

Meta-analysis of Yield QTLs Derived from Inter-specific Crosses of Rice Reveals Consensus Regions and Candidate Genes

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Abstract Several reports on mapping and introgression of quantitative trait loci (QTLs) for yield and related traits from wild species showed their importance in yield improvement. The aim of this study was to locate common major effect, consistent and precise yield QTLs across the wild species of rice by applying genome-wide QTL meta-analysis for their use in marker-aided selection (MAS) and candidate gene identification. Seventy-six yield QTLs reported in 11 studies involving inter-specific crosses were projected on a consensus map consisting of 699 markers. The integration of 11 maps resulted in a consensus map of 1,676 cM. The number of markers ranged from 32 on chromosome 12 to 96 on chromosome 1. The order of markers between consensus map and original map was generally consistent. Meta-analysis of 68 yield QTLs resulted in 23 independent meta-QTLs on ten different chromosomes. Eight meta-QTLs were less than 1.3 Mb. The smallest confidence interval of a meta-QTL (MQTL) was 179.6 kb. Four MQTLs were around 500 kb and two of these correspond to a reasonably small genetic distance 4.6 and 5.2 cM, respectively, and suitable for MAS. MQTL8.2

was 326-kb long with a 35-cM interval indicating it was in a recombination hot spot and suitable for fine mapping. Our results demonstrate the narrowing down of initial yield QTLs by Meta-analysis and thus enabling short listing of QTLs worthy of MAS or fine mapping. The candidate genes shortlisted are useful in validating their function either by loss of function or over expression.

Keywords Meta-analysis · *Oryza sativa* · Wild species · Yield · Marker-assisted selection · Candidate genes

Introduction

Rice is a major staple food crop for more than half of the world's population. When all developing countries are considered together, rice provides 27% of dietary energy supply and 20% of dietary protein intake (www.fao.org). The observed levelling-off of yield in rice cultivars along with the adverse effects of climate and deteriorating environmental health in rice growing areas are of concern in today's food security priorities. It is increasingly being recognized that exploitation of gene pools of wild progenitor species is the fastest and acceptable approach to achieve the twin goals of high productivity and adaptability in any crop (Gur and Zamir 2004; McCouch et al. 2007; Kovach and McCouch 2008; Swamy and Sarla 2008). It is therefore important to identify QTLs from wild × cultivated crosses and to introgress those in cultivated varieties through marker-aided selection (MAS). This would provide impetus to marker-assisted breeding on one hand and enable gene discovery on the other for sustainable rice production (Fridman et al. 2004; Ashikari and Matsuoka 2006).

Yield is governed by several quantitative trait loci (QTLs) across the genome and their effect changes with

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the genomic and environmental context. So far only few yield QTLs have been successfully used in MAS (Liang et al. 2004). Most of the QTLs for yield have been mapped in early generations (F_2 , BC_2 , and BC_2F_2), in limited number of environments and genetic backgrounds. Use of such QTLs in MAS is less likely to yield desired results because of their inconsistent performance in subsequent generations and in different environments. However, it is difficult to evaluate the mapping populations in all possible environments to identify such large effect and consistent QTLs across the genetic backgrounds.

The most precise major effect yield QTLs identified at the same chromosomal location across studies are more useful in MAS and positional cloning to identify candidate genes (Swamy and Sarla 2008; Price 2006). Different approaches can be followed to find precise location of common large effect QTLs across the studies. One approach is the bibliographic review of QTLs affecting a trait and their comparison across studies for co-location and effect, which is supported by a statistical analysis and graphical representation (Chardon et al. 2004). Another approach is the joint analysis of raw data collected from mapping populations in several experiments. However, this approach is impossible due to unavailability of raw data from individual studies and vastly differing data structures.

QTL meta-analysis is an approach to identify consensus QTL across studies, to validate QTL effects across environments/genetic backgrounds and also to refine the QTL positions on the consensus map (Goffinet and Gerber 2000). QTL meta-analysis requires independent QTLs for the same trait obtained from different plant populations, different locations, or different environmental conditions (Goffinet and Gerber 2000). The consistent QTL identified by meta-analysis for a set of QTLs at a

confidence interval of 95% is called as meta-QTL (MQTL). The meta-QTL with smallest confidence interval (CI) and having consistent and large effect on the trait is useful in MAS. In plants, the concept of meta-analysis has been applied to the analysis of QTLs/genes for blast resistance (Ballini et al. 2008), root traits in rice (Courtois et al. 2009), plant height in *Poaceae* family (Lin et al. 1995), lint fiber length in cotton (Rong et al. 2007), cyst nematode resistance in soybean (Guo et al. 2006), fusarium head blight in wheat (Loffler et al. 2009), flowering time (Chardon et al. 2004), and drought tolerance in maize (Hao et al. 2010) and disease resistance in cocoa (Lanaud et al. 2009) (Table 1).

QTL regions harbor many genes; among them few key genes may be more important in the regulation of a complex trait. Meta-QTL regions with refined positions are more accurate for short listing candidate genes. The common candidate genes shortlisted across the meta-QTLs are more likely candidates regulating the yield. Superior alleles of such key genes can also be mined from different sources and incorporated in elite cultivars to develop new varieties.

In this study, QTL meta-analysis was carried for yield QTLs reported from inter-specific crosses to develop a consensus map and to identify consensus yield QTLs. This should provide MQTLs with high effects and small CIs for possible use in MAS or fine map to deduce candidate genes for gene discovery.

Materials and Methods

There are mainly three steps in identifying consensus QTLs for yield from inter-specific crosses. Firstly, in a bibliographic review of QTL mapping studies, reliable data on

Table 1 Previous reports on meta-analysis of QTLs of different traits in crop plants

S number	Crop	Trait	No of studies included for meta-analysis	Software used for meta-analysis	Number of QTLs/genes projected on consensus map	Number of meta-QTLs	Candidate genes	References
1	Rice	Blast resistance	–	–	435	165		Ballini et al. 2008
2	Rice	Root traits	24	Meta-QTL	306	119		Courtois et al. 2009
3	Wheat	Early maturity	13	Biomercator	84	18	<i>Ppd</i> , <i>Vrn</i>	Hanocq et al. 2007
4	Wheat	Fusarium head blight	23	Meta-QTL	101	19		Loffler et al. 2009
5	Maize	Flowering time	22	Biomercator	313	62	<i>ZFL1</i> , <i>ZFL2</i>	Chardon et al. 2004
5	Maize	Drought tolerance	22	Biomercator	239	39		Hao et al. 2010
6	Cotton	Lint fiber length	–	Biomercator	196	20		Rong et al. 2007
7	Soy bean	Cyst nematode resistance	17	–	62	7		Guo et al. 2006
8	Cocoa	Disease resistance	16	Biomercator	76	13		Lanaud et al. 2009

QTLs for yield was compiled (Supplementary Table 1). Secondly, a consensus map was created and on this consensus map QTLs of individual studies were projected. In the third step, a meta-analysis was performed on QTL clusters to identify the consensus MQTL.

Bibliographic Review and Synthesis of Yield QTL Data

QTL information was collected from 11 published reports involving inter-specific crosses in rice. The details of the wild species, size of the mapping population, number of markers used and yield QTLs identified are given in Table 2. These studies involved one of the four wild species *Oryza rufipogon*, *Oryza grandiglumis*, *Oryza glumaepatula*, or *Oryza nivara* as the donor parents and *Oryza sativa* as recipient parent. The *O. sativa* recipients were *indica*, tropical *japonica*, or temperate *japonica*. In all, 76 QTLs were reported for yield per plant or yield per plot and the QTLs with additive effect were either derived from wild allele or cultivated allele (Xiao et al. 1998; Moncada et al. 2001; Septiningsih et al. 2003; Brondani et al. 2002; Marri et al. 2005; Tian et al. 2006; Yoon et al. 2006; Tan et al. 2007; Kaladhar 2006; Swamy 2008).

