Theor Appl Genet (2001) 103:153–160

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Impact of epistasis and QTL×environment interaction on the developmental behavior of plant height in rice (*Oryza sativa* L.)

Received: 19 May 2000 / Accepted: 27 October 2000

Abstract QTLs with epistatic effects and environmental interaction effects for the developmental behavior of plant height in rice were studied by conventional and conditional methods for quantitative trait loci (QTLs) by mapping with a doubled-haploid population of 123 lines from IR64/Azucena in three environments. The results showed that epistatic effects were important and most epistasis could be detected only by conditional QTL mapping, while most non–epistatic QTLs could be detected by both conventional and conditional methods. Many modificative QTLs showed only epistatic effects without their own additive effects at some stages. QTL×environment (*QE*) interaction effects were detected more often than QTL main effects for plant-height behavior, which might indicate that gene expression could be greatly affected by the environment. No QTLs had effects during the whole of ontogeny. Conditional QTL mapping might be a valid way to reveal dynamic gene expression for the development of quantitative traits, especially for epistatic effects.

Keywords Quantitative trait locus (QTL) · Epistatic effects · QTL by environment interaction effects · Developmental behavior · Conditional QTL mapping

Introduction

Plant height in rice is generally considered to be controlled by both qualitative and quantitative genes (Huang et al. 1996). At least 60 dwarfing genes, designated *d*–1 to *d*–60, have been identified in rice by classical genetic analysis (Kinoshita 1995). Some polygenes for the quantitative behavior of plant height and its components in rice were recently mapped on molecular linkage groups (Cho et al. 1994; Li et al. 1995; Xiao et al. 1995; Huang et al. 1996; Lin et al. 1996; Yan et al. 1998). Since the development of plant-height is controlled by genes expressed selectively at different growth stages, dynamic QTL mapping is needed to understand the genetics of plant height growth behavior. Zhu (1995) proposed conditional statistical methods for understanding the dynamics of the causal genetic effects and variance components in developmental quantitative traits. Using this methodology, Atchley and Zhu (1997) analyzed conditional epigenetic variability in mice, and Yan et al. (1998) detected QTLs with additive and/or additive by environment interaction effects for the developmental behavior of plant height.

Recently, epistatic effects were considered as important for complex traits by many researchers (Lark et al. 1995; Eshed and Zamir 1996; Cockerham and Zeng 1996; Yu et al. 1997). Hence, genetic models for QTL mapping assuming no epistasis could lead to a biased estimation of QTL parameters. QTL×environment interaction is another important component for quantitative traits. Significant *QE* interactions have been reported (Paterson et al. 1991; Lu et al. 1996; Zhuang et al. 1997; Yan et al. 1998). QTLs detected in one environment but not in another might indicate *QE* interaction (Veldboom and Lee 1996). But it is impossible to estimate the real *QE* interaction by simply comparing QTLs detected in multiple environments.

Zhu (1998) proposed an indirect method to map QTLs with *QE* effects using predicted total genotype×environment (*GE*) interaction effects. It was shown that some QTLs had both genetic main effects and *QE* interaction effects, even though they could be detected in two environments (Yan et al. 1998). Recently, a new methodology was proposed for directly mapping QTLs with additive and epistatic effects, as well as their *QE* interaction, based on mixed linear model approaches

Communicated by H.C. Becker

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(Wang et al. 1999; Zhu 1999), and the software QTLMapper version 1.0 was developed (Wang et al. 1999) for analyzing the experimental data.

In the present research, the dynamic behavior of plant height at different stages of rice were analyzed for detecting QTLs with additive and epistatic effects as well as their *QE* interaction effects by combining the statistical procedures for analyzing conditional genetic effects (Zhu 1995) and the QTL mapping method based on mixed model approaches (Wang et al. 1999; Zhu 1999). The temporal gene expressions including additive effects, additive×additive epistatic effects, and their *QE* interaction effects for plant height, are also discussed.

Materials and methods

Materials

A population of 123 DH lines derived from a cross between irrigated *indica* variety IR64 and upland *japonica* variety Azucena (Guiderdoni et al. 1992) was used in the experiments. IR64 is a semi-dwarf variety carrying the *sd*–1 gene (IRRI 1975). The genetic map of this population, containing 175 markers distributed among 12 chromosomes covering 2005 cM with an average distance of 11.5 cM between markers (Huang et al. 1997), was used for QTL mapping.

