the donor line compared to Thatcher and its derivatives (Table 1). Kochumadhavan *et al.* [5] reported that petkus rye derived winter wheats Aurora, Burgas 2, Clement, Kavkaz and Skorospelka 35, all carrying *Pm8* conferred high resistance (score 1) to powdery mildew. In the present study spring wheat cultivars, namely, HD 2687, HS 240 and WH 542 carry the the same cereale rye derived resistance gene *Sr31* *Lr26* *Yr9* and *Pm8*. However, the gene *Pm8* is not expressed in these wheats which can be attributed to the suppression of *Pm8* by a dominant gene *Su Pm8* located on chromosome 1AS of wheat genome [6,7]. Tomar and Menon [8] reported fast rusting to stem rust on the backcross derivatives with genes *Lr28* or *Lr32*. Backcross derivatives with genes *Lr32* and *Lr37* were also associated with terminal clubbiness of spikes.

The gene *Lr9* has been transferred from *Ae. umbellulata* to common wheat [9]. It has been reported that *Lr9* conferred seedling resistance to 13 Indian races of *Puccinia recondita* Rob. ex. Desm. [10]. However, the gene *Lr9* could not be exploited in hard red spring wheats [11] because of its linkage with genes for inferior baking quality, but the same resistance had been incorporated into US soft red winter wheats including Abe, Arthur 71 and Riley 67. Races of *P. recondita* virulent on cultivars with *Lr9* in the United States have been reported [12]. Huerta Espino [13]

Table 1. Adult plant response of *Aegilops* derived genes to stem rust, leaf rust, stripe rust and powdery mildew and the genotype of stocks with regards to hybrid necrosis

Stock	Source	Gene(s) present	Reaction to			Response to powdery mildew	Hybrid necrosis gene present
			Stem rust	Leaf rust	Stripe rust		
Abe	<i>Aegilops umbellulata</i>	<i>Sr36</i> , <i>Lr9</i> <i>Pm6</i>	10R MR	F-40S+	40S	1	ne1 ne2
Transfer	<i>Ae. umbellulata</i>	<i>Lr9</i>	90S	F-40S+	40S	3	Ne1 ne2
Thatcher*6/R.L.5406	<i>Ae. squarrosa</i> var. <i>meyeri</i>	<i>Sr21</i> , <i>Sr33</i> <i>Lr21</i>	20MR- 40MR	20MR- 30MR	70S	3	ne1 ne2
Thatcher*6/R.L.5404	<i>Ae. squarrosa</i> var. <i>strangulata</i>	<i>Lr22a</i>	90S	30MR MSS 60MR MSS	F-TMR	3	ne1 ne2
CS 2A/2M 4/2	<i>Ae. speltoides</i> <i>Ae. Comosa</i>	<i>Sr34</i> , <i>Lr28</i> <i>Yr8</i>	90S	F	F	0	Ne1 ne2
C 86-8/Kalyansona	<i>Ae. squarrosa</i>	<i>Lr32</i>	70S	F	90S	3	ne1 ne2
Thatcher*8/VPM 1(R.L.6081)	<i>Ae. ventricosa</i>	<i>Sr38</i> , <i>Lr37</i> <i>Yr17</i>	10MR- 20MR,MS	F	15MS- 20S	4	ne1 ne2
W 3531	<i>Ae. speltoides</i>	<i>Sr32</i>	TR MR-10R MR	F-TR	30S	2	Ne1 ne2
Compare Thatcher	<i>Ae. comosa</i>	<i>Sr34</i> , <i>Yr8</i>	90S 70S	F-5R-10MR 90S	F 80S	1 3	Ne1 ne2 ne1 ne2

+ = Rust reactions observed during 1999-2000 season indicating ineffectivity of *Lr9*, R MR reactions of stem rust appear late at maturity.

Table 2. Adult plant response to rusts and seedling response to powdery mildew in Indian bread wheat cultivars carrying *Aegilops* derived genes

