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Full Length Article

Mapping Quantitative Trait Loci for Important Agronomic Traits and Developing Potential Near-Isogenic Lines in Wheat

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Abstract

Tailoring wheat cultivars with good agronomic traits and high yield has always been the objective of breeders. However, most of these traits are quantitative. Therefore, it is of great significance to excavate the stable quantitative trait loci (QTL) associated with agronomic characters of wheat for marker assisted selection (MAS) breeding. In the current study, 160 BC_3F_3 introgression lines (ILs) from Lumai14 and Jing411 were used for a linkage map construction. Quantitative trait loci (QTL) for 10 agronomic traits, including heading date (HD), plant height (PH), first internode length (FIL), length from flag leaf pulvinus to spike base (LPSB), spike length (SL), number of valid tillers (NT), fertile spikelet number per main spike (FSN), grain number per main spike (GNS), grain weight per plant (GWP) and thousand grain weight (TGW) were mapped under six environments. One hundred and fifty six SSR markers were anchored in the linkage map of the ILs and every chromosome contained 7.42 markers in average. A total of 46 QTLs for the above traits were identified on all chromosomes except for 2D and 5D. Among them, *QHd-7D*, *QFil-4A*, *QLpsb-4A-1*, *QSl-1D-2* and *QFsn-7B* were detected in 2, 2, 2, 4 and 3 environments, respectively. In addition, 10 QTL clusters were also found. Moreover, analysis of genetic background for 160 lines found that the IL 30 and IL 86 contained 4 and 3 introgressed chromosomal segments from donor parent, Jing411, respectively, and one of these donor segments harbored *QFil-4A* for FIL and *QLpsb-4A-1* for LPSB. So the two lines and the recurrent parent, Lumai14, can be regarded as potential near-isogenic lines for further fine mapping.

Keywords: Wheat; Agronomic traits; Introgression Lines; Marker assisted selection; QTL

Introduction

Wheat (*Triticum aestivum* L.) is one of the important food crops, and more than one third of the population consumes it as a staple food around the world (Brenchley *et al.*, 2012). Developing wheat varieties with good agronomic traits has been one of the major breeding objectives for breeders. Heading date (HD) is not only closely related to the maturity, but also directly or indirectly affects the wheat production and many other important agronomic traits. There are many quantitative traits in wheat that are related to yield such as plant height (PH), spike length (SL), number of valid tillers (NT), grain number per spike (GNS), fertile spikelet number per main spike (FSN) and 1000 grain weight (TGW) (Wu *et al.*, 2012). With the application of molecular biology and quantitative genetics in plant breeding program, quantitative trait loci (QTLs) for many agronomic and yield-related traits were detected using either double haploid (DH), or recombinant inbred line (RIL) and F_2 genetic populations. QTLs controlling agronomic and yield-related traits had been mapped on all 21 chromosomes in wheat (Wang *et al.*, 2011; Wu *et al.*, 2012; Mason *et al.*, 2013; Nguyen *et al.*, 2015; Hussain *et al.*, 2017). However, it was very difficult for these QTLs to be used in developing new varieties, because they were often subject to both genetic background and environments. Therefore, it is very important to detect the QTLs, which are less or not affected by genetic background and environments (Woo *et al.*, 2008). Thus, these QTLs will be more applicable for marker assisted breeding program. Quantitative trait loci identified using introgression line populations are not affected by genetic background, and can be used to pyramiding breeding. In the present study, an introgression line population was developed from Lumai14 and Jing411. Genetic background of all lines was determined using SSR markers. Quantitative trait loci controlling 10 important agronomic traits, *i.e.*, HD, PH, FIL, LPSB, NT, SL, FSN, GNS, grain weight per plant (GWP) and TGW were mapped across six different environments. The objectives of this study were to (1) detect stably expressed QTLs controlling agronomic traits across different environments and (2) develop potential near-isogenic lines in wheat. The purpose was to provide a

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foundation for fine mapping, map-based cloning, marker assisted selection and pyramiding programs in wheat.

Materials and Methods

Plant Materials

A BC_3F_3 IL population (Fig. 1) comprised of 160 introgression lines (IL1-IL160) derived from Lumai14 and Jing411, was used in this study. Recipient parent, Lumai14, was an irrigated-land high-yield cultivar developed by the Yantai Academy of Agricultural Sciences, Shandong, China, whereas, Jing411 used as donor parent that had been widely grown as one of the main varieties at the Northern Winter Wheat Region of China in 1990s (Xu *et al.,* 2014; Zhai *et al.,* 2015).

Field Trials and Traits Evaluation

The ILs population and their parents were grown at experimental farm of Shanxi Agricultural University, Taigu, China (37°25′N, 112°35′E) (Wang *et al.,* 2015). The experiments were carried out under six environments from 2013 to 2017, including 2013–2014 drought stress (DS) (E1), 2013–2014 well-watered (WW) (E2), 2014–2015 DS (E3), 2014–2015 WW (E4), 2015–2016 DS (E5), 2016–2017 DS (E6). All of the trials were irrigated before sowing. Plants under drought stress only relied on natural precipitation during the whole growing period after sowing. The rainfall in E1, E3, E5 and E6 was 187, 103.5, 189 and 138mm (http://data.cma.cn/), respectively. Well-watered treatments were irrigated with 650 m^3 ha^{-1} at the pre-overwintering period, seedling establishment, flowering, mid-grain-filling stage, respectively. All the trials were performed in randomized complete block design with three replications. All the ILs along with their parents was planted on rows of 2.5 m length. The rows were separated 0.25 m apart and fifty seeds were sown in each row. Heading date (HD), PH, FIL, LPSB, NT, SL, FSN and GNS, were measured in the field. GWP and TGW were evaluated in the experiment room. Data was recorded from five randomly selected plants from each row and then averaged.

