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ORIGINAL PAPER

Conditional QTL mapping for plant height with respect to the length of the spike and internode in two mapping populations of wheat

Fa Cui · Jun Li · Anming Ding · Chunhua Zhao · Lin Wang · Xiuqin Wang · Sishen Li · Yinguang Bao · Xingfeng Li · Deshun Feng · Lingrang Kong · Honggang Wang

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Abstract Plant height (PH) in wheat is a complex trait; its components include spike length (SL) and internode lengths. To precisely analyze the factors affecting PH, two $F_{8:9}$ recombinant inbred line (RIL) populations comprising 485 and 229 lines were generated. Crosses were performed between Weimai 8 and Jimai 20 (WJ) and between Weimai 8 and Yannong 19 (WY). Possible genetic relationships between PH and PH components (PHC) were evaluated at the quantitative trait locus (QTL) level. PH and PHC (including SL and internode lengths from the first to the fourth counted from the top, abbreviated as FIITL, SITL, TITL, and FOITL, respectively) were measured in four environments. Individual and the pooled values from four trials were used in the present analysis. A QTL for PH was mapped using data on PH and on PH conditioned by PHC using IciMapping V2.2. All 21 chromosomes in wheat were shown to harbor factors affecting PH in two populations, by both conditional and unconditional QTL mapping methods. At least 11 pairwise congruent QTL were identified in the two populations. In total, ten unconditional QTL and five conditional QTL that could be detected in the conditional analysis only have been verified in no less than three trials in WJ and WY. In addition, three QTL on the short arms of chromosomes 4B, 4D, and 7B were mapped to positions similar to those of the semi-dwarfing genes *Rht-B1*, *Rht-D1* and *Rht13*, respectively. Conditional QTL mapping analysis in WJ and WY proved that, at the QTL level, SL contributed the least to PH, followed by FIITL; TITL had the strongest influence on PH, followed by SITL and FOITL. The results above indicated that the conditional QTL mapping method can be used to evaluate possible genetic relationships between PH and PHC, and it can efficiently and precisely reveal counteracting QTL, which will enhance the understanding of the genetic basis of PH in wheat. The combination of two related populations with a large/moderate population size made the results authentic and accurate.

Abbreviations

PH	Plant height
PHC	Plant height components
SL	Spike length
FIITL	The first internode length from the top
SITL	The second internode length from the top
TITL	The third internode length from the top
FOITL	The fourth internode length from the top
WJ	Recombinant inbred line population derived from the cross between Weimai 8 and Jimai 20
WY	Recombinant inbred line population derived from the cross between Weimai 8 and Yannong 19

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F. Cui, J. Li, A. Ding, and C. Zhao contributed equally to this work.

F. Cui · J. Li · A. Ding · C. Zhao · S. Li · Y. Bao · X. Li · D. Feng · L. Kong · H. Wang (✉)
State Key Laboratory of Crop Biology, Shandong Key Laboratory of Crop Biology, Taian Subcenter of National Wheat Improvement Center, College of Agronomy, Shandong Agricultural University, Taian 271018, China
e-mail: hgwang@sdau.edu.cn

F. Cui
e-mail: sdaucf@126.com

L. Wang
Municipal Academy of Agricultural Sciences, Jining 272031, Shandong, China

X. Wang
Municipal Academy of Agricultural Sciences, Zaozhuang 277100, Shandong, China

Introduction

Plant height is an important agronomic trait for morphogenesis and grain yield formation in wheat. An appropriate plant height is a prerequisite for attaining the desired yield in wheat breeding programs. The introduction of dwarfing traits into plants has achieved tremendous increases in wheat yields during the 'Green Revolution' (Peter 2003). Therefore, it is essential to elucidate the genetic basis of plant height to further increase yield.

Classical genetic studies indicated that plant height in bread wheat was a complex trait controlled by both Mendelian genes and quantitative genes, and almost all 21 chromosomes harbored factors affecting it (Law et al. 1973; Snape et al. 1977). Most dwarfing genes have now been well characterized, and closely linked molecular markers have been developed for marker-assisted selection in wheat breeding programs (Ellis et al. 2005; Zhang et al. 2008). Among the dwarfing genes, *Rht-B1* and *Rht-D1*, which have been successfully utilized in wheat breeding programs worldwide, are located on the short arms of chromosomes 4B and 4D, respectively (Börner et al. 2002; Cadalen et al. 1998; Huang et al. 2003). They both originated from natural mutations and confer gibberellic acid (GA) insensitivity. *Rht13* on chromosome 7BS has been verified to produce a marked reduction in height and gibberellin sensitivity (Ellis et al. 2005).

With the rapid development of molecular marker technology in wheat, increasing numbers of QTL studies have been conducted in an attempt to dissect the genetic basis of plant height. Most of these studies have focused on the final plant height without considering its developmental behavior or the influence of its component traits (Kato et al. 1999; Keller et al. 1999; Börner et al. 2002; Huang et al. 2003; Sourdille et al. 2003; Huang et al. 2004; Liu et al. 2005; McCartney et al. 2005; Huang et al. 2006; Marza et al. 2006; Klahr et al. 2007; Zhang et al. 2008; Chu et al. 2008; Wang et al. 2009; Mao et al. 2010). By considering developmental behavior, Wang et al. (2010) and Wu et al. (2010) have documented dynamic QTL for plant height in wheat after Zhu (1995) introduced the new methodology for conditional genetic analysis to identify QTL expressed at certain stages of the life cycle. More recently, a method for multivariable conditional analysis was proposed for analyzing the contributions of component traits to a complex trait and for investigating the genetic relationship between two traits at the QTL level (Wen and Zhu 2005). To our knowledge, few reports of QTL analysis based on this methodology have been reported (Guo et al. 2005; Zhao et al. 2006; Liu et al. 2008a). However, none of them considered plant height and its components in wheat.

Biologically, plant height in wheat equals spike length plus all of its internode lengths above the ground. A desirable plant type is partially determined by combining these components. Previous studies have shown that the internode has a great influence on the lodging resistance of crops. Dunn and Briggs (1989) and Stanca et al. (1979) indicated that cultivars with shorter basal internodes were prone to lodging resistance. Pinthus (1973) showed that longer lower internode length resulted in lodging sensitivity in wheat. A recent report indicated that the third internode position had an effect on the bending stress of the barley stem (Tavakoli et al. 2009). In addition, Kato et al. (1999) showed that QTL for final wheat plant height was not completely consistent with those for culm length and spike length when they partitioned the plant height into these two components. These results indicated that the components at the QTL level had different effects on plant height. To date, no report has documented a QTL analysis of the relationships between plant height and all of its components in wheat. Therefore, characterizing the genetic relationships between plant height and its components at the QTL level will enhance the understanding of molecular mechanisms regulating plant height. This understanding will provide a theoretical basis for breeding programs designed to increase lodging resistance based on selecting desirable cultivars, and in turn attaining the desired yield levels.

Population size has a great effect on the estimation of QTL number and genetic effect (Beavis 1998; Mackay 2001; Schön et al. 2004; Vales et al. 2005; Zou et al. 2005; Buckler et al. 2009). The precision and efficiency of QTL detection will be enhanced by combining more than two related populations (Kumar et al. 2007; Ma et al. 2007; Buckler et al. 2009). For the present study, we performed QTL detection for plant height based on the combination of two related populations, one of which was a large population with up to 485 lines and the other was smaller comprising 229 lines. Both unconditional mapping methods and conditional mapping methods for multivariable conditional analysis were utilized. The objectives of this study were to: (1) accurately identify all the genetic factors affecting plant height, (2) specify the genetic relationships between plant height and its components at the QTL level and (3) discuss the effect of combining two related populations of different size on the efficiency and precision of QTL detection.

Materials and methods

Experimental populations and their evaluation

Two $F_{8:9}$ recombinant inbred line (RIL) populations derived from crosses between three Chinese common wheat varieties, i.e., between Weimai 8 and Jimai 20 (WJ) and between Weimai 8 and Yannong 19 (WY), comprising 485 and 229 lines, respectively, were used in the present study. Weimai 8 is a large-panicle type of the ideotype model and was released by Weifang Municipal Academy of Agricultural Sciences, Shandong, China in 2003; Jimai 20 and Yannong 19, two superior quality wheat varieties, are multi-panicle types, and they were released by Crop Research Institute, Shandong Academy of Agricultural Sciences, China in 2003, and by Yantai Municipal Academy of Agricultural Sciences, Shandong, China in 2001, respectively. They are all semi-dwarfing varieties, but Weimai 8 is slightly taller than the other two varieties, and Jimai 20 is the shortest among the three varieties. In addition, the common parent Weimai 8 is a 1BL/1RS translocation line, whereas the other two parents have the common 1B chromosome. The parents together with the RILs were evaluated in four environments in Shandong province, China; Tai'an in 2008–2009 (E1), and Tai'an in 2009–2010 (E2), Zaozhuang in 2009–2010 (E3) and Jining in 2009–2010 (E4). A two-row plot with rows 2 m long and 30.0 cm apart was used, and 50 seeds were planted in each row. From each plot, five representational leading tillers in the middle row were selected before harvest as samples to measure plant height (PH), the spike length (SL), the first internode length (FIITL) from the top, the second internode length (SITL) from the top, the third internode length (TITL) from the top, and the fourth internode length (FOITL) from the top. PH was measured from ground level to the tip of the spike, excluding awns, SL was measured from the base of the spike to the tip, excluding awns, FIITL was measured from the base of the spike to the first node from the top, SITL was measured from the first node to the second, and so on. All lengths were reported in centimeters. The average of the results from representative samples was used in data analysis.

