Conditional genetic analysis on quantitative trait loci for yield and its components in rice☆

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Abstract

Conditional mapping method was used to analyze QTLs for rice yield and its components: number of productive panicles, number of full-filled grains, and kilo-grain weight. By unconditional mapping, some pleiotropic or closely linked QTLs were detected; by conditional mapping, QTL number of yield decreased greatly after excluding the effect from full grain, which indicated that full grain gave the most contribution to yield. The phenomenon was discussed that small number of QTLs for yield seems not to fit too much the very complex trait that is generally believed controlled by many genes. [Life Science Journal. 2007;4(1):71−76] (ISSN: 1097−8135).

Keywords: quantitative trait locus; conditional genetics; rice yield; yield components

1 Introduction

Yield is a very important trait in rice breeding, and as a complex quantitative trait can be dissected into a number of causal components such as number of productive panicles per plant, number of full-filled grains per panicle and kilo-grain weight. A number of studies have been made to locate QTLs for yield and its components[1−3]. However, in these studies, the contribution of each component to yield has not been analyzed in detail. Conditional QTL mapping approach provides a useful tool for understanding contributions of the causal components in multi-component traits. Therefore, the present studies used the unconditional and conditional QTL mapping for yield and its components to reveal the contribution of each component to yield.

2 Materials and Methods

2.1 Materials

A population of 123 double haploid (DH) lines derived from a cross between an irrigated *indica* variety IR64 and an upland *japonica* variety Azucena[4] were used in the experiments. 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[5] was used for QTL mapping.

2.2 Field experiment

The 123 DH lines and their parents, IR64 and Azucena, were grown in a randomized complete design with two replications at Hainan in 1995 and Hangzhou of China in 1996, 1998. Hainan and Hangzhou show great difference in climate, soil conditions, day length, and even 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 four lines with eight plants per line. At the maturity stage, 6 central plants of each plot were measured.

2.3 Phenotipic measurement

Observations were taken on the six central plants of each plot at Hainan in 1995 and Hangzhou in 1996 and 1998 for the productive panicle number per plant (panicle number, PN), full grain number per panicle (full grain, FG), and the weight of 1000 grains (kilo-grain weight, KW). The yield per plant (YD) was calculated as the formula of $YD = PN \times FG \times KW/1000$.

2.4 Phenotypic and genotypic correlations

Phenotypic and genotypic correlation coefficients among different traits were calculated using MINQUE (1)[6].

2.5 QTL analysis for yield and yield components

With the unconditional and conditional QTL mapping procedures[7], QTLs with additive and additive × additive epistatic effects as well as their environmental

interaction effects in DH population could be searched for multi-component quantitative traits such as yield and its components. The conditional genetic effects of the yield given its component will indicate the net effects of gene expression excluding those of the given component, revealing the contribution of the left components on the formation of yield. The conditional phenotypic value was obtained by the mixed model approaches for conditional genetics of quantitative traits[8]. The likelihood ratio value of 11.5, which is equal to a LOD score of 2.5[9], was used as a threshold for detection of QTL or epistasis.

3 Results and Analysis

3.1 Phenotypic variation

The phenotypic values of the parents and the DH population for yield and its components were presented in Table 1. The parent IR64 was observed to be inferior to Azucena for full grain number per panicle under three environments, for kilo-grain weight at Hainan 1995 and Hangzhou 1998, and for calculated yield at Hangzhou 1996, but superior to Azucena for yield and its components at other situations. The data presented in Table 1 also indicated transgressive variation in the DH population for yield and its components in three environments with skew and kurt values being less than 1.0 except a few cases suggesting that the data were like normal distribution and suitable for QTL analysis.

