RESEARCH ARTICLE

Introgression of a leaf rust resistance gene from *Aegilops caudata* to bread wheat

AMANDEEP KAUR RIAR[1], SATINDER KAUR[1], H. S. DHALIWAL[1,2], KULDEEP SINGH[1] and PARVEEN CHHUNEJA[1*]

[1]*School of Agricultural Biotechnology, Punjab Agricultural University, Ludhiana 141 004, India*
[2]*Present address: Akal School of Biotechnology, Eternal University, Baru Sahib 173 101, India*

Abstract

Rusts are the most important biotic constraints limiting wheat productivity worldwide. Deployment of cultivars with broad spectrum rust resistance is the only environmentally viable option to combat these diseases. Identification and introgression of novel sources of resistance is a continuous process to combat the ever evolving pathogens. The germplasm of nonprogenitor *Aegilops* species with substantial amount of variability has been exploited to a limited extent. In the present investigation introgression, inheritance and molecular mapping of a leaf rust resistance gene of *Ae. caudata* (CC) acc. pau3556 in cultivated wheat were undertaken. An F_2 population derived from the cross of *Triticum aestivum* cv. WL711 – *Ae. caudata* introgression line T291-2 with wheat cultivar PBW343 segregated for a single dominant leaf rust resistance gene at the seedling and adult plant stages. Progeny testing in F_3 confirmed the introgression of a single gene for leaf rust resistance. Bulked segregant analysis using polymorphic D-genome-specific SSR markers and the cosegregation of the 5DS anchored markers (*Xcfd18*, *Xcfd78*, *Xfd81* and *Xcfd189*) with the rust resistance in the F_2 population mapped the leaf rust resistance gene (*LrAC*) on the short arm of wheat chromosome 5D. Genetic complementation and the linked molecular markers revealed that *LrAC* is a novel homoeoallele of an orthologue *Lr57* already introgressed from the 5M chromosome of *Ae. geniculata* on 5DS of wheat.

[Riar A. K., Kaur S., Dhaliwal H. S., Singh K. and Chhuneja P. 2012 Introgression of a leaf rust resistance gene from *Aegilops caudata* to bread wheat. *J. Genet.* **91**, 155–161]

Introduction

Rusts are the most devastating fungal diseases posing a threat to wheat production worldwide. Leaf rust, caused by the heteroecious basidiomycete *Puccinia triticina* is a major disease in most of the wheat-growing areas where its epidemics cause significant yield losses (German *et al.* 2007; Kolmer *et al.* 2007; Park *et al.* 2007). Development and deployment of cultivars with host genetic resistance is the most eco-friendly way to reduce the losses. A total of 67 leaf rust resistance genes (*Lr*) and 48 stripe rust resistance genes (*Yr*) have been catalogued so far (McIntosh *et al.* 2008, 2010). Most of these leaf rust and stripe rust resistance genes condition a hypersensitive reaction and interact with the pathogen in a gene-for-gene fashion. Virulence in the pathogen population has been evolving rapidly following the deployment of many of these resistance genes, thus, necessitating a constant search and transfer of the new and effective sources of rust resistance.

The germplasm of wild relatives and progenitor species of cultivated wheat comprise an excellent reservoir of useful traits, including disease resistance that can be exploited for wheat improvement (Dyck *et al.* 1990; Khush and Brar 1992). A number of leaf rust resistance genes have been introgressed from the wild relatives to the wheat cultivars through interspecific hybridization. Various *Aegilops* species have been reported to possess resistance to several wheat diseases (Gill *et al.* 1983, 1985; Kuraparthy *et al.* 2007a,b; Chhuneja *et al.* 2008; Schneider *et al.* 2008). Numerous wheat-*Aegilops* addition, substitution and translocation lines have been developed to dissect and introgress many agronomically useful traits into the wheat gene pool (Friebe *et al.* 2000). Several genes for resistance to leaf rust and stripe rust have been introgressed from *Aegilops* and *Thinopyrum* species to cultivated wheat: for example *Ae. umbellulata* (*Lr9*); *Thinopyrum ponticum* (*Lr19*, *Lr24* and *Lr29*); *Ae. ventricosa* (*Lr37*, *Yr17*); *Th. intermedium* (*Lr38*); *Ae. speltoides* (*Lr28*, *Lr35*, *Lr36*, *Lr51* and *Lr66*); *Ae. tauschii* (*Lr21*, *Lr22a*, *Lr32*, *Lr39*, *Lr40*, *Lr41* and *Yr28*); *Ae. geniculata* (*Lr57*,

*For correspondence. E-mail: pchhuneja@pau.edu.

