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QTL Dissection of Grain Weight and Filling Rate in Wheat RILs Grown in Contrasting Thermo-Pluviometric Conditions

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Abstract A total of 103RILs of bread wheat derived from WH-730× HUW-510 were evaluated for grain filling process under normal and late sown field conditions during *rabi* 2011 and *rabi* 2012. The process of grain filling was characterized by estimating 4 parameters of grain development, namely final grain weight, maximum grain filling rate, thousand grain weight and grain filling duration by fitting non-linear logistic regression and highly significant genotypic differences was observed all three traits. A total of 19 QTLs were detected through composite interval mapping for final grain weight (W), grain filling rate (R), grain filling duration (GFD) and thousand grain weight (TGW) across all the four experiments, which were found beneficial for increasing the grain filling rate (R) and reducing the grain filling duration (GFD) to counteract the terminal heat stress. These QTLs may be exploited for genetic improvement of the wheat. Some of the markers identified during the present study may prove useful for marker-assisted selection.

Keywords Bread wheat, Grain filling components, Linkage map, QTL mapping.

Introduction

Wheat (*Triticum aestivum* L., 2n = 42, AABBDD genomes) is an allohexaploid species with seven groups of homeologous chromosomes and is the third highest growing cereal crop after maize and rice. It is one of popular food grains due to its farmer friendly properties and better nutritional properties. Global wheat production in 2017 amounted to 754 million tons, which is 2.7% more than in 2016 (FAO 2017). The demand for wheat in the developing world is projected to increase by 60% by 2050 but its production is expected to be affected negatively by climate change and natural resource depletion. Therefore, an immediate research is required to overcome these negative climatic impacts on grain production of wheat. The number of kernels per unit area and kernel weight are two major factors in determining the grain yield of wheat (Calderini and Reynolds 2000). Kernel weight is a complex quantitative trait, which is controlled by a number of genes and significantly influenced by the environment and determined by grain-filling process (Daynard et al. 1971). Grain filling process is very crucial and dynamic process in wheat growth as dura-

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tion and rate of this process determines the individual grain size, grain weight and ultimately the economics of the crop. Grain filling duration (GFD) is much influenced by temperature (Pinthus and Shalom 1978, Knott and Gebeyhou 1987) while grain filling rate (GFR) appears to be largely under the genetic control (Nass and Reisser 1975, Van Sanford 1985). A thorough understanding of the grain filling process will be helpful to break the current yield plateau and to increase the yield potential of wheat. Exposure of bread wheat genotypes to high temperatures significantly decreases the grain weight and has tens physiological maturity.

Integrated genetic maps involving molecular and phenotypic markers provide a direct means for investigating the number of genes influencing a trait, their location along the chromosomes and the effects of variation in their dosage. Development of SSR markers, which are PCR-compatible, co-dominantly inherited has greatly facilitated linkage map construction and use in plant breeding (Kannan et al. 2014) as these can be multiplexed for simultaneous marker genotype characterization at a number of loci within or across linkage groups. Quantitative trait loci (QTL) analysis is a powerful tool for qualitative and quantitative genetic analysis of complex traits (Liu 1998, Shah et al. 1999). Very limited reports are available on QTL for grain filling in wheat (Wang et al. 2009). Recently, identification of new microsatellite markers linked to grain filling rate as indicator for heat tolerance genes in a F_2 wheat population have been reported by Barakat et al. (2011, 2012) and in RIL population by Pandey et al. (2013). However, the knowledge gained so far on QTL for grain filling in wheat is still incomplete. Therefore, our objectives were to estimate parameters on a logistic model describing the dependency of grain filling rate and grain filling duration, to detect and quantify the QTLs associated with final grain weight (W), grain filling rate (R), grain filling duration (GFD) and thousand grain weight (TGW) and to identify the molecular markers linked to these QTLs also.

(We thank Directorate of Wheat Research (DWR), Karnal for providing the mapping population).

Materials and Methods

Plant materials

A total of 103 RILs derived by single seed descent from individual F_2 plants of WH-730 × HUW-510 cross of bread wheat along with parents were studied.

