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QTL mapping for developmental behavior of plant height in wheat (*Triticum aestivum* L.)

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Abstract A recombinant inbred line (RIL) population with 305 lines derived from a cross of Hanxuan 10 × Lumai 14 was used to identify the dynamic quantitative trait loci (QTL) for plant height (PH) in wheat (*Triticum aestivum* L.). Plant heights of RILs were measured at five stages in three environments. Total of seven genomic regions covering PH QTL clusters on different chromosomes identified from a DH population derived from the same cross as the RIL were used as the candidate QTLs and extensively analyzed. Five additive QTLs and eight pairs of epistatic QTLs significantly affecting plant height development were detected by unconditional QTL mapping method. Six additive QTLs and four pairs of epistatic QTLs were identified using conditional mapping approach. Among them, three additive QTLs (*QPh.cgb-1B.3*, *QPh.cgb-4D.1*, *QPh.cgb-5B.2*) and three pairs of epistatic QTLs (*QPh.cgb-1B.1–QPh.cgb-1B.3*, *QPh.cgb-2A.1–QPh.cgb-2D.1*, *QPh.cgb-2D.1–QPh.cgb-5B.2*) were common QTLs detected by both methods. Three QTLs (*QPh.cgb-4D.1*, *QPh.cgb-5B.3*, *QPh.cgb-5B.4*) were expressed under both drought and well-water conditions. The present data are useful for wheat genetic manipulations through molecular marker-assisted selection (MAS), and provides new insights into understanding the genetic mechanism and regulation network underlying the development of plant height in crops. Our result in this study indicated that combining unconditional and conditional mapping methods could make it possible to reveal not only the stable/conserved QTLs for the developmental traits such as plant height but also the dynamic expression feature of the QTLs.

Keywords Wheat (*Triticum aestivum* L.) · Plant height · Developmental behavior · Quantitative trait locus (QTL) · Recombinant inbred line (RIL)

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Introduction

Plant height, an important agronomic trait in cereal crops, not only determines plant architecture but also contributes a lot to grain yield. Machado et al. (2002) found that plant height explained 61% of the variation in grain yield in corn. Another similar study indicated that the weight of the grains was reduced when reducing plant height in wheat (Zapata et al. 2004). As

we know, the spectacular increases in wheat and rice yields during the 'Green Revolution' were achieved by the introduction of dwarfing traits into the plants (Peter 2003). Semi-dwarf plants possessed short, strong stalks and did not lodge. Furthermore, a greater proportion of assimilation partitioned into the grain, resulting in further yield increases and higher harvest index. Therefore, the reduced plant height has been widely used as the ideal trait in crop breeding program for high-yield varieties. For example, the dwarf trait derived from Norin 10 is now present in >70% of current commercial wheat cultivars world-wide (Evans 1998).

Plant height in wheat is generally considered to be controlled by both qualitative and quantitative genes (Tang et al. 2007). The reduced plant height in Norin 10 is controlled by two dwarfing genes, namely *Rht-B1b* and *Rht-D1b*, which are semi-dominant alleles of homologous genes on chromosomes B and D (Boerner et al. 1996).The effect of each gene on plant height is similar and their combined effect is additive. It was found that the wheat *Rht* genes encode growth repressors that are normally suppressed by gibberellin (GA) (Peng et al. 1999). Regarding the quantitative genetics of plant height, a number of quantitative trait loci (QTL) were detected to govern the trait by molecular mapping in wheat (Ahmed et al. 2000; Zhang et al. 2008). In these QTL studies, plant height was only measured at maturation (harvest) without considering the effects due to distinct gene expression at different developmental stages.

However, the development of plant height is a complex dynamic process that is controlled by a network of genes as well as by environmental factors. According to the theory of developmental genetics, genes are selectively expressed at different growth stages. The development of morphological traits occurs through the actions and interactions of many genes that might behave differentially during growth periods (Atchley and Zhu 1997). QTL mapping by phenotypic data measured at a single time point is too simple to reveal the genetic control of developmental processes of the target quantitative traits (Peat and Whittington 1965; Wu 1987; Xu and Shen 1991). It is necessary, therefore, to understand the dynamics of gene expression for a trait at different developmental stages as a basis for quantitative trait manipulation (Xu 1997). Recently, time-related QTL mapping has been used to reveal the genetic basis of developmental characters such as grain filling (Takai et al. 2005), growth rate (Li et al. 2006), blast resistance (Li et al. 2008) and tiller number (Yan et al. 1998a; Wu et al. 1999) in rice, plant height in maize (Yan et al. 2003), and seed weight in soybean (Teng et al. 2009). So far, no report has documented the dynamic analysis of QTLs for plant height in wheat.

We have identified a number of QTLs associated with dynamic development of plant height in wheat using a doubled haploid population derived from a cross of Hanxuan 10 × Lumai 14 (published separately). In the present research, a recombinant inbred line population (RILs) derived from a same cross was used to investigate the dynamic QTLs for developmental behavior of plant height in wheat with time-dependent measures evaluated in three environments. Both conditional and unconditional QTLs for plant height were examined using a more effective statistical mapping method (Zhu 1995; Wang et al. 1999). Furthermore, the temporal gene expressions including additive effects, additive × additive epistatic effects, and their *QE* (QTL main effects and environments interaction) effects for plant height are discussed. The information obtained in this study provides new insights into understanding the genetic mechanism and regulation network underlying the development of plant height in crops and also benefits crop genetic manipulations through molecular marker-assisted selection (MAS).

