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Article

Genetic Dissection of QTL Associated with Grain Yield in Diverse Environments

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Abstract: Wheat (*Triticum aestivum* L.) breeding programs strive to increase grain yield; however, the progress is hampered due to its quantitative inheritance, low heritability, and confounding environmental effects. In the present study, a winter wheat population of 159 recombinant inbred lines (RILs) was evaluated in six trials under rainfed, terminal drought, and fully-irrigated conditions, over four years. Quantitative trait locus/loci (QTL) mapping was conducted for grain yield main effect (GY) and the genotype × environment interaction (GEI) effect. A total of 17 QTL were associated with GY and 13 QTL associated with GEI, and nine QTL were mapped in the flanking chromosomal regions for both GY and GEI. One major QTL *Q.Gy.ui-1B.2*, explaining up to 22% of grain yield, was identified in all six trials. Besides the additive effect of QTL associated with GY, interactions among QTL (QTL × QTL interaction), QTL × environment, and QTL × QTL × environment were also observed. When combining the interaction effects, QTL *Q.Gy.ui-1B.2* along with other QTL

explained up to 52% of the variation in grain yield over the six trials. This study suggests that QTL mapping of complex traits such as grain yield should include interaction effects of QTL and environments in marker-assisted selection.

Keywords: *Triticum aestivum*; QTL × QTL interaction; grain yield; genotype × environment interaction

1. Introduction

Wheat is one of the most important crops, and breeding for improved grain yield has been a major objective in wheat breeding programs throughout the world. Progress on genetic improvement of grain yield using phenotypic evaluation has been hampered because it is under quantitative genetic control, has a low heritability, and is confounded by environmental effects [1–5]. Quantitative trait locus/loci (QTL) analysis has been proved to be an effective approach for identifying chromosomal regions conferring quantitative traits and estimating the relative effects of each region [6]; however, the genetic and physiological complexity of grain yield makes it difficult to identify major QTL that are consistently associated with improved grain yield under a variety of environmental conditions and in different mapping populations.

Exploring genotype × environment interaction (GEI) is another important aspect for studying adaptability of genotypes with high yielding potential. Plants could change their phenotypic expression to adapt to different environments (also called phenotypic plasticity), and the GEI was caused by response differences of genotypes to environmental change [7]. Several studies have been conducted to measure and understand the nature of GEI [8–12]. However, most of them mainly focused on effects of environmental covariates rather than the genetic attributes of GEI. More recently, Gauch *et al.* [10] proposed a new strategy, analyzing the GEI using additive main effects and multiplicative interaction (AMMI) model. In this method, the GEI matrix was compressed into several interaction principal components (IPCs), which were then used as genetic traits in QTL analysis to represent the differences of genotypes in responding to the environmental changes. Therefore, QTL that are responsible for GEI could be detected. Besides the IPCs from the AMMI model, environmental sensitivity score (standardized differences in trait values measured in different environments) has also been used in QTL mapping to understand the GEI [7].

In addition to GEI, the interaction effects of QTL × QTL, QTL × environment and QTL × QTL × environment play important roles in gene network regulation and plant adaptability [13]. Studies of the QTL × QTL interaction (QQI, or QTL epistasis) and QTL × environment interaction (QEI) have been conducted in several crops, including rice (*Oryza sativa* L.) [14,15], corn (*Zea mays ssp. mays* L.) [16,17], cotton (*Gossypium hirsutum* L.) [18], and the model plant *Arabidopsis thaliana* [7,19]. These studies showed that QQI and QEI effects were common for some complex traits and needed to be examined to better understand the genetic control of these traits.

In wheat, QQI studies have been conducted for coleoptile length [20], plant height [21,22], *Fusarium* head blight resistance [23–25], end-use quality [26,27], grain protein content [28], pre-harvest sprouting [29,30], water-soluble carbohydrates [31], and yield and yield components [32,33].

Particularly, Kumar *et al.* [32] and Wu *et al.* [33] demonstrated that analyzing QQI and QQEI would be helpful for improving GY through marker-assisted selection (MAS) because the estimation of the main-effect QTL might be biased if QQI and QEI were not examined.

The present study used spatially adjusted phenotypic data and advanced statistical method (AMMI) to identify QTL associated with the grain yield main effect and GEI effect, and also studied the QQI, QEI, and QQEI of grain yield.

2. Materials and Methods

2.1. Plant Materials

A population of 159 $F_{8:10}$ recombinant inbred lines (RILs) were used in this study. The population was derived from the cross between Rio Blanco (PI 531244) and IDO444 (PI 578278) [34]. Rio Blanco is a hard white winter wheat cultivar with high yielding and good quality released by Agripro Biosciences, Inc. Mission, KS [35]. It carries the dwarf allele *Rht-B1b* at *Rht-B1* locus and the tall allele *Rht-D1a* at *Rht-D1* locus, and has been widely used as a parent in hard white winter wheat breeding programs [36–38]. IDO444, developed by University of Idaho, Aberdeen, ID, is a tall hard red winter wheat germplasm that carries tall alleles at both *Rht-B1* and *Rht-D1* loci. IDO444 was released as germplasm based on its disease resistance and improved grain yield under rainfed production conditions in the Pacific Northwest [39].

2.2. Trial Conditions and Trait Evaluations

The mapping population was planted in six location-year environments (six trials) in southeastern Idaho, including Aberdeen (42.96° N, 112.83° W, elevation 1342 m) in harvesting years 2006 (06AB) and 2010 (10AB), Arbon Valley (42.89° N, 112.61° W, elevation 1525 m) in harvesting year 2007 (07AR), Rockland (42.57° N, 112.88° W, elevation 1417 m) in harvesting years 2007 (07RK) and 2011 (11RK), and Blackfoot (43.19° N, 112.35° W, elevation 1371 m) in harvesting year 2010 (10BF). Fertilizer was applied based on a soil test before sowing (data not shown). Herbicides and fungicides were applied to control weeds and diseases when necessary (data not shown). The trial 06AB was an irrigated trial. The trials 10AB and 10BF were terminal drought (TD) environments where water stress was applied when all plots completed anthesis. The trials 07RK, 07AR, and 11RK were three non-irrigated trials (rainfed) and only received rainfall during the growing season. Total rainfall (estimated) in growing seasons (1 September to 31 July) in trials 06AB, 07AR, 07RK, 10AB, 10BF, and 11RK were 334, 296, 255, 183, 273, and 430 mm, respectively. Total rainfall (estimated) from 1 March to 31 July in 06AB, 07AR, 07RK, 10AB, 10BF and 11RK were 150, 132, 118, 101, 167, and 225 mm, respectively (data from National Climate Data Center [40]). Overhead irrigation system was used in 06AB and 10AB trials, whereas wheel irrigation system was used in 10BF. The estimated irrigation water was 376, 208, and 508 mm for 06AB, 10AB, and 10BF, respectively.

In each trial, parents and RILs were planted in a randomized complete block design with two replicates. Seeding rate was 2.0 million kernels per hectare for trials in 07RK, 07AR, and 11RK; while 2.5 million kernels per hectare in 06AB, 10AB, and 10BF. Plots in trials 07AR, 07RK and 11RK

were 3-m long and 1.5-m wide with four rows; plots in trial 06AB were 1.5-m long and 1.5-m wide with 7 rows; and plots in trials 10AB and 10BF were 3-m long and 1.5-m wide with 7 rows.

In all six trials, plots were harvested using a Wintersteiger Classic small plot combine (Wintersteiger Inc., Salt lake City, UT, USA) equipped with a Harvest Master weighing system (Juniper Systems, Inc., Logan, UT, USA). Grain yield (GY, ton/hectare) was determined from the grain weight of each plot at 12% moisture. Heading date (HD, day) was recorded as days from 1 January to the date when 50% of the spikes were fully visible above the flag leaf collar in a plot. Plant height (HT, cm) was determined after maturity as the height of the stem to the tip of the spike excluding awns.

