RESEARCH ARTICLE

Quantitative trait loci for rice yield-related traits using recombinant inbred lines derived from two diverse cultivars

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Abstract

The thousand-grain weight and spikelets per panicle directly contribute to rice yield. Heading date and plant height also greatly influence the yield. Dissection of genetic bases of yield-related traits would provide tools for yield improvement. In this study, quantitative trait loci (QTL) mapping for spikelets per panicle, thousand-grain weight, heading date and plant height was performed using recombinant inbred lines derived from a cross between two diverse cultivars, Nanyangzhan and Chuan7. In total, 20 QTLs were identified for four traits. They were located to 11 chromosomes except on chromosome 4. Seven and five QTLs were detected for thousand-grain weight and spikelets per panicle, respectively. Four QTLs were identified for both heading date and plant height. About half the QTLs were commonly detected in both years, 2006 and 2007. Six QTLs are being reported for the first time. Two QTL clusters were identified in regions flanked by RM22065 and RM5720 on chromosome 7 and by RM502 and RM264 on chromosome 8, respectively. The parent, Nanyangzhan with heavy thousand-grain weight, carried alleles with increased effects on all seven thousand-grain weight QTL, which explained why there was no transgressive segregation for thousand-grain weight in the population. In contrast, Chuan7 with more spikelets per panicle carried positive alleles at all five spikelets per panicle QTL except *qspp5*. Further work on distinction between pleiotropic QTL and linked QTL is needed in two yield-related QTL clusters.

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Introduction

Rice is the staple food for most of the people in the world. With the increasing world population, rice yield is still a hot topic in rice breeding despite the increasing grain yield after the green revolution (Ashikari *et al.* 2005; Song *et al.* 2007). Thousand-grain weight (TGW), grain number per panicle (GPP) and panicle number per plant are the three yield components. However, TGW and GPP were often focussed in the past QTL mapping studies due to their direct contribution to yield. For these traits, numerous QTLs were identified in the last decades (http://www.gramene.org/qtl/index.html). Some major QTLs were also fine mapped and cloned in last several years. For instance, grain shape/TGW QTL, *GS3*, *GW2* and *qSW5/GW5* were cloned on the basis of QTL mapping (Fan *et al.* 2006; Song *et al.* 2007; Shomura *et al.* 2008; Weng *et al.* 2008). For GPP, *Gn1a* was also isolated by map-based cloning strategy (Ashikari *et al.* 2005). Recently, Huang *et al.* (2009) reported that *DEP1* not only affects the erect panicle but also the grain number per panicle. On the other hand, plant height (PH) and heading date (HD) were highly associated with rice grain yield, and much attention has been paid to unveil their complex genetic basis. Among the plant height genes, the semi-dwarf gene *sd1* is the most dominant compared to other plant height genes which is responsible for green revolution in rice (Spielmeyer *et al.* 2002). Besides, several dozens of genes/QTLs for rice heading date were mapped. Of them, *Hd1*, *Hd3a* and *Ehd1* were cloned which play important roles in rice flowering pathway (Yano *et al.* 2000; Kojima *et al.* 2002; Doi *et al.* 2004). Interestingly, the recently cloned genes, *Ghd7* and *Ghd8*, had major effects not only on HD and PH but also on rice yield (Xue *et al.* 2008; Yan *et al.* 2011). In addition, few yield QTLs were fine mapped, such as *gw8.1* and *gw9.1* controlling grain weight (Xie *et al.* 2006, 2008), *GPP1*, *gpa7* and *SPP3b/TGW3b* controlling spikelets per panicle (SPP)/GPP (Tian *et al.* 2006; Liu *et al.* 2009, 2010), and so on. However, yield traits are

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quantitatively inherited and their genetic basis is thus explained only in part by these cloned genes. Hence, it is necessary to detect QTLs/genes associated with yield traits using more populations in order to understand their genetic bases well.

