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ORIGINAL PAPER

Identification of novel QTLs for seedling and adult plant leaf rust resistance in a wheat doubled haploid population

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Abstract Pyramiding of genes that confer partial resistance is a method for developing wheat (*Triticum aestivum* L.) cultivars with durable resistance to leaf rust caused by *Puccinia triticina*. In this research, a doubled haploid population derived from the cross between the synthetic hexaploid wheat (SHW) (×*Aegilotriticum* spp.) line TA4152-60 and the North Dakota breeding line ND495 was used for identifying genes conferring partial resistance to leaf rust in both the adult plant and seedling stages. Five QTLs located on chromosome arms 3AL, 3BL, 4DL, 5BL and 6BL were associated with adult plant resistance with the latter four representing novel leaf rust resistance QTLs. Resistance effects of the 4DL QTL were contributed by ND495 and the effects of the other QTLs were contributed by the SHW line. The QTL on chromosome arm 3AL had large effects and also conferred seedling resistance to leaf rust races MJBJ, TDBG and MFPS. The other major QTL, which was on chromosome arm 3BL, conferred seedling resistance to race MFPS and was involved in a significant interaction with a locus on chromosome arm 5DS. The QTLs and the associated molecular markers identified in this research can be used to develop wheat cultivars with potentially durable leaf rust resistance.

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Introduction

Wheat leaf rust, caused by the fungus *Puccinia triticina* Eriks., is the most common disease of wheat and can result in yield reduction of 5–15% or greater depending on the stage of crop development when the initial infection occurs (Samborski 1985; Kolmer 1996). The most economical and preferable method for controlling wheat leaf rust is the utilization of host plant resistance, and great efforts have been made to introgress resistance genes from related wild or cultivated species into wheat (McIntosh et al. 1995).

To date, more than 60 leaf rust resistance genes (*Lr* genes) have been identified and mapped to specific chromosomes (McIntosh et al. 2008). However, many of the *Lr* genes identified confer race-specific resistance, and have been frequently overcome by the appearance of new virulent races. *P. triticina* is highly variable with 50–60 races being identified in the US annually (Kolmer et al. 2008). Therefore, to achieve effective and long-lasting leaf rust resistance, it is essential to identify new resistance sources in wheat germplasm and to develop wheat cultivars with combinations of effective resistance genes (Messmer et al. 2000; McIntosh et al. 1995; Oelke and Kolmer 2005).

Quantitative trait locus (QTL) analysis is a powerful tool for identifying genes with both major and minor effects and estimating the number and chromosomal location of genes involved. Chromosome mapping of new *Lr* genes can lead to the identification of molecular markers suitable for

marker-assisted selection (MAS). In the case of leaf rust, QTL analysis has been used to detect genomic regions containing major resistance genes such as *Lr34* on chromosome arm 7DS (Suenaga et al. 2003; Schnurbusch et al. 2004), and other loci that condition minor levels of resistance located on different chromosomes (Suenaga et al. 2003; Schnurbusch et al. 2004; Messmer et al. 2000; William et al. 2006; Xu et al. 2005). Combinations of loci that condition quantitative resistance (Xu et al. 2005) would be preferable for developing cultivars with durable resistance since more than one gene would be involved and thus would be more difficult for the *P. triticina* population to overcome.

In the current work, a doubled haploid (DH) population derived from the cross between a synthetic hexaploid wheat (SHW) line and a North Dakota hard red spring wheat breeding line (Chu et al. 2008a) was evaluated for reaction to leaf rust at the adult plant stage in the field and at the seedling stage in the greenhouse. QTL analysis led to the identification of novel QTLs governing partial leaf rust resistance at both stages.

Table 1 Infection type (IT) and leaf infected area (IA) means of parental wheat lines TA4152-60 and ND495 as well as the derived double haploid population (Pop.) to *Puccinia triticina* in field and greenhouse tests

Experiment	ND495	TA4152-60	Pop. AVG	Pop. range
Field (adult plant)				
Infection type	2.3	0.8	2.1	0.4–3.0
Leaf infected area (%)	35.0	5.0	25.5	1.0–80.0
Greenhouse (seedling)				
Race MJBJ	3.0	2.5	2.6	1.0–3.0
Race TDBG	3.0	2.5	2.5	0.5–3.0
Race MFPS	2.0	3.0	2.4	0.5–3.0

