ISSN 1479-2621

Plant Genetic Resources: Characterization and Utilization (2020) **18**(4); 211–221
doi:10.1017/S1479262120000222

QTL mapping for stripe rust and powdery mildew resistance in *Triticum durum–Aegilops speltoides* backcross introgression lines

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Received 31 October 2019; Accepted 18 July 2020 – First published online 17 August 2020

Abstract

Wheat, a major food crop, faces significant yield constraints due to losses caused by various diseases, especially rusts and powdery mildew. Since the causal organisms are always evolving, there is a never-ending hunt for new genes/quantitative trait loci (QTLs) for resistance to control the damage. For this purpose, *Triticum durum–Aegilops speltoides* backcross introgression lines (DS-BILs) developed in our wide hybridization programme were screened against stripe rust and powdery mildew at both seedling and adult plant stages. DS-BILs showed complete to moderate resistance at the adult plant stage while varying resistance and susceptibility at the seedling stage. A total of 1095 single-nucleotide polymorphisms (SNPs) identified on 14 chromosomes of *T. durum*, using genotyping by sequencing, were used for QTL mapping. Eleven unique QTLs, across six chromosomes (chr1B, chr2A, chr2B, chr3B, chr6B and chr7B) were identified for resistance, four QTLs for field mixture of stripe rust pathotypes, two QTLs for stripe rust pathotype 78S84 and five QTLs for field mixture of powdery mildew pathotypes using stepwise regression-based likelihood ratio test for additive effect of markers and single-marker analysis. Eleven DS-BILs carrying multiple QTLs were identified which will serve as a useful resource to transfer the respective resistance to susceptible cultivars to develop all stage resistant elite cultivars where QTL for stripe rust resistance *QYrAs.pau-2A.1* (LOD 3.8, PVE 24.51 linked to SNP S2A_16016633) and QTL for powdery mildew resistance *QPmAs.pau-6B* (logarithm of the odds (LOD) 3.2, phenotypic variation explained (PVE) 17.75 linked to SNP S6B_26793381) are major targets of the transfer.

Keywords: *Aegilops speltoides*, crop wild relatives, disease resistance, powdery mildew, QTL, stripe rust, *Triticum durum*, wheat

Introduction

Stripe rust and powdery mildew caused by *Puccinia striiformis* and *Blumeria graminis* are two economically significant fungal foliar diseases of wheat which are a significant constraint for sustainable wheat production, hampering both yield and quality (Elkot *et al.*, 2015; Bariana *et al.*, 2016; Bansal *et al.*, 2017; Lan *et al.*, 2017). In recorded history, diseases and pests have caused substantial wheat yield losses ranging from 50 to 100% under epidemic conditions (Figueroa *et al.*, 2018). The long-term use of chemical pesticides has had a significant negative impact on the environment as well as on human health.

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Thus, a holistic approach of introduction of disease resistance genes is much more lucrative and sustainable. McIntosh *et al.* (2017) have reported characterization and deployment of more than 70 genes for each of these diseases from elite wheat genotypes, landraces and crop wild relatives to counter the problem of biotic stress on wheat production.

In wheat, disease resistance has been characterized into two categories based on their action across the lifecycle of the plant (Chen, 2005). Firstly, the all-stage resistance (ASR) caused by seedling stage resistance genes, which start acting from the seedling stage and remain active throughout the plant life. These genes are mostly race-specific. Secondly, the adult plant resistance (APR) caused by genes that are primarily responsible for moderate to complete resistance at the adult plant stage only. APRs may confer hypersensitive reaction or provide more durable resistance to plants by providing slow rusting type resistance (Venkata *et al.*, 2008; Niks *et al.*, 2015). This type of durable resistance is crucial as it does not exert evolutionary stress on the causal organism by retarding the development of disease progression. Although APR is a durable form of resistance, only a small number of resistance genes have been known to confer this particular type of resistance (Kankwatsa *et al.*, 2017).

Several *Aegilops* species have been exploited to transfer genes for resistance to wheat, against various insect pests, powdery mildew and rust diseases that have been commercially used (Kaur *et al.*, 2018). Kishii (2019) has compiled a list of genes identified or transferred from various *Aegilops* species, including *Aegilops speltoides*, which have been the sources of leaf rust resistance genes (*Lr28*, *Lr35*, *Lr36*, *Lr37*, *Lr47*, *Lr51* and *Lr66*), stem rust resistance genes (*Sr32*, *Sr39* and *Sr47*), powdery mildew resistance genes (*Pm1d*, *Pm12*, *Pm32* and *Pm53*) and green bug resistance gene (*Gb5*). Apart from disease resistance, *Aegilops* species have been reported to possess resistance to abiotic stresses like heat, salinity and drought tolerance (Monneveux *et al.*, 2000; Colmer *et al.*, 2006; Rawat *et al.*, 2008; Liu *et al.*, 2015; Awlachew *et al.*, 2016).

During field examination of various crop wild relatives of wheat (at the School of Agricultural Biotechnology, Punjab Agricultural University) for more than 20 years, selected accessions of *Ae. speltoides*, the putative wheat B genome donor (Zhang *et al.*, 2018), were found to be resistant to most of the diseases prevailing in the field. In this study, *Triticum durum–Ae. speltoides* backcross introgression lines (DS-BILs), developed through limited backcrossing followed by selfing, were evaluated for resistance against the two major wheat diseases, stripe rust and powdery mildew, and quantitative trait locus (QTL)/genes were mapped using single-nucleotide polymorphisms (SNPs) developed through genotyping by sequencing (GBS).