Development of Consensus Map

Genetic maps comprising a large number of genetic markers have been published in rice (McCouch et al. 2002; Temnykh et al. 2001). In the present study, rice map of Temnykh et al. (2001) was used as reference map, on which the markers of 11 studies were projected to develop a consensus map (Fig. 2). Chromosomes connected with less than two common markers to the reference map were excluded before creation of the consensus map.

QTL Projections

For all the QTLs, 95% CI on their respective original maps was estimated using the approach described by Darvasi and Soller (1997):

$$CI = \frac{530}{NR^2}$$

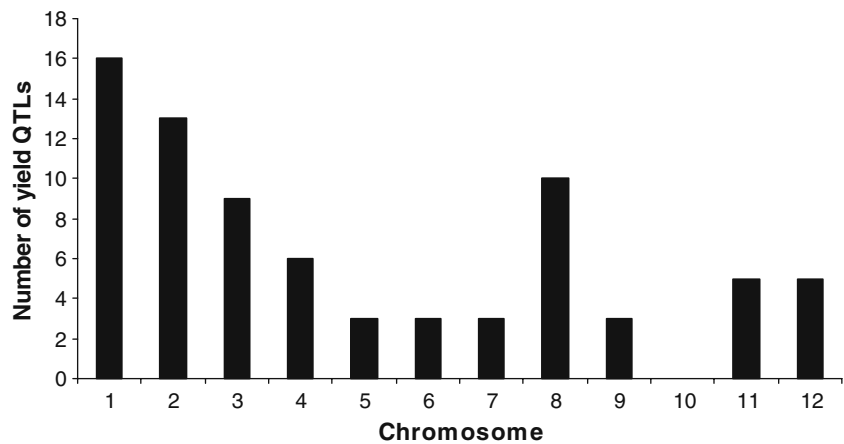
Where *N* is the population size and *R*² the proportion of the phenotypic variance explained by the QTL. Re-estimation of CI was conducted to control heterogeneity of CI calculation methods across studies. Projection of QTL positions was performed by using a simple scaling rule between the original QTL flanking marker interval and the corresponding interval on the consensus chromosome. For a given QTL position, the new CI on the consensus linkage

Table 2 Overview of yield QTLs identified from inter-specific crosses of rice

S	Wild species (genome) number and accession used	Recurrent Parent	Mapping population	Population size	Number of markers	Markers used	QTL analysis	Number of locations used for phenotyping	Yield QTLs identified	References
1	<i>Oryza rufipogon</i> (AA) IRGC105491	Ce64	BC ₂	300	102	RFLP, SSLP	SMA	1	7	Xiao et al. 1998
2	<i>O. rufipogon</i> IRGC105491	Jefferson	BC ₂ F ₂	353	104	SSR, RFLP	IM and CIM	3	5	Thomson et al. 2003
3	<i>O. rufipogon</i> IRGC105491	IR64	BC ₂ F ₂	285	131	SSR, RFLP	IM and CIM	2	3	Septiningsih et al. 2003
4	<i>O. rufipogon</i> IRGC105491	Catapo	BC ₂ F ₂	274	125	SSLP, RFLP	IM and CIM	2	2	Moncada et al. 2001
5	<i>O. rufipogon</i> IC22015	IR58025A	BC ₂	251	80	SSR	IM and CIM	1	10	Marri et al. 2005
6	<i>O. rufipogon</i> IRGC105491	Teqing	ILs	120	179	SSR	SMA	1	6	Tan et al. 2007
7	<i>O. rufipogon</i> IRGC105491	Guichao 2	ILs	159	129	SSR	SMA	2	2	Tian et al. 2006
8	<i>Oryza glumaepatula</i> (AA)×BG90-2	RS19	BC ₂ F ₂	96	150	SSR, STS	SMA	2	7	Brondani et al. 2002
9	<i>Oryza grandiglumis</i> (CCDD) IRGC101154	Hwaseongbyeon	BC ₃ F ₅	150	51	SSR	SMA	1	1	Yoon et al. 2006
10	<i>Oryza nivara</i> (AA) IRGC81848	Swarna	BC ₂ F ₂	227	100	SSR	IM and CIM	1	17	Swamy 2008
11	<i>O. nivara</i> (AA) IRGC81832	Swarna	BC ₂ F ₂	245	75	SSR	IM and CIM	1	16	Kaladhar 2006

SMA single marker analysis, IM interval mapping, CIM composite interval mapping

Fig. 1 Distribution of yield QTLs on rice chromosomes



group was approximated with a Gaussian distribution around the most likely QTL position. All projections of QTL onto the consensus map were performed using the Biomecator 2.0 (Arcade et al. 2004) (www.genoplante.org).

Meta-analysis

The meta-analysis was performed on the QTL clusters on each chromosome using the Biomecator 2.0 (Arcade et al. 2004). The Akaike information criterion (AIC) was used to select the QTL model on each chromosome (Akaike 1974). According to this criterion, the QTL model with least AIC value is considered the significant model indicating the number of meta-QTLs.

Insilico Identification of Candidate Genes

The 23 meta-QTLs were analyzed for the presence of genes regulating yield traits based on the comparative genomics approach with *O. sativa* Nipponbare sequences (www.rapdatabase.org). Gene content was noted based on annotated data of homologous regions in Nipponbare using RAP, Build 5 (www.rapdatabase.org). It is assumed that the genes identified in Nipponbare regions are homologous and collinear to those underlying the yield enhancing QTLs mapped in different studies involving different donor wild species and recipients.

