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Mapping main effect QTL and epistatic interactions for leaf rust and yellow rust using high density ITMI linkage map

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Abstract

The present study was undertaken to identify QTL for leaf rust (LR) and stripe or yellow rust (YR) using ITMI-mapping population under Indian environmental conditions. A high density framework linkage map consisting of 1,345 markers was used to conduct single and two locus QTL analyses using QTLCartographer and QTLNetwork. A total of 14 main-effect QTL (M-QTL) for LR and 12 M-QTL for YR were detected. Among all these M-QTL, 7 for LR and 4 for YR were novel, and have not been reported in earlier studies using same population. Eight significant Q×Q interactions for each trait were also identified, which involved 16 epistatic-QTL (E-QTL) for LR and 14 E-QTL (including 2 M-QTL) for YR. Four genomic regions had QTL for both LR and YR. The phenotypic variation explained (PVE) ranged from 2.16% - 29.07% for M-QTLLR and from 0.80%-7.05% for E-QTL. Epistasis contributed a significant portion of the PVE (26.01% for LR and 31.51% YR) for the two traits. Minor environment interactions were observed for YR.

Keywords: Epistasis; Leaf Rust; QTL; Wheat; Yellow Rust.
Abbreviation: APR: adult plant resistance; E-QTL: epistatic QTL; LR: leaf rust; M-QTL: main-effect QTL; PVE: phenotypic variation explained; YR: yellow rust.

Introduction

Leaf rust (LR) caused by *Puccinia triticina* Eriks. and stripe or yellow rust (YR) caused by *Puccinia striiformis* f. sp. tritici are two important diseases of wheat. Leaf rust or brown rust, is distributed worldwide, and represents one of the most important fungal pathogen of wheat. Similarly, yellow rust is of particular importance in slightly cooler and wetter areas of the temperate and maritime regions and at higher altitudes, and in regions with hot summers where wheat is grown as a winter crop. According to an estimate, under favorable conditions in Asia, leaf rust could affect wheat production on 60 m ha (63%) and yellow rust on 43 m ha (45%), (Singh et al., 2004). In India, as much as 0.8 to 1.5 mt of wheat production was lost due to leaf rust epidemics during 1971-1973, further underlying the importance of the disease (Govindu, 1977). Stripe rust is also fast becoming a major productivity constraint in North Western Plains Zone of India. The use of fungicides to control rust diseases, inflates the cost of production, besides causing environmental pollution hazards to human health. Therefore, development and use of resistant varieties containing diverse genes for resistance against these rust diseases is the most-efficient and environmentally sustainable means of reducing losses due to these diseases. In view of this, selection for rust resistance has become an integral part of the strategic Indian wheat breeding programme. At present, more than 70 *Lr*-genes (*Lr1* through *Lr68*, in addition to some temporary designations) conferring resistance to leaf rust have been identified in wheat (http://www.ars.usda.gov/mwa/cdl; Herrera-Foessel et al., 2011, 2012; McIntosh et al., 2011; Ingala et al., 2012). Most of the major *Lr* genes confer race-specific resistance, although several other genes like *Lr12*, *Lr13*, *Lr34*, *Lr68*, *LrSV1* and *LrSV2* also provide durable leaf rust resistance in wheat worldwide (Roelfs et al., 1992; Herrera-Foessel et al., 2012; Ingala et al., 2012). Gene *Lr34* has been most widely used in wheat breeding programs because it provides durable resistance and has association with yellow rust resistance (*Yr18*) and tolerance to barley yellow dwarf virus infection (McIntosh, 1992; Singh, 1993). Similarly, for yellow rust, more than 50 *Yr*-genes designated as *Yr1* through *Yr49* along with some temporary designations such as *YrH52* (Peng et al., 1999) or *YrnsB1* and *Yr30* (Börner et al., 2000) have been described (http://www.ars.usda.gov/mwa/cdl; Li et al., 2011; Herrera-Foessel et al., 2011; McIntosh et al., 2011). Adult plant resistance (APR) genes to yellow rust have been mapped on a number of wheat chromosomes, which include *Yr18* on chromosome 7D (Singh et al., 2000, 2001; Bariana et al., 2001; Boukhatem et al., 2002), *Yrns-B1* on 3BS (Börner et al., 2000), (Singh et al., 2000), *Yr29* on chromosome 1B (William et al., 2003a, b), and *Yr31* on chromosome 2BS (Singh et al., 2003). However, non-specific, adult plant or quantitative resistance, is generally considered to be durable, polygenically controlled, and is effective at the adult plant stage. The genetic basis of this type of resistance has not been explored in as much details as the major gene controlled resistance nor has it been widely exploited for improving resistance of wheat varieties. Nonetheless, due to the recent availability of molecular markers a few attempts have been made at the dissection of polygenic/quantitative leaf/yellow rust resistance in wheat using QTL analysis. In the past, QTL