Molecular Markers Detection and Linkage Map Construction

Genomic DNA of all ILs and their parents were extracted using a modification of the phenol-chloroform method described by Devos *et al.* (1992). Five hundred and sixty-five simple sequence repeat (SSR) markers evenly distributed on 21 chromosomes of wheat were selected from a high-density microsatellite consensus map for bread wheat published by Somers *et al.* (2004). Polymerase chain reaction (PCR) was performed using following thermal profile: initial degradation of DNA at 95℃ for 4 min followed by 36 cycles of 95℃ for 59 s, annealing for 59 s and elongation at 72℃ for 60 s and final extension at 72℃ for 7 min. The PCR products were separated using 8% non-denatured polyacrylamide gel electrophoresis (PAGE) and visualized by silver staining (Marklund *et al.,* 1995; Cui *et al.,* 2014a; Zhai *et al.,* 2015). These markers were employed on both parents and polymorphic markers were selected for further studies. The order, location and distance between markers on the chromosomes of polymorphic SSR markers screened in this study were anchored according to a high-density microsatellite consensus map reported by Somers *et al.* (2004). A genetic linkage map of the IL population was constructed using Map Draw software.

Data Analysis and QTL Mapping

Basic statistical analysis and correlation analysis of 10 important agronomic traits of wheat IL population across six environments were performed using DPS v9.50 statistical analysis software. QTL was detected by likelihood ratio test based on stepwise regression for additive QTL (RSTEP-LRT-ADD) using IciMapping 4.0 (Li *et al.,* 2007; Cui *et al.,* 2014b). The threshold LOD values were calculated using 1000 permutations with a type 1 error of 0.05. All QTLs were named by following "QTL + trait + chromosome" formula (Liu *et al.,* 2014; Sraphet *et al.,* 2017; Teng *et al.,* 2018).

Results

Markers Selection and Linkage Map Construction

A total of 156 polymorphic markers between parents were selected from 565 pairs of primers, accounting for 27.61% of effective amplification. Every chromosome had 7.42 markers in average and the average length between two loci on the chromosome was 16.47 cM. The number of polymorphic markers ranged from 3 to 15 on each chromosome (Fig. 2).

Analysis of Introgression Fragments

The genotypes of 160 ILs were explored using 156 polymorphic SSR markers selected from parents screening. The results showed that the genetic background of Lumai14 was 93.2% in this ILs population, was close to its theory value (93.8%). All of 156 markers were anchored in the linkage map of the ILs, according to the international wheat consensus SSR map (Somers *et al.,* 2004). The range of the number of segments from donor parent in all lines was from 2 to 25. Among them, seven lines (IL 45, 77, 78, 84, 85, 99, 100) contained 2 donor segments, while the IL 132 had 25.

Phenotypic Variation of Important Agronomic Traits

Recipient Lumai14 was characterized by longer HD, lower PH, fewer NT, shorter SL, less FNS, less GNS, lower GWP and lower TGW, compared with donor Jing411. The means of HD, NT, SL, GNS and GWP in most of the environments

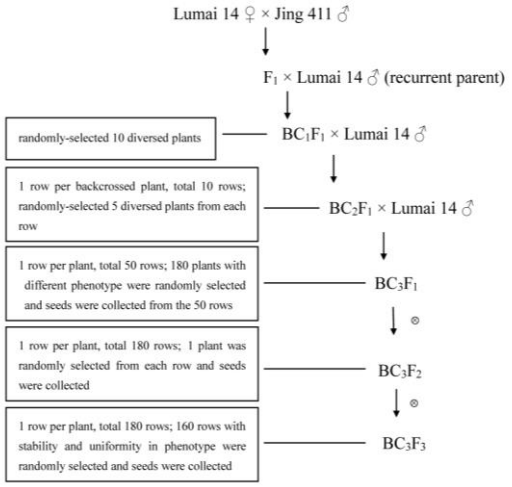

Fig. 1: The scheme of development of introgression line population (BC_3F_3)

and PH in all environments for ILs were between their parents. Except HD in E1 and E4, NT in E4 and FNS in all environments, the minimum values of all observed traits for ILs under six environments were less than that of the low-parent, and the maximum values were greater than the parent of the high value. There was segregation for all investigated traits in IL population with the coefficients of variation (CV) ranging from 0.35 to 60.25%. Length from flag leaf pulvinus to spike base had the highest variation with CV values of 22.19–60.25%, while NT was the least variation with CVs of 0.35–0.53% (Table 1). All traits investigated in the IL population showed transgressive segregation.

Correlations of Important Agronomic Traits

Heading date showed a highly significant negative correlation with PH and LPSB and TGW across all the six environments. Positive correlations existed between PH and all the other seven traits except for SL and GNS. The most significant correlation were observed among FIL, LPSB and TGW. In particular, the correlation coefficient between FIL and LPSB was 0.88 (Table 2). Besides, significantly positive correction also observed between NT and SL, FSN, GNS and GWP, and between SL and FSN, GNS and GWP. There were also significantly positive correlations between FSN and GNS and GWP, between GWP and GNS and TGW.