Materials and methods

Plant material

Eighty-nine BC_2F_{10} DS-BILs developed from durum wheat cultivar PDW274 and *Ae. speltoides* accession #pau3809 were used in the study. Details of the development of the DS-BILs can be found in Awlachew *et al.* (2016). *Ae. speltoides* acc. pau3809 was crossed with *T. durum* cv. PDW274 as female and F_1 was backcrossed to *T. durum*. All the BC_1 plants were backcrossed and BC_2F_1s selfed to generate homozygous BILs of *Ae. speltoides* in *T. durum* background. This set of *T. durum–Ae. speltoides* backcross introgression lines will be denoted as DS-BILs henceforth in this paper.

Seedling screening

For screening against stripe rust (YR), and powdery mildew (PM), 89 DS-BILs along with recurrent parent PDW274 and susceptible check WL711, a hexaploid wheat cultivar susceptible to both the diseases, were planted in bread boxes with 10 seeds of each genotype (with one row of control check each) and were kept in different temperature- and moisture-controlled glass houses maintained specifically for each disease. The first leaves of 7-day germinated seedlings were inoculated with respective disease spores. For YR, two sets of the same BILs were inoculated, one with *P. striiformis* (*Pst*) pathotype 78S84 and other with a mixture of pathotypes collected from open field. For PM, a mixture of *B. graminis* (*Bg*) pathotypes collected from open field was used for inoculation. The inoculated bread boxes for each disease were placed separately in water-filled trays covered with a black sheet for 24 h at 100% relative humidity. After the incubation, the bread boxes were maintained in separate glasshouses for disease development. For YR, disease scoring was done using Stakamans' scale (Visioni *et al.*, 2018) after 14 days when susceptible control showed complete susceptibility for respective pathotypes. Similarly, for scoring disease in PM, a linear scale of 0–9 was used (Yang *et al.*, 2017).

Molecular analysis

DNA extraction of 89 DS-BILs along with PDW274 and *Ae. speltoides* acc. pau3809 was done using the cetyl trimethylammonium bromide (CTAB) method (Saghai-Maroof *et al.*, 1984). DNA was genotyped using GBS. The raw reads generated by GBS were subjected to SNP calling using the TASSELGBSv2 pipeline in TASSELv5.2 (Glaubitz *et al.*, 2014). The SNPs were called against the A and B genomes of wheat reference genome refseqV1.0. The vcf file generated using the pipeline was filtered for depth at 3

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(DP3) and converted to HapMap format. The TASSEL output was then filtered for homozygous SNPs for each parental line, and the polymorphic SNPs between the two parental lines were selected. Furthermore, the SNPs were filtered for 20% missing data, and remaining SNPs were used for mapping. The distribution of SNPs along 14 chromosomes is presented in online Supplementary Fig. S1.

QTL mapping

For mapping, the disease resistance, scoring of the diseases was converted into linear scale as per Yang *et al.* (2017) and 1095 SNPs were used for mapping using the CSL functionality of QTL IciMapping V4.1.0.0 employing single marker analysis (SMA) and stepwise regression-based likelihood ratio test (RSTEP-LRT) (Wang *et al.*, 2016). QTLs detected at LOD (logarithm of odds) score ≥ 2.0 and PVE (phenotypic variation explained) > 9.0 were considered to be significant.

Introgression profile of DS-BILs

Introgression profiling of *Ae. speltoides* fragments in *T. durum* background of 89 DS-BILs were done using GGT2 (van Berloo, 2008).

Postulation of candidate genes

The physical positions of the mapped SNPs in the introgressed segments were used to identify the candidate genes conferring resistance to diseases in the annotated wheat genome present at https://wheat-urgi.versailles.inra.fr/Seq-Repository/Annotations. Jbrowse functionality was used to manually hunt for the candidate genes in the designated regions of the annotated wheat genome. Gene names and functions were identified from https://web.persephonesoft.com/?data=genomes.

Results

Evaluation of rust and powdery mildew resistance

Recipient parent PDW274 was completely susceptible at the seedling stage against stripe rust pathotype Pst78S84 and mixture of pathotypes while donor *Ae. speltoides* acc. pau3809 showed complete resistance. PDW274 depicted moderate resistance against stripe rust at the adult plant stage under artificial epiphytotic conditions. PDW274 thus might carry an APR gene for stripe rust while *Ae. speltoides* acc. pau3809 harbours ASR gene(s). Seedling screening of the DS-BILs against Pst78S84 showed wide variation ranging from complete resistance to complete susceptibility (Figs. 1a and 2a) with most of the DS-BILs showing susceptible reaction. Similarly, when DS-BILs were tested at the seedling stage with a mixture of stripe rust pathotypes collected from open field, most genotypes were highly susceptible (YR score of 8) and 12 DS-BILs were moderately susceptible (YR score of 5.33) with only two DS-BILs (DS-BIL6 and DS-BIL16) as completely resistant (YR score of 2.67). However, the DS-BIL panel was completely resistant at the adult plant stage under artificial epiphytotic conditions in the field.