Analysis of molecular and biochemical markers

Various molecular markers, including G-SSR, EST-SSR, ISSR, STS, SRAP and RAPD, were used to genotype the three parents and their derived lines. Of these, relevant information regarding G-SSR markers, including BARC, CFA, CFD, CFT, GWM, GDM, GPW, WMC and PSP codes, as well as PCR-based STS markers of the MAG code, were taken from the GrainGenes Web site (http://wheat.pw.usda.gov). Relevant information about EST-SSR markers prefixed CFE, KSUM and CNL were publicly available (http://wheat.pw.usda.gov/ITMI/EST-SSR/). EST-SSR markers of SWES and WW codes were developed and kindly provided by Professor Sishen Li, College of Agronomy, Shandong Agricultural University, China. EST-SSR markers with the prefixes CWEM, EDM and CWM were published in reference articles by Peng and Lapitan (2005), Mullan et al. (2005) and Gao et al. (2004), respectively. ISSR markers were developed by the University of British Columbia Biotechnology Laboratory (UBCBL) (Nagaoka and Ogihara 1997). Relevant information about chromosome 1RS-specific markers of rye were detailed by Zhao et al. (2009), and functional markers, were detailed by Liu et al. (2008b) and Liang et al. (2010). The differences of high molecular weight glutenin subunits (HMW-GS) at *Glu-a1*, *Glu-b1* and *Glu-d1* between the parents were detected and used as biochemical markers.

Each PCR reaction for G-SSR, EST-SSR and PCR-based STS markers was conducted in a total volume of 25 μl in a TaKaRa PCR thermal cycler or in a Bio-Rad 9600 thermal cycler, following the proportion described by Röder et al. (1998). Amplifications were performed using a touchdown PCR protocol detailed by Hao et al. (2008). The PCR reaction volume and PCR protocol for SRAP and ISSR markers followed the proportion and procedure detailed by Li et al. (2007b), and for RAPD markers, by Suenaga et al. (2005). The types of high molecular weight glutenin subunits (HMW-GS) were detected by using sodium dodecyl sulphate polyacrylamide gel electrophoresis (SDS-PAGE) (Singh and Shepherd 1991). Markers of BARC, CFA, CFD, GWM, GDM, and WMC codes were screened against the nullisomic–tetrasomic stocks of Chinese Spring (CSNT) to assign them to chromosomes, where possible.

Construction of the genetic linkage map

Linkage groups were constructed by MAPMAKER 3.0 (Lander et al. 1987). First, the "ANCHOR" command was used to locate marker loci on chromosomes based on the CSNT identification and the public genetic maps in GrainGenes 2.0 (http://wheat.pw.usda.gov/GG2/index.shtml). Then, the assignment of the remaining loci to chromosomes was made using the "ASSIGN" command at a LOD score of 3.0. Based on the linkage group defined above, JoinMap, version 3.0 (Biometris, Wageningen, The Netherlands, http://www.joinmap.nl), was used to construct the linkage map, and centimorgan units were calculated using the Kosambi mapping function (Kosambi 1944).

Data analysis and QTL mapping

To estimate variance and covariance components, all six traits were first analyzed with the MINQUE method proposed by Zhu (Zhu 1992). Based on these components, genetic correlation coefficients were estimated between PH and PH components (PHC). Significance levels of the genetic correlation coefficients were derived by a jackknife resampling procedure. Phenotypic correlation coefficients between PH and PHC were calculated from the trait means for the four environments. Basic statistical analysis was implemented by the software SPSS13.0 (SPSS, Chicago, USA). Conditional genetic analysis was conducted based on the phenotypic values of PH conditioned on each of PHC, which were obtained by the method described by Zhu (Zhu 1995). Conditional phenotypic values $y_{(PH|PHC)}$ indicate the value of PH without the influences of PHC.

Both the observed phenotypic values ($y_{(PH)}$) and the conditional phenotypic values ($y_{(PH|PHC)}$) obtained from each environment of E1, E2, E3 and E4, and the pooled data collected from the average of the four environments above (P) were used for QTL mapping analyses. Inclusive composite interval mapping by IciMapping 2.0 was used based on stepwise regression of simultaneous consideration of all marker information (Li et al. 2007a). The walking speed for all QTL was 1.0 cM. A LOD score of 2.5 was set as a threshold for declaring the presence of a QTL.

Table 1 Phenotypic values for PH of three parents and the two RIL populations in four growing environments and its components in wheat

Trait[a]	Environment[b]	Parent			WJ[c]				WY[c]			
		Weimai 8	Jimai 20	Yannong 19	Mean	SD	Min.	Max.	Mean	SD	Min.	Max.
PH (cm)	E1	86.67	73.60	81.87	98.31	9.25	66.43	129.20	94.767	10.36	68.07	122.53
	E2	77.80	69.30	75.20	90.25	8.67	55.44	118.54	87.41	8.87	64.80	113.00
	E3	71.80	62.50	69.30	91.54	7.93	61.60	116.00	89.13	8.97	61.00	119.20
	E4	85.30	73.30	84.50	95.50	8.79	63.83	124.33	96.59	10.48	67.70	143.70
SL (cm)	E1	10.84	9.02	9.34	10.03	1.29	6.98	15.14	9.80	1.21	7.10	13.39
	E2	10.58	9.36	8.60	10.05	1.18	7.10	15.16	9.21	0.97	6.88	12.18
	E3	12.00	10.50	10.02	11.45	1.41	8.10	16.40	10.71	1.26	7.70	14.80
	E4	10.89	9.41	9.55	10.39	0.87	7.91	13.34	9.89	0.80	7.55	14.65
FIITL (cm)	E1	27.70	22.75	27.5	26.21	3.24	12.4	37.13	28.11	3.56	19.67	40.53
	E2	25.42	23.64	25.5	29.52	3.28	21.46	41.14	31.39	3.67	22.10	45.34
	E3	25.70	23.33	25.27	31.00	3.81	20.87	44.67	31.79	3.68	21.97	42.13
	E4	27.70	27.00	26.30	29.07	3.92	8.67	50.67	31.19	3.54	22.00	43.00
SITL (cm)	E1	17.40	13.33	16.33	21.16	2.31	12.45	27.98	20.09	2.85	13.57	27.72
	E2	14.60	13.68	15.10	20.71	2.54	13.96	30.58	20.69	3.15	14.02	27.12
	E3	14.10	12.07	14.40	20.08	2.26	12.93	28.53	19.04	2.80	11.73	25.33
	E4	16.80	15.00	17.00	21.37	2.61	13.67	32.67	20.91	3.40	12.00	30.00
TITL (cm)	E1	12.93	9.67	10.67	16.29	2.12	8.33	21.95	14.40	2.85	7.85	20.70
	E2	11.26	11.46	12.80	15.06	2.16	7.58	20.64	14.22	1.76	8.96	19.44
	E3	10.93	9.83	11.77	15.64	2.08	8.57	21.10	14.44	2.43	8.13	20.70
	E4	15.70	11.00	13.00	16.52	2.68	8.70	21.67	15.41	2.76	8.00	22.17
FOITL (cm)	E1	9.10	8.67	7.33	13.33	2.46	6.22	19.31	10.98	3.03	7.85	20.70
	E2	7.50	6.74	6.74	9.41	1.77	4.32	16.14	9.78	1.57	6.38	14.90
	E3	7.90	6.37	11.77	10.89	2.27	4.50	18.83	10.57	2.06	6.13	16.33
	E4	8.70	6.00	8.70	10.76	1.99	5.17	25.80	10.45	1.95	5.20	18.33

SD standard deviation

[a] *PH* plant height; *SL*, *FIITL*, *SITL*, *TITL* and *FOITL* indicate the five component traits of PH, i.e., spike length, the first internode length counted from the top, the second internode length counted from the top, the third internode length counted from the top and the forth internode length counted from the top, respectively

[b] E1, E2, E3 and E4 represent the environments of 2008–2009 in Taian, 2009–2010 in Taian, 2009–2010 in Zaozhuang and 2009–2010 in Jining, respectively

[c] WJ and WY represent the populations derived from the cross between Weimai 8 and Jimai 20 and between Weimai 8 and Yannong 19, respectively

Results

Phenotypic variation of traits and correlations with plant height

The final PH and PHC for the two RIL populations and the parents in four environments are shown in Table 1. Among the four environments, significant differences of PH existed at the 0.05 level between Weimai 8 and Jimai 20, but did not exist between Weimai 8 and Yannong 19 (data not shown). However, the phenotypic variations among the RIL lines were obvious in both populations. Strong transgressive segregations were observed for PH in all environments, with some lines being taller than the taller parent or shorter than the shorter parent in WJ and WY, respectively, indicating that alleles with positive effects are distributed among the parents. PH segregated continuously and followed a normal distribution in WJ and WY (Fig. 1), indicating that PH was a typical quantitative trait controlled by a few minor genes and that the data were suitable for QTL analysis. The evaluation of the genetic and phenotypic correlations between PH and PHC is listed in Table 2 and shows a highly significant positive correlation with all of PHC except SL in both populations. Higher correlation coefficients were observed between PH and SITL and between PH and TITL in WJ, but were observed between

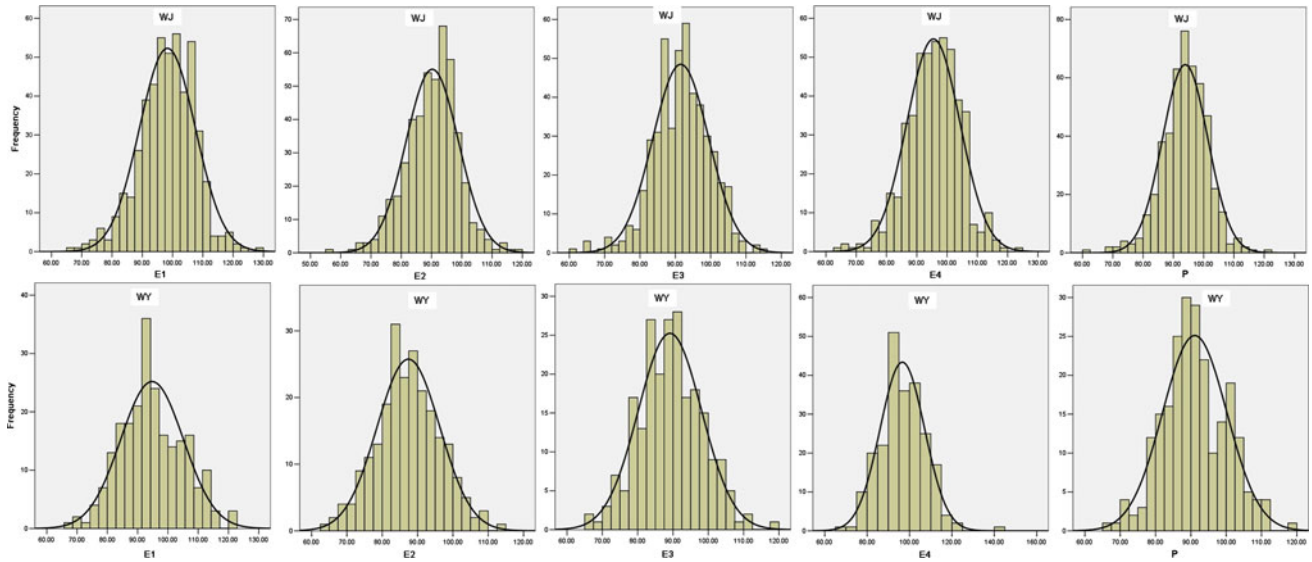

Fig. 1 Phenotypic distribution of wheat plant height in progeny derived from the WJ and WY. The *abscissa* shows the mean values of plant height and the ordinate indicates the frequency of distribution. *Letters* above each graph indicate the corresponding population name. A letter *E* plus a *numeral*, or the letter *P*, below each graph indicates the trial. The WJ population was derived from the cross between Weimai 8 and Jimai 20. The WY population was derived from the cross between Weimai 8 and Yannong 19. *E1* 2008–2009, Tai'an, *E2* 2009–2010, Tai'an, *E3* 2009–2010, Zaozhuang, *E4* 2009–2010, Jining, *P* the average data calculated from the four trials

