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Identification of gene (s) controlling grain yield and some morphological traits in bread wheat under water deficit condition using SSR markers

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ABSTRACT: Drought is the most important abiotic stress affecting production of wheat in the world. The objective of this research was Identification of QTL for grain yield and some morphological traits and determination of gene function of each QTL and its share in determining the phenotypic trait variance. To identify loci controlling traits related with drought tolerance in wheat, 142 and 121 recombinant inbred line were derived from a cross between Azar2 (drought tolerant) and 87Zhong291 varieties were evaluated under rainfed and supplementary irrigation. Characteristics measured were as follows: grain yield, plant height, spike length, flag leaf length, flag leaf width, second leaf length and second leaf width. Parental polymorphism was assessed using SSR and ISSR. 24 SSR and 16 ISSR polymorphic markers were used to screen population. Linkage analysis assigned 40 polymorphic markers in population map consisted of 45 SSR and AFLP markers. Transgressive segregation was observed for all the studied traits as revealed by phenotypic distribution. Using QTL Cartographer, composite interval mapping (CIM) for all traits were conducted. Based on composite interval mapping, 71 QTL were identified for the studied traits under rainfed and supplementary irrigation. The QTL was detected across two environments: ISSR25_2-CFA2257 contributed by parent 87Zhong291 explains more than 40%, of the total phenotypic variance for grain yield. In this study, we have reported some strong and stable QTLs for grain yield and second leaf width. These QTL could be used efficiently in wheat breeding programs.

Keywords: Composite interval mapping, Drought, Quantitative trait locus, Simple sequence repeats, Wheat

INTRODUCTION

According to FAO statistics, wheat (*Triticum aestivum* L.) is one of the most important crops worldwide, ranking fourth in terms of total food production after sugar cane, maize and rice. Based on FAO statistics, cultivation and production of wheat in Iran were 7 million hectares and 13.8 million tons respectively (FAO, 2012). Because of increasing population in the world, wheat production is not sufficient even in areas with high performance levels of wheat. For this reason, producing stress tolerant varieties and improve the performance of cultivated varieties is the main objectives of wheat breeding.

Abiotic stresses, especially drought and heat are main limiting factor for production of wheat in most regions of the world (Maphosa, 2013). Despite of recent researches, drought tolerance is still considered a big obstacle for wheat production. This challenge is resulted from quantitative nature of drought tolerance that controlled by genotype-environment factors interaction. In addition to this reason, interaction between drought and other stresses was occurred (Didb *et al.*, 2007).

Grain yield and the majority of economic traits of wheat just like other crop are quantitative in nature that controlled by many genes. Each of genes has a small effect on the phenotype. So, these traits are characterized by genotype-environment interaction and usually show a low heritability. Due to the quantitative nature of aforementioned traits, it is complex to study and identify responsible genes in the genome by conventional quantitative genetic strategies (Hai *et al.*, 2008).

However, by the development of molecular markers and powerful statistical methods, it is possible to dissect complex quantitative traits by QTL analysis (Doerge, 2002). In QTL mapping, many markers can be used such as Simple Sequence Repeats (SSR), Amplified Fragment Length Polymorphism (AFLP), Inter Simple Sequence Repeat (ISSR) and Random Amplified Polymorphic DNA (RAPD).

SSR and ISSR markers because of high genomic coverage and high polymorphism are useful markers to QTL mapping (Babu *et al.,* 2004; Collard *et al.,* 2005). In wheat with its large genome (approx. 16 Gbp), quantitative traits have been mapped in several studies (Börner *et al.,* 2002; Groos *et al.,* 2002; McCartney *et al.,* 2005; Verma *et al.,* 2005; Kumar et al., 2007; Pushpendra *et al.,* 2007; Zhang *et al.,* 2010; Tang *et al.,* 2011; Kadam *et al.,* 2012; Chesnokov *et al.,* 2013; Yu, 2014; Shukla *et al*., 2015).

The objectives of this study are following as: (1) Identification of QTL for grain yield (GY), plant height (PHT), spike length (SL), flag leaf length (FLL), flag leaf width (FLW), second leaf length (SLL) and second leaf width (SLW) traits, (2) Determining gene function of each QTL and its share in determining the phenotypic trait variance and (3) Analysis of the reliability and stability of QTL under widely different environments. The detection of QTL controlling grain yield and morphological traits under extremely different environments is expected to help unraveling the complex genetic nature of yield related traits.

MATERIALS AND METHODS

A. Plant material and field trials for trait evaluation

Recombinant inbred lines (RILs) population of F9 generation comprising 142 and 121 lines was derived from a cross between the Azar2 with 87Zhong291 (Rustaei *et al.,* 2010). Azar2 is a winteral cultivar and drought resistant. 87Zhong291 has intermediate grow type with high potential for rainfed climate.

This mapping population was grown at the dry research station located in Maragheh, Iran in an Alpha-lattice design with two replications in rainfed (RC) and supplementary irrigation conditions (SIC). Traits measured were following as: GY, PHT, SL, FLL, FLW, SLL and SLW.

