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ORIGINAL ARTICLE

Quantitative trait loci identification and meta-analysis for rice panicle-related traits

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Abstract Rice yield is a complex trait controlled by quantitative trait loci (QTLs). In the past three decades, thousands of QTLs for rice yield traits have been detected, but only a very small percentage has been cloned to date, as identifying the QTL genes requires a substantial investment of time and money. Meta-analysis provides a simple, reliable, and economical method for integrating information from multiple QTL studies across various environmental and genetic backgrounds, detecting consistent QTLs powerfully and estimating their genetic positions precisely. In this study, we aimed to locate consistent QTL regions associated with rice panicle traits by applying a genome-wide QTL meta-analysis approach. We first conducted a QTL analysis of 5 rice panicle traits using 172 plants in 2011 and 138 plants in 2012 from an F_2 population derived from a cross between Nipponbare and H71D rice cultivators. A total of 54 QTLs were detected, and these were combined with 1085 QTLs collected from 82 previous studies to perform a meta-analysis using BioMercator v4.2. The integration of 82 maps resulted in a consensus map with 6970 markers and a total map length of 1823.1 centimorgan (cM), on which 837 QTLs were projected. These QTLs were then integrated into 87 meta-quantitative trait loci (MQTLs) by meta-analysis, and the 95 % confidence intervals (CI) of them were smaller than the mean value of the original QTLs. Also, 30 MQTLs covered 47 of the 54 QTLs detected from the cross between Nipponbare and H71D in this study. Among them, the two major and stable QTLs, *spp10.1* and *sd10.1*, were found to be included in MQTL10.4. The three other major QTLs, *pl3.1*, *sb2.1*, and *sb10.1*, were included in MQTL3.3, MQTL2.2, and MQTL10.3, respectively. A total of 21 of the 87 MQTLs' phenotypic variation were >20 %. In total, 24 candidate genes were found in 15 MQTLs that spanned physical intervals <0.2 Mb, including genes that have been cloned previously, e.g., *EP3*, *LP*, *MIP1*, *HTD1*, *DSH1*, and *OsPNH1*. However, it would be beneficial to identify a greater number of candidate genes from these MQTLs. Mining new genes that modulate yield and its related traits would assist researchers to better understand the relevant molecular mechanisms. The MQTLs found in this study that have small physical and genetic intervals are useful not only for marker-assisted selection and pyramiding, but they also provide important information of rice yield and related gene mining for future research.

Keywords QTL analysis · Meta-analysis · Rice panicle traits · Yield · MQTL

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Introduction

Rice is a staple food for more than 3.5 billion people worldwide. However, owing to the impacts of population growth, changing climates, and limited arable land, it is

imperative that scientists find ways of meeting the increasing demand for high-yielding rice. Rice yield is a complex trait that is composed of three component traits: number of panicles per plant, number of grains per panicle, and grain weight, which are all considered quantitative traits (Xing and Zhang 2010). These traits are controlled by quantitative trait loci (QTLs). Genetic dissection of yield and its component traits by molecular marker linkage maps has resolved hundreds of QTLs. Though numerous important genes have been found to regulate these traits (Ashikari et al. 2005; Fan et al. 2006; Li et al. 2011a, b; Song et al. 2007; Wang et al. 2012), our knowledge of the gene networks that control rice yield is still limited. Integration of results from multiple QTL studies will enhance our knowledge of the genetic basis for dissection of complex traits (Veyrieras et al. 2007). BioMercator, a genetic map compilation and QTL meta-analysis software program, offers wizards to run analyses and display input and output maps through an accessible graphical user interface (Arcade et al. 2004; Sosnowski et al. 2012). Recently, BioMercator has been used for QTL meta-analysis in several crops, especially maize and soybean (Griffiths et al. 2009; Jin et al. 2013; Li et al. 2013; Qi et al. 2011; Truntzler et al. 2010; Zhang et al. 2014). Though a large number of QTLs have been detected, there are a few reports on QTL meta-analysis of rice yield-related traits (Ballini et al. 2008; Courtois et al. 2009; Swamy and Sarla 2011). The key limitations to integrating results from multiple studies are the use of diverse mapping populations and different molecular markers, which hinder comparisons of QTL positions and validation of conserved QTLs. Thus, it is of significant value for gene mining and genomics-assisted breeding of rice to construct a high-density consensus map and conduct a meta-analysis for rice panicle traits.

In this study, QTLs for five panicle-related traits, including panicle length (PL), number of primary branches (NPB), number of secondary branches (NSB), spikelets per panicle (SPP), and seed setting density (SD), were identified using an F_2 population derived from a cross between Nipponbare and H71D rice cultivars. The 54 QTLs detected in this study together with 1085 previously reported QTLs collected from 80 maps were combined to perform a meta-analysis. Our main objectives were: (1) to detect QTLs for the five panicle-related traits, and identify major and stable QTLs across different years; (2) to identify MQTLs from the large number of reported QTLs and refine their positions; and (3) to mine candidate genes from the MQTLs with small genetic and physical intervals, which may be useful in marker-assisted selection (MAS) and pyramiding. The results obtained from this research may provide valuable information for improving panicle composition traits in rice breeding.

Materials and methods

Plant materials and QTL mapping for panicle-related traits

An F_2 population was developed from a cross between Nipponbare and H71D rice cultivars. The F_1 generation was self-fertilized to produce the F_2 generation in an experimental field at the South China Agricultural University (23°09′N, 113°20′E), Guangzhou, China. The parents and the F_2 population were planted in two-row plots in a randomized, complete block design from July to November of 2011 and 2012. The spacing between rows and between plants within a row was 20 cm. After maturity, we randomly harvested 172 plants in 2011 and 138 plants in 2012 to test traits and conducted a QTL analysis using IciMapping v3.2 (Li et al. 2008). In total, 123 single sequence repeat (SSR) markers distributed evenly on 12 whole chromosomes were used to prepare the framework linkage map. Inclusive composite interval mapping, which was used in this study, has been proposed for additive QTL mapping. A permutation test (1000 permutations) was used to determine the logarithm of odds (LOD) threshold (Li et al. 2007, 2012). The relative contribution of the genetic component (R^2) was calculated, and described as the proportion of phenotypic variation (PVE) that could be resolved. QTLs with PVE >20 % were considered major QTLs. Moreover, QTLs detected in both of the studied years were considered stable.