Table 2 Genetic and phenotypic correlations between plant height and its components and phenotypic and genetic variances of plant height and plant height conditioned on its components

Trait[a]	Correlation		Directed and conditioned variances	
	Genetic	Phenotypic	V_G	V_P
PH	–/–	–/–	49.564/70.151	86.890/111.37
SL	0.041/0.029	0.036/0.023	49.519/70.126	84.709/110.95
FIITL	0.641**/0.697**	0.635**/0.675**	26.672/33.145	58.184/69.596
SITL	0.730**/0.781**	0.730**/0.749**	20.252/24.031	55.017/61.750
TITL	0.737**/0.855**	0.715**/0.824**	19.962/15.493	47.336/52.457
FOITL	0.683**/0.844**	0.683**/0.820**	23.889/16.656	48.827/49.392

For each entry, the first figure refers to WJ and the second to WY

–, No available data

[a] For abbreviations, see Table 1

** Correlation is significant when $p < 0.01$ level

PH and TITL and between PH and FOITL in WY. These findings indicate a strong stable genetic association between PH and TITL. A significant positive correlation between PH and SL was not observed in either WJ or in WY, indicating a weak genetic association between PH and SL. In both WJ and WY, conditioning PH on FIITL, SITL, TITL and FOITL led to a strong reduction of variance, while PH conditioned on the SL showed variances nearly as high as the unconditioned PH (Table 2), confirming the results of genetic and phenotypic correlations between PH and PHC.

Construction of genetic linkage maps

The genetic map constructed based on the WJ population included 344 loci on the wheat chromosomes spanned 2,855.5 cM, with an average density of one marker per 8.30 cM. There were six linkage gaps with linkage distances >50 cM. Marker distribution ranged from 45 on chromosome 4A to 3 on chromosomes 4D and 7D. The WY population was used to establish a genetic map consisting of 358 loci distributed in 27 linkage groups with six linkage gaps, and it covered 3,010.70 cM of the whole genome with an average distance of 8.41 cM between the adjacent loci. The number of markers per chromosome ranged from 40 on chromosome 1B to 3 on chromosome 3D. The two linkage maps contained 69 common loci. The chromosomal locations and the orders of the markers in the two maps were generally in agreement with published reports in GrainGenes 2.0 (http://wheat.pw.usda.gov/GG2/index.shtml). Positions of the loci common to the two maps were approximately in accordance. In addition, a 1BL/1RS translocation event was confirmed by the linkage maps of chromosome 1B in both WJ and WY. Functional markers and biochemical markers were accurately mapped to their corresponding chromosomes. The recommended map distance for genome-wide QTL scanning is an interval length less than 10 cM (Doerge 2002). Thus, the maps were suitable for genome-wide QTL scanning in this study. The two linkage maps will be reported in another paper.

Conditional and unconditional QTL mapping in the WJ population

Up to 53 QTL distributed throughout the wheat genome, except for chromosomes 4B, 5A and 7D, were identified by both unconditional and conditional QTL analysis methods (Table 3). Together, these QTL explained 11.31–43.82% of the phenotypic variation in the individual traits. The major QTL from Weimai 8 with positive additive effects of 3.73 cm accounted for 14.88% of the phenotypic variance in E4. It was detected at a similar position as *Rht-D1* in the linkage group 4D, and it was significant in all environments. Another QTL with a moderate effect of 1.14 cm was detected on chromosome 7B between *Xedm105.2* and *Xgwm344*, a position similar to *Rht13*, but it exhibited significance only in E2 by unconditional analysis.

In total, 25 QTL with additive effects ranging in absolute size from 0.98 to 3.73 cm of the PH were detected by the unconditional QTL mapping method (Table 3). Of these QTL, 15 were detected in only one environment, three in two environments, four in three environments, two in four environments, and one in all five trials. Of these QTL, one was detected on each of the chromosomes 1A, 1D, 2A, 2D, 4D, 6A and 6B, two each on 3B, 4A, 5B and 7B, three each on 2B and 7A and four on 5D.

When PH was conditioned on SL, all of the ten unconditional QTL in E1, 9 of 13 in E2, 4 of 9 in E3, 3 of 3 in E4 and 3 of 11 in P still showed additive effects nearly as great as those detected by the unconditional analysis method (Table 5), indicating a weak genetic association between these two traits. The QTL mapping for PH conditioned on FIITL detected 2 each of the 10, 13, and 9 unconditional QTL in E1, E2 and E3, respectively, and they each showed an additive effect similar to that of its corresponding unconditional QTL. In addition, 3 of 9 unconditional QTL for PH in E3, 2 each of 3 and 11 in E4 and P, respectively, were detected when the influence of FIITL on PH was excluded, with an enhanced or reduced additive effect. QTL analysis of PH, excluding the influence of SITL, detected one QTL each in E1 and E2 with an additive effect equal to that of the corresponding unconditional QTL; when the influence of SITL on PH was excluded, 2, 4, 2, 0 and 1 conditional QTL with reduced or enhanced additive effect were detected in E1, E2, E3, E4 and P, respectively. Ignoring the influence of TITL on PH, conditional mapping identified 2 each out of 10 and 9 unconditional QTL in E1 and E3, respectively, 11 of 13 in E2, 1 of 3 in E4, 3 of 11 in P; however, only one conditional QTL each in E1 and E2, two conditional QTL in P, showed an additive effect similar to those of the unconditional QTL. When PH was conditioned on FOITL, 18 of 46 unconditional QTL (including the overlapping QTL detected in different environments) in five trials could still be identified, including two each in E1 and E4, six in E2, three in E3 and five in P. Among them, one conditional QTL that was detected in E1, five in E2, two in E4 and three in P, showed a lower or higher value for the additive effect compared to the corresponding unconditional QTL.

In addition, conditional QTL mapping analysis revealed numerous additional additive QTL that could not be identified by unconditional QTL mapping methods (Table 5). Among the five PHC, only five extra QTL were detected when PH was conditioned on SL in all five trials; nine additional QTL were detected when PH was conditioned

Table 3 Unconditional and conditional QTL with significant additive effects for plant height in the WJ population

Chrom[a]	Pos[b]	Interval Marker[c]	Add [E/PVE(%)][d]					
			PH	PH|SL	PH|FIITL	PH|SITL	PH|TITL	PH|FOITL
Ch-1A	30	*Xedm80.4-Glu-a1*				−1.20 (E2/3.29)		
Ch-1A	70	*Xwmc333-BE470813*	−1.64 (E3/4.23)	−1.50(E3/3.56)	−1.42 (E3/4.29)	−1.24 (E3/3.51)	−1.01 (E3/2.39)	−1.68 (E3/5.65)
						−0.76 (P/2.21)		
Ch-1B	18	*PrCEN-2-Xwmc134*			−1.31 (E2/.43)			
Ch-1D-2	24	*Xbarc346.1-Xswes226.1*	−2.48 (E3/3.21)	−2.66 (E2/3.40)				
				−2.48 (E3/3.23)				
				−2.20 (P/3.11)				
Ch-2A	39	*Xpsp3088-Xcfa2263*					0.82 (P/2.14)	1.09 (E4/2.52)
								1.06 (P/3.35)
Ch-2A	49	*Xgwm356-Xgwm382.3*	2.18 (E2/4.63)	1.96 (E2/3.85)	1.99 (E1/4.29)		1.32 (E2/3.17)	2.07 (E2/5.65)
			1.78(P/4.33)	1.40(P/2.68)			1.38 (E4/4.72)	1.63 (P/6.72)
Ch-2A	59	*Xbarc1138-Xcfa2043.1*					−0.87 (E4/2.26)	−1.11 (P/3.84)
Ch-2A	166	*Xissr813-Xbarc15*				−1.43 (E2/4.64)	−1.60 (E3/5.77)	
Ch-2B	26	*Xcft3391-Xpsp3065.1*	1.68 (E2/3.66)	1.37 (E2/2.43)	1.41 (E2/3.94)		0.93 (E2/1.74)	1.20 (E2/2.50)
			1.47 (E3/3.34)	1.33 (P/3.07)	1.16 (E3/2.82)		1.25 (E3/3.59)	1.57 (E3/4.96)
			1.39 (P/3.35)		1.01 (P/2.95)			0.94 (P/4.06)
Ch-2B	56	*Xbarc13-IB267*	−1.68 (E3/4.37)		−1.47 (E1/2.94)	−1.46 (E3/4.81)		−1.39(E1/3.02)
					−1.55 (E3/5.03)	−1.06 (P/4.20)		
					−0.94 (P/2.55)			
Ch-2B	63	*Xcfd188-Xwmc764.2*			1.64 (E1/3.42)			
					1.72 (P/5.56)			
Ch-2B	81	*Xpsp3034-Xedm97.1*					−1.33 (E4/5.67)	
Ch-2B	97	*Xcfe230-Xwmc617.1*					1.00 (E4/3.26)	
Ch-2B	154	*Xwmc344.2-Xwmc344.4*	−1.46 (E3/3.13)		−1.35 (E3/3.56)		0.80 (P/2.13)	
					−1.13 (P/3.52)			
Ch-2D-1	37	*STS01-Xwmc181.1*	1.68 (E1/2.66)	1.68 (E1/2.67)	1.78 (E1/3.62)			1.18 (E2/2.01)
			1.84 (E2/3.76)	1.73 (E2/3.33)				1.52 (E3/4.05)
			1.52 (E3/3.05)	1.67 (E3/3.82)				
			1.82 (P/4.95)	1.46 (P/3.18)				
Ch-3A	1	*Xmag896.3-Xbarc1113*			1.60 (E1/3.40)			
Ch-3A	18	*Xmag896.2-Xswes185*			1.26 (E2/2.99)		−0.96 (P/2.65)	
					0.91 (P/2.24)			
Ch-3A	49	*Xmag896.1-ww176*				−1.24 (E3/3.56)	−1.53 (E3/5.49)	