2.3. Statistical Analysis

Broad sense heritability (h_B^2) and the adjusted means (Best Linear Unbiased Estimates, BLUEs) were calculated from a spatial model in the computer program ASReml-R [41,42]. For trials 06AB, 07AR and 07RK, only replicates were used to adjust the spatial variation due to the incomplete data in the row and column directions; while for trials 10AB, 10BF and 11RK, replicate, row and column were used to adjust the spatial variation. Best spatial model were selected based on the log-likelihood value. RILs were first fitted as random effect to estimate h_B^2 according to the equation:

$$h_B^2 = \sigma_g^2/(\sigma_g^2 + \sigma_e^2/r) \quad (1)$$

where σ_g^2 is the genetic variance, σ_e^2 is the error variance and r represents the number of replications. RILs were then used as fixed effect to obtain the BLUEs for use in Pearson's correlation and QTL analyses.

Analysis of variance (ANOVA) was estimated to test the effect of genotype × environment interaction (GEI) for each trait. In order to account for the heterogeneous variance of the environments, the inverse of the variance of individual environments were used as weights in the ANOVA model. The AMMI method [9] was conducted to obtain the first two interaction principal components of the GEI effect (IPC1 and IPC2) across six environments. The standard deviation of BLUEs of GY (GYsd) was calculated across six environments to represent the environmental sensitivity of genotypes.

2.4. QTL Analysis

The whole genome linkage map developed based on this RIL population was previously obtained, and the map included 739 markers with the average density of 6.7 cM per marker [34]. The 159 RILs and the two parents were later genotyped with the Illumina Infinium 9K SNP iSelect platform [43] in the USDA-ARS genotyping lab at Fargo, North Dakota. A total of 999 SNPs showed polymorphisms between the two parents. Markers with high segregation distortion (χ^2 test at $\alpha = 0.01$) were removed for both the SNPs and the markers used in previous maps. The maps were constructed using software MSTmap [44] and Mapmaker/EXP 3.0b [45]. The SNP names in the map were "IWA" (Illumina wheat Design A) plus the index number of the SNP, such as "IWA7179". The full SNP names and indexes can be accessed from Cavanagh *et al.* [43]. The marker groups and the marker order in each group were determined in MSTmap, and the marker orders were checked in Mapmaker 3.0b using the "ripple" function. Map distances were calculated using Kosambi function in Mapmaker and given in centi-Morgan (cM).

BLUEs of RILs of each trait in individual environments and the GEI related traits (the IPCs and GYsd) were used separately in QTL analysis in Windows QTL Cartographer 2.5 [46]. Composite interval mapping (CIM) method was applied to identity the potential QTL associated with the traits investigated. Model 6 was used with 5 control markers, 10 cM window, and forward and backward regression method (probability for into and out 0.05). A QTL with LOD score ≥2.5 ($\alpha = 0.05$) was declared as a significant QTL in order to detect potential QTL across different environments. Genomic regions of the corresponding QTL were determined with the 1-LOD support interval method [47].

For QTL closely located and associated with the same trait, stepwise multiple regression using the peak marker of each QTL was conducted, and the QTL that were not significant in the model were excluded. If QTL identified for the same trait but coming from different environments had overlapped confidence interval, they are supposed to be the same QTL and given the same name. QTL × environment interaction (QEI), QTL × QTL interaction (QQI, QTL epistasis) and QTL × QTL × environment interaction (QQEI) were tested by ANOVA method using the peak markers of the QTL associated with GY, IPCs and GYsd in R [42]. Accumulative effect of GY QTL without and with the QQI were tested by stepwise multiple regression in R [42], and the coefficient of determination (R^2) from the stepwise multiple regression model was the total amount of phenotypic variation explained by all the QTL left in the model.

3. Results

3.1. Phenotypic Analysis of GY, HD, and HT

The broad sense heritability and the BLUEs of GY, HD, and HT of the two parents and RILs in six trials are summarized in Table 1. GY of IDO444 was significantly greater than that of Rio Blanco in four of the six trials, which comprised of three RF and one TD trials. Grain yield of Rio Blanco was significantly greater than that of IDO444 in one irrigated trial 06AB and one terminal drought trial 10BF. The broad sense heritability of GY was greater than 0.50 in all trials except for in 07RK. Distributions of GY in the RIL population exhibited continuous variation in all trials (Figure 1), and the significant transgressive segregation was also observed in both lower and higher yield (Table 1 and Figure 1).

Field conditions greatly affected GY and HT as expected, but had almost no effects on HD (Table 1). Mean GY of the RILs in irrigated trial 06AB was much higher than that in RF and TD trials, almost twice as much of GY in TD trials (10AB and 10BF), and four times as much of GY in RF trials (07RK, 07AR, and 11RK).

Compared to HD and HT, GY had relatively low broad sense heritability in the six trials (Table 1). All three traits had the lowest heritability in 07RK. Traits GY and HD showed lower heritability in rainfed condition than the other conditions. Under terminal drought condition, HD and HT still had very high heritability, but GY showed lower heritability. Of all six trials, GY10AB had the lowest heritability among grain yield, and heritability of HT in environment 07RK was the lowest among all the traits (only 0.08), indicating a strong environment effect in 07RK.

Table 1. The broad sense heritability (h_B^2) and mean BLUE values of grain yield (GY, ton/hectare), heading date (HD, day), and plant height (HT, cm) of the two parents and the 159 recombination inbred lines in six trials.

Trait	Env [a]	Parent [b]			RILs [c]				h_B^2
		ID	RB	Diff	Mean	Std. Dev.	Min.	Max.	
GY	06AB	8.88	9.18	−0.30	8.46	0.80	6.24	10.28	0.63
	07AR	2.39	2.08	0.32	2.30	0.29	1.36	2.93	0.53
	07RK	2.10	1.30	0.80	1.51	0.33	0.67	2.17	0.33
	10AB	6.48	6.08	0.40	6.45	0.69	4.46	8.01	0.55
	10BF	5.02	5.45	−0.43	4.96	0.51	3.74	6.27	0.52
	11RK	1.91	0.59	1.32	1.39	0.31	0.65	2.29	0.57
HD	06AB	160	152	8	157	2.46	152	164	0.70
	07AR	167	161	6	164	1.71	159	170	0.78
	07RK	159	160	NS	160	1.02	158	163	0.40
	10AB	169	163	6	168	2.66	163	174	0.78
	10BF	174	164	10	171	1.98	166	176	0.77
	11RK	181	175	6	176	2.56	171	183	0.59
HT	06AB	103.1	74.4	28.7	84.6	8.15	68.6	105	0.81
	07AR	80.5	57.4	23.1	69.2	7.20	52.1	86.4	0.79
	07RK	59.9	51.8	8.1	53.6	4.65	43.2	67.3	0.08
	10AB	104.0	81.2	22.8	98.8	6.53	83.8	121.6	0.47
	10BF	109.2	86.4	22.8	97.1	8.53	76.2	121.9	0.83
	11RK	64.4	43.8	20.6	54.7	5.77	42.2	67.6	0.62

Env: environment; h_B^2: broad sense heritability; [a] 06AB was an irrigated trial, 10AB and 10BF were terminal-drought trials, and 07RK, 07AR, and 11RK were rainfed trials; [b] ID: IDO444; RB: Rio Blanco; Diff: difference between IDO444 and Rio Blanco (IDO444–Rio Blanco): NS means not significant at α = 0.05, numbers mean significant at α = 0.05; [c] Std. Dev.: standard deviation.