It is important to construct a population for QTL mapping. Variety of populations were used for mapping in past years, such as, F_2, double haploid (DH), recombinant inbred lines (RIL) and back cross (BC) populations. DH and RIL populations were preferred for QTL mapping because they can be used for field experiments with replicates over several years and locations. In addition, population from the inter-subspecies cross between *indica* and *japonica* was helpful to uncover the QTLs controlling the complex agriculturally important traits, since they had been diverged in many different characteristics by domestication in different geographical regions. Hence, intersubspecies populations were developed for QTL mapping in most research groups, in which a large number of QTLs had been identified (Xiao *et al.* 1996; Yano *et al.* 2001; Yan *et al.* 2003; Nonoue *et al.* 2008). To our present knowledge, it is advantageous to construct a mapping population using two parents which display a huge polymorphism in the genome. In such a population, more QTLs/genes are likely to be discovered attributing to diverse alleles. In this study, RIL population derived from a cross between two contrasting cultivars, Nanyangzhan (*japonica*) with few SPP but large grains and Chuan7 (*indica*) with more SPP but small grains were used to (i) detect QTL for PH, HD, SPP and TGW; and (ii) to evaluate the power of QTL detection for yield components as compared with other reports.

Materials and methods

Mapping population and field experiment

Mapping population consisted of 185 RILs derived from a cross between two rice cultivars Nanyangzhan and Chuan7 by single-seed descent. In 2006 and 2007 rice growing seasons, F_7, F_8 populations and two parent cultivars were planted in a bird-net-equipped field on the experimental farm of Huazhong Agricultural University in Wuhan, P. R. China. The randomized complete block design with two replicates was adopted in field trials. After one month from sowing, 10 seedlings of each line were arranged for one row in the main experimental field with a distance of 16.5 cm between plants within a row and 26.4 cm between rows. Eight individuals in the middle of each row were harvested to score the traits.

Trait measurement

HD was determined from the date of sowing to the emergence of the first panicle. At ripening stage, PH was measured from field surface to the top of the highest panicle of each plant, individually. Plants were individually harvested for collection of panicle number, spikelet number and grain yield. SPP was calculated by counting the total number of SPP divided by its panicle number. TGW was measured as the grain weight per plant divided by its grain number multiplied by 1000; yield per plant was calculated as the grain weight per plant.

Data analysis

A genetic linkage map of 164 SSR markers was constructed (Bai *et al.* 2010). Composite interval mapping (CIM) was performed for QTL analysis in RILs using the software Windows QTL Cartographer 2.5 (Wang *et al.* 2007). Window size was set at 10 cM and stepwise regression analysis was used to detect cofactors. QTL main effects were estimated using the maximum-likelihood estimation method. For the four investigated traits, the LOD threshold was determined at the experiment-wise significance level of 0.05 by computing 1000 permutations, and the LOD threshold ranged from 2.9–3.3. Heritability for the traits was calculated based on the experiments, using the formula: $H^2 = \delta_g^2 / \left(\delta_g^2 + \delta_{ge}^2/n + \delta_e^2/nr\right)$, where δ_g^2, δ_e^2 and δ_{ge}^2 were the estimates of genetic (G), G × E (environment) and error variance with $n = 2$ being the number of environments and $r = 2$ being the number of replicates. Two-way ANOVA was performed for genotype and environment interactions for the five traits using Microsoft Excel.

Results

Phenotypic variation of the RIL population

According to the results of Duncan's test, a highly significant difference in TGW and SPP ($P \leq 0.01$), and a significant difference in HD ($P \leq 0.05$), between the two parents Nanyangzhan and Chuan7 were observed (table 1). Nanyangzhan has a typical large grain size of over 43.3 g per thousand grains and small panicle of 91 SPP with an earlier heading date. In contrast, Chuan7 had an extremely small grain size of 11.4 g per thousand grains and large panicle of 208 SPP with a late heading date; whereas, there was no significant difference in plant height and yield between parents. However, variation of PH in RILs population was very wide from 63.0 to 189.0 cm and 84.1 to 170.4 cm in 2006 and 2007, respectively. A similar situation was found for yield. Transgressive segregation was observed for HD, PH, SPP and yield except TGW (table 1). In particular, SPP exhibited broad distribution in the RILs, in which the maximum of SPP was three times more than its minimum in both years.

Heritability and correlation

HD, PH, SPP and TGW showed higher broad sense heritability ranging from 79.4% to 90.0%, whereas the heritability of yield was only 33.5% (table 1). PH was significantly positively correlated with TGW and yield in two years; TGW,

Table 1. Heritabilities and distributions of heading date, plant height, spikelets per panicle, thousand-grain weight and yield in the experimental materials for two years.