Table 3 continued

Chrom[a]	Pos[b]	Interval Marker[c]	Add [E/PVE(%)][d]					
			PH	PH|SL	PH|FIITL	PH|SITL	PH|TITL	PH|FOITL
Ch-3B	3	*Xcft3374.1-Xcft3374.2*	1.37 (E1/2.13)	1.36 (E1/2.09)				
			1.04 (P/1.85)					
Ch-3B	53	*Xcft53-Xgwm566*	−1.77 (E1/3.18)	−1.67 (E1/3.20)	−1.40 (E2/3.93)	−1.63 (E1/4.04)		
				−1.36 (P/3.26)		−1.36 (E2/4.22)		
Ch-3D	12	*Xbarc52-BE7905.1*			−1.85 (E1/2.94)		−1.62 (E1/2.55)	−0.78 (P/2.00)
Ch-4A	0	*Xapr1.14.1-Xapr1.14.2*				1.01 (E4/2.72)		
Ch-4A	28	*Xapr1.8.1-Xcfe253*	−2.04 (E1/4.88)	−2.04 (E1/4.85)		−1.58 (E1/3.82)	−1.50 (E1/3.56)	
						−0.85 (P/2.73)	−0.87 (P/2.74)	
Ch-4A	97	*Xwmc262-Xapr1.5.3*	−1.78 (E3/5.02)		−1.48 (E3/4.74)	−1.36 (E4/4.22)		
Ch-4A	124	*Xcwm48-Xbarc61*			1.56 (E1/3.25)	1.22 (E4/4.30)	1.46 (E1/3.35)	
					1.55 (E4/2.92)			
Ch-4A	173	*Xwmc524-Xcfe29*					−1.25 (E1/2.42)	
							−0.78 (P/2.22)	
Ch-4A	175	*Xbarc346.2-ww46*					1.16 (E4/4.35)	
Ch-4A	190	*Xbarc346.2-ww46*				2.02 (E1/5.20)		1.25 (P/3.68)
Ch-4D	23	*Xcfd23 –Xswes536*	3.09 (E1/7.62)	3.12 (E1/7.74)	1.84 (E4/5.95)		1.57 (E2/4.03)	2.33 (E4/10.87)
			2.49 (E2/5.49)	2.33 (E2/4.83)			1.49 (E4/6.68)	
			1.69 (E3/3.45)	1.73 (E3/3.23)				
			3.73 (E4/14.88)	3.96 (E4/16.21)				
			2.45 (P/7.81)	2.36 (P/6.64)				
Ch-5B	5	*Xissr853-Xmag467*	1.91 (E2/4.79)	1.93 (E2/4.93)		1.20 (E2/3.33)	1.35 (E2/3.74)	1.60 (E2/4.51)
Ch-5B	146	*Xgwm499-Xissr854.2*	1.87 (P/3.54)					1.62 (P/4.96)
Ch-5B	123	*Xissr821-Xissr880.2*				1.40 (E4/2.95)	1.53 (E1/3.74)	2.05 (E4/5.17)
Ch-5B	194	*Xwmc73-Xgwm335*				−1.63 (E3/5.39)	−1.40 (E2/3.49)	−1.37 (E1/2.57)
						−1.31 (E4/4.43)	−1.25 (E3/3.14)	
						−1.22 (P/4.80)	−1.00 (P/3.16)	
Ch-5D-1	12	*Xmag2999-Xwmc765*				1.41 (E2/4.53)		
Ch-5D-1	60	*Xswes558.5-Xswes558.1*	−1.72 (E2/3.08)			−1.60 (E2/3.47)	−1.20 (E2/2.35)	
						−1.53 (E4/2.91)		
						−1.42(P/3.38)		
Ch-5D-2	26	*Xcfd78-Xcfd189*	1.70 (E2/3.53)	1.62 (E2/3.22)			1.50 (E2/4.32)	
Ch-5D-2	54	*Xcfd18-Xbarc133*	2.28 (P/8.55)		1.54 (P/6.62)			

Table 3 continued

Chrom[a]	Pos[b]	Interval Marker[c]	Add [E/PVE(%)][d]					
			PH	PH|SL	PH|FIITL	PH|SITL	PH|TITL	PH|FOITL
Ch-5D-2	71	*Xbarc133-Xcfe242.1*	2.07 (E1/4.37)	2.08 (E1/4.39)	2.15 (E1/5.82)	1.61 (E4/4.73)		
			1.77 (E2/3.76)	1.66 (E2/3.37)	1.90 (E2/6.92)			
					1.64 (E3/5.43)			
Ch-6A	59	*Xcfe87.2-Xcinau191*		−1.53 (E2/2.57)		−1.45 (E2/4.06)	−1.04 (E2/1.93)	
				−1.56 (P/3.57)				
Ch-6A	146	*Xpsp3152-Xcfe273.2*	−1.58 (E1/2.93)	−1.58 (E1/2.91)			−1.21 (E2/3.03)	
Ch-6B	5	*Xcwm75-Xswes131.1*					−1.28 (E1/2.64)	
Ch-6B	29	*Xswes131.2-Xswes131.4*	−1.62 (E1/3.01)	−1.62 (E1/3.06)				−1.14 (E2/2.31)
Ch-6B	45	*Xcwm90.5-Xmag2053.1*			1.27 (E4/3.06)			
Ch-6B	157	*Xswes180.1-Xswes180.2*					0.88 (P/2.79)	
Ch-6D	39	*Xgwm95-Pr119.1*					−1.99 (E3/2.86)	
Ch-6D	80	*Xapr1.2.3-Xbarc154*					2.53 (E1/2.88)	
							1.81 (E4/2.95)	
							2.49 (P/3.43)	
Ch-7A	4	*Xgwm473-Xedm16.1*	−1.84 (E1/3.74)	−1.86 (E1/3.80)			−1.12 (E2/2.52)	−1.46 (E4/4.88)
			−1.43 (E2/2.59)	−1.92 (E2/4.66)			−1.09(P/4.06)	−1.23 (P/4.82)
			−1.78 (E4/3.87)	−1.98 (E4/4.85)				
			−1.68 (P/4.70)	−1.63 (P/4.39)				
Ch-7A	68	*Xcfe261-ww160.2*	−1.45 (E2/2.71)	−1.29 (E2/2.14)	−1.40 (E4/3.67)		−1.24 (E2/3.07)	−1.24 (E2/2.61)
			−1.85 (E4/4.27)	−1.66 (E4/3.48)				−1.20 (P/4.58)
			−1.70(P/4.86)					
Ch-7A	165	*Xedm16.2-Xcfa2173.1*	2.19 (E1/5.61)	2.19 (E1/5.59)		1.52 (E1/3.55)	2.08 (E1/6.92)	2.00 (E1/6.24)
			1.26 (E2/2.11)	1.32 (E2/2.32)		1.61 (E2/3.12)	1.51 (E2/4.76)	
			0.98 (P/1.70)			1.32 (E4/5.13)	1.06 (P/4.09)	
						1.18 (P/5.25)		
Ch-7B-1	10	*Xedm105.2-Xgwm344*	1.14 (E2/1.71)		0.98 (P/2.86)	1.76 (E2/7.08)	1.40 (E2/4.03)	
Ch-7B-1	69	*Xcfe223-Xissr844.2*				−0.80 (P/2.28)	−1.74 (E2/5.92)	
							−1.42 (E3/4.38)	
							−1.00 (P/3.35)	
Ch-7B-2	15	*Xcnl142-Xpsp3033*		−2.00 (E2/3.98)			−1.02 (E2/2.06)	

Table 3 continued

Chrom[a]	Pos[b]	Interval Marker[c]	Add [E/PVE(%)][d]					
			PH	PHISL	PHIFIITL	PHISITL	PHITITL	PHIFOITL
Ch-7B-2	43	*Xbarc1073-Yp-7B-2*	1.90 (E2/2.82)	2.13 (E2/3.55)		1.19 (E2/1.92)	1.89 (E2/4.40)	2.60 (E2/6.72)
			1.49 (E3/2.01)	1.84 (P/3.54)			1.57 (P/5.26)	
			1.40 (P/2.05)					

[a] Chromosome on which the QTL was detected

[b] Estimation of the QTL position on the corresponding chromosome

[c] Flanking markers of the QTL

[d] Numerals before parentheses are estimates of the additive effect of the QTL. Positive values indicate that Weimai 8 alleles increase the plant height. Negative values indicate that Weimai 8 alleles reduce plant height. E and numerals in parentheses indicate the environment in which the QTL was detected and the percentage of phenotypic variance explained by the additive effects of the mapped QTL, respectively. Of the environments, P indicates that the data were derived from the average of the four environments. For the remaining abbreviations, see Table 1

on FOITL, while up to 31 additional QTL were identified when the influence of TITL was eliminated. Conditional QTL analysis detected 16 and 22 additional QTL when the influence of FIITL and SITL was excluded, respectively. The total numbers of additional QTL above included several overlapping QTL that were reproducibly detected in different environments.