Cultivar	Gene(s) present	Adult plant reaction to			Seedling response to powdery mildew
		Stem rust	Leaf rust	Stripe rust	
C 306*2/Abe	<i>Lr9</i>	90S	F-50S+	F	4
C 306*9//CS2A/2M 4/2	<i>Lr28</i>	90S	F	F	2
C 306*4//C 86-8/Kalyansona F4	<i>Lr32</i>	90S	F	F	3
C 306*2//Thatcher*8/VPM 1	<i>Sr38 Lr37 Yr17</i>	20MS	F	F	4
C 306		90S	90S	F	3
HD 2009*3/Abe	<i>Lr9</i>	40S	F-50S+	90S	4
HD 2009*3//cs/2A/2M 4/2	<i>Lr28</i>	60S	F	90S	2
HD 2009		40S	60S	100S	3
HD 2285*6/Abe	<i>Lr9</i>	30MS	F-40S+	30S	2
HD 2285*7//CS 2A/2M 4/2	<i>Lr28</i>	50MS,S	F	30S	2
HD 2285*5//C 86-8/Kalyansona F4	<i>Lr32</i>	50MS,S	F	30S	3
HD 2285*5//Thatcher*8/VPM 1	<i>Sr38 Lr37 Yr17</i>	20MS	F	10MS	4
HD 2285		30MS	100S	30S	3
HD 2329*5/Abe	<i>Lr9</i>	80S	F-40S+	80S	4
HD 2329*7//CS 2A/2M 4/2	<i>Lr28</i>	90S	F	90S	2
HD 2329*5//C 86-8/Kalyansona F4	<i>Lr32</i>	90S	F	90S	3
HD 2329*5//Thatcher*8/VPM 1	<i>Sr38 Lr37 Yr17</i>	50MS	F	40MS	4
HD 2329		80S	90S	90S	3
HD 2402*4/Abe	<i>Lr9</i>	30S	F-30S+	F	4
HD 2402*3//CS 2A/2M 4/2	<i>Lr28</i>	40S	F	F	2
HD 2402		30S	100S	F	3
HD 2687*2//CS 2A/2M 4/2	<i>Sr31, Lr26, Lr28, Yr9, Pm8</i>	10RMR	F	F	2
HD 2687*2//C 86-8/Kalyansona F4	<i>Sr31, Lr26, Lr32, Yr9, Pm8</i>	10RMR	F	F	3
HD 2687*3//Thatcher*8/VPM 1	<i>Sr31, Sr38, Lr26, Lr37</i>	5RMR	F	F	4
HD 2687	<i>Sr31, Lr26, Yr9, Pm8</i>	10R,MR	80S	F	3
HS 240*3/Abe	<i>Sr31, Lr9, Lr26, Yr9, Pm8</i>	10R,MR	F-30S+	F	4
HS 240*6//CS 2A/2M 4/2	<i>Sr31, Lr26, Lr28, Yr9, Pm8</i>	5R MR	F	F	2
HS 240*2//C 86-8/Kalyansona F4	<i>Sr31, Lr26, Lr32, Yr9, Pm8</i>	5R MR	F	F	3
HS 240*2//Thatcher*8/VPM 1	<i>Sr31, Sr28, Lr26, Lr37, Yr9, Yr17, Pm8</i>	F	F	F	4
HS 240	<i>Sr31, Lr26, Yr9, Pm8</i>	5R MR	70S	F	3
HUW 234*6/Abe	<i>Lr9</i>	20MS S	F-50S+	F	4
HUW 234*5//CS 2A/2M 4/S	<i>Lr28</i>	40MS S	F	F	2
HUW 234*5//C 86-8/Kalyansona F4	<i>Lr32</i>	40MS S	F	F	3
HUW 234*5//Thatcher*8/VPM 1	<i>Sr38, Lr37, Yr17</i>	15MS S	F	F	4
HUW 234		20MS S	100S	F	3
J 24*7//CS 2A/2M 4/2	<i>Lr28</i>	90S	F	100S	2
J 24*3//C 86-8/Kalyansona F4	<i>Lr32</i>	90S	F	100S	3
J 24		90S	100S	100S	3
Kalyansona*4/Abe	<i>Lr9</i>	80S	F-50S+	90S	4
Kalyansona*10//CS 2A/2M 4/2	<i>Lr28</i>	90S	F	90S	2
Kalyansona*5//C 86-8/Kalyansona F4	<i>Lr32</i>	90S	F	90S	3
Kalyansona*5//Thatcher*8/VPM 1	<i>Sr38, Lr37, Yr17</i>	20MS	F	10MS	4
Kalyansona		80S	80S	90S	3
Lok-1*5/Abe	<i>Lr9</i>	70S	F-50S+	90S	4
Lok-1*7//CS 2A/2M 4/2	<i>Lr28</i>	90S	F	80S	2
Lok-1*5//C86-8/Kalyansona F4	<i>Lr32</i>	90S	F	80S	3
Lok-1*5//Thatcher*8/VPM 1	<i>Sr38, Lr37, Yr17</i>	20MS	F	30MS	4
Lok-1		70S	80S	80S	3
NI 5439*4/Abe	<i>Lr9</i>	90S	F-50S+	100S	4
NI 5439*7//CS 2A/2M 4/2	<i>Lr28</i>	90S	F	100S	2

Table 2. (Contd.)