Results

Overview

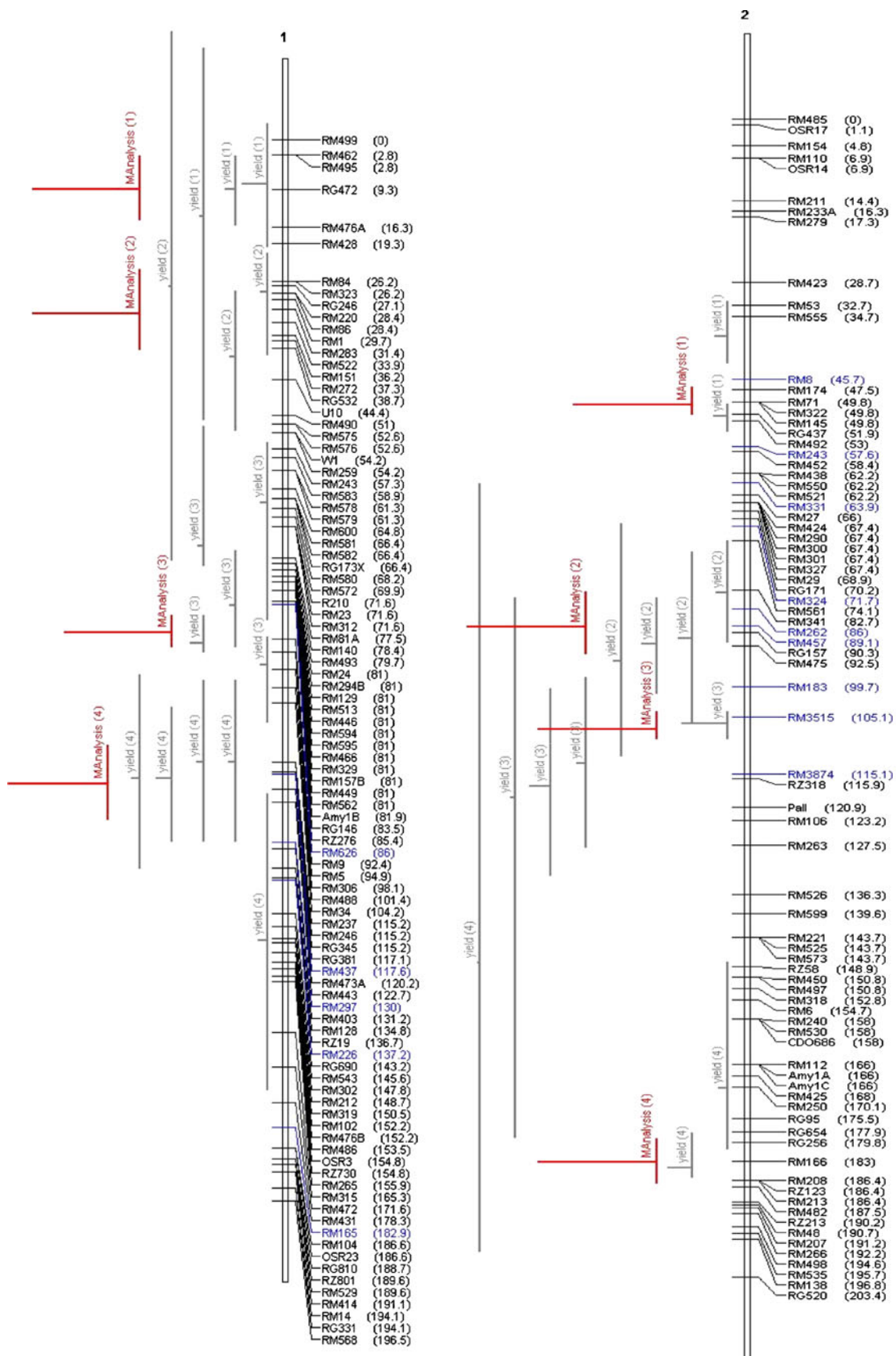
In the 11 populations of rice derived from inter-specific crosses, population size ranged from 96 (Brondani et al. 2002) to 353 lines (Thomson et al. 2003). The number of markers used ranged from 80 (Marri et al. 2005) to 150 (Moncada et al. 2001). The number of locations for phenotyping varied

from 1 to 3. Almost all the studies covered all the chromosomes except chromosome 4, 6, 7, 10, 11, and 12 in Marri et al. (2005) and chromosomes 7, 9, and 10 in Kaladhar (2006). From the 11 studies, 76 yield QTLs were reported which were distributed on all the chromosomes except on chromosome 10. The number of QTLs per population ranged from 1 to 24. The proportion of QTLs per chromosome ranged from three QTLs each on chromosomes 5, 6, and 7 to 16 yield QTLs on chromosome 1. The distribution of yield QTLs on different chromosomes showed that chromosomes 1, 2, and 8 have the highest number of 16, 13, and ten QTLs, respectively (Fig. 1). The number of yield QTLs ranged from three to nine on other chromosomes. The trait increasing allelic effect was derived from the wild species in 43 out of the 76 QTLs. Of these 27% QTLs were from *O. nivara*, 29% were from *O. rufipogon*, 1% from *O. grandiglumis* and 43% from *O. sativa*. In *O. glumaepatula* × *O. sativa* study the trait increasing QTL alleles were derived only from *O. sativa* (Brondani et al. 2002).

Development of Consensus Map

The linkage map of rice by Temnykh et al. 2001 is a widely used reference map. This map contained most of the markers used in the 11 QTL mapping studies from inter-specific crosses and marker orders were almost same. In developing consensus map at least two markers should be common between the reference map and projected maps. After integration of all the maps no marker inversions were found between the projected and reference map. The consensus map contained 699 markers including SSR, RFLP, AFLP markers, and genes. The map covered a total length of 1,676 cM with an average distance of 3 cM between markers.

Fig. 2 Chromosome wise output of meta-QTLs identified by meta-analysis of 68 reported yield QTLs. Vertical lines on the left of chromosomes indicate the confidence interval, horizontal lines indicate the variance, MQTLs are in red. Markers and genetic distance (cM) are shown on the right of chromosomes



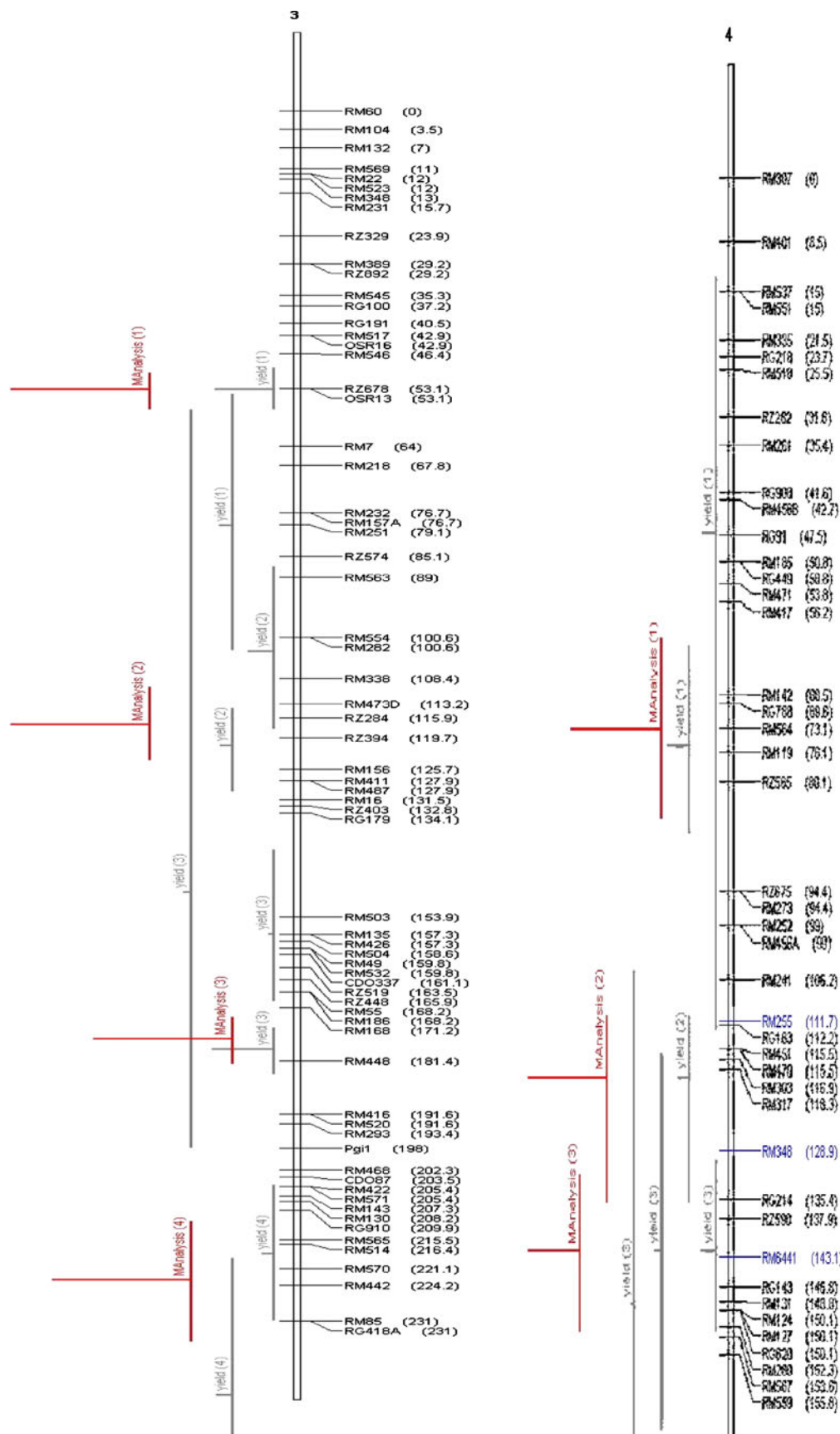


Fig. 2 (continued)