Conditional and unconditional QTL mapping in the WY population

Unconditional and conditional QTL analysis of PH jointly identified 58 QTL distributed on all 21 wheat chromosomes except 3D and 5B in all five trials (Table 4). These QTL explained 2.53–22.43% of the phenotypic variance with the additive effects in absolute size ranging from 1.06 to 7.77 cm. A QTL with the highest additive effect value was detected on chromosome 5D in a very small interval (Fig. 2). It is an allele from Weimai 8 with additive effects of 7.77 cm on height reduction, and it was detected in three of the five trials by unconditional QTL analysis methods. The QTL on 4B between *Xcau8.1* and *Xgwm495*, a position similar to that of *Rht-B1*, was detected by the conditional QTL analysis method.

Unconditional QTL mapping analysis of PH detected a total of 34 putative additive QTL exhibiting from 30.27 to 53.73% of the phenotypic variance in the individual trials, 19 being environment-specific QTL that can be detected in only one environment, 12 and 3 being partly environment-independent QTL detected in two and three environments, respectively. By this method, we were unable to identify any QTL that can be detected in all five trials, suggesting a strong influence of environmental effects on the expression of the PH. Of these QTL, one was found on chromosomes 1B, 2B, 2D, 3B, 6B and 7B, two on 2A, 4A, 4D and 7A, three on 1D, 5D, 6D, 6A and 7D and five on 1A.

Of 13 QTL detected in unconditional mapping in E1, 7, 9, 2, 2 and 3 were still significant when the influence of SL, FIITL, SITL, TITL and FOITL on PH was excluded, albeit 4, 4, 0, 2 and 3 of them exhibited reduced or enhanced additive effects (Table 5). Of the two unconditional QTL detected in E2, the conditional QTL on 7D showed an equal additive effect value to the unconditional QTL when the influence of FOITL on PH was excluded; the same was seen for the QTL detected on 2A when the influence of SL on PH was excluded. The effect was reduced to 1.46 cm when the influence of FIITL on PH was eliminated. The QTL detected on 7D showed an enhanced effect from −2.27 to −3.84 cm when PH was conditioned on the FIITL. Overall, 10, 2, 3, 0, and 1 of the 12 unconditional QTL detected in E3 could still be identified when PH was conditioned on its five component traits: SL, FIITL, SITL, TITL and FOITL, respectively. Of these, three each were

Table 4 Unconditional and conditional QTL with significant additive effects for plant height in the WY population

Chrom	Pos	Interval Marker	Add [E/PVE(%)]					
			PH	PH|SL	PH|FIITL	PH|SITL	PH|TITL	PH|FOITL
Ch-1A	11	*BE470813.2-BE470813.3*	2.86 (E1/7.63)	2.33 (E1/5.09)	3.26 (E1/11.13)			
			2.00 (P/4.89)	1.98 (P/4.77)				
Ch-1A	73	*Xcfe26.3-Xcfe257.2*	4.47 (E1/12.89)	4.60 (E1/13.63)	3.56 (E1/6.93)	2.58 (E3/7.18)	2.06 (E1/5.36)	2.53 (E1/7.56)
			3.36 (E3/7.25)	3.11 (E3/6.27)				2.00 (E4/4.63)
			3.12 (P/8.19)	3.09 (P/8.03)				
Ch-1A	83	*Xcfa2147-Xcwm109.1*	−2.25 (E4/2.57)					−1.76(E4/4.6)
Ch-1A	93	*Xme3em2.8-Xcfe26.1*	−2.38 (E1/5.07)	−2.11 (E1/4.00)		−1.60 (E2/5.89)		
			−1.66 (E3/3.22)	−1.78 (E2/4.09)		−1.28 (P/4.47)		
				−1.67 (P/3.24)				
Ch-1A	137	*Xmag3124-Xcfe242.3*	1.55 (P/2.81)	1.74 (E1/2.76)	1.92 (E1/3.70)			
				1.55 (P/2.84)	1.50 (P/4.84)			
Ch-1B-1	17	*Xwmc719-Glu-b1*		−2.99 (E1/7.32)			−1.48 (E1/4.69)	
Ch-1B-1	25	*Xbarc80-Xwmc367*	2.69 (E1/3.16)	5.23 (E1/11.94)	2.50 (P/7.28)	2.78 (E1/6.58)		
			4.06 (P/9.31)	4.05 (P/9.26)				
Ch-1B-1	54	*Xgwm11-Xbarc61.2*						5.49(E3/5.50)
Ch-1B-2	11	*Xcfe254-Xmag972.1*			−2.70 (E3/8.78)			
Ch-1D	35	*Xcfd48.2-Xcfe78.1*	3.11 (E4/6.13)	2.25 (E1/4.71)	1.82 (E1/2.72)			
				2.37 (E2/7.34)	2.15 (E3/6.14)			
					1.855(P/7.67)			
Ch-1D	62	*Xcfd48-UMN25*	2.14 (P/4.43)	2.11 (P/4.30)				
Ch-1D	79	*Xcwm70.2-Xcfd61*					−3.84 (E2/14.96)	-1.93(E4/4.52)
							−2.69 (P/11.67)	-1.55(P/4.80)
Ch-1D	99	*Xcwm63.1-ww127.1*	3.40 (E4/13.87)	3.13 (E4/11.45)			1.77 (E2/6.67)	2.44(E2/9.17)
			2.16 (P/5.35)	2.19 (P/5.45)			1.58 (P/8.94)	2.58(E4/14.15)
								2.20(P/15.67)
Ch-2A	34	*Xwmc453-Xbarc212*	3.83 (E2/14.69)	2.21 (E1/3.15)	1.46 (E2/3.80)			
			3.24 (P/8.91)	3.85 (E2/15.21)	1.74 (P/4.64)			
				3.29 (P/9.18)				
Ch-2A	50	*Xcfe175.1-Xwmc177*				−1.774 (P/7.42)	−3.07 (E1/22.43)	−2.16 (E1/7.76)
							−1.41 (P/6.41)	
Ch-2A	101	*Xme3em6.1-Xbarc15*				−2.06 (E1/7.50)		
Ch-2A	106	*Xbarc15-Xgwm558*	2.14 (E1/4.11)	2.84 (E1/7.15)	3.38 (E1/6.36)	2.33 (E1/9.49)	1.31 (P/6.44)	1.54 (E4/4.22)
			2.89 (P/9.98)	2.87 (P/9.84)				1.52 (P/7.98)
Ch-2A	169	*Xpsp3029.2-Xwmc181.2*				2.81 (E1/8.44)	1.72 (E1/4.05)	2.11 (E1/5.44)
						2.56 (E2/9.19)	1.78 (E4/8.15)	
						3.36 (P/17.24)		
Ch-2B-1	48	*Xwmc580.2-Xwmc441*	3.35 (E1/5.30)	2.41 (E1/2.76)				
			3.11 (E4/7.88)	2.78 (E4/6.72)				

Table 4 continued

Chrom	Pos	Interval Marker	Add [E/PVE(%)]					
			PH	PH|SL	PH|FIITL	PH|SITL	PH|TITL	PH|FOITL
Ch-2B-1	94	*Xgwm129-Xmag3478*				−1.84 (E3/4.92)	−1.60 (E3/5.51)	
Ch-2D	12	*Xwmc181.1-Xcfd53*					−1.46 (E1/4.70)	
Ch-2D	111	*Xcwm70.1-Xcwm83*			2.51 (E3/8.30)			
Ch-2D	130	*Xcau14.2-ww160.1*	−2.34 (E4/3.17)	−4.37 (E1/7.56)			−4.25 (E2/16.97)	−3.38 (E2/7.72)
				−2.31 (P/3.09)				
Ch-3A	68	*Xcfa2193-Xbarc197.1*						−1.41 (E4/4.15)
								−1.80 (P/9.97)
Ch-3B	82	*Xbarc344-Xcfe3292*	−2.12 (P/4.06)	−2.13 (P/4.09)		−3.00 (E4/12.60)		
CH-4A-1	34	*Xcfe89.3-Xbarc170*	−2.02 (E3/3.64)	−2.44 (E3/5.30)	−2.22 (E3/6.43)	−1.70 (E3/5.77)	−1.58 (E1/5.95)	−1.37 (E1/4.03)
CH-4A-2	0	*Xissr810.2-Xbarc1047*	−2.11 (E1/4.18)	−2.65 (E3/6.36)	−2.64 (E1/7.19)	−1.88 (E3/7.10)	−1.86 (E4/8.89)	−1.66 (E1/5.83)
			−2.62 (E3/6.22)		−2.19 (E3/6.38)			
					−1.26 (P/3.53)			
CH-4B-1	63	*Xcau8.1-Xgwm495*			−2.03 (E1/3.76)		−1.74 (E1/4.35)	−2.47 (E1/11.94)
							−2.19 (E4/12.74)	−1.69 (E4/6.23)
								−1.06 (P/3.71)
CH-4D-1	43	*Xcau17.4-Xcau17.3*	2.83 (E1/6.55)	2.50 (P/6.66)	2.66 (E1/6.45)	2.31 (E3/9.30)		
			2.54 (P/6.84)					
CH-4D-2	19	*Xcau17.1-Xcfd71*	2.11 (E1/3.69)		2.06 (E1/3.91)			
Ch-5A-1	0	*Xcwm17.1-Xmag3273*				1.47 (E1/3.73)		
Ch-5A-1	32	*Xcfa2163.2-Xcwm216*					4.66 (E2/17.23)	4.74 (E2/18.44)
								4.64 (E3/16.66)
Ch-5A-1	105	*Xbarc151-Xwmc524*					1.99 (E1/8.84)	
							1.49 (E4/5.65)	
Ch-5A-2	32	*Xwmc327.2-Xwmc3277.*						−1.93 (E4/5.06)
CH-5D	42	*Xgwm190-Xbarc28.2*	−7.77 (E1/6.91)	−3.82 (E3/6.93)	−7.07 (E1/6.47)	−2.29 (E4/5.64)	−3.53 (E1/3.60)	
			−4.36 (E3/9.05)	−4.59 (P/4.37)	−3.94 (E2/7.98)	−3.19 (P/4.32)	−3.44 (P/6.92)	
			−4.61 (P/4.43)		−2.29 (E4/5.64)			
					4.95 (P/10.23)			
CH-5D	57	*Xbarc133-ww152*	−2.73 (P/4.66)	−2.77 (P/4.79)				
CH-5D	103	*Xcau18.2-Xgwm66.4*				1.39 (E2/4.30)		
CH-5D	163	*Xcfe242.2-Xbarc320*	−2.30 (E4/6.28)	−2.06 (E4/5.21)		−1.79 (E1/5.35)		
Ch-6A	1	*Xbarc23-Xbarc204.1*				−2.84 (E3/7.50)		
Ch-6A	47	*Xgwm427-Xcfa2104*	2.46 (E3/5.42)	2.02 (E3/3.61)	1.89 (E4/7.33)		2.00 (E2/9.02)	1.85(E2/5.55)
Ch-6A	75	*Xcfe179.2-ww179*	3.22 (E3/8.97)	2.82 (E2/10.11)	1.66 (E2/7.00)	−2.12 (E1/8.19)	−1.51 (E2/5.11)	
			−1.55 (P/2.92)	3.28 (E3/9.26)		−1.57 (E2/5.75)		
				−1.53 (P/2.86)				
Ch-6A	106	*Xissr808-BE606386*					−1.96 (E2/8.62)	
Ch-6A	151	*Xpsp3152-Xcfe179.3*	−2.39 (E4/7.07)	−2.44 (E4/7.56)				−1.61 (E4/5.90)