Screening for powdery mildew with a mixture of powdery mildew (*Bg*) pathotypes collected from open field, identified 40 DS-BILs to be completely to moderately resistant with a score ranging from 0 to 3.3 while rest of the DS-BILs were highly susceptible, whereas recipient parent PDW274 showed complete susceptibility while *Ae. speltoides* showed complete resistance with a score of 0 (Figs. 1b and 2c).

QTL mapping

The results of QTL mapping using RSTEP-LRT for the additive effect of markers and single-marker analysis (SMA) are presented in Table 1. For stripe rust against field mixture of pathotypes, two QTLs (*QYrAs.pau-2A.1* and *QYrAs.pau-7B*) were mapped on chromosomes 2A and 7B with SMA (LOD score 3.8 with PVE 24.51% and LOD score 2.4 with PVE 10.06%) and RSTEP_LRT (LOD score 2.6 with PVE 13.83% and LOD score 2.4 with PVE 10.06%) with resistance allele contributed by *Ae. speltoides*. Also, for the same field mixture of pathotypes, two QTLs were mapped with only SMA, QTL *QYrAs.pau-1B* on chromosome 1B with LOD score 2.0 with PVE 11.64% and QTL *QYrAs.pau-2B* on chromosome 2B with LOD score of 2.2 and PVE 12.8%. These QTLs also had resistance allele contributed by *Ae. speltoides*. For stripe rust, two QTLs, *QYrTd.pau-2A.2* and *QYrTd.pau-3B* were mapped against *Pst* 78S84 on chromosomes 2A and 3B with both algorithms SMA (LOD score 2.9 with PVE 14% and LOD score 4.1 with PVE 19.29%) and RSTEP-LRT (LOD score 2.1 with PVE 9.4% and LOD score 4.1 with PVE 19.29%). PDW274 contributed resistance alleles for both the QTLs. However, the mapping could not be conducted for adult plant data as the whole of the population was resistant.

Similarly, for powdery mildew against field pathotypes at the seedling stage, five QTLs located on chromosomes 2A, 2B, 3B and 6B were detected using both algorithms. With SMA, QTLs *QPmAs.pau-2A.2*, *QPmAs.pau-2B* and *QPmAs.pau-6B* at a LOD score of 2.02 with PVE 11.49%, LOD score of 2.3 with PVE 14.05% and LOD score of 3.2 with PVE 17.75% were detected, respectively. With RSTEP-LRT, QTLs *QPmAs.pau-2A.1*, *QPmAs.pau-3B* and *QPmAs.pau-6B* were detected, respectively at an LOD score of 2.0 with PVE 9.16%, LOD score of 2.4 with PVE 12.89% and LOD score of 3.2 with PVE 17.75%. *Ae.*

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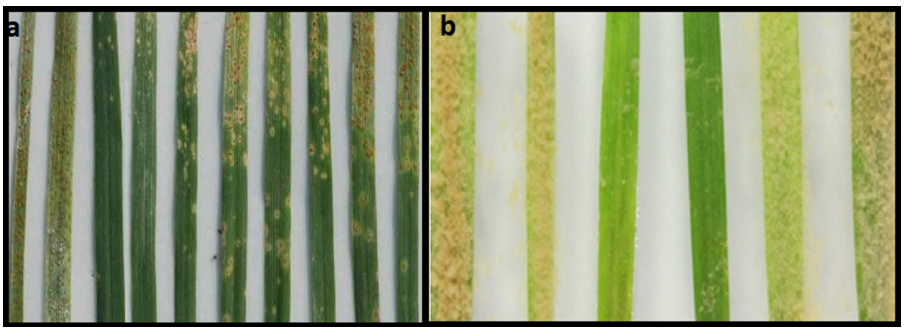

Fig. 1. Disease reaction of tested genotypes for (a) stripe rust pathotypes, and (b) powdery mildew pathotypes. The first three leaves represent susceptible check *T. aestivum* cv WL711, *T. durum* cv. PDW274 and *Ae. speltoides* acc pau3809, serially. Succeeding leaves represent reactions of DS-BILs.