Field experiment

The 123 DH lines and their parents, IR64 and Azucena, were grown in a randomized complete design with two replications at Hainan Island in 1995, and at Hangzhou in 1996 and 1998. Hainan Island is located in the Southern China Sea at an 18° north latitude. Hangzhou is located in southeastern China at about a 30° north latitude. These two sites showed a great difference in climate, soil conditions, day length, and rice growing seasons. The experiment was conducted from early December 1995 to late April 1996 at Hainan, where rice can grow well all year round. At Hangzhou, experiments were carried out from late May to early November in 1996 and middle May to middle October in 1998.

In all environments, the germinated seeds were sown in a seedling bed and the seedlings were transplanted to a paddy field 30 days later, with a single plant per hill spaced at 15×20 cm. Each plot included three to four lines with eight plants per line. After transplanting, plant height (from the surface of the soil to the tip of the plant) was measured every 10 days for the five central plants (fixed through all growth stages) of each plot until heading. A total of nine measurements were conducted during the whole rice growth period.

Statistical analysis

QTLs with additive and additive×additive epistatic effects, as well as their environmental interaction effects in the DH population, were mapped by QTLMapper version 1.0 (Wang et al. 1999). For conventional analysis of plant height at the final stage (90 days after transplanting), the phenotypic value of the *k*–th DH line in environment *h* can be partitioned by the following mixed linear model (Zhu 1999)

$$\begin{aligned} y_{hk} = {} & \mu + a_i x_{A_{ik}} + a_j x_{A_{jk}} + aa_{ij} x_{AA_{ijk}} \\ & + u_{E_{hk}} e_{E_h} + u_{A_i E_{hk}} e_{A_i E_h} + u_{A_j E_{hk}} e_{A_j E_h} + u_{AA_{ij} E_{hk}} e_{AA_{ij} E_h} \\ & + \sum_{f(h)} u_{M_{fk(h)}} e_{M_{f(h)}} + \sum_{l(h)} u_{MM_{lk(h)}} e_{MM_{l(h)}} + \varepsilon_{hk}, \end{aligned} \tag{1}$$

where μ is the population mean; a_i and a_j are the additive effects (fixed effects) of two putative loci Q_i and Q_j, respectively; aa_{ij} is the additive×additive epistatic effect (fixed effect) between the two loci; $x_{A_{ik}}$, $x_{A_{jk}}$ and $x_{AA_{ijk}}$ are the coefficients of these genetic main effects; e_{E_h} is the random effect of environment h with a coefficient $u_{E_{hk}}$; $e_{A_iE_h}$ (or $e_{A_jE_h}$) is the random additive×environment interaction effect with a coefficient $u_{A_iE_{hk}}$ (or $u_{A_jE_{hk}}$) for Q_i (or Q_j); $e_{AA_{ij}E_h}$ is the random epistasis×environment interaction effect with a coefficient $u_{AA_{ij}E_{hk}}$; $e_{M_{f(h)}}$ is the random effect of marker f nested within the h–th environment with a coefficient $u_{M_{fk(h)}}$, $e_{MM_{l(h)}}$ is the random effect of the l–th marker×marker interaction nested within the h–th environment with a coefficient $u_{MM_{lk(h)}}$; ε_{hk} is the random residual effect. The marker factors $e_{M_{f(h)}}$ and $e_{MM_{l(h)}}$ in the model are used to absorb additive and epistatic effects of background QTLs for controlling the noise. The QTLs detected by this conventional mapping method would indicate the cumulative gene effects from the initial time to the final time (90 days after transplanting).

Conditional QTL analysis was conducted with the phenotypic value at time *t*, given the phenotypic behavior at time (*t*–1), using QTLMapper version 1.0 (Wang et al. 1999). Like that in Equation (1), the conditional value $y_{hk(t|t-1)}$ can be partitioned as

$$\begin{aligned} y_{hk(t|t-1)} = {} & \mu_{(t|t-1)} + a_{i(t|t-1)} x_{A_{ik}} + a_{j(t|t-1)} x_{A_{jk}} + aa_{ij(t|t-1)} x_{AA_{ijk}} \\ & + u_{E_{hk}} e_{E_{h(t|t-1)}} + u_{A_i E_{hk}} e_{A_i E_{h(t|t-1)}} + u_{A_j E_{hk}} e_{A_j E_{h(t|t-1)}} \\ & + u_{AA_{ij} E_{hk}} e_{AA_{ij} E_{h(t|t-1)}} + \sum_{f(h)} u_{M_{fk(h)}} e_{M_{f(h)(t|t-1)}} \\ & + \sum_{l(h)} u_{MM_{lk(h)}} e_{MM_{l(h)(t|t-1)}} + \varepsilon_{hk(t|t-1)}, \end{aligned} \tag{2}$$

with all the parameters defined as conditional effects. The QTLs detected by conditional mapping will reflect the net expression of genes during the time period from time (*t*–1) to time *t*, independent of the genetic effects before time (*t*–1).

