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META-ANALYSIS OF QTL ASSOCIATED WITH STARCH PASTING VISCOSITY IN RICE (*ORYZA SATIVA* L.)

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Abstract

Rapid Visco Analyzer (RVA) profiles are important traits for indicating rice quality, which are controlled by quantitative trait loci (QTL). In the past two decades, hundreds of QTL for rice RVA profiles have been detected, but without an integration study. Consistent QTL regions associated with rice RVA profiles by QTL meta-analysis with genetic information of 592 QTL for eight RVA profiles were studied. A total of 82 meta-QTL for RVA profiles were detected on 12 chromosomes. MQTL possessed narrower confidence intervals than the initial QTL and candidate genes were identified within each MQTL. These MQTL and candidate genes are beneficial for future marker-assisted selection gene cloning.

Introduction

Rice quality is a complex trait that is composed of four components: milling, appearance, nutrition, cooking and eating quality (Bao 2012). In particular, cooking and eating quality is deemed to be the most important trait affecting consumer acceptability of rice and is determined by several important indicators (Xu *et al*. 2015). The starch viscosity properties by using RVA profile represents pasting behavior and is based on rice flour that has been subjected to a standard temperature-programmed heat-hold-cool-hold protocol. The RVA starch paste viscosity characteristics are described using the following eight parameters: peak viscosity (PKV), hot paste viscosity (HPV), cool paste viscosity (CPV), peak time (PeT), pasting temperature (PaT), breakdown viscosity (BDV), setback viscosity (SBV) and consistency viscosity (CSV). These traits are controlled by quantitative trait loci (QTL). There are a number of QTL have been detected (Bao *et al*. 2000, 2002, Zhang *et al.* 2007, Liu *et al.* 2011, Yang *et al*. 2012, Hsu *et al.* 2014 and Zheng *et al*. 2012), but no report on QTL meta-analysis of rice RVA profiles. To integrate results from several studies by using diverse mapping populations, multiple environments, and different molecular markers, QTL meta-analysis can narrow down the regions of QTL, compare QTL positions, and validate conserved QTL compared with the initial QTL.

In this study, 592 QTL for RVA profiles from 13 maps in rice was collected. These QTL were used to perform meta-analysis to refine QTL position on Bio Mercator V4.2 (Versailles, France). Identification of meta-QTL (MQTL) provides high credibility QTL combined multiple studies and narrowed confidence intervals (CI) of initial QTL. These MQTL obtained from meta-analysis provide resources for rice breeding and gene mining in future.

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Materials and Methods

QTL of eight RVA profiles and their genetic maps were collected from publications and public databases based on following principles. It was necessary to obtain detailed information about QTL, including QTL name, trait, different environments, time, chromosome of QTL, LOD scores, R2 values (phenotypic variation explained, PVE), confidence intervals and QTL positions. These collected data were edited in text document of Bio Mercator v3 format.

The consensus map was obtained by Wu *et al.* (2016). All markers shown on each linkage used package LinkageMapView in R (Ouellette *et al.* 2018). All the QTL projections were performed according to Wu *et al.* (2016).

Based on the integrated consensus map and initial QTL projections, a QTL meta-analysis according to the QTL clusters on each linkage group (LG) of the consensus map to identify MQTL using BioMercator V4.2 and algorithms from the MetaQTL software (Wu *et al.* 2016) were performed. Usually, the lowest AIC value was used to select the best QTL model for each LG and then calculated QTL from the optimum model is regarded as the meta-QTL (MQTL) (Wu *et al.* 2016). The study was conducted in Mianyang, Sichuan, P.R. China.

Results and Discussion

To collect genetic map and QTL information for rice RVA profiles, Gramene (www. gramene.org), QTARO (http://qtaro.abr.affrc.go.jp/) and recent reports in the literature up to 2018 were amined. A total 13 studies were identified which reported 592 QTL for RVA profiles (Table 1).