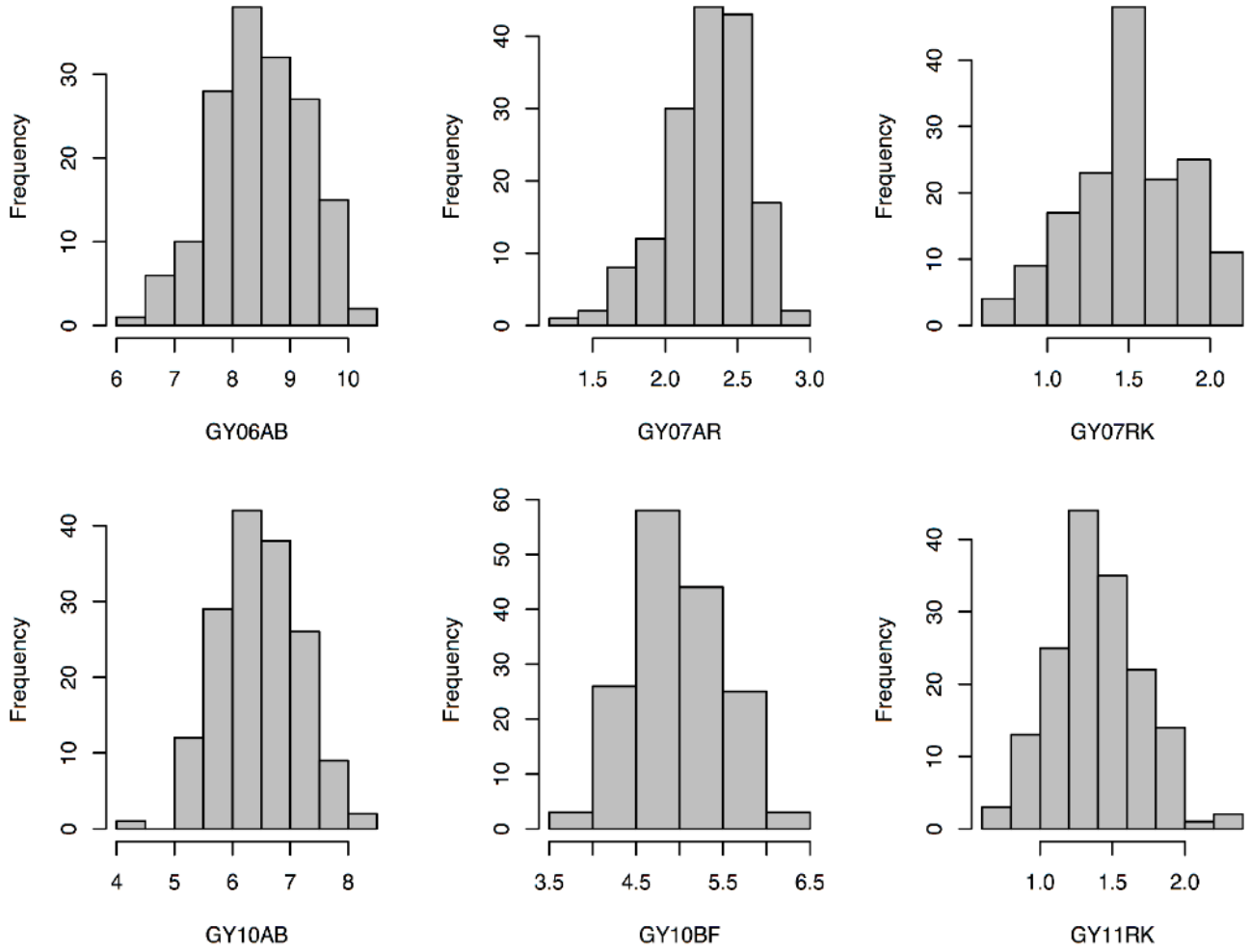
Correlation between grain yield, HD, and HT were analyzed for individual environments and summarized in Table 2. Correlation coefficients (*r*) were low in general and there was no significant correlation between grain yield with HD and HT in irrigated trial 06AB. The *r* between grain yield and HT was higher than that between grain yield and HD in two rainfed and one terminal drought trial. HD showed consistently negative correlation with grain yield in 4 out of 6 trials; whereas HT showed positive correlation with grain yield under the three rainfed conditions and negative correlation with grain yield in the terminal drought trial 10AB.

Table 2. Phenotypic correlations between grain yield (GY), heading date (HD), and plant height (HT) in the 159 RILs over six environments.

Trait	GY					
	06AB	07AR	07RK	10AB	10BF	11RK
HD	NS	−0.18 *	−0.21 **	−0.28 **	−0.19 *	NS
HT	NS	0.37 **	0.34 **	−0.38 **	NS	0.30 **

NS: not significant; * significant at α = 0.05, ** significant at α = 0.01.

Figure 1. Histograms of grain yield in six environments.



3.2. Enrichment of the Previous Genetic Maps

By adding 413 SNPs to the previous map derived from this population, the average interval between two markers was reduced from 6.7 to 3.4 cM, which excluded markers with high segregation distortion (χ^2 test at $\alpha = 0.01$). The map used in the QTL analysis included 413 SNPs, 342 DArTs, 106 SSRs, and 1 sequence-tagged-site (STS) marker from the semi-dwarf gene *Rht-B1*, representing all the 21 chromosomes except 1D and 5D.

3.3. QTL Associated with the Grain Yield

A total of 17 QTL located on 14 chromosomal regions (1A-1, 1B-1, 2B-1, 2B-2, 2D, 3B-1, 3B-2, 4B, 5A-1, 5B-2, 6B-2, 7A-4, 7A-5, and 7B-1) were associated with grain yield derived from the six individual trials (Figure 2 and Table 3). The QTL *Q.Gy.ui-1B.2* on chromosomal region1B-1 was associated with grain yield and significant across all six trials and explained 6%–22% of the yield variation. IDO444 contributed the high yielding allele for this QTL. The remaining 16 QTL each explained 6%–16% of the variation of grain yield but mostly were significant in only one trial. Besides *Q.Gy.ui-1B.2* that was detected in all trials, two QTL (*Q.Gy.ui-2B.2* and *Q.Gy.ui-3B.1*) were identified in trial 06AB, two (*Q.Gy.ui-5A.1* and *Q.Gy.ui-5B.1*) in 07RK, three (*Q.Gy.ui-2B.1, Q.Gy.ui-2D* and

Q.Gy.ui-7B) in 07AR, four (*Q.Gy.ui-1A, Q.Gy.ui-4B, Q.Gy.ui-6B* and *Q.Gy.ui-7A.2*) in 10AB, four (*Q.Gy.ui-3B.2, Q.Gy.ui-5B.2, Q.Gy.ui-6B* and *Q.Gy.ui-7A.1*) in 10BF, and one (*Q.Gy.ui-1B.1*) in 11RK. QTL *Q.Gy.ui-1B.1 and Q.Gy.ui-1B.2* on chromosome segment 1B-1 were 8.5 cM apart, and each explained 22% of grain yield in 11RK trial. Additional four QTL, *Q.Gy.ui-1A*, *Q.Gy.ui-3B.1*, *Q.Gy.ui-4B*, and *Q.Gy.ui-7B*, explained 11%, 12%, 16%, and 11% of grain yield variation in 10AB, 06AB, 10AB and 07AR, respectively.

Figure 2. Distribution of QTL for grain yield (GY), heading date (HD), plant height (HT) and three traits related to genotype × environment interactions (IPC1, IPC2 and GYsd).