B. Markers analysis

The DNA was isolated from the leaf tissue of parental genotypes and RILs of 14-day-old seedlings using CTAB extraction protocol (Saghai-Maroof *et al.,* 1984). In all, 299 SSR primers (153 gwm, 50 barc, 10 cfd, 23 cfa, 50 wmc, 13 gdm) were used in this study. Among the 299 primer pairs evaluated, 24 pair polymorphic primers of suitable banding patterns were used. ISSR primers were used for saturating genetic map. Totally, nine ISSR primers were evaluated, five ISSR primers produced suitable banding pattern for scoring. PCR reactions were performed on a programmable thermal controller (Bio-Rad Company) in a total volume of 10 µl containing 1x buffer, 50 mmol l^{-1} $MgCl_2$, 250 mmol l^{-1} dNTPs, 3 ng μl^{-1} of each primer, 5U μl^{-1} Taqpolymerase and 100ng of genomic DNA as template. After an initial denaturing step for 5 min at 94°C, 35 cycles were performed for 1 min at 94°C, 1 min at 46-66 °C (depending on the primer pair used), and 2 min at 72 °C, followed by a final extension step of 7 min at 72°C. SSR and ISSR primers were resolved on 6% polyacrylamide gel with silver stained, 4% polyacrylamide gel by ethidium bromide staining and 3% agarose gel, followed by ethidium bromide staining.

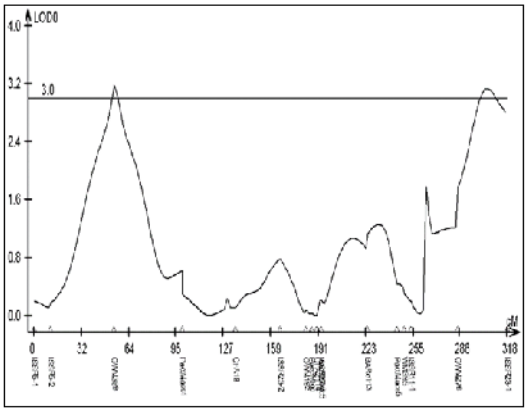
C. Molecular map construction

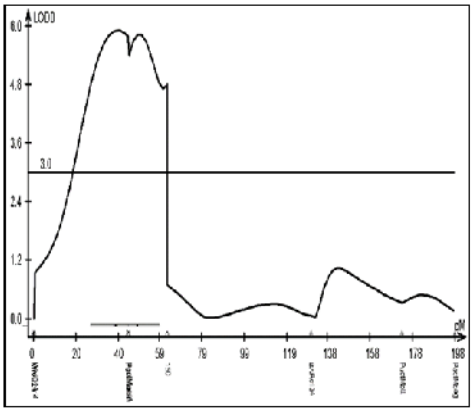
Deviation of the Mendelian ratio in 142 and 121 individuals of the F9 population was tested. Linkage analyze was performed byLOD≥3 and the maximum distance of 50 centimorgan (cM) between two neighboring markers. Linkage map was prepared by QTX 20 Map Manager (Manly and Olson, 1999) and Kosambi function (Kosambi, 1943) was used for converting recombination frequency to (cM) map distance (Fig. 1). Analysis of genotypic and phenotypic data, determining relationship between them and identification of QTL was performed by 2.5 QTL Cartographer software (Wang *et al.,* 2005). Furthermore, by using this software, data analysis was done as composite interval mapping.

RESULTS

A. Frequency distribution of traits

Histograms showing frequency distributions of mean values of seven metric traits (under RC and SIC) are presented in Fig. 2.