Cultivar	Gene(s) present	Adult plant reaction to			Seedling response to powdery mildew
		Stem rust	Leaf rust	Stripe rust	
NI 5439*5//C 86-8/Kalyansona F4	<i>Lr32</i>	90S	F	100S	3
NI 5439*5/Thatcher*8/VPM 1	<i>Sr38, Lr37, Yr17</i>	20MS	F	30MS	4
NI 5439		90S	90S	100S	3
PBW 226*5/Abe	<i>Lr9</i>	20S	F-40S+	F	4
PBW 226*5//CS 2A/2M 4/2	<i>Lr28</i>	40S	F	F	2
PBW 226*5//C 86-6/Kalyansona F4	<i>Lr32</i>	40S	F	F	3
PBW 226*5/Thatcher*8/VPM 1	<i>Sr38, Lr37, Yr17</i>	15MS-15S	F	F	4
PBW 226		20S	90S	F	3
Sonalika*7/Abe	<i>Lr9</i>	60S	F-30S+	60S	4
Sonalika*8//CS 2A/2M 4/2	<i>Lr28</i>	80S	F	70S	2
Sonalika*5//C 86-8/Kalyansona F4	<i>Lr32</i>	80S	F	70S	3
Sonalika*5/Thatcher*8/VPM 1	<i>Sr38, Lr37, Yr17</i>	20S	F	30MS	4
Sonalika		60S	80S	60S	3
WH147*5/Abe	<i>Lr9</i>	90S	F-60S+	90S	4
WH147*7//CS 2A/2M 4/2	<i>Lr28</i>	100S	F	90S	2
WH147*5//C 86-8/Kalyansona F4	<i>Lr32</i>	100S	F	90S	3
WH147*5/Thatcher*8/VPM1	<i>Sr38, Lr37, Yr17</i>	20MS-20S	F	10MS	4
WH147		90S	90S	90S	3
WH542*5/Abe	<i>Sr31, Lr9, Lr26, Yr9, Pm8</i>	15R MR	F-40S+	F	4
WH542*6//CS 2A/2M 4/2	<i>Sr31, Lr26, Lr28, Yr9, Pm8</i>	15R MR	F	F	2
WH542*5//C 86-8/Kalyansona F4	<i>Sr31, Lr26, Lr32, Yr9, Pm8</i>	10R MR	F	F	2
WH542*3/Thatcher*8/VPM 1	<i>Sr31, Sr38, Lr26, Lr37, Yr9, Yr17, Pm8</i>	5R MR	F	F	4
WH542	<i>Sr31, Lr26, Yr9, Pm8</i>	10R MR	80S	F	3

+ = Susceptible reactions recorded during 1999-2000 season indicating ineffectivity of *Lr9*.

also reported field isolates with virulences for *Lr9* from Italy, Burundi and Pakistan. *Lr9* consistently displayed total immunity to leaf rust at Wellington for over 25 years until it was rendered ineffective during September 1998 by a new pathotype (Menon unpublished). The isolate with virulence for *Lr9* is similar to the pathotype 77-5 with additional virulence for *Lr9* (Nayar Pers. Comm.). However, this gene continues to be very effective in many other parts of the world.

Aegilops squarrosa derived genes *Lr21* and *Lr22a* conferred moderate resistance to leaf rust at adult plant stage. The lines carrying these genes were reported to be susceptible in seedling stage to most of the prevalent Indian races of the leaf rust pathogen [14], but these were found to carry a high degree of adult plant resistance. According to McIntosh (Pers. Comm.) the *Lr21* stock possesses a linked gene for stem rust resistance with a same specificity as *Sr21* and also with *Sr33* which confers moderate resistance to stem rust. The gene *Lr22a* in the Thatcher background tested in the current study also exhibited resistance to stripe rust compared to the other Thatcher derivatives.

This also suggest the possibility of genetic linkage between *Lr22a* and stripe rust resistance.

The *Ae. speltoides* derived resistance gene *Lr28* was very effective in determining resistance to leaf rust. The gene *Lr28* has been reported [10] to confer seedling resistance to 10 prevalent Indian races of leaf rust. The translocation derivatives 3/8 and 4/2 were also resistant to stripe rust (*Puccinia striiformis* West.) at Wellington apparently due to the presence of *Yr8*. The line Compare, produced through homoeologous recombination on 2D, carries the linked genes *Sr34* and *Yr8* from *Aegilops comosa*. *Yr8* conferred high resistance to stripe rust whilst *Sr34* was totally ineffective against stem rust. From the results in Table 1 it appears that line CS 2A/2M 4/2 also possess resistance to powdery mildew additional to that shown by other Chinese Spring based lines such as Transfer. The only available strain of *Ae. comosa* possessed excellent adult plant resistance to all the three rusts as well as seedling resistance to powdery mildew (Table 3). *Ae. squarrosa* derived resistance gene *Lr32* and *Ae. ventricosa* derived gene *Lr37* confer total immunity to