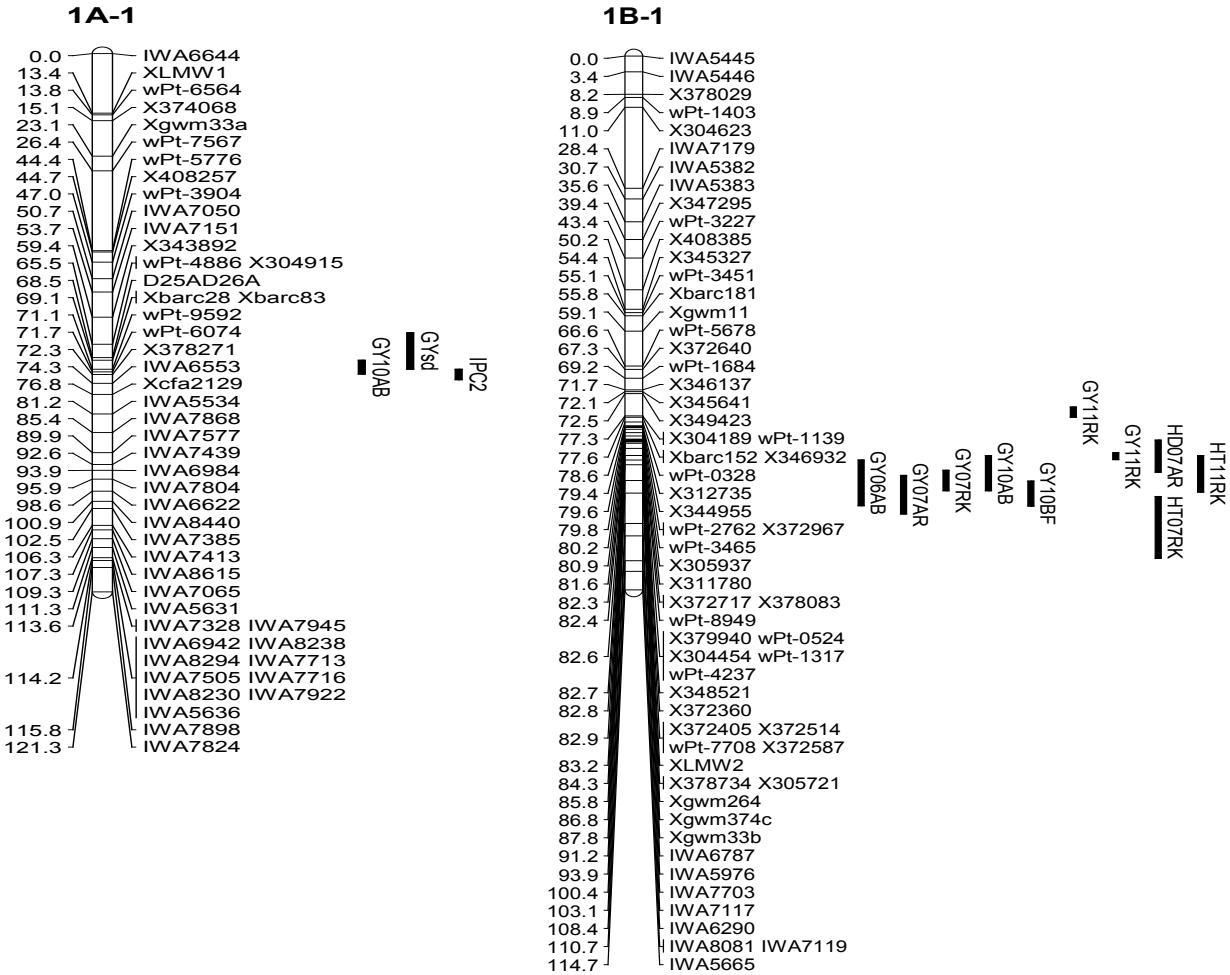


Figure 2. *Cont.*

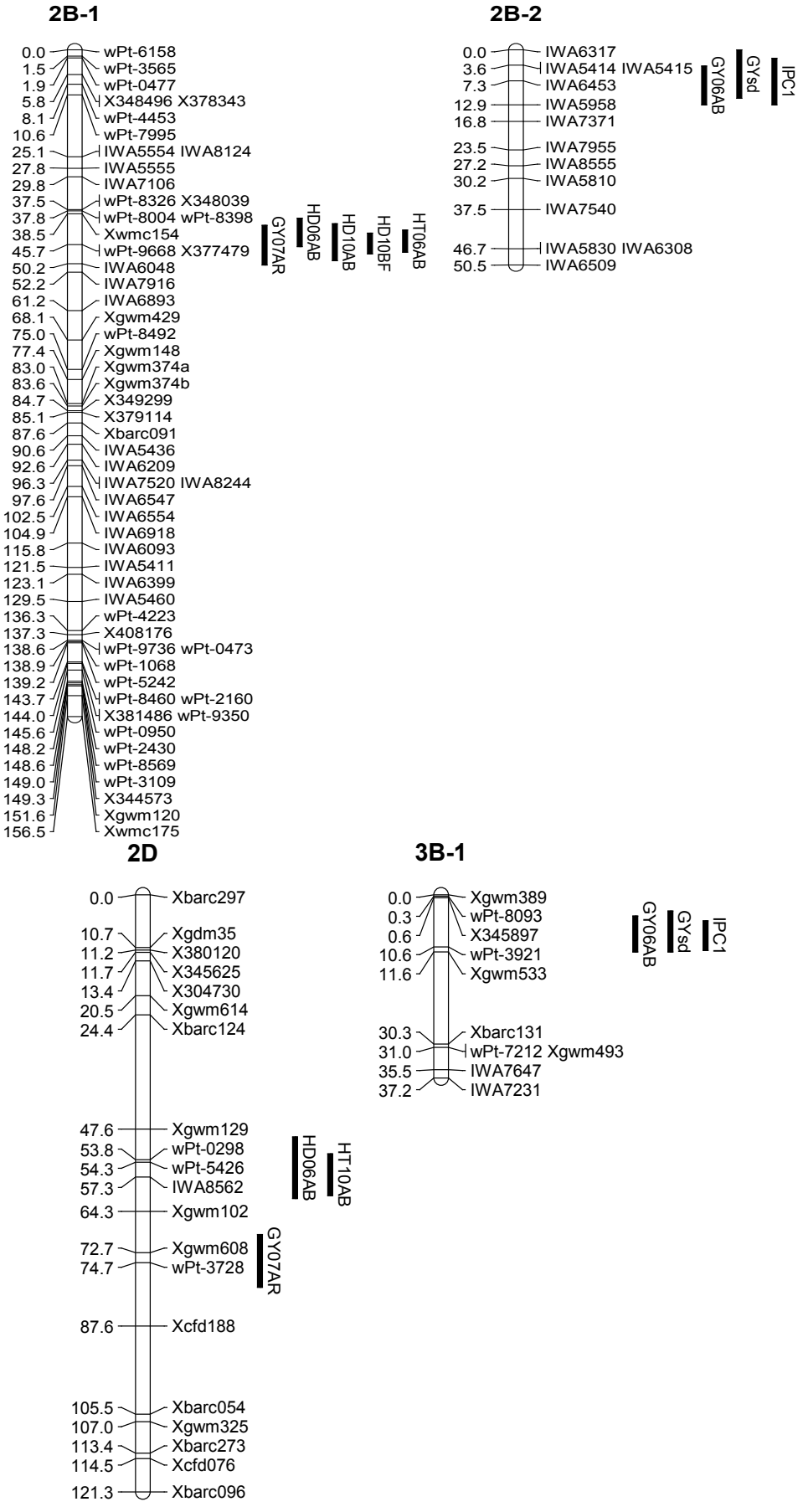


Figure 2. *Cont.*

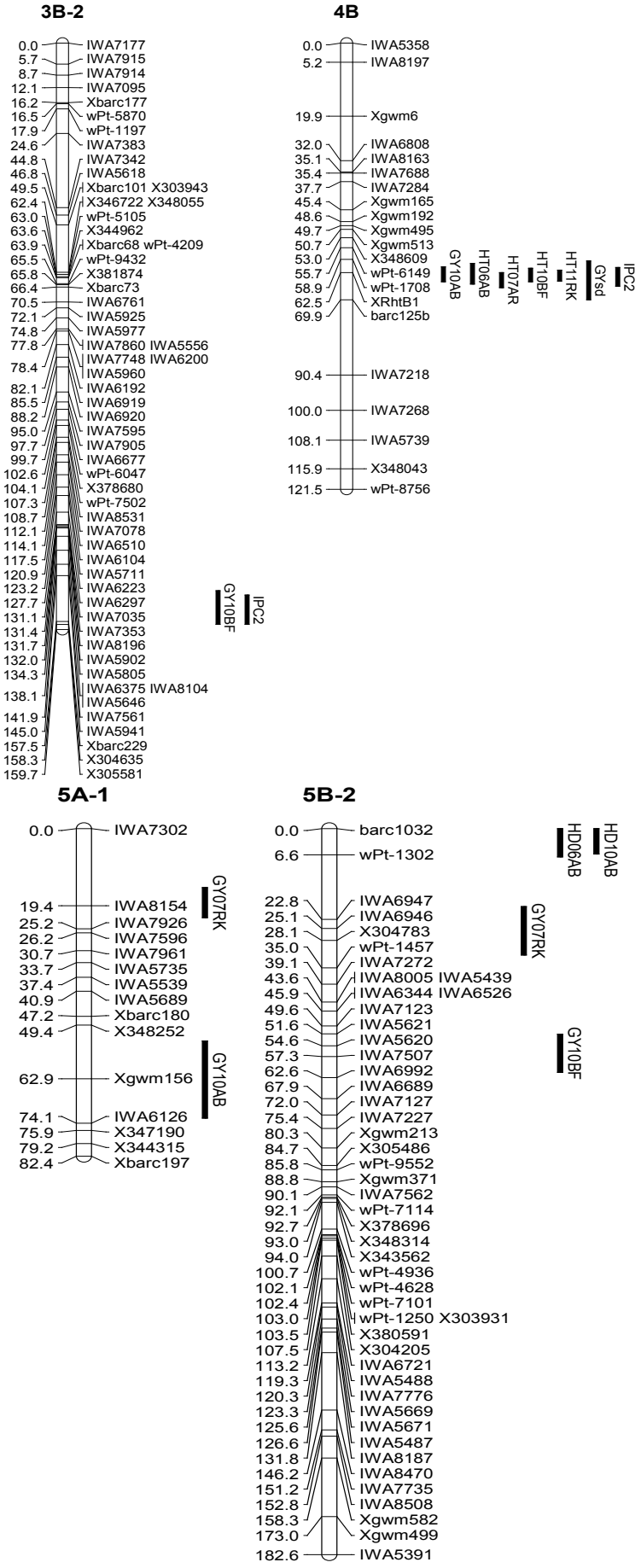


Figure 2. *Cont.*

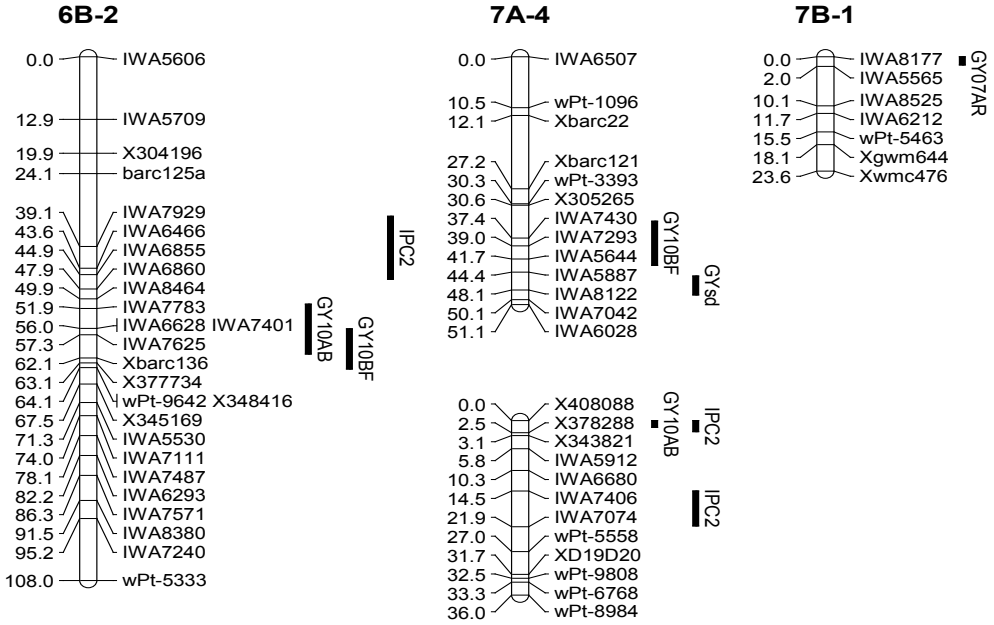


Table 3. QTL of grain yield identified in Rio Blanco/IDO444 population in six environments.

QTL	Env.	Chr.	Position	Peak Marker	LOD	Add [a]	R^2 (%)
Q.Gy.ui-1A	10AB	1A-1	71.71	X115497	6.1	0.23	11
Q.Gy.ui-1B.1	11RK	1B-1	77.31	X304189	9.5	0.14	22
Q.Gy.ui-1B.2	11RK	1B-1	85.81	Xgwm264	9.6	0.15	22
	07RK	1B-1	91.21	IWA6787	3.7	0.10	8
	06AB	1B-1	92.21	IWA6787	4.8	0.25	9
	10AB	1B-1	92.21	IWA6787	3.2	0.17	6
	10BF	1B-1	93.21	IWA5976	3.4	0.14	7
	07AR	1B-1	93.91	IWA5976	4.3	0.09	9
Q.Gy.ui-2B.1	07AR	2B-1	45.71	X116276	3.9	0.08	8
Q.Gy.ui-2B.2	06AB	2B-2	8.31	IWA6453	4.0	−0.23	8
Q.Gy.ui-2D	07AR	2D	74.71	X119684	2.9	0.07	6
Q.Gy.ui-3B.1	06AB	3B-1	10.61	X116345	6.1	0.28	12
Q.Gy.ui-3B.2	10BF	3B-2	156.01	Xbarc229	3.4	−0.15	8
Q.Gy.ui-4B	10AB	4B	62.51	XRhtB1	8.3	−0.27	16
Q.Gy.ui-5A.1	07RK	5A-1	19.41	IWA8154	3.5	0.13	8
Q.Gy.ui-5A.2	10AB	5A-1	65.91	Xgwm156	2.8	0.16	6
Q.Gy.ui-5B.1	07RK	5B-2	25.11	IWA6946	2.8	−0.08	6
Q.Gy.ui-5B.2	10BF	5B-2	54.61	IWA5620	4.2	−0.15	8
Q.Gy.ui-6B	10AB	6B-2	57.01	IWA7625	2.9	0.15	5