Keywords. alien introgression; molecular mapping; leaf rust; *Puccinia triticina*; *Triticum aestivum*; *Aegilops caudata*.

Yr40); *Ae. triuncialis* (*Lr58*); *Ae. longissima* and *T. dicoccoides* (*Lr53*, *Yr15*, *Yr35*, *Yr36*) (McIntosh *et al.* 2008, 2010) and commercially exploited.

Aegilops species with C, U, and M genomes have been identified as very good sources of resistance to leaf rust and stripe rust (Valkoun *et al.* 1985; Singh *et al.* 2000). *Ae. caudata*, a diploid nonprogenitor species of wheat with CC genome carries resistance genes against several wheat diseases, especially rust and powdery mildew in addition to genes for high protein and lysine (Friebe *et al.* 1992; Potz *et al.* 1996). This article describes introgression of a leaf rust resistance gene from a rust resistant accession of *Ae. caudata* L. acc. pau#3556 into bread wheat and molecular mapping of the leaf rust resistance gene.

Materials and methods

Plant material

Ae. caudata L. acc. pau3556 was crossed with *T. durum* cv. WH868 and an amphiploid was synthesized which was further crossed with a Chinese Spring stock, CS (Ph^1), carrying an inhibitor for *Ph1* locus (Chen *et al.* 1994), for the induction of homeologous chromosome pairing. The F_1 was further crossed and backcrossed with a high yielding but rust susceptible wheat cv. WL711. Homozygous F_8 introgression lines with $2n = 42$ chromosomes have been developed that are resistant to both leaf rust and stripe rust. One of the wheat–*Ae. caudata* introgression lines, T291-2, was crossed with wheat cv. PBW343 for transferring the alien gene(s) to a well adapted background and to generate the mapping population.

Disease screening

The selected homozygous introgression line T291-2 and its parents were analysed for leaf rust resistance both at the seedling and adult plant stage for two years. The F_2 population derived from the cross T291-2/PBW343 was screened for leaf rust resistance at the seedling stage against the most virulent and prevalent pathotype 77–5 (avirulence/virulence formula: *Lr9*, *Lr18*, *Lr19*, *Lr24*, *Lr25*, *Lr28*, *Lr29*, *Lr32*, *Lr41*, *Lr45*/p*Lr1*, *Lr2*, *Lr3*, *Lr10*, *Lr11*, *Lr12*, *Lr13*, *Lr14*, *Lr15*, *Lr16*, *Lr17*, *Lr18*, *Lr20*, *Lr21*, *Lr22*, *Lr23*, *Lr26*, *Lr27*+*Lr31*, *Lr33*, *Lr36*, *Lr37*, *Lr42*, *Lr43*, *Lr44*, *Lr46*) to study the inheritance of the introgressed leaf rust resistance. The terminal disease severity for leaf rust against mixture of pathotypes (77-2, 77-5 and 104-2) was tested at the adult plant stage in the field.

For seedling tests, first leaf of seven-day-old seedling(s) of each plant was inoculated individually with uridiniospores – talc mixture keeping inoculum density of 6–8 uridiniospores over a microscopic field area of 2.92 mm^2. The inoculated seedlings were incubated in a dark chamber maintained at 20°C±1°C at 100 per cent relative humidity for 16 h. After incubation, the trays were shifted to glasshouses maintained at 20°C±2°C (Nayar *et al.* 1997). Fourteen days after inoculation, the infection types were recorded using the scale proposed by Stakman *et al.* (1962). At seedling stage plants with the disease reaction 0; , ; , 1 and 2 were considered as resistant and those with 3 and above as susceptible. Disease severity for parents and mapping population was assessed at the adult plant stage in open experimental field. This material was repeatedly spray-inoculated with mixture of uridiniospores of leaf rust races (77-2, 77-5 and 104-2), suspended in water (1 g inoculum per 10 L of water, using one drop of Tween-20 as dispersant). The observations on terminal disease severity were recorded as the percentage of leaf area covered with rust urediospores, according to the modified Cobb's scale (Peterson *et al.* 1948) which included disease severity (per cent leaf area affected) and infection type viz. 0, immune; R, resistant; MR, moderately resistant; MS, moderately susceptible; S, susceptible. Chi square test was applied for studying the inheritance of the gene under study in the F_2 population.