for adult plant resistance to LR and YR were reported using ITMI- (Nelson et al., 1997; Singh et al., 2000; Börner et al., 2002; Boukhatem et al., 2002) and several other mapping populations (Börner et al., 2000; Bariana et al., 2001; Singh et al., 2001; Boukhatem et al., 2002; Suenaga et al., 2003; William et al., 2003a,b; Ramburan et al., 2004; Mallard et al., 2005; Christiansen et al., 2006; Chu et al., 2009; Singh et al., 2009; Jagger et al., 2011; Prins et al., 2011; Agenbag et al., 2012). But, the studies involving identification of QTL for LR and YR under Indian environmental conditions are limited (Chhuneja et al., 2006). Moreover, recent studies also, demonstrated the role of epistatic and environmental interactions in controlling disease resistance in bread wheat (Ma et al., 2006). In the present study we used a high-density map comprising 1,345 markers to dissect the polygenic resistance against leaf and yellow rusts under Indian environmental conditions and to find out the role of epistatic and environmental interactions in the genetic control of these two diseases. This is likely to help in better understanding of the quantitative genetic control of the two diseases and also in designing suitable strategies for efficient use of resistance sources in wheat-breeding programs.

Material and methods

Plant material and phenotypic data recording

One hundred and ten (110) recombinant inbred lines (RILs) of the ITMI-population were used in the present study (for more details, see Nelson et al., 1995). Seeds of the above mapping population were initially provided by Dr. R.P. Singh of CIMMYT, Mexico. The RILs along with two parental genotypes were raised for three years (2001-2002, 2002-2003 and 2003–2004) in the experimental area of Punjab Agricultural University, Ludhiana, Punjab, which is a major wheat growing area of Northern India (Chhuneja et al., 2006). Each genotype was planted in pair rows of 1 m with row-to-row distance of 20 cm. The routine agronomic practices were followed for raising the crop. The infector rows (a mixture of susceptible wheat genotypes) were planted after every 20 rows as well as around the population. To initiate the disease epidemic, infector rows and experimental population were sprayed with 1 g of mixture of LR/YR urediospores (leaf rust pathotypes 77-1, 77-2, 77-5, 104-2 and stripe rust pathotypes 46S102, 46S103 and 46S119) suspended in 10 litre of water with 2-3 drops of Tween 20 as dispersant solution. The inoculations of LR and YR were done in the evening on alternate days beginning from end of December to mid of January each year. At adult plant stage, data were recorded as percentage of leaf area covered with rust urediospores, according to modified Cobb's scale (Peterson et al., 1948).

Framework linkage map

The published framework linkage map of ITMI-population (Song et al., 2005) and marker segregation data of 1,345 markers were retrieved from Graingenes database (http://wheat.pw.usda.gov.). The map represented a total genetic distance of 2,654 cM with an average distance of 1.97cM between any two markers.

Statistical analysis

Single-locus QTL analysis to identify main effect QTL for LR and YR was carried out by composite interval mapping (CIM) using QTL Cartographer V2.5 (Wang et al., 2007). In this method, model 6 with forward and backward step-wise regression with five markers as cofactors to control genetic background and a 10 cM genome-wide scan window, were used for the detection of QTL. A LOD score of 2.5 was used for suggesting the presence of a putative QTL. The experiment-wise threshold LOD scores for the detection of definitive QTL were calculated based on 1000 permutations at $P \leq 0.05$ (Churchill and Doerge, 1994). The QTL with LOD scores below the threshold LOD were considered as only 'suggestive QTL' and those with LOD scores above the threshold were considered as 'definitive QTL'. A QTL detected in more than half of the environments was considered a 'consistent QTL'. The peaks of the LRs (likelihood ratios) in the linkage map were taken as putative positions of the QTL. Confidence intervals (CI) were obtained using positions ± 2 LOD away from the peak. QTL detected with overlapping confidence intervals (also called as support intervals) were treated as the same. The relative contribution of a genetic component (R^2 or h^2) was calculated as the proportion of the PVE. Another software QTLNetwork 2.0 (Yang et al., 2008), which is based on Mixed-model-based composite interval mapping (MCIM; Zhu, 1999; Yang et al., 2007), was used to conduct two-locus QTL analysis which allows identification of QTL involved in epistatic (QQ or E-QTL) and environmental interactions (QE or QQE), in addition to the identification of main effects QTL. A significance threshold of $P<0.05$ was used to select associated markers, and to declare putative main effect or epistatic QTL. The QTL were designated according to the standard nomenclature for QTL as recommended for wheat (McIntosh et al., 1998) and in continuation to those followed by us in our earlier studies involving QTL analyses (Kumar et al., 2009).