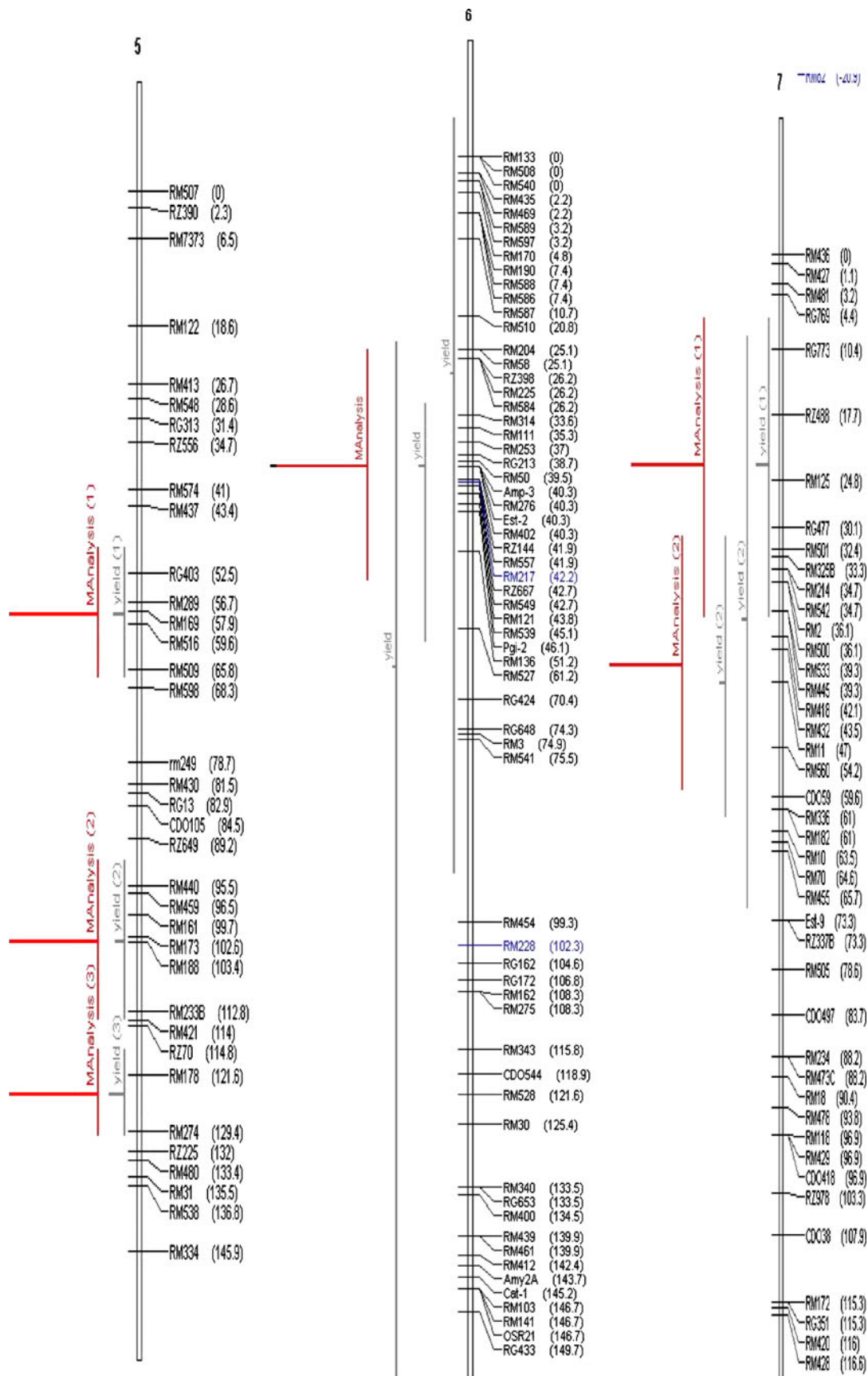


Fig. 2 (continued)

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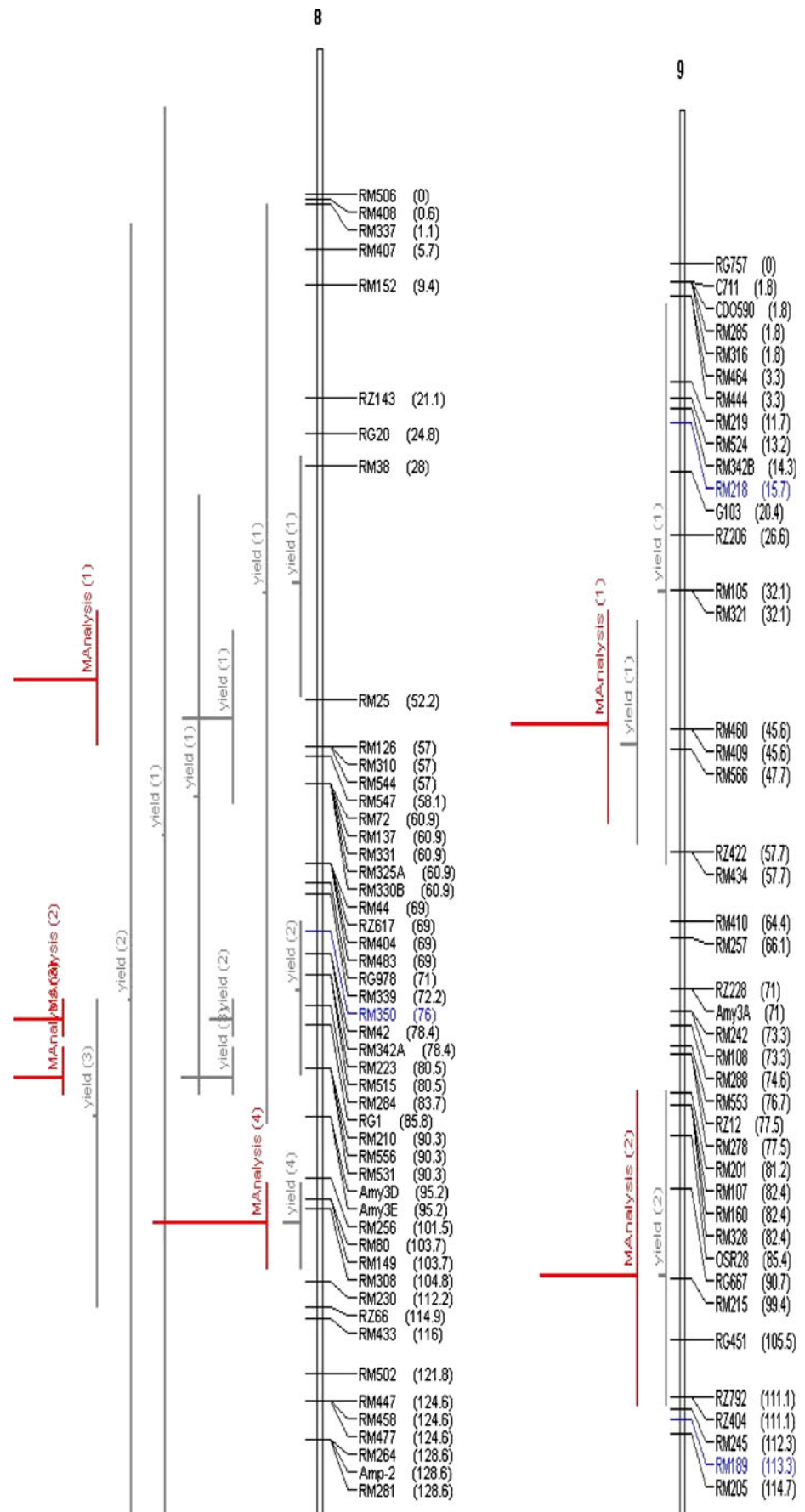