Traits	Year	Population (mean±SD)	Range	Nangyanzhan (mean±SD)	Chuan7 (mean±SD)	Heritability
HD (d)	2006	92.9 ± 7.9 ab	70.0–115.3	87.2 ± 1.9 b	98.7 ± 2.3 a	89.0%
	2007	81.1 ± 5.2 b	71.8–100.1	83.2 ± 1.6 b	96.6 ± 2.7 a	
PH (cm)	2006	132.4 ± 22.1 b	63.0–189.0	145.6 ± 4.1 a	146.0 ± 4.6 a	90.5%
	2007	129.6 ± 20.6 b	84.1–170.4	140.3 ± 5.7 a	144.0 ± 5.4 a	
SPP	2006	104.2 ± 29.0 Bb	61.2–201.3	92.5 ± 12.5 Bc	210.2 ± 18.2 Aa	79.4%
	2007	122.6 ± 38.0 B	60.2–241.3	88.6 ± 6.7 C	206.7 ± 13.9 A	
TGW (g)	2006	20.0 ± 4.7 Bb	11.6–33.2	44.3 ± 1.6 Aa	11.4 ± 0.7 Bc	90.0%
	2007	18.9 ± 3.8 Bb	11.7–29.1	42.3 ± 2.0 Aa	11.5 ± 0.6 Bc	
Yield (g)	2006	10.3 ± 6.5 b	2.5–29.8	19.3 ± 1.9 a	16.8 ± 2.0 a	33.5%
	2007	12.3 ± 5.6 b	1.5–29.6	14.1 ± 1.5 ab	19.8 ± 2.2 a	

A, B and C, ranked by Duncan test at $P \leq 0.01$; a, b and c, ranked by Duncan test at $P \leq 0.05$.

SPP and yield were negatively correlated with HD, respectively. Further, SPP and TGW were positively correlated with yield, but a negative correlation was detected between them in both years (table 2).

Heading date

Totally, four HD QTLs were located on chromosomes 3, 5, 6 and 11, respectively. Of these, *qhd3* and *qhd6* were detected repeatedly in two years. In addition, *qhd5* and *qhd11* were identified in only one year. The four QTLs explained 7.6% to 27.7% of phenotypic variance, individually. *qhd6* was a major QTL explaining up to 27.7% of phenotype variance, Chuan7 allele of *qhd6* delayed HD. In contrast, Nanyangzhan alleles of *qhd5* and *qhd11* showed an increasing effect (figure 1; table 3).

Plant height

A total of four PH QTLs were identified in the mapping population. Two major QTLs, *qph1* and *qph8*, were detected in both years, located on chromosomes 1 and 8, respectively. Their LOD scores were more than 10 and explained over 24% of the phonotype variance. *qph6* and *qph12* were identified only in 2006. They had small additive effects and explained less than 6% of phenotype variance (table 3).

Table 2. The correlation coefficients among five traits.

	PH	HD	SPP	TGW	Yield
PH		0.01	0.07	0.21*	0.36**
HD	0.24*		−0.21*	−0.27**	−0.20*
SPP	0.07	−0.21*		−0.38**	0.35**
TGW	0.42**	−0.17	−0.28*		0.04
Yield	0.32**	−0.27*	0.15	0.40**	

The correlation coefficients in 2006 and 2007 are below and above the diagonal, respectively. Significant at $\alpha = 0.05^*$ and $\alpha = 0.01^{**}$.

Spikelets per panicle

Five SPP QTLs were identified on chromosomes 3, 5, 7, 8 and 10, respectively. *qspp5* was detected only in 2006, and Nanyangzhan allele increased the trait value. On the contrary, the other four QTLs, Chuan7 allele increased trait value and was detected only in 2007.

Thousand-grain weight

A total of seven QTLs were detected for TGW. Of them, *qtgw3a* was a major QTL, which is located on the centromere region of chromosome 3 in both years. It explained over 24% of phenotype variance with large LOD scores of more than 15. In addition, *qtgw2*, *qtgw7* and *qtgw9* were stably identified in two years, although they explained less than 11.0% of phenotype variance. *qtgw3b*, *qtgw5* and *qtgw8* were only identified in 2007. Of all the QTLs detected here, Nanyangzhan carried alleles with increasing effects.

A two-way ANOVA test showed that genotype, environment and the G × E interaction were highly significant in the five traits (table 4).