Table 4 continued

Chrom	Pos	Interval Marker	Add [E/PVE(%)]					
			PH	PH|SL	PH|FIITL	PH|SITL	PH|TITL	PH|FOITL
Ch-6B	39	*Xcwm109.6-Xissr818*	2.07 (E4/2.80)			1.69 (E1/4.73)		
Ch-6B	45	*Xswes180.1-Xmag3469*				−2.87 (E4/9.03)		
CH-6D	47	*Xswes123.8-Xcfe127*	2.91 (E3/7.65)	3.09 (E3/8.68)				
CH-6D	61	*Xswes123.1-Xswes123.9*	−1.88 (E4/4.33)	−2.13 (E4/5.70)				
CH-6D	90	*Xcfe87.1-Xissr841.1*	2.09 (E3/3.96)	1.93 (E3/3.34)	1.90 (E1/3.55)			
CH-6D	110	*Xbarc096-Xgwm469*					−1.61 (E1/6.13)	
Ch-7A	24	*Xissr847-Xgwm60*						−1.79 (E4/6.95)
Ch-7A	92	*Xcfe284-ww160.2*	−4.15(E4/9.14)		−2.64(E4/10.91)			−3.68 (E4/11.05)
Ch-7A	101	*ww160.4-ww160.3*	2.36 (E4/4.65)	2.32 (P/4.49)				
CH-7B	74	*Xcfa2106-Xwmc364.1*				2.02 (P/7.55)		
CH-7B	138	*Xcau12.4-ww121*	−1.80 (E1/3.01)	−1.65 (E1/2.53)				
			−2.59 (E3/6.06)	−2.63 (E3/6.23)				−1.64 (E3/6.53)
			−2.00 (P/4.86)	−2.01 (P/4.90)				
CH-7D	2	*Xissr814.2-Xswm5.1*						1.51 (E4/4.01)
CH-7D	38	*Xmag2934.1-Xmag2934.2*	1.74 (E1/2.66)		1.67 (E1/2.73)			2.37 (E2/9.07)
			2.61 (E3/5.52)		1.58 (E2/6.04)			
CH-7D	56	*Xcfd4-Xgwm44*	−2.78 (E1/7.12)		−2.52 (E1/6.42)	−1.87 (E3/7.18)		−2.09 (E1/9.41)
			−2.27 (E2/6.55)		−3.84 (E2/14.96)			−2.26 (E2/8.28)
Ch-7D	125	*Xgdm67-Xswes558.1*	−2.75 (E3/6.66)	−3.07 (E3/8.33)				

For abbreviations, see Table 1, for title description see Table 3

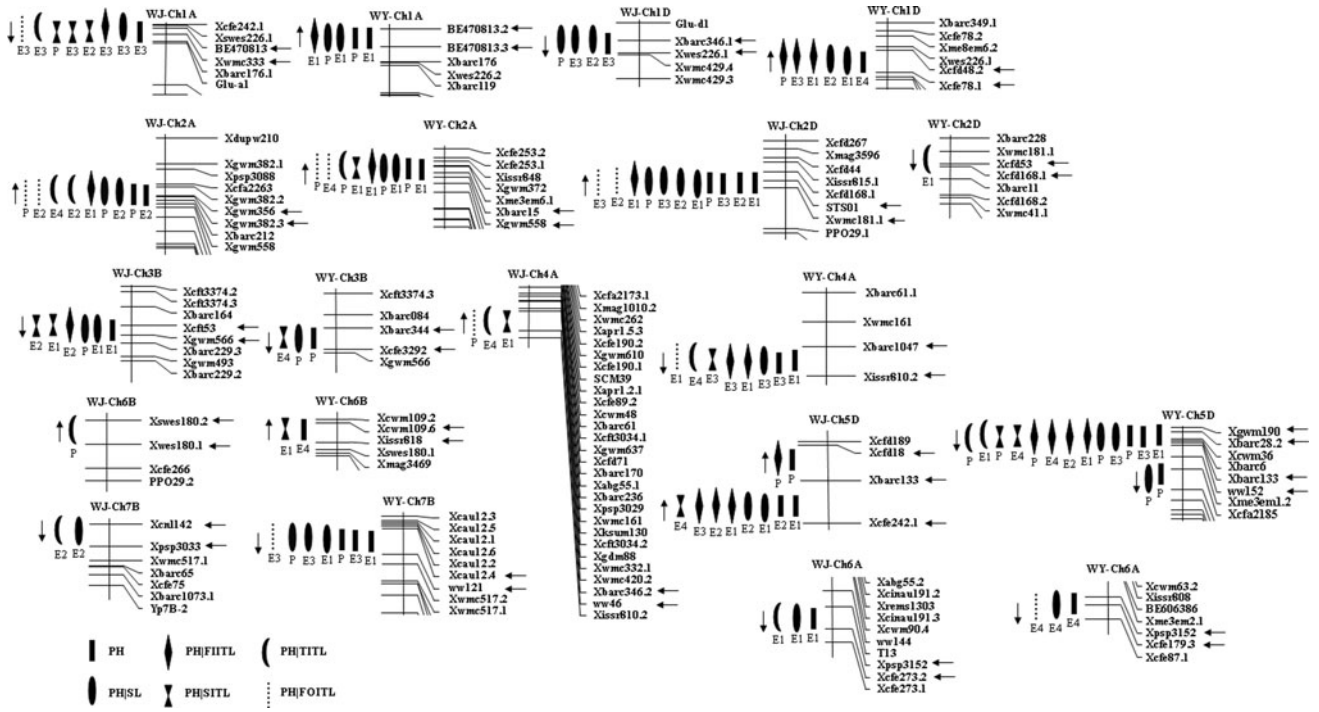

Fig. 2 Comparison of congruent QTL detected in both WJ and WY populations. The unconditional and conditional QTL symbols are described at the bottom left of this Figure; they were placed on the left of their corresponding chromosomes to represent a significant QTL. An uppercase letter *E* plus a *numeral*, 1, 2, 3 or 4, or the uppercase letter *P*, underneath a *QTL symbol* indicates that the corresponding QTL was detected in Tai'an (2008–2009), Tai'an (2009–2010), Zaozhuang (2009–2010), Jining (2009–2010), and in the average data calculated from the four trials, respectively. The pair markers that were each marked by a *horizontal arrow* on the right of the linkage map indicate the flanking markers of the corresponding QTL. A QTL with height-increasing alleles and height-reducing alleles from Weimai 8 were marked by an *upward vertical arrow* and by a *downward arrow* on the left of QTL symbols, respectively. The two linkage maps based on WJ and WY populations were marked by 'WJ-Ch' and 'WY-Ch', respectively

Table 5 Number of unconditional and conditional QTL detected in different environments

En[a]	Uncon[b]	Cond[c]				
	PH	PH|SL	PH|FIITL	PH|SITL	PH|TITL	PH|FOITL
E1	10/13	10 + 0 + 0/3 + 4+4	2 + 0 + 6/5 + 4 + 4	1 + 2 + 1/2 + 0 + 6	1 + 1 + 6/0 + 2 + 8	1 + 1+2/0 + 3 + 4
E2	13/2	9 + 2 + 2/1 + 0+3	2 + 0 + 3/0 + 2 + 3	1 + 4 + 5/0 + 0 + 4	1 + 10 + 5/0 + 0 + 7	1 + 5+1/1 + 0 + 5
E3	9/12	4 + 0 + 0/7 + 3 + 0	2 + 3 + 1/1 + 1 + 3	0 + 2 + 2/0 + 3 + 4	0 + 2 + 5/0 + 0 + 1	3 + 0+0/0 + 1 + 2
E4	3/11	3 + 0 + 0/4 + 1 + 0	0 + 2 + 2/0 + 1 + 2	0 + 0 + 8/0 + 0 + 3	0 + 1 + 6/0 + 0 + 4	0 + 2+2/0 + 4 + 8
P	11/14	3 + 3 + 3/14 + 0 + 3	0 + 2 + 4/1 + 3 + 2	0 + 1 + 6/0 + 1+4	2 + 1 + 9/0 + 3 + 2	2 + 3+4/1 + 1 + 3
Total	46/52	29 + 5 + 5/ 29 + 8 + 10	6 + 7 + 16/ 7 + 11 + 14	2 + 9 + 22/ 2 + 4 + 21	4 + 15 + 31/ 0 + 5 + 22	7 + 11 + 9/ 2 + 10 + 22

For each entry, the first figure refers to WJ and the second to WY

The numbers above included several overlapped QTL detected in various environments

[a] Environment in which each QTL was detected. For abbreviations, see Table 1

[b] Number of unconditional QTL

[c] Number of conditional QTL. The first Arabic numerals before the "+" indicate the number of QTL detected in both unconditional and conditional analyses with equal additive effects (additive effect of conditional QTL ranged less than 10% of that of the corresponding unconditional QTL); the middle Arabic numerals indicate the number of QTL detected in both unconditional and conditional analyses with reduced or enhanced additive effects; the third Arabic numerals following a "+" indicate the number of QTL that was detected only in conditional analysis