Experimental design

The present study comprised of 103 F_{10} RILs derived by single seed descent from individual F_2 plants of WH-730 × HUW-510 cross of bread wheat along with parents (Table 1) provided by Directorate of Wheat Research, Karnal and maintained at the Wheat Section, Department of Genetics and Plant Breeding, CCS Haryana Agricultural University, Hisar. The experiment was laid out in α -design with two replications, in *rabi* 2011 and *rabi* 2012 having four row plot of 2 m length of 20 × 5 cm spacing between and within rows,

Table 1. Mean, range and heritability for average single grain weight (W), maximum grain filling rate (R), grain filling duration (GFD) and thousand grain weight (TGW) in the WH-730 × HUW-510 RIL population and their parents evaluated under both normal and late sown experiments of *rabi* seasons 2010-11and 2011-12 each (LS-11, 15-11and NS-12, LS-12 respectively). W-final grain weight, R-maximum grain filling rate, GFD-grain filling duration, TGW-thousand grain weight, NS-11-normal sown experiment of *rabi* season 2010-11, LS-11-late sown experiment of *rabi* season 2010-11, NS-12-normal sown experiment of *rabi* season 2011-12, LS-12-late sown experiment of *rabi* season 2011-12.

			RIL population (all 4 environment)								
	Parents		NS-11		LS-11		NS-12		LS-12		
Trait	HUW-510	WH-730	Mean	Range	Mean	Range	Mean	Range	Mean	Range	h^2 (%)
W	39.02	39.16	42.49	30.55-62.31	40.79	29.57-66.65	49.23	32.7-65.27	42.21	29.57-66.65	67
R	0.13	0.14	0.13	0.07-0.2	0.12	0.07-0.2	0.14	0.08-0.2	0.13	0.07-0.2	75
GFD	604.42	490.15	578.73	410.67-955.08	610.73	368.74-909.38	615.76	445.67-772.91	546.55	368.74-909.38	67
TGW	38.40	39.50	38.74	26.99-49.76	34.14	24.57-42.87	45.49	30.53-59.45	38.53	28.19-47.29	84.75

respectively. This location typically experiences moderate drought during the pre and post-anthesis periods and the soil was clay loam with a pH 7.1-8. The average annual rainfall was 455 mm with 27 rainy days (a day with minimum of 2.5 mm rainfall).

The field trials were carried out at the experimental area of Wheat Section, Department of Genetics and Plant Breeding, CCSHAU, Hisar in four different environments by adopting two dates of sowings (normal and late) in each of the two *rabi* seasons of 2011 and 2012. These four experiments were coded adopting the last two digits of year of harvest that is NS-11, LS-11 and NS-12, LS-12 for normal sown (NS) and late sown (LS) experiments in respective years.

Trait evaluation

A total of four traits comprising W, R, GFD and TGW were evaluated in the present study described as follows :

Measurement of W. R and GFD

The 50% heading time of each line was recorded and 50-60 simultaneously heading spikes in each line were tagged and sampled at a 5 days interval after anthesis upto maturity. Then grains were separated from glumes, kept at 105^0C for 10 minutes and then at 70^0C until reaching a constant weight. At this stage, the number of total grains and their weight was recorded.

Accumulated growing degree days (GDD) from anthesis were calculated by summing daily – degree days as :

$$(T_n) = \frac{(T_{max} + T_{min})}{2} - T_b$$

where, T_{max} and T_{min} are maximum and minimum temperature in centigrade, respectively and T_6 is the base temperature (5^0C) (Yasuda and Shimoyama 1965).

The grain weight data from each plot was fitted by non-linear regression to a logistic curve as described by Darroch and Baker (1990). Grain development rate (GDR) and grain filling duration (GFD) were calculated for each genotype in each replication. Thus, grain development parameters were estimated from each of the 840 (105 × 2 × 2) fitted logistic growth curves and each logistic curve contained at least 6 samplings of grain growth at different stages of grain development in each replication of four different experiments. TGW (g) was measured as the average weight of two independent samples of 1,000 grains from each plot.