Table 1. Phenotypic values of yield and yield components for the DH population and its parents under three environments

Trait	Env.	Parents		DH population					
		IR64	Azucena	Mean	Max	Min	Stdev	Skew	Kurt
Panicle number	1	6.1	3.5	6.7	11.6	3.8	1.5	0.5	0.1
	2	13.4	10.1	8.9	15.3	4.5	2.4	0.6	−0.1
	3	9.0	4.9	7.5	12.2	3.0	2.1	0.35	−0.52
Full grain	1	46.8	66.5	37.0	106.7	0.7	18.1	0.5	1.1
	2	35.7	78.8	94.1	182.1	20.3	32.0	0.1	−0.4
	3	60.9	95.5	69.2	127.3	15.3	25.7	0.11	−0.43
Kilo-grain weight	1	27.1	29.0	27.0	40.3	19.3	4.2	0.4	−0.1
	2	25.6	24.9	25.4	33.8	17.8	2.9	0.2	0.2
	3	25.6	28.2	23.0	30.8	16.0	3.4	0.23	−0.44
Yield	1	7.7	6.7	7.0	20.7	1.1	3.3	0.77	1.71
	2	12.2	19.8	19.3	34.3	6.1	6.4	0.30	−0.49
	3	14.0	13.2	11.9	23.0	1.7	4.4	0.16	·−0.02

Env. 1, 2, 3 represent Hainan in 1995, Hangzhou in 1996 and 1998.

3.2 Correlations between yield and each of its components

Significant positive correlations were discovered between yield with each of its components while the components showed negative correlations between each other (Table 2). Because of significant correlations between yield with its components, the unconditional and conditional QTL mapping could be used to fully dissect the contributions of yield components to yield.

Table 2. Genotypic correlations (upper triangle) and phenotypic correlations (lower triangle) among yield and yield components

	Panicle number	Full grain	Kilo-grain weight	Yield
Panicle number		−0.06*	−0.16**	0.14 **
Full grain	−0.02		−0.08*	0.53**
Kilo-grain weight	−0.12**	−0.04		0.07*
Yield	0.19**	0.50**	0.08*	

* and ** represent significance level of $P = 0.01$ and 0.005, respectively.

3.3 Unconditional QTLs and their effects for yield components and yield

All of the QTLs with additive effects and/or additive × additive epistasis effects and their putative positions in the genome detected by unconditional mapping for yield components and yield were presented in Table 3. QTL for each trait was named as abbreviation of the trait name with the number of chromosome on which the

QTL was located. If there were more than one QTL in a chromosome, the serial number was added after chromosomal number separated by a hyphen. The positions of these QTLs were indicated by the marker interval bracketing the concerned QTL with the estimated distance in Morgon (M) from the left marker. There were totally 11, 9, 17 and 10 QTLs for panicle number, full grain, kilo-grain weight and yield, respectively.

In Table 4, the estimated unconditional additive effects and the additive × additive epistatic effects at significance level of 0.01 or 0.005 under three environments for each trait were presented. Among the total QTLs with additive and additive × additive epistasis effects for yield components and yield, 9, 6, 11 and 8 QTLs were found with additive main effect (a) and/or additive × environment interaction effect (ae) for each trait, respectively. QTLs within a same marker interval

between yield and each of its components were found, such as Yd1-2 and Pn1, Yd1-1 and Kw1-1, Yd2 and Fg2-2. These three pairs of QTLs had also similar directions of effects. A QTL Fg4 for full grain was found with relatively large a and ae effects within marker interval RG163-RZ590, also closely linked with QTL Pn4 for panicle number and QTL Yd4 for yield. There were 8, 7, 11 and 5 digenic epistatic interactions with epistatic main effects and/or epistasis by environment interaction effects were detected to be associated with the yield components and yield, respectively (Table 4). There were 1, 3, 8 and 2 interactions included the loci without detectable QTL additive effects for each trait, respectively. Unlike the situation of additive QTLs, no similar epistatic interactions between yield and each of its components were found.