The leaf rust infection types (ITs) were recorded following Long and Kolmer (1989), in which: *0* no uredinia or hypersensitive flecks, *semicolon* (;) no uredinia but hypersensitive necrotic or chlorotic flecks, *1* small uredinia surrounded by distinct necrosis, *2* small to medium uredinia surrounded by necrosis or chlorosis, *3* moderate size uredinia without chlorosis, *4* large size uredinia without chlorosis. In this table, the IT listed above were converted into 0, 0.5, 1, 2, 3 and 4, respectively

Materials and methods

Plant materials

A DH population from the cross between the SHW line TA4152-60 and the North Dakota hard red spring wheat breeding line ND495 was previously described (Chu et al. 2008a). The mapping population consists of 120 DH lines that were used to construct whole genome linkage maps and identify QTLs governing important agronomic traits as well as resistance to foliar disease (Chu et al. 2008a, b). In this research, the 120 lines were used for identification and mapping of QTLs conferring leaf rust resistance. The parental line TA4152-60 is an elite SHW line that was synthesized at the International Maize and Wheat Improvement Center (CIMMYT) from a cross between the durum wheat variety 'Scoop 1' and the *Aegilops tauschii* accession WPI358 (TA2516), and was originally identified as moderately resistant to leaf rust (Mujeeb-Kazi et al. 2000). The other parental line, a hard red spring wheat breeding line ND495, is a selection from 'Justin*2/3/ND 259/Conley//ND 112'. Our field observations indicated that the SHW line was resistant whereas ND495 was moderately susceptible to leaf rust (Table 1; Fig. 1).

Disease reaction evaluation

Field experiments to evaluate adult plant leaf rust resistance were conducted in 2007 and 2008 in Fargo, ND, using randomized complete block designs (RCBDs). Two replicates were included in the 2007 experiment, which was planted on May 16. For each replicate, fifteen seeds of each line were sown in a 90 cm-long row with 30 cm of distance between rows. The 2008 nursery was planted on May 14, and included three replicates that were planted in hill plots with seven seeds per line. To check the uniformity of infection, the two parental lines were planted after every thirty lines in both years. Disease severities were scored in late July when acceptable levels of leaf rust appeared on the susceptible parent ND495. Since leaf rust is very diverse for virulence it can be assumed that a number of different races were present in the plots at Fargo in both years. The leaf rust infection types (ITs) were scored using the system developed by Roelfs and Martens (1988) and Long and Kolmer (1989), in which: 0 = neither uredinia nor hypersensitive flecks, semicolon (;) = no uredinia but hypersensitive necrotic or chlorotic flecks, 1 = small uredinia surrounded by distinct necrosis, 2 = small to medium uredinia surrounded by necrosis or chlorosis, 3 = moderate size uredinia without chlorosis, and 4 = large size uredinia without chlorosis. ITs of 0, semicolon (;) and 1 were considered as resistant, those of 2 and 3 were moderately resistant and moderately susceptible, respectively, and that of 4 was highly susceptible. When used for data analysis, the ITs were converted into 0, 0.5, 1, 2, 3 and 4, respectively. The leaf infected area (IA) of the parent and each progeny line was also recorded in the percentage scale using the modified Cobb scale (Peterson et al. 1948).

To determine if the leaf rust resistance loci conferred race-specific resistance or if these differed from the