Materials and methods

Plant materials

A population of 305 RILs derived from a cross of Hanxuan 10 × Lumai 14 was used in this experiment. Hanxuan 10, the female parent, is a drought-tolerant variety from Shanxi Academy of Agricultural Sciences, which is released in 1966 and still widely cultivated in arid and barren areas in China. Lumai 14, the male parent, is a high-yielding variety adapted to abundant water and fertile conditions from Yantai Institute of Agricultural Sciences, Shandong Province, and widely grown during the 1990s in northern China. A total of 305 lines and their parents were grown on the experimental farm (39°48′ N, 116°28′ E, 46 m altitude) of the Institute of Crop Sciences, Chinese Academy of Agricultural Sciences in Beijing

in 2005 and 2006. The experimental unit was a two-row plot with a length of 2 m, and 30 cm between the rows. The plant materials were managed under two water regimes in 2006. One was drought stress (06DS) with a total of 137 mm rainfall in the whole growth season of wheat (from October 1, 2006 to June 10, 2007). And the other was well watered (06WW) with 750 m^3/hm^2 at each stage of pre-overwintering, jointing, flowering and grain filling, respectively. In 2005, only one water regime (drought stress, 05DS) was performed with a total of 128.8 mm rainfall in the whole wheat growth season.

Measurement of plant height

Plant height (from the surface of the soil to the tip of the plants) was measured firstly at the jointing stage (more than 50% of the plants had two nodes over ground). After that, the measurement was conducted every 7 days through flowering stage. A total of five different time points were taken for measuring plant height during the whole wheat growth period, which were designated as S1 (stage 1), S2 (stage 2), S3 (stage 3), S4 (stage 4) and S5 (stage 5), respectively. The average of plant height in each RIL was used in data analysis. For conditional analysis, S1|S0 indicates the time interval from the initial time of plant growth to stage 1, i.e. period 1; S2|S1 the time interval from stage 1 to stage 2, i.e. period 2 and so on.

Molecular markers and linkage map construction

Total of 28 candidate SSR makers were used in this study. These SSR makers were selected from the seven genetic linkage groups of wheat (on the chromosome of 1B, 2A, 2B, 2D, 3D, 4D and 5B, respectively) covering plant height QTLs, which were identified from a doubled haploid (DH) population derived from the same cross as the present RILs established by our lab (Jing et al. 1999; Hao et al. 2003; Zhou et al. 2005; Yang et al. 2007a, b; Wu et al. 2010). Benefiting from same ancestors, we are able to compare the QTLs for wheat plant height detected in both populations so as to find the functional QTLs that work in different genetic backgrounds and environments. The seven linkage groups consisting of the 28 markers cover a total of 305.87 cM genomic regions with an average interval of 14.6 cM between adjacent marker loci. The QGAStation v1.0 (http://ibi.zju.edu.cn/software/qga/) was employed for constructing molecular marker linkage maps (groups) in the present RILs population.

QTL detection

Both unconditional QTL and conditional QTL were detected with the mixed linear model using the software of QTL Network version 2.0 (http://ibi.zju.edu.cn/software/qtlnetwork/). The threshold to declaring QTL is set to P value of 0.05 by permutation method. Here, unconditional and conditional phenotypic values were arranged in same data file for QTL mapping. Unconditional phenotypic valves were the data measured at different stages. Conditional phenotypic value at time t given phenotypic values at time $(t - 1)$ were predicted by the software QGA Station 1.0 (http://ibi.zju.edu.cn/software/qga/). Unconditional QTLs indicate the cumulative effects of QTLs from the initial time to time t, conditional QTLs the cumulative effects of QTLs from time $t - 1$ to time t. QTL were named according to the rule of "QTL + trait + research department + chromosome" (McIntosh et al. 1999).

Basic statistical analysis was implemented by the software SPSS13.0.

Results

Phenotypic variation of wheat plant height

The phenotypic values of plant height from the RIL population and their parents in three environments at five developmental stages are presented in Table 1. Variation of plant height for all plants investigated increased as the trait developed. The female parent Hanxuan 10 grew significantly higher than the male parent Lumai 14 at all stages in three environments. For anyone of the both parents, plant height showed no significant difference between the well-watered (06WW) and the drought-stress (05DS and 06DS) conditions. During the period from stage 1 to stage 5, plant heights showed a persistent increasing trend in the RIL population with the fastest growth rate from stage 2 to stage 3 in WW condition and stage 1 to stage 2 under DS condition. Plant height segregated continuously among the RIL population, and transgressive segregation were also observed in certain stages (stage 1 of 06DS, stage 2 and stage 3 of DS 05). The skewness for the distributions of plant height in the RILs

Table 1 Phenotypic values of plant height (cm) for the RIL population and its parents in five different measuring stages evaluated in three environments