	10BF	6B-2	60.31	Xbarc136	2.6	0.12	5
Q.Gy.ui-7A.1	10BF	7A-4	37.41	IWA7430	3.6	−0.14	7
Q.Gy.ui-7A.2	10AB	7A-5	0.01	X408088	4.3	−0.20	8
Q.Gy.ui-7B	07AR	7B-1	0.01	IWA8177	5.3	−0.10	11

Env.: environment; Chr.: chromosome; LOD: logarithm of the odds ratio; Add: additive effect; R^2: the phenotypic variation explained by a QTL; [a] Positive values alleles from IDO444 increased the value of the trait, negative values alleles from Rio Blanco increased the value of the trait.

3.4. QTL Related to Genotype × Environment Interaction

QTL associated with GEI (or phenotypic plasticity) is summarized in Table 4. By using data of IPC1, IPC2, and GYsd, 13 QTL were identified (two for IPC1, six for IPC2, and five for GYsd) to be associated with GEI. Nine of the 13 QTL were located in the flanking regions of the QTL associated with GY. QTL on chromosome segments 1A-1, 2B-2, 3B-1 and 4B were associated with two of the three GEI traits. QTL on 3B-1 explained 15% and 12% of variation of IPC1 and GYsd, respectively. QTL on 4B flanking *Rht-B1* explained 17% and 8% of variation of IPC2 and GYsd, respectively. QTL on 1A-1 and 2B-2 had smaller effect than that of on 3B-1 and 4B.

Table 4. QTL identified for genotype × environment interaction of grain yield.