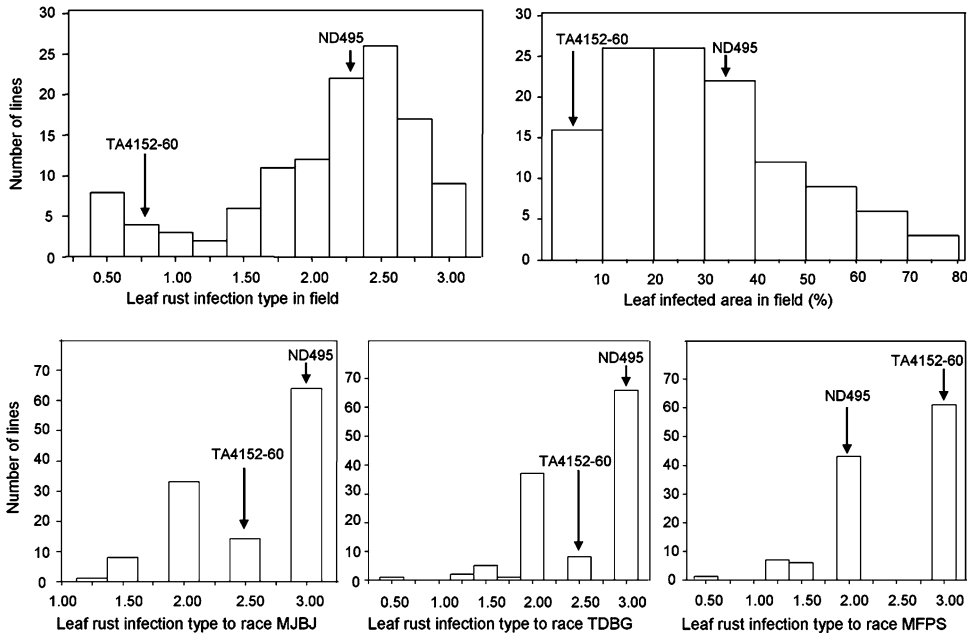

Fig. 1 Histograms of leaf rust infection type (IT) distribution in wheat lines of the TA4152-60 × ND495 derived double haploid population in field tests and greenhouse tests with races TDBG, MJBJ and MFPS of *Puccinia triticina*. The leaf rust ITs were the same as those denoted in Table 1

known *Lr* genes, leaf rust races MJBJ, TDBG and MFPS were used for the greenhouse evaluation of seedling plants. These races are common and widespread throughout the Great Plains region (Kolmer et al. 2008). Race MJBJ is virulent on *Lr1*, *Lr3*, *Lr10*, *Lr16*, *Lr14a*, *Lr14b* and *Lr24*; race TDBG is virulent on *Lr*1, *Lr2a*, *Lr2c*, *Lr3*, *Lr10*, *Lr14b* and *Lr24*, and race MFPS is virulent on *Lr1*, *Lr3*, *Lr3ka*, *Lr10*, *Lr14a*, *Lr14b*, *Lr17*, *Lr24*, *Lr26* and *Lr30*. In greenhouse testing, six to eight seeds of each DH line were planted in 3.5-cm^2 plastic pots in vermiculite (Sunshine Strong-Lite Medium Vermiculite Premium Grade, JR Johnson Horticultural Supplies, St. Paul, MN) as described by Oelke and Kolmer (2004). Seedlings were watered daily, and fertilized at emergence with 20–20–20 NPK soluble fertilizer (Spectrum Group, St. Louis). After approximately 8 days of growth in a greenhouse at 18–22°C with 16 h of supplemental light, when the first leaf was fully expanded, the seedlings were inoculated by atomizing urediniospores of the individual isolates suspended in Soltrol 170 oil (Chevron Phillips Chemical Company, Woodlands, TX). After 30 min of air drying, the inoculated seedlings were incubated in a mist chamber at 18°C and 100% relative humidity for 16–24 h, and then were moved back to the greenhouse for further incubation. ITs were recorded 12 days post inoculation.

Molecular mapping and QTL analysis

The linkage maps developed for this DH population consist of 632 markers and span 3,811.5 cM with an average density of one marker per 6.03 cM (Chu et al. 2008a). A subset of 449 markers spaced 5–20 cM apart giving the most complete genome coverage was used for QTL detection.

Bartlett's χ^2 was calculated (SAS Institute 2006) to test for homogeneity of variances among the 2 years of IT and IA to determine if years could be combined. QTL analysis was done first by identifying individual markers significantly ($P < 0.001$) associated with leaf rust resistance through single-factor regression analysis using the computer program Map Manager QTX (Manly et al. 2001), and then by simple interval mapping (SIM) and composite interval-regression mapping (CIM) to evaluate marker intervals putatively associated with trait phenotypes using the computer program Windows QTL Cartographer (V2.5) (Wang et al. 2007), and further verified by Map Manager QTX (Manly et al. 2001). The critical LOD threshold of 3.2 in this DH population was determined by a test with 5,000 permutations that yield an experiment-wise significance level of 0.05. Markers with significant ($P < 0.001$) main effects were tested against all other markers to identify significant ($P < 0.000001$) interactions (Manly et al. 2001). Markers with the most significant effect for each QTL were assembled into multiple regression models to determine the coefficient of determination (R^2) using the computer program QGENE (Nelson 1997), which is the total amount of variation explained by the model.