Env.[a]	Stage	Parent			RIL population			
		Hanxuan 10	Lumai 14	*t* Value	Mean ± SD	Range	Skew.	Kurt.
06WW	1	41.88	36.88	2.83*	31.63 ± 0.29	19–44	0.114	−0.544
	2	66.38	44.50	9.50**	49.45 ± 0.50	32–70	0.013	−0.969
	3	96.75	57.75	21.50**	70.33 ± 0.78	45–99	−0.213	−1.252
	4	100.13	66.75	20.46**	82.67 ± 1.02	51–115	−0.325	−1.415
	5	120.75	74.75	23.12**	98.13 ± 1.08	64–135	−0.203	−1.286
06DS	1	45.88	36.75	5.31**	36.40 ± 0.25	25–47	−0.165	−0.656
	2	65.75	42.00	25.09**	52.46 ± 0.49	34–68	−0.172	−1.162
	3	91.00	52.75	19.81**	66.65 ± 0.79	40–92	−0.328	−1.400
	4	102.25	64.25	15.15**	82.45 ± 1.01	50–115	−0.265	−1.314
	5	111.25	70.00	15.52**	90.10 ± 1.01	55–122	−0.243	−1.308
05DS	1	42.75	36.25	2.70*	39.06 ± 0.33	24–53	−0.080	−0.606
	2	55.00	39.50	6.20**	59.28 ± 0.65	37–80	−0.293	−1.261
	3	69.25	43.00	8.34**	76.87 ± 0.90	46–102	−0.418	−1.416
	4	90.75	53.25	14.39**	87.27 ± 1.02	48–118	−0.414	−1.330
	5	101.25	69.50	19.52**	93.97 ± 0.97	55–112	−0.385	−1.252

[a] 06WW: well-watered condition in 2006; 06DS: rainfed condition in 2006; 05DS: rainfed condition in 2005

"*" and "**" Significance at 0.05 and 0.01 probability levels, respectively

population were all less than 1 in absolute values (Table 1), suggesting that the trait approximately followed normal distributions, and the experimental data of this research were suitable for QTL analysis.

Unconditional QTL mapping for wheat plant height development

The chromosomal regions and estimated genetic effects of unconditional QTL affecting wheat plant height at different developmental stages evaluated in three environments are presented in Table 2 (additive QTLs) and Table 3 (epistatic QTLs), respectively. Independent analysis on the data coming from different environments indicated that only one main additive QTLs (*QPh.cgb-4D.1*) and one pair of epistatic QTLs (*QPh.cgb-1B.1–QPh.cgb-1B.3*) worked at all the five developing stages in three environments. Of these, *QPh.cgb-4D.1* expressed steadily in all growth stages in three environments, but had different effect values at the different developing stages. This QTL explained phenotypic variation from 7.88 to 16.43% of the total. However, the other additive QTL, *QPh.cgb-5B.2*, was detected only at the first stage under 06WW condition, which accounted for 3.80% of the total phenotypic variation. The epistatic QTLs, *QPh.cgb-1B.1* and *QPh.cgb-1B.3*, were detected at each of the five stages in 06WW environment, while the two QTLs were found only at stage 2 and 4 in 06DS environment. The contribution rate due to additive by additive interaction effect of these two QTLs varied from 3.66 to 4.86%. No epistatic QTL was detected under 05DS condition.

When the data of three environments were analyzed together, more QTLs significantly affecting plant height development were detected (Fig. 1), which included five additive QTLs (*QPh.cgb-1B.3*, *QPh.cgb-2B.1*, *QPh.cgb-2D.1*, *QPh.cgb-4D.1*, and *QPh.cgb-5B.2*) and eight pairs of epistatic QTLs (*QPh.cgb-1B.1–QPh.cgb-1B.3*, *QPh.cgb-2A.1–QPh.cgb-2D.1*, *QPh.cgb-2D.1–QPh.cgb-5B.2*, *QPh.cgb-1B.1–QPh.cgb-3D.2*, *QPh.cgb-2D.1–QPh.cgb-5B.1*, *QPh.cgb-1B.1–QPh.cgb-3D.1*, *QPh.cgb-2D.1–QPh.cgb-4D.1*, and *QPh.cgb-1B.3–QPh.cgb-3D.1*). Among them, an additive QTL, *QPh.cgb-4D.1*, and a pair of epistatic QTLs, *QPh.cgb-1B.1–QPh.cgb-1B.3*, were detected at all developing stages, and the contribution rate varied from 5.95 to 15.95% for the additive effect of the *QPh.cgb-4D.1*, and 2.01–3.48% for the epistatic effects of the paired QTLs, respectively. The other four additive QTLs, *QPh.cgb-5B.2*,

Table 2 Additive effect of QTL detected by unconditional mapping

Env.	QTL	Marker interval	S1[a]		S2		S3		S4		S5	
			A[b]	R^2 (%)[c]	A	R^2 (%)	A	R^2 (%)	A	R^2 (%)	A	R^2 (%)
06WW	*QPh.cgb-4D.1*	*Xgwm192–Xgwm165*	1.80	10.88	3.63	12.44	6.22	15.17	8.23	15.44	8.49	14.74
	QPh.cgb-5B.2	*Xgwm213–Xgwm371*	−1.09	3.80								
06DS	*QPh.cgb-4D.1*	*Xgwm192–Xgwm165*	1.41	7.88	3.65	13.58	6.28	14.70	8.36	16.43	7.93	14.34
05DS	*QPh.cgb-4D.1*	*Xgwm192–Xgwm165*	2.12	9.44	4.71	12.38	7.04	14.46	8.16	15.22	7.43	13.63
Three env.	*QPh.cgb-1B.3*	*Xgwm582–WMC156*	0.53	2.39								
	QPh.cgb-4D.1	*Xgwm192–Xgwm165*	1.69	5.95	3.84	10.12	6.44	14.10	8.15	15.95	8.34	13.96
	QPh.cgb-5B.2	*Xgwm213–Xgwm371*	−0.84	1.44	−1.56	1.51						
	QPh.cgb-2B.1	*WMC477–WMC272*					1.81	1.14	2.06	0.88		
	QPh.cgb-2D.1	*BARC168–WMC18*									3.13	1.47