The conditional phenotypic value ($y_{hk(t|t-1)}$ of plant-height behavior was obtained by the mixed model approaches for the conditional genetics of developmental quantitative traits (Zhu 1995). The likelihood-ratio threshold was chosen at α=0.01 for claiming putative QTLs, of which their genetic effects were further tested by a *t*-test with the jack-knifing re-sampling procedure. QTLs were presented when genetic main effects (*a* and *aa*) or *QE* interaction effects (*ae* and *aae*) were significantly different from zero (P≤0.01).

Results

Phenotypic variation

The phenotypic values of plant height for the DH population and its parents at nine measuring stages were collected in three environments (data not shown). The parent Azucena showed a greater plant height than IR64 at all stages in all three environments. Both DH lines and their parents had a lower plant height in Hainan at all stages than in Hangzhou for 1996 and 1998, with plant height being slightly shorter in 1996 than in 1998. The plant height of the DH population segregated continuously and both skewness and kurtosis values were less than 1.0 at most stages, which suggested that the plant-height behavior of the DH population was suitable for QTL analysis. Transgressive segregants from lines higher than the tall parent, Azucena, to lines lower than the short parent, IR64, were observed at all stages in all three environments.

QTLs for plant-height development

As a contrast for the conditional mapping of net QTL effects during different growth periods, conventional mapping was conducted for plant height at the final stage (the 9th stage) at which plant height was the accumulated result of genetic main effects and *QE* effects at all previous stages. The main effect is the accumulated effect expressed in the same way across different environments, while the interaction effect is the deviation due to a specific environment. At a specific environment, the total effect of a QTL could include the main effects plus *QE* interaction effects at that environment.

Seventeen QTLs with an additive main effect (*a*) and/or an additive×environment interaction effect (*ae*) were identified to specific chromosomal regions in the linkage map by conventional and conditional mapping (Table 1). For plant height they were named as “Ph” with the relevant chromosomal number. If there was more than one QTL in a chromosome, the serial number was added after the chromosomal number. Of the 17 QTLs, there were 12 affecting plant height at the final stage with *a* and/or *ae* effects, and these 12 QTLs also had conditional *a* and/or *ae* effects at some specific stages. The other five QTLs were found only by conditional mapping.

The 12 QTLs at the final stage were detected on 10 out of the 12 chromosomes (except chromosomes 11 and 12). Of these 12 QTLs, five had significant additive main effects at the 0.005 level, with one being positive (7.15 cm) and four negative (–3.7 to –16.27 cm). The short parent IR64 contributed alleles for decreasing plant height at QTLs Ph1–2, Ph3–2, Ph4–2 and Ph8, but for increasing plant height at Ph2–2. This suggested that alleles for plant height were dispersed within the two parents. Ten QTLs had significant *ae* interaction effects at the final stage. Of these ten QTLs, there was only one with *ae* effects in all three environments, while six QTLs had *ae* effects in two environments and three QTLs in only one environment. In Hainan, four QTLs had *ae* effects to decrease plant height, and three to increase. In Hangzhou, there were one decrease and three increases in 1996, whith four decreases and two increases in 1998. At the final stage, there were three QTLs (Ph1–2, Ph4–2 and Ph8) with both additive main effects (*a*) and additive *QE* interaction effects (*ae*).

All QTLs detected at the final stage were found to have both conditional *a* and *ae* effects at specific stages, except that QTL Ph10 had no *a* effect at any stage. Conditional effects, revealing the net effects of gene expression from time (*t*–1) to *t*, were selectively expressed at different stages. In Table 1, there were nine QTLs with conditional *a* and/or *ae* effects at about two to four stages, eight QTLs at five to seven stages. The conditional net effects of a QTL could have unequal magnitudes for gene effects at different stages, even in reverse directions, although usually the directions of the conditional effects were consistent with the final directions. QTLs with conditional effects for reverse directions might indicate that the expression of a gene or genes could change significantly during ontogeny, even counteracting each other, and result in the failure of detecting cumulative effects at the final stage. When combined with conditional mapping, more QTLs would be found than by only conventional mapping. In the present study, there were five QTLs with only conditional additive main effects and/or additive *QE* interaction effects, but without conventional effects.

In Table 1, ten QTLs had only conditional *a* effects without conventional *a* effect s, and seven QTLs had only conditional *ae* effects without conventional *ae* effects. The *ae* effects might be more extensive than the *a* effects. There were two QTLs (Ph10 and Ph11–1) with only *ae* effects but no *a* effects over the whole growing period, while no QTL with only *a* effects and no *ae* effects was found. This indicated that environments could affect the expression of genes for developmental traits.