Results

Evaluation of leaf rust in the DH population

Homogeneity tests indicated the ITs data were homogeneous ($x^2_{df=1} = 1.51, P = 0.22$) among the two field

experiments, therefore the datasets were combined (Table 1; Fig. 1). The mean ITs of the field tests were used for QTL analysis. In field tests, the SHW line (TA4152-60) had chlorotic flecks and was resistant, while the common wheat line ND495 had moderate size uredinia surrounded by chlorosis and was moderately susceptible, the mean ITs of the DH lines varied from highly resistant to moderately susceptible (Table 1; Fig. 1). The leaf IA data from the 2 years of field experiments were also combined because they were homogeneous across years ($x^2_{df=1} = 0.22, P = 0.64$). The mean IA of both parents and DH lines were consistent with the IT data, and statistical analysis further showed that the data of IT and IA were highly correlated ($r = 0.80$, $P < 0.0001$).

In the seedling tests, the SHW line was moderately resistant to moderately susceptible to leaf rust races MJBJ and TDBG, while ND495 was moderately susceptible to the same races (Table 1). Using race MFPS, ND495 was moderately resistant and the SHW line was moderately susceptible. The mean ITs of the whole population to the three races was near 2.5, suggesting that most lines in the population were moderately susceptible to these three races (Table 1; Fig. 1). The intermediate ITs of the parental lines indicated that genes conferring partial resistance segregated in this population. The transgressive segregation for lower IT in the seedling and field tests indicated that some progeny lines had leaf rust resistance derived from both parents.

Identification of QTLs

Single-factor regression, SIM, and CIM analysis of the combined field IT data for reaction to leaf rust revealed five QTLs associated with resistance (Table 2; Fig. 2). Four QTLs located on chromosome arms 3AL (designated as *QLr.fcu-3AL*), 3BL (*QLr.fcu-3BL*), 5BL (*QLr.fcu-5BL*) and 6BL (*QLr.fcu-6BL*) were significantly associated with resistance contributed by the SHW parent TA4152-60, and one QTL located on chromosome arm 4DL (*QLr.fcu-4DL*) was contributed by ND495. The total phenotypic variation explained by the five QTLs in the multiple regression model was 58%.

The QTLs *QLr.fcu-3AL* and *QLr.fcu-3BL* had the largest effects for leaf rust resistance in the field experiments. *QLr.fcu-3AL* explained 18% of the phenotypic variation and *Xfcp586* was the most significant marker within the interval. *QLr.fcu-3BL* explained 19% of the trait variation and *Xbarc164 was* the most significant marker within the interval (Table 2; Fig. 2). The two QTLs each reduced the IT by 0.6 in the field experiments. The three remaining QTLs, *QLr.fcu-4DL*, *QLr.fcu-5BL* and *QLr.fcu-6BL*, showed smaller effects on leaf rust resistance and explained 13, 7 and 12% of the phenotypic variation, respectively (Table 2).

QTLs *QLr.fcu-3AL*, *QLr.fcu-3BL*, *QLr.fcu-4DL* and *QLr.fcu-5BL* were also significant in the analysis of leaf IA (Table 2). The peak interval of *QLr.fcu-3BL* was shifted proximal relative to the *QLr.fcu-3BL* peak for the IT data; however, the most significant marker was still *Xbarc164*, which was also the most significant marker associated with the IT data (Fig. 2). *QLr.fcu-4DL* contributed by ND495, was significant only in the single-factor regression for IA and not in the CIM. *QLr.fcu-5BL* derived from ND495 had a slightly greater effect on leaf IA than on IT (Table 2).

Table 2 Composite interval mapping (CIM) analysis of QTLs associated with resistance to *Puccinia triticina* in field and greenhouse tests to specific leaf rust races in the TA4152-60 × ND495 derived doubled haploid population

QTL[a]	Marker interval[b]	Peak position (cM)	R^2 value					Logarithm of the odds (LOD)				
			Field IT	Field IA	MJBJ	TDBG	MFPS	Field IT	Field IA	MJBJ	TDBG	MFPS
QLr.fcu-3AL (TA4152-60)	*Xcfa2183–Xgwm666*	99.4–129.6	0.18	0.10	0.36	0.30	0.12	7.4	3.90	17.0	13.9	4.7
QLr.fcu-3BL (TA4152-60)	*Xbarc164–Xfcp544*	113.8–137.9	0.19	0.20	NS	NS	0.15	9.2	8.30	NS	NS	4.9
QLr.fcu-4DL (ND495)	*Xgdm61–Xcfa2173*	43.3–66.9	0.13	0.07	NS	NS	NS	4.6	2.85	NS	NS	NS
QLr.fcu-5BL (TA4152-60)	*Xgdm116–Xbarc59*	140.1–156.4	0.07	0.10	NS	NS	NS	3.9	4.85	NS	NS	NS
QLr.fcu-6BL (TA4152-60)	*Xbarc5–Xgwm469.2*	84.4–90.7	0.12	NS	NS	NS	NS	3.9	NS	NS	NS	NS
Multiple regression[c]	–	–	0.58	0.41	–	–	0.25	–	–	–	–	–