Table 3. QTLs with additive effect and/or additive × additive epistatic effect for yield and yield components

Panicle number			Full grain			Kilo-grain weight			Yield		
QTL	Marker interval	Distance(M)	QTL	Marker interval	Distance(M)	QTL	Marker interval	Distance(M)	QTL	Marker interval	Distance(M)
Pn1	RZ730-RZ801	0.12	*Fg1*	*RG345-RG381*	*0*	Kw1-1	RG532-W1	0.14	Yd1-1	RG532-W1	0
Pn2-1	RG544-RG171	0.04	Fg2-1	RG437-RG544	0.08	Kw1-2	RZ801-RG810	0.02	Yd1-2	RZ730-RZ801	0.22
Pn2-2	RZ213-RZ123	0	Fg2-2	RZ123-RG520	0.12	*Kw2-1*	*PalI-RZ58*	*0*	Yd2	RZ123-RG520	0
Pn3	Pgi_1-CDO87	0.06	Fg3	RZ284-RZ394	0.06	Kw2-2	RG256-RZ213	<u>0.1</u>	*Yd3*	*RZ574-RZ284*	*0.1*
Pn4	RZ675-RG163	0.16	Fg4	RG163-RZ590	0.02	*Kw3-1*	*RG104-RG348*	*0.06*	Yd4	RZ590-RG214	0.02
Pn6	RG162-RG172	0	*Fg6*	*RG162-RG172*	*0.02*	Kw3-2	RZ337A-RZ448	0.06	Yd6	RZ398-RG213	0
Pn7	PGMS007-CDO69	0.16	*Fg8*	*TGMSI02-A10K250*	*0.02*	Kw4	RZ262-RG190	0.08	*Yd8*	*RZ66-AC5*	*0*
Pn8-1	RG20-A5J560	0.1	Fg9	RZ12-RG667	0.06	Kw5-1	RG229-RG13	0.16	Yd10	RZ625-CDO93	0
Pn8-2	*RZ66-AC5*	*0.24*	Fg12	RG463-RG901	0.02	*Kw5-2*	*RZ70-RZ225*	*0*	Yd11-1	Adh1-RG1094	0.06
Pn9	CDO590-C711	0				Kw6	RG172-CDO544	0.06	Yd11-2	Npb44-RG247	0
Pn10	*CDO93-CDO98*	*0*				*Kw7*	*RZ337B-CDO497*	*0.12*			
						Kw8	RG418B-Amp-2	0			
						Kw9-1	*C711-G103*	*0.12*			
						Kw9-2	RZ228-RZ12	0			
						Kw10	RG134-RZ500	0.02			
						Kw11	*RG247-RG103*	*0.24*			
						Kw12	RG958-RG181	0.3			

The QTLs with both additive and epistatic effects were presented in regular form while the QTLs involved in epistasis but without additive effects were presented in bold italic letters, and the QTLs with only additive effects but no epistatic effects were notified with underling lines.

3.4 QTLs and their effects for yield conditional on each of its components

All of the QTLs with additive effects and/or additive × additive epistasis effects and their putative positions in the genome for yield conditional on each of its components were presented in Table 5. There were totally 13, 5 and 12 QTLs for yield conditional on panicle number, full grain and kilo-grain weight, respectively.

The estimated conditional additive effects and the additive × additive epistatic effects at significance level of 0.01 or 0.005 under three environments were presented in the Table 6. The conditional QTL effects of the yield given the observed phenotype of yield component indicated the net effects of gene expression from the other components that was independent to the causal effects from the given component. When yield was conditional on panicle number, 10 QTLs with conditional ad-

ditive main effects and/or conditional additive × environment interaction effects were detected. The number of QTLs was more than that of unconditional yield. This might indicate that after excluding the negative interference of panicle number, the other two left components might give larger contribution to yield. When yield was conditional on full grain, three QTLs with conditional additive main effects and/or conditional additive × environment interaction effects were detected. This might indicate that after excluding the effect on yield from full grain, the other two left components gave little contribution to yield. This was consistent with that the full grain had the larger genotypic correlation of 0.53 with yield than those of 0.14 and 0.07 that the panicle number and kilo-grain weight had. When yield was conditional on kilo-grain weight, seven QTLs with conditional additive main effects and/or conditional additive

× environment interaction effects were detected. This might indicate that after excluding the effect on yield from kilo-grain weight, the other two components gave nearly the same contribution to yield with that in the situation of including the effect from kilo-grain weight, which meant that kilo-grain weight was not considerably important for the formation of yield in this study.