Epistasis for plant-height development

Using QTLMapper version 1.0, additive×additive epistatic main effects (*aa*) and epistasis×environment interaction effects (*aae*) could be analyzed along with *a* main effects and *ae* interaction effects. In the present study, epistasis was found for only seven pairwise genes at final and previous stages by both conventional and conditional mapping methods. Most epistasis was only revealed at some specific stages by conditional mapping. This was markedly different from the situation of QTLs with *a* and/or *ae* effects, being detectable in most cases at both final and previous stages by both conventional and conditional mapping.

A total of 71 epistatic of pairwise genes (Table 2) were identified by conventional and/or conditional mapping, of which 60 did not appear at the final stage. Of the 11 epistatic genes found at the final stage, three were identified only by conventional mapping. The other eight were found by both conventional and conditional mapping methods, but at no more than three developmental stages (1.5 stages on average), less than the developmental stages at which additive effects of the QTLs were identified (4.75 stages on average). Of the 60 found only by the conditional method, epistatic effects of four pairs of QTLs (Ph1–2 Ph4–2, Ph1–2 Ph8, Ph3–1 Ph3–2 and Ph6–1 Ph8) were identified at two stages, the remainder could be identified at only one stage. This might indicate that epistatic effects existed mostly for a short time period, so that they would hardly be observed during different developmental stages. This was implied by the fact that short gene expression existed for epistatic effects but with long expression for additive effects and that modified genes could act mostly in very specific situations.

The epistasis×environment interaction effect (*aae*) was an important component of the total *QE* interaction effects. At the final stage, only six pairs of QTLs had both *aa* and *aae* effects, while four other pairs had only *aae* effects and one pair only an *aa* effect. It was shown that *aae* effects were more often detected than *aa* effects just as *ae* effects were more often detected than *a* effects. Sixty pairs of QTLs were detected with condition-

Table 1 Estimated additive (*a*) and additive×environment interaction (*ae*) effects of QTLs for plant height (cm) at final and specific stages in three environments. Final indicates the final stage (from initial time to 90 days), 90D|80D indicates the stage from 80 days to 90 days, and so on. QTL Ph6–1 and Ph11–2 were not listed in this Table because they had no *a* or *ae* effect

QTL	Marker interval	Distance (M)	Stage	*a* effect	*ae* in 95 Hainan	*ae* in 96 Hangzhou	*ae* in 98 Hangzhou
Ph1–1	RG532–	0.1	70D|60D	−0.73**			
	W1		60D|50D			0.43**	
			40D|30D				0.30*
Ph1–2	RZ730–	0.22	**Final**	**−16.27****	**−0.99***		**1.08***
	RZ801		80D|70D	−0.77**	−1.19**		1.30**
			70D|60D	−1.02**	−0.78**	0.83**	
			60D|50D	−1.62**		−1.05**	
			40D|30D	−1.08**	0.85**		−1.03**
			30D|20D			0.93**	
			20D|10D		−0.73**		0.81**
			10D|Initial	−2.85**		1.47**	−1.49**
Ph2–1	RG437–	0	50D|40D	0.62**			
	RG544		30D|20D	−0.54**			
			20D|10D		0.56**	−0.74**	
Ph2–2	Amy1AC–	0.04	**Final**	**7.15****			
	RG95		50D|40D	0.44*	0.47*	−0.59*	
			40D|30D			−0.32**	
			10D|Initial			0.49**	−0.55**
Ph3–1	RZ574–	0.36	**Final**		**−2.68****		
	RZ284		90D|80D	0.48*	−0.64**		
			70D|60D	−0.57*			
			60D|50D			−1.42**	1.51**
			30D|20D	0.7**			
			10D|Initial	1.03**	−0.86**		
Ph3–2	Pgi–1–	0.06	**Final**	**−5.08****			
	CDO87		90D|80D		−0.68**	1.05**	
			70D|60D		0.88**	1.83**	−2.71**
			60D|50D			−2.34**	2.52**
			50D|40D	0.56**			
			40D|30D		−1.18**		
			30D|20D	−1.19**			0.58**
			20D|10D	−0.56**			
Ph4–1	RG218–	0	**Final**			**−0.93****	**2.56****
	RZ262		80D|70D			−1.78**	1.07**
			70D|60D		−0.57**	0.8**	−0.28**
			60D|50D			0.29*	−0.40*
			50D|40D	0.93**	1.03**	−0.98**	
			40D|30D		0.4**	−1.12**	0.72**
Ph4–2	RZ590–	0	**Final**	**−4.88****	**2.54****		
	RG214		80D|70D	0.81*			1.09**
			60D|50D			0.89**	
			40D|30D		0.84**		−0.89**
			30D|20D	−1.82**			
			10D|Initial	−1.14**		−1.10**	
Ph5	RZ649–	0.2	**Final**		**−1.99****	**1.74****	
	RZ67		60D|50D		−0.30**	0.30**	
			50D|40D			−0.63**	
			40D|30D			−0.28*	
			20D|10D	0.49**	0.62**		
Ph6–2	RG653–	0.1	**Final**		**−2.8****	**3.76****	
	Amy2 A		90D|80D		−0.23*		
			50D|40D	0.87**		1.08**	
			40D|30D				0.80**
Ph7–1	RG511–	0.16	80D|70D	0.79*	−1.3**		
	RG477		50D|40D			0.22**	
Ph7–2	CDO418–	0.08	**Final**		**1.95****	**2.16****	**−4.00****
	RZ978		70D|60D		0.5**	0.47**	−0.97**
			40D|30D	−0.75**			
			10D|Initial	0.78*			