DNA extraction and molecular marker screening

Genomic DNA was isolated from seedlings of parents and RILs using a CTAB protocol (Doyle and Doyle 1990). The standard protocol for PCR experiment was used. Then amplicons were resolved in 2.5% (w/v) agarose gel and the products were visualized by staining with ethidium bromide (2.0 μl of 10 mg/ml).

Linkage map construction and QTL analysis

Linkage analysis was performed to construct the genetic map using MAPMAKER/EXP version 3.0b (Lander and Botstein 1989) while for QTL analysis Windows QTL Cartographer version 2.5 used to determine the position and effects of QTLs averaged over all the environments (means) using CIM method (Basten et al. 2005).

Statistical analysis

The alpha (α) design described earlier was used for the analysis of grain development parameters. The statistical analysis was performed using PROC GLM of SAS. All possible pair wise treatment comparisons were performed using LSMEANS statement of PROC GLM (SAS Institute 1985).

Results

Linkage map of the RIL. population
WH-730 × HUW-510

To perform selective genotyping QTL method, 300 SSRs were screened for polymorphism in a sub-set of 37 lines representing both tails of distribution from WH-730/HUW-510 RIL populations. Genetic map was constructed using 99 SSR markers and generated 21 linkage groups. The total linkage coverage and aver-

Table 2. Simple correlation analysis for average single grain weight (W), maximum grain filling rate (R), grain filling duration (GFD) and thousand grain weight (TGW) in the WH-730 ×HUW-510 RIL population of bread wheat evaluated in the normal and late sown experiment of *rabi* season of 2010-11 (NS-11, LS-11) and 2011-12 (NS-12, LS-12) respectively. *-Significant at 5%, **-Significant at 1%, W-final grain weight, R-maximum grain filling rate, GFD-grain filling duration, TGW-thousand grain weight, NS-11-normal sown experiment of *rabi* season 2010-11, LS-11-late sown experiment of *rabi* seasons 2010-11, NS-12-normal sown experiment of *rabi* season 2011-12, LS-12-late sown experiment of *rabi* season 2011-12.

Experimental code	Characters	Final grain weight (W)	Rate (R)	Grain filling duration (GFD)	Thousand grain weight (TGW)
2010-11	W (mg)	1	0.227**	0.508**	-0.184*
(NS-11)	R (mg/seed/GDD ^{0}C)		1	-0.593**	0.339**
	GFD (GDD ^{0}C)			1	0.266**
	TGW				1
	W (mg)	1	0.180**	0.456**	0.211*
(LS-11)	R (mg/seed/GDD ^{0}C)		1	-0.675**	0.084
	GFD (GDD ^{0}C)			1	0.130
	TGW				1
2011-12	W (mg)	1	0.471**	0.386**	0.765**
(NS-12)	R (mg/seed/GDD ^{0}C)		1	-0.545**	0.585**
	GFD (GDD ^{0}C)			1	0.550
	TGW				1
	W (mg)	1	0.317**	0.602**	0.451**
(LS-12)	R (mg/seed/GDD ^{0}C		1	-0.457**	0.229*
	GFD (GDD ^{0}C)			1	0.133
	TGW				1

age interval distance were 1847.9 and 18.66 cM/marker, respectively.

Phenotypic variation and correlation analysis

Parental phenotypic variation and the distribution among RILs for W, R, GFD and TGW evaluated under both normal and late sown experiments during *rabi* 2011 and *rabi* 2012 (NS-11, LS-11 and NS-12, LS-12 respectively) were shown in Table 1. In all four experiments, the measured target traits varied in the RIL population following a continuous distribution representing a normal phenotypic segregation for QTL mapping. The estimated heritability varied from 67 (W and GFD) to 84.6% (TGW). A highly significant association was observed between final grain weight (W) with maximum grain filling rate (GFD) and grain filling duration in all four experiments (Table 2), whereas, highly significant negative ($p < 0.001$) association of grain filling duration with maximum grain filling rate was consistent across all the four experiments, while the GFD exhibited highly significant association with thousand grain weight across all the four experiments except in late sown experiment of *rabi* 2011 season 2010-11 (LS-11). In general, the strength of association of GFD was consistently strong with W and R with positive and negative directions, respectively across all the four experiments.