[a] The first measure time, i.e. stage 1, S2 indicates the second measure time, i.e. stage 2 and so on

[b] Additive effect

[c] Rate of contribution. Hereinafter same

Table 3 Epistatic effects of QTLs detected by unconditional mapping

Env.	QTL_i	Marker interval	QTL_j	Marker interval	S1		S2		S3		S4		S5	
					AA[a]	R^2 (%)	AA	R^2 (%)	AA	R^2 (%)	AA	R^2 (%)	AA	R^2 (%)
06WW	*QPh.cgb-1B.1*	*Xgwm131–Xgwm273*	*QPh.cgb-1B.3*	*Xgwm582–WMC156*	1.23	4.86	1.91	3.96	2.99	3.99	3.75	3.66	4.45	4.19
06DS	*QPh.cgb-1B.1*	*Xgwm131–Xgwm273*	*QPh.cgb-1B.3*	*Xgwm582–WMC156*			1.93	4.17			3.69	3.66		
Three env.	*QPh.cgb-1B.1*	*Xgwm131–Xgwm273*	*QPh.cgb-1B.3*	*Xgwm582–WMC156*	0.92	2.01	1.97	2.97	3.39	3.18	3.83	3.48	3.80	3.41
	QPh.cgb-2A.1	*Xgwm275–Xgwm425*	*QPh.cgb-2D.1*	*BARC168–WMC18*	0.73	1.62			1.86	1.71			2.84	1.71
	QPh.cgb-2D.1	*BARC168–WMC18*	*QPh.cgb-5B.2*	*Xgwm213–Xgwm371*	0.57	0.79	1.14	0.97					2.82	1.51
	QPh.cgb-1B.1	*Xgwm131–Xgwm273*	*QPh.cgb-3D.2*	*Xgdm8–Xgwm645*					1.85	1.02				
	QPh.cgb-2D.1	*BARC168–WMC18*	*QPh.cgb-5B.1*	*Xgwm67–Xgwm213*					2.34	2.25	3.02	2.48		
	QPh.cgb-1B.1	*Xgwm131–Xgwm273*	*QPh.cgb-3D.1*	*Xgwm341–Xgdm8*							2.44	1.05		
	QPh.cgb-2D.1	*BARC168–WMC18*	*QPh.cgb-4D.1*	*Xgwm192–Xgwm165*									−2.07	1.31
	QPh.cgb-1B.3	*Xgwm582–WMC156*	*QPh.cgb-3D.1*	*Xgwm341–Xgdm8*									3.07	2.21

[a] Interaction effect of additive by additive

QPh.cgb-2B.1, *QPh.cgb-1B.3* and *QPh.cgb-2D.1*, were identified at stage 1 and 2, stage 3 and 4, stage 1 and stage 5, respectively. *QPh.cgb-2D.1–QPh.cgb-5B.2*, another pair of epistatic QTLs, were detected at stage 1, 2, and 5, while the epistatic QTLs, *QPh.cgb-2A.1–QPh.cgb-2D.1*, were found at stage 1, 3, and 5. The paired QTLs with epistatic effect detected only in two stages were *QPh.cgb-2D.1–QPh.cgb-5B.1* at stage 3 and 4. The four pairs of epistatic QTLs detected only at one stage were *QPh.cgb-1B.1–QPh.cgb-3D.2*