Table 4. Unconditional QTL effects for yield per plant and its components

Trait		Additive effect					Additive × additive epistatic effect				
	QTL	a	ae_1	ae_2	ae_3	QTLi	QTLj	aa	aae_1	aae_2	aae_3
PN											
	Pn1	0.37**	-0.39**		0.48*	Pn1	Pn3	0.30*			
	Pn2-1	0.54**	0.45**	-1.42**	0.97**	Pn1	Pn7	0.37*			
	Pn2-2	-0.57**				Pn1	Pn8-1		-0.32**	-1.34**	1.66**
	Pn3	0.48*		0.70*		Pn2-1	Pn3			-0.26*	0.18*
	Pn4	0.91**	0.46**	1.14**	-1.60**	Pn3	Pn4	-0.42*	-0.36**	-0.89**	1.25**
	Pn6	-1.86**		-0.67**	0.60**	Pn3	Pn9			0.17**	-0.16**
	Pn7				-0.20**	Pn6	Pn8-1				-1.53**
	Pn8-1	-2.55**	0.56**	1.90**	-2.45**	***Pn8_2***	***Pn10***				-0.56*
	Pn9			-0.26**	0.26**						
FG											
	Fg2-1		3.47**	9.86**	-13.33**	***Fg1***	Fg9		3.79*	-6.24**	
	Fg2-2		-1.40**		1.59**	Fg2-1	***Fg8***	7.91*			
	Fg3		-0.97*	7.15**	-6.18**	Fg2-2	Fg4	3.67*			4.80*
	Fg4	-9.70**	8.23**	-6.88**		Fg3	Fg4			-1.62**	1.60**
	Fg9	4.12*	5.52**	3.34**	-8.87**	Fg3	Fg9	-6.05**		-9.99**	5.98**
	Fg12	-3.46*			-1.42**	Fg4	***Fg6***	3.90*		4.14*	
						Fg9	Fg12		-4.33*		4.61*
KW											
	Kw1-1		-0.70*		0.62**	Kw1-1	***Kw2-1***	0.54*			
	Kw1-2	-0.80**		-0.71*	0.61*	Kw1-2	***Kw3-1***		-0.41**	-2.14**	2.54**
	Kw2-2		-0.18**			Kw1-2	Kw6	0.62**	2.34**	-2.00**	-0.34**
	Kw3-2	-0.57*	-0.91**		0.78**	Kw1-2	Kw8	0.47*			
	Kw4	0.76*				***Kw2-1***	***Kw3-1***	0.51*		-0.39*	0.39**
	Kw5-1			-1.81*	1.11*	Kw3-2	***Kw5-2***		-0.37**		0.35**
	Kw6		1.56**	-0.32**	-1.25**	Kw4	Kw12		-0.85*		
	Kw8		0.35**		-0.35**	Kw5-1	***Kw11***	1.24**			-0.74*
	Kw9-2	-0.46**			-0.69**	Kw6	***Kw9-1***		0.29**		-0.36**
	Kw10	0.80**		0.32**	-0.40**	***Kw7***	Kw8	0.72*			
	Kw12		0.85*			Kw9-2	***Kw11***		-1.45**	1.24**	0.21**
YD											
	Yd1-1	-1.47**	-2.62**	1.10**	1.52**	Yd1-1	***Yd8***		0.88**	-2.77**	1.89**
	Yd1-2	1.24**	-1.84**	2.29**		Yd1-2	Yd6		-0.25**		0.41*
	Yd2			-0.64**	0.45**	***Yd3***	Yd10	1.08*			
	Yd4	-1.42**	1.54**	-1.60**		Yd4	Yd11-1		0.27**	-0.71**	0.44**
	Yd6	1.06**	1.03**	-2.81**	1.78**	Yd11-1	Yd11-2	-1.48*			
	Yd10	1.09*									
	Yd11-1	2.01**									
	Yd11-2	-1.56*									

a, aa, ae_1, ae_2, ae_3, aae_1, aae_2, aae_3 represent additive main effect, epistatic main effect and additive × environment interaction effect, epistasis × environment interaction effect at Hainan in 1995, at Hangzhou in 1996 and 1998, respectively. * and ** represent the significance level of $P=0.01$ and 0.005, respectively. The forms of bold italic letter and the underling lines have the same meaning with those in Table 3.