QTL analysis

A total of 17 putative QTLs were detected for W, R, GFD and TGW in all four environments (NS-11, LS-11, NS-12 and LS-12) are listed in Table 3.

Three QTL for W were mapped on chromosomes 1A, 2A, 4A and 6A. One in NS-12, whereas two QTL were found in LS-11 (Table 3). Two QTLs, namely QW. hau-1A and QW. hau-6A in the intervals wmc336-Xgwm164, and wmc254-barc 113 were with a LOD value of 4.5 and 3.2 respectively and both with -3.63 mg of additive effect were detected in LS-11 experiment explaining about a total of 48% variations. The increasing effect was contributed by WH-730 allele in the LS-11experiment. These QTLs were tightly linked with left marker of the interval on chromosome 1A and 6A respectively. The QTL, QW. hau-1A was also detected in LS-12 experiment. The increased additive effect was contributed by WH-730 parent. One major QTL, (QW. hau-2A) in the interval Xgwm 95-Xgwm 275 with over-

Table 3. Location and effects of QTLs for average single grain weight (W), maximum grain filling rate (R), grain filling duration (GFD) and thousand grain weight (TGW) in the WH-730 × HUW-510 RIL population detected through composite interval mapping (CIM). a W-final grain weight, R-maximum grain filling rate, GFD-grain filling duration, TGW-thousand grain weight, b The interval of LOD peak value foe QTL, c The logarithm of the odds, d Additive effect at putative QTL. Positive values indicate a positive effect of HUW-510 alleles, whereas negative values indicate the contribution of the WH-730 allele, e Percentage of the phenotypic variation explained, N-11-normal sown experiment of *rabi* season 2010-11, LS-11- late sown experiment of *rabi* season 2010-11, NS-12-normal sown experiment of *rabi* season 2011-12, LS-12-late sown experiment of *rabi* season 2011-12.

Trait[a]	QTL	Experiment	Marker or interval[b]	LOD[c]	Add[d]	R^2[e] (%)
W	QW.hau-1A	LS-11	wmc-336-Xgwm164	4.5	-3.63 (mg)	29
	QW. hau-6A	LS-11	wmc-254-barc113	3.2	-3.63 (mg)	19
	QW.hau-2A	NS-12	Xgwm95-Xgwm275	4.3	5.17 (mg)	23
	QW. hau-1A	LS-12	wmc336-Xgwm164	4.6	-4.72 (mg)	27
R	QR.hau-1A.1	NS-11	Xgwm164-wmc120	2.9	-0.042 (mg/seed/GDD^{0}C)	27
	QR.hau-1A.2	NS-11	wmc120-wmc 93	4.3	-0.042 (mg/seed/GDD^{0}C)	27
	QR.hau-1A.3	NS-11	wmc120-wmc 93	2.9	-0.042 (mg/seed/GDD^{0}C)	27
	QR.hau-6D.1	LS-11	barc21-barc196	3.7	-0.014 (mg/seed/GDD^{0}C)	26
	QR.hau-2A.1	NS-12	barc1005-wmc382	6	-0.019 (mg/seed/GDD^{0}C)	40
	QR.hau-2A.2	NS-12	Xgwm95-Xgwm275	4.1	0.015 (mg/seed/GDD^{0}C)	23
GFD	QGfd.hau-5B	NS-11	wmc500.1-cfa2104	3.4	-67.07 (GDD^{0}C)	48
	QGfd.hau-6D	LS-11	barc21-barc196	2.9	57.82 (GDD^{0}C)	24
	QGfd.hau-3A.1	NS-12	wmc215-wmc169	2.7	38.91 (GDD^{0}C)	24
	QGfd.hau-3A.2	NS-12	wmc169-wmc112	3.1	39.68 (GDD^{0}C)	23
	QGfd.hau-3B	LS-12	barc344-Xgwm544	4.8	-72.66 (GDD^{0}C)	21
TGW	QTgw.hau-2D	NS-11	wmc41-cfd233	5	-3.41(g)	43
	QTgw.hau-6B	LS-11	Xgwm 626-barc18	4.7	-2.83 (g)	25
	QTgw.hau-2A	NS-12	Xgwm95-Xgwm275	3.9	3.94 (g)	20
	QTgw. hau-2A	LS-12	Xgwm95-Xgwm275	6.1	3.43 (g)	29

all phenotypic variation of 22.50%, at a LOD value of 4.3 with an increasing additive effect of 5.17mg was detected in NS-12 experiment. The allele with an increasing effect for W was contributed by HUW-510 parent.