Molecular studies

Bulked segregant analysis (BSA) was used for mapping the introgressed leaf rust resistance. DNA of the parental lines WL711 and PBW343, T291-2, and F_2 plants was isolated using the modified method of Saghai-maroof *et al.* (1994). The DNA of 10 rust resistant and 10 susceptible F_2 plants was bulked to generate resistant (R) and susceptible (S) bulks. In the F_1 from the cross of *T. durum* – *Ae. caudata* amphiploid and CS (Ph^I), C genome chromosomes from the amphiploid and D genome chromosomes from Chinese Spring were in hemizygous state and hence had higher probability of pairing and recombining. So the D-genome SSR markers were used for detecting *Ae. caudata* introgressions and mapping leaf rust resistance gene introgressed in the wheat background. A total of 164 D-genome-specific SSR markers (including CFD, GWM, CFA, WMC, GDM and BARC series) were tested for polymorphism and BSA. The PCR products were resolved either on 2.5% agarose or 8% denaturing PAGE gel.

Data analysis and genetic mapping

The mapping software Mapmaker v3.0 (Lander *et al.* 1987) was used to determine the linkage between the introgressed gene and the markers. Maximum LOD score of 3.0 and maximum recombination fraction of 0.20 were used. The markers were screened on F_2 plants and their linkage with the rust resistance locus was confirmed by working out the recombination distance in centimorgan (cM). Leaf rust resistance data of the F_2 derived F_3 progenies were converted to susceptible as A, resistant as B and segregating as H and computed with marker data for determining the distance between the leaf rust resistance gene and the linked markers. The

computer program Mapchart v2.1 developed by Voorrips (2002) was used to construct the linkage map for the chromosome carrying leaf rust resistance gene.

Results

WL711 – *Ae. caudata* introgression line T291-2 showed complete resistance at the seedling stage against pathotype 77-5 (figure 1a). When tested at the adult plant stage, the T291-2 exhibited complete resistance against a mixture of pathotypes 77-2, 77-5 and 104-2 of *P. triticina* (figure 1b) indicating the introgression of a leaf rust resistance gene.

Inheritance studies

T291-2/PBW343 F_2 population was tested against the *Pt* pathotypes to study the inheritance of leaf rust resistance introgressed from *Ae. caudata* into *T. aestivum* cv. WL711. At the seedling stage, F_2 population of 286 plants when screened against race 77-5 segregated into 208 R and 78 S showing a goodness of fit to 3:1 segregation with chi-square of 0.79 (table 1) indicating that a single dominant gene governed resistance to 77-5 (figure 1a). The same plants were transplanted in field and screened against a mixture of leaf rust races. At the adult plant stage, 284 F_2 plants depicted leaf rust reaction ranging from complete resistance to complete susceptibility (figure 1b) segregating into 206 R and 78 S plants (table 1) with a Chi-square value of 0.92 (*P* value) for 3:1 segregation ratio confirming that a single gene was segregating for leaf rust resistance in this population. All the F_2 plants resistant at the seedling stage also remained resistant at the adult plant stage indicating that the gene under study was effective throughout the life of the plant. The progeny testing in F_3 generation at the seedling stage confirmed the segregation of a single gene for leaf rust resistance (data not given).