Data collection and QTL meta-analysis

Five panicle-related traits in rice, PL, NPB, NSB, SPP, and SD, were surveyed in this study. QTLs of these five traits and their genetic map information were collected from publications and public databases based on the following principles. First, it was necessary to obtain detailed information about the genetic maps, including cross type, population size, and genetic distances of each marker. Those QTLs that had available LOD scores, R^2 values, and map positions were integrated with our analysis. If any of these variables were missing, the map and QTLs would be discarded. Second, data, such as the name of the cross parents, symbol of QTLs, chromosome, linkage, location, and environment, were collected and organized into a BioMercator v3 format text document. Finally, 1139 rice panicle trait QTLs were collected from 82 QTL maps (Supplemental Table 1), including the 54 QTLs identified from this study (the maps were named 2011-Wu and 2012-Wu).

Meta-analysis was performed on the QTL clusters for each chromosome using BioMercator v4.2 and Veyrieras's algorithm (Veyrieras et al. 2007). The lowest Akaike information criterion (AIC) value was used to select the best

QTL model for each chromosome, which was considered a significant model indicating the number of MQTLs.

Results

Evaluation of panicle-related traits

Statistically significant or very significant differences were observed for the five panicle-related traits between Nipponbare and H71D in the 2 years (Table 1). According to the values of skewness and kurtosis, all traits showed a pattern of continuous distribution in the F_2 populations. Transgressive segregations were observed for four of the traits over the 2 years studied, with the exception of the number of primary branches.

QTL analysis of five panicle-related traits

A total of 123 SSR markers were used to genotype 172 plants and 138 plants in 2011 and 2012, respectively. A linkage map covering 12 whole rice chromosomes was constructed, and the total length of this map was 1927 cM. The average interval of markers was 15.7 cM. A total of 54 QTLs for the five panicle-related traits, distributed on 11 chromosomes (except chromosome 4), were identified by QTL analyses using inclusive composite interval mapping; with LOD values ranging from 2.51 to 6.94 (Table 2). For the single traits, the number of QTLs ranged from 6 (for PL) to 14 (for SD), individually explaining 6.31 % (NPB) to 52.6 % (SPP) of the PVE. In total, 7 of the 54 QTLs individually explained >20 % of the PVE and were, thus, considered major QTLs. A total of 10 of the 54 QTLs were considered stable QTLs as they were detected in both 2011 and 2012. Also, two major and stable QTLs in the same interval of RM147–RM228, *spp10.1* and *sd10.1*, were considered important for improving these traits through MAS.

Meta-QTL analysis of rice panicle-related traits

We collected 1139 QTLs for rice panicle-related traits from 82 QTL maps (Supplemental Table 1). Pre-consensus maps for all twelve chromosomes suitable for meta-analysis were created by integration of six genetic maps (Supplemental Table 2). The pre-consensus maps were then used to construct an integrated consensus map for the 82 QTL maps. This integrated consensus map covered a genetic length of 1823.1 cM, including 6970 markers, and 837 QTLs were projected onto it (Fig. 1; Table 3, and Supplemental Table 3). The average genetic distance between markers on the 12 chromosomes ranged from 0.19 to 0.5 cM.

A meta-analysis of the 837 QTLs was then performed. The AIC was used to select the QTL model on each chromosome. The number of MQTLs per chromosome was short-listed according to the QTL model. In total, 87 MQTLs were identified with a confidence interval (CI) of 95 %. The number of MQTLs identified on each chromosome varied from four to ten (Table 4; Fig. 2). The PVE of the MQTLs varied from 2 to 32 %. Among the 87 MQTLs, 21 had PVEs >20 %. The CIs (95 %) of all MQTLs were narrower than their mean values of the original QTLs. The CIs (95 %) of MQTLs varied from 0.04 cM between the intervals RM480–RZ225 on chromosome 5 to 18.3 cM between the intervals RZ797–RM229 on chromosome 11. The physical length of these MQTLs varied from

Table 1 Performance of panicle traits of the two parents and their F_2 populations

Trait	Year	Parents		F_2 population			
		Nipponbare	H71D	Range	Mean ± SD	Kurtosis	Skewness
PL[a]	2011	22.2 ± 1.5	26.3 ± 1.5*	19.7–34.1	26.5 ± 2.6	−0.117	−0.032
	2012	19.8 ± 1.1	27.0 ± 1.3**	17.7–33.1	24.7 ± 2.8	−0.239	0.001
NPB	2011	8.8 ± 1.2	15.6 ± 1.6**	10.0–21.0	13.6 ± 2.2	0.297	0.514
	2012	7.6 ± 1.1	17.4 ± 3.1**	8.0–19.0	12.2 ± 2.2	0.137	0.455
NSB	2011	19.5 ± 1.9	72.0 ± 16.9**	15.0–93.0	52.8 ± 14.2	0.038	0.234
	2012	15.4 ± 3.0	63.8 ± 14.0**	10.0–75.0	37.4 ± 14.4	−0.319	0.371
SPP	2011	109.7 ± 12.7	367.9 ± 85.2**	37.0–459.0	187.0 ± 107.8	−1.015	0.276
	2012	107.0 ± 16.6	368.0 ± 73.5**	81.0–466.0	230.5 ± 84.2	−0.381	0.542
SD[b]	2011	5.0 ± 0.5	13.9 ± 2.8**	3.2–17.7	10.1 ± 2.7	0.143	0.474
	2012	5.5 ± 0.6	13.7 ± 3.0**	4.1–17.0	9.2 ± 2.9	−0.521	0.486

PL panicle length, *NPB* number of primary branches, *NSB* number of secondary branches, *SPP* spikelets per panicle, *SD* seed setting density

[a] The unit of panicle length is centimeter

[b] The unit of seed setting density is grains per centimeter

*, ** Statistically significant at 0.05 and 0.01 probability levels, respectively

Table 2 Identification of QTLs for five panicle-related traits in the F_2 population and their genetic parameters estimated in 2011 and 2012