Quantitative Trait Loci for Agronomic Traits

For 10 traits investigated in the present study, a total of 46 QTLs were identified which explained 2.75–11.72% of the phenotypic variations. Among them, the favorable alleles of 34 QTLs detected were contributed from the donor parent Jing411, while the favorable alleles of the rest 12 QTLs mapped were derived from recipient Lumai14. The number of QTLs for individual trait varied from 2 to 10, namely 5 QTLs for HD, 3 QTLs for PH, 2 QTLs for FIL, 5 QTLs for LPSB, 2 QTLs for NT, 10 QTLs for SL, 2 QTLs for GNS, 4 for FSN, 6 QTLs for GWP and 7 QTLs for TGW. These QTLs mapped were distributed on 19 of the 21 wheat chromosomes except for 2D and 5D. And they were more frequently detected on chromosomes 3B, 3D, 4A, 4D, 5A, 5B, 6A, 7A and 7B (Fig. 2 and Table 3). Among them, *QSl-1D-2* for SL that was located close to the marker Xbarc62 on 1D chromosome was identified simultaneously in E1 E3, E4 and E6. The QTL accounted for 11.72, 4.29, 5.18 and 6.86% of the phenotypic variation, respectively. Alleles of this QTL derived from Jing411 cultivar increased spike length. Moreover, *QFsn-7B* distributed on 7B chromosome controlling FSN was detected at the same time across E1, E2 and E6 environment. The phenotypic variations expressed of this QTL were 9.50, 4.25 and 4.09%, respectively. In addition, *QFil-4A* for FIL and *QLpsb-4A-1* for LPSB distributed near the marker Xwmc707 on chromosome 4A were detected simultaneously in E3 and E4 and their alleles were contributed from donor Jing411 as well. *QHd-7D* for HD that was located near the Xwmc671 locus on chromosome 7D was detected in E1 and E5. It explained 11.71 and 8.77% of the phenotypic variation. The additive effect estimated at the location of this QTL showed that Lumai14 allele reduced the days to ear emergence.

Quantitative traits loci for related traits tend to cluster on chromosomes. In the present study, 10 QTL clusters were found. They located on 1A, 1B, 1D, 4A, 4D, 5B, 6A, 7A and 7B chromosomes, respectively (Fig. 2). There were 6 QTL clusters on chromosome 1B, 1D, 4A, 7A (2) and 7B with the favorable alleles contributed from donor parent Jing411. Among them, the QTL cluster near the Xwmc809 on the 7A chromosome was related to four traits including FIL, LPSB, SL and NT. The QTL clusters on 1D (Xgdm126) and 7A (Xgwm60) were associated with three traits, viz. NT, FSN and GWP, PH, LPSB and GWP, respectively. Three clusters included two traits were located on 4A (FIL and LPSB), 1B (SL and GWP) and 7B (FSN and TGW). In contrast, the favorable alleles of *QSl-5B* and *QGns-5B* in the near of Xwmc371 on chromosome 5B cluster were contributed from recipient parent Lumai14. The three remaining clusters distributed on 1A, 6A and 4D were contributed by both Jing411 and Lumai14.

Developing Potential Near-isogenic Line

Genome-wide scanning and QTL mapping found that the IL 30 and IL 86 had 4 and 3 introgression segments from Jing411, respectively. One of those introgression segments anchored *QFil-4A* for FIL and *QLpsb-4A-1* for LPSB. And the two QTLs were repeatedly detected in E3 and E4. Their positive alleles were from donor parent Jing411, and their additive effects were 0.80 and 0.95, 0.52 and 0.66, respectively (Fig. 2 and Table 3).

Table 1: Phenotypic analysis of important agronomic traits in ILs and their parents under multiple environments