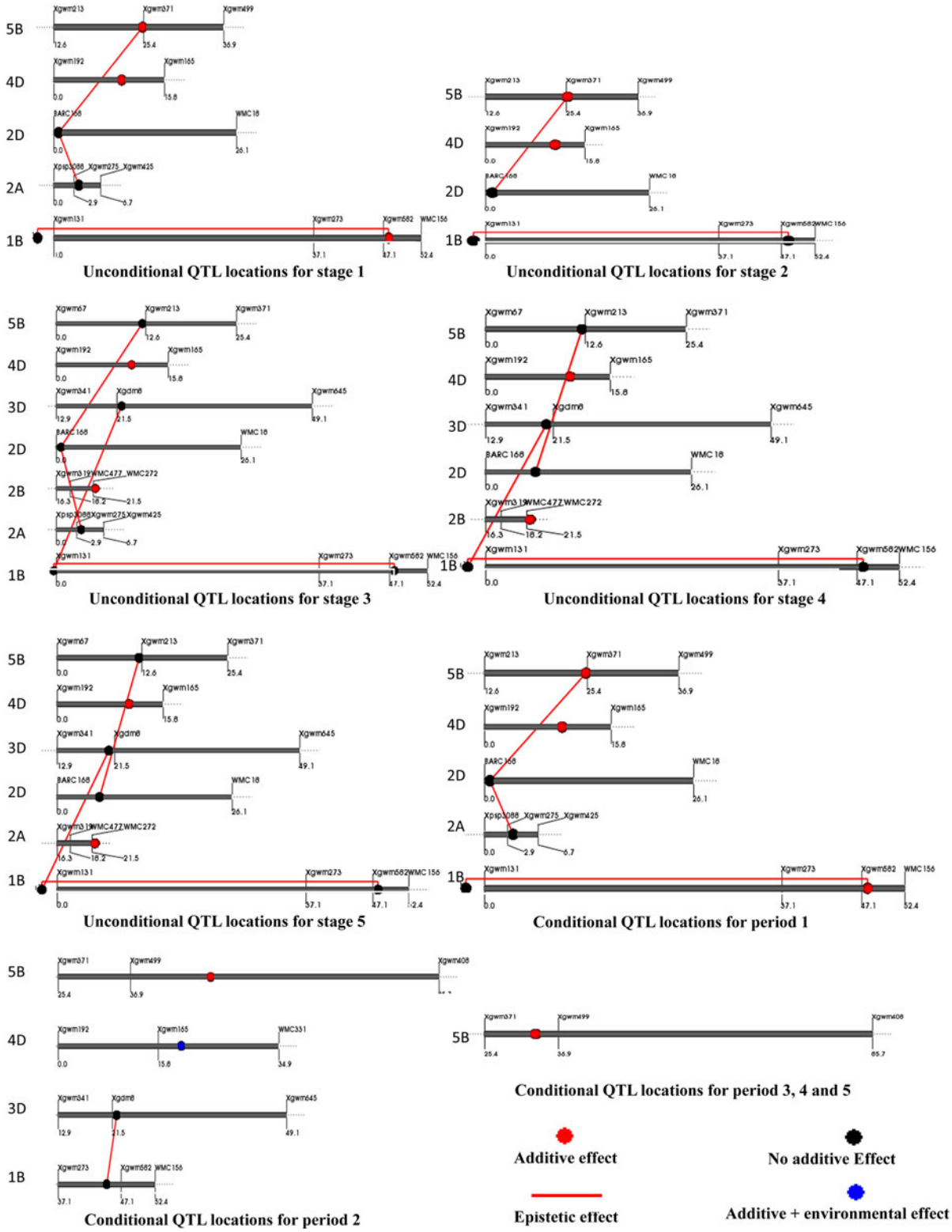

Fig. 1 Chromosome locations of QTLs affecting wheat plant height

at stage 3, *QPh.cgb-1B.1–QPh.cgb-3D.1* at stage 4, *QPh.cgb-1B.3–QPh.cgb-3D.1* and *QPh.cgb-2D.1–QPh.cgb-4D.1* at stage 5, respectively.

As described above, it is clear that some QTLs detected by integrated analysis using data of all three environments were not found by separate analysis based on each data of single environment indicating that wheat plant height is significantly controlled by genotype and environment interactions. At a given environment, the total effect of a QTL on the trait include the genetic main effects and *QE* interaction at that environment. Here, QTLs detected with genetic main effects revealed that genes at these genomic regions would express independent of environments. However, QTLs detected with *QE* interaction effects demonstrated that the gene expression at these loci was environment-dependent. In the present study, *QPh.cgb-4D.1* in all three environments, *QPh.cgb-1B.1–QPh.cgb-1B.3* (epistatic QTLs) in two environments, and *QPh.cgb-5B.2* only in one environment were detected by genetic main effect. The QTLs detected by *QE* interaction effect included three additive QTLs (*QPh.cgb-1B.3*, *QPh.cgb-2B.1* and *QPh.cgb-2D.1*) and seven pairs of epistatic QTLs (*QPh.cgb-2A.1–QPh.cgb-2D.1*, *QPh.cgb-2D.1–QPhcgb-5B.2*, *QPh.cgb-1B.1–QPh.cgb-3D.2*, *QPh.cgb-2D.1–QPh.cgb-5B.1*, *QPh.cgb-1B.1–QPh.cgb-3D.1*, *QPh.cgb-2D.1–QPh.cgb-4D.1* and *QPh.cgb-1B.3–QPh.cgb-3D.1*). Therefore, integrated analysis all phenotypic values of different environments is a more effective method to map QTL for developmental behavior of the target trait, and the independent analysis of phenotypic values of different environments is just a better way to find the common QTLs for the trait in a given environment. At the same time, the results of the unconditional QTL mapping suggest that more QTLs could be detected from phenotypic data collected at different time points across plant development than at the final stage. The detection of different QTLs at different stages indicates that genes governing wheat plant height might be expressed differently during the growth season.

Conditional QTL mapping for wheat plant height development

Plant height at a specific stage is the accumulated result of genetic main effects and *QE* effects at all previous stages. Such cumulative gene effects can be inferred by unconditional QTL mapping. However, the temporal expression patterns of the related genes cannot be fully revealed by the unconditional QTL mapping. The conditional genetic effects at time t given the phenotypic values observed at $(t-1)$ will indicate the net effects of gene expression from time $(t-1)$ to t, which are independent of the casual effects (Zhu 1995). Therefore, conditional QTL will reveal the gene expression at the specific period from time $(t-1)$ to t at that locus. QTL detected at period 1 indicates the cumulative gene expression from the initial time to the time point. Thus, these QTLs were equivalent to the unconditional QTLs at stage 1. QTL detected at period 2 conditioned on period 1 indicates the net effects of gene expression at the period from the first measuring time to the second measuring time and so on.