In the three conditional analysis cases, common QTLs between unconditional yield and yield conditional on each of its components were identified. They were Yd1-2 and Yd|Kw1-2, Yd6 and Yd|Fg6, Yd11 and Yd|Pn11. Between yield conditional on panicle number and yield conditional on kilo-grain weight, a common QTL Yd|Pn4 or Yd|Kw4 was identified. This QTL had effect on yield after excluding the causal effects from panicle number and kilo-grain weight, but missed after excluding the effects from full grain, so this QTL might be through affection on full grain to improve the yield. In fact, this QTL was really identified for full grain by unconditional mapping, and a closely linked QTL Yd4 was identified for final yield.

There were 7, 2 and 9 digenic epistatic interactions with epistatic main effects and/or epistasis by environment interaction effects were detected to be associated with the yield conditional on panicle number, full grain and kilo-grain weight, respectively (Table 6). While no similar epistatic interaction was identified among yield and yield conditional on its components, a pair of interaction Fg4 and Fg6 for full grain by unconditional mapping were found similar with the interaction Yd|Pn4 and Yd|Pn6-2 for yield conditional on panicle number, in which Fg4 and Yd|Pn4 were pleiotropic or closely linked genes, thus resulting the association of the two pairs of interactions between full grain and the formation of yield.

Table 5. Loci with QTL additive effect and/or with additive × additive epistatic effect for yield conditional on each of its components

YD|PN			YD|FG			YD|KW		
QTL	Marker interval	Distance (M)	QTL	Marker interval	Distance (M)	QTL	Marker interval	Distance (M)
Yd|Pn1-1	W1-RG173	0	Yd|Fg3	Pgi-1-CDO87	0.12	Yd|Kw1-1	U10-RG532	0.04
Yd | Pn1-2	*RZ730-RZ801*	*0.2*	*Yd | Fg4*	*RZ675-RG163*	*0.08*	Yd|Kw1-2	RZ730-RZ801	0.22
Yd|Pn2	RG654-RG256	0	*Yd | Fg5*	*RZ70-RZ225*	*0*	Yd|Kw3-1	RG348-RZ329	0.12
Yd | Pn3	*RG348-RZ329*	*0.06*	Yd|Fg6	RZ398-RG213	0.02	*Yd | Kw3-2*	*Pgi-1-CDO87*	*0*
Yd|Pn4	RG163-RZ590	0.02	Yd|Fg8	A5J560-A3E396	0.06	Yd|Kw4	RG163-RZ590	0
Yd|Pn5	RZ67-RZ70	0.08				*Yd | Kw5*	*RZ556-RG403*	*0.16*
Yd|Pn6-1	Est-2-RZ144	0				*Yd | Kw7*	*CDO59-RG711*	*0*
Yd|Pn6-2	RG172-CDO544	0.04				*Yd | Kw8-1*	*RZ143-RG20*	*0*
Yd | Pn8	*RG1-Amy3DE*	*0.1*				Yd|Kw8-2	AG8 _ Aro-RZ617	0.02
Yd|Pn10	RG134-RZ500	0				Yd|Kw10	G1084-RG257	0
Yd|Pn11	Adh1-RG1054	0.06				Yd|Kw11	RG103-RG1109	0.08
Yd|Pn12-1	AF6-RG457	0.08				*Yd | Kw12*	*RG463-RG901*	*0*
Yd|Pn12-2	RG958-RG181	0						

The forms of bold italic letter and the underling lines have the same meaning with those in Table 3.