Trait	Year	QTL	Marker interval	Position	LOD	PVE (%)	A
PL	2011	*pl3.1*	RM473D–RM6080	90	2.52	20.37	−2.33
PL	2011	*pl3.2*	RM156–RM16	141	2.66	13.03	−1.34
PL	2012	*pl6.1*	RM136–RM3	82	3.23	15.22	−1.13
PL	2011	*pl9.1*	RM201–RM205	91	2.82	14.28	−1.23
PL	2011	*pl12.1*	RM277–RM519	103	3.19	15.85	−0.52
PL	2012	*pl12.2*	RM519–RM270	113	3.04	15.99	−0.38
NPB	2011	*pb1.1*	RM495–RM84	4	3.04	7.17	−0.7
NPB	2012	*pb1.2*	RM428–RM1	24	2.80	10.32	−0.59
NPB	2012	*pb2.1*	RM5345–RM1358	46	2.76	10.51	−0.86
NPB	2011	*pb2.2*	RM1358–M29	91	2.66	13.31	−0.73
NPB[a]	*2011*	*pb3.1*	*RM523–RM231*	*0*	*2.55*	*10.29*	*−0.89*
NPB	*2012*	*pb3.1*	*RM523–RM231*	*0*	*2.51*	*8.03*	*−0.73*
NPB	2011	*pb3.2*	RM16–RM6266	148	6.17	16.00	0.67
NPB	2011	*pb6.1*	RM204–RM584	35	2.65	6.31	−0.38
NPB	2011	*pb7.1*	RM82–RM214	11	3.41	12.53	−0.39
NPB	2011	*pb8.1*	RM152–RM310	47	6.30	17.90	−1.25
NPB	2011	*pb10.1*	RM222–RM311	5	2.92	13.26	−0.74
NPB	2011	*pb10.2*	RM311–RM304	25	3.33	8.44	−0.26
NPB	2011	*pb10.3*	RM147–RM228	84	4.96	19.67	0.15
NSB	*2011*	*sb1.1*	*RM495–RM84*	*4*	*5.05*	*15.92*	*−7.1*
NSB	*2012*	*sb1.1*	*RM495–RM84*	*7*	*3.06*	*10.09*	*−6.29*
NSB	2012	*sb1.2*	RM84–RM490	17	3.84	13.75	−7.32
NSB	2012	*sb1.3*	RM490–RM578	57	2.66	9.24	−3.81
NSB	2011	*sb1.4*	RM578–RM580	98	2.69	12.59	−3.3
NSB	2011	*sb2.1*	RM1358–RM29	89	5.42	25.02	−8.3
NSB	2011	*sb2.2*	RM262–RM263	128	3.07	11.55	−7.28
NSB	2012	*sb6.1*	RM584–RM276	58	3.06	9.29	−5.67
NSB	2011	*sb8.1*	RM310–RM339	62	4.08	13.86	−8.07
NSB	2011	*sb10.1*	RM304–RM147	63	3.92	21.35	−11.36
SPP	2011	*spp1.1*	RM495–RM84	5	3.47	13.10	−34.97
SPP	2012	*spp1.2*	RM84–RM490	22	4.00	15.12	−38.27
SPP	2012	*spp1.3*	RM490–RM578	58	2.92	10.68	−33.3
SPP	2011	*spp1.4*	RM23–RM24	111	2.81	12.03	−38.2
SPP	2011	*spp2.1*	RM555–RM5345	30	3.26	12.38	−41.44
SPP	2012	*spp2.2*	RM262–RM263	146	3.37	11.37	−36.26
SPP	2012	*spp6.1*	RM584–RM276	58	3.25	10.40	−32.85
SPP	2011	*spp8.1*	RM152–RM310	34	3.07	13.76	−36.68
SPP	*2011*	*spp10.1*	*RM147–RM228*	*87*	*4.87*	*25.67*	*−33.33*
SPP	*2012*	*spp10.1*	*RM147–RM228*	*87*	*3.72*	*52.62*	*−64.29*
SPP	2011	*spp11.1*	RM167–RM202	47	3.20	14.59	−45.65
SD	*2011*	*sd1.1*	*RM495–RM84*	*2*	*4.41*	*11.35*	*−1.15*
SD	*2012*	*sd1.1*	*RM495–RM84*	*6*	*5.79*	*15.45*	*−1.64*
SD	2012	*sd1.2*	RM84–RM490	19	4.57	17.36	−1.6
SD	2012	*sd1.3*	RM578–RM580	76	3.36	12.97	−1.54
SD	2011	*sd1.4*	RM23–RM24	113	4.23	10.81	−0.71
SD	2012	*sd2.1*	RM154–RM211	0	2.80	6.52	−1.12
SD	2012	*sd2.2*	RM29–RM341	106	3.08	10.57	−1.39
SD	2011	*sd2.3*	RM475–RM262	121	3.43	9.30	−0.56
SD	2012	*sd5.1*	RM164–RM274	90	4.06	13.20	−1.41
SD	2012	*sd7.1*	RM10–RM505	53	3.25	11.90	0.68