Results and discussion

Phenotypic analyses

LR and YR scores of RILs at adult plant (AP) stage were not normally distributed and were skewed towards resistance in all the environments (for more details, see Chhuneja et al., 2006). This suggested non-uniform distribution of loci controlling these traits in the RILs of the mapping population. The rank correlations between different pairs of environments were positive and highly significant, for both LR and YR scores, suggesting that the disease scores of RILs in different environments varied in the same direction and that RIL × environment interactions were generally absent. Also mean LR and YR scores were significantly and positively correlated (Table 1), suggesting the possibility of linked/common QTL for the two diseases.

QTL analyses

The detailed results of single- and two-locus QTL analyses for LR and YR are presented in Tables 2-4.

(a) *Main effect QTL for LR and YR*

Quantitative genetic control of LR and YR:

For LR, a total of 14 M-QTL (12 detected by single-locus analysis and 5 detected by two-locus analysis; 3 being common) located on 9 different chromosomes were detected during the present study (Tables 2-4). In the past, QTL for LR were reported on at least 18 chromosomes (Nelson et al., 1997; William et al., 1997; Messmer et al., 2000; Börner et al., 2002; Schnurbusch et al., 2004a; Navabi et al., 2005; Xu

Table 1. Simple and rank correlation coefficients between leaf rust (LR) and yellow rust (YR) scores of RILs of ITMI-mapping population of wheat.

	LR			YR			LR-YR
Environment[c]	I-II	I-III	II-III	I-II	I-III	II-III	AE-AE
Simple correlation	0.73***	0.78***	0.69***	0.72***	0.58***	0.64***	0.30**
Rank correlation	0.79***	0.82***	0.73***	0.74***	0.52***	0.65***	0.30**

[c]Environment I = Ludhiana 2002, II = Ludhiana 2003, III = Ludhiana 2004, AE= pooled data of all the environments; ** Significant at P <0.01, ***significant at P<0.001

Table 2. QTL for leaf rust (LR) and yellow rust (YR) detected in ITMI-mapping population of wheat by single-locus analysis using QTL Cartographer.

QTL*[k]	Environment [c]	Flanking markers[e]	Position (cM)	CI (cM)	LOD	a	R^2 (%)[x]
LR							
QLr.ccsu-1A.1	III	Xbarc263-Xcdo426	17.31	14.6-22.3	2.82	-6.73	6.83
QLr.ccsu-1A.3[k]	II	Xgwm99-Xmwg912	117.01	110.8-122.9	2.62	-7.09	7.39
QLr.ccsu-2A.2	III, AE	Xgwm359-Xbcd1184	56.41 -57.81	54.6-60.5	1.31-3.07	7.70	2.95-8.83
QLr.ccsu-2A.3	II, AE	Xfbb353-Xbcd543	84.81	83.3-86.7	2.54-3.26	6.99	6.90-6.93
QLr.ccsu-2B.1	II, AE	Xfba62-Xfba345	59.91	57.0-60.4	3.56-6.42	11.21	11.52-17.33
QLr.ccsu-2D.2	II, AE	Xfba64-Xfbb68	64.01	54.3-65.8	2.02-3.03	-7.08	5.14-6.32
QLr.ccsu-3A.2	I	Xfba175-Xcdo638	45.01	44.4-45.2	3.83	8.69	10.69
QLr.ccsu-3B.1[k]*	I, III, AE	Xbarc75-Xbarc133	9.01-13.81	4.6-17.1	1.72-3.16	6.43	2.89-6.62
*QLr.ccsu-5B.4**	II, III, AE	Xcdo1326-Xbarc140	97.41-99.41	93.2-103.4	1.22-3.61	-7.57	2.55-8.37
QLr.ccsu-5B.5	I, II, AE	Xbarc142-Xbarc69	108.31-119.11	104.6-141.4	2.02-2.71	-7.10	4.38-7.34
QLr.ccsu-7B.1	I, III, AE	Xcn18-Xfbb195	28.21 -30.31	24.3-30.5	1.24-4.74	8.42	2.16-10.69
*QLr.ccsu-7D.1**	I, II, III, AE	Xbcd1872-Xwg834	6.71-8.71	2.2-13.1	8.12-11.10	13.76	23.47-29.07
YR							
QYr.ccsu-1A.1[k]	I,II, III, AE	Xgwm99-XksuE11.1	115.01-118.31	111.4-120.1	1.25-2.53	-7.28	2.51-8.93
QYr.ccsu-1B.1	III, AE	Xcdo1189-Xgwm259	88.11-91.51	81.4-95.1	2.04-2.64	-6.06	6.63-9.79
QYr.ccsu-2A.1	II	Xbcd152-Xpsr903	71.61	71.1-71.7	9.50	10.37	24.30
QYr.ccsu-2B.1	I	Xmwg950-Xtam72	20.51	19.2-21.7	2.67	4.93	7.58
*QYr.ccsu-2B.2**	III, AE	Xgwm630-XksuF11	32.71-33.01	29.3-34.9	1.34-3.58	5.92	3.72-10.62
QYr.ccsu-2B.3	III, AE	Xbarc167-Xgwm129	37.31	36.0-37.7	1.84-3.33	5.87	5.86-10.96
QYr.ccsu-2B.4	III, AE	Xgwm55.1-Xbcd1119	39.71-40.51	38.4-42.1	4.03-5.19	7.74	11.04-14.13
QYr.ccsu-3B.1[k] *	I, II, III, AE	Xfbb166- Xcdo460	11.11-21.61	8.0-27.6	3.27-5.46	8.78	10.10-18.74
QYr.ccsu-3B.2	I, II, III, AE	Xgwm566-XksuH7	60.61-63.91	50.1-68.8	1.21-2.78	-5.10	3.15-6.25
QYr.ccsu-7A.1	III, AE	Xbarc121 -Xfba354	77.71-78.31	76.8-81.8	1.08-4.21	8.50	3.98-12.10
QYr.ccsu-7B.2	II	Xfbb67-XksuD2.2	86.51	71.0-101.6	3.07	6.20	9.14
QYr.ccsu-7D.1	II, III, AE	Xbarc154-Xbarc352	21.11-23.11	18.0-26.0	2.20-5.04	8.60	5.71-13.32