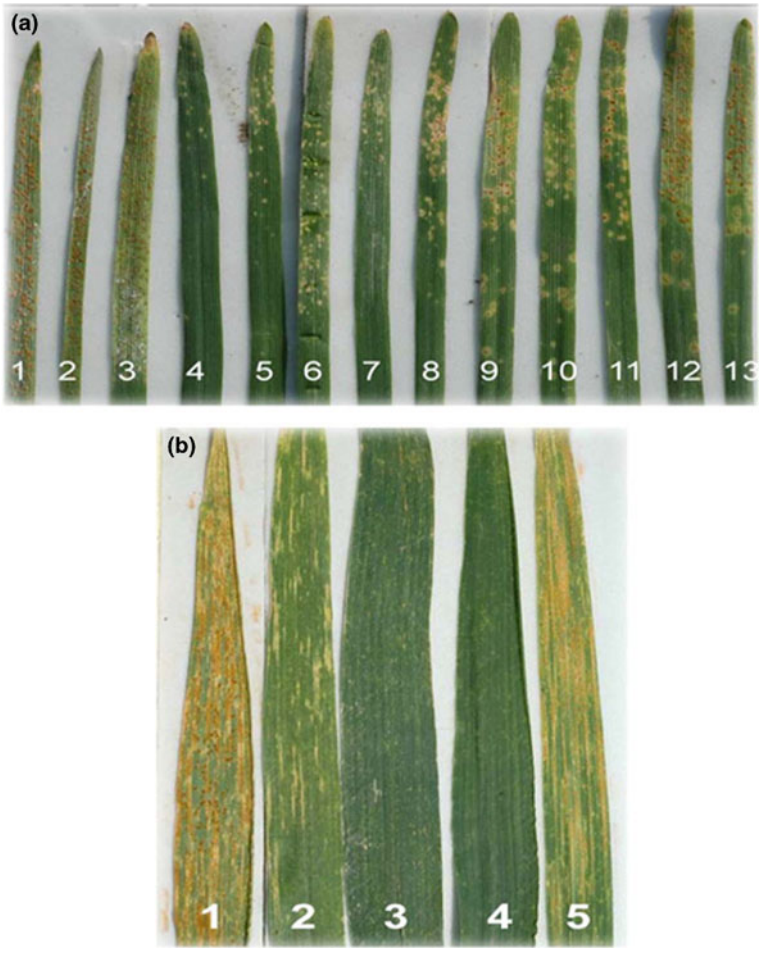

Figure 1. Leaf rust reaction of the parents, wheat – *Ae. caudata* introgression lines and representative F_2 plants developed from the cross: *T. durum* cv. WH868 – *Ae. caudata* acc. pau 3556/CS(*Ph*^{1})//WL711/3/PBW343. (a) Reaction at the seedling stage against leaf rust pathotype 77–5; 1 (WL711); 2 (PBW343); 3 (WH868); 4 (ILT291-2), 5 (ILT279–6); 6–13 (representative F_2 plants). (b) Leaf rust reaction at the adult plant stage against a mixture of pathotypes 77-2, 77-5 and 104-2; 1 (WL711); 2 (IL T291-2); 3-5 (representative F_2 plants).

Table 1. Segregation for leaf rust (*Puccinia triticina*) resistance in the F_2 population derived from WL711–*Ae. caudata* IL(T291-2)/PBW343 at the seedling and adult plant stage.

Stage	Resistant plants	Susceptible plants	Total plants	χ^2 (3:1)	*P* value
Seedling	208	78	286	0.79	0.37
Adult plant	206	78	284[a]	0.92	0.33

[a]Two plants did not survive after transplanting.

Molecular characterization and graphical genotyping of the donor wheat–Ae. caudata introgression line T291-2

WL711, *Ae. caudata*, PBW343, WH868, and the donor introgression line T291-2, were assayed for polymorphism using SSR (simple sequence repeat) markers. A total of 164 selected D-genome primers were amplified on the parents. A total of 98 primers were found to be polymorphic and 42 were nonpolymorphic among the two parents with 11 primers giving null allele in *Ae. caudata* and hence behaved as dominant markers. Overall, 70% primers, including dominant markers were observed to be polymorphic when resolved on 2.5% agarose gel. Maximum number of polymorphic markers were detected for chromosome 2D (81.8%) and minimum for chromosome 1D (58.8%). To define the size of the alien introgression and to identify the translocation/recombination break point, graphical genotypes for the D-genome chromosomes were generated for the donor introgression line T291-2. Out of the 98 D-genome polymorphic markers amplified, 15 markers showed introgression for *Ae. caudata* specific alleles or 15.3% introgression of the alien chromatin. As per the consensus wheat linkage map at Komugi (http://www.shigen.nig.ac.jp/wheat/komugi/maps/markerMap.jsp) and consensus map of Somers *et al.* (2004), the 15 markers that showed introgression mapped on wheat chromosomes 2D, 3D, 4D, 5D, 6D, and 7D with maximum introgression on chromosome 5D followed by chromosome 6D (figure 2). The introgression of *Ae. caudata* chromatin to the A and B genome chromosomes of wheat (not tested) might have also occurred. Except for one marker *Xcfd76* which detected interstitial introgression, all the other markers detected terminal introgressions as expected since the terminal transfers have higher occurrence during induced homeologous pairing in wide crosses as compared with the interstitial transfers.