Trait[1]	Environment[2]	Parent		Introgression Lines					
		Lumai14	Jing411	Mean	S.D.[3]	Variation	Skewness	Kurtosis	CV (%)[4]
HD(d)	E1	216.7	213.7	215.0	0.86	214.0-218.0	1.05	1.33	0.40
	E2	218.3	214.7	217.1	1.14	214.7-219.3	-0.62	-0.27	0.52
	E3	216.0	215.3	215.5	1.15	213.0-219.0	0.55	0.38	0.53
	E4	218.3	216.3	218.4	1.05	216.7-221.0	0.26	-0.43	0.48
	E5	221.3	220.0	221.4	0.82	219.3-223.0	0.94	3.56	0.37
	E6	219.0	217.7	218.7	0.76	217.3-220.3	-0.14	-0.05	0.35
PH(cm)	E1	64.2	78.3	69.0	9.08	53.8-85.9	0.18	-1.22	13.17
	E2	84.7	96.5	87.2	10.98	65.4-103.8	0.01	-1.28	12.60
	E3	48.0	58.4	50.9	5.20	42.2-60.8	0.27	-0.68	10.21
	E4	52.1	63.9	55.9	6.25	44.7-71.7	0.40	-0.37	11.19
	E5	60.4	68.3	60.3	7.79	48.4-74.7	0.42	-0.50	12.91
	E6	65.4	83.5	72.1	10.35	55.8-90.8	0.30	-1.13	14.35
FIL(cm)	E1	21.2	23.3	22.8	2.85	17.7-28.8	0.16	-0.80	12.63
	E2	28.5	29.1	31.0	3.51	23.7-37.6	0.11	-0.90	11.33
	E3	17.0	18.4	19.7	4.60	14.1-24.4	1.24	1.30	23.33
	E4	18.6	20.9	20.7	3.21	14.7-27.8	0.24	-0.10	15.50
	E5	20.6	21.6	18.7	2.68	14.3-26.6	1.09	2.40	14.35
	E6	21.1	21.8	20.8	2.09	17.4-25.8	0.61	0.45	10.06
LPSB(cm)	E1	5.0	5.7	5.4	2.12	0.9-9.7	0.04	-0.53	39.08
	E2	10.4	9.5	11.8	2.63	6.2-16.6	0.13	-0.71	22.19
	E3	3.7	2.2	4.6	2.20	0.1-9.4	0.46	0.00	47.64
	E4	3.4	3.3	4.2	2.51	0.1-10.4	0.09	0.58	60.25
	E5	5.6	3.4	3.3	1.64	1.0-8.5	1.31	3.00	50.15
	E6	5.7	3.0	4.0	1.52	1.7-8.6	0.58	1.53	38.25
NT	E1	2.8	4.0	3.0	0.61	2.0-4.7	0.76	1.51	19.98
	E2	3.8	4.4	3.6	0.69	2.5-4.7	0.21	-0.22	18.94
	E3	1.5	3.4	2.1	0.67	1.0-3.6	0.58	0.39	31.96
	E4	1.9	3.7	2.2	0.66	1.2-3.5	0.55	0.52	30.13
	E5	2.6	4.0	2.7	0.78	1.6-4.1	0.95	1.42	28.76
	E6	3.9	3.5	3.7	0.66	2.9-4.7	0.58	0.89	17.83
SL(cm)	E1	8.8	9.1	8.6	0.50	7.6-10.3	0.40	0.88	5.77
	E2	8.7	9.4	8.9	0.56	7.7-10.2	0.04	-0.12	6.31
	E3	8.0	9.1	8.5	0.52	7.5-9.5	0.24	0.59	6.17
	E4	8.8	9.5	8.8	0.53	7.5-10.3	-0.14	0.99	6.01
	E5	7.9	8.1	8.1	0.47	7.2-9.9	0.61	2.35	47.35
	E6	9.0	9.4	9.3	0.55	8.1-11.0	0.34	0.91	5.89
FNS	E1	14.2	18.2	15.2	0.74	13.9-16.6	-0.03	0.14	4.88
	E2	14.9	18.8	15.4	0.67	14.3-16.9	0.06	-0.05	4.34
	E3	14.4	18.8	15.0	0.83	13.0-16.9	-0.20	0.21	5.52
	E4	16.1	18.3	15.3	0.77	14.0-17.1	-0.08	0.19	5.00
	E5	15.7	18.5	15.6	0.82	13.7-17.0	-0.32	1.02	5.27
	E6	16.1	18.1	16.0	0.85	14.5-17.7	0.33	-0.13	5.31
GNS	E1	33.8	38.9	32.9	4.48	25.8-41.2	0.18	0.38	13.60
	E2	40.3	47.4	39.1	4.17	30.8-47.9	0.11	-0.38	10.67
	E3	33.7	46.4	34.4	5.30	20.8-48.1	0.21	0.30	15.41
	E4	39.0	46.7	39.1	4.79	30.6-47.8	-0.02	-0.40	12.27
	E5	36.2	40.2	33.3	6.04	25.1-45.3	0.52	0.49	18.13
	E6	33.9	38.3	35.1	3.71	30.1-43.5	0.21	0.60	10.59
GWP(g)	E1	3.4	6.1	4.4	0.99	2.9-6.8	0.52	0.16	22.67
	E2	4.0	8.3	7.1	1.49	4.0-10.9	0.13	-0.06	21.18
	E3	2.7	6.7	3.7	1.45	1.5-7.1	0.83	0.64	39.65
	E4	3.7	7.8	4.3	1.41	1.6-7.8	0.45	0.05	32.92
	E5	4.7	6.9	4.7	2.86	2.3-8.3	1.54	3.51	36.18
	E6	2.8	3.3	3.6	0.96	2.3-5.7	0.72	0.72	27.07
TGW(g)	E1	30.8	32.9	36.7	3.38	29.6-43.5	-0.06	0.13	9.21
	E2	30.9	40.6	42.5	4.45	32.3-50.8	-0.11	-0.40	10.48
	E3	37.4	42.6	39.7	4.49	30.9-50.4	-0.21	-0.07	11.03
	E4	38.6	43.8	40.7	4.67	32.6-51.4	0.02	0.25	11.76
	E5	36.3	40.3	42.3	3.52	35.9-50.1	0.04	2.33	8.33
	E6	23.4	26.5	32.0	4.46	23.2-40.2	-0.05	-0.58	13.92

[1]: HD: heading date; PH: plant height; FIL: first internode length; LPSB: length from flag leaf pulvinus to spike base; SL: spike length; NT: number of valid tillers; FSN: fertile spikelet number per main spike; GNS: grain number per main spike; GWP: grain weight per plant; TGW: thousand grain weight

[2]: E1: 2013-2014 drought stress (DS); E2: 2013-2014 well-watered (WW); E3: 2014-2015 DS; E4: 2014-2015 WW; E5: 2015-2016 DS; E6: 2016-2017 DS

[3]: S.D.: standard deviation

[4]: CV: coefficient of variation

Table 2: Correlation coefficients for important agronomic traits in ILs under multiple environments