Fig. 2 (continued)

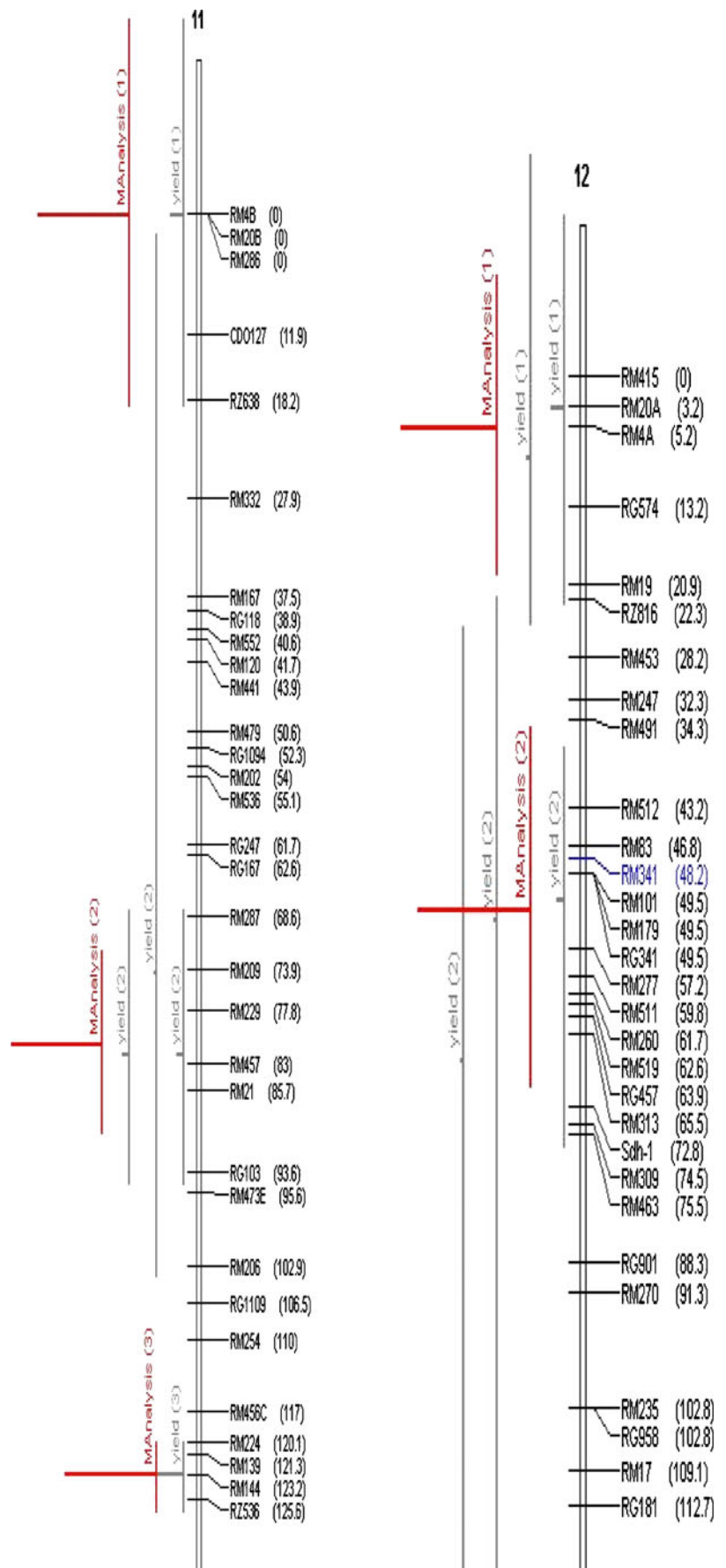
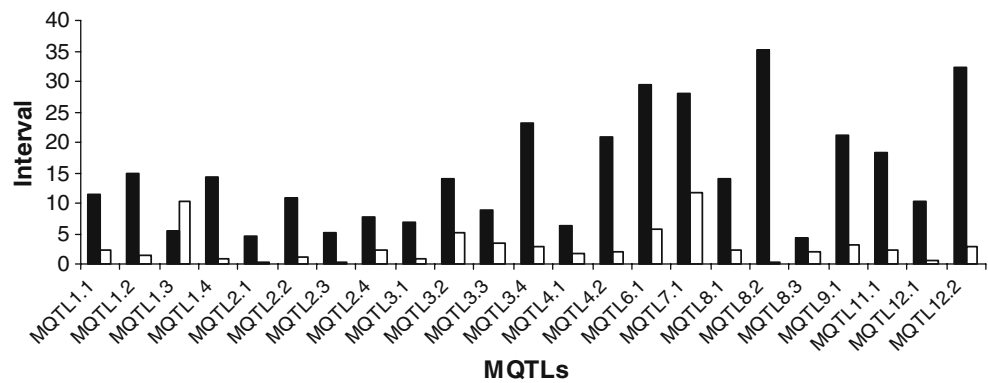