A total of six major QTLs for maximum grain filling rate R were detected in the RIL population. The QTLs included three loci on chromosome 1A, 1 on 6D and 2 on 2 Aidentified in NS-11, LS-11 and NS-12 experiments respectively. In NS-11 experiment, three QTLs, namely QR.hau-1A.1, QR. hau-1A.2 and QR.hau-1A.3 were detected. QR.hau-1A.1 was detected in the interval Xgwm164-wmc120 at a LOD value of 2.9 explaining 26.56% of phenotypic variation, whereas both QR.hau-1A.2 at a LOD score of 4.3, and QR.hau-1A.3 at a LOD score of 2.9 were detected in the interval wmc120-wmc93 explaining 26.57 and 26.55% of phenotypic variance, respectively. All these three QTLs together explained about 79.68% of the total phenotypic variance.The QTL allele with increasing effect (0.042 mg/seed/GDD^{0}C) was contributed by WH-730 parent. The QTL (QR.hau-6D) in the interval barc21-barc196 was detected in LS-11experiment at a LOD value of 3.7 explaining about 25.67% of total phenotypic variation and an allele with increasing additive effect (0.014 mg/seed/GDD^{0}C) was contributed by WH-730 parent (Table 3). Two QTLs for R were detected in the NS-12 experiment which together explained about 63.82% of total variation out of which one QTL (QR.hau-2A.1) explained 40.37% of the phenotypic variation for R, at a LOD score of 6 and the allele with increasing rate of grain filling was contributed by the parent WH-730. Another QTL (QR.hau-2A.2) was detected in the interval (Xgwm95-Xgwm275) at a LOD score of 4.1 and the QTL with increasing additive effects (0.015 mg/seed/GDD^{0}C) for rate of grain filling was contributed by HUW-510 parent. This QTL explained 23.45% of phenotypic variation in the rate of grain filling. No QTL for R was detected in LS-12 experiment. Marker Xgwm-95 and barc21were found to be closely linked to the QTL for R on the chromosomes 2A and 6D, respectively.

For GFD, a total of five QTLs which major effects were detected in the WH-730 × HUW-510 RIL population across the four experiments.The QTL (QGfd.hau-5B) in the interval wmc500.1-cfa2104 on chromosome 5B at a LOD score of 3.4 explaining 48% of phenotypic variance to GFD was detected in the NS-11 experiment. The HUW-510 allele at this QTL had a decreasing effect on grain filling duration. The other QTL (QGfd.hau-6D) for GFD was detected on 6D chromosome in the interval barc21-barc196 at a LOD value of 2.9 in the LS-11 experiment. This QTL explained 24.24% of total variation for GFD in the experiment of LS-11. The WH-730 allele at this QTL had a decreasing effect on grain filling duration. In NS-12, two QTLs, namely QGfd.hau-3A.1 and QGfd.hau-3A.2 for GFD were detected on 3A chromosome in the intervals wmc215-wmc169 and wmc169-wmc112 and contributed 24.12 and 22.80% phenotypic variation, respectively. The WH-730 allele at these QTLs decreased the growing degree days for grain filling duration. In LS-12 experiment only one QTL (QGfd.hau-3B) was detected on chromosome 3B in interval barc 344-Xgwm544 explaining 21% of phenotypic variation for the trait (Table 3). The HUW-510 allele at this QTL decreased the grain filling duration. Marker barc-21 was closely linked to QTL (QGfd.hau-6D) on 6D chromosome in the LS-11 experiment.