Mapping of leaf rust resistance

Among the 15 markers showing introgression, only three 5D-specific markers, *Xcfd81*, *Xcfa2104* and *Xgwm190*, generated polymorphic DNA fragments between R and S bulks. These three markers amplified an additional introgression line specific allele in the resistant bulks which was absent in the susceptible bulks. This is evident from the fact that some of the rust resistant F_2 plants of the R bulk could be heterozygous while the susceptible F_2 plants of the S bulk were homozygous recessive. Another three markers (*Xcfd18*, *Xcfd78* and *Xcfd189*) which were mapped on 5D behaved as dominant markers, showing null allele in the T291-2. Two hundred and sixtyfour F_2 plants were analysed with the informative 5D specific SSR markers for studying the cosegregation of these markers with the leaf rust resistance gene introgressed from *Ae. caudata* to *T. aestivum*. All the four markers (*Xcfd18*, *Xcfd78*, *Xcfd189* and *Xcfd81*) showed goodness of fit to the

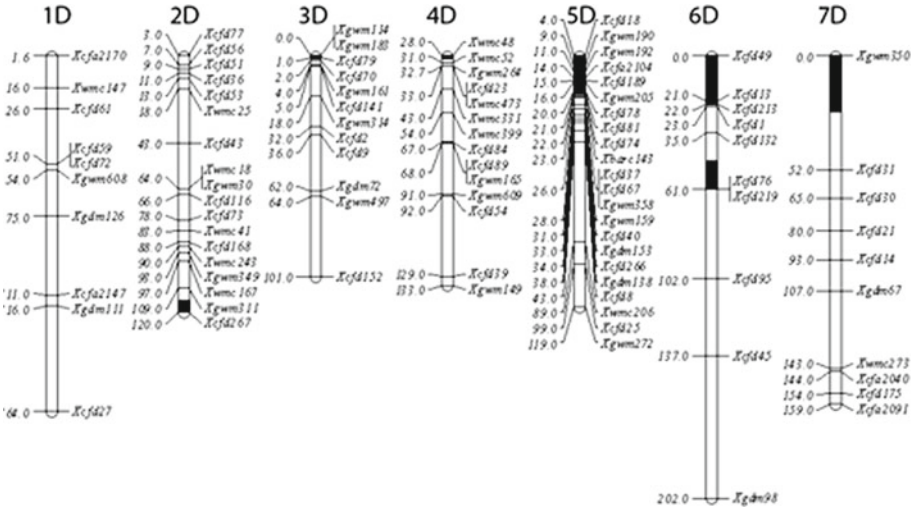

Figure 2. Graphical genotyping of a wheat–*Ae. caudata* introgression line T291-2 based on SSR markers using software GGT32. Black areas indicate *Ae. caudata* specific introgression and white areas indicate wheat specific alleles. Map distances are according to the Somers *et al.* (2004).

Figure 3. *In vitro* amplification profile of WL711–*Ae. caudata* ILT291-2/PBW343 derived F_2 population for SSR marker *Xcfd81* on 8% PAGE using LICOR DNA Analyzer for WL711 (1); PBW343 (2); WH868 (3, 4); IL T291-2 (5); ILT279–6 (6) Negative control (7); F_2 plants (8–64) with leaf rust reactions of the $F_{2:3}$. R (resistant), H (segregating) and S (susceptible) depict the leaf rust reaction of the $F_{2:3}$ progenies.

expected 1:2:1/1:3 segregation ratio (data not given) and cosegregated with the leaf rust resistance gene in this F_2 population and thus confirming that the leaf rust resistance gene from *Ae. caudata* had introgressed on to wheat chromosome 5D. Figure 3 shows the segregation pattern for the marker *Xcfd81* in the F_2 population. Leaf rust resistance gene *LrAC* was observed to be terminal to *Xcfd18*, *Xcfd78* and *Xcfd189* as the closest markers at a distance of 0.4 cM, followed by *Xcfd81* at a distance of 0.6 cM (figure 4). The marker order was in correspondence with the consensus map of Somers *et al.* (2004).

Allelic test with Lr57

Leaf rust resistance gene *LrAC* introgressed from *Ae. caudata* acc. pau3556 mapped on the short arm of wheat chromosome 5D. Another leaf rust resistance gene *Lr57*, introgressed from M genome of *Ae. geniculata* had been mapped earlier by our group at about the same location (Kuraparthy *et al.* 2007a). The introgression lines carrying *LrAC* and *Lr57* demonstrated phenotypic differences. T291-2 was taller than WL711–*Ae. geniculata* ILs T756-2, T598 and T550, carrying *Lr57-Yr40* and WL711. T291-2 had red seed colour against amber seed colour of WL711–*Ae. geniculata* ILs carrying *Lr57*. To confirm whether *LrAc* was allelic to *Lr57*, ILT756-2 carrying *Lr57*, was crossed with T291-2 and the F_2 population was screened at the seedling and adult stage against *Pt* pathotype 77-5 and mixture of pathoptypes, respectively. A total of 320 F_2 plants were screened and all were found to be resistant, indicating that *LrAC* might be a homoeoallele of *Lr57*.