Trait	HD	PH	FIL	LPSB	NT	SL	FSN	GNS	GWP
PH	-0.44**								
	-0.61**--0.26**								
FIL	-0.32**	0.82**							
	-0.02--0.50**	0.60**-0.92**							
LPSB	-0.25**	0.71**	0.88**						
	-0.44**-0.038	0.59**-0.87**	0.68**-0.95**						
NT	-0.10	0.02	-0.01	-0.02					
	-0.24**--0.05	-0.03-0.15	-0.16*-0.25**	-0.18**-0.24**					
SL	0.14	-0.18*	-0.09	-0.12	0.19*				
	-0.19**-0.49**	-0.49**-0.17**	-0.29**-0.10	-0.34**-0.06	0.03-0.45**				
FSN	-0.04	0.01	0.05	-0.01	0.21**	0.27**			
	-0.30**-0.22**	-0.05-0.15	-0.09-0.19*	-0.08-0.09	-0.09-0.39**	0.21**-0.36**			
GNS	0.09	-0.18*	-0.13	-0.11	0.27**	0.31**	0.51**		
	-0.05-0.37**	-0.37**--0.06	-0.25**-0.02	-0.20**-0.02	0.04-0.54**	0.17*-0.50**	0.34**-0.67**		
GWP	-0.14	0.14	0.15	0.11	0.63**	0.22**	0.35**	0.53**	
	-0.33**-0.06	0.07-0.24**	-0.19*-0.34**	-0.04-0.29**	0.51**-0.76**	0.07-0.55**	0.12-0.53**	0.28**-0.71**	
TGW	-0.28**	0.43**	0.36**	0.30**	0.01	-0.07	0.02	0.05	0.39**
	-0.47**--0.16**	0.19*-0.64**	-0.02-0.66**	0.05-0.59**	-0.09-0.22**	-0.48**-0.12	-0.15-0.17*	-0.34**-0.39**	0.29**-0.52**

HD: heading date; PH: plant height; FIL: first internode length; LPSB: length from flag leaf pulvinus to spike base; NT: number of valid tillers; SL: spike length; FSN: fertile spikelet number per main spike; GNS: grain number per main spike; GWP: grain weight per plant; TGW: thousand grain weight

Correlation coefficients between the averaged important agronomic traits are shown on top; of each correlation pair, the first and the second values are the minimum and maximum correlation coefficient values among 6 environments tested, respectively