[k] Indicate the co-localized QTL for LR and YR; *indicate the QTL detected by both QTL Cartographer and QTLNetwork; [c] environment I = Ludhiana 2002, II = Ludhiana 2003, III = Ludhiana 2004, AE=pooled data of all the three environments; [e] markers in bold represent definitive QTL; position indicates the distance (cM) between QTL and the first marker of the relevant chromosome; CI= confidence intervals, obtained by marking positions ±2 LOD from the peak; a = additive effect of the QTL, positive value indicate that the allele for increased trait value is contributed by W7984 (Synthetic), negative value indicate that the allele for increased trait value is contributed by Opata 85. [x]contributions: R^2 (LR), environment I= 55.83%, environment II= 70.87%, environment III= 56.88%, AE= 75.91%, R^2 (YR), environment I= 30.8%, environment II= 69.47%, environment III= 86.88%, environment AE= 86.74%

et al., 2005; Leonova et al., 2007; Naz et al., 2008; Singh et al., 2009). Similarly, for YR, single-locus analysis identified as many as 12 M-QTL, including two M-QTL identified by two-locus analysis (Tables 2 and 3). The identification of a large number of M-QTL for LR and YR in the present study with a wide range of PV (2.16 - 29.07% for LR and 2.51-24.30% for YR), confirmed quantitative genetic control of LR and YR as reported in some earlier studies (Nelson et al., 1997; Messmer et al., 2000; Börner et al., 2002; Suenaga et al., 2003; Schnurbusch et al., 2004a; Mallard et al., 2005; Naz et al., 2008; Singh et al., 2009; Jagger et al., 2011; Prins et al., 2011; Agenbag et al., 2012). A comparison with earlier studies also showed that more QTL for LR and YR were detected during the present study than in the earlier studies, where up to 8 QTL for LR (Nelson et al., 1997; William et al., 1997; Messmer et al., 2000; Börner et al., 2002; Schnurbusch et al., 2004a) and upto10 QTL for YR (Prins et al., 2011) were reported. This may be attributed to the use of high density ITMI-linkage map and also due to the expression of new QTL as a result of host interaction with leaf rust races specific to Indian environments.