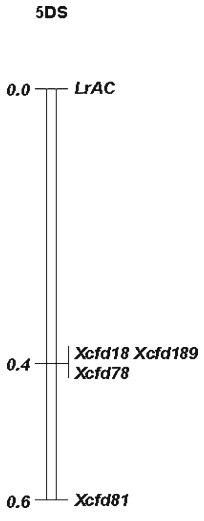

Figure 4. Linkage map of short arm of chromosome 5D carrying an introgressed segment with leaf rust resistance gene (*LrAC*) from *Ae. caudata* based on an F_2 population derived from cross *T. durum* cv. WH868–*Ae. caudata* acc. pau3556/ CS(*Ph*^{1})/ WL711/3/PBW343.

Discussion

This study reports the introgression of a leaf rust resistance gene from *Ae. caudata* into cultivated wheat and its mapping. The line T291-2 ($2n = 42$) was used for mapping the gene for leaf rust resistance introgressed from *Ae. caudata* acc. pau 3556 to hexaploid wheat background. Inheritance studies of leaf rust resistance in F_2 population at seedling and adult plant stages suggested the introgression of a dominant gene for rust resistance. There was no distortion in the observed segregation ratio, which is otherwise a serious problem with the alien introgressions (Endo 1990; Prins and Marais 1999; Marais *et al.* 2005), indicating that the alien segment carrying leaf rust resistance must be capable of normal transmission through male gamete with no segregation distortion.

Most of the translocations were expected to be on the D-genome chromosomes as compared to their A and B genome counterparts because *T. durum–Ae. caudata* amphiploid (AABBCC) was crossed with CS(*Ph*^{1}) (AABBDD) and C genome of *Ae. caudata* and D genome from *CS(Ph*^{1}*)* was expected to be in hemizygous state and hence had higher probability of pairing. Molecular characterization of the donor introgression line T291-2 and the molecular

mapping in F_2 population using D-genome-specific SSR markers showed that the leaf rust resistance gene from *Ae. caudata* was located on the short arm of wheat chromosome 5D which has been tentatively designated as *LrAC*. The alien fragments introgressed from nonprogenitor species are not expected to recombine with their wheat counterparts in the presence of functional *Ph1* locus. However, in the present study, some recombination has been observed between *LrAC* and the linked markers. Similar spontaneous recombination between 5D chromosome of wheat and its homeologue 5M chromosome of *Ae. geniculata* had also been observed earlier (Liu *et al.* 2011).

No apparent linkage drag could be observed in the parental introgression line in WL711 and its derived backcross progenies in PBW343 background, indicating this to be a compensating transfer which could be deployed and exploited commercially. The transfers were made through induction of homeologous pairing which leads to compensating transfers between homeologous chromosomes only.

Homeologous group 5 of wheat contains nine catalogued genes for rust resistance. Most of these genes have been mapped on the long arm of homeologous group 5 chromosomes. Only three leaf rust resistance genes were mapped on the short arm of homeologous group 5 chromosomes (McIntosh *et al.* 2010). *Lr52* and an uncatalogued gene have been located on the short arm of chromosome 5B. A pair of linked leaf rust and stripe rust resistance genes *Lr57* and *Yr40*, introgressed from 5M chromosome of *Ae. geniculata* to bread wheat at the Punjab Agricultural University (Kuraparthy *et al.* 2007a) has been mapped on distal region of 5DS. The *LrAC*, mapped during the present investigation, also mapped in the same region. The graphical genotyping of the introgression line T291-2 indicated the replacement of almost complete short arm of chromosome 5D from *Ae. caudata* with breakpoint at the centromere whereas the alien introgression from *Ae. geniculata* mapped in less than 3.5% of the distal region of the short arm of 5D chromosome of wheat. Allelic tests conducted between the wheat–*Ae. geniculata* IL and wheat–*Ae. caudata* IL indicated that *LrAC* might be a homoeoallele of *Lr57*. Mapping of three rust resistance genes in the same chromosomal region indicated that the short arm of homeologous group 5 in the C and M genome *Aegilops* species might harbour additional genes for resistance to biotic stresses.

