QTL for grain colour and yield traits in bread wheat and their correspondence in rice genome

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ABSTRACT

In bread wheat, QTL analysis was conducted using the *PW* RIL population, derived from PH132 (red wheat) × WL711 (white wheat), and the *ITMI*pop, derived from Opata85 × W7984. The *PW*-population was used for grain color and yield traits, but *ITMI*pop was used for only yield traits. Besides main-effect QTL, epistasis was also detected for all of the traits. A major QTL for grain colour (PV up to 36.18%) was mapped on 3BL in the *PW*-population, and another major QTL controlling six yield traits was located on 2DS in both populations (PV explained for individual traits varied from 8.93% to 19.81% in *PW* population and from 13.00% to 37.85% in *ITMI*pop). The QTL for grain colour was physically mapped to the distal 19% region of 3BL, while the QTL controlling the yield traits was physically mapped to distal bin of 2DS covering 53% of the arm length. Comparative mapping revealed that the wheat genomic region harbouring the major QTL for grain colour is orthologous to the rice chromosome 1 region distal to the red pericarp (*Rd*) gene and the QTL controlling yield traits could be an orthologue of a recently cloned major rice QTL (*Ghd7*) on chromosome 7. The above orthologous relationships between wheat and rice may be exploited for development of markers closely associated with two wheat QTL for marker-aided selection and cloning of QTL.

INTRODUCTION

Wheats are classified as either red or white on the basis of their grain colour. Due to their end-use properties, the demand for white wheat is growing world-wide. Mostly, white wheats are susceptible to pre-harvest sprouting (PHS) and the red wheats are tolerant to PHS. Therefore, there is a need to combine white grain colour with PHS tolerance (PHST) in bread wheat. In the past, loci controlling grain colour were assigned to group 3 chromosomes, but information on genetic analysis of grain colour at the genome-wide scale is largely missing[1]. Besides eliminating the red color of the grain, improvement of yield and its component traits is also an important objective of most wheat breeding programmes around the world. QTL studies conducted in the past suggested complex genetic control of these traits, which involved main effect QTL (M-QTL), QTL × QTL interactions (epistasis) and QTL × environment interactions[2]. In the present study in bread wheat, we studied the genetic control of grain colour and yield traits, leading to the detection of major QTL, and identified orthologous rice genomic regions for the major QTL thus identified.

MATERIALS AND METHODS

Mapping populations

Two mapping populations were used during the present study. The first population (*PW*-population) comprised 100 RILs and was derived from PH132 (red wheat) × WL711 (white wheat)[3] and the second population (*ITMI*pop) comprised 110 RILs and was derived from Opata85 × W7984[4]. The parents along with the RILs of the two populations were evaluated over two years (2003-2004 and 2004-2005) at two different locations, Meerut and Ludhiana, representing major wheat growing areas of Northern India.

Genetic stocks

Nullisomic–tetrasomic (NT) and ditelosomic (DT) lines for chromosome 3B and five terminal deletion lines of 3BL of Chinese Spring were used in the present study[5]. The seed material of NT and DT lines was kindly provided by B. S. Gill, Kansas State University, Kansas, USA and the seed material of deletion lines was kindly provided by T. R. Endo, Kyoto University, Japan,.

Recording of data

Data on colour of NaOH soaked grains was recorded visually on a scale of 1 to 5 (1=white colour; 5 = red colour) in the *PW*-population, and data on nine yield and yield-contributing traits {PY = plot yield (g/m^2), TN = tiller number/ m^2, SPW = single spike weight (g), SL = spike length (cm), NSL = number of spikelets/spike, SC = spike compactness, NS = number of seeds/spike, SW = seed weight /spike (g) and TGW = 1000 grains weight (g)} were recorded on both populations (*PW* and *ITMI*pop).

Framework genetic map

An updated framework linkage map of the *PW*-population consisting of 217 loci was used during the present study. For ITMI*pop*, the published framework linkage map of Song et al[4] and segregation data of 1345 markers available at Graingenes (http://wheat.pw.usda.gov) were used.

QTL analysis

Single-locus QTL analysis was carried out by composite interval mapping (CIM) using QTL Cartographer V2.5[6]. A LOD score of 2.5 was used for suggesting the presence of a putative QTL. QTLNetwork 2.0[7] was used to conduct two-locus QTL analysis to identify main

effect QTL (M-QTL), QTL × QTL (QQ epistasis) interactions, and QTL × environment interactions (QE or QQE). P<0.05 was used to select markers and to declare presence of M-QTL and E-QTL.

Wheat-rice comparative genomic analysis

The nucleotide sequences were retrieved from NCBI (http://www.ncbi.nlm.nih.gov/) for RFLP markers mapped on the ITMI linkage map[4,8], mapped rice markers and rice BAC/PAC clones. Rice-wheat comparative genomic analysis was carried out with the help of BLASTn using Gramene (http://www.gramene.org/Multi/blastview) and Graingenes (http://wheat.pw.usda.gov/GG2/blast.shtml) databases. At least 70% nucleotide similarity for not less than 100 bases with an *e* value of $<e^{-20}$ was used for detecting significant matches.