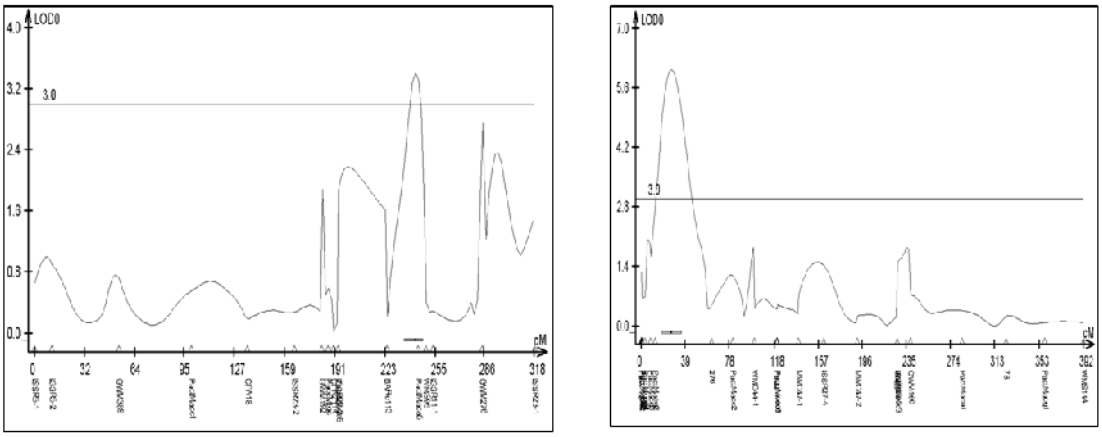
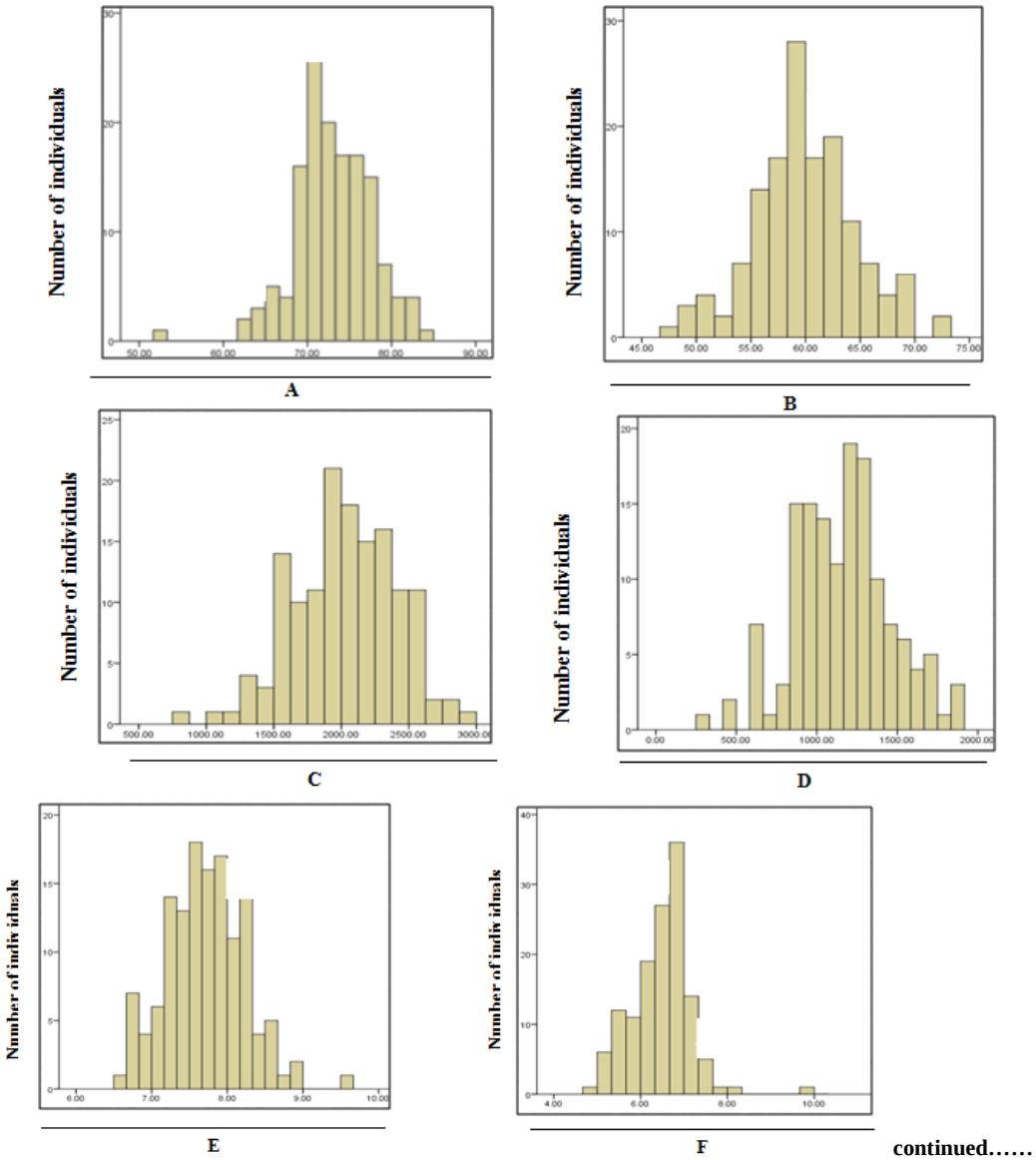


Fig.1. LOD values and maximum points of diagram for QTLs related with studied trait in bread wheat.