Three QTLs with major effects were detected for TGW across four experiments. The QTLs were found to be distributed one each individually on three different chromosomes,namely 2A, 6B and 2D. The QTL (QTgw.hau-2D) was detected in the interval wmc41-efd233 on chromosome 2D at a LOD of 5 and explaining 42.9% of the variance of TGW in the NS-11 experiment. The WH-730 allele at the QTL had increasing effect on TGW (Table 3). In LS-11 experiment, QTL (QTgw. hau-6B) was detected at a LOD score of 4.7 in the interval Xgwm626 - barc18 on chromosome 6B. The QTL accounted 25.14% of phenotypic variance of the trait. In NS-12, QTL (QTgw.hau-2A) was found to be located in the interval Xgwm95-Xgwm275 on the chromosome 2A with LOD value of 3.9 and accounted 20.27% phenotypic variance of TGW. The HUW-510 allele had a increasing effect on TGW. This QTL (QTgw.hau-2A) was also identified the LS-12 experiment at a LOD score of 6.1. The QTL accounted 28.61% of phenotypic variance of the trait. The allele from HUW-510 contributed high seed weight.

Discussion

A well-known relationship is reported by various scientists between yield and its related traits with quantitative trait loci (QTL), which are highly affected by environmental conditions (Borner et al. 2002). Similarly, in the present study also numerous QTL have been detected with all the traits i.e., W, R, GFD and TGW varying from one to three, which may be due to different agronomical conditions like average temperature, sunlight and rainfall, were detected across all four environments. The present results are in agreement with those reported earlier that the QTL analysis should be conducted in various environments for a specific trait.

No precise information regarding the single grain weight (W) in bread wheat has been reported using the QTL analysis till present date. However, several attempts had been carried out to establish the QTLs for TGW, that is closely related with W, and also present on chromosome 1A (Wang et al. 2009). In present study, four major QTLs were found for single grain weight, one on 1A, 2A, 4A and 6A chromosomes (Fig. 1) in all the four experiments (NS-11, LS-11, NA-12 and LS-12), while the QTL, QW-hau-1A was common in both the late sown experiments (LS-11 and LS-12). The second and third QTL namely QW.hau-6A and QW. hau-2A for W was detected on 6A and 2A chromosome, respectively. Similar results are also reported of having significant region for (TGW) 1A, 2A and 6A chromosome (Huang et al. 2004, Huang et al. 2006, Golabadi et al. 2010 and Wang et al. 2009).

Another important trait of grain filling process in wheat is maximum grain filling rate (R) and very less reports on QTL for this trait are present. In present study, six QTLs were identified for R by CIM method. Three QTLs namely QR.hau-1A.1, QR.hau-1A.2 and QR.hau-1A.3 were detected on 1A chromosome, while two QTL, QR.hau-2A.1 and QR.hau-2A.2, on 2A chromosome in NS-11 and NS-12 experiments, respectively (Fig. 1), whereas QTL, QR.hau-6D WAS identified in the interval barc21-barc196, on 6D chromosome. Similar results were reported by Wang et al. (2009) for maximum grain filling rate on 1A, 2A and 6D chromo-