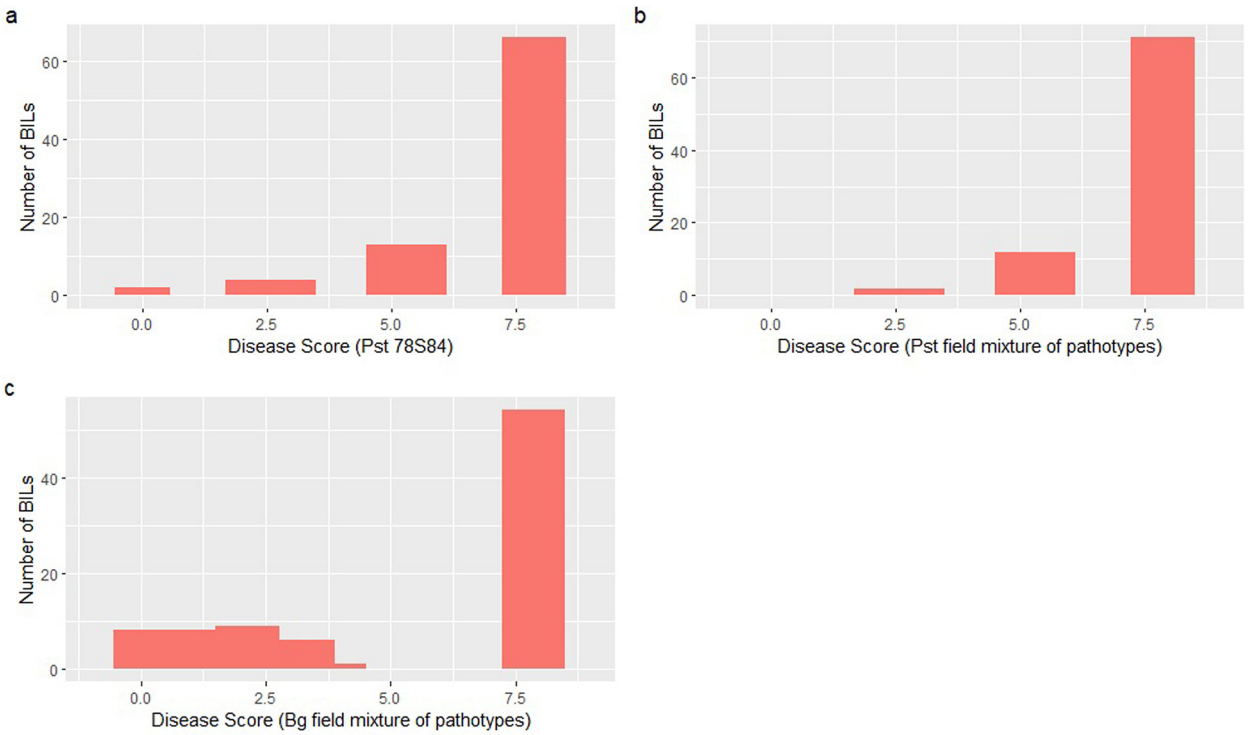

Fig. 2. Frequency distribution of the disease score of *T. durum–Ae. speltoides* DS-BILs for (a) stripe rust pathotype Pst 78S84, (b) mixture of pathotypes of stripe rust and (c) mixture of pathotypes of powdery mildew. PDW274 was highly susceptible with reaction score of 8 for all the stripe rust and powdery mildew pathotypes. *Ae. speltoides* acc. pau3809 was highly resistant with reaction score of 0.

speltoides contributed all the resistance alleles in these QTLs. Fig. 3 summarizes the mapped QTLs along with the linked markers on the physical map of the DS-BILs.

Since both the parents contributed to resistance for these diseases, QTLs mapped on segments donated by respective parents were studied. Studying the introgression in the resistant lines and the resistance donor fragments, 11 lines carrying multiple QTLs, mapped during this study, were identified. These lines are summarized in Table 2. Out of these six lines, namely DS-BIL6, DS-BIL8, DS-BIL16, DS-BIL18, DS-BIL20 and DS-BIL53 had three or four loci, for YR and PM, whereas other lines had two loci each. DS-BIL6 and DS-BIL16 had all the four loci (*QYrAs.pau-1B*, *QYrAs.pau-2A.1*, *QYrAs.pau-2B* and *QYrAs.pau-7B*) mapped for YR using field mixture of pathotypes and were completely resistant to stripe rust. However, lines with two or three loci showed moderate susceptibility. For PM, *QPmAs.pau-2A.1*, *QPmAs.pau-2B*

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Table 1. Summary of the QTL mapping using single marker analysis (SMA) and RSTEP-LRT for additive effect of markers algorithms of QTL ICI mapping

				Marker position				
	Trait name	QTL	SNP marker name	Chr.	Phy. position (Mb)	LOD	PVE (%)	Add
RSTEP-	Pst field pathotypes	*QYrAs.pau-2A.1*	S2A_16016633	S2A	16.01	2.6	13.83	0.6621
LRT	Pst field pathotypes	*QYrAs.pau-7B*	S7B_708445814	S7B	708.44	2.4	10.06	0.8519
	Pst 78S84	*QYrTd.pau-2A.2*	S2A_766158316	S2A	766.15	2.2	09.42	−0.6615
	Pst 78S84	*QYrTd.pau-3B*	S3B_743818730	S3B	743.81	4.1	19.29	−1.2189
	Bg field pathotypes	*QPmAs.pau-2A.1*	S2A_43146710	S2A	43.15	2.0	09.16	1.7895
	Bg field pathotypes	*QPmAs.pau-3B*	S3B_775092221	S3B	775.09	2.4	12.89	2.4370
	Bg field pathotypes	*QPmAs.pau-6B*	S6B_26793381	S6B	26.79	3.2	17.75	2.2547
SMA	Pst field pathotypes	*QYrAs.pau-1B*	S1B_626229235	S1B	626.22	2.0	11.64	0.4094
	Pst field pathotypes	*QYrAs.pau-2A.1*	S2A_16016633	S2A	16.01	3.8	24.51	0.8815
	Pst field pathotypes	*QYrAs.pau-2B*	S2B_27896451	S2B	27.89	2.2	12.80	0.4638
	Pst field pathotypes	*QYrAs.pau-7B*	S7B_708445814	S7B	708.44	2.4	10.06	0.8518
	Pst 78S84	*QYrTd.pau-2A.2*	S2A_766158316	S2A	766.15	2.8	14.00	−0.8065
	Pst 78S84	*QYrTd.pau-3B*	S3B_743818730	S3B	743.81	4.1	19.29	−1.2189
	Bg field pathotypes	*QPmAs.pau-2A.2*	S2A_771507864	S2A	771.507	2.1	11.49	2.1681
	Bg field pathotypes	*QPmAs.pau-2B*	S2B_791958961	S2B	791.958	2.3	14.05	2.2938
	Bg field pathotypes	*QPmAs.pau-6B*	S6B_26793381	S6B	26.793	3.2	17.75	2.2547