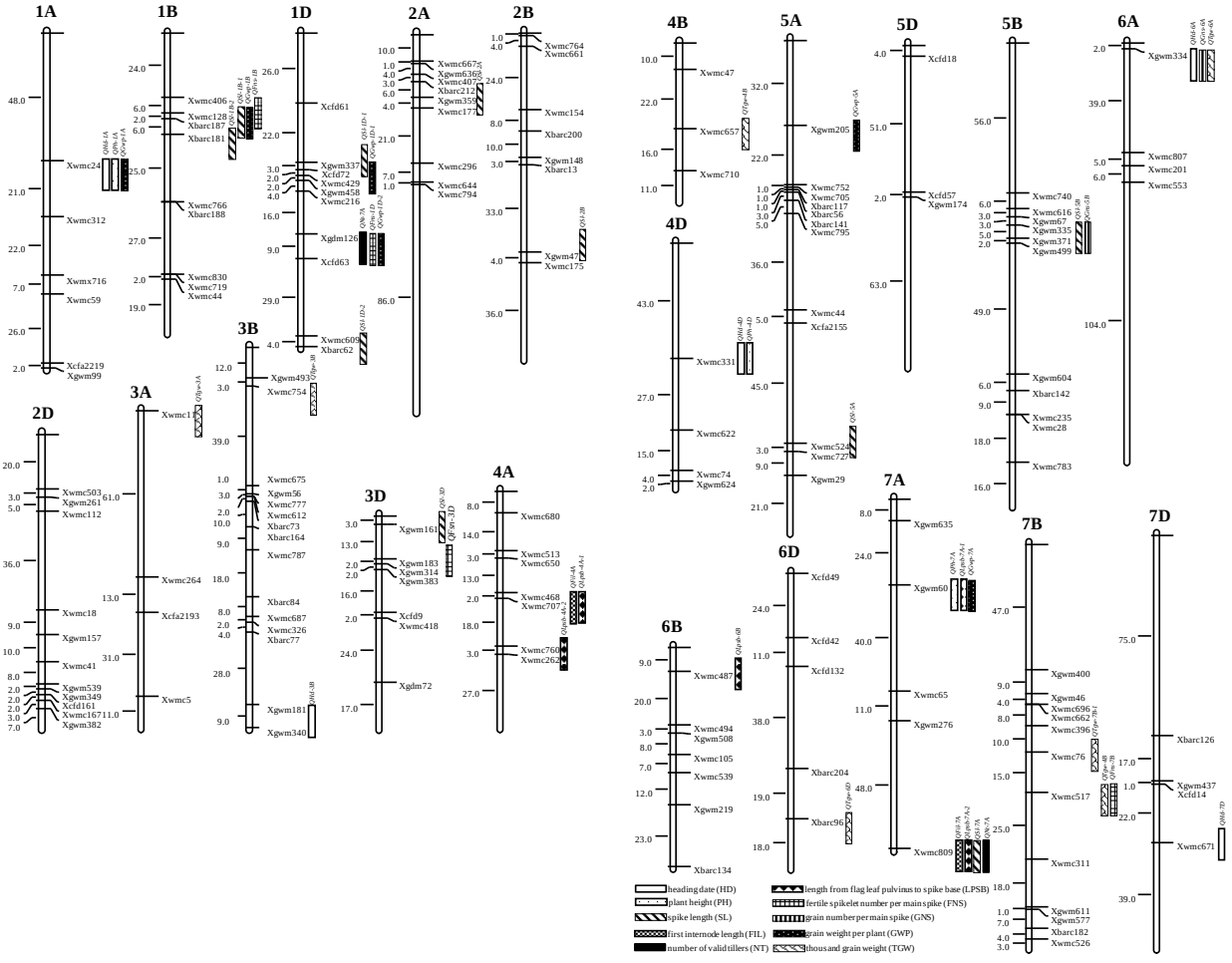

Fig. 2: Distribution of QTLs for important agronomic traits on the genetic linkage map. The map distance in cM are shown on the left. The QTLs are listed on the right

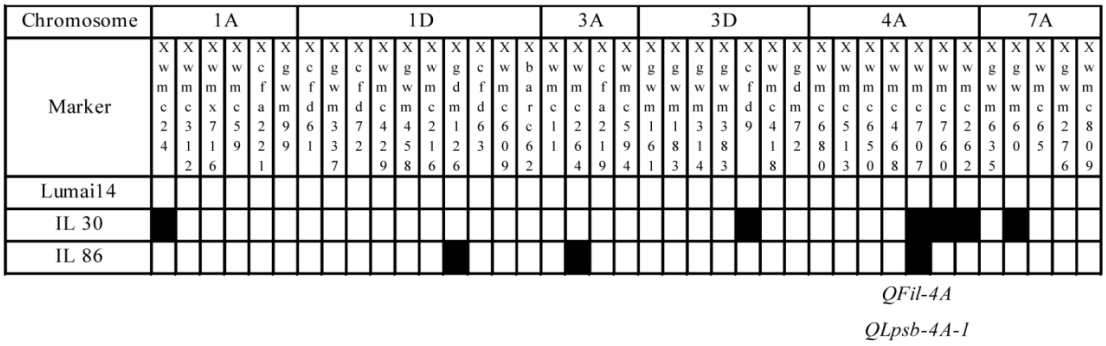

Fig. 3: The distribution of introgression fragments in the IL 30 and 86. The chromosomes not shown weren't substituted segments from donor

On the other hand, FIL and LPSB of the two lines were longer than those of receptor Lumai14 across all environments. Significant difference of FIL existed between IL 30 and Lumai14 in E1, E2, E3, E4 and E6, but did between IL 86 and Lumai14 in E1 and E2. For LPSB, difference between IL 30 and Lumai14 was significant in E1 and E2, but did between IL 86 and Lumai14 in E2. It was more interesting that there was no significant difference for FIL and LPSB between IL 30 and 86 under all 6 environments. This indicated that *QFil-4A* and *QLpsb-4A-1* played an increasing FIL and LPSB role. Therefore, the IL 30 and 86 and their recurrent parent can be regarded as potential near-isogenic lines.

Discussion

To date, many QTLs for agronomic traits were mapped, using DH, RIL and F_2 populations (Ramya *et al.,* 2010; Cui *et al.,* 2011; Naruoka *et al.,* 2011; Nguyen *et al.,* 2015; Leng *et al.,* 2017; Yan *et al.,* 2017). However, it is still difficult to use all of these QTLs in wheat breeding due to less phenotypic effects (Xie *et al.,* 2006). Their phenotypic expression is generally affected by pleiotropic effects of genes for non-target traits (Woo *et al.,* 2008). For an introgression population, the genotypes of all lines are very similar to those of the recurrent parent, and mainly exhibit differences in specific chromosomal segments. Phenotypic differences between lines and the recurrent parent can generally be attributed to introgressed donor segments. Also, due to differences in the numbers and locations of introgressed fragments from donor parents, IL populations may include superior lines with aggregated beneficial genes from the donor parent. Therefore, mapping QTL by introgression population has been an underlying approach for combining marker-based. QTL discovery with elite cultivar improvement (Huang *et al.,* 2003). This strategy has been successfully applied in identifying and transferring valuable QTLs from un-adapted germplasm into elite breeding lines for diploid plants such as rice (Wang *et al.,* 2013; Suzuki *et al.,* 2015; Ye *et al.,* 2015; Singh *et al.,* 2018). In wheat, Merchuk-Ovnat *et al.* (2016) first explored that introgression of ancestral QTLs from wild emmer wheat can enhance drought resistance and productivity in elite wheat varieties. In the present study, it was found that the IL 30 and 86 were introgressed few donor fragments and carried the alleles increased FIL and LPSB (Fig. 3). So the two lines can be regarded as underlying near-isogenic lines. They can be used for fine mapping by crossing and backcrossing with recipient Lumai14.

So far, an increasing number of studies for important agronomic characters in wheat have been reported (Wu *et al.,* 2012). And QTLs for agronomic traits have been located on all 21 chromosomes in wheat (Carter *et al.,* 2011; Cui *et al.,* 2012; Zhang *et al.,* 2012; Cui *et al.,* 2014b; Liu *et al.,* 2014). In the present study, 46 QTLs controlling 10 agronomic traits were detected on 19 chromosomes; the exceptions were 2D and 5D. Some loci found here were identical to those detected in previous studies.