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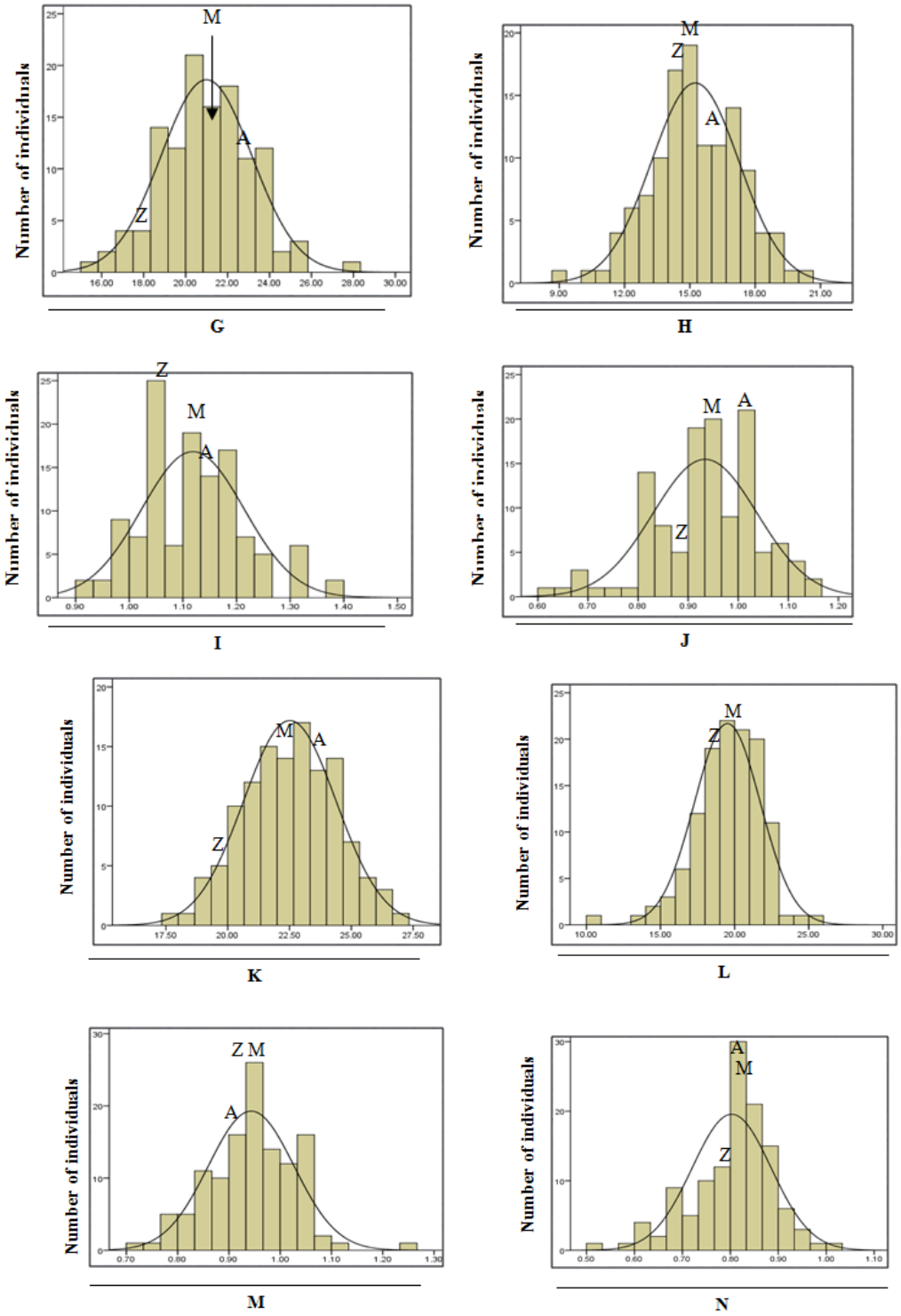

Fig. 2. Distribution of GY and morphological traits in the population of bread wheat.A) PHT (supplementary irrigation), B) PHT (rainfed), C)GY (supplementary irrigation), D) GY (rainfed), E) SL (supplementary irrigation), F)SL (rainfed), G) FLL (supplementary irrigation), H) FLL (rainfed), I) FLW (supplementary irrigation), J) FLW (rainfed), K) SLL (supplementary irrigation), L) SLL (rainfed), M) SLW (supplementary irrigation), N) SLW (rainfed). (Z: 87Zhong291, A: Azar2 and M: Mean of population).

Transgressive segregation was observed for all the studied traits as revealed by frequency distributions under two conditions.

B. Data analysis and linkage mapping

Linkage analysis assigned 40 polymorphic markers in population map consisted of 45 SSR and AFLP markers. The linkage map with 142 individuals, representing 68 markers to 8 linkage groups and map with121 individual, 67 markers were assigned to 9 linkage groups. In the first map, 17 markers and in the second map, 18 markers were as signed to any linkage groups. For GY, PHT and SL, the markers were assigned to eight linkage groups. So the linkage map with 24SSR, 31AFLP markers and 13 markers ISSR, were covered 1310c M of the wheat genome with distance between two neighboring markers19.26cM. Linkage groups 1, 2, 3, 4, 5, 6, 7 and 8, respectively have 3, 17, 8, 23, 8, 2, 3 and 4 markers (Fig. 3).