In order to identify the temporal expression patterns of the genes associated with wheat plant height development, conditional QTL mapping approach was further employed in this study. Total five, three and three additive QTLs significantly affecting plant height were detected in 06WW, 06DS, and 05DS environments, respectively (Table 4). Of these, two QTLs (*QPh.cgb-4D.1*, *QPh.cgb-5B.3*) were detected in all three environments, although the expression periods of *QPh.cgb-5B.3* showed some different in three environments.

When the data of three environments were analyzed together, total of six additive QTLs (Table 4) and four pairs of epistatic QTLs (Table 5) were detected (Fig. 1). Among them, three additive QTLs, *QPh.cgb-1B.3*, *QPh.cgb-4D.1* and *QPh.cgb-5B.2*, were detected at period 1 (from the initial time to the first measuring time point), which were identical with unconditional additive QTLs at stage 1. Two additive QTLs, *QPh.cgb-4D.2* and *QPh.cgb-5B.4*, were detected at period 2 (from the first measuring time point to the second measuring time point). Only one additive QTL, *QPh.cgb-5B*, was detected at the last three periods (period 3, period 4, period 5). In addition, QTL *QPh.cgb-4D.2* at period 2 showed not only additive main effects but also *QE* effects. For epistatic QTLs, *QPh.cgb-1B.1–QPh.cgb-1B.3*, *QPh.cgb-2A.1–QPh.cgb-2D.1* and *QPh.cgb-2D.1–QPh.cgb-5B.2* were detected at period 1, while *QPh.cgb-1B.2–QPh.cgb-3D.2* was found at period 2. Notably, three pairs of epistatic QTLs (*QPh.cgb-2A.1–QPh.cgb-2D.1*, *QPh.cgb-2D.1–QPh.cgb-5B.2* and *QPh.cgb-1B.2–QPh.cgb-3*) detected by integrated analysis on

Table 4 Additive effects of QTLs detected by conditional mapping

Env.	QTL	Marker interval	S1|S0[a]		S2|S1		S3|S2		S4|S3		S5|S4	
			A	R^2 (%)	A	R^2 (%)	A	R^2 (%)	A	R^2 (%)	A	R^2 (%)
06WW	*QPh.cgb-4D.1*	*Xgwm192–Xgwm165*	1.80	10.88								
	QPh.cgb-5B.2	*Xgwm213–Xgwm371*	−1.09	3.80								
	QPh.cgb-1B.3	*Xgwm582–Xgwm156*			−0.75	5.03						
	QPh.cgb-5B.4	*Xgwm499–Xgwm408*			1.191	3.56			1.158	5.24		
	QPh.cgb-5B.3	*Xgwm371–Xgwm499*									1.33	5.98
06DS	*QPh.cgb-4D.1*	*Xgwm192–Xgwm165*	1.41	7.88								
	QPh.cgb-5B.4	*Xgwm499–Xgwm408*					0.72	4.37				
	QPh.cgb-5B.3	*Xgwm371–Xgwm499*							0.81	4.01	1.50	9.43
05DS	*QPh.cgb-4D.1*	*Xgwm192–Xgwm165*	2.12	9.44								
	QPh.cgb-4D.2	*Xgwm165–WMC331*			1.13	4.16						
	QPh.cgb-5B.3	*Xgwm371–Xgwm499*					1.25	6.41				
Three env.	*QPh.cgb-1B.3*	*Xgwm582–WMC156*	0.53	2.39								
	QPh.cgb-4D.1	*Xgwm192–Xgwm165*	1.69	5.95								
	QPh.cgb-5B.2	*Xgwm213–Xgwm371*	−0.84	1.44								
	QPh.cgb-4D.2	*Xgwm165–WMC331*			0.56	0.77						
	QPh.cgb-5B.4	*Xgwm499–Xgwm408*			1.05	1.84						
	QPh.cgb-5B.3	*Xgwm371–Xgwm499*					0.74	2.71	0.76	2.76	1.15	3.17

[a] The time interval from the initial time of plant growth to stage 1, i.e. period 1; S2|S1 the time interval from stage 1 to stage 2, i.e. period 2 and so on

all the data were not detected when phenotypic values in three environments were analyzed independently. These results from conditional QTL mapping also evidence that using all phenotypic data obtained in different environments is an effective method to map QTL for developmental traits.

Overall, five additive QTLs and eight pairs of epistatic QTLs significantly affecting plant height growth were detected by unconditional QTL mapping method, while six additive QTLs and four pairs of epistatic QTLs were detected by conditional mapping method. Of them, three additive QTLs (*QPh.cgb-1B.3*, *QPh.cgb-4D.1*, *QPh.cgb-5B.2*) and three pairs of epistatic QTLs (*QPh.cgb-1B.1–QPh.cgb-1B.3*, *QPh.cgb-2A.1–QPh.cgb-2D.1*, *QPh.cgb-2D.1–QPh.cgb-5B.2*) are common QTLs detected by two different methods. Two additive QTLs (*QPh.cgb-2B.1*, *QPh.cgb-2D.1*) and five pairs of epistatic QTLs (*QPh.cgb-1B.1–QPh.cgb-3D.2*, *QPh.cgb-2D.1–QPh.cgb-5B.1*, *QPh.cgb-1B.1–QPh.cgb-3D.1*, *QPh.cgb-2D.1–QPh.cgb-4D.1*, *QPh.cgb-1B.3–QPh.cgb-3D.1*) were identified only by unconditional mapping method, whereas three additive QTLs (*QPh.cgb-4D.2*, *QPh.cgb-5B.3*, *QPh.cgb-5B.4*) and one pairs of epistatic QTLs (*QPh.cgb-1B.2–QPh.cgb-3D.2*) were identified only by conditional mapping. The result indicated that combining unconditional and conditional mapping methods could reveal the dynamic gene expression for quantitative traits.