leaf rust at adult plant stage at Wellington. Pathotypes of leaf rust prevalent in India were avirulent on *Lr32* and *Lr37* at the seedling stage (Tomar-unpublished). Sawhney and Sharma [16] observed that *Lr32* displayed 2 reaction against Indian leaf rust pathotypes in the seedling stage. The backcross derivatives with *Lr32* were also observed to carry enhanced resistance to head blight caused by *Fusarium graminearum* compared to the recurrent parents (Menon unpublished). Although the linked genes *Sr38* and *Yr17* in the donor line displayed moderate resistance to stem rust and stripe rust respectively, the authors could not combine this moderate resistance with total immunity to leaf rust conferred by *Lr37* in the backcross derivatives of HD 2329, Lok 1 and Sonalika whereas the same could be combined in HD 2285, Kalyansona, NI 5439 and WH 147.

Aegilops speltoides derivatives possessing *Sr32* showed a high degree of resistance to stem rust. It is significant to note that the line W 3531 carrying *Sr32* also exhibited excellent mature plant resistance to leaf rust which could be due to genes *Lr12/Lr31* alongwith the adult plant resistance gene *Lr34* imparting durable resistance to leaf rust in the Chinese Spring background. Similarly the line Compair in the Chinese Spring background exhibited resistance to leaf rust.

Kihara *et al.* [17] reported that *Aegilops squarrosa* included numerous forms with resistance to stem rust and leaf rust. Kerber and Dyck [18] determined a higher frequency (44.7%) of forms resistant to leaf rust than to stem rust in a study of 85 accessions. Most of the 18 accessions tested in the present study did not possess adequate resistance to all the three rusts but more particularly to stem rust (Table 3). Four strains showed resistance to leaf rust and a similar number including one strain of *Ae. squarrosa* var. *strangulate* exhibited high degree of resistance to stripe rust. These results are in agreement with those of Kerber and Dyck [18] indicating that more forms of

Table 3. Number of accessions of *Aegilops* resistant to wheat rusts and powdery mildew

Species	No. of accessions tested	Number of accessions resistant to			
		Stem rust	Leaf rust	Stripe rust	Powdery mildew
<i>Aegilops squarrosa</i>	18	0	4	4	14+(4)
<i>Aegilops speltoides</i>	17	14	17	9	17
<i>Aegilops umbellulata</i>	3	0	3	2	3
<i>Aegilops comosa</i>	1	1	1	1	1

(+) = moderately resistant, with limited growth of mycelium. Accessions displayed hypersensitive flecks with small and moderate size of uredia with necrosis and chlorosis were considered to be resistant while large uredia with or without necrosis or chlorosis were categorized as susceptible.

Aegilops squarrosa are resistant to leaf rust than to stem rust.

Most of the 17 accessions of *Aegilops speltoides* evaluated by us (Table 3) exhibited high degree of resistance to all the three rusts. Table 3 shows that the majority of accessions of *Aegilops* were resistant to powdery mildew. However, four accessions belonging to three varieties of *Ae. squarrosa*, viz., anthera (1), meyeri (1) and typica (2) possessed only moderate resistance (score 2) to powdery mildew.

Hybrid necrosis

Hybrid necrosis, expressed as progressive death of F_1 hybrids, frequently noted in inter and intraspecific wheat crosses. Hybrid necrosis caused by the interaction of complementary genes *Ne1* and *Ne2*. Lines, Transfer (*Lr9*), CS 2A/2M 4/2 (*Sr34 Lr28* and *Yr8*), W 3531 (*Sr32*) and Compair (*Sr34/Yr8*) are in Chinese Spring background and carry a weak allele of *Ne1*. Weak expression of hybrid necrosis can be precluded through judicious and careful selection of genotypes which are normal particularly in the progenies of early backcross generation. Hybrid necrosis can also be precluded by using a non-carrier variety as a bridge in crosses between *Ne1* carriers and *Ne2* carriers. The other stocks tested were found to be non carriers.

Acknowledgements

The authors express their appreciation and gratitude to Drs. R.N.sawhney, Indian Agricultural Research Institute, New Delhi (now supranational) and R.A. McIntosh, University of Sydney, Australia for their generous supply of donor seed and critically going through the manuscript. The authors also thank Mr. S. Bojan, IARI Regional Station, Wellington, India for technical assistance.

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