Discussion

Repeatability of QTL detection depend on the crosstalk of its genetic effects and environment

A total of 20 QTLs were identified in this study. Of them, eight were detected in common in both years. Additional two QTLs could also be commonly detected in two years if the LOD threshold decreased to 2.0, an empirical threshold of LOD score in rice (Vanooijen 1999). For TGW with the highest heritability, five out of seven QTLs were commonly detected in both years; however, for SPP with the lowest heritability, only one out of five QTLs were repeatedly detected. For PH and HD with modest heritability, half QTLs were repeatedly identified. For any traits, the major QTLs, such as *qhd3*, *qhd6*, *qph1*, *qph8* and *qtgw3*, could be repeatedly detected in this study. In addition, the minor

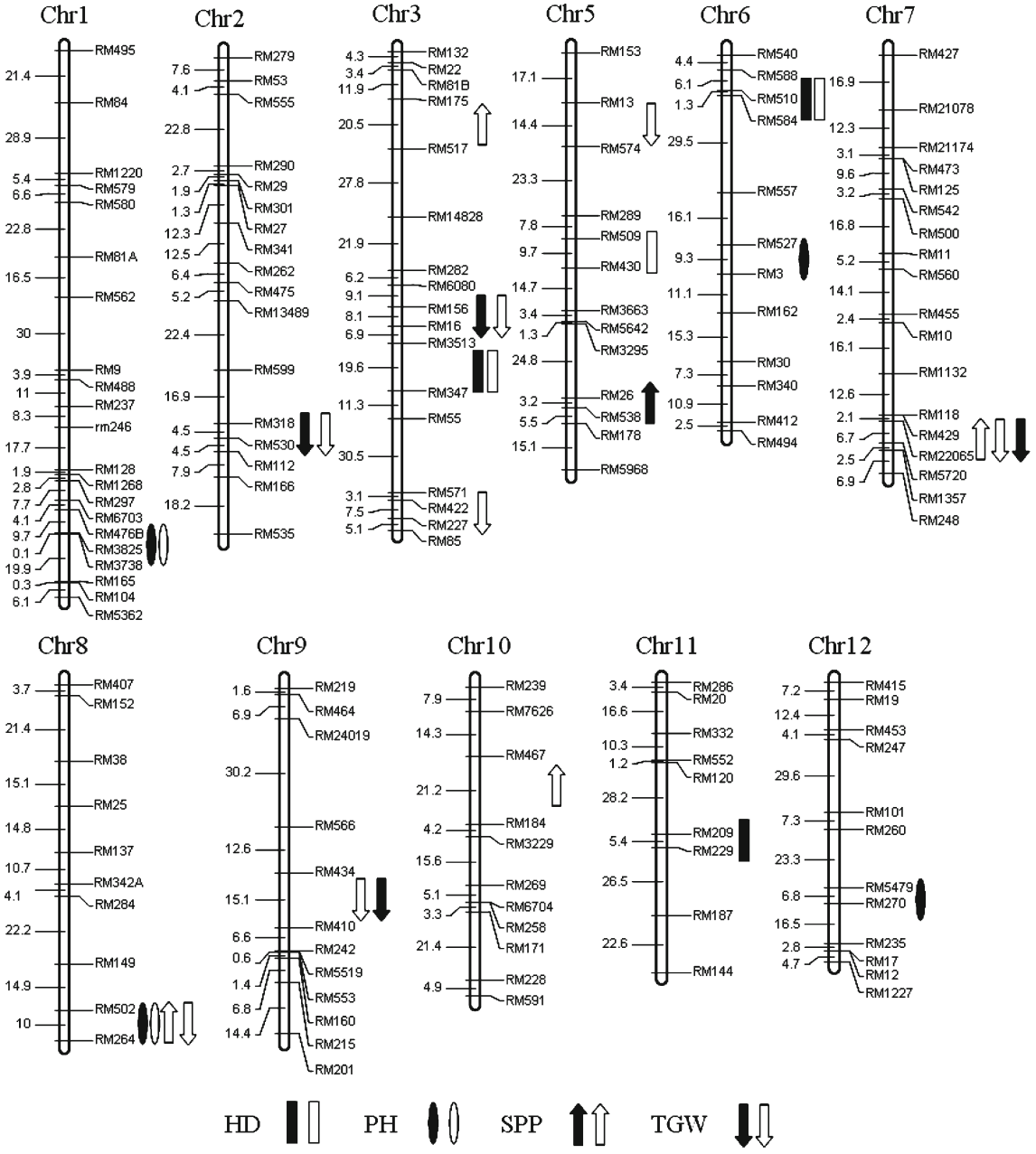

Figure 1. Genetic linkage map showing QTL positions detected in the RIL population. Black and white shapes indicated QTL identified in 2006 and 2007, respectively.