Discussion

Plant height is an important agronomic trait for morphogenesis and grain yield formation in cereal crops, which is controlled by both Mendelian genes and quantitative genes. To date, none of the quantitative genes for wheat plant height is identified biochemically and physiologically although *Rht-B1b* and *Rht-D1b* responsible for the reduced plant height have been cloned and functionally characterized (Boerner et al. 1996; Peng et al. 1999). Recently, a number of QTLs affecting wheat plant height have been detected by QTL mapping (Ahmed et al. 2000; Zhang et al. 2008). Most of those QTL analysis just used the phenotypic data at the harvest stage, which did not reveal dynamic expressions of the QTLs during the development of the trait. In the present

Table 5 Epistatic effects of QTLs detected by conditional mapping

Env.	QTL_i	Marker interval	QTL_j	Marker interval	S1|S0		S2|S1	
					AA	R^2 (%)	AA	R^2 (%)
06WW	*QPh.cgb-1B.1*	*Xgwm131–Xgwm273*	*QPh.cgb-1B.3*	*Xgwm582–WMC156*	1.23	4.86		
Three env.	*QPh.cgb-1B.1*	*Xgwm131–Xgwm273*	*QPh.cgb-1B.3*	*Xgwm582–WMC156*	0.92	2.01		
	QPh.cgb-2A.1	*Xgwm275–Xgwm425*	*QPh.cgb-2D.1*	*BARC168–WMC18*	0.73	1.62		
	QPh.cgb-2D.1	*BARC168–WMC18*	*QPh.cgb-5B.2*	*Xgwm213–Xgwm371*	0.57	0.79		
	QPh.cgb-1B.2	*Xgwm273–Xgwm582*	*QPh.cgb-3D.2*	*Xgdm8–Xgwm645*			0.67	1.35

study, the unconditional and conditional QTL mapping methods were employed to investigate the developmental behavior of wheat plant height over the whole growth season under different field conditions and the main-effect QTLs with potential for MAS in breeding program.

The present data showed that the genes controlling wheat plant height had an obvious dynamic characteristic as the development. The number of the QTLs and their effects on the trait both were different at different period. For example, by conditional method, three additive QTLs detected at period 1 and only one at the final period (Table 4). The QTL *QPh.cgb-5B.3* explained 2.71, 2.76 and 3.17% of total phenotypic variation at period 3, 4 and 5, respectively. Total of six additive QTLs and four pairs of epistatic QTLs were identified by conditional QTL analysis. None of them were simultaneously detected at any particular developmental period, nor was any QTL detected at all the five periods. Five additive QTLs (*QPh.cgb-1B.3*, *QPh.cgb-4D.1*, *QPh.cgb-4D.2*, *QPh.cgb-5B.2* and *QPh.cgb-5B.4*) and three pairs of epistatic QTLs (*QPh.cgb-1B.1–QPh.cgb-1B.3*, *QPh.cgb-2A.1–QPh.cgb-2D.1* and *QPh.cgb-2D.1–QPh.cgb-5B.2*) were not identified at the final period. These results indicated that some QTLs function for a short time, some work for a longer period under very specific situation, but none of genes controlling plant heights could express throughout the entire growth process. It is consistent with theory of developmental genetics that gene expresses selectively at different developmental periods.

In addition, the expression of some QTLs may be varied at different stages. For example, additive QTL, *QPh.cgb-2D.1*, acted at some stages (e.g. stage 5), but also had epistatic effects with other four QTLs (*QPh.cgb-2A.1*, *QPh.cgb-5B.2*, *QPh.cgb-5B.1* and *QPh.cgb-4D.1*) at some stages (stages1, 2, 3 and 5). However, six epistatic QTLs (*QPh.cgb-1B.1*, *QPh.cgb-1B.2*, *QPh.cgb-2A.1*, *QPh.cgb-3D.1*, *QPh.cgb-3D.2*, *QPh.cgb-5B.1*) showed no additive effects at any stage tested here. This kind of epistatic QTLs might be considered as modifying gene.

QTL epistasis and QTL environment interaction profoundly affect plant development, especially those quantitative traits. It was reported that epistatic QTLs and *QE* interaction influenced *Brassica* flowering time (Long et al. 2007), rice tiller number (Yan et al. 1998a; Wu et al. 1999) and plant height development (Yan et al. 1998b; Cao et al. 2001). Compared with those studies by only analyzing the main effects of individual QTLs, our integrate approach revealed that an epistatic effect existed extensively during the whole period of growth for the developmental behavior of wheat plant height. As mentioned above, total eight pairs of epistatic QTLs were identified. The reason for so much epistasis might be that QTL interactions occur at different stages under certain situations. The interaction between QTLs and background or modifying loci might be the prevalent form of epistasis affecting the behavior of quantitative traits (Doebley et al. 1995; Yu et al. 1997).