NS non-significant; *IT* infection type, *IA* leaf infected area

[a] The parent contributing effects for resistance is shown in parentheses

[b] The marker interval of *QLr.fcu-3BL* for field leaf infected area (IA) was different (see Fig. 2)

[c] Mutiple regression models included the most significant markers in each marker interval

The QTLs *QLr.fcu-3AL* and *QLr.fcu-3BL*, which had the largest effects for the field experiments, also had significant effects for resistance in seedling tests (Table 2; Fig. 2). *QLr.fcu-3AL* was significantly associated with seedling resistance to races MJBJ and TDBG (Table 2; Fig. 2). For resistance to race MFPS, QTLs *QLr.fcu-3AL* and *QLr.fcu-3BL* both had significant effects (Table 2; Fig. 2). In addition, a significant interaction between marker *Xbarc164* (the most significant marker of *QLr.fcu-3BL*) and *Xgwm159* (a locus on chromosome arm 5DS) was associated with seedling IT caused by race MFPS (Table 3). When DH lines were grouped into four categories based on the allelic state of markers *Xbarc164* and *Xgwm159*, the group of DH lines with the TA4152-60 alleles at *Xbarc164* and ND495 alleles at *Xgwm159* had a mean IT of 2.0 to race MFPS, which was significantly less than the three other possible genotypes (Table 3). Since the 5DS marker *Xgwm159* showed no direct effect on leaf rust resistance through QTL analysis, the interaction between *Xbarc164* and *Xgwm159* indicated that certain alleles from chromosome arm 5DS in ND495 could significantly improve the expression of *QLr.fcu-3BL*, the QTL carried by TA4152-60. No significant interactions between these loci were detected for IT to races MJBJ and TDBG.

Discussion

In this research, five QTLs were shown to be associated with adult plant resistance to leaf rust in the DH population derived from the cross between TA4152-60 and ND495. Among these, four QTLs, including two with large effects on chromosome arms 3AL and 3BL, were derived from TA4152-60, whereas the QTL on chromosome arm 4DL was contributed by ND495. TA4152-60 carried more leaf rust resistance QTLs, which is consistent with the field observation that this line was more resistant than ND495 (Table 1).

The two QTLs with major effects for leaf rust resistance were unique in that one of these, *QLr.fcu-3BL,* conditioned race-specific resistance in seedling tests yet was also associated with resistance of adult plants in the field, where presumably multiple races were present. The other QTL with major effects, *QLr.fcu-3AL*, conditioned seedling and field resistance to more than one race. QTLs for leaf rust resistance in wheat have previously been assumed to condition race non-specific resistance that is expressed only in adult plants (Messmer et al. 2000, Xu et al. 2005). The race-specificity, or lack thereof, of *QLr.fcu-3BL* should be investigated further with other races. In this study the field tests were conducted in two environments that may have affected the significance levels of the three minor QTLs. Additional environments may have either increased or decreased the relative contributions of the minor QTLs.

It was surprising that the QTLs derived from TA4152-60 were on the A and B genomes, which indicated that these must have been derived from Scoop 1, the durum wheat parent of TA4152-60, and not *Ae. tauschii.* Although *Ae. tauschii* has been a source of leaf rust resistance genes such as *Lr21*, *Lr22a*, and *Lr42* (McIntosh et al. 1995) none of the resistance QTLs in this study were derived from this wild wheat relative. Genes *Lr14a* and *Lr23* (McIntosh et al. 1995) were derived from tetraploid wheat and express very low IT to avirulent races in seedling plants. The resistances associated with the QTLs in TA4152-60 are different compared to these genes since they do not confer very low IT in seedlings. Leaf rust resistance genes derived from tetraploid wheats that express incomplete or partial resistance in adult plants have also not been previously mapped. The use of synthetic wheats may be a useful approach to transfer leaf rust resistance from durum wheat to hexaploid wheat.