Table 1 (continued)

QTL	Marker interval	Distance (M)	Stage	*a* effect	*ae* in 95 Hainan	*ae* in 96 Hangzhou	*ae* in 98 Hangzhou
Ph8	Amy3DE–RZ66	0.1	**Final**	–3.7**		2.74**	–2.39**
			90D|80D	–0.54*	0.59*		
			80D|70D		–0.64**	0.95**	
			60D|50D	–0.88**		0.59**	–0.74**
			50D|40D			1.08**	
			40D|30D			–0.33**	0.34**
			20D|10D		–0.66**	–0.17**	0.83**
			10D|Initial		0.37**		
Ph9	RZ422–Amy3ABC	0.24	**Final**		1.94**		–1.94**
			80D|70D		1.17*		–1.08**
			70D|60D	–0.99**	–0.26*		
			60D|50D			–0.24**	0.45**
			40D|30D		0.43**	0.25**	–0.66**
			30D|20D	0.56**			
			20D|10D			–0.24**	0.24**
Ph10	RG134–RZ500	0.02	**Final**				–0.95**
			80D|70D				–0.18**
			60D|50D		1.23**		–0.97**
Ph11–1	CDO127–RZ638	0	50D|40D		0.2*	0.98**	–1.09**
			20D|10D			–0.27**	
Ph12	RG901–CDO344	0	70D|60D	0.77**			
			60D|50D			1.02**	
			50D|40D	0.93**			
			40D|30D			–0.32**	
			30D|20D			–0.71*	0.53*
			20D|10D		–0.54**		
			10D|Initial	–0.94*	1.43**		–0.99*

* $P<0.01$ and ** $P<0.005$, respectively

al epistatic effects, with only 23 pairs having both *aa* and *aae* effects, 30 pairs having only *aae* effects, and seven pairs having only *aa* effects. This is consistent with the situation at the final stage where *aae* interaction effects were more often detectable than *aa* main effects. This also indicated that environments could greatly affect the gene expression for epistatic effects on developmental traits.

QTLs involved in epistasis could have no additive or additive by environment interaction effects. There were two QTLs (Ph6–1 and Ph11–2) involved in epistasis but with no *a* or *ae* effects at any stage. These were located between the marker intervals *Amp–3–Est–2* and *RG1109–RZ536*, respectively. The distances of these two QTLs from the left marker were 0 and 0.14 Morgans, respectively. These kind of QTLs might be considered as modifying genes. But other QTLs with their own effects (*a* and/or *ae*) could also have modifying effects at some specific stages. For example, Ph2–2 had no *a* or *ae* effects during stages from 50 days (50D) to 90 days (90D), but with epistatic effects (*aa* and/or *aae*) with three QTLs (Ph3–1, Ph2–1 and Ph11–2) at the stage of 80D–90D, two QTLs (Ph3–2 and Ph6–1) at the stage of 60D–70D, and one QTL (Ph8) at stage of 50D–60D, respectively. By conditional analysis of QTLs with *aa* and *aae* effects, gene expression modified by other genes or environments could be appropriately studied for developmental traits.

Discussion

In the present study, we used a new method for mapping QTLs with additive and epistatic effects, as well as their *QE* interaction effects, for developmental behavior. This analytical method, compared with those involved studying only the main effects of individual QTLs, might reveal more important information for plant breeding.