Table 2 continued

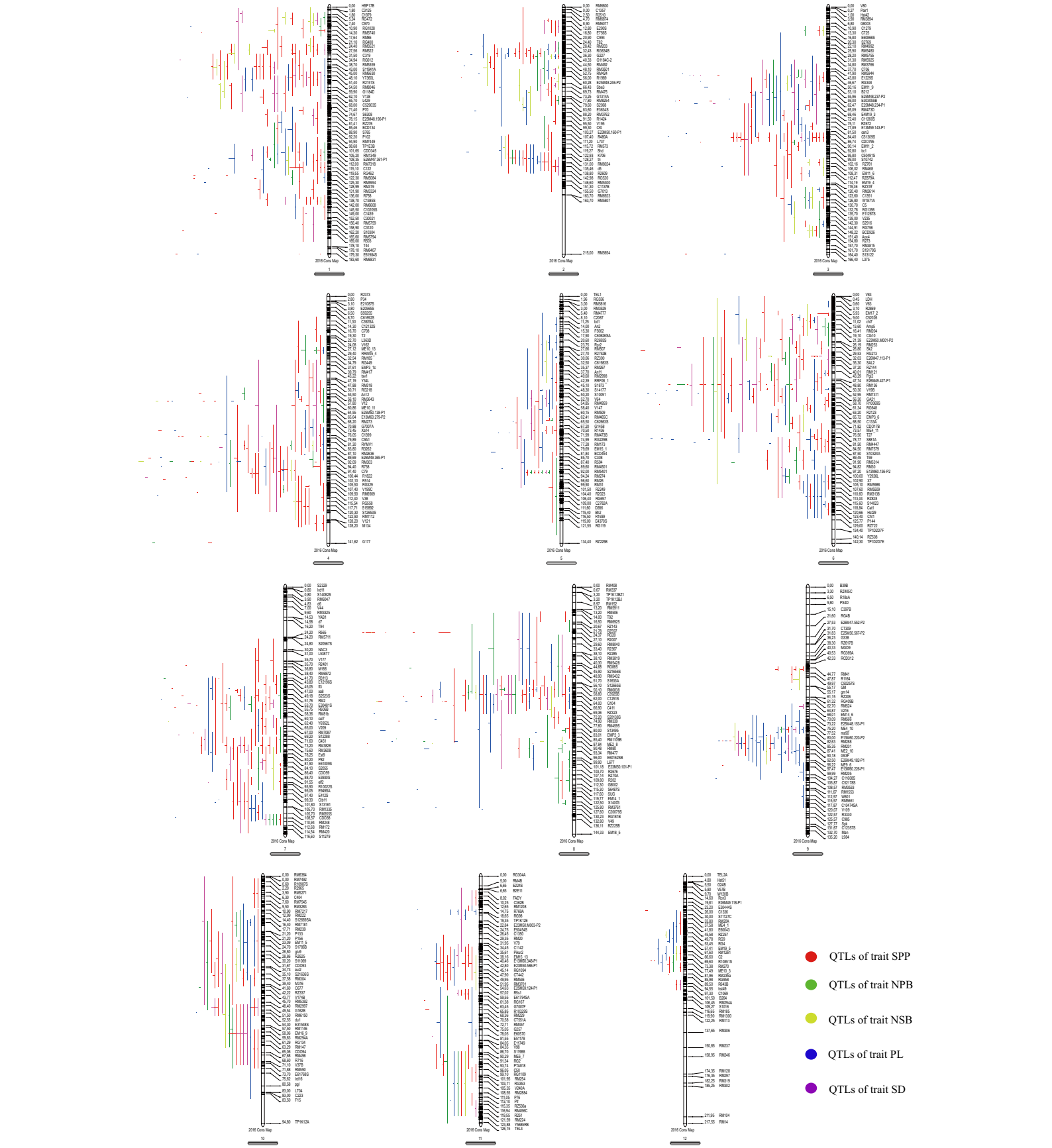
Trait	Year	QTL	Marker interval	Position	LOD	PVE (%)	A
SD	2012	*sd7.2*	RM505–RM234	62	5.99	15.20	1.44
SD	2012	*sd8.1*	RM152–RM310	24	2.85	9.50	−1.51
SD	*2011*	*sd10.1*	*RM147–RM228*	*87*	*6.94*	*24.58*	*−0.72*
SD	*2012*	*sd10.1*	*RM147–RM228*	*87*	*3.19*	*45.33*	*−2.06*

PL panicle length, *NPB* number of primary branches, *NSB* number of secondary branches, *SPP* spikelets per panicle, *SD* seed setting density, *Position* genetic map position by centimorgen (cM), *PVE* percentage of phenotypic variance explained by QTL, *A* the additive effect of QTL; negative values indicate that alleles from H71D increased the trait score

[a] Rows in italics represent QTLs detected in both 2011 and 2012

0.04 to 9.17 Mb. Furthermore, 30 MQTLs covered 47 of the 54 QTLs detected from the cross between Nipponbare and H71D in this study. Among them, the two major QTLs, *spp10.1* and *sd10.1*, were found to be included in MQTL10.4. The three other major QTLs, *pl3.1*, *sb2.2,* and *sb10.1*, were included in MQTL3.3, MQTL2.2, and MQTL10.3, respectively (Table 4). A total of 15 MQTLs spanned physical intervals <0.2 Mb. These MQTLs with small genetic and physical intervals might be regarded as important regions for MAS, fine mapping, candidate gene identification, and functional analysis.

MQTLs with precise and narrow physical intervals are useful in mining and listing of candidate genes. The potential of a few important genes or gene families related to yield have already been proved in rice and other crops, e.g., cell division-controlling genes, sugar transport protein-like genes, cytochrome P450 encoding genes, cytokinin oxidase genes, PPR repeat-containing protein-like genes, zinc finger-like protein encoding genes, F-box genes, and genes with no apical meristem (Swamy et al. 2011; Swamy and Sarla 2011). The genes present in the 15 MQTLs with physical length <0.2 Mb from the present study were analyzed based on several rice databases (http://www.ricedata.cn, http://shigen.nig.ac.jp/rice/oryzabase/, and http://rice.plantbiology.msu.edu/cgi-bin/gbrowse/rice/). In MQTL1.4, *Os01g20910* was a zinc finger C3HC4-type domain containing a protein-encoding gene. This type of gene enhances growth of transgenic tobacco (Zeba et al. 2009). A CCT motif family protein-encoding gene, *Os02g05470*, was found in MQTL2.1. In rice, *Ghd7* that is regarded as an important regulator of heading date and yield potential also encodes a CCT motif family protein (Weng et al. 2014). Two reported genes, *LP* and *EP3*, were found in the physical region of MQTL2.2. *LP* is an F-box gene that enhances grain yield by improving rice panicle architecture (Li et al. 2011a, b). The *EP3* gene also encodes putative F-box protein, which is involved in the development of several organs including the rice panicle (Piao et al. 2009). The candidate gene in MQTL2.6 may be *Os02g43820*, an AP2 domain containing a protein-encoding gene. AP2 transcriptional factor, a cross-talk factor involved in signal transduction pathways of salicylic acid, jasmonic acid, ethylene, and abscisic acid, plays a role in various biological functions, including plant development, flower development, fruit and seed maturation, wounding, pathogen defense, and so on. Overexpression of *OsAP2-39*, a gene contained in an AP2 domain, leads to a reduction in yield by decreasing the biomass and the number of seeds in the transgenic rice lines (Yaish et al. 2010). Two reported genes, *MIP1* and *HTD1*, were found in MQTL4.1. *MIP1* interacted with *MOC1* both in vitro and in vivo. The overexpression of *MIP1* resulted in enhanced tillering and reduced plant height (Krupovič et al. 2008). The *HTD1* gene encodes an ortholog of *Arabidopsis MAX3*. Complementation analyses of *HTD1* confirmed that the defect in *HTD1* is responsible for both high tillering and dwarf phenotypes in the *htd1* mutant (Zou et al. 2006). The candidate gene *Os05g32350* in MQTL5.5 was also a zinc finger C3HC4-type domain containing protein-encoding gene, similar to *Os01g20910* in MQTL1.4. Five F-box genes (*OsFBDUF30*, *OsFBX186*, *OsFBDUF31*, *OsFBDUF32,* and *OsFBDUF33*) were found in MQTL6.1. The F-box gene family has been shown to play an important role in regulating various developmental processes and stress responses. Also, several F-box genes have been characterized to regulate important and diverse physiological processes, such as hormonal response, embryogenesis, seed germination, seedling development, floral organogenesis, lateral root formation, leaf senescence, pathogen resistance, and abiotic stress responses (Ikeda et al. 2007; Li et al. 2015; Song et al. 2012). In MQTL6.2, *Os06g11860* is an ethylene-responsive transcription factor (ERF) gene. ERF, with a single AP2 domain, is one of the largest subfamilies of the AP2/ERF transcription factor family. Though most of the ERFs are activators of stress-responsive genes, there are at least two ERF genes (*MFS1* and *OsAP37*) associated with grain yield in rice (Ramegowda et al. 2014; Ren et al. 2012). Two reported genes, *BU1* and *DSH1*, were found in the region of MQTL6.3. *BU1* is a brassinosteroid-induced gene. Rice plants with overexpression of *BU1* showed enhanced bending of the lamina joint, increased grain size, and resistance to brassinazole, an inhibitor of brassinosteroid biosynthesis (Tanaka et al. 2009). The product of *DSH1* is a dihydrosphingosine C4 hydroxylase, which may be involved