Trait [a]	QTL	Chr.	Position	Peak Marker	LOD	Add	R^2 (%)
IPC1	*Q.Gypc1.ui-2B*	2B-2	8.31	IWA6453	3.6	−0.19	8
	Q.Gypc1.ui-3B	3B-1	10.61	X116345	6.2	0.26	15
IPC2	*Q.Gypc2.ui-1A*	1A-1	71.71	X115497	5.2	−0.19	9
	Q.Gypc2.ui-3B	3B-2	157.51	Xbarc229	2.9	0.14	5
	Q.Gypc2.ui-4B	4B	62.51	XRhtB1	9.2	0.26	17
	Q.Gypc2.ui-6B	6B-2	39.11	IWA7929	3.0	−0.14	5
	Q.Gypc2.ui-7A.1	7A-5	0.01	X408088	3.0	0.15	5
	Q.Gypc2.ui-7A.2	7A-5	20.51	IWA7074	3.2	0.16	6
GYsd	*Q.Gysd.ui-1A*	1A-1	68.51	D25AD26A	2.9	0.07	6
	Q.Gysd.ui-2B	2B-2	3.61	IWA5414	3.5	−0.07	7
	Q.Gysd.ui-3B	3B-1	7.61	X116345	4.8	0.10	12
	Q.Gysd.ui-4B	4B	64.51	XRhtB1	3.5	−0.08	8
	Q.Gysd.ui-7A	7A-4	48.11	IWA8122	2.9	−0.07	6

Chr.: chromosome; LOD: logarithm of the odds ratio; Add: additive effect; R^2: the phenotypic variation explained by a QTL; [a] GYsd: standard deviation of grain yield from 6 environments; IPC1: the first interaction principal component of genotype × environment effect; IPC2: the second interaction principal component of genotype × environment effect.

3.5. QTL × QTL Interaction

QTL × QTL interaction (QQI) analysis was performed on five QTL (*Q.Gy.ui-1A*, *Q.Gy.ui-1B.2*, *Q.Gy.ui-3B.1*, *Q.Gy.ui-4B* and *Q.Gy.ui-7B*) that showed relatively larger effects on grain yield (Table 5). Among the five QTL, *Q.Gy.ui-1A* had significant interaction with all the other four QTL except *Q.Gy.ui-7B*, and *Q.Gy.ui-4B* had significant interaction with both *Q.Gy.ui-1B.2* and *Q.Gy.ui-3B.1*. The total phenotypic variation explained by the QQI ranged from 5% to 31% (Table 5). Some QQI were significant in several environments. For example, *Q.Gy.ui-3B.1* and *Q.Gysd.ui-1A* had significant interaction effect in 07AR, 10AB and 10BF. Some QQI were significant in the environments where both QTL were identified, such as *Q.Gy.ui-4B* × *Q.Gy.ui-7A.2*; some QQI were significant in the environments where only one of the two QTL was identified, such as *Q.Gy.ui-4B* × *Q.Gy.ui-7A.2*, and some QQI were significant in the environments where neither QTL was identified, such as *Q.Gy.ui-4B* × *Q.Gy.ui-1A*.

Table 5. QTL × QTL interactions detected in the six trials among *Q.Gy.ui-1A*, *Q.Gy.ui-1B.2*, *Q.Gy.ui-3B.1*, *Q.Gy.ui-4B* and *Q.Gy.ui-7B*, and with other QTL associated with grain yield.

Q1	Q2	Environment	Interaction Effect [a]	R^2 (%)
Q.Gy.ui-1A	*Q.Gy.ui-1B.2*	10AB	0.46	17
	Q.Gy.ui-3B.1	10AB, 10BF	0.5	12
	Q.Gysd.ui-3B.1	10BF, 11RK	0.45	8
	Q.Gy.ui-3B.2	11RK	−0.21	5
	Q.Gy.ui-4B	07RK	−0.32	9
Q.Gy.ui-1B.2	*Q.Gy.ui-2B.1*	07RK	−0.34	17
	Q.Gy.ui-4B	07RK	−0.2	11
	Q.Gy.ui-5A.1	07AR	0.19	8
	Q.Gy.ui-6B	10BF	0.32	14
	Q.Gy.ui-7A.2	06AB	−0.52	12
Q.Gy.ui-3B.1	*Q.Gysd.ui-1A*	07AR, 10AB, 10BF	0.18	6
	Q.Gy.ui-2D	07AR	−0.19	10
	Q.Gy.ui-4B	10BF	−0.38	9
Q.Gy.ui-4B	*Q.Gysd.ui-1A*	07RK, 11RK	−0.29	8
	Q.Gy.ui-7A.1	10AB	−0.42	22
	Q.Gy.ui-7A.2	10AB	−0.74	31
Q.Gy.ui-7B	*Q.Gy.ui-2B.2*	10AB	0.49	5
	Q.Gy.ui-2D	06AB	−0.59	6

[a] Interaction effects were estimated as A + D − B − C, where A and D represent the means of genotypes same as the two parents, and B and C represent means of recombination genotypes.

3.6. QTL × Environment Interaction

Of the 30 QTL associated with GY main effect and GEI effect (Tables 3 and 4), 18 QTL (12 peak markers) showed significant QEI effect (Table 6). Eight of the 12 peak markers were identified for the GEI effects (GYsd, IPC1 or IPC2). The QTL *Q.Gy.ui-1B.2*, which was identified in all six trials, also showed significant QEI effect.

Table 6. QTL showing significant QTL × environment interaction effect for grain yield.

Marker	Chr.	Position	QTL	Trait	R^2 (%)
D25AD26A	1A-1	68.51	*Q.Gysd.ui-1A*	GYsd	6
X115497	1A-1	71.71	*Q.Gy.ui-1A*	GY10AB	11
X304189	1B-1	77.31	*Q.Gy.ui-1B.1*	GY11RK	22
Xgwm264	1B-1	85.81	*Q.Gy.ui-1B.2*	GY11RK	22
IWA5976	1B-1	93.91	*Q.Gy.ui-1B.2*	GY07AR, GY10BF	7–24
IWA5414	2B-2	3.61	*Q.Gysd.ui-2B*	GYsd	4–7
IWA6453	2B-2	8.31	*Q.Gy.ui-2B.2, Q.Gypc1.ui-2B*	GY06AB, IPC1	8
X116345	3B-1	7.61	*Q.Gysd.ui-3B, Q.Gy.ui-3B.1, Q.Gypc1.ui-3B*	GYsd, GY06AB, IPC1	6–12
Xbarc229	3B-2	156.01	*Q.Gy.ui-3B.2, Q.Gypc2.ui-3B*	GY10BF, IPC2	4–8
XRhtB1	4B	64.51	*Q.Gysd.ui-4B, Q.Gy.ui-4B, Q.Gypc2.ui-4B*	GYsd, GY10AB, IPC2	5–17
IWA8122	7A-4	48.11	*Q.Gysd.ui-7A*	GYsd	6
X408088	7A-5	0.01	*Q.Gy.ui-7A.2, Q.Gypc2.ui-7A.1*	GY10AB, IPC2	4–8

Chr.: chromosome; Marker: peak markers of each QTL; Trait: traits for which the QTL were identified.

3.7. QTL × QTL × Environment Interaction of Grain Yield

A total of nine pairs of QTL showed significant QQEI (Table 7). These QTL pairs mostly showed QQI in trials 06AB and 10AB. The two peak markers of QTL *Q.Gy.ui-7A.2* also showed significant QQI and QQEI effect. The two QTL *Q.Gy.ui-7B* and *Q.Gy.ui-3B.1* did not show significant QQI in any trials but showed significant QQEI effect.

Table 7. QTL pairs that showed significant QTL × QTL × environment interactions.

Marker-1	Marker-2	Identified in [a]	QTL-1	QTL-2
IWA6787	X408088	AB06	*Q.Gy.ui-1B.2*	Q.Gy.ui-7A.2
IWA6453	IWA8154	AB06	*Q.Gy.ui-2B.2*	Q.Gy.ui-5A.1
IWA6453	IWA8122	AB06	*Q.Gy.ui-2B.2*	Q.Gysd.ui-7A
IWA5620	IWA5887	AB06	*Q.Gy.ui-5B.2*	Q.Gy.ui-7A.1
IWA5887	IWA6453	AB06	*Q.Gy.ui-7A.1*	Q.Gy.ui-2B.2
IWA7430	IWA7625	AB10	*Q.Gy.ui-7A.1*	Q.Gy.ui-6B
IWA5887	IWA7430	AB10	*Q.Gy.ui-7A.1*	Q.Gy.ui-7A.1
X408088	XRhtB1	AB10	*Q.Gy.ui-7A.2*	Q.Gy.ui-4B
IWA8177	X116345	NA	*Q.Gy.ui-7B*	Q.Gy.ui-3B.1

Marker-1 and Marker-2 were the peak markers of QTL-1 and QTL-2, respectively; [a] Environments where the interaction between the two QTL (QQI) were identified.