Zhang *et al.* (2008) found *Qph4D* controlling PH was located on 4D chromosome (Xbarc334-Xwmc331). In the current research, *QPh-4D* (Xwmc331), explained 5.56% of the phenotypic variation was also identified at the same position of the same chromosome. And *QPh-3A* for PH on the chromosome 3A detected in present study was only 5cM apart from the QTL controlling this trait detected by Liu *et al.* (2014). So they may be the same QTL. For FSN, *QFsn-7B* was located near the marker Xwmc517 of chromosome 7B in E1, E2 and E6 in the present study. The QTL accounted for 4.09–9.50% of the phenotypic variation. Wang *et al.* (2011) also found a QTL for FSN in the same region. Cui *et al.* (2012) found *QFsn.WY.7B.1a* was also mapped in the same interval. This fully demonstrated that this region of the chromosome 7B distributed the locus that controlled the FSN. For TGW, the *QTgw-4B* evaluated near the Xwmc657 of chromosome 4B in the current research was apart 2–7cM from *QTgw.wa-4B* (Xbarc20-Xwmc238) detected simultaneously across three conditions (Wang *et al.,* 2011).

Besides this the QTL controlling TGW were also observed that were located at the flanking marker Xcfd39-Xbarc20 on chromosome 4B (Huang *et al*., 2006; Heidari *et al*., 2011; Liu *et al*., 2014). According to the wheat genetic linkage map made by Somers *et al.* (2004), *QTgw-4B*

Table 3: QTLs for important agronomic traits in wheat ILs under multiple environments

Trait[1]	QTL[2]	Chromosome	Marker	LOD[3]	Add[4]	PVE(%)[5]	Donor of positive allele	Environment[6]
HD	*QHd-1A*	1A	Xwmc24	2.49	-0.31	8.62	Lumai14	E6
	QHd-3B	3B	Xgwm340	3.28	0.55	6.02	Jing411	E4
	QHd-4D	4D	Xwmc331	2.59	-0.27	4.92	Lumai14	E4
	QHd-6A	6A	Xgwm334	3.38	-0.36	9.51	Lumai14	E5
	QHd-7D	7D	Xwmc671	3.44	-0.71	11.21	Lumai14	E2
				4.28	-0.48	8.77	Lumai14	E5
PH	*QPh-1A*	1A	Xwmc24	2.68	2.44	5.59	Jing411	E3
	QPh-4D	4D	Xwmc331	2.76	1.72	5.56	Jing411	E4
	QPh-7A	7A	Xgwm60	2.82	2.17	6.07	Jing411	E4
FIL	*QFil-4A*	4A	Xwmc707	2.86	0.80	5.57	Jing411	E3
				3.36	0.95	5.93	Jing411	E4
	QFil-7A	7A	Xwmc809	4.13	2.18	6.38	Jing411	E5
LPSB	*QLpsb-4A-1*	4A	Xwmc707	2.57	0.52	3.80	Jing411	E3
			Xwmc707	3.25	0.66	4.71	Jing411	E4
	QLpsb-4A-2	4A	Xwmc760	2.63	0.58	3.89	Jing411	E3
	QLpsb-6B	6B	Xwmc487	5.39	1.16	5.93	Jing411	E5
	QLpsb-7A-1	7A	Xgwm60	3.92	0.48	4.21	Jing411	E5
	QLpsb-7A-2	7A	Xwmc809	4.58	1.32	6.24	Jing411	E5
NT	*QNt-1D*	1D	Xgdm126	5.21	0.16	4.86	Jing411	E6
	QNt-7A	7A	Xwmc809	3.65	0.47	3.55	Jing411	E5
SL	*QSl-1B-1*	1B	Xbarc187	2.74	0.54	4.73	Jing411	E2
	QSl-1B-2	1B	Xbarc181	3.47	0.78	5.46	Jing411	E4
	QSl-1D-1	1D	Xgwm337	2.55	0.15	3.56	Jing411	E2
	QSl-1D-2	1D	Xbarc62	7.21	0.76	11.72	Jing411	E1
			Xbarc62	2.64	0.49	4.29	Jing411	E3
			Xbarc62	3.05	0.54	5.18	Jing411	E4
			Xbarc62	3.90	0.64	6.86	Jing411	E6
	QSl-2A	2A	Xgwm359	3.45	-0.17	7.12	Lumai14	E6
	QSl-2B	2B	Xgwm47	2.97	-0.27	4.96	Lumai14	E2
	QSl-3D	3D	Xgwm161	3.50	-0.17	4.94	Lumai14	E2
	QSl-5A	5A	Xwmc524	4.38	0.21	6.26	Jing411	E2
	QSl-5B	5B	Xgwm371	3.65	-0.18	7.24	Lumai14	E6
	QSl-7A	7A	Xwmc809	4.78	0.45	7.99	Jing411	E1
FSN	*QFsn-1B*	1B	Xwmc128	3.83	-0.59	4.71	Lumai14	E1
	QFsn-1D	1D	Xgdm126	3.05	0.21	5.70	Jing411	E3
	QFsn-3D	3D	Xgwm183	2.69	0.24	3.30	Jing411	E1
	QFsn-7B	7B	Xwmc517	7.27	0.30	9.50	Jing411	E1
			Xwmc517	2.73	0.18	4.25	Jing411	E2
			Xwmc517	3.35	0.23	4.09	Jing411	E6
GNS	*QGns-5B*	5B	Xgwm371	3.65	-0.90	3.95	Lumai14	E6
	QGsn-6A	6A	Xgwm334	3.23	-1.37	2.75	Lumai14	E6
GWP	*QGwp-1A*	1A	Xwmc24	3.67	0.71	6.03	Jing411	E3
	QGwp-1B	1B	Xbarc187	3.01	1.43	3.59	Jing411	E5
	QGwp-1D-1	1D	Xwmc429	8.83	0.40	8.78	Jing411	E6
	QGwp-1D-2	1D	Xgdm126	4.16	0.20	3.94	Jing411	E6
	QGwp-5A	5A	Xgwm205	3.49	0.64	5.88	Jing411	E3
	QGwp-7A	7A	Xgwm60	3.19	0.31	4.95	Jing411	E1
TGW	*QTgw-3A*	3A	Xwmc11	2.88	0.87	3.92	Jing411	E5
	QTgw-3B	3B	Xwmc754	3.82	1.17	5.28	Jing411	E5
	QTgw-4B	4B	Xwmc657	3.53	1.71	4.74	Jing411	E4
	QTgw-6A	6A	Xgwm334	2.63	2.04	4.84	Jing411	E6
	QTgw-6D	6D	Xbarc96	4.82	1.21	6.92	Jing411	E5
	QTgw-7B-1	7B	Xwmc76	2.52	-1.33	3.56	Lumai14	E1
	QTgw-7B-2	7B	Xwmc517	3.87	1.45	6.01	Jing411	E3