Table 3 Yield QTLs identified by meta-analysis

S number	MQTL	Chromosomes	QTL region	AIC value	QTL model	Number of initial QTL	Mean variance of initial QTL (R^2)	shortest CI of initial QTL (cM)	Mean Initial CI (cM)	MQTL CI (95%) (cM)	Physical length of MQTL (Mb)	KB/cM	Coefficient of Reduction in length from shortest initial QTL to MQTL	Coefficient of reduction in length from mean initial QTL to MQTL	MQTL rank for MAS/fine mapping
1	MQTL1.1	1	RM499–RM428	163.4	4	3	9.3	6.9	13.1	11.3	2.2	196.2	0.6	1.1	
2	MQTL1.2	1	RM323–RM151			3	6.0	13.5	28.9	15.0	1.3	89.6	0.9	2.0	
3	MQTL1.3	1	RM626–RM9			5	5.7	11.6	24.2	5.5	10.2	1,856.9	2.1	4.4	
4	MQTL1.4	1	RM246–RM443			5	9.4	2.9	14.6	14.2	1.00	70.7	0.2	1.0	7
5	MQTL2.1	2	RM174–RM492	137.4	4	2	10.5	36.9	37.9	4.6	0.28	60.8	8.0	8.2	2
6	MQTL2.2	2	RM341–RM475			4	7.7	10.0	17.6	10.9	1.06	97.4	0.9	1.7	
7	MQTL2.3	2	RM3874–RM3515			4	14.6	10.8	26.5	5.2	0.18	34.5	2.0	5.1	1
8	MQTL2.4	2	RG654–RM208			3	16.0	25.7	41.4	7.8	2.36	302.7	3.3	5.3	
9	MQTL3.1	3	RM546–OSR13	97.86	4	2	14.0	12.7	13.9	7.0	0.98	140.7	1.8	2.0	3
10	MQTL3.2	3	RM338–RM156			2	10.7	9.2	10.7	13.9	5.08	365.1	0.6	0.7	
11	MQTL3.3	3	RM168–RM448			3	12.0	8.4	12	8.9	3.39	381.0	0.9	1.4	
12	MQTL3.4	3	RM130–RM85			2	20	7.6	20	23.1	2.95	128.0	0.3	0.9	
13	MQTL4.1	4	RM417–RM119	54.45	2	2	12.2	5.4	12.9	6.3	1.82	288.5	0.9	5.6	4
14	MQTL4.2	4	RM348–RM124			3	6.4	7.3	6.8	21.0	2.09	99.6	0.4	0.3	
15	MQTL6.1	6	RM204–RM136	26.05	1	3	27.1	20.1	27.1	29.5	5.58	189.2	0.7	1.0	
16	MQTL7.1	7	RM501–RM11		1	2	14.2	12.3	13.2	27.9	11.8	425.7	0.4	0.5	
17	MQTL8.1	8	RM38–RM25	98.83	3	5	20	12.2	17.1	14.1	2.26	160.5	0.9	1.2	
18	MQTL8.2	8	RM342–RM515			3	2.7	14.8	32.9	35.1	0.33	9.3	0.4	0.9	
19	MQTL8.3	8	RM248–RM210			2	4.2	8.1	22.4	4.4	1.92	435.3	1.8	5.1	5
20	MQTL9.1	9	RM105–RM434	23.72	1	2	13.9	7.8	13.9	21.1	3.16	149.9	0.3	0.7	
21	MQTL11.1	11	RM287–RM21		1	3	7.3	32.8	26.6	18.4	2.41	130.8	1.8	1.4	
22	MQTL12.1	12	RM20A–RG574	44.4	2	2	11.8	5.2	12.6	10.3	0.59	57.2	0.5	1.2	6
23	MQTL12.2	12	RM179–RM511			3	6.6	19.0	19.1	32.3	2.94	91.2	0.6	0.6	
Total						68									7

AIC Akaike information criterion, CI confidence interval, cM centimorgan, MQTL meta-QTL

Fig. 3 Genetic and physical interval of MQTLs

Meta-analysis

A total of 76 QTLs were reported for yield from 11 studies involving inter-specific crosses. All these QTLs were projected on the consensus map and meta-analysis was performed on the QTL clusters on each chromosome. The meta-analysis of 76 QTLs resulted in identification of 31 meta-QTLs on 11 chromosomes (Fig. 2). However, at eight QTL regions meta-QTLs (three on chromosome 5, two on chromosome 11, and one each on chromosome 4, 7, and 9, respectively) had only one initial QTL. Meta-analysis by definition involves more than two QTLs in a QTL cluster. So, only 23 meta-QTLs with two or more QTLs are considered for further analysis. The number of meta-QTLs along with their AIC values and confidence intervals is given in Table 3. The number of meta-QTLs identified on each chromosome varied from one to four. There were four meta-QTLs each on chromosomes 1, 2, and 3, three on chromosome 8, two each on chromosomes 4, 11, and 12, and one meta-QTL each on chromosomes 6, 7, and 9. In general the confidence intervals of all the meta-QTLs were narrower than their respective original QTLs. Fifteen of the 23 meta-QTLs were narrower than the mean of its initial QTLs. The confidence intervals of the meta-QTLs varied from 4.4 cM between the marker intervals RM248–RM210 on chromosome 8 to 35.1 cM between the marker intervals RM342–RM515 also on chromosome 8. At seven loci on chromosomes 1, 2, 3, 8, and 11, MQTLs were narrower than the smallest QTL reported in that region. At four QTL clusters the meta-analysis reduced the confidence intervals to around 5 cM. These were RM626–RM9 (5.5) on chromosome 1, RM174–RM492 (4.6) and RM3874–RM3515 (5.2) on chromosome 2 and RM248–RM210 (4.4) on chromosome 8. The physical length of the MQTLs varied from 0.18-Mb (RM3874–RM3515) to 11.8 Mb (RM501–RM11) (Fig. 3). At three MQTL regions the physical length was around 500 kb. These regions were RM3874–RM3515 (0.18 Mb), RM174–RM492 (0.28 Mb) on chromosome 2, RM342–RM515 on chromosome 8 (0.34 Mb), and RM20A–

RG574 (0.59 Mb) on chromosome 12. It is interesting to note that the two MQTLs on chromosome 2 with small physical interval also had small genetic interval. These regions are important for MAS and functional analysis to identify the candidate genes for yield.

Genes Underlying Meta-QTLs of Yield

The gene content was analyzed in the 23 meta-QTL regions to deduce the candidate genes. Most of the genes present in the MQTLs were genes for hypothetical and expressed proteins, pseudo-genes, genes for signal transduction, stress tolerance and transposable elements. The presence of specific kinds of transposons and retrotransposons may have some functional significance. However, there were many annotated genes/gene families which were common across the MQTL regions; these may be probable candidate genes for yield (Table 4). In eight MQTL regions with less than 1.3-Mb LRR kinase, NAM, pentatricopeptide repeat proteins, cytokinin oxidase, F-box protein, AP2-domain-containing proteins and zinc-finger transcription factors were present. Over all in most of the MQTLs, cytochrome P450, pentatricopeptide (PPR) repeat-containing protein-like, zinc-finger (AN1-like)-like protein, no apical meristem (NAM) and F-box like protein genes were commonly observed. The candidacy of these genes in yield and yield traits has already been proved in other crops.

Discussion

Naturally Occurring Alleles for Yield Improvement

Wild progenitors have emerged as an important gene pool for mapping of yield QTLs in several crops (McCouch et al. 2007; Swamy and Sarla 2008). They are rich source of naturally occurring alleles for the further improvement of yield and also crosses with wild species generate lot of new and unknown variations in the form of transgressive segregants but rarely exploited; these new variations are

Table 4 Meta-QTL regions tagged with QTLs for different yield components and candidate genes