Novel QTL for LR and YR

The alignment of the molecular map of ITMI-population used during the present study with the earlier linkage maps involved in QTL analysis for LR and YR, suggested that 7 of the 14 M-QTL for LR (*QLr.ccsu-1A.2*, *QLr.ccsu-1A.3*, *QLr.ccsu-2B.*1, *QLr.ccsu-2D.I*, *QLr.ccsu-3A.2*, *QLr.ccsu-5B.4*, *QLr.ccsu-5B.5*) identified during the present study were new (Nelson et al., 1997; William et al., 1997; Messmer et al., 2000; Börner et al., 2002; Schnurbusch et al., 2004a; Navabi et al., 2005; Naz et al., 2008; Singh et al., 2009). Seven new QTL included two consistent (*QLr.ccsu-5B.4*, *QLr.ccsu-5B.5*) and one definitive QTL (*QLr.ccsu-2B.*1). Similarly, for YR, 4 of the 12 M-QTL (*QYr.ccsu-1A.1*, *QYr.ccsu-2A.1*, *QYr.ccsu-3B.2*, *QYr.ccsu-7B.2*) were novel; the remaining 8 M-QTL were reported earlier using ITMI- and other mapping populations (Börner et al., 2000, 2002; Bariana et al., 2001; Singh et al., 2001; Boukhatem et al., 2002; Suenaga et al., 2003; William et al., 2003a, b; Ramburan et al., 2004; Mallard et al.,2005; Navabi et al., 2005; Christiansen et al., 2006; Lin and Chen 2007; Khlestkina et al., 2007; Jagger et al., 2011; Prins et al., 2011; Agenbag et al., 2012).The four novel QTL includes two

consistent QTL (*QYr.ccsu-1A.1*; *QYr.ccsu-3B.2*) and one definitive QTL (*QYr.ccsu-2A.1*). It is interesting that the new QTL detected during the present study were not reported even when the same population was used in earlier studies (Nelson et al., 1997, Börner et al., 2002). This suggested that the expression of these novel QTL may be sensitive to environmental conditions and the reported novel QTL express only under Indian environmental conditions. This also suggests that there is a need to study the genetics of these rust diseases under varied environments representing the conditions of different wheat growing regions of the world to enable identification of all the different QTL conferring resistance against LR and YR around the world. This will help in developing resistant varieties for a particular regions or environments.

Major QTL for LR

Two major M-QTL (*QLr.ccsu-2B.1*, *QLr.ccsu-7D.1*explaining >15% PV) for LR were identified, one each on 2B and 7D. Among these QTL, the QTL (*QLr.ccsu-2B.1*) on 2B is novel, while the second major QTL *QLr.ccsu-7D.1* may represent the very important durable and slow rusting resistance gene *Lr34* (Nelson et al., 1997). Major QTL in the region of *Lr34* was reported in a number of earlier studies using several different mapping populations including the ITMI-population (Nelson et al., 1997; Börner et al., 2002; Suenaga et al., 2003; Schnurbusch et al., 2004a; Navabi et al., 2005; Prins et al., 2011). This also suggested widespread occurrence of *Lr34* in different wheat genotypes.

Major QTL for YR

One of the two major M-QTL (*QYr.ccsu-2A.1*) for YR was identified on 2AS and was located ~30cM distal to the QTL reported by Christiansen et al., (2006) suggesting that this QTL could be a novel QTL for YR. The second major QTL *QYr.ccsu-3B.1* on 3BS for YR most likely corresponds to the adult plant YR resistance gene *Yr30*/QTL identified earlier using a number of different mapping populations including ITMI-population (Singh et al., 2000; Börner et al., 2000; Suenaga et al., 2003; Khlestkina et al., 2007).

Another important genomic region for YR on chromosome 2B

In the past, the genomic region defined by marker interval *Xmwg950-Xgwm129* on 2B was reported to carry a solitary QTL/gene for YR (Börner et al., 2002; Boukhatem et al., 2002; Ramburan et al., 2004; Mallard et al., 2005). However, the use of high density linkage map of ITMI-population, during the present study, allowed us to further dissect this 20 cM region into 4 different QTL for YR, each with narrow confidence intervals (Table 2). Individual QTL of this cluster explained 7.58-14.13 % PV for YR. This QTL cluster may be a good candidate for future studies on YR.