QTLs of trait SPP
QTLs of trait NPB
QTLs of trait NSB
QTLs of trait PL
QTLs of trait SD

◀**Fig. 1** The integrated consensus map constructed by BioMercator. The integrated consensus map contained 6970 markers (the majority of them are hidden; for details, see Supplemental Table 3) covering a length of 1823.1 cM, and 837 QTLs were projected on it. The names of the QTLs are hidden on the map to make it more legible. *Vertical lines* on the left of the chromosomes indicate the CI of each QTL, while *horizontal lines* indicate PVE. Markers and genetic distance (cM) are shown on the right of the chromosomes

Table 3 Details of the integrated map

Chromosome	No. of markers	No. of QTLs	Length (cM)	Average (cM)
1	964	113	183.6	0.19
2	731	69	215	0.29
3	824	89	167.5	0.20
4	577	87	141.6	0.25
5	522	42	134.4	0.26
6	682	114	142.3	0.21
7	538	80	118.6	0.22
8	500	97	144.3	0.29
9	406	45	137	0.34
10	320	36	94.8	0.30
11	472	45	126.5	0.27
12	434	20	217.5	0.50
Total	6970	837	1823.1	

No. number

in plant viability or reproductive processes. The phenotype of sterility is apparently caused by loss of function of *DSH1* in the stigma (Imamura et al. 2007). The candidate gene in MQTL6.7 is *OsPNH1*. The *OsPNH1* gene plays an important role in the formation of the shoot apical meristem and in leaf adaxial cell specification. Ethylene is a hormone involved in various aspects of growth, development, and responses to biotic and abiotic stresses in plants. In MQTL7.1, a product of the candidate gene *Os07g15540* is a putative ethylene receptor, which may play an important role in the ethylene-signaling pathway. In the 0.19-Mb region of MQTL8.1, we found two F-box genes (*OsFBDUF40* and *OsFBDUF41*) and a putative zinc finger family gene (*Os08g03310*). *Os11g05380* is a putative cytochrome P450 gene in MQTL11.2. Cytochrome P450s are essential for plant steroid hormone biosynthesis and inactivation (Nomura and Bishop 2006). *OsARF1*, a candidate gene reported in the 0.06-Mb region of MQTL11.5, has been shown to be essential for growth in vegetative organs and seed development (Attia et al. 2009; Waller et al. 2002). In MQTL11.8, a putative leucine-rich repeat receptor protein-encoding gene, *Os11g47240*, was found. Leucine-rich repeat receptor protein-encoding gene proteins play key roles in a variety of biological pathways, such as plant morphogenesis, meristematic growth, embryogenesis, pollen self-incompatibility, environmental signal processing, hormone regulation, pathogen defense, abscisic acid early signaling, brassinosteroid signaling, negative regulator-programmed cell death, germination speed, and tolerance to oxidative stress (Park et al. 2014). In total from the present study, 24 candidate genes were found from 15 MQTLs, which spanned a physical interval length <0.2 Mb. Additional candidate genes could be mined from other MQTL regions that were >0.2 Mb.

Discussion

Challenges for identifying QTL genes

Complex traits are features whose properties are determined by both genetic and environmental factors. The most economically important traits in both plants, including rice yield, and animals are categorized into complex traits. Rice grain yield is such a complex trait controlled by quantitative trait loci (QTLs), which is a genetic concept used to explain the inheritance of non-Mendelian traits. A QTL is a particular fragment of the chromosome that correlates with variation of certain phenotypes (the quantitative trait). QTL analysis is a statistical method that links two types of information—phenotypic data (trait measurements) and genotypic data (usually molecular markers)—in an attempt to explain the genetic basis of variation in complex traits (Miles and Wayne 2008). Since the first paper on the subject of plant QTL analysis was published in 1988 (Paterson et al. 1988), thousands of plant QTL studies have been published. With advances in genotyping technology and the development of quantitative genetic analytical techniques over the last three decades, QTL analysis has become an innovator within crop science research (Meng and Long 2008). In April 2008, 8646 rice QTLs were documented in the Gramene database, which had been extracted from 247 reports published between 1994 and 2007 (Ni et al. 2009). Though thousands of QTLs for rice yield traits have been documented, to date, only a few of them with large effects have been cloned, as to identify QTL genes is a slow and difficult process (Korstanje and Paigen 2002). First, at least one large mapping populations should be constructed through years of cross and self-cross; second, a large number of polymorphic markers need to be developed, and the phenotypic data of the mapping population need to be collected, then construct a high-density genetic map using these polymorphic markers to genotyping the mapping population, and finally combine the phenotypic data with the genotypic data to identify QTLs. However, it is very time-consuming, laborious, and costly to build large mapping populations, collect the phenotypic data and genotyping the mapping population to construct a high-density genetic map, and evaluate QTLs in multiple environments or different years. Identification of major and stable QTLs