Epistasis was recognized as early as 90 years ago by Bateson (1909) to describe the situation where the action of one locus masks the allelic effects at another locus. But in classical statistical genetics, epistasis was used as a statistical abstraction, so that less attention was paid to the molecular and physiological nature of the gene interactions involved (Tachida and Cockerham 1989). Now, however, studies of QTLs have begun to bridge the gap between continuous variation within populations and the genetic mechanisms that generate that variation (Phillipsa 1998). It was shown by the results of the present study that an epistatic effect (*aa* or *aae*) existed extensively during the whole period of growth for the developmental behavior of plant height. The reason for so much epistasis might be that QTLs interact with each other at different stages under certain situations. This support the possibility that 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).

Table 2 Estimated epistatic (*aa*) and epistasis × environment interaction (*aae*) effects of QTLs for plant height (cm) at final and specific stages in three environments

QTL$_i$	QTL$_j$	Stage	*aa* effect	*aae* in 95 Hainan	*aae* in 96 Hangzhou	*aae* in 98 Hangzhou
Ph1–1	Ph1–2	**Final**		**–1.21****		
		80D|70D		–0.55**		0.30**
	Ph3–2	60D|50D				0.41**
	Ph7–2	90D|80D	–0.43**	0.43**		–0.58**
	Ph8	50D|40D			–0.23**	0.24**
	Ph9	**Final**		**–1.46****	**4.23****	**–3.69****
		90D|80D	–0.31*		–0.79**	
		80D|70D			´ 1.41**	–1.41**
Ph1–2	Ph2–1	10D|Initial	–0.92**	0.25**		
	Ph3–1	10D|Initial	–0.89*			
	Ph4–2	80D|70D				0.57*
		20D|10D	–0.33*	–0.58**	0.49**	0.28**
	Ph6–2	70D|60D	0.73**		–0.81**	0.52**
	Ph7–2	80D|70D			–0.87**	0.78**
	Ph8	70D|60D	–0.99**	1.08**	–0.84**	
		60D|50D		– 1.37**	1.17**	
	Ph9	50D|40D			–0.39**	0.28**
	Ph11–1	60D|50D				0.38**
Ph2–1	Ph2–2	90D|80D	–0.73**			–0.97**
	Ph3–1	10D|Initial		0.26**		
	Ph7–2	70D|60D	–0.62**		–0.92**	
	Ph12	40D|30D		0.80**		–0.98**
Ph2–2	Ph3–1	**Final**		**3.25****	**–4.37****	**1.13****
		90D|80D		0.56**	–0.88**	
	Ph3–2	70D|60D	0.82**	0.38**	–0.99**	0.61**
	Ph4–2	50D|40D			–0.25**	0.21*
	Ph5	40D|30D			0.22**	
	Ph6–1	70D|60D	–0.61*	0.62*		–0.90**
	Ph6–2	10D|Initial			0.47**	–0.48**
	Ph7–2	40D|30D		0.44**		–0.32*
	Ph8	**Final**	**–3.43****	**1.37****		**–1.54****
		60D|50D				–0.49**
	Ph9	**Final**	**–2.67***	**1.20***	**–1.65****	
	Ph10	10D|Initial			–0.37**	
	Ph11–2	90D|80D				0.27**
Ph3–1	Ph3–2	90D|80D	0.55**		1.04**	
		70D|60D		0.86**		–0.55**
	Ph4–2	10D|Initial	–0.96*			
	Ph5	**Final**	**3.38****	**3.48****	**–2.62****	
	Ph6–1	80D|70D		–0.98**	0.62**	0.36**
	Ph6–2	70D|60D	0.87**			
	Ph7–2	10D|Initial	0.87*			
	Ph9	**Final**	**–3.08****			
		20D|10D	0.39**			
	Ph12	30D|20D		–0.94**	0.53**	0.56**
Ph3–2	Ph5	30D|20D		0.21*		
	Ph6–1	60D|50D	–0.90**			0.65*
	Ph6–2	50D|40D		0.22**	–0.83**	0.71**
	Ph8	**Final**	**3.79****	**1.54****	**–1.52****	
		60D|50D		0.60**	–0.54**	
	Ph9	10D|Initial			–0.34**	
	Ph10	30D|20D	–0.83**	–0.60**	0.11*	0.48**
	Ph11–2	50D|40D	0.53**	–0.71**	0.67**	
Ph4–1	Ph7–2	70D|60D			0.38**	
	Ph9	60D|50D		0.59**	–0.43**	
	Ph11–2	40D|30D	–0.53**	–0.22**	0.55**	–0.39**
	Ph12	60D|50D				–0.22**
Ph4–2	Ph6–2	50D|40D				–0.55*
	Ph7–1	**Final**		**–3.65****	**3.96****	
		80D|70D		–0.70**	0.72**	
		30D|20D	0.50**			
	Ph7–2	80D|70D	0.71**			
	Ph8	30D|20D				–0.31**
	Ph10	60D|50D				–0.29**
	Ph11–1	30D|20D			0.29**	–0.35**