The initial QTL were distributed on all 12 LGs; the highest number was on LG06, followed by LG01, LG02, LG04, and LG07 (Fig.1A). The phenotypic variance explained by the initial QTL ranged from 1.2 to 79.04% and the LOD value varied from 0.59 to 79.16 (Fig.1B).

Table 1. Details of references used for this study.

Map name	Cross name	Population type	Population size	Marker number	QTL number	References
2000-Bao	ZYQ8×JX17	DH	132	124	25	(Bao *et al.* 2000)
2002-Bao	IR64×Azucena	DH	135	460	13	(Bao *et al.* 2002)
2007-Zhang	Nikken2×Milyang23	RIL	111	83	34	(Zhang *et al.* 2007)
2011-Liu	Asominori×IR24	CSSLs	66	79	168	(Liu *et al.* 2011)
2011-Nguyen	Koshihikari×Guichao2	RIL	184	65	28	(THOA 2011)
2011-Than	Koshihikari×Nanjing11	RIL	140	152	30	(Hanh 2011)
2012-Yang	9311×Nipponbare	RIL	190	200	75	(Yang *et al.* 2012)
2012-Zheng	Koshihikari×Kasalath	RIL	182	104	37	(Zheng *et al.* 2012)
2014-Hsu	TNG78×TCS17	RIL	190	89	27	(Hsu *et al.* 2014)
2015-Shao	Koshihikari×9311	CSSLs	138	53	10	(Shao *et al.* 2015)
2017-Yao	Zhongyouzao8×Toyonishiki	RIL	153	236	97	(Yao *et al.* 2017)
2017-Zhang	Sasanishiki×Habataki	RIL	85	202	41	(Jie *et al.* 2017)
2018-Zhang	CJ06×TN1	DH	95	69	7	(Sheng-Hao *et al.* 2018)

The new consensus map contained 9732 markers which was up to 1750.4 centimorgan (cM) long with an average marker density of 4.17 loci per cM and 12 LGs on which 7297 loci were mapped (Fig. 2). This new consensus map contains more markers and higher marker density, making it more suitable for the present QTL meta-analysis.

Then a meta-analysis of the 370 QTL was performed, the QTL model of each chromosome was selected by the lowest AIC. In total, 82 MQTL (~22.1%) were obtained with a confidence interval (CI) of 95%. The number of MQTL on each chromosome varied from 4 to 10. The PVE of these MQTL varied from 0.03 to 0.45, 18 MQTL had PVE > 0.2. Confidence interval of 92.68% of all MQTL was narrowed down compared with their mean values of the original QTL (Table 2).

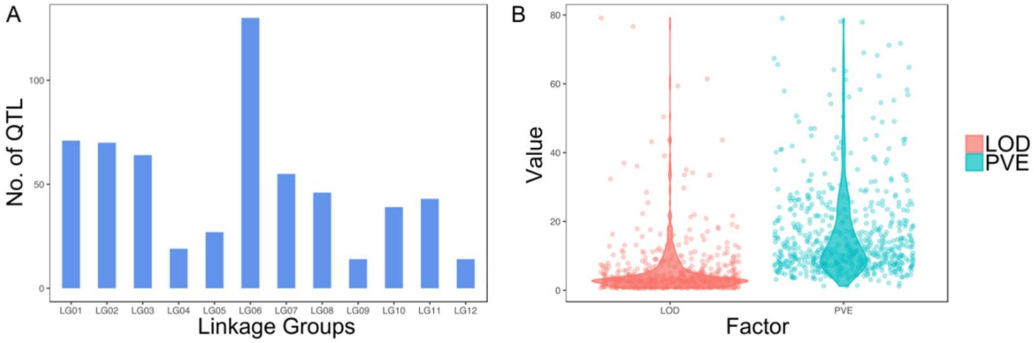

Fig. 1. Summary of initial QTL. A. Distribution of all the initial QTL on 12 LGs; B. Phenotypic variances and LOD value of each initial QTL. PVE, phenotypic variance explained by the QTL.