(b) *Epistatic QTLfor LR and YR*

A total of 16 E-QTL for LR and 14 E-QTL for YR which were involved in 8 significant digenic epistatic interactions for each of the two traits were detected following two locus QTL analyses. Although no M-QTL for LR was involved in epistasis, two M-QTL for YR were also involved in epistasis. Epistasis contributed 26.01% (LR) and 31.51% (YR) of the total PV for the two traits with individual epistatic interactions contributing from 0.80% to 6.21% for LR and from 1.40% to 7.05% for YR. For both LR and YR, in almost half of the epistatic interactions, parental two locus combinations enhanced resistance whereas, in the remaining half of the interactions, recombinant two locus combinations enhanced resistance. During the present study, the PVE due to M-QTL and QQ interactions together explained almost all the fixable (additive and additive × additive) genetic component that controls the genetic variation in LR and YR resistance in wheat, which is in agreement with the recent earlier findings of Feng et al., (2007). A dissection of the heritable component, in the present study, clearly showed that QQ epistatic interactions play an equal or even more important role in LR and YR resistance. Epistatic effects for LR and YR have been observed in wheat using classical genetic approaches (Milus and Line, 1986; Wagoire et al., 1998; Ahamed et al., 2004; Feng et al., 2007). In addition, a recent study by Datta et al., (2007), while investigating the genetic basis of LR resistance in three released wheat cultivars viz. DWR195, RAJ3765 and HP1731, observed that in two of the three wheat genotypes (DWR195 and RAJ3765) complementary gene action was responsible in imparting resistance. In the past, not very serious efforts were made to understand the role of epistasis in the genetic control of LR and YR. This may be attributed to the lack of the availability of suitable statistical tools in the past and partly also to the belief that the genes for disease resistance are mainly additive. But, in the recent past, with the availability of suitable statistical tools (Zhu et al., 1999; Yang et al., 2007, 2008) for the detection of two locus interactions, a number of studies have shown the role of epistasis in disease resistance in wheat (Jia et al., 2005; Ma et al., 2006; Rosewarne et al., 2008). Rosewarne et al., (2008) in addition to detecting 3 QTL for LR and 6 QTL for YR, identified an epistatic interaction for YR between two marker intervals explaining 7% PV for the trait. The results of the present study as well as earlier studies using both the classical and modern genetic approaches clearly indicated that epistatic interactions between minor QTL may play a significant role in enhancing overall resistance to LR and YR in a cultivar. Therefore, to select a cultivar with a high level of resistance, breeders need to select for all resistance enhancing QTL/genes.

(c) *Interactions of LR and YR with environment*

In the present study, only few QTL × environmental interactions for YR and no such interactions for LR were observed (Tables 3 and 4), which is also supported by high rank correlations observed between different pairs of environments, both for LR and YR scores (Table 1). This may be attributed to the fact that the present investigation was carried out at a single location, where the environmental conditions and pathogen population may not have varied over the years. In a recent study involving variable environments (different climatic conditions, altitudes and soil types), which were distantly located, a large proportion of QTL for LR in wheat showed interaction with environments (Naz et al., 2008). This suggested an importance of selection of diverse environments for QTL studies aiming at the detection of QTL × environment interactions. However, the QTL not involved in Q × E interactions should be the target of marker assisted selection (MAS) aimed at improvement in resistance to LR and YR.

(d) *Co-localized/linked QTL for LR and YR*

Four co-localized QTL for LR and YR:

During the present study, 4 genomic regions including the

Table 3. QTL with main effects and those involved in interaction with environment for leaf rust (LR) and yellow rust (YR) detected in ITMI-mapping population of bread wheat using QTLNetwork [x].

QTL*[k]	Flanking markers	Position	CI (cM)	a	h^2a (%)	Q × E interactions	
						Env.	h^2ae (%)
LR							
QLr.ccsu-1A.2	Xbarc162-Xgwm164	38.3	38.0-39.3	-3.30	01.95	-	-
QLr.ccsu-2D.1	Xfbb279-Xwsu1	36.2	34.2-37.2	-5.02	04.49	-	-
QLr.ccsu-3B.1[k]*	Xbarc75-Xgwm533.1	10.0	7.5-16.1	3.21	01.84	-	-
*QLr.ccsu-5B.4**	Xcdo348-Xcdo1326	96.5	94.9-97.4	-3.09	01.71	-	-
*QLr.ccsu-7D.1**	Xbcd1872-Xwg834	7.7	5.7-9.6	11.26	22.64	-	-
YR							
*QYr.ccsu-2B.2**	Xwsu1-Xfbb47	28.5	27.5-30.7	6.07	9.06	II	2.77
QYr.ccsu-3B.1[k]*	Xfbb166-Xgwm493	19.4	17.1-21.6	5.49	7.42	-	-

[x] Contributions: h^2a (LR) = 32.63%, h^2a (YR) = 16.48%, h^2ae (YR)= 2.77%; *indicate the QTL detected by both QTL Cartographer and QTLNetwork; [k] indicate the co-localized QTL for LR and YR; position indicates the distance (cM) between QTL and the first marker of the relevant chromosome; CI is the confidence interval of QTL position; a is the additive effect of the QTL, positive value indicate that the allele for increased trait value is contributed by W7984 (Synthetic), negative value indicate that the allele for increased trait value is contributed by Opata 85; ae is the effect of the QTL × environment interaction; h^2a and h^2ae are the percentages of the phenotypic variations explained by a and ae, respectively; Env. = environment in which Q × E was detected for the particular QTL

Table 4. QTL involved in QQ (aa) and QQE (aae) interactions for leaf rust (LR) and yellow rust (YR) in ITMI-mapping population of bread wheat detected using QTLNetwork[x].