Table 2 (continued)

QTL_i	QTL_j	Stage	*aa* effect	*aae* in 95 Hainan	*aae* in 96 Hangzhou	*aae* in 98 Hangzhou
Ph5	Ph8	80D|70D	0.81*			
	Ph9	40D|30D	–0.85**			0.64*
Ph6–1[a]	Ph7–1	50D|40D	–0.66**			
	Ph8	60D|50D	–0.46**			
		40D|30D			0.29**	–0.24**
	Ph11–2	70D|60D				–0.91**
Ph6–2	Ph10	90D|80D	–0.49**	0.47**	–0.77**	
	Ph12	50D|40D		–0.20**	0.16*	
Ph7–1	Ph8	80D|70D	–1.05**			–0.99**
	Ph9	50D|40D	–0.86**		–0.73**	
	Ph11–1	10D|Initial		–0.43**	–1.28**	1.71**
Ph7–2	Ph12	**Final**	**–2.78****		**–2.34****	**2.77****
Ph8	Ph9	**Final**	**4.36****		**3.29****	**–2.60****
		70D|60D	0.61**		0.26**	
		60D|50D			0.69**	–0.60**
		50D|40D	–0.64**			
	Ph11–2	90D|80D	–0.66**	0.73**	–0.94**	
	Ph12	80D|70D	0.69*	–1.01**		
Ph9	Ph12	30D|20D		0.26**	–0.35**	
Ph10	Ph12	60D|50D		0.29**		
Ph11–1	Ph12	70D|60D	–0.84**	0.87**		
Ph11–2	Ph12	70D|60D	0.53**	0.63**		–0.87**

[a] Indicates QTLs without additive or additive×environment interaction effects at any stage

The *QE* interaction is clearly an important component affecting trait development. Understanding *QE* interaction is of importance to the breeding scheme, to marker-assisted selection and to map-based gene cloning. Usually, *QE* effects are treated as random effects, especially in different years. This implies that QTLs would be affected by different environments. For the final plant height, some QTLs (e.g. Ph1–2, Ph2–2 and Ph3–2) primarily had additive main effects, but others (e.g. Ph3–1, Ph4–1, Ph5, Ph6–2, Ph7–2, Ph9 and Ph10) only had *ae* interaction effects. This was implied by the fact that while some QTLs have only *QE* effects, the gene expression of some QTLs could be mainly induced by the environment. Selection on these *QE*-interaction QTLs could result in unstable offspring. This suggests that selection should be applied especially on QTLs with additive main effects.

A major QTL for plant height linked to marker RZ730 on chromosome 1 was inferred to be the location of the *sd*–1 gene (Yan et al. 1998). In the present study, a major QTL Ph1–2 was detected with a distance of 22 cM from the marker RZ730. For this QTL, the alleles to decrease plant height were contributed from IR64. Significant epistasis and *QE* interaction effects were also found at this locus. This indicated that a major gene or QTL could also interact with other genes under different environments.

Twelve QTLs with significant *a* and/or *ae* effects for final plant height were determined by the conventional method. But by combining with the conditional method, 17 QTLs were significantly identified with time–dependent measures. By conditional QTL mapping, extra gene expression at specific periods could be detected. The failure of detecting QTLs at the final stage of growth by conventional QTL mapping could be due to the fact that some QTLs might have opposite effects at different stages. These kinds of QTLs are also important for plant breeding since they can affect the developmental pattern of agronomic traits. In the present study, a conditional analysis of plant height was conducted for nine stages after transplanting. Since the lines of the DH population studied could have variation in their developmental stage at a specific time, the results obtained for plant height might be confounded with the variation in heading date. QTLs with conditional positive effects in early stages could therefore be an indicator for selecting earliness of heading date.

Acknowledgements We thank Dr. N. Huang for providing the research materials and molecular marker data and Drs Z.C. Xu, P.K. Pathak; Z.H. Ye; P.Y. Liu and some undergraduates in the Departments of Agronomy and Biology for helping to collect the phenotypic data. The authors are very grateful to two anonymous referes for their helpful and valuable suggestions. The present research was supported by a key grant from the National Natural Science Foundation of China.