Table 6. QTL effect (g) for yield per plant conditional on each of its components

Trait	QTL	a	ae_1	ae_2	ae_3	QTLi	QTLj	aa	aae	aae_2	aae_3
YD|PN											
	Yd|Pn1-1		-0.22**	2.08**	-1.86**	Yd|Pn1-1	Yd|Pn6-1		0.54*		-0.61*
	Yd|Pn2	-0.97*				*Yd | Pn1-2*	Yd|Pn4		-0.36*	0.53**	
	Yd|Pn4	-1.31**	1.72**	-1.40**		Yd|Pn2	Yd|Pn5	-2.07**	-1.55**	-1.37**	2.92**
	Yd|Pn5	1.61**	-1.61**	2.96**	-1.34**	*Yd | Pn3*	*Yd | Pn8*	-1.41**	0.74*		
	Yd|Pn6-1		1.91**	-2.15**	0.24*	Yd|Pn4	Yd|Pn6-2		-1.15*	1.19*	
	Yd|Pn6-2		-0.69**	0.61*		Yd|Pn5	Yd|Pn11		-0.39*		
	Yd|Pn10		-0.62**	0.94*		Yd|Pn12-1	Yd|Pn12-2	-0.97**			
	Yd|Pn11	0.87*									
	Yd|Pn12-1			2.41**	-1.36**						
	Yd|Pn12-2	0.90*									
YD|FG											
	Yd|Fg3	1.17**	0.14**	-0.71**	0.57**	*Yd | Fg4*	*Yd | Fg5*	-0.96**	0.77*		-0.49*
	Yd|Fg6	-2.02**				Yd|Fg6	Yd|Fg8	2.23**	-1.32**	1.69**	
	Yd|Fg8				0.95*						
YD|KW											
	Yd|Kw1-1	-0.82**				Yd|Kw1-1	*Yd | Kw12*	-0.80*			
	Yd|Kw1-2	1.32**				Yd|Kw1-2	*Yd | Kw8-1*			1.40*	
	Yd|Kw3-1	-0.77**	0.90*	-1.52**		Yd|Kw1-2	Yd|Kw8-2				0.52*
	Yd|Kw4	-1.64**	1.73**	-3.34**		Yd|Kw3-1	Yd|Kw4		0.34*	-0.43**	
	Yd|Kw8-2		-2.25**		2.43**	*Yd | Kw3-2*	Yd|Kw4		0.48**		
	Yd|Kw10	0.46*				Yd|Kw4	*Yd | Kw7*	-1.35**	1.18*		-0.95*
	Yd|Kw11				-0.51**	Yd|Kw4	*Yd | Kw12*			0.66**	-0.44**
						Yd | Kw5	Yd|Kw8-2				-1.40*
						Yd|Kw8-2	Yd|Kw11	0.87*			

a, ae_1, ae_2, ae_3, aa, aae_1, aae_2, aae_3, * and ** have the same meaning with those in Table 4. The forms of bold italic letter and the underling lines have the same meaning with those in Table 3.

4 Discussion

Conditional mapping technique permits detection of the net QTL effect of the integrated trait excluding the causal genetic effects of the given component. The unique feature of the conditional mapping approach is that it exploits the variability of integrated trait conditioned on variability of the given component to detect QTLs. In contrast, unconditional mapping for the final integrated trait allows identification of the QTLs based on the integrated effect of all its components. The variation in the population caused by such integrated effects can be made leveled by the opposite effects of the components in the formation of the final trait so that some QTLs will be made undetectable or biased by unconditional mapping.

In this study, conditional mapping helped to identify more QTLs for yield conditional on its components than those detected only for final yield. Other studies[10,11] also indicated that a relative small number of QTLs for final yield seemed not fitting too much the complex trait that was generally believed controlled by many genes. The conditional mapping might give an explanation for this phenomenon and the components contribute to the final yield oppositely, so that many genes would not be detected.

Practically, the formation of yield is a very complex biological pathway and genetic dissection of yield seems considerably difficult. Previous studies using molecular markers have indicated some putative QTLs controlling yield and its components. However, in these studies the phenotypic values of the final trait were used for QTL mapping. With the conditional approach, not only we mapped QTLs for yield but also we investigated the net effects on yield from its components. It was also found that when compared to other components, full grain gave the highest contribution in this study. So genetic investigation on full grain might be also useful in capture genes for final yield.

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