and *QPmAs.pau-3B* provided complete resistance individually. The other two PM QTLs conferred moderate resistance only in combination.

Introgression profile of DS-BILs

Introgression profile of DS-BILs was studied to visually identify the regions of introgression harbouring QTLs which would finally help in the selection of BILs as a pre-breeding material for rust resistance. The introgression profile is given in online Supplementary Fig. S2. Since *Ae. speltoides* is known to carry genes epistatic to *Ph1* locus of wheat (Millet, 2007; Colas *et al.*, 2008; King *et al.*, 2018), called *Ph* suppressors, which lead to homoeologous recombination of the alien genome with wheat chromosomes and are responsible for introgression of *Ae. speltoides* segments to both A and B genomes of *T. durum*, as seen in online Supplementary Fig. S2.

Postulation of candidate genes

The regions of 50 kb on both sides of the linked markers with respective QTLs were scanned to identify the candidate genes. The identified genes for each of the QTL mapped in this study are listed in Table 3. All the genes identified were high confidence genes as per annotation v1.1. For each target locus, genes known to be involved in different pathways of pathogen–host interactions and pathogenesis were identified and will be validated by developing mapping populations from the selected DS-BILs. No gene was detected in 50 kb region harbouring QTL *QPmAs.pau-3B*, hence a region of 500 kb was scanned on both sides of the linked SNP and candidate genes around the target loci were identified (Table 3).

Discussion

Stripe rust and powdery mildew are major constraints to wheat production worldwide. Wheat breeding programmes, to counter these hindrances, need continuous identification and introgression of new disease resistance genes from diverse sources including crop wild relatives. The work in hand describes the transfer and mapping of new genes/QTL for stripe rust and powdery mildew resistance from *Ae. speltoides*. During this study on a set of *T. durum–Ae. speltoides* introgression lines, two major genic loci effective against stripe rust pathotype *Pst* 78S84 were identified. Five genic loci were identified against field mixture of *Bg* pathotypes. Four loci were identified against field mixture of *Pst* pathotypes collected from the field. These QTLs were present on the terminal ends of the respective chromosomes (Fig. 3) which have been reported to have recombination hot spots of the chromosomes. The phenotypic data of the DS-BILs showed that a large number of loci might be responsible for resistance reaction as the variability of different reaction types shows the

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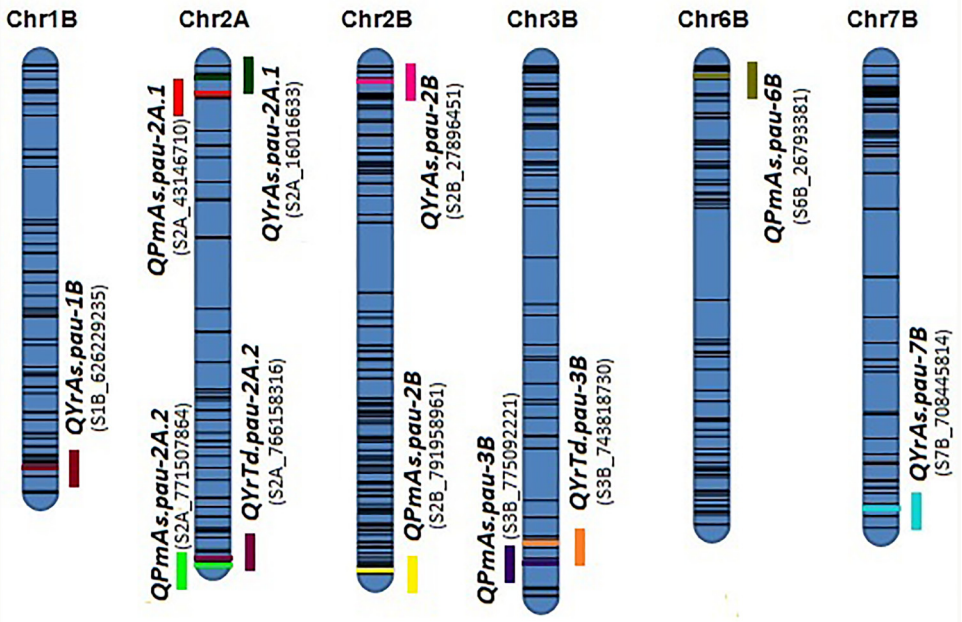

Fig. 3. Summary of the mapped QTLs for stripe rust and powdery mildew in the *T. durum–Ae. speltoides* introgression lines. Mapped QTLs are represented as bars alongside the carrier chromosomes. The black lines represent the SNP positions along the length of the chromosomes. The coloured lines on chromosomes and bars alongside represent the positions of QTLs. QTL names, and SNPs linked to the QTLs are presented alongside the coloured bars.