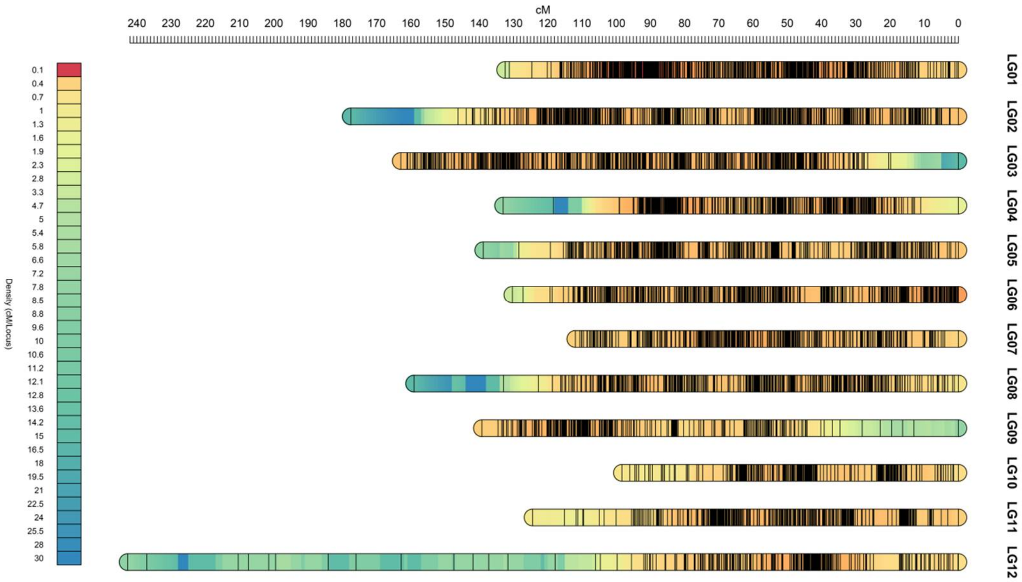

Fig. 2. Overview of the new integrated consensus map. Distribution of 7297 loci on 12 linkage groups (LGs), the different colors on the left indicated different density of markers (cM/locus), the rule above the figure indicated the genetic distance in cM, each linkage group shown on the right.

Rice starch past viscosity (RVA profiles) are easy-measure traits for indicating rice quality with numerous genetic researches which were carried out to identify QTL for eight RVA profiles. This is the first study for meta-analysis of RVA profiles, integrating the location of hundreds of

Table 2. MQTL of rice RVA profiles and candidate genes in the regions.