RESULTS AND DISCUSSION

QTL analysis for grain colour

A summary of results of single and two-locus QTL analyses for grain colour is presented in Table 1. The results confirmed earlier reported loci for grain colour on group 3 chromosomes in bread wheat[1] and also identified 8 new loci. A major M-QTL (*QGc.ccsu-3B.1*) on 3B explained 15.28% to 40.42% PV and corresponds to the red grain colour locus *R-B1* earlier identified[1,8]. Further, two-locus analysis also showed significant role of QQ epistatic interaction in the genetic control of grain colour in bread wheat. However, the QTL for grain colour did not show any interaction with environment. Complementary epistasis for purple grain colour in wheat[9] and red grain colour in rice[10] was also reported in earlier studies. Further, only 4 (one each on 1D, 2B, 3B and 6B) of the 12 QTL for grain colour were co-localized with QTL for PHS (unpublished results). Thus the remaining 8 QTL may be exploited for combining white grain colour with PHS tolerance in bread wheat genotypes.

Table 1. Summary of the results of single-locus and two-locus QTL analyses for grain colour and yield traits in bread wheat.

	Grain colour	**Yield traits**	
	***PW*- population**	***ITMI*pop**	***PW*-population**
Single-locus analysis			
Total QTL	6	69	109
Chromosomes involved	2B, 2D, 3B, 5D, 6B	19 (except 5A and 6D)	20 (except 7D)
Range of PVE for individual QTL	3.22% - 40.42%	2.94% - 38.73%	2.09% - 37.85%
Two-locus analysis			
Total QTL	10	89	155
Chromosomes involved	1D, 2B, 2D, 3A, 3B, 3D, 6B	19 (except 6D and 7D)	All 21
Total M-QTL	4	18	31
Total E-QTL	6	74	125
Total QQ interactions[a]	4	38 (1-9)	68 (3-10)
Total QE interactions	Nil	4	7
Total QQE interactions	Nil	7	5
Range of PVE for individual M-QTL	6.05%-11.28%	0.74% - 35.65%	0.46% - 21.52%
Range of total PVE of M-QTL for individual trait	34.55%	3.80% - 43.50%	10.02% - 58.67%
Range of PVE due to QE	Nil	3.03% - 13.26%	0.79% - 5.56%
Range of PVE by individual QQ	0.82%-13.09%	0.36% - 34.72%	0.99% - 9.87%
Range of PVE due to QQ for individual trait	21.54%	1.76% - 64.10%	11.56% - 33.12%
Range of PVE due to QQE	Nil	1.27 - 41.93%	1.0% - 10.16%

[a] Figure in parenthesis is the range of QQ interaction for individual trait.

QTL analysis for yield and yield contributing traits

The results of single-locus and two-locus QTL analyses for yield traits are summarized in Table 1. For different yield traits, a few major (explaining >15% PV) and a number of minor (explaining <15% PV) QTL were detected. An important QTL on 2DS (range of PV for different traits =8.93% to 19.81% in P*W*-population and 13.00% to 37.85% in *ITMI*pop) was also reported to influence a number of traits in earlier studies in bread wheat[2]. This suggested the importance of the genomic region on 2DS harbouring the above QTL in exercising genetic control over several important traits in bread wheat.

Another highlight of the present study was that epistatic (QQ) interactions explained a higher proportion of PV for five traits (SPW, SL, SC, SW and TGW) in *PW*-population and for four traits (SPW, SC, NS and SW) in *ITMI*pop. Moreover, nearly half (54/106) of the digenic QQ interactions in both the populations involved alleles belonging to different parents at the two QTL (recombinant types) resulting in higher trait values. This type of epistasis may contribute to fixable heterotic effects for yield traits in bread wheat. Marker-assisted selection (MAS) may be exploited for fixation of interacting alleles at different loci to harness the heterotic effects in pure lines breeding of wheat. Further, QE and QQE were mainly involved in controlling the phenotypic variation in PY, TN and SPW in both the populations.

Physical and comparative mapping of major QTL

During the present study, the major QTL (*QGc.ccsu-3B.1*) on 3B for grain colour (see above) was physically mapped in the distal bin (3BL11-0.81-1.00) of 3BL covering 19% of the arm length. This is reported as a recombinogenic region with high gene density[11]. Comparative analysis revealed that the wheat genomic region containing *R-B1* locus has homology with the rice genomic region, ~ 16Mb distal to the rice red pericarp locus *Rd* on chromosome 1. This is contrary to the previous results suggesting orthologous relationship between the *R*-locus of wheat and *Rd*-locus of rice. As a result of the above relationship between wheat and rice genomic regions and the presence of the grain colour QTL *QGc.ccsu-3B.1* in the gene-rich recombinogenic region of 3BL, fine mapping of the QTL (*QGc.ccsu-3B.1*) for grain colour may be carried out to develop closely linked markers and for its map-based isolation.

Another major QTL on 2DS influencing yield traits (see above) was physically mapped to the distal bin (2DS5-0.47-1.00) of 2DS covering 53% of the arm length, which is reported as a gene rich region[11]. BLASTn analysis showed that sequences of RFLP markers flanking the above QTL had high homology with rice sequences in the genomic region of chromosome 7 which contains a major QTL *Ghd7*, which is reported to control several traits including spikelets per panicle, number of grains per panicle, heading date and plant height in rice[12]. This suggests an orthologous relationship between the major wheat QTL and the rice QTL *Ghd7*. Map-based cloning of *Ghd7* revealed that this gene encodes CCT domain protein which has crucial roles in regulation processes, photoperiodic flowering, vernalization, circadian rhythms and light signaling[13]. The sequence information of *Ghd7* could be a candidate for the isolation of the above major QTL in wheat.

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