involvement of additive effects of multiple loci. Despite this, 11 loci were identified to provide resistance when mapping was done using RSTEP-LRT for the additive effect of markers and SMA. Since there were few sites on different chromosomes where there was low coverage/density of SNPs, and this hindered identifying QTLs (if present) in these locations. All the QTLs detected in the current study had good marker density (one SNP per 2.03 Mb against genomic average of one SNP per 8.60 Mb) in the genomic regions harbouring target QTL. To explain the residual resistance, which was not mapped in this study, a higher density of SNPs providing more coverage of the genome and a bigger set of the DS-BILs can be used. All the selected DS-BILs with different QTL combinations can be used in breeding programmes for marker-assisted transfer of the respective QTLs to the hexaploid backgrounds providing a good source of resistance.

Various designated genes, temporarily designated genes and QTLs for YR and PM reported from various studies have been compiled in online Supplementary Fig. S3 (source: www.wheat.pw.usda.gov). QTL *QYrAs.pau-1B* reported herein has been found in the vicinity of designated

Table 2. Summary of the resistant DS-BILs along with QTLs present in these DS-BILs

Genotype	QTLs present			
DS-BIL6	*QYrAs.pau-1B*	*QYrAs.pau-2A.1*	*QYrAs.pau-2B*	*QYrAs.pau-7B*
DS-BIL8	*QPmAs.pau-2A.2*	*QPmAs.pau-2B*	*QPmAs.pau-6B*	
DS-BIL16	*QYrAs.pau-1B*	*QYrAs.pau-2A.1*	*QYrAs.pau-2B*	*QYrAs.pau-7B*
DS-BIL18	*QPmAs.pau-2A.2*	*QPmAs.pau-2B*	*QPmAs.pau-6B*	
DS-BIL20	*QPmAs.pau-2A.2*	*QPmAs.pau-2B*	*QPmAs.pau-6B*	
DS-BIL32	*QPmAs.pau-2B*	*QPmAs.pau-6B*		
DS-BIL40	*QPmAs.pau-2A.2*	*QPmAs.pau-6B*		
DS-BIL45	*QYrTd.pau-3B*	*QYrTd.pau-2A.2*	*QPmAs.pau-6B*	
DS-BIL53	*QPmAs.pau-2A.2*	*QPmAs.pau-2B*		
DS-BIL55	*QYrTd.pau-2A.2*	*QPmAs.pau-3B*		
DS-BIL56	*QYrTd.pau-3B*	*QYrTd.pau-2A.2*		

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Table 3. Postulation of genes present in the survey sequence of wheat genome refseqV1.0

QTL	Trait	Distance from SNP	Chr	Reference gene/gene ID	Function
QYrAs.pau-1B	Pst field pathotypes	+4.59	chr1B	*TraesCS1B01G393400*	RING/U-box superfamily protein (zinc finger)
		−14.76	chr1B	*TraesCS1B01G393600*	Disease resistance protein (NBS-LRR class)
QYrAs.pau-2A.1	Pst field pathotypes	0	chr2A	*TraesCS2A01G038100*	L-gulonolactone oxidase
QPmAs.pau-2A.1	Bg field pathotypes	+13.05	chr2A	*TraesCS2A01G090000*	26S protease regulatory subunit
		+1.31	chr2A	*TraesCS2A01G090100*	Leucine-rich repeat receptor-like protein kinase
		−33.07	chr2A	*TraesCS2A01G090200*	Zinc-finger protein
QYrTd.pau-2A.2	Pst 78S84	+6.45	chr2A	*TraesCS2A01G567300*	Auxin response factor
QPmAs.pau-2A.2	Bg field pathotypes	−39.24	chr2A	*TraesCS2A01G577900*	Glutathione S-transferase
QYrAs.pau-2B	Pst field pathotypes	0	chr2B	*TraesCS2B01G057300*	Zinc finger family protein
QYrTd.pau-3B	Pst 78S84	+5.51	chr3B	*TraesCS3B01G499200*	Glutathione S-transferase
QPmAs.pau-3B	Bg field pathotypes	+352.75	chr3B	*TraesCS3B01G535300*	Glutathione S-transferase
		+388.74	chr3B	*TraesCS3B01G535500*	Protein enhanced disease resistance 2
		+469.71	chr3B	*TraesCS3B01G535700*	Glutathione S-transferase
QPmAs.pau-6B	Bg field pathotypes	+24.08	chr6B	*TraesCS6B01G044800*	receptor kinase 1
		0	chr6B	*TraesCS6B01G044900*	Mitochondrial transcription termination factor-like
		−47.40	chr6B	*TraesCS6B01G045000*	Mitochondrial transcription termination factor-like
QYrAs.pau-7B	Pst field pathotypes	+29.70	chr7B	*TraesCS7B01G443600*	RING/U-box superfamily protein (zinc finger)

Distance from SNP represents the distance of start site of the gene to SNP linked with QTL, where + sign represents the gene was found downstream of the SNP and − sign gene was found upstream, 0 represents the SNP was present inside the gene, and all distances are in kilobases.