MQTL[a]	Chr (LG)[b]	MQTL Position (cM)	Weight[c]	Marker Interval[d]	MQTL CI (cM)[e]	No. of projected QTL[f]	CI of projected QTL (cM)[g]	Physical start (bp)[h]	Physical end (bp)[h]	Physical length of MQTL (bp)	No. of candidate genes	Cloned gene[i]
MQTL1.1	7	47.43	0.29	E476S-RM8133	1.07	11	18.13	9,325,545	9,391,431	65,886	12	
MQTL1.2		68.65	0.03	RM6716-RM5	2.5	1	2.51	23,120,856	23,326,243	205,387	32	
MQTL1.3		71.54	0.13	R1928-RM3366	0.23	5	1.06	22,074,383	25,106,668	3,032,285	425	
MQTL1.4		73.9	0.03	R3072-RM1349	1	1	1.02	23,113,645	25,071,392	1,957,747	274	
MQTL1.5		77.56	0.1	R2635-RM237	2.43	4	6.35	24,187,312	26,815,834	2,628,522	364	*GIF2*
MQTL1.6		93.91	0.28	C2340-RM6117	0.31	11	6.2	34,471,055	36,007,539	1,536,484	241	*OsGAMYB*
MQTL1.7		99.78	0.12	RM3324-RM265	0.01	4	4.02	31,719,884	35,197,724	3,477,840	548	*OsGAMYB*
MQTL2.1	7	40	0.12	RM2939-RM7636	2.35	5	7.92	7,421,029	7,664,319	243,290	29	*FUWA*
MQTL2.2		46.69	0.07	RM1081-RM5812	0.69	2	0.98	11,183,432	15,900,167	4,716,735	662	*OsSWEET4*
MQTL2.3		52.74	0.09	S2525-RM550	5.82	4	11.96	10,001,543	12,464,529	2,462,986	348	*OsSWEET4*
MQTL2.4		66.49	0.17	RM341-RZ386	2.39	7	7.55	19,342,016	19,653,251	311,235	41	*OsBEIIb*
MQTL2.5		70.96	0.07	S2068-RZ166	0.84	2	1.22	20,147,800	21,475,633	1,327,833	178	
MQTL2.6		87.14	0.2	R1737-S14054	0.63	8	13.11	25,458,461	25,442,875	15,586	3	
MQTL2.7		107.59	0.25	RM6122-RM530	0.05	10	16.75	28,435,730	30,538,241	2,102,511	338	*OsNF-YB1*
MQTL3.1	7	44.17	0.03	RM4853-RM523	4	1	4	1,397,197	3,497,275	2,100,078	347	
MQTL3.2		58.97	0.29	OSR16-RM1338	1.01	10	14	6,061,222	8,393,689	2,332,467	350	*OsPE*
MQTL3.3		71.94	0.07	RG369-RM282	1.98	2	7.16	8,965,020	12,408,792	3,443,772	515	
MQTL3.4		79	0.21	C606-C269A	5.29	7	17.1	10,368,893	12,544,690	2,175,797	327	
MQTL3.5		106.67	0.12	S1466-R19	3.43	5	25.24	22,990,172	24,600,376	1,610,204	218	
MQTL3.6		125.19	0.19	RZ745-C1351	0.58	6	3.9	28,473,627	28,358,120	115,507	13	
MQTL3.7		148.88	0.09	E10579S-RM16157	0.98	3	7.33	34,343,147	35,158,692	815,545	155	*GPA3*
MQTL4.1	6	16.73	0.12	RS9-RM3524	1.41	2	2	23,240,937	22,893,791	347,146	58	
MQTL4.2		25.85	0.21	E20565S-RM3892	0.77	3	8.97	362,983	1,136,610	773,627	127	*OsARG*
MQTL4.3		54.32	0.2	RM1359-RM1155	2.66	4	18.47	20,032,558	20,516,294	483,736	75	*GIF1*
MQTL4.4		62.09	0.13	S12568-C1087	1.77	2	2.51	22,332,343	22,168,354	163,989	29	
MQTL4.5		77.23	0.08	E31962S-R2737	6.65	1	6.7	24,766,251	29,341,162	4,574,911	697	
MQTL4.6		89.04	0.27	RZ590-R1427	2.4	5	23.11	32,634,557	34,158,649	1,524,092	245	*FLO2*
MQTL5.1	8	20.39	0.1	R2693S-R3332	1.94	2	2.77	2,044,855	2,100,423	55,568	8	

(Contd.)