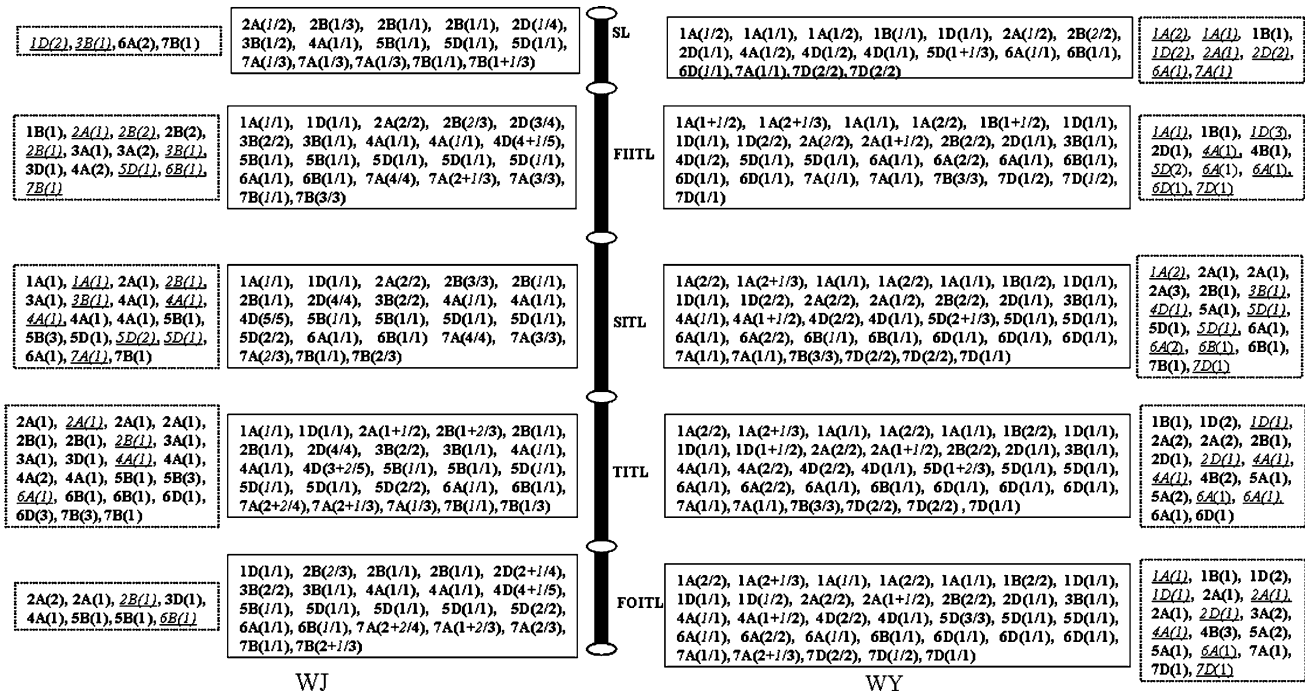

Fig. 3 Correlations between plant height and its components at the QTL level. The central *vertical black line* indicates a stem of wheat, and the white ellipses within it indicate the nodes. The abbreviations for the five plant height components are placed at the right of the stem. The text boxes with the solid borders describe the QTL for PH contributed by its nearby component trait. For example, **7B(1 + *1*/3)**, in the solid text box on the left of SL, indicates that a QTL for PH was detected on chromosome **7B** in **3** trials by unconditional QTL mapping methods, but this QTL was completely contributed by SL in **1** trial and was partially contributed by SL in *1* trial. That is to say, if an unconditional QTL for PH was completely contributed by its component trait, the numeral in *parentheses* before the *slash* was marked by *bold* typeface, but marked by *italic* typeface if partially contributed by its component trait. Contents of the text boxes with *dashed borders* indicate the conditional QTL for PH with an additive effect opposite to that for its conditioned trait. For example, *1D(2)*, in the dashed text box on the left of SL, indicates a QTL that can be detected by both unconditional and conditional mapping methods but in different environments on *1D*, and it showed additive effect opposite to that of SL in *2* trials; **6A(2),** in the dashed text box on the left of SL, indicates a QTL that can only be detected by conditional mapping methods in **2** trials on chromosome 6A. That is to say, we distinguished the conditional QTL for PH based on whether it showed significance by unconditional mapping methods, but in different environments, by marking letters in *italics* with *underline* or in *bold* typeface, respectively. The numeral in parentheses indicates the number of environments in which the QTL for plant height that could only be detected by conditional QTL analysis. For each text, the left of the stem refers to WJ and the right refers to WY

detected from analysis when PH was conditioned on SL and SITL, one each was detected from analysis when PH was conditioned on the FIITL and the FOITL, respectively, and they showed different additive effects compared to their corresponding unconditional QTL, either reduced or enhanced. None of the 11 unconditional QTL detected in E4 were significant when PH was conditioned on SITL or TITL, but four were unchanged when PH was conditioned on SL. When PH was conditioned on FIITL and FOITL, one and four showed obvious different additive effects, respectively. All 14 unconditional QTL detected in P showed significant and unchanged additive effect values when PH was conditioned on SL, but none of them could be identified with equal additive effects when PH was conditioned on each of its four internode lengths, with the exception of PH conditioned on FIITL and FOITL. However, 3, 1, 3 and 1 of the 14 unconditional QTL detected in P still showed significant additive effects, either reduced or enhanced, when PH was conditioned on FIITL, SITL, TITL and the FOITL, respectively.

The fewest additional conditional QTL were detected when PH was conditioned on SL, being 4, 3, 0, 0 and 3 in E1, E2, E3, E4 and P, respectively (Table 5), followed by PH conditioned on FIITL, being 4, 3, 3, 2 and 2 in E1, E2, E3, E4 and P, respectively. When PH was conditioned on SITL, TITL and FOITL, the total number of additional QTL was similar, being 6, 8 and 4 in E1, 4, 7 and 5 in E2, 4, 1 and 2 in E3, 3, 4 and 8 in E4 and 4, 2 and 3 in P, the total being 21, 22 and 22, respectively.

Common QTL resolved in both populations

Based on common markers in two genetic maps, comparisons of congruent QTL were conducted (Fig. 2). Up to 11 pairwise QTL were common to the two populations, albeit most of them were detected in different environments by

either the unconditional or the conditional method. Of these, one pairwise each with height-reducing alleles from the common parents Weimai 8 were mapped to chromosomes 3B, 6A and 7B, and one pairwise each with height-enhancing alleles from Weimai 8 were detected on chromosome 2A and 6B. The remaining six pairwise common QTL alleles from Weimai 8 exhibited opposite additive effects in two different populations, one pairwise each located on chromosomes 1A, 1D, 2D, 4A, and two pairwise on 5D. Interestingly, the major QTL detected on chromosome 5D in the WY population shared a common flanking marker, *Xbarc133*, with one in the WJ population; more than one QTL with either a strong or moderate effect can be detected near this common marker in almost all environments by either unconditional or conditional QTL mapping methods in WJ, indicating an authentic QTL.

Discussion

Relationship between plant height and its components

Conditional QTL mapping analysis provides an efficient tool to reveal relationships between PH and PHC. For example, when performing conditional QTL analysis of PH conditioned on SL (PH|SL), there are four possible results: (1) a QTL detected by the unconditional method can be identified with a similar or equal effect, indicating that this QTL for PH is independent of SL; (2) a QTL detected by the unconditional method can be identified with either a greatly reduced or a greatly enhanced effect, suggesting that this QTL for PH is partially, but not completely, associated with SL; (3) a QTL detected by the unconditional method cannot be identified, meaning that this QTL for PH is entirely contributed by SL; (4) an additional QTL can be detected by the conditional mapping method, which means that the expression of the QTL for PH is completely suppressed by SL, and the effects could only be identified by eliminating the influence of SL. This suggests that the additional QTL has an opposite additive effect on PH and SL.

Of the 46 unconditional QTL for PH in WJ and 52 in WY, 29 each were independent of SL, while in WJ, only 6 were independent of FIITL, 2 of SITL, 4 of TITL, and 7 of FOITL. In WY, 7 were independent of FIITL, 2 of SITL, and 2 of FOITL. This indicated that there is weak genetic association between PH and SL, but strong association between PH and each of the four internode lengths (Table 5). This finding confirmed the results of the correlation analysis and variance analysis between PH and PHC (Table 2). Of the 25 unconditional QTL for PH in WJ, 11, 15, 18, 12 and 14 were entirely contributed by SL, FIITL, SITL, TITL and FOITL, respectively, and 3, 5, 5, 8 and 3 were partially contributed by SL, FIITL, SITL, TITL and FOITL, respectively. In addition, 1, 2, 0, 5 and 5 QTL were either entirely or partially contributed by SL, FIITL, SITL, TITL and FOITL in different trials, respectively (Table 3; Fig. 3). Of the 34 unconditional QTL for PH in WY, 12, 21, 29, 30 and 23 were entirely due to variation in SL, FIITL, SITL, TITL and FOITL, respectively, and 6, 3, 2, 0 and 4 were partially due to variation in SL, FIITL, SITL, TITL and FOITL, respectively. In addition, 1, 4, 3, 4 and 4 QTL were either entirely or partially due to variation in SL, FIITL, SITL, TITL and FOITL in different trials, respectively (Table 4; Fig. 3). From Fig. 3, Tables 3 and 4 together, we concluded that there were more QTL for PH with opposite additive effects for TITL than for the other four traits. The largest number of new QTL was identified by excluding the influence of TITL on PH in WJ, while the largest number of new QTL that were consistent among various environments were detected by conditioning PH on TITL in WY. By removing the influence of SL on PH, the fewest extra QTL for PH were revealed in both populations, indicating the fewest QTL for PH with additive effects opposite to that of SL, followed by FIITL in WY, but by FOITL in WJ (Fig. 3). Taking the reproducibility of QTL detection over environments into consideration, the number of QTL for PH with additive effect opposite to that of its corresponding component traits arranged in proper order were TITL, SITL, FIITL, FOITL and SL in WJ, and TITL equal to FOITL, SITL, FIITL and SL in WY, respectively (Table 5). In conclusion, these results of WJ and WY together demonstrate that, at the QTL level, SL had the least level contribution to PH among all the five PHC considered, followed by FIITL. TITL had the strongest influence on PH, followed by SITL and FOITL.