Regarding QTL environment interaction, no strong effect was detected to affect wheat plant height in this study although the trait varied in the RIL population in three environments. Most QTL obtained in three environments were found to have genetic main effects. Only one conditional QTL (*QPh.cgb-4D.2*) (Fig. 1) at the period 2 showed an obvious interaction with environment although eight QTLs were detected in three environments. This indicated that wheat plant height QTLs detected here showed no obvious interaction with environment. The similar phenomenon was also found by Yan et al. (2003). They found some different plant height of maize between two different locations, but only one QTL detected for

plant height showed obvious interaction with environment. They explained this phenomenon in the following two possible reasons: (1) QTLs with strong effect rarely interact with environment because of their major effect, and the interactions between environment and QTLs with weak effect were masked by other effects due to the limitation of the statistical method. (2) The plant height possesses a high heritability capacity and is a little affected by environment.

Under two different water conditions, QTLs for wheat plant height showed some difference. Five additive QTLs, *QPh.cgb-1B.3*, *QPh.cgb-4D.1*, *QPh.cgb-5B.2*, *QPh.cgb-5B.3* and *QPh.cgb-5B.4*, were detected under well watered condition. And four additive QTLs, *QPh.cgb-4D.1*, *QPh.cgb-4D.2*, *QPh.cgb-5B.3* and *QPh.cgb-5B.4*, were identified under drought stress condition. Of these QTLs, two (*QPh.cgb-1B.3*, *QPh.cgb-5B.2*) are specific for well watered condition, while one (*QPh.cgb-4D.2*) is specific for drought stress condition. Three (*QPh.cgb-4D.1*, *QPh.cgb-5B.3* and *QPh.cgb-5B.4*) are simultaneously identified under both environments. These specific or common main-effect QTLs can be used in wheat plant height breeding with molecular marker assisted selection.

Both unconditional and conditional QTL mapping were performed in this study so that we could get more understanding on the mechanism underlying wheat plant height development. Unconditional mapping can detect the accumulated result of genetic main effects and *QE* effects at the measuring time *t*. The conditional mapping can reveal the gene expression at the specific period from time $(t - 1)$ to t at that locus, reflecting the net effects of gene expression from time $(t - 1)$ to t. Here, three additive QTLs (*QPh.cgb-4D.2*, *QPh.cgb-5B.3* and *QPh.cgb-5B.4*) and one pair of epistatic QTLs (*QPh.cgb-1B.2–QPh.cgb-3D.2*) were detected by conditional mapping method, but weren't detected by unconditional mapping strategy. One possible explanation is that genes with very small genetic effects in a certain growth period would be undetectable by the unconditional approach. In contrast, two additive QTLs (*QPh.cgb-2B.1*, *QPh.cgb-2D.1*) and five pairs of epistatic QTLs (*QPh.cgb-1B.1–QPh.cgb-3D.2*, *QPh.cgb-2D.1–QPh.cgb-5B.1*, *QPh.cgb-1B.1–QPh.cgb-3D.1*, *QPh.cgb-2D.1–QPh.cgb-4D.1*, and *QPh.cgb-1B.3–QPh.cgb-3D.1*) were detected by unconditional mapping, but weren't identified by conditional mapping. One possible reason was that the genes with opposite genetic effects were expressed at the same or nearby locations at previous growth periods. As a result, the variation of cumulative gene effects could be diminished to the point of being undetectable. Therefore, a combination of conditional and unconditional mapping of QTL with the concept of genetic effects has provided us insight into the complexity of QTLs for the development of quantitative traits. In other words, dynamic mapping of QTLs based on both conventional and conditional methods would be a powerful tool to reveal the genetic expression of developmental behavior of quantitative traits.

The combination of developmental quantitative genetics and molecular linkage map makes it easier than ever to analyze the developmental behavior of important agronomic traits (Atchley and Zhu 1997; Price and Tomos 1997; Yan et al. 1998a, b; Cao et al. 2001). Selection of DNA markers is one of factors affecting the accuracy and efficiency of QTL mapping. In the present study, 28 SSR makers were selected from the seven genomic regions on different chromosomes of wheat genetic linkage map. All these genomic regions are important for wheat plant height, which were identified using a DH population derived from the same cross as that for the present RIL population. This genetic linkage map constructed using the DH population consisted of 395 marker loci, including 132 amplified fragment length polymorphisms (AFLP) and 263 simple sequence repeats (SSR) (Jing et al. 1999; Hao et al. 2003; Zhou et al. 2005; Yang et al. 2007a, b). The size of the RIL population used here is larger than that of the DH population. Mapping QTLs with those 28 makers covering the seven genomic regions in a bigger population could reduce the false positives, and also validate the QTLs identified previously using the DH population. Fortunately, all of the eight additives QTLs have been detected in the present study had already been confirmed by a combination of unconditional and conditional mapping methods in the same genomic regions of the DH population (Wu et al. 2010). Therefore, we could conclude that QTLs can be detected repeatedly in the different type of populations derived from the same parents to a certain extent and the QTLs identified here are authentic.

In conclusion, the most important merit of the present study is to uncover the dynamic characterization

of the main-effect and epistatic QTLs as well as their environmental interactions for wheat plant height under three different field conditions. Eight main-effect QTLs were identified using the two populations, having a potential for MAS and cloning the target gene in further fine mapping. Combining conditional and unconditional mapping strategies for QTL analysis could unravel more important information for understanding the molecular mechanism governing quantitative traits in plants.

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