genes *Yr29/Lr46* and QTL *QYr.cim-1BL* (Lan *et al.*, 2014). Similarly, QTL *QYrAs.pau-2A.1* was found in the vicinity of *Yr56* where some QTLs for YR have also been reported like *QYr.sun-2A_Wollaroi*, *QYr.tam-2AS_TAM111*, *QYr.ucw-2A.2(IWA422)*, *QYr.ufs-2A_Cappelle-Desprez_Yr16* and *QYr.inra_2AS.1_Recital* (Maccaferri *et al.*, 2015). QTL *QYrAs.pau-7B* has been physically located in the vicinity of stripe rust resistance genes *Yr52* and *Yr59* (McIntosh *et al.*, 2017). Interestingly, QTL *QYrTd.pau-3B* mapped from tetraploid donor PDW274 in the current study was found in the same genomic region as QTL *QYrEDWL.par-3BL* which was mapped in the tetraploid background of Ethiopian spring wheat by Liu *et al.* (2017). For PM, QTL *QPmAs.pau-6B* is located in the region harbouring QTL *QPm#66-2B* (Ben-David *et al.*, 2014). Other QTLs reported in this study could also be traced to the same arm, or close vicinity of genes/QTLs reported in the literature, as is depicted in online Supplementary Fig. S3. It was not possible to compare exact locations of the other QTLs mapped in this study with reported genes or QTL as most of the reported genes or QTLs have been mapped on the based-on linkage; whereas in the current study, genes/QTLs have been physically mapped to specific chromosome regions.

Studying the annotated reference of wheat genome refseqV1.0 showed the genes present in the genomic regions of mapped QTLs. Various categories of these genes are NBS-LRR protein family responsible for disease resistance, receptor or receptor-like proteins/motifs like Zinc finger, ubiquitin pathway proteins like ubiquitin regulator units and glutathione S transferase (GST), antioxidant pathway enzymes like L-gulonolactone oxidase, various kinases, auxin response factors (ARFs) and mitochondrial transcription termination factor-like (mTERF) proteins (Table 3). All these are known for their action in pathogen recognition, reactions, being involved in various biotic and abiotic stresses or plant-pathogenesis pathways. A complete list of genes is given in online Supplementary Table S1. The role of other genes/proteins in plant pathogenesis is either yet not reported or not well documented.

QYrAs.pau-1B and *QPmAs.pau-2A.1* loci harboured genes with NBS-LRR and zinc finger motifs. NBS-LRR genes are from the most abundant disease resistance

https://doi.org/10.1017/S1479262120000222 Published online by Cambridge University Press

gene family in plant genomes, and zinc finger motifs have been reported to be major motifs linked with the response of plants to various biotic and abiotic stresses (DeYoung and Innes, 2006; McHale *et al.*, 2006; Lee and Yeom, 2015; Dubey and Singh, 2018). Zinc finger motif was also found in the region of QTL *QYrAs.pau-2B* and *QYrAs.pau-7B*. PM QTL *QPmAs.pau-3B* was found to be located in the genomic region having the gene coding for protein-enhanced disease resistance 2 which induces resistance by negative regulation of salicylic acid in biotrophic pathogens like PM (Tang *et al.*, 2005). Zhang *et al.* (2019) suggested that in wheat, pathogen resistance genes can be activated by alternate splicing regulators in salicylic pathways, down-regulating its synthesis. L-gulonolactone oxidase (in the region of QTLs *QYrAs.pau-2A.1*) is a key enzyme in the formation of ascorbate. Thus, the regulation of this enzyme is essential in the regulation of ascorbate formation in plants (Gullner and Kômíves, 2007). Ascorbate is one of the major antioxidants of plants (Potters *et al.*, 2010; Paciolla *et al.*, 2016) and second, being glutathione, both act against reactive oxygen species (ROS) produced under biotic stresses (Kuźniak, 2010). Being part of the ascorbate–glutathione cycle, it takes part in signal transduction in biotic stress besides regulating the expression of nuclear genes as a response to invading pathogen providing both local and systematic defence (Sarowar *et al.*, 2005; Kuźniak, 2010).

QTL *QPmAs.pau-2A.1* region also annotated gene for regulatory subunit of 26S proteasome subunit. Proteasome, which is a part of the ubiquitin-proteasome system (UPS), functions by removal of misfolded and defective proteins along with eliminating short-lived proteins (Vierstra, 2009). Along with this, various pathways are controlled by UPS which include response to biotic and abiotic stresses (Sadanandom *et al.*, 2012), and acts as one of the major systems in plant immunity (Üstün *et al.*, 2016). Besides immunity, their role in defence responses by the production of ROS and forming hypersensitive reactions were reported (Marino *et al.*, 2012). Üstün *et al.* (2016) showed that proteasome mutants impaired/reduced systematic acquired resistance (SAR) on secondary infection and concluded that proteasome is essential for the pathogen-associated molecular pattern (PAMP) triggered immunity (PTI) and SAR. In a study involving *Arabidopsis* with loss of function mutants, Yao *et al.* (2012) reported that 26S regulatory subunit of proteasome, RPN1a, is essential for resistance. It induced cell death when *Arabidopsis* was infected by powdery mildew, concluding its effect on basal defence and resistance protein-mediated defence. Dielen *et al.* (2010) in a review on UPS (26S) highlighted the involvement of the system in defence mechanisms regardless of pathogen type.