The donor introgression line T291-2 was moderately resistant to stripe rust resistance also. The F_2 population under study could not be screened for stripe rust resistance since one of the parents PBW343 was resistant to stripe rust pathotypes due to the presence of *Yr27*. However, with the emergence of *Yr27* virulence (78S84), PBW343 now gives completely susceptible reaction at the adult plant. T291-2, however, still has high level of resistance against stripe rust and the F_5 population derived from T291-2/PBW343 showed segregation in response to rust infection at the adult plant stage. The mapping of stripe rust resistance of *Ae. caudata* segregating in this population is under progress. Leaf rust resistance gene *LrAC* introgressed from *Ae. caudata* to 5DS of hexaploid wheat is a putatively new gene or an orthologue of *Lr57* since as per the published evidence no other leaf rust resistance gene has been transferred from the C genome of *Ae. caudata* to bread wheat. *Ae. caudata* is one of the most resistant representatives in the group of less closely related species with homeologous genomes from where no rust resistance genes has been transferred to wheat (Valkoun *et al.* 1985). The wheat–*Ae. caudata* T291-2 with a high level of leaf rust resistance can be exploited for wheat germplasm enhancement through marker-assisted selection.

Acknowledgements

Financial assistance was provided by the USDA-ARS under the Project IN-ARS-842 and Department of Biotechnology, Government of India, in the form of various research grants are gratefully acknowledged.

References

Chen P. D., Tsujimoto H. and Gill B. S. 1994 Transfer of *Ph*^{I} genes promoting homeologous pairing from *Triticum speltoides* to common wheat. *Theor. Appl. Genet.* **88**, 97–101.

Chhuneja P., Kaur S., Goel R. K., Aghaee-Sarbarzeh M., Prashar M. and Dhaliwal H. S. 2008 Transfer of leaf rust and stripe rust resistance from *Aegilops umbellulata* Zhuk. to bread wheat (*Triticum aestivum* L.). *Genet. Res. Crop Evol.* **55**, 849–859.

Dyck P. L., Kerber E. R. and Marters J. W. 1990 Transfer of a gene for stem rust resistance from *Aegilops caudata* to common wheat. *Can. J. Plant Sci.* **70**, 931–934.

Endo T. R. 1990 Gametocidal chromosomes and their induction of chromosome mutations in wheat. *Jpn. J. Genet.* **65**, 135–152.

Friebe B., Schubert V., Bluthner W. D. and Hammer K. 1992 C-banding pattern and polymorphism of *Aegilops caudata* and chromosomal constitutions of the amphiploid *T. aestivum–Ae. caudata* and six derived chromosome additional lines. *Theor. Appl. Genet.* **83**, 589–596.

Friebe B., Qi L. L., Nasuda A., Zhang P., Tuleen N. A. and Gill B. S. 2000 Development of a complete set of *Triticum aestivum–Aegilops speltoides* chromosome addition lines. *Theor. Appl. Genet.* **101**, 51–58.

German S., Barcellos A., Chaves M., Kohli M., Campos P. and Viedma L. 2007 The situation of common wheat rusts in the southern Cone of America and perspectives for control. *Aust. J. Agric. Res.* **58**, 620–630.

Gill B. S., Browder L. E., Hatchett J. H., Harvey T. L., Martin T. J., Raupp W. J. *et al*. 1983 Disease and insect resistance in wild wheats. In *Proceedings of the 6th International Wheat Genetics Symposium* (ed. S. Sakamoto), pp. 785–792. Faculty of Agriculture, Kyoto University, Japan.

Gill B. S., Sharma H. C., Raupp W. J., Browder L. E., Hatchett J. H., Harvey T. L. *et al*. 1985 Evaluation of *Aegilops* species for resistance to wheat powdery mildew, wheat leaf rust, Hessian fly and greenbug. *Plant Breeding* **69**, 314–316.

Khush G. S. and Brar D. S. 1992 Overcoming the barriers in hybridization. In *Distant hybridisation of crop plants* (ed. G. Kallo and J. B. Chawdhury), pp. 47–61. Springer, Berlin, Germany.

Kolmer J. A., Jin Y. and Long D. L. 2007 Wheat leaf and stem rust in the United States. *Aust. J. Agric. Res.* **58**, 631–638.

Kuraparthy V., Chhuneja P., Dhaliwal H. S., Kaur S., Bowden R. L. and Gill B. S. 2007a Characterization and mapping of cryptic alien introgression from *Aegilops geniculata* with new leaf rust and stripe rust resistance genes *Lr57* and *Yr40* in wheat. *Theor. Appl. Genet.* **114**, 1379–1389.