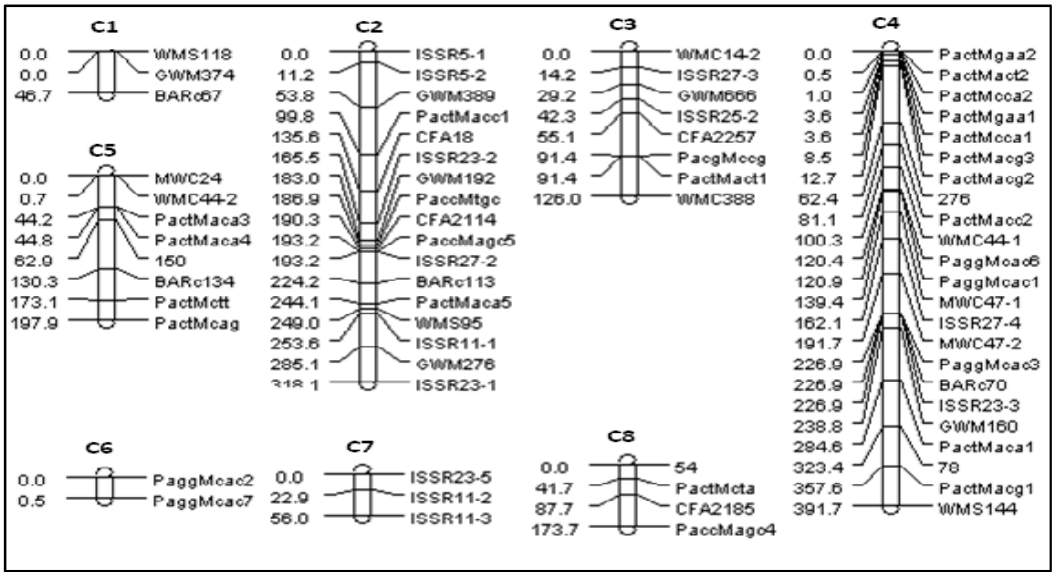

Fig. 3. Linkage map of the population of recombinant inbred lines of bread wheat derived from crosses 87Zhong291 and Azar2 with 142 individuals for GY, PHT and SL.

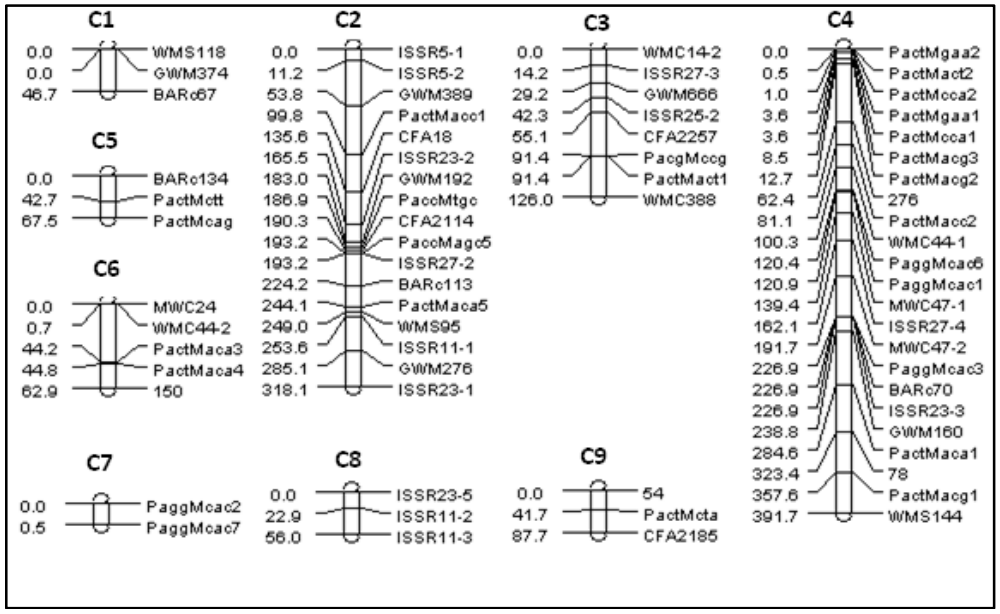

Fig. 4. Linkage map of the population of recombinant inbred lines of bread wheat derived from crosses 87Zhong291 and Azar2 with 121 individuals for FLL, FLW, SLL and SLW.

In the second map, the markers were assigned to 9 linkage groups that the linkage map with 28SSR, 26AFLP markers and 13 markers ISSR, were covered 1157cM of the wheat genome with distance between two neighboring markers17.26cM. Linkage groups 1, 2, 3, 4, 5, 6, 7, 8and 9, respectively had 3, 17, 8, 23, 3, 5, 2, 3 and 3 markers (Fig. 4).

C. QTL analysis

QTL for grain yield (GY). In SIC, twenty QTL were detected on groups 2, 3, 4, 5 and 8, respectively, explaining a total of 60% of the phenotypic variance for GY. The QTL were detected across two environments: ISSR25_2-CFA2257 contributed by parent 87Z hong 291 explains more than 40%, of the total phenotypic variance for GY (Table 1). Ten QTL on groups 2, 3, 4 and 5, respectively, were detected for GY in RC. These QTL explain up to 25% of phenotypic variation for GY (Table 2). Among the detected QTL, one QTL (PacMaca5-Xwms95) was found, for which Azar2 contributed the positive allele, explaining about 18% of the total phenotypic variation of GY.