QTL[k]i	Flanking markers i	Position (CI)i	QTL j	Flanking markers j	Position (CI)j	aa	h^2 (%)	Q × Q × E interactions	
								Env.	h^2aae(%)
LR									
QLr.ccsu-1B.1	Xbarc302-Xglk136	41.6 (39.3-42.6)	*QLr.ccsu-5B.3*	Xbcd1030-Xcdo504	80.7 (74.6-83.7)	4.45	3.54	-	-
QLr.ccsu-1D.1[k]	Xbarc99-Xbarc169	59.3 (52.1-63.5)	*QLr.ccsu-5B.2*	Xtam72-XksuA1	38.0 (37.3-38.4)	-4.56	3.71	-	-
QLr.ccsu-2A.1	Xcdo456.2-Xbarc124	28.6 (26.6-32.6)	*QLr.ccsu-3A.3*	Xgwm666.1-Xgwm30	52.0 (51.7-53.1)	-3.66	2.40	-	-
QLr.ccsu-3A.1	Xfbb370-Xglk683	4.8 (2.0-5.7)	*QLr.ccsu-3B.3*	Xfbb177-Xmwg818	76.1(75.0-77.6)	3.84	2.63	-	-
QLr.ccsu-3B.2	Xfbb156-XATPase.2	68.0 (67.3-69.2)	*QLr.ccsu-3D.1*	Xbcd907-XgbxG265	13.3 (10.1-15.7)	5.90	6.21	-	-
QLr.ccsu-3B.4[k]	Xfbb378-Xgwm108	93.1 (93.1-95.1)	*QLr.ccsu-5B.1*	Xgwm68-Xmwg561	30.3 (29.7-32.4)	-4.24	3.21	-	-
QLr.ccsu-4A.1	Xcdo475-XksuD9	62.7 (61.9-63.7)	*QLr.ccsu-6D.1*	Xbcd1821-Xbcd342	6.4 (5.4-7.4)	-4.43	3.51	-	-
QLr.ccsu-5B.5	Xbarc59-Xabc310.2	121.7 (120.4-131.7)	*QLr.ccsu-7A.1*	Xcdo347-Xfba134	116.2 (110.3-120.2)	-2.12	0.80	-	-
YR									
QYr.ccsu-1D.1[k]	Xbarc99-Xbarc169	53.3 (52.1-60.3)	*QYr.ccsu-7B.1*	Xwg686-Xgwm302	55.8 (49.6-64.3)	3.65	3.27	I, III	1.98-2.46
QYr.ccsu-2A.2	Xgwm294-Xbcd161	75.9 (75.6-76.5)	*QYr.ccsu-5B.1*	Xcdo959-Xfbb121.1	10.0 (7.0-12.8)	4.67	5.37	-	-
QYr.ccsu-2A.3	Xgwm122-Xgwm249	78.9 (77.7-79.3)	*QYr.ccsu-5B.1*	Xcdo959-Xfbb121.1	11.0 (8.0-13.8)	2.64	1.71	-	-
QYr.ccsu-3B.3[k]	Xfbb378-Xgwm108	93.1 (91.5-95.1)	*QYr.ccsu-4B.1*	Xbcd1262-Xbcd749	16.3 (15.1-18.1)	3.76	3.48	-	-
QYr.ccsu-4A.1	Xbarc138-Xfba147	23.6 (21.9-24.3)	*QYr.ccsu-5D.1*	Xbarc286-Xgwm639	68.8 (66.8-72.0)	-5.36	7.05	III	3.45
QYr.ccsu-4A.2	Xfba231-Xfbb154	66.5 (64.7-69.2)	*QYr.ccsu-5D.1*	Xbarc286-Xgwm639	68.8 (66.8-72.0)	-2.39	1.40	-	-
QYr.ccsu-5D.2	Xbarc347-Xcdo1508	84.4 (82.4-86.4)	*QYr.ccsu-5D.4*	Xbarc144-Xbcd87	163.8 (161.0-164.8)	-4.70	5.44	-	-
QYr.ccsu-5D.3	Xfbb26-Xgwm271	96.9 (95.2-99.4)	*QYr.ccsu-5D.5*	Xgwm565-Xgwm654	167.7 (167.5-168.7)	-3.92	3.79	-	-

[x] Contributions: epistasis, h^2aa (LR) = 26.01%, h^2aa (YR) = 31.51%, environment interactions, h^2aae (YR) = 1.98 – 3.45%; [k] indicate the co-localized QTL for LR and YR; CI is the confidence interval (cM); aa is the additive by additive interaction between two loci i and j, positive value indicate that QQ interactions with parental two locus combinations has increased trait values , negative value indicate that QQ interactions with recombinant two locus combinations has increased trait values; aae is the effect of the epistasis × environment interactions; h^2aa, h^2aae are the percentages of the phenotypic variations explained by aa, and aae, respectively; Env. = environment in which aae interaction was detected.