Table 4 MQTLs of rice panicle traits and candidate genes/QTLs in the regions

MQTL	QTL model	Interval	Position[a]	PVE (%)	No. of initial QTL	Mean initial CI[b]	MQTL CI (95 %)[c]	Physical length of MQTL (Mb)	Partial initial QTLs[d]	Candidate genes
MQTL1.1	9	RM323–RG246	16.22	13	15	15.48	1.51	0.71	*pb1.1; pb1.2; sb1.1; sb1.2; spp1.1; spp1.2; sd1.1; sd1.2*	
MQTL1.2		RM6289–RM151	31.65	12	13	11.5	2.88	0.54		
MQTL1.3		S11122–RM6613	49.79	22	24	18.8	3.29	0.32	*sb1.3*; *spp1.3*; *sd1.3*	
MQTL1.4[e]		*RM3412–L429*	*65.46*	*5*	*7*	*23.22*	*7.55*	*0.2*	*sb1.4*	*Os01g20910*
MQTL1.5		E25M60.448–P1–RM23	77.53	3	1	6	5.33	0.68	*spp1.4*	
MQTL1.6		RZ744–BCD134	83.82	4	6	20.02	8.46	1.03	*sd1.4*	
MQTL1.7		RM7202–C10728S	112.16	13	15	18.7	2.06	0.74		
MQTL1.8		RM128–RG101	123.25	12	13	15.59	3.2	0.67		
MQTL1.9		E50125S–RM3290	147.65	16	19	14.4	0.32	0.29		
MQTL2.1	7	*S12817S–E290S*	*12.44*	*8*	*5*	*10.29*	*2.39*	*0.11*		*Os02g05470*
MQTL2.2		*RM5699–C980*	*42.29*	*32*	*20*	*12.87*	*1.5*	*0.07*	*pb2.1*; *sb2.1*; *spp2.1*; *sd2.1*	*EP3; LP*
MQTL2.3		RM424–RM27	52.86	11	9	18.97	2.51	0.83	*pb2.2*; *sd2.2*	
MQTL2.4		RG157–RM475	68.25	13	9	19.11	3.25	0.54	*sb2.2*	
MQTL2.5		V219–E3634S	83.2	7	4	16.9	9.18	0.46		
MQTL2.6		*RM7245–RM5706*	*108.87*	*4*	*3*	*25.38*	*14.92*	*0.04*	*spp2.2*	*Os02g43820*
MQTL2.7		Lsi1–RM5460	132.76	26	18	20.06	0.83	2.51		
MQTL3.1	10	S2514–RM3126	16.31	3	3	6.78	3.93	0.47		
MQTL3.2		G62–RZ16	48.59	24	22	20.29	2.4	0.84	*pb3.1*	
MQTL3.3		RM214–RM1164	67.94	16	14	23.83	2.53	2.08	*pl3.1*	
MQTL3.4		S14055–RM168	80.84	3	3	12.91	4.4	1.94		
MQTL3.5		RZ1000–RM6974	88.48	22	19	14.13	1.82	1.19		
MQTL3.6		RZ403–RG96B	92.18	4	2	4.88	2.95	0.29	*pb3.2*	
MQTL3.7		sh4–RM468	105.86	6	5	11.43	3.16	1.56		
MQTL3.8		RZ879A–RZ474	112.77	4	2	6.96	3.93	2		
MQTL3.9		TB1–CDO122	125.27	7	6	11.86	2.61	0.43		
MQTL3.10		R2224–chl1	149.67	10	8	13.74	0.42	0.89		
MQTL4.1	7	S10983–RM185	30.92	7	6	14.35	2.6	1.81		
MQTL4.2		E50621-RM119	57.95	18	17	25.43	2.61	1.19		
MQTL4.3		RM241–RM1388	77.54	7	4	18.81	7.47	1.82		

Table 4 continued

MQTL	QTL model	Interval	Position[a]	PVE (%)	No. of initial QTL	Mean initial CI[b]	MQTL CI (95 %)[c]	Physical length of MQTL (Mb)	Partial initial QTLs[d]	Candidate genes
MQTL4.4		*RM3288–RM6590*	*85.35*	*20*	*15*	*20.97*	*3.16*	*0.11*		*MIP1*; *HTD1*
MQTL4.5		RM349–RM3474	98.75	30	31	23.68	3.16	2.79		
MQTL4.6		RG214–RM6909	109.21	13	10	18.8	1.06	0.21		
MQTL4.7		RM5879–G177	131.19	6	4	15.63	2.39	2.73		
MQTL5.1	6	GA478–E60961	22.32	12	6	13.8	4.59	0.33		
MQTL5.2		BLE3–RM289	51.3	8	4	21.92	0.7	5.47		
MQTL5.3		S21985–V147	56.78	14	4	12.38	5.53	7.14		
MQTL5.4		G1458–RM1237	67.34	16	8	21.26	0.84	0.38		
MQTL5.5		*C1239–RG13*	*73.39*	*20*	*8*	*18.67*	*2.77*	*0.1*	*sd5.1*	*Os05g32350*
MQTL5.6		RM480–RZ225	95.94	28	12	12.8	0.04	0.25		
MQTL6.1	8	*S21003S–RZ516*	*10.82*	*13*	*15*	*10.8*	*0.53*	*0.11*	*pb6.1*	*OsFBDUF30*; *OsFBX186*; *OsFBDUF31*; *OsFBDUF32*; *OsFBDUF33*
MQTL6.2		*RG213–RM50*	*29.59*	*4*	*5*	*14.87*	*4.7*	*0.09*	*sb6.1*; *spp6.1*	*Os06g11860*
MQTL6.3		*RM6779–RM7088*	*34.49*	*10*	*10*	*9.44*	*0.3*	*0.16*		*BU1*; *DSH1*
MQTL6.4		RM5585–RM136	44.55	5	3	5.66	2.23	1.15		
MQTL6.5		RM8240–RM6162	53.74	27	36	26.3	0.56	0.32	*pl6.1*	
MQTL6.6		C709C–S20510	66.2	9	10	10.26	2.27	2.02		
MQTL6.7		*PNH1–RM7579*	*84.21*	*19*	*22*	*15.87*	*2.11*	*0.04*		*OsPNH1*
MQTL6.8		*L124–S14023*	*113.86*	*12*	*13*	*14.17*	*0.35*	*0.55*		
MQTL7.1	7	*RM1186–RM3767*	*49.6*	*21*	*15*	*12.5*	*1.51*	*0.08*	*pb7.1*	*Os07g15540*
MQTL7.2		R430–RM7110	55.92	15	13	15.42	3.52	0.33		
MQTL7.3		RM432–RM7087	65.9	9	7	11.48	3.67	0.4		
MQTL7.4		S1082–C529	75.86	19	14	10.23	2.55	1.48	*sd7.1*	
MQTL7.5		CDO497–RM182	85.29	8	7	12.27	1.57	3.6	*sd7.2*	
MQTL7.6		C50076S–RM118	93.97	10	6	13.64	3.2	1.23		
MQTL7.7		CDO38–RM248	110.55	17	16	13.34	0.28	0.38		
MQTL8.1	8	*RZ143–RZ597*	*21*	*14*	*12*	*17.52*	*3.18*	*0.19*	*sd8.1*	*OsFBDUF40*; *Os08g03310*; *OsFBDUF41*
MQTL8.2		RM3231–E60560S	47.44	5	6	28.36	3.1	0.34		
MQTL8.3		RM3181–C1251S	60.25	25	27	17.87	1.17	0.6	*pb8.1*; *spp8.1*	
MQTL8.4		E3835S–RM3395	65.34	17	14	16.24	3.29	0.86	*sb8.1*	
MQTL8.5		RM339–RG28	76.41	5	7	28.97	5.44	1.44		