References:

Atchley WR, Zhu J (1997) Developmental quantitative genetics, conditional epigenetic variability and growth in mice. Genetics 147:765–776

Bateson W (1909) Mendel's principles of heredity. Cambridge University Press, Cambridge, UK

Cho YG, Eun MY, McCouch SR, Cae YA (1994) The semi–dwarf gene, *sd*–1, of rice (*Oryza sativa* L.). II. Molecular mapping and marker–assisted selection. Theor Appl Genet 89:54–59

Cockerham CC, Zeng ZB (1996) Design with marker loci. Genetics 143:1437–1456

Doebley J, Stec A, Gustus C (1995) *Teosinte branched l* and the origin of maize: evidence for epistasis and the evolution of dominance. Genetics 141:333–346

Eshed Y, Zamir D (1996) Less–than additive epistatic interactions of quantitative trait loci in tomato. Genetics 143:1807–1817

Guiderdoni E, Galinato E, Luistro J, Vergara G (1992) Anther culture of tropical japonica/ indica hybrids of rice (*Oryza sativa* L.). Euphytica 62:219–224

Huang N, Courtois B, Khush GS, Lin HX, Wang GL, Wu P, Zheng KL (1996) Association of quantitative trait loci for plant height with major dwarfing genes in rice. Heredity 77:130–137

Huang N, Parco A, Mew T, Magpantay G, McCouch S, Guiderdoni E, Xu J, Subudhi P, Angeles ER, Kush GS (1997) RFLP mapping of isozymes, RAPDs and QTLs for grain shape and brown plant hopper resistance in a doubled-haploid rice population. Mol Breed 3:105–113

IRRI (1975) Parentage of IRRI crosses IR–IR 50000, International Rice Research Institute, Manila, The Philippines

Kinoshita T (1995) Report of committee on gene symbolization, nomenclature and linkage groups. Rice Genet Newslett 12:9–153

Lark KG, Chase K, Adler FR, Mansur LM, Orf JJ (1995) Interactions between quantitative trait loci in soybean in which trait variation at one locus is conditional upon a specific allele at another. Proc Natl Acad Sci USA 92:4656–4660

Li Z, Pinson SRM, Stansel JW, Park WD (1995) Identification of quantitative trait loci (QTLs) for heading date and plant height in cultivated rice (*Oryza sativa* L.). Theor Appl Genet 91: 374–381

Lin HX, Zhuang JY, Qian HR, Lu J, Min SK, Xiong ZM, Huang N Zheng KL (1996) Mapping QTLs for plant height and its components by molecular markers in rice (*Oryza sativa* L.). Acta Agron Sinica 22:257–263

Lu C, Shen L, Tan Z, Xu Y, He P, Chen Y, Zhu L (1996) Comparative mapping of QTLs for agronomic traits of rice across environments using a doubled-haploid population. Theor Appl Genet 93:1211–1217

Paterson AH, Damon S, Hewitt JD, Zamir D, Rabinowitch HD, Lincoln SE, Lander ES, Tanksley SD (1991) Mendelian factors underlying quantitative traits in tomato: comparison across species, generations, and environments. Genetics 127: 181–197

Phillipsa PC (1998) The language of gene interaction. Genetics 149:1167–1171

Tachida H, Cockerham CC (1989) A building block model for quantitative genetics. Genetics 121:839–844

Veldboom LR, Lee M (1996) Genetic mapping of quantitative trait loci in maize in stress and nonstress environments: II. Plant height and flowering. Crop Sci 36:1320–1327

Wang DL, Zhu J, Li ZK, Paterson AH (1999) Mapping QTLs with epistatic effects and QTL×environment interactions by mixed linear model approaches. Theor Appl Genet 99:1255–1264

Xiao J, Li J, Yuan L, Tanksley SD (1995) Identification of QTLs affecting traits of agronomic importance in a recombinant inbred population derived from a subspecific rice cross. Theor Appl Gent 92:230–244

Yan J, Zhu J, He C, Benmoussa M, Wu P (1998) Molecular dissection of developmental behavior of plant height in rice (*Oryza sativa* L.). Genetics 150:1257–1265

Yu SB, Li JX, Xu CG, Tan YF, Gao YJ, Li XH, Zhang Q, Maroof MAS (1997) Importance of epistasis as the genetic basis of heterosis in an elite rice hybrid. Proc Natl Acad Sci USA 94:9226–9231

Zhu J (1995) Analysis of conditional genetic effects and variance components in developmental genetics. Genetics 141:1633–1639

Zhu J (1998) Mixed model approaches for mapping quantitative trait loci. Hereditas 20(Suppl):137–138

Zhu J (1999) Mixed model approaches of mapping genes for complex quantitative traits. J Zhejiang Univ (Natural Science) 33:327–335

Zhuang JY, Lin HX, Lu J, Qian HR, Hittalmani S, Huang N, Zheng KL (1997) Analysis of QTL×environment interaction for yield components and plant height in rice. Theor Appl Genet 95:799–808