marker intervals *Xgwm99-XksuE11.1* (*QLr.ccsu-1A.3, QYr.ccsu-1A.1*) on 1A, *Xbarc99-Xbarc169* (*QLr.ccsu-1D.1, QYr.ccsu-1D.1*) on 1D, *Xbarc75-Xcdo460* (*QLr.ccsu-3B.1, QYr.ccsu-3B.1*) and *Xfbb378-Xgwm108* (*QLr.ccsu-3B.4, QYr.ccsu-3B.3*) on 3B, contained one QTL each for both LR and YR (Tables 2-4). This co-localization of the QTL for the two traits is also supported by the significant positive correlations observed between mean scores for LR and YR during the present study. In the past, only one of these genomic regions on 3B (*Xbarc75- Xcdo460*) was reported to carry QTL/gene for LR and YR in two separate studies involving ITMI-population (Nelson et al., 1997; Singh et al., 2000; Börner et al., 2002); the QTL in the remaining three genomic regions were reported for the first time.

Linked QTL for LR and YR, in a 7DS region for Lr34 and Yr18

In addition to the above co-localized QTL, one M-QTL each for LR (*QLr.ccsu-7D.1*) and YR (*QYr.ccsu-7D.1*), separated by ~15cM interval, were detected in the distal region of chromosome arm 7DS (Table 2). Five markers were mapped in the above interval of ~15 cM between the two QTL and the marker *Xwg834* most closely linked with QTL for LR (*QLr.ccsu-7D.1*) was placed at ~2.9 cM, while the most closely linked marker *Xbarc154* with the QTL for YR (*QYr.ccsu-7D.1*) was placed at ~2.0 cM. These markers may be used for exploitation of the above QTL in wheat breeding programmes, using MAS. Earlier, durable and slow rusting resistance QTL/genes *Lr34* and *Yr18*, that are linked with each other, were reported in the same genomic region in which the above two QTL were mapped during the present study (Nelson et al., 1997; Singh et al., 2000, 2001; Börner et al., 2002; Boukhatem et al., 2002; Suenaga et al., 2003; Schnurbusch et al., 2004a, b). Therefore, we assume that the QTL for LR and YR detected during the present study may represent the QTL/genes *Lr34* and *Yr18*. In the past, co-localization/linkage between genes for resistance against several diseases in wheat and rye were reported. For instance, complete linkage between the slow rusting gene for yellow rust (*Yr29*) and the leaf rust resistance gene, *Lr46*, on 1BL of wheat was reported by William et al. (2003a, b). Similarly, linkage among the 3 genes (*Yr17, Lr37* and *Sr38*) on chromosome arm 2AS was also reported in wheat (Bariana and McIntosh, 1993). A recent study also found that slow-rusting genes *Lr67*and *Yr46* in wheat are pleiotropic or closely linked (Herrera-Foessel et al., 2011). Furthermore, in case of rye, linkage between the genes for resistance against leaf rust (*Lr26*), stem rust (*Sr31*), stripe rust (*Yr9*) and powdery mildew resistance (*Pm17*) on chromosome 1R of rye was reported (Hsam et al., 2000; Mago et al., 2002). The two co-localized QTL, one each on 1A (*QLr.ccsu-1A.3, QYr.ccsu-1A.1*) and 3B (*QLr.ccsu-3B.1, QYr.ccsu-3B.1*) and the linked QTL for LR and YR on 7DS, had additive effect and the alleles for increased resistance for both LR and YR at each of these co-localized/linked QTL is contributed by a single parent i.e. either W7984 or Opata85. Therefore, selection of desirable alleles at the flanking markers of the QTL regions harboring these co-localized/linked QTL may help in simultaneous improvement in LR and YR. However, the other two co-localized QTL, one each on 1D (*QLr.ccsu-1D.1, QYr.ccsu-1D.1*) and 3B (*QLr.ccsu-3B.4, QYr.ccsu-3B.3*) had epistatic effect and the QTL alleles for increased resistance to LR at these loci is associated with decreased resistance to YR and *vice versa*. So, the simultaneous improvement in LR and YR using these QTL may not be successful.

Conclusions

The present study, in addition to confirming the earlier results, identified several QTL expressing specifically in Indian environmental conditions. Significant role of epistatic interactions was also observed for both the leaf rust and the yellow rust. These results suggest the need to study the genetic control for resistance expressed in response to specific races of leaf rust and yellow rust prevalent in Indian sub-continent environments. This will help in developing resistant cultivars for Indian sub-continent environments, using MAS. In addition, there is a need to involve larger mapping populations in the future studies for the detection of interacting loci for leaf rust and yellow rust globally.

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