SI number	MQTL	Chromosome	QTL region	Interval (Mb)	Tagged QTLs	Candidate genes
1	MQTL1.1	1	RM499–RM428	2.2	<i>ph1</i> , <i>tn1</i> (Li et al. 2006) <i>np1.1</i> , <i>sf1.1</i> , <i>gw1.1</i> (Swamy and Sarla 2008)	Putative LRR protein kinase Putative arm repeat-containing protein Putative nodulin-like protein Zinc-finger transcription factor Putative seed specific protein Putative hexose transporter Putative AP2-domain-containing protein Putative myb-like transcription factor
2	MQTL1.2	1	RM323–RM151	1.3	<i>gpl1.1</i> (Septiningsih et al. 2003) <i>spp</i> , <i>gpp</i> , <i>fgp</i> (Brondani et al. 2002) <i>ph1.1</i> (Kaladhar 2006)	Putative MAR binding protein Putative cytochrome P450 Putative auxin-induced protein Putative hexokinase Putative 6-phospho-1-fructokinase Zinc-finger protein like Putative pollen specific protein Always early 1 protein like Basic helix-loop-helix protein like Putative cytokinin oxidase Phytocyanin protein like
3	MQTL1.3	1	RM626–RM9	10.2	<i>bm1.1 I</i> (Swamy and Sarla 2008)	Pentatricopeptide (PPR) repeat protein Seed specific protein, AP-3 complex delta subunit-like protein F-box protein like Zinc-finger protein like Fertility restorer-like protein NAM-like protein
4	MQTL1.4	1	RM246–RM443	1.00	<i>ppl1.1</i> , <i>gpl1.1</i> (Xiao et al. 1998) <i>gw2.1</i> , <i>gpl2.1</i> , <i>ph2.1</i> (Moncada et al. 2001) <i>cl</i> (Yoon et al. 2006) <i>ph1.4</i> , <i>nt1.4</i> , <i>pl1.3</i> , <i>gw1.7</i> (Kaladhar 2006)	Gibberellin response modulator-like Leaf senescence protein like Mitogen-activated protein kinase-like
5	MQTL2.1	2	RM174–RM492	0.28	<i>gw2.1</i> (Kaladhar 2006)	F-box family protein like Putative pentatricopeptide early nodulin Putative LRR receptor-like kinase Putative CLAVATA1 receptor kinase Putative aux/IAA protein
6	MQTL2.2	2	RM341–RM475	1.06	<i>spp2</i> (Yoon et al. 2006) <i>pl2.1</i> , <i>nsp2.1</i> , <i>nt2.2</i> , <i>pl2.2</i> , <i>gnp2.1</i> (Kaladhar 2006) <i>snp2.1</i> , <i>np2.1</i> , <i>nt2.1</i> , <i>gnp2.1</i> (Marri et al. 2005)	AP2-domain-containing protein, myb family transcription factor-like tetra-tricopeptide repeat-containing protein Pentatricopeptide repeat-containing protein Putative NAC domain protein Putative auxin-responsive factor Kelch repeat-containing F-box family protein Putative bHLH transcription factor Putative cytochrome P450 zinc-finger, cryptochrome 1a leucine zipper protein like

Table 4 (continued)

Sl number	MQTL	Chromosome	QTL region	Interval (Mb)	Tagged QTLs	Candidate genes
7	MQTL2.3	2	RM3874–RM3515	0.18	<i>pw2.1</i> (Swamy and Sarla 2008)	Putative leucine-rich protein enhancer of shoot regeneration
8	MQTL2.4	2	RG654–RM208	2.36	<i>ph2.1</i> , <i>gpl2.1</i> (Moncada et al. 2001) <i>sn.1</i> , <i>gn2.1</i> , <i>pw2.1</i> , <i>pl2.1</i> (Marri et al. 2005) <i>ph2.1</i> , <i>bm2.2</i> (Swamy and Sarla 2008)	No apical meristem like protein PPR repeat Zinc-finger protein like F-box protein like
9	MQTL3.1	3	RM546–OSR13	0.98	<i>nt3.1</i> , <i>nsp3.1</i> , <i>gnp3.1</i> (Kaladhar 2006)	Putative cytochrome p450
10	MQTL3.2	3	RM338–RM156	5.08	<i>gw3.1</i> (Thomson et al. 2003) <i>lw3</i> , <i>gw3</i> (Yoon et al. 2006)	Zinc-finger-like protein F-box-domain-containing protein like Cytokinin synthase like hAT dimerisation domain Auxin-induced protein like Myb-like transcription pentatricopeptide-like HGWP repeat-containing protein like Cytochrome <i>c</i> oxidase Putative leucine-rich repeat Putative zinc-finger protein Jasmonate-induced protein like Sucrose synthase Arm repeat protein like Early flowering 4 like Glucose-6-phosphate dehydrogenase
11	MQTL3.3	3	RM168–RM448	3.39	<i>nt3.2</i> , <i>nsp3.2</i> , <i>gnp3.2</i> (Kaladhar 2006)	Indole-3-acetate beta-glucosyltransferase Putative oxalate oxidase HGWP repeat-containing protein like Zinc-finger transcription factor like Putative gibberellin response modulator Putative LRR receptor-like protein kinase F-box domain like Putative MYB transcription factor Pentatricopeptide repeat
12	MQTL3.4	3	RM130–RM85	2.95	<i>nt3.3</i> , <i>np3.1</i> , <i>nsp3.3</i> , <i>gnp3.3</i> (Kaladhar 2006)	Zinc-finger protein like bHLH transcription factor like Auxin-induced protein WRKY1 like bHLH transcription factor like Putative NAC domain transcription factor hAT family dimerisation domain
13	MQTL4.1	4	RM417–RM119	1.82		Putative AP2 domain Pentatricopeptide
14	MQTL4.2	4	RM348–RM124	2.09	<i>ph</i> , <i>pl</i> , <i>pbr</i> , <i>sbr</i> , <i>sn</i> (Li et al. 2006)	WRKY17 like ankyrin like Putative gibberellin 7-oxidase Pentatricopeptide repeat IAA-transcription factor like HGWP repeat-containing protein like Putative LIGULELESS1 Auxin-induced protein like Putative Jasmonate <i>O</i> -methyltransferase

Table 4 (continued)

Sl number	MQTL	Chromosome	QTL region	Interval (Mb)	Tagged QTLs	Candidate genes
15	MQTL6.1	6	RM204–RM136	5.58	<i>pss6.1</i> (Thomson et al. 2003) <i>gw6, pl6, spp6, lw6, tt6</i> (Yoon et al. 2006) <i>ns6.1, gp6.1</i> (Kaladhar 2006)	Putative unusual floral organs Putative flowering locus D auxin response factor MADS box protein Basic helix-loop-helix protein F-box family protein-like Putative AP2 domain HGWP repeat-containing protein like Fertility restorer like Pentatricopeptide repeat-containing protein Leucine zipper-containing protein like Putative cytochrome P450 Sucrose synthase G protein coupled receptor-related-like WRKY17-transcription factor Putative auxin-growth promoter Putative myb family transcription factor Zinc-finger-like protein
16	MQTL7.1	7	RM501–RM11	11.8	<i>tnr, pnr, gw, gpp</i> (Brondani et al. 2002) <i>qfg7, qss7</i> (Tian et al. 2006)	Putative pentatricopeptide repeat Myb family transcription factor like HGWP repeat-containing protein-like Leaf senescence related protein Xylulose kinase-like protein Cytochrome P450-like protein Auxin-regulated protein F-box protein-like protein Helix-loop-helix-like protein Putative pentatricopeptide CLAVATA1 receptor kinase Putative F-box protein Putative cytochrome P450 HGWP repeat-containing protein like AP2 domain protein NAC protein-like Senescence-associated protein like Putative zinc-finger protein Putative male fertility protein Putative zinc-finger protein
17	MQTL8.1	8	RM38–RM25	2.26	<i>gpp8.1, gpl8.1, pss8.1</i> (Xiao et al. 1998)	Putative NAC domain protein
18	MQTL8.2	8	RM342–RM515	0.33	<i>tnr, pnr, plht</i> (Brondani et al. 2002) <i>qfg8, qgw8, qga8</i> (Tian et al. 2006) <i>nt8.1, np8.1, nsp8.1, gnp8.1</i> (Kaladhar 2006)	Putative senescence-associated protein F-box protein family like Putative myb-related protein Auxin-induced protein-related-like protein AP2 domain transcription factor like
19	MQTL8.3	8	RM248–RM210	1.92	<i>ph8.1, pl8.1, gpl8.2</i> (Xiao et al. 1998)	Leucine zipper protein like Zinc finger Male fertility protein like Leaf senescence protein like
20	MQTL9.1	9	RM105–RM434	3.16	<i>pl9, sbr9</i> (Li et al. 2006) <i>pl9.1, gpp9.1, spp9.1, tt9.1</i> (Thomson et al. 2003)	