Kuraparthy V., Sood S., Chhuneja P., Dhaliwal H. S., Kaur S., Bowden R. L. and Gill B. S. 2007b A cryptic wheat-*Aegilops triuncialis* translocation with leaf rust resistance gene *Lr58*. *Crop Sci.* **47**, 1995–2003.

Lander E. S., Green P., Abrahamson J., Barlow A., Daly M. J., Lincoln S. E. and Newburg L. 1987 MAPMAKER: an interactive computer package for constructing primary genetic linkage maps of experimental and natural populations. *Genomics* **1**, 174–181.

Liu W., Rouse M., Friebe B., Jin Y., Gill B. S. and Pumphrey M. O. 2011 Discovery and molecular mapping of a new gene conferring resistance to stem rust, *Sr53*, derived from *Aegilops geniculata* and characterization of spontaneous translocation stocks with reduced alien chromatin. *Chromosome Res.* **19**, 669–682.

Marais G. F., Pretorius Z. A., Wellings C. R., McCallum B. and Marais A. S. 2005 Leaf rust and stripe rust resistance genes transferred to common wheat from *Triticum dicoccoides*. *Euphytica* **143**, 115–123.

McIntosh R. A., Yamazaki Y., Dubcovsky J., Rogers W. J., Morris C. F., Somers D. J. *et al*. 2008 Catalogue of gene symbols for wheat. Proceedings of the 11th International Wheat Genetics Symposium. Brisbane, Australia.

McIntosh R. A., Yamazaki Y., Rogers W. J., Morris C. F. and Devos K. M. 2010 Catalogue of gene symbols for wheat (http://www.shigen.nig.ac.jp/wheat/komugi/genes/download.jsp).

Nayar S. K., Prashar M. and Bhardwaj S. C. 1997 Manual of current techniques in wheat rusts. Research Bulletin No.2, Regional Station, Flowerdale, Shimla India.

Park R. F., Bariana H. S. and Wellings C. R. 2007 Preface to 'global landscapes in cereal rust control'. *Aust. J. Agric. Res.* **58**, 469.

Peterson R. F., Campbell A. B. and Hannah A. E. 1948 A diagnostic scale for estimating rust severity on leaves and stem of cereals. *Can. J. Res.* **26**, 496–500.

Potz H., Schubert V., Houben A., Schubert I. and Weber W. E. 1996 Aneuploids as a key for new molecular cloning strategies: development of DNA markers by microdissection using *Triticum aestivum–Aegilops markgraffi* chromosome addition line B. *Euphytica* **89**, 41–47.

Prins R. and Marais G. F. 1999 A genetic study of the gametocidal effect of the *Lr19* translocation of common wheat. *S. Afr. J. Plant Soil* **16**, 10–14.

Saghai-maroof M. A., Biyashev R. M., Yang G. P., Zhang Q. and Allard R. W. 1994 Extraordinarily polymorphic microsatellite DNA in barley: species diversity, chromosomal locations, and population dynamics. *Proc. Natl. Acad. Sci. USA* **91**, 5466–5470.

Schneider A., Molnar I. and Molnar Lang M. 2008 Utilisation of *Aegilops* (goatgrass) species to widen the genetic diversity of cultivated wheat. *Euphytica* **163**, 1–19.

Singh H., Tsujimoto H., Sakhuja P. K., Singh T. and Dhaliwal H. S. 2000 Transfer of resistance to wheat pathogens from *Aegilops triuncialis* into bread wheat. *Wheat Info. Serv.* **91**, 5–10.

Somers D. J., Isaac P. and Edwards K. 2004 A high density microsatellite consensus map for bread wheat (*Triticum aestivum* L.). *Theor. Appl. Genet.* **109**, 1105–1114.

Stakman E. C., Stewart D. and Loegering W. Q. 1962 Identification of physiologic races of *Puccinia graminis* var. *tritici* USDA Agri Res Serv Bull (Revised Washington D. C.).

Valkoun J., Hammer K., Kucerova D. and Bartos P. 1985 Disease resistance in the genus *Aegilops* L.—stem rust, leaf rust, stripe rust, and powdery mildew. *Kulturpflanzen* **33**, 133–153.

Voorrips R. E. 2002 Map chart: software for the graphical presentation of linkage maps and QTLs. *J. Hered.* **93**, 77–78.

Received 1 December 2011, in final revised form 5 March 2012; accepted 9 March 2012
Published on the Web: 12 July 2012