3.8. The Pyramiding Effect of QTL for Grain Yield in the Six Environments

An accumulative effect of all QTL in each environment was estimated by a step-wise multiple regression (Table 8). The additive effect of all QTL explained 31%, 24%, 18%, 49%, 36%, and 21% in 06AB, 07AR, 07RK, 10AB, 10BF and 11RK, respectively. When the QQI effect was considered, the explained phenotypic variation was 39%, 24%, 21%, 52%, 41%, and 24%, respectively (Table 9). QQI effect was not significant in the pyramiding for GY07AR.

Table 8. Total phenotypic variation (R^2) explained by all the QTL for grain yield in each trial.

Trait	QTL	R^2 (%)
GY06AB	*Q.Gy.ui-1B.2, Q.Gy.ui-2B.2, Q.Gy.ui-3B.1*	31
GY07AR	*Q.Gy.ui-1B.2, Q.Gy.ui-2B.1, Q.Gy.ui-2D, Q.Gy.ui-7B*	24
GY07RK	*Q.Gy.ui-1B.2, Q.Gy.ui-5A.1, Q.Gy.ui-5B.1*	18
GY10AB	*Q.Gy.ui-1A, Q.Gy.ui-1B.2, Q.Gy.ui-4B, Q.Gy.ui-5A.2, Q.Gy.ui-6B, Q.Gy.ui-7A.2*	49
GY10BF	*Q.Gy.ui-1B.2, Q.Gy.ui-3B.2, Q.Gy.ui-5B.2, Q.Gy.ui-6B, Q.Gy.ui-7A.1*	36
GY11RK	*Q.Gy.ui-1B.1*	21

Table 9. Total phenotypic variation (R^2) of grain yield explained by QTL main effect and interaction effect.

Trait	QTL [a]	R^2 (%)
GY06AB	*Q.Gy.ui-1B.2, Q.Gy.ui-3B.1, Q.Gy.ui-1B.1/Q.Gy.ui-7A.2, Q.Gy.ui-2B.2/Q.Gy.ui-5A.1*	39
GY07AR	*Q.Gy.ui-1B.2, Q.Gy.ui-2B.1, Q.Gy.ui-2D, Q.Gy.ui-7B*	24
GY07RK	*Q.Gy.ui-5B.1, Q.Gy.ui-1B.2/Q.Gy.ui-2B.1*	21
GY10AB	*Q.Gy.ui-1A, Q.Gy.ui-1B.2, Q.Gy.ui-5A.2, Q.Gy.ui-6B, Q.Gy.ui-4B/Q.Gy.ui-7A.2*	52
GY10BF	*Q.Gy.ui-5B.2, Q.Gy.ui-7A.1, Q.Gy.ui-1B.2/Q.Gy.ui-6B, Q.Gy.ui-3B.2/Q.Gy.ui-7A.2*	41
GY11RK	*Q.Gy.ui-2D, Q.Gy.ui-1B.1/Q.Gy.ui-3B.2*	24

[a] QTL-1/QTL-2 means the interaction effect of QTL-1 and QTL-2 including their additive effects.

4. Discussion

Improvement of grain yield is an essential target in all wheat breeding programs. Genetic dissection of QTL associated with grain yield would help us gain a better understanding of the genetic mechanisms controlling grain yield and provide insight into developing improved breeding schemes using molecular marker assisted selection. Numerous studies have targeted identification of more additive QTL associated with grain yield; however, few studies have analyzed the non-additive QTL effect [13] contributing to grain yield variation. The present study not only focused on identifying major additive QTL but also elucidated several non-additive interaction effects contributing to grain yield, with an attempt to develop a breeding scheme or a genetic architecture to improve grain yield using MAS.

4.1. Major QTL Associated to Grain Yield

Out of 17 QTL associated with the main effect of grain yield, five QTL (*Q.Gy.ui-1A*, Q.*Gy.ui-1B.2*, *Q.Gy.ui-3B.1*, *Q.Gy.ui-4B*, and *Q.Gy.ui-7B)* explained over 10% of phenotypic variation (Table 3). Especially, the QTL *Q.Gy.ui-1B.2* was identified in all six trials and explained 22% of the phenotypic variation of gain yield in 11RK, one rain-fed trial. The interaction of this QTL with *Q.Gy.ui-1A, Q.Gy.ui-2B.1, Q.Gy.ui-4B, Q.Gy.ui-5A.1, Q.Gy.ui-6B and Q.Gy.ui-7A.2* explained 8% to 17% of grain yield variation over five of the six trials (Table 5). This QTL was located in the flanking region of the QTL associated with HT in 07RK and 11RK, two rain-fed trials, and with HD in 07AR, another rain-fed trial (Figure 2). QTL for grain yield on chromosome 1B have been reported in several studies [3,48–52], but the positions of the reported QTL were different from that of *Q.Gy.ui-1B.2* identified in the present study, so *Q.Gy.ui-1B.2* is most likely to be a novel QTL for grain yield.

The QTL *Q.Gy.ui-1A* explained 11% of grain yield only in the terminal drought trial 10AB, but it had significant interaction effect with three other major QTL (*Q.Gy.ui-1B.2*, *Q.Gy.ui-3B.1*, and *Q.Gy.ui-4B*) in one terminal drought trial 10BF and two rainfed trials 07RK and 11RK (Table 5). In addition, this QTL was co-located with two GEI QTL (GYsd and IPC2), so it might be related to plant responses to environmental changes. This QTL was close to marker *Xbarc83*, where QTL associated with spike number per plant, spikelet number per spike, and thousand-grain weight were identified [53].

The QTL *Q.Gy.ui-3B.1* explained 12% of grain yield only in the irrigated trial 06AB; however, its interaction with *Q.Gy.ui-1A*, *Q.Gy.ui-2D*, *Q.Gy.ui-4B* and *Q.Gysd.ui-1A* explained 6%–12% of grain yield in trials other than 06AB (Table 5). *Q.Gy.ui-1A* and *Q.Gysd.ui-1A* were co-located, and their

interactions with *Q.Gy.ui-3B.1* showed in both terminal drought trials (10AB and 10BF). The QTL *Q.Gy.ui-3B.1* was located in the flanking region of a major QTL associated with yield in durum wheat (*Triticum durum* Desf.) [3]. This QTL was also co-located with two QTL associated with GEI (*Q.Gysd.ui-3B* and *Q.Gyipc1.ui-3B*), it might be related to the adaptation to different environments.

The QTL *Q.Gy.ui-4B* explained 16% of the phenotypic variation of grain yield only in the terminal drought trial 10AB; however, its interaction with *Q.Gy.ui-7A.2* and *Q.Gy.ui-3B.1* explained 31 and 10% of the phenotypic variation of grain yield in the two terminal drought trials 10AB and 10BF, respectively. This QTL with peak marker *XRhtB1* was located in the position of the semi-dwarf gene *Rht-B1*, and had high yield allele from Rio Blanco (*Rht-B1b*). One GEI QTL, *Q.Gysd.ui-4B*, also had peak marker *XRhtB1*, so it is possible that both *Q.Gy.ui-4B* and *Q.Gysd.ui-4B* were the pleiotropic effect of *Rht-B1*gene, but this needs to be validated with additional experiments.

Currently, QTL associated with grain yield have been mapped on all 21 chromosomes of bread wheat [1–5,32,48–50,52,54–61], but common QTL are still rare. Some of the QTL identified in the present study confirm the previously reported ones. The QTL *Q.Gy.ui-2B.1* identified in GY07AR was co-located with a HD QTL (possibly related to *Ppd-B1* gene) and might be the same QTL reported by McCartney *et al.* [4]; and the QTL *Q.Gy.ui-4B* that was detected at the locus *Rht-B1* was also detected by Cuthbert *et al.* [1].