QTL for plant height (PHT). In RC, by using composite interval mapping (CIM), one QTL for PHT was located between PactMacg2- 276 markers in linkage group 4. Four QTL on groups 2, 4 and 5 were identified explaining nearly 27% of the total phenotypic variance of PHT in SIC (Table 3).

QTL for Spike length (SL). On the basis of data from RCa total of 5 QTL for SL were identified on groups 2, 3 and 4, respectively. These QTL totally explained 28.98% of the phenotypic variance of SL (Table 3). Two QTL associated with SL were identified on group 5 in SIC. These QTL explain up to 33% of phenotypic variation for SL.

Table 1: Linkage group, Marker intervals, Position (cM), LOD, Additive effect and Phenotypic Variance Explained of QTLs related with GY in bread wheat in SIC.

Linkage group	Marker intervals	Position	LOD	A	PVE (%)
2	ISSR5_2-Xgwm389	39.80	6.12	0.0119	0.10
2	Xgwm389-PactMacc1	3.20	5.74	0.0113	0.08
2	PactMacc1-CFA18	33.20	5.01	0.0316	0.60
2	Xbarc113-PactMaca5	3.80	4.48	0.0378	0.60
2	PactMaca5-Xwms95	3.90	3.16	0.0303	5.40
3	ISSR27_3-Xgwm666	11.80	3.04	0.1415	1.90
3	Xgwm666-ISSR25_2	1.80	5.70	0.060	0.29
3	ISSR25_2-CFA2257	1.70	4.62	-0.4971	40.46
3	CFA2257-PacgMccg	1.90	5.60	-0.18	2.70
3	CFA2257-PacgMccg	21.90	4.26	-0.127	4.50
3	PactMact1-Xwmc388	31.60	5.43	0.0389	0.10
4	0-PactMgaa2	0.0001	5.06	-0.067	0.19
4	PactMacg2-276	41.30	3.72	-0.026	0.48
4	PactMacc2-Xwmc44_1	17.90	4.27	0.075	0.34
4	Xwmc47_1-ISSR27_4	1.60	4.11	-0.046	0.27
4	Xgwm160-PactMaca1	9.20	3.08	0.010	0.10
4	PactMacg1-Xwms144	29.60	4.47	-0.0018	0.25
5	Xbarc134-PactMctt	1.70	3.74	-0.0081	0.058
5	Xwmc44_2-PactMaca3	1.30	6.54	0.016	0.22
8	CFA2185-PaccMagc4	3.30	.15	0.047	1.53

Table 2: Linkage group, Marker intervals, Position (cM), LOD, Additive effect and Phenotypic Variance Explained of QTLs related with GY in bread wheat in RC.

Linkage group	Marker intervals	Position	LOD	A	PVE (%)
2	Issr5_2-Xgwm389	39.80	3.83	0.022	0.43
2	Xgwm389-pactMacc1	3.20	3.85	-0.73	0.46
2	PactMacc1-CFA18	33.20	3	-0.87	0.91
2	Xbarc113-PactMaca5	3.80	5.17	-0.76	0.37
2	PacMaca5-Xwms95	3.90	3.26	-0.83	18.26
3	Xgwm666-Issr25_2	1.80	4.73	0.091	0.70
3	Issr25_2-CFA2257	8.70	4.19	-0.15	2.90
4	0-PactMgaa2	0.001	3.23	0.028	0.86
4	PactMacg2-276	43.30	3.07	-0.16	0.20
5	Xwmc24-Xwmc44_2	4	4.67	0.013	0.65

Table 3: Trait, Linkage group, Marker intervals, Position, LOD, Additive effect and Phenotypic Variance Explained of QTLs related with plant height and spike length in bread wheat. A) PHT (SIC), B) PHT (RC), C) SL (SIC), D)SL (RC).

Traits	Linkage group	Marker intervals	Position (cM)	LOD	A	PVE (%)
A	2	ISSR5_2-Xgwm389	42.60	3.18	1.205	5.00
	2	Xgwm276-ISSR23_1	20.01	3.13	1.59	5.30
	4	PactMacg3- pactMacg2	4.21	3.39	-1.56	8.20
	5	Xwmc24-Xwmc44_2	0.71	4.14	1.46	8.90
B	4	PactMacg2-276	14.01	6.03	-0.015	2.40
C	5	Xwmc44_2-PactMaca3	38.01	5.90	0.258	17.40
	5	PactMaca4-150	4.01	5.82	0.243	16.50
D	2	Xbarc113-PactMaca5	17.80	3.41	0.62	11.00
	3	ISSR25_2-CFA2257	12.00	3.19	-0.36	2.40
	4	PactMgaa2-PactMact2	0.01	4.59	0.38	7.70
	4	PactMacg2-276	4.00	7.74	-0.04	0.28
	4	PactMacg2-276	49.70	4.12	-0.21	7.60

QTL for Flag leaf length (FLL) Flag leaf width (FLW). For FLL in RC, four QTL were located in linkage groups2,3and 9, respectively (Table 4). Additive effect of these QTL was positive and four QTL totally explain more than 8% of the total phenotypic variance for this trait. For FLL trait in SIC in just one QTL on group 2 was identified (Table 4). Additive effect of the QTL was positive and explained 10% of the phenotypic variation. Seven QTL were detected in linkage groups2,3 and 9 for FLW under RC, respectively (Table 4). These QTL explain up to 13% of phenotypic variation for this trait. In this study, no QTLs for FLW in SIC have been estimated.