Table 4 (continued)

Sl number	MQTL	Chromosome	QTL region	Interval (Mb)	Tagged QTLs	Candidate genes
21	MQTL11.1	11	RM287–RM21	2.41	<i>cl11, gl11</i> (Yoon et al. 2006) <i>nt11.1, sf11.1, bm11.1</i> (Kaladhar 2006) <i>ph11.1, pl11.1, sf11.1, bm11.1</i> (Swamy and Sarla 2008)	HGWP repeat-containing protein-like Arm repeat-containing protein like Putative cytochrome P450 pentatricopeptide Putative teosinte branched1 Putative gibberellin-induced protein 1 bHLH transcription factor Putative fertility restorer homologue A Zinc-finger domain 3 like Pentatricopeptide repeat proteins Putative auxin-independent growth promoter Putative cytochrome P450 SAP domain-containing protein like F-box protein like
22	MQTL12.1	12	RM20A–RG574	0.59	<i>spp, gpp</i> (Tan et al. 2007)	Putative NAM Zinc-finger transcription factor Putative AP2-1 protein PPR repeat-containing protein like
23	MQTL12.2	12	RM179–RM511	2.94	<i>gpp12.1, ph12.1, pl12.1, gn12.1</i> (Xiao et al. 1998) <i>pl12, sn12</i> (Li et al. 2006) <i>pl12.1, nsp12.1, nfg12.1, bm12.1</i> (Swamy and Sarla 2008)	HGWP repeat-containing protein like Zinc knuckle domain like

created because of many genetic and epigenetic factors (Wang et al. 2005; Dong et al. 2006). Among the wild species, AA genome progenitors of cultivated rice are more useful in introgression. It is clear from the overview of QTLs that 29% and 27% of the yield enhancing QTLs were from AA genome wild progenitors such as *O. rufipogon* and *O. nivara* than the genetically distant wild species such as *O. glumaepatula* and *O. grandiglumis*. Favorable effect of wild allele introgression from AA genome species has been reported in several previous studies (Xiao et al. 1998; Thomson et al. 2003; Tian et al. 2006; Rahman et al. 2008). The prevalence of favorable QTLs for yield from wild species is maximum on chromosomes 1, 2 and 8. QTLs for yield were not identified on chromosome 10.

Meta-analysis of QTLs

Meta-analysis reduced the total 68 QTLs to 23 (33%) independent meta-QTLs on ten different chromosomes. In general the MQTLs were narrower than their mean of the initial QTLs. At seven meta-QTL regions confidence interval was narrower than the smallest QTL in that region. At six of these loci the confidence interval was reduced to less than 8 cM, with a reduction in length by 1.8 times of the smallest QTLs. Similarly, the highest reduction of QTL

length was observed on chromosome 2, the MQTL was 8 times smaller than smallest QTL in the group and located to a confidence interval of only 4.6 cM. Four MQTLs had physical interval of around 500 kb and three of these also had reasonably less genetic distance. These four QTLs also had high mean PV of more than 10%. The markers flanking each of these four QTLs are suitable for MAS to increase the yield of elite cultivars. MQTL 8.2 was 326Kb long with a 35-cM interval indicating it was in a recombination hot spot and suitable for fine mapping. If the selected few high-priority, trait-increasing, major effect MQTLs is pooled by marker-aided selection, it may lead to increased yield even in the presence of extensive phenotypic buffering, that obviously takes place (Fu et al. 2009) and yet an yield increase of about 15–20% can be easily expected by marker-aided introgression of these high-priority yield QTLs.

It is clear from our study that the meta-analysis is useful in identifying consensus and precise QTLs. In the earlier meta-QTL studies for different traits in wheat, maize, cotton, and soybean, 10% to 21% reduction in total QTL was reported by QTL meta-analysis and the average reduction in the CI of the QTL varied from two to four times of the original QTLs (Guo et al. 2006; Ballini et al. 2008; Rong et al. 2007; Courtois et al. 2009; Loffler et al.

2009; Hao et al. 2010; Lanaud et al. 2009). In some of these studies, MQTLs were used for deducing candidate genes also. In wheat for Fusarium head blight resistance four MQTLs were recommended for MAS after meta-analysis (Loffler et al. 2009).

Identification of Candidate Genes

Map based cloning of QTLs is the commonly used approach for identification of candidate genes underlying the complex traits. Using this approach candidate genes have been identified for heading date, tiller number, submergence tolerance, grain number, and grain yield in rice (Yano et al. 2001; Salvi and Tuberosa 2005; Ashikari et al. 2005, Xu et al. 2006). However, this approach is time consuming and results depend on the effect and consistency of the QTLs across the generations. A combination of meta-analysis and comparative in silico mapping can be an efficient and rapid approach for identifying new candidate genes for trait variation. Based on this approach candidate genes were deduced for flowering time and drought tolerance in maize (Chardon et al. 2004; Hao et al. 2010) and for lint fiber length in cotton (Rong et al. 2007). In the present study in silico candidate gene analysis of meta-QTLs resulted in several candidate genes involved in yield. Some of the important genes/gene families with sufficient evidence to support their candidacy in rice and other crops are listed and discussed further. The genes were cytochrome P450, cytokinin oxidase, PPR repeat-containing protein-like, zinc-finger (AN1-like)-like protein, F-box-like protein, and NAM-like proteins.

Cytochrome P450 is a high-priority gene family associated with yield. This is supported by recent report of a rice brassinosteroid deficient mutant *osdwarf 4-1* encoding a cytochrome P450 protein increasing biomass and grain yield under dense planting (Sakamoto et al. 2005). Cytochrome P450 also has a role in homeostasis of cytokinin which regulates growth, development in wheat and grain yield in rice (Ashikari et al. 2005; Xin et al. 2010). PPR repeats are present in promoter region of *Rf* genes of rice, regulate embryogenesis and fertility restoration in rice (Bentolila et al. 2002; Akagi et al. 2004; Xu et al. 2009; Wang et al. 2010). Thus, association of PPR genes with 15 out of 23 meta-QTLs for yield may be through increase in fertility. Zinc-finger (AN1-like)-like proteins are known to be involved in stress tolerance and in the regulation of rice plant architecture (Zhang et al. 2010). Suppression of this gene resulted in drastic increase in leaf and tiller angles, shortened shoot height and reduced grain production in rice (Mukhopadhyay et al. 2004; Wang et al. 2008). F-box proteins play an important role in floral development and stress tolerance. They express during various stages of panicle and seed development regulating the grain yield (Jain et al. 2007). The shortlisted common candidate genes underlying precise

meta-QTLs can be used for further function analysis to define functions and to identify important yield enhancing genes in rice. In addition, the presences of specific kinds of transposable elements have some functional significance in yield improvement. The large amount of variation that is usually observed in inter-specific crosses is mainly because of many genetic and epigenetic factors, including transposable elements (Wang et al. 2005; Yu et al. 2010).

Conclusions

Meta-analysis of yield QTLs helped to identify the most precise and concise MQTLs. The meta-QTLs with a small physical and genetic interval are useful in MAS/pyramiding. The QTLs for use in MAS are also targets for fine mapping and positional cloning for gene discovery. The shortlisted candidate genes underlying meta-QTLs can be cloned to unravel the molecular mechanisms regulating yield. In breeding rice for higher yield, this study provides insights into the location of important loci introgressed from wild species of rice.

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