4.2. QTL × Environment Interactions

In the present study, 12 peak markers (19 QTL) responsible for GY or GEI showed significant QEI (Table 6). Shen *et al.* [18] defined three types of QEI: (1) QTL identified in all environments showed QEI, such as the *Q.Gy.ui-1B.2*; (2) QTL identified only in parts of the environments showed QEI, such as the *Q.Gy.ui-2B.2* from 06AB; and (3) QTL not identified in any individual environments showed QEI, such as *Q.Gysd.ui-7A*. Here, the second type QEI was the most common, and it also supports why QTL for the same trait usually are identified only in specific environments. In practice, if MAS was performed on QTL that have QEI effect, the selected plant thus could be more likely to adapt to different environments. However, due to QEI effect either changes in magnitude or changes in the direction of additive effects, it might be more practical to use QEI that only showed changes in magnitude of effect and will not have opposite effect in different environments.

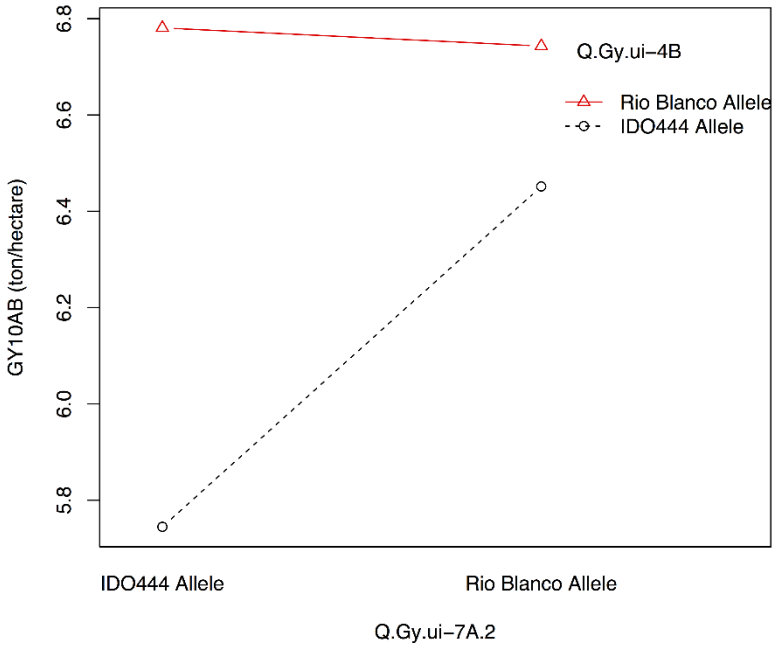
4.3. QTL × QTL Interactions

The present study identified several QQI in individual environments, but no common QQI were found in all the environments (less than 4 environments), indicating that interactions between QTL were also affected by environments.

Different types of QQI were identified in the present study. Based on the marker combination effect, both synergistic (parental genotype combination favored) and antagonistic epistasis (recombination favored) were identified (Table 5). In addition to this, one special type of interaction was also observed, that is, when marker A was a specific allele (from IDO444 or Rio Blanco), the two alleles of marker B had no difference but had higher grain yield than when marker A was the other allele. For example, both *X408088* (*Q.Gy.ui-7A.2*) and *XRhtB1* (*Q.Gy.ui-4B*) (Figure 3) were significantly associated with GY10AB, but *XRhtB1* had an epistatic effect over *X408088*. When *XRhtB1* was the allele from Rio

Blanco, the two alleles of *X408088* had no difference but still had higher yield than when *XRhtB1* was the allele from IDO444; in this case, selection the allele from Rio Blanco of marker *XRhtB1* is enough although both markers were significant for GY10AB. This could save time and effort in MAS. Not only could the use of that QQI increase the selection efficiency, but also could increase the selection response (Tables 8 and 9). Therefore, for some complex traits like grain yield, the interaction between QTL could be as important as the QTL main effect [15].

Figure 3. Interaction between two QTL for grain yield in 10AB.



4.4. QTL for Genotype × Environment Interactions

Via *et al.* [62] developed two models, allelic sensitivity model and gene regulation model, to explain genotype × environment interaction (GEI). The allelic sensitivity model proposes that GEI was caused by the differential expression of loci in different environments, and the gene regulation model proposes that some specific genes might sense environmental changes and regulate (enhance or suppress) the expression of related genes. However, these two models are not mutually exclusive and might work together to explain the process [7]. In the present study, we used the first two principal components (IPC1, IPC2) of GEI matrix and the standard deviation (GYsd) of GY across six trials as indicators of the response differences of genotypes to environmental changes. A total of 13 QTL were identified for these three traits (IPC1, IPC2 and GYsd), and nine of them were co-located with QTL for the GY main effect in individual environments (Tables 3 and 4, Figure 2), so these nine GEI QTL, which were related to the different responses of genotypes to the environmental changes, might just be a subset of QTL associated with GY. However, it is also possible that some QTL associated with GY were just QTL controlling the response to environmental changes, not for GY *per se*. The first possibility would be consistent with the expectation of the allelic sensitivity model [7]. The four QTL that were not co-located with QTL responsible for GY might only play a role in regulation. Overall, the results here suggest that both the allelic sensitivity model and the gene regulation model could be involved in the GEI, but allelic sensitivity model might have a greater influence on grain yield. As far as we know, no previous studies

on QTL mapping of environmental sensitivity have been conducted, except that Gauch *et al.* [10] introduced the AMMI method in QTL mapping using the pre-harvest spouting study in wheat as an example. Another study on *Arabidopsis* was conducted by Ungerer *et al.* [7], and they also found that most of the environmental sensitivity QTL were co-located with the main effect QTL.

4.5. Pleiotropic QTL

In the present study, the co-location between grain yield and traits associated with GEI (IPC1, IPC2 and GYsd) has already been discussed. Of interest here is the pleiotropic effect of QTL associated with HD and HT. The population used in present study had segregation for the semi-dwarf gene *Rht-B1* (4B), and the photoperiod sensitivity gene *Ppd-B1* (2B) might also be segregating in the population based on the QTL mapping results for heading date. These two genes play major roles in the ability of wheat plants to adapt in different environments, so some QTL associated with HD or HT might have pleiotropic effect with GY or GEI traits. The QTL mapping results confirmed this hypothesis. The pleiotropic effect between QTL of HD and GY happened on chromosome 2B-1 (*Q.Gy.ui-2B*) at the position of the *Ppd-B1* gene. Compared with the potential *Ppd-B1* gene on chromosome 2B, the *Rht-B1* gene on chromosome 4B had a greater effect on grain yield, but mainly for grain yield in terminal drought condition (10AB and 10BF). The *Rht-B1* region not only had pleiotropic effect on GY from 10AB to 10BF, but also on GEI traits GYsd and IPC2, so this locus might play an important role on regulating plant response to environmental changes.

5. Conclusions

The present study was an attempt to dissect the genetic basis of wheat grain yield and genotype × environment interactions using QTL mapping method. One major QTL on chromosome 1B was identified in all of the six trials, and explained up to 22% of grain yield variation. Most of the QTL for GEI were co-located with QTL for grain yield main effect. Interaction effects (QQI, QEI, QQEI) were common in the present study, suggesting that future QTL mapping and marker-assisted selection of complex traits like grain yield should include QQI and QEI.

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Author Contributions

Junli Zhang implemented the field trials, and did data analysis, genetic map construction, and primary writing of the manuscript. Jianli Chen is the project leader and corresponding author who oversaw all activities related to the project implementation and manuscript development. Chenggen Chu is a collaborator who contributed to genetic map construction and manuscript development. Weidong Zhao and Justin Wheeler provided technical assistance in field trials and genotyping of the mapping population. Edward J. Souza originally developed the mapping population and contributed to manuscript

development. Robert S. Zemetra is a collaborator who contributed to field trials and manuscript development.

Conflicts of Interest

The authors declare no conflict of interest.

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