Table 4: Trait, Linkage group, Marker intervals, Position, LOD, Additive effect and Phenotypic Variance Explained of QTLs related with A)FLL(RC), B)FLL(SIC), C) FLW (RC), D)SLL (RC) and E) SLW (RC).

Traits	Linkage Group	Marker intervals	Position	LOD	A	PVE
A	2	Xbarc113-PactMaca5	1.80	3.97	0.046	5.00
	3	CFA2257-PacgMccg	5.90	5.41	0.005	0.02
	3	PactMact1-Xwmc388	29.6	4.42	0.028	0.47
	9	54-PactMcta	6.00	4.85	0.028	2.90
B	2	PactMtgc-CFA2114	0.10	3.24	0.10	10.00
C	3	CFA2257-PacgMccg	3.90	5.09	0.11	8.90
	3	PactMact1-Xwmc388	29.60	4.01	0.012	0.10
	4	PactMgaa2-PactMact2	0.01	3.53	0.0076	0.40
	4	PactMacg2-276	37.30	3.73	-0.0095	0.50
	4	PactMacg1-Xwms144	29.40	3.89	-0.0113	0.70
	9	54-PactMcta	6.01	3.74	0.02	2.80
	9	PactMcta-CFA2185	33.30	3.82	-0.003	0.04

QTL for Second leaf length (SLL) and Second leaf width (SLW). Based on the data of the RC a total of eight QTL were detected on groups 2, 3, and 4, explaining a total of 22.65% of the phenotypic variance for SLL (Table 5). For second leaf length in SIC no QTL have been estimated. Nine QTL on linkage groups 2, 3, 4 and 9 were identified explaining nearly 36% of the total phenotypic variance of SLW in RC (Table 5). For second leaf width in SIC no QTL have been detected.

DISCUSSION

A.QTL analysis of traits

Considering that the genetic length of the whole hexaploid wheat genome is about 4000 cM, our maps have about 62% coverage. Numerous QTL for GY, PHT, SL, FLL, FLW, SLL and SLW were detected with QTL numbers varying from zero to twenty, depending on the traits and environments. Despite the fact that the positions of QTL derived from different environments are probably stable within a genome but the effects of QTL may differ between environments. Thus, a QTL analysis should be based on various environments (Hai *et al.*, 2008).

Studies showed that selection for grain yield in the segregative generation is more efficient than direct selection. Therefore, cultivars with high grain yield under drought stress have high potential to maintain their grain yield at maximum level (Quarrie *et al.*, 2006).

Table 5: Trait, Linkage group, Marker intervals, Position, LOD, Additive effect and Phenotypic Variance Explained of QTLs related with A)SLL (RC) and B) SLW (RC).

Traits	Linkage Group	Marker intervals	Position	LOD	A	PVE
A	2	ISSR5_2-Xgwm389	40.01	4.45	0.007	0.31
	2	PactMacc1-CFA18	33.20	4.08	0.006	0.17
	2	CFA18-ISSR23_2	29.40	4.14	0.0006	0.07
	2	ISSR23_2-Xgwm192	14.50	5.01	0.117	10.70
	2	Xbarc113-PactMaca5	1.80	5.90	0.047	6.90
	3	CFA2257-Pacgmccg	3.90	5.37	0.010	0.10
	3	PactMact1-Xwmc388	31.60	5.71	0.052	1.50
	4	PactMacg1-Xwms144	31.40	5.42	-0.022	2.90
B	2	ISSR5_2-Xgwm389	34.01	4.21	0.0031	0.05
	2	Xgwm389-PactMacc1	8.01	4.40	0.0003	0.0005
	3	CFA2257-PacgMccg	6.01	3.37	-0.065	5.40
	3	CFA2257-PacgMccg	36.31	3.73	-0.184	8.38
		PactMact1-Xwmc388	28.01	4.60	-0.122	17.90
	4	PactMgaa2-PactMact2	0.01	4.13	0.0082	0.54
	4	PactMacg2-276	38.01	4.21	-0.0086	0.47
	4	Xgwm160-PactMaca1	8.01	3.43	0.0113	0.87
	9	54-PactMcta	6.01	4.22	0.020	2.50