[1]: HD: heading date; PH: plant height; FIL: first internode length; LPSB: length from flag leaf pulvinus to spike base; NT: number of valid tillers; SL: spike length; FSN: fertile spikelet number per main spike; GNS: grain number per main spike; GWP: grain weight per plant; TGW: thousand grain weight
[2]: QTL, quantitative trait loci
[3]: LOD, logarithm of the odds
[4]: Add, additive effect, positive and negative values indicate that phenotypic variation are contributed by Jing411 and Lumai14, respectively
[5]: PVE, phenotypic variation explained
[6]: E1: 2013-2014 drought stress (DS); E2: 2013-2014 well-watered (WW); E3: 2014-2015 DS; E4: 2014-2015 WW; E5: 2015-2016 DS; E6: 2016-2017 DS

detected in the present study was located in the middle of the above interval, suggesting that it may be the same QTL. In the current study, *QSl-1D-1*, with the positive allele being from donor Jing411, was mapped near the marker Xgwm337 of the 1D chromosome; it explained 3.56% of the phenotypic variation. Deng *et al.* (2017) found that *Qfw1D1-1* was located in the flanking marker Xcfd183-Xgwm337 in E1, E2 and E3, accounting for the explained

phenotype variation ranging from 23.38 to 24.60%. It may be pleiotropic or tightly linked QTL. On the other hand, in the present study, *QSl-1D-2*, explained 4.29–11.29% of the phenotypic variation, was mapped repeatedly in E1, E3, E4 and E6. It was distributed in the vicinity of marker Xbarc62 on 1D chromosome. And the *QSl-1D-2* from donor parent Jing411 increased SL. But it has not reported by other researches, so it may be a novel QTL controlling SL. It may be used in improvement of SL as superior gene in future wheat molecular breeding.

Two or more QTLs were detected in the vicinity of a marker or flanking marker on the same chromosome, indicating that the chromosome region is a QTL hot-spot region. Many previous researches reported that the distribution of QTLs for different traits of wheat presented compartmentalization, forming the QTL cluster (Groos *et al.*, 2003; Quarrie *et al.*, 2005), the QTL of regionalization tended to show close linkage or multiple effects (Huang *et al.*, 2006; Ma *et al.*, 2007). The existence of QTL-rich regions in wheat genome was observed in the current study. For example, *QFil-7A*, *QLpsb-7A-2*, *QNt-7A* and *QSl-7A* were identified at the near of Xwmc809 on chromosome 7A. The *QFil-4A* and *QLpsb-4A-1* detected in E3 and E4 were also distributed on the 4A- Xwmc707 vicinity.

In particular, these QTLs were contributed by the donor parent Jing411, Moreover, their phenotypic values of FIL and LPSB performed significant correlation in all 6 environments, suggesting that there may be pleiotropic or tightly linked QTL responsible for both traits. It is interesting that *QHd-4D* and *QPh-4D* linked to 4D-Xwmc331 in the current study was also associated with biological yield QTL *QBy-4D*, grain yield *QGy-4D* and straw yield *QSy-4D* detected by Li *et al.* (2014), showing that the chromosomal region carried a large number of target genes.

Conclusion

In the present study, a genetic map was constructed using an ILs population. A total of 46 additive QTLs and 10 QTL clusters were identified. Among them, *QHd-7D*, *QLpsb-4A-1*, *QSl-1D-2* and *QFsn-7B* observed were identified in 2, 2, 2, 4 and 3 environments, respectively. We found that QTLs for SL, NT, FSN and GWP were co-located in the same genomic region. The QTL *QFil-4A* and QTL *QLpsb-4A* distributed on chromosome 4A were simultaneously mapped, and the phenotypes between the two traits showed significantly positive correlation. These QTLs may be pleiotropi QTL or closely-linked gene, which can be used in pyramiding breeding. Moreover, we found two potential near-isogenic lines (IL 30 and IL 86) of FIL and LBSP for further fine mapping.

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