TGW QTLs, *qtgw7, qtgw8* and *qtgw9*, were also identified in both years. In contrast, some minor QTLs were only identified in single year, such as *qhd5*, *qph6* and *qspp10*. Based on the present knowledge, some genes/QTLs' expression, such as HD, PH and SPP genes, trended to be induced and/or affected by environmental factors (photoperiod, temperature and others). Analogically, these related QTLs were probably sensitive to environments. Further, highly significant interactions between genotype and environment for all five traits were observed in this study (table 4). Thus, some QTLs were identified only in some specific environments.

Comparing QTL detection with previous studies

Using populations derived from combination between Nipponbare (*japonica*) and Kasalath (*indica*), 16 HD QTLs were consecutively identified (Yano *et al.* 2001; Matsubara *et al.* 2008). Four HD QTL were identified in this study. The major HD QTL, *qhd6*, was located at the same region as *Hd3a* mapped by Monna *et al*. (2002). In the region of RM3513–RM347 at the end of the long arm of chromosome 3, *qhd3* was corresponding to the locus of *Hd6* mapped by Yamamoto *et al.* (2000). *qhd5* (RM509-RM430) was likely to be

Table 3. QTL for heading date, plant height, spikelets per panicle and thousand-grain weight detected in the RIL population derived from the cross between Nanyangzhan and Chuan7.

Trait	QTL	Interval	2006			2007		
			LOD[c]	A[a]	V%[b]	LOD[c]	A[a]	V%[b]
HD (d)	*qhd3*	RM3513–RM347	4.2	−2.7	11.0	5.8	−2.1	15.4
	qhd5	RM509–RM430				4.1	1.5	7.6
	qhd6	RM510–RM584	8.5	−4.4	27.7	11.2	−2.4	20.7
	qhd11	RM209–RM229	3.7	2.6	10.0			
PH (cm)	*qph1*	RM3825–RM3738	12.8	−10.8	26.4	11.9	−14.0	37.3
	qph6	RM527–RM3	3.6	−5.2	5.9			
	qph8	RM502–RM264	12.4	10.2	24.0	10.1	11.9	28.4
	qph12	RM5479–RM270	3.8	−5.2	5.9			
SPP	*qspp3*	RM175–RM517				3.6	−10.9	6.6
	qspp5	RM26–RM538	3.0	10.6	11.3			
	qspp7	RM22065–RM5720	2.7[c]	−10.1	11.3	5.3	−12.9	11.5
	qspp8	RM502–RM264				4.6	−11.8	9.3
	qspp10	RM467–RM184				4.3	−14.4	14.2
TGW (g)	*qtgw2*	RM318–RM530	3.1	1.3	7.1	3.0	0.8	4.2
	qtgw3a	RM156–RM16	15.3	2.7	33.0	15.2	1.9	24.3
	qtgw3b	RM422–RM227				4.3	1.0	6.0
	qtgw5	RM13–RM574				6.8	1.4	12.6
	qtgw7	RM22065–RM5720	6.0	1.6	11.0	4.7	1.1	7.5
	qtgw8	RM502–RM264	2.1[c]	0.9	3.5	3.9	1.0	6.0
	qtgw9	RM434–RM410	3.3	1.3	7.1	3.1	0.9	5.3

[a]A additive effect, positive additive effect means Nanyangzhan allele increasing trait values. [b]Variance explained by the QTL. [c]QTL with LOD ≥ 2.9 in one year but 2.0 ≤ LOD ≤ 2.9 in the other years are also listed.

Table 4. Summary of effects resolved by two-way ANOVA of the five traits of RIL population measured in two environments.

Traits	Variation	*df*	MS	*F*	*P*
HD	E	1	33413.95	967.07	< 0.0000
	G	184	185.45	5.37	< 0.0000
	G×E	184	44.02	1.27	< 0.0000
	Error	370	34.55		
PH	E	1	1499.30	46.35	< 0.0000
	G	184	1629.83	50.38	< 0.0000
	G×E	184	119.87	3.71	< 0.0000
	Error	370	32.35		
SPP	E	1	64258.94	362.32	< 0.0000
	G	184	3341.40	18.84	< 0.0000
	G×E	184	690.88	3.90	< 0.0000
	Error	370	177.35		
TGW	E	1	26.73	13.39	0.0003
	G	184	65.22	32.68	< 0.0000
	G×E	184	5.00	2.51	< 0.0000
	Error	370	2.00		
Yield	E	1	6313.15	5004.73	< 0.0000
	G	184	48.26	38.25	< 0.0000
	G×E	184	24.36	19.31	< 0.0000
	Error	370	1.26		