Some of the QTLs characterized in this study may be new sources of leaf rust resistance in wheat. Previously, Messmer et al. (2000) reported a QTL conferring leaf rust resistance on chromosome 3A in a recombinant inbred population derived from ‘Forno’ × ‘Oberkulmer’. The 3A QTL found by Messmer et al. (2000) and the 3A QTL found in this study may be identical. Messmer et al. (2000) also reported a leaf rust resistance QTL on the distal end of chromosome arm 4DL, but the QTL *QLr.fcu-4DL* detected in this research was located in the proximal region of chromosome arm 4DL, therefore, *QLr.fcu-4DL* is probably different from the one identified by Messmer et al. (2000). The QTLs *QLr.fcu-4DL*, *QLr.fcu-3BL*, *QLr.fcu-5BL* and *QLr.fcu-6BL*, have chromosome locations that have not been previously implicated in leaf rust resistance; therefore these are potentially new unexploited genes for leaf rust resistance in wheat.

None of the QTLs characterized in this study conditioned high levels of resistance. The parental line TA4152-60 only had moderate seedling resistance. The transgressive segregation of progeny lines with better resistance than either parent indicated that these QTLs had some additive characteristics and could be combined to develop highly resistant germplasm.

The TA4152-60 line was more susceptible to race MFPS than ND495. The results indicated that resistance to race MFPS conditioned by *QLr.fcu-3AL* and *QLr.fcu-3BL* was contributed by TA4152-60. However, the significant interaction between *QLr.fcu-3BL* and *Xgwm159* on chromosome arm 5DS indicated that *QLr.fcu-3BL* was only effective when ND495 alleles were present at the *Xgwm159* locus. Bai and Knott (1992) reported that genes on chromosomes 1D and 3D suppressed the resistance genes on chromosomes 2B and 4B. TA4152-60 may carry a suppressor on