ARF (in the region of QTL *QYrTd.pau-2A.2*) in various studies has been explained as a mediator of auxin to biotic and abiotic stresses (Ghanashyam and Jain, 2009; Fu and Wang, 2011; Bouzroud *et al.*, 2018). Bouzroud *et al.* (2018) reported that ARFs have a vital role in alteration (activation or repression) of the rate of transcription of auxin-responsive genes. Both biotic and abiotic stress-responsive genes are enriched in *cis*-elements of 5′-regulatory units in ARFs. They showed that under stress conditions, ARFs are actively regulated at the post-transcriptional level. Besides this, Fu and Wang (2011) reported that pathogen produced indole acetic acid (IAA) by the action of ARFs can cause either resistance to a necrotrophic pathogen (through ethylene signalling or camalexin biosynthesis), susceptibility by cell wall expansion or stomatal opening (through host IAA biosynthesis or IAA conjugation), basal resistance by IAA conjugation (differential regulation) or resistance to biotrophic pathogen (through indole glucosinolate biosynthesis and/or salicylic acid signalling).

High inducibility of GST in biotic stress in response to bacterial, fungal or viral infection by up-regulation of key defence enzymes has been reported in various studies (Gullner and Kômíves, 2007; Taylor *et al.*, 2012; Gullner *et al.*, 2018). In our study, QTLs *QPmAs.pau-2A.2*, *QYrTd.pau-3B* and *QPmAs.pau-3B* were found to be linked to GST gene/s. These authors have reported that besides its role in detoxification of various toxic substances and as antioxidative in reaction in infected cells, it also regulates the expression of various protective genes. Changes in expression of GSTs are reported to be modifying symptoms of a disease and sometimes the rate of multiplication of pathogens. Some GSTs with peroxidase activity are also known to detoxify lipid hydroperoxidases.

QTL *QPmAs.pau-6B* region was found to carry three genes, one of receptor kinase 1 and two of mTERF gene. Receptor kinases are known to be modulating plant defence responses. Receptor-like kinases (RLKs) and receptor-like proteins (RLPs) act as pattern recognition receptors (PRRs) (Tang *et al.*, 2017) and thus lead to first defence response. Multi-protein immune complexes of PRRs and other RLKs are formed at the surface of interaction. The two broad classes of receptors are, one in the cytoplasm with NB-LRR and the other on the cell surface with RLKs and RLPs (Jones and Dangl, 2006; Jones *et al.*, 2016). In wheat, *TaRLK-R1,2,3* (Zhou *et al.*, 2007) and *LRK10* (Feuillet *et al.*, 1997) have been involved in plant immunity where *TaRLK-R1* has also been cloned (Qin *et al.*, 2012). Wang and Bouwmeester (2017) suggested that PRRs recognize not only the invading organism's surface effectors but also damage-associated molecular patterns. PTI acts as a primary defence, and ETI acts as a secondary defence by recognition of by-products of effector specific resistance genes (Shi *et al.*, 2016). Thus, they both result in biotrophic pathogens' growth reduction. While mTERFs are best known to act against abiotic stresses and since only eight plant mTERFs are known to be characterized, very little is known about their action against biotic stresses (Babiychuk *et al.*, 2011; Vardhan and Kousar, 2015; Chen *et al.*, 2017; Pan *et al.*, 2019). However, mTERFs

https://doi.org/10.1017/S1479262120000222 Published online by Cambridge University Press

are known to show changed nuclear gene expression, which could support their role in various stresses.

The inference from this outcome requires studying the functions, activation, deactivation or alteration in the rate of expression of these loci in the process of development of resistance to specific diseases. However, regions having *Ae. speltoides* specific introgression may carry novel genes. In either case, there is a need to study the regions countering resistance at the transcriptional level to evaluate the actual cause of resistance in DS-BILs which would further help in the identification of unique pathways of development of disease resistance genotypes.

While several lines did contain large segment substitutions from *Ae. speltoides*, it is difficult to detect the QTLs that are close to each other with opposite effects. Hence, transferring them to different backgrounds can identify some additional genes or QTL. To conclude, despite the selected 11 DS-BILs being a good source of resistance to YR and PM, only the functional study of the regions could elaborate on the effect of these loci/QTLs in providing disease resistance.

Supplementary material

The supplementary material for this article can be found at https://doi.org/10.1017/S1479262120000222.

Acknowledgements

The financial support provided by the Department of Biotechnology, Ministry of Science and Technology, Government of India in the form of DBT Programme Support (grant no. BT/PR/5468/AGR/02/851/2012 dated 15.5.2012) is gratefully acknowledged. The supply of the rust inoculum by the Indian Institute of Wheat and Barley Research Station, Flowerdale, Shimla, India is also gratefully acknowledged.

Author contribution

GSD conducted disease screening, QTL mapping and manuscript writing; SK, JK and RS helped in the development of material and disease screening; ND supervised the study, helped in writing the manuscript; JP conducted genotyping by sequencing; PC designed the study, provided the basic genetic material, supervised the study and finalised the manuscript. All the authors have read the manuscript and approved it.

Conflict of interest

The authors declare that they have no conflict of interest.

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