The results described above demonstrate that some unconditional QTL for PH were contributed by more than one component traits, based on whether the QTL could be identified by conditional analysis (Tables 3, 4). In QTL mapping, the likelihood of detecting a QTL is dependent on the ratio between the variance caused by the QTL's effect and the total variance of the trait as well as the size of the mapping population (Lander and Botstein 1989). In conditional QTL analysis, effects on QTL contributed by a conditional trait are reduced and the QTL with effects below a certain threshold become virtually undetectable. Thus, it is reasonable to obtain the results described, which indicated that the unconditional QTL for PH was strongly influenced by the conditional traits, indicating a pleiotropic QTL. Notably, there was a difference in the conditional mapping results in different environments. The environment plays an important role in controlling gene

expression, especially for quantitative traits, and could account for the above differences.

Common QTL resolved in both populations

In bread wheat, a variety of complex traits has been subjected to QTL analysis (Keller et al. 1999; Kato et al. 1999; Börner et al. 2002; Huang et al. 2006; Wang et al. 2009, 2010; Wu et al. 2010). However, in the majority of these cases, each study involved a single mapping population, and only unconditional QTL mapping analysis was conducted. Consequently, only a limited number of QTL could be detected in each study, and the result was not conclusive. With the rapid development of molecular marker technology, additional research on QTL effects in more than one different or related genetic backgrounds is warranted. Kumar et al. (2007) have used two independent RIL populations to conduct QTL analysis, but only a solitary QTL for spikelets per spike was common between the two populations. Ma et al. (2007) identified a large number of common QTL using RILs and RIL-derived IF_2 populations. Buckler et al. (2009) used a set of 5000 RILs (maize Nested Association Mapping population, NAM), comprising 25 related individual RIL populations, to dissect QTL for flowering time in maize; they identified numerous small-effect QTL that were shared among families.

In this report, two related RIL populations were subjected to unconditional and conditional QTL mapping methods to identify QTL for PH. Up to 11 pairwise congruent QTL were detected in the two populations (Fig. 2). Because of the limited number of common loci in the two genetic maps, precise prediction and definition of common QTL in the two populations were hampered, though positions of most QTL identified in the two populations are of high congruency. The results show that QTL from the common parent in the two related populations can be detected repeatedly to a certain extent, and the comparable QTL are authentic.

Comparison of the present study to previous studies

PH in wheat has been subjected to QTL analysis in many other reports, but in most QTL experiments, population size has been limited by the cost of marker genotyping and/or the cost of trait phenotyping. The limited population sizes can lead to an underestimation of QTL number, overestimation of QTL effects, and failure to quantify QTL interactions (Vales et al. 2005). Beavis (1998) suggested that as many as 200 individuals might still be too few for reliable QTL detection. Buckler et al. (2009) utilized NAM (Nested Association Mapping population) comprising 5,000 RILs, to dissect QTL for flowering time in maize; they concluded that, with large enough samples, additive QTL models could accurately predict the phenotype. False positive QTL may be caused by parental sharing when the RIL population is not large enough to permit completely random mating (Zou et al. 2005). Schön et al. (2004) exploited a large experimental population, 976 F_5 maize testcross progenies, for QTL detection, and found a large effect of sample size on power of QTL detection and accuracy and precision of QTL estimates. To our knowledge, there has been no report on QTL analysis for PH in wheat with a mapping population of more than 400 progenies. The present WJ mapping population included 485 $F_{8:9}$ RILs and the WY mapping population included 229 $F_{8:9}$ RILs, enhancing the accuracy and precision of QTL detection of PH.

Classical genetic studies indicated that the genetic control of PH in bread wheat is complex, and most chromosomes harbor factors that can affect it (Law et al. 1973). Almost all of the 21 chromosomes were found to contribute to genetic variation for PH in the case of the substitution of lines of Cappelle-Desprez into Chinese Spring (Snape et al. 1977). This finding has been confirmed by various other reports of QTL detection for PH in wheat (Kato et al. 1999; Keller et al. 1999; Börner et al. 2002; Huang et al. 2003; Sourdille et al. 2003; Huang et al. 2004; Liu et al. 2005; McCartney et al. 2005; Huang et al. 2006; Marza et al. 2006; Klahr et al. 2007; Zhang et al. 2008; Chu et al. 2008; Wang et al. 2009; Wang et al. 2010; Mao et al. 2010; Wu et al. 2010). Therefore, it was not surprising that, in the present study, many QTL were detected on almost all of the 21 chromosomes, in two mapping populations by both unconditional and conditional methods.

To date, numerous major effects on PH have been identified and 25 semi-dwarfing genes have been named (Worland et al. 1998; Zhang et al. 2008). The two most common semi-dwarfing genes, *Rht-B1* and *Rht-D1*, have been successfully utilized in wheat breeding programs worldwide and are located on the short arms of chromosomes 4B and 4D, respectively. *Rht13* on chromosome 7BS has been well characterized, and it markedly reduces PH (Ellis et al. 2005). The major QTL detected in WJ on the short arm of chromosome 4D is located in approximately the same region as the dwarfing gene *Rht-D1*, corresponding to the QTL detected by McCartney et al. (2005), Huang et al. (2006), Zhang et al. (2008), Chu et al. (2008), Wang et al. (2009), Mao et al. (2010), Wu et al. (2010) and Wang et al. (2010) (Table 3). Fortunately, it can be reproducibly identified in the WY population between interval *Xcau17.4* and *Xcau17.3*, but it only has a moderate effect (Table 4). Through conditional analysis, we showed that each component considered, except SL, completely or partially contributed to this QTL. The QTL detected by the conditional mapping method in WY on the short arm of chromosome 4B was detected between *Xcau8.1* and

Xgwm495, a position similar to that of *Rht-B1* and consistent with the QTL detected by Sourdille et al. (2003), Huang et al. (2003), (2006), Zhang et al. (2008), Wu et al. (2010) and Mao et al. (2010), but this QTL cannot be reproducibly identified in the WJ population (Table 4). Conditional analysis indicated that this QTL may have an opposite effect than that of FOITL in three environments, of TITL in two environments and of SITL in one environment. A moderate QTL on the short arm of chromosome 7B was mapped to a position similar to *Rht13*, but it can be detected in a single environment in WJ. Conditional analysis indicated that FIITL and TITL had no effect on this QTL, while SL and FOITL both contributed to it, and SITL exhibited a negative effect.

The major QTL detected in WY on chromosome 5D, between *Xgwm190* and *Xbarc28.2*, has not been reported elsewhere. It can be reproducibly detected in the WJ population in the same position, but with reduced additive effects (Tables 3, 4; Fig. 2). Conditional analysis indicated that FOITL completely contributed to this QTL, while SL, SITL and TITL partially contributed to it, and FIITL had no influence on this QTL. Interestingly, this QTL mapped between 41.9 and 45.5 cM on chromosome 5D, a very small interval; therefore, both *Xgwm190* and *Xbarc28.2* can be simultaneously utilized for marker-assisted selection (MAS) in wheat breeding programs. A QTL located on chromosome 2DL had a moderate effect, and was identified in four of the five trials by the unconditional mapping method in WJ, but was detected in only one environment by conditional analysis in WY. It corresponds to the QTL detected by Marza et al. (2006) and Wang et al. (2009) (Tables 2, 3; Fig. 2). Notably, this QTL is located at a similar position to that of the polyphenol oxidase (PPO) gene. One of this QTL's flanking markers, *STS01*, is a functional PPO gene marker; thus, the correlation between the PH and PPO deserves further study. Conditional analysis indicated that SL had no contribution to this QTL, but SITL and TITL completely contributed to it. The contribution of FIITL and FOITL varied in different environments.

If a QTL is independent of the environment, the implication is that its expression is stable regardless of differences in environment, and it can be of great value for MAS. In the present study, three QTL on chromosome 7A, two on 7B, and one each on 1A, 2B, 2D, 4D and 5D were identified by the unconditional mapping method and were significant in more than three trials. Furthermore, five additional conditional QTL were verified in up to three environments. Of these, one was revealed in WJ when PH was conditioned on SITL in E3, E4 and P and on TITL in E2, E3 and P. It was located on the long arm of chromosome 5B between *Xwmc73* and *Xgwm355* and corresponded to the QTL identified by Klahr et al. (2007) and Wang et al. (2010). The QTL on chromosome 7B between *Xcfe223* and *Xissr844.2* was detected in WJ in E2, E3 and P when PH was conditioned on TITL. McCartney et al. (2005) and Zhang et al. (2008) have detected QTL for PH in this interval. The QTL on 4B between *Xcau8.1* and *Xgwm495*, a position similar to that of *Rht-B1*, was significant in WY in E1, E4 and P when PH was conditioned on FOITL. The remaining two additional conditional QTL consistent in three trials were both novel QTL that have not been reported previously. Of these, the QTL on 6D between *Xapr1.2.3* and *Xbarc154* was identified in WJ in E1, E4 and P when the influence of TITL on PH was excluded; the QTL on 2A between *Xpsp3029.2* and *Xwmc181.2* showed significance in E1, E2 and P in WY when PH was conditioned on SITL. The results described above indicated that the conditional mapping method can efficiently and accurately reveal counteracting QTL by their components.

Above all, the number of QTL detected in WJ and WY was almost equal, but the QTL detected in WY showed greater additive effects than those found in WJ. Disregarding the difference in genetic background of the two populations, we came to the conclusion that population size had little influence on the estimation of QTL number, but had a great influence on the estimation of QTL effects, indicating that QTL effects can be overestimated with small mapping populations.

In summary, the combination of conditional and unconditional mapping methods applied to two related populations can precisely dissect factors affecting PH and evaluate possible genetic relationships between PH and PHC at the QTL level. In addition, a large population size can enhance the authenticity and accuracy of the QTL detection.

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