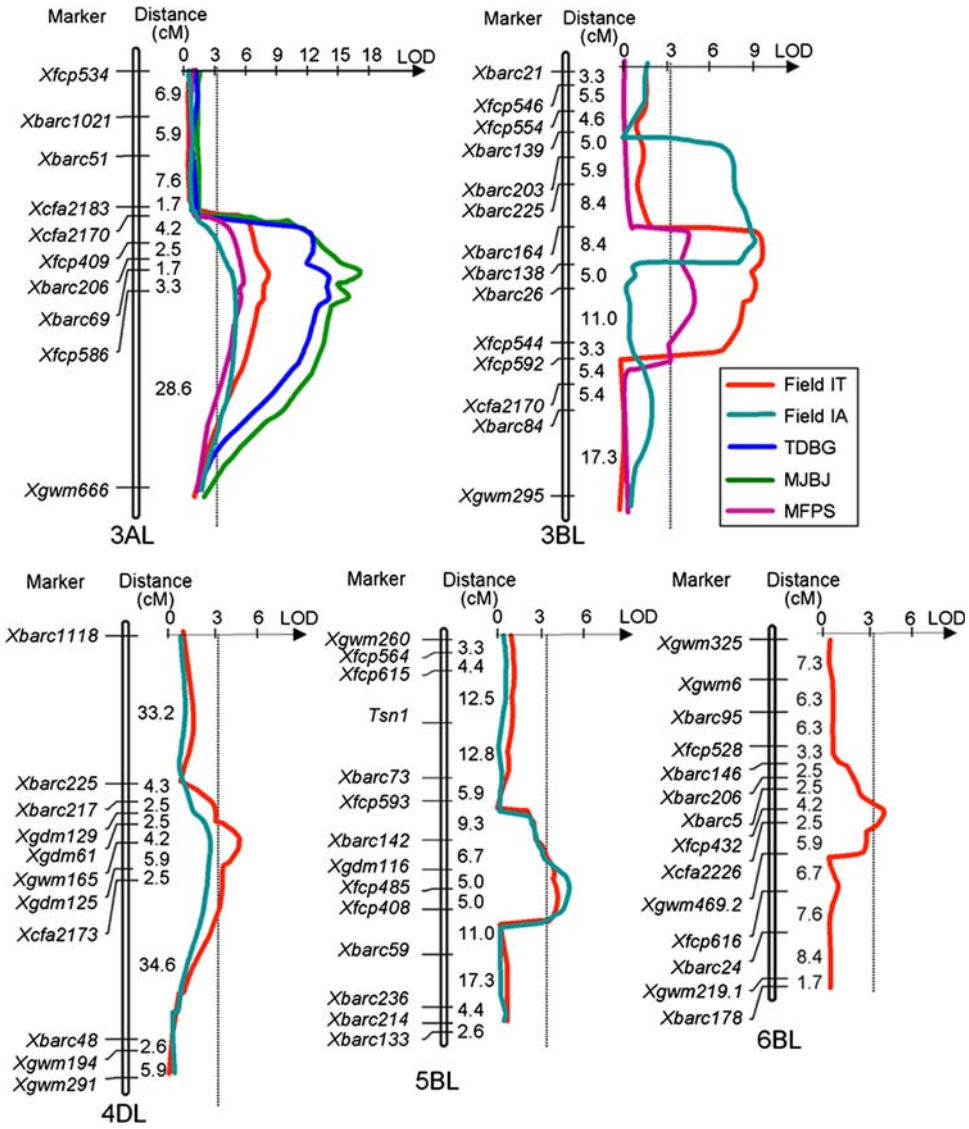

Fig. 2 Composite interval regression maps of QTLs associated with leaf rust resistance in the TA4152-60 × ND495 derived double haploid population. The positions of marker loci are shown to the *left* of the linkage groups and centiMorgan (cM) distances between loci are shown along the right. The *vertical dotted line* represents the logarithm of the odds (*LOD*) significance threshold of 3.2 in this research. *Red*, *cyan*, *blue*, *green* and *purple lines* indicate QTLs associated with leaf rust resistance identified in field tests of infection type (IT) and leaf infected area (IA) and greenhouse tests with races TDBG, MJBJ and MFPS of *Puccinia triticina*, respectively. The LOD and R^2 values for each QTL are listed in Table 2

Table 3 The interaction between markers *Xbarc164* (3BL) and *Xgwm159* (5DS) on seedling infection type (IT) to race MFPS of *Puccinia triticina*

Marker allele state combination		No. of lines	Mean IT ($LSD_{0.05} = 0.3$)[a]
Xbarc164 (3BL)	*Xgwm159* (5DS)		
TA4152-60	ND495	31	2.0a
TA4152-60	TA4152-60	18	2.5b
ND495	TA4152-60	35	2.5b
ND495	ND495	36	2.8b

[a] Numbers followed by the same letter are not significantly different from one another at the probability level of $P < 0.05$

chromosome arm 5DS that affects the expression of *QLr.fcu-3BL*, which could partially explain why TA4152-60 was susceptible to race MFPS even though it carries the resistance QTLs. The higher susceptibility to race MFPS in TA4152-60 might also be due to the background effect on the leaf rust resistance genes. Dyck and Samborski (1974) found that *Lr2* alleles expressed the most resistance in the Thatcher background but were least effective in Red Bobs. Pretorius et al. (1990) also reported that the expression of *Lr22a* was background dependant. In addition, the moderate resistance in ND495 to race MFPS indicated that the line might carry additional resistance QTLs with minor effects,

but were not detected in this research. Overall, marker coverage of the chromosomes in our population was quite good, but a few gaps are known to exist (Chu et al. 2008a, b). If minor QTLs exist within one or more of the gaps of the linkage map, they would have gone undetected. Also, the relatively small population size makes it difficult to detect all QTLs with minor effects.

In conclusion, our research revealed five QTLs conferring adult plant resistance to leaf rust in the TA4152-60 × ND495 derived DH population. The effects of all identified QTLs were additive and thus progeny lines with combinations of these QTLs expressed increased resistance. The synthetic wheat line TA4152-60 contributed four QTLs, and the common wheat line ND495 contributed one. The major QTLs on chromosomes 3AL and 3BL conditioned adult plant resistance in field experiments and the QTL on 3BL also conferred seedling resistance to a specific race, and the QTL on 3AL conditioned seedling resistance to all races tested. Since the chromosome 7DS region in wheat is associated with partial resistance to leaf rust, stripe rust, and powdery mildew (Spielmeyer et al. 2005), the QTLs described in this study potentially may also confer resistance to other wheat pathogens. The QTLs and the associated molecular markers identified in this research will be useful for accumulating partial leaf rust resistance to develop wheat cultivars with potentially long-lasting resistance.

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