G, genotype; E, environment; G×E, genotype×environment interaction.

qDTH-5 detected from a BC_2F_2 population (Milyang 23/*Oryza rufipogon*//Milyang 23) (Cho *et al.* 2003). Besides, *qhd11* was closely linked to *dth11.1* flanked by the region between RM167 and RM209 detected in the population between cultivar and wild rice (Septiningsih *et al.* 2003). Interestingly, the mapping populations in which *qDTH-5* and *dth11.1* were respectively identified had one wild rice as a parent. Among four PH QTLs, *qph1* was very near to the *sd1* locus that caused the first green revolution (Spielmeyer *et al.* 2002), which probably indicated *qph1* in this study is

the locus of *sd1*. The *qph6* and *qph12* loci were similar to *cl6* and *cl12* reported by Rahman *et al.* (2007), respectively. However, *qph8* was detected as a major QTL for the first time in this population, which had an approximate effect to *qph1*. Thus, isolation of *qph8* would be significant in both uncovering its genetic basis and making strategy of its application in breeding. Among seven TGW QTLs, *qtgw3a* and *qtgw5* were also frequently identified by previous researchers in different populations (Xing *et al.* 2002; Lin and Wu 2003; Thomson *et al.* 2003; Ma *et al.* 2004). These two QTLs were mapped to the same region of *GS3* and *GW5* which were the most important genes for grain length and grain width in rice, respectively (Zhang 2007). The *qtgw8* and *qtgw9* loci were first found in present study, the later was identified in both years in spite of a minor effect. With the major QTLs being cloned (such as *GS3* and *GW5*/*qSW5*), and the minor QTLs should be considered as targets for cloning. Three of five SPP QTLs, *qspp5*, *qspp7* and *qspp8*, were new QTLs found in this study. They had a potential to increase the grain yield to some extent. Interestingly, *qspp7* and *qspp8* were just located on the two QTL hot-spot regions of chromosomes 7 and 8, respectively. Hence, isolation of these QTLs was also helpful to explore QTL hot spots' genetic mechanism.

Taken together, six of 20 QTLs were detected in this study for the first time. This suggested that populations derived from diverse parents in both phenotype and genotype were more chance to detect QTL. The accessions with contrasting phenotype characters are recommended as parents for developing the mapping population in future.

Genetic dissection of the QTL clusters

There were two QTL clusters on chromosomes 7 and 8. The major PH QTL, *qph8*, was located on the end of the long arm of chromosome 8, which explained more than 24.0% of phenotype variance in present population. Its additive value was close to that of *qph1* (*sd1*) with opposite directions (table 3). There were two minor QTLs *qspp8* and *qtgw8* around the region of *qph8*. One may ask whether they are linked QTLs or a pleiotropic QTL with effects on PH, SPP and TGW. Accordingly, a similar question also exists in that *qtgw7* and *qspp7* were identified in the same region between RM22065 and RM5720. In previous reports, some QTLs showed pleiotropic effects, such as cloned gene *GS3* which is a major gene for grain length/weight with a minor effect in grain width and thickness, and *Ghd7* showed a pleiotropic effects in PH, HD, and SPP (Fan *et al.* 2006; Xue *et al.* 2008). Besides, Zhang *et al.* (2006) reported that one QTL was mapped to the short arm of chromosome 8 that conducted simultaneously four traits (SPP, GPP, HD and PH). On the other hand, *Hd3* was first identified as a single HD QTL located on the short arm of chromosome 6 (Yamamoto *et al.* 1998). However, Monna *et al.* (2002) reported that *Hd3a* and *Hd3b* were two distinct QTLs in the *Hd3* region. In the present study, the low mapping resolution is not enough to clearly answer the question. However, a clear answer to the questions is a key step to make a breeding design to utilize them. Developing near-isogenic lines for the target regions is an efficient way to resolve the question.

In conclusion, the population derived from diverse parents showed more opportunities for detection of new QTL. If these QTLs identified in this study will be validated in the near-isogenic lines in further study, they can be utilized for rice yield improvement by marker assisted selection for favourable alleles. In addition, two QTLs hot spots and QTL *qtgw9* would be worth fine mapping and cloning in future in order to unveil their genetic characteristics.

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