Table 4 continued

MQTL	QTL model	Interval	Position[a]	PVE (%)	No. of initial QTL	Mean initial CI[b]	MQTL CI (95 %)[c]	Physical length of MQTL (Mb)	Partial initial QTLs[d]	Candidate genes
MQTL8.6		RM42–RM1109	83.88	5	3	11.27	3.3	0.39		
MQTL8.7		RG1–RM502	92.2	19	19	17.68	2.54	4.85		
MQTL8.8		R2027–RM3761	125.69	9	9	18	0.36	0.33		
MQTL9.1	7	C11804S–C11325S	45.66	10	5	5.64	1.37	0.86		
MQTL9.2		R10783S–RZ206	55.14	3	1	10.78	9.07	5.42		
MQTL9.3		RG553–RM105	66.37	2	1	2.7	2.79	3.33		
MQTL9.4		RM410–RM1896	79.35	22	8	9.18	1.48	5.88		
MQTL9.5		RM6051–RM160	86.34	31	17	14.48	3.02	6.96	*pl9.1*	
MQTL9.6		C356B–RM6854	91.28	18	7	9.2	1.22	4.16		
MQTL9.7		RZ792–RM1189	100.68	14	6	9.96	0.69	6.23		
MQTL10.1	4	C51175SA–RM8207	17.35	31	12	22.06	2.37	2.79	*pb10.1*	
MQTL10.2		RM6144–RM304	37.59	26	9	16.65	3.36	3.05	*pb10.2*	
MQTL10.3		S11014–RM6150	50.66	25	7	14.75	3.24	0.32	*sb10.1*	
MQTL10.4		RM147–RM228	63.32	17	7	25.6	4.06	1.3	*pb10.3*; *spp10.1*; *sd10.1*	
MQTL11.1	8	S10637B–Rcn1	15.95	11	5	7.31	1.84	0.25		
MQTL11.2		*RM2459–CDO127*	*18.5*	11	*5*	*9.24*	*1.76*	*0.17*		*Os11g05380*
MQTL11.3		la–RM479	43.45	26	12	17.14	4.71	9.17	*spp11.1*	
MQTL11.4		E61794SA–RM4862	60.05	14	5	6.44	1.78	0.51		
MQTL11.5		*RZ797–RM229*	*68.1*	2	*3*	*29.39*	*18.3*	*0.06*		*OsARF1*
MQTL11.6		E60570–E51178	80.42	7	2	9.9	3.85	0.39		
MQTL11.7		G4001–RG1109	98.69	19	10	25.12	4.26	0.34		
MQTL11.8		RZ536a–RM144	115.84	11	3	10.14	1.45	0.13		*OsWAK121*; *OsWAK122*; *OsWAK123*; *Os11g47240*
MQTL12.1	6	C3029S–Rcn3	13.3	5	1	15.17	15.19	0.32		
MQTL12.2		RZ737–RM20A	33.05	9	2	17.9	13.08	0.24		
MQTL12.3		S14025–RM511	52.54	21	4	18.54	5.02	4.29	*pl12.1*	
MQTL12.4		R10851S–C11001SB	69.67	28	6	15.34	6.17	2.59	*pl12.2*	
MQTL12.5		E20994S–RM259	79.27	26	5	13.61	5.43	2.63		
MQTL12.6		C87–RM2854	95.39	11	2	9.29	2.71	0.66		