QTL analysis on grain yield in wheat was first demonstrated by Araki *et al.* (1999). Subsequently, studies showed that grain yield QTL were detected on almost all chromosomes of wheat (Kato *et al.,* 2000; Huang *et al.,* 2006; McCartney *et al*., 2005; Kirigwi *et al.,* 2007; Snape *et al.* 2007; Kumar and Sharma, 2007). Based on the data of two environments, a total of thirty QTL on five groups for GY were detected in the present study. Moreover, in the Chuanmai42 × Chuannong16mapping population, Tang *et al.* (2011) detected nineteen QTL for grain yield in seven different conditions. According to additive effect of major QTL of ISSR25_2-CFA2257 and PacMaca5-Xwms95, the positive allele of these QTL is contributed by the parent Azar2. The most significant QTL detected for grain yield in present study were located on groups 2 and 3. Various QTL studies have showed the most important grain yield QTL are located on chromosome 5 (Kato *et al.,* 2000; Quarrie *et al.,* 2005; Huang *et al.,* 2006; Cuthbert *et al.,* 2008). Considering the high percentage of phenotypic variance explained by QTL (ISSR25_2-CFA2257) in the population could be concluded that selection for this trait in supplementary irrigation can be effective. In this study some stable QTL for grain yield were detected under RC and SIC. The additive effect of these QTL depends on conditions, which showed the favorable allele came from both 87Zhong291 and Azar2 parents. This kind of QTL was less affected by the environmental conditions and is useful for Marker-based selection (MAS). Earlier studies have demonstrated QTL for PHT on 19 of the 21 wheat chromosomes, except 6B and 6D (Borner *et al.,* 2002; Draeger *et al.,* 2007; Maccaferri *et al.,* 2008; Wang *et al.,* 2009; Shukla *et al.,* 2015).

In the present study, five QTL for PHT were located on 3 groups based on two environments. According to additive effect of these QTL, PHT enhancing allele at this locus was contributed by two parents. The significant QTL for PHT under SIC was located on group 5 flanked by markers Xwmc24-Xwmc44_2 explaining 8.9% of phenotypic variation with positive allele coming from 87Zhong291. This QTL was co-located with QTL for GY (RC). Co-location of plant height QTL with GY has been showed in previous studies also (Kirigwi *et al.,* 2007; Peleg *et al.,* 2009; Kadam *et al.,* 2012; Shukla *et al.,* 2015).

SL is one of the most significant components of spike characteristics. several studies reported that QTLs for SL were located on chromosomes 1A, 1B, 1D,2D, 3B, 3D, 4A, 5A, 5D, 6A,6B, 7A, 7B, 7D (Sourdille *et al.,* 2000; Marza *et al.,* 2006; Cui *et al.,* 2012; Yu, 2014).Seven QTL were identified for spike length. Those in linkage groups 2, 4 (PactMgaa2-PactMact2) and 5 showed a positive effect from the 87Zhong291 allele, whereas QTLs 3 and 4 showed a negative effect. The SL enhancing allele under RC at Xbarc113-PactMaca5 locus was contributed by 87Zhong291 parent. This QTL explained 11% of phenotypic variation for SL and co-located with QTL for GY and FLL traits under RC. Another QTL for SL under RC, PactMacg2-276 explained 7.60% of phenotypic variation with positive allele coming from drought resistant parent Azar2. This QTL co-located with GY (both conditions) and PHT (RC). In wheat, SL is reported to be correlated with GY and PHT (Chesnokov *et al.,* 2013).

Chesnokov *et al*. (2013) reported that QTL for FLL and FLW were mainly located on chromosomes 5A. These researchers identified sixteen QTL on 6 chromosomes in ten region × year conditions. In this study twelve QTL for FLL and FLW was located on 4 groups. The strongest effect QTL for FLL under SIC, was located on chromosome 2 flanked by markers PactMtgc-CFA2114 explaining 10% of PV with positive allele coming from the Azar2 parent. Studies of Thorne (1965), Inoue *et al*. (2004) and Rafr'que (2006), showed that between the yield and flag leaf area was a significant positive correlation. But in this study, despite of FLL and FLW of Azar2 was larger than the 87Zhong291, but the GY of Azar2 was lower than the 87Zhong291. There is no report on QTL for SLL and SLW in wheat. Our studies revealed nineteen QTL on 4 groups. We report here major QTL for SLW trait on group 3 in the Azar2/87Zhong291 RIL population under RC. This QTL explained 17.9% of phenotypic variation and was co-located with QTL for GY(SIC), FLL and FLW (RC) and SLL under (RC) with positive allele coming from 87Zhong291.

According to our findings, For GY, PHT, SL, FLL, FLW, SLL and SLW, 44 and 27 QTL were located, under RC and SIC, respectively. According to the number of located QTLs for traits and the degree of explanation phenotypic variance of each QTL (from 0/0005 to 40.46%) indicated that these traits controlled by number of major and minor genes. In this study, we have reported some strong and stable QTLs for grain yield and second leaf width. These QTL could be used efficiently in wheat breeding programs.

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