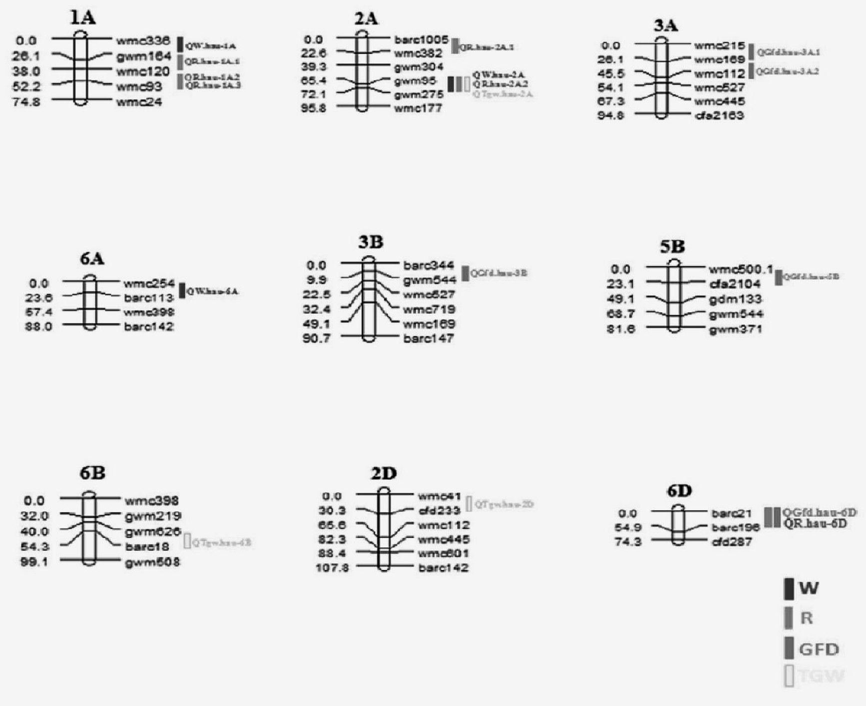

Fig. 1. A genetic map derived from the cross WH-730 × HUW-510 showing the location of QTLs.

some. This difference may be due to different genetic background in the mapping population and method phenotyping for R itself.

The grain filling duration (GFD) is an important factor that is closely associated with yield. A total of five QTLs were identified in present study. The QTLs namely, Gfd.hau-6D was detected on common chromosomal region of QTL for R (Fig. 1), which may be either due to pleiotropic effect of the single putative QTL or two tightly linked QTLs and this could only be established by saturating the region by more markers and studying larger size of mapping population. Other important QTLs for GFD wmc500.1-cfa2104 and barc344-Xgwm544 were found on 5B and 3B chromosomes, respectively, which are in accordance with other reported data earlier (Wang et al. 2009, Mohammadi et al. 2008). Two more QTLs for GFD were detected on 3A but no such result has been reported earlier.

The close relation has been identified between thousand grain weight (TGW) and single grain weight (W) as the region on 2A for TGW is common to that of the QTL for W also occupying the interval between Xgwm95 and Xgwm275 markers (Fig. 1). QTLs for thousand-grain weight (TGW) were detected on 2A, 6B and 2D. Many QTLs for TGW on 2A and 6B were reported earlier (Huang et al. 2004, 2006) and 2D (Wang et al. 2009, Huang et al. 2004, 2006, Borner et al. 2002). The QTL detected on 6B accounting 28.14% variability for the trait at LOD value of 4.7. The QTL for TGW on 2A had a high precision of its location (Cl=7.0cM) with one – LOD support value 6.1cM and tightly linked with left flanking marker (Xgwm95) at a distance of 0.01cM. This QTL may be useful for MAS in genetic improvement of thousand grain weight and ultimately the grain yield.

Pleiotropic effects and QTL pyramiding for breeding

Three groups of co-located QTLs were detected. In the first group, the co-located QTLs for W, R and

TGW were detected in the interval between Xgwm95-Xgwm275 on chromosome 2A. The alleles HUW-510 at these QTLs had an increasing effect on these traits. This explained the highly significant positive correlations observed among these traits in the population. The second group of co-located QTLs for GFD and R was detected in the interval between barc21-barc196 on 6D chromosome. The QTL alleles with increasing effect at these QTLs were being contributed by different parents, namely HUW-510 allele for GFD and WH-730 allele for R. This explained the highly significant negative correlation between GFD and R observed in present population.

A number of QTLs for increasing the grain filling rate (R) and reducing the grain filling duration (GFD) were found to be useful to counteract the terminal heat stress. These QTLs may be exploited for genetic improvement of the wheat. Specially, the QTLs for R identified on 1A chromosome, namely QR.hau-1A.1; QR.hau-1A.2, and QR.hau-1A.3, and QTLs for GFD on (QGfd.hau-3A.1, QGfd.hau-3A.2) from the donor parent WH-730 and the QTL for TGW on 2A from HUW-510 parent are promising QTLs for genetic improvement of these respective traits through MAS. So, a QTL pyramiding scheme seemed to be useful for high-yield breeding based on the idex of efficiently accumulating beneficial QTL by using MAS.

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