Mb Mega base

[a,b,c] units are cM

[d] Partial initial QTLs were from the 54 QTLs detected in this study

[e] The rows in italics indicate that the region of these MQTLs was <0.2 Mb

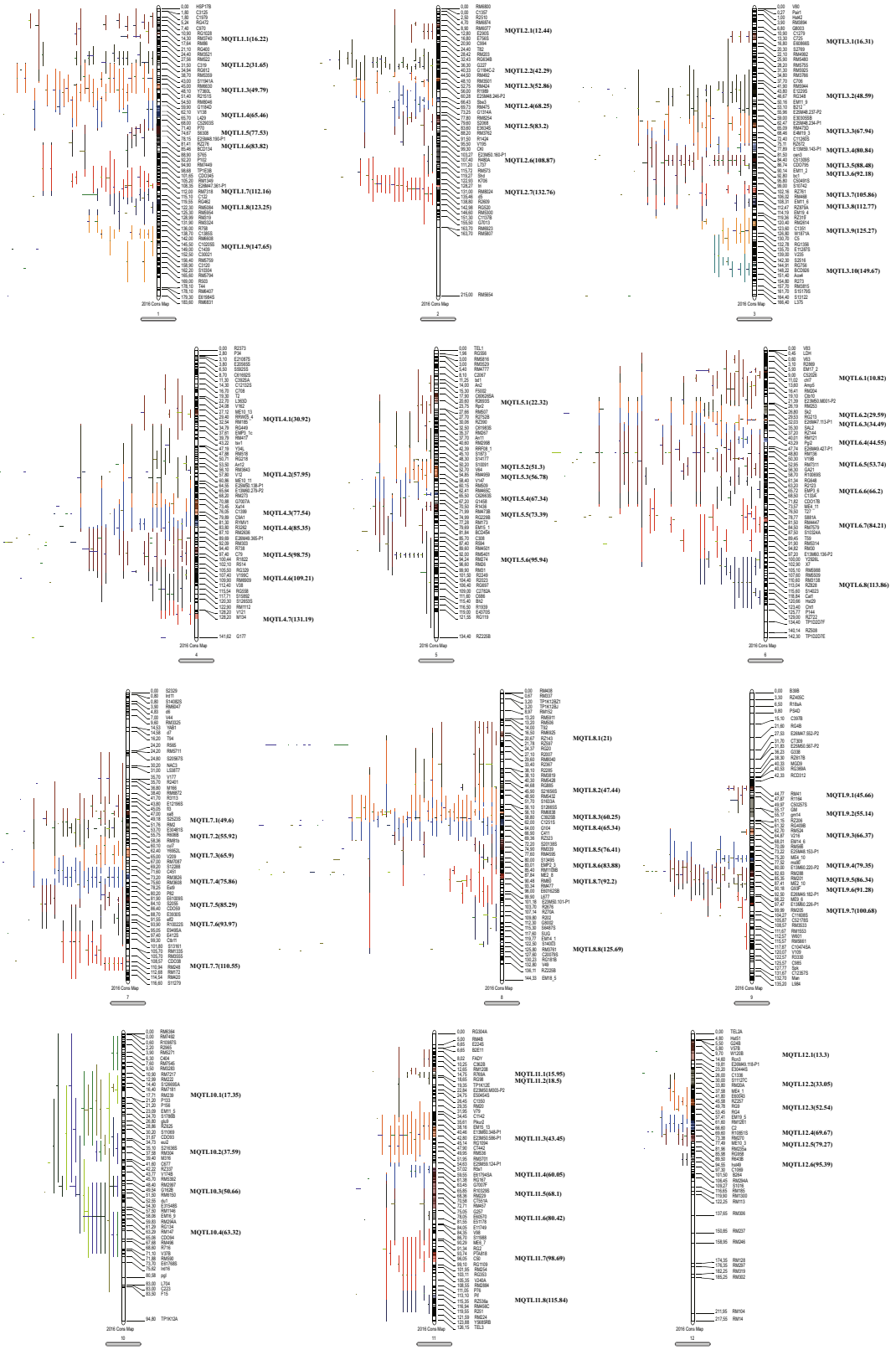


Fig. 2 Meta-analysis results for rice panicle-related traits. *Vertical lines* on the left of the chromosomes indicate the CI of each QTL; *horizontal lines* indicate the PVE. The *colors* of *vertical lines* on the left of the chromosomes correspond to the best model of MQTLs for each chromosome. 87 MQTLs were shown on the right of the chromosomes. Figures in *brackets* indicate the position of the MQTLs in the consensus map

is still so difficult, let alone to recognizing QTLs with small genetic effects.

Meta-analysis of quantitative trait loci

Recently, being a new developing method of candidate gene approach, digital candidate gene approach has been primarily applied to identify potential candidate genes in some studies. Integrated identification approach (including literature-based meta-analysis) is one of the digital candidate gene approaches (Zhu and Zhao 2007). Meta-analysis is a statistical powerful tool can be used for QTL detection and precise estimation of their genetic effects by integrating information from multiple QTL studies. By this method, we only need to collect previously reported QTL information and perform a meta-analysis; then, candidate genes can be mined from the MQTLs with small genetic and physical intervals. Hence, this method is simple and labor-saving, but also save money. Also, a meta-analysis is stronger than those of individual studies and can give greater insight into the genetic architecture of complex traits (Wu and Hu 2012). BioMercator is such a good tool that has been used for QTL meta-analysis to integrate information from multiple QTL studies, detect MQTLs, and estimate their genetic effects precisely (Arcade et al. 2004; Sosnowski et al. 2012; Swamy et al. 2011). Recently, a number of studies have reported on QTL meta-analysis using BioMercator software (Delourme et al. 2013; Huang et al. 2011; Khowaja et al. 2009). Some of these studies have mined a large number of candidate genes (Shinozuka et al. 2012; Swamy et al. 2011; Zhang et al. 2014). Thus, meta-analyses can be quite useful and beneficial for QTL analysis and candidate gene mining. However, the reliability of these results is not clear. The premise to gain reliable results is quality control of data and a large enough total sample. For QTL meta-analysis, collecting data as much as possible are necessary as well as building a QTL mapping population, which may be useful for candidate gene identification in the follow-up study.

Conclusion

In this study, we first conducted a QTL analysis of five panicle-related traits using an F_2 population derived from a cross between Nipponbare and H71D rice cultivars. A total of 54 QTLs were identified. Seven of the 54 QTLs individually explained >20 % of the PVE and were thus considered major QTLs. Two major and stable QTLs in the same interval of RM147–RM228, *spp10.1* and *sd10.1*, were considered important for improving these traits through MAS. Then, we performed a meta-analysis of the 54 QTLs together with 1085 previously reported QTLs using BioMercator v4.2 software. From these results, we build a rice high-density consensus map with 6970 markers. The map covered a total length of 1823.1 cM, and 837 QTLs were projected into 87 MQTLs. A total of 47 of the 54 QTLs detected in this study were comprised in 30 MQTLs. The PVE of 21 among the 87 MQTLs was >20 %. In total, 24 candidate genes were found in 15 MQTLs spanning a physical interval length <0.2 Mb. The high-density consensus map and the MQTLs with small physical and genetic intervals described from the present study are useful not only for MAS and pyramiding, but they also provide important information for gene fine mapping and positional cloning for future research.

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Compliance with ethical standards

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Conflicts of interest All authors have no conflicts of interest to declare.

Ethical standards This article does not describe any studies with human participants or animals performed by any of the authors.

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