MQTL[a]	Chr (LG)[b]	MQTL Position (cM)	Weight[c]	Marker Interval[d]	MQTL CI (cM)[e]	No. of projected QTL[f]	CI of projected QTL (cM)[g]	Physical start (bp)[h]	Physical end (bp)[h]	Physical length of MQTL (bp)	No. of candidate genes	Cloned gene[i]
MQTL5.2		27.6	0.05	RM3853-RM17920	5.88	1	5.92	4,104,395	3,077,140	1,027,255	139	*Chalk5; GS5*
MQTL5.3		41.82	0.16	S16612S-S1873	11.78	4	34.62	4,665,325	6,791,412	2,126,087	279	*GSE5/GW5/qSW5*
MQTL5.4		58.01	0.12	Grh1-S12928	3.03	3	21.64	7,779,385	6,936,886	842,499	132	
MQTL5.5		72.82	0.17	S2692-G366	7.17	4	14.99	19,588,424	20,266,481	678,057	86	*FLO4/OsPPDKB*
MQTL5.6		81.87	0.18	RM430-RM18707	1.04	3	4.33	18,753,924	20,603,108	1,849,184	225	*FLO4/OsPPDKB*
MQTL5.7		83.98	0.12	RM3351-E10316S	0.5	3	5.46	20,759,230	21,198,987	439,757	68	
MQTL5.8		98.16	0.09	E12114S-C246	0.6	2	10.35	26,464,157	26,999,172	535,015	96	*OsSSIVb*
MQTL6.1	7	5.72	0.29	RM8075-C52026	0.77	27	8.42	1,351,321	1,913,030	561,709	90	*Wx*
MQTL6.2		7.98	0.07	RM7639-RM8074	0.39	3	0.82	1,415,183	1,416,185	1,002	1	
MQTL6.3		12.95	0.23	RM587-RZ516	1.39	21	0.88	2,292,845	2,562,212	269,367	49	
MQTL6.4		16.88	0.05	R2291-C226A	2.38	4	8.67	2,498,863	3,540,219	1,041,356	180	*OsSSI/SSS1*
MQTL6.5		31.77	0.12	R1966-R1954	3.53	10	16.79	4,796,628	4,938,469	141,841	19	
MQTL6.6		42.07	0.12	S1553-RM549	2.26	11	10.34	6,648,404	6,977,637	329,233	44	*ALK/SSIIa*
MQTL6.7		55.54	0.13	S20510-E769S	0.23	11	12.13	17,555,674	17,940,296	384,622	49	
MQTL7.1	7	7.26	0.03	S2329-RM6222	5.8	1	5.8	36,140	1,006,777	970,637	164	
MQTL7.2		27.56	0.23	Rc-E10534S	1.92	8	8.35	6,062,889	6,433,104	370,215	60	
MQTL7.3		38	0.08	S4774-C1023A	3.39	2	4.78	4,734,626	7,235,197	2,500,571	347	*RP6*
MQTL7.4		41.74	0.09	C636-R1582	2.81	4	15.56	7,627,634	8,145,902	518,268	92	*OsAPL4/OsAGPL4*
MQTL7.5		48.89	0.08	RM6427-RM560	2.55	2	7.06	17,450,492	19,584,215	2,133,723	285	
MQTL7.6		62.31	0.22	RM1048-RM3753	3.12	8	10.38	20,165,312	23,661,338	3,496,026	544	
MQTL7.7		68.06	0.05	S11177-E61009S	3.87	1	4	19,276,524	23,604,108	4,327,584	657	
MQTL7.8		74.6	0.04	RM3753-RM505	3.09	1	3.1	23,661,220	24,527,944	866,724	142	
MQTL7.9		81.91	0.17	R2286-R1245	4.45	6	13.59	21,245,036	24,298,862	3,053,826	478	
MQTL7.10		91.6	0.03	RM7441-R1789	0.03	1	0.71	24,988,890	26,530,892	1,542,002	253	
MQTL8.1	10	2.11	0.04	RM337-RM6925	3.5	1	3.49	153,299	648,272	494,973	77	*FSE1*
MQTL8.2		28.25	0.06	RM5068-RM1111	3.66	2	5.84	3,157,859	4,773,862	1,616,003	230	*OsMST5*
MQTL8.3		33.66	0.08	RM22420-RM8020	3.19	2	4.94	3,335,440	4,516,920	1,181,480	178	*OsMST5*
MQTL8.4		45.48	0.07	RM547-RM8243	5.02	2	7.1	5,592,402	8,936,626	3,344,224	500	
MQTL8.5		68.29	0.14	RM8264-RM515	6.01	4	13.81	19,835,907	20,286,538	450,631	74	
MQTL8.6		87.69	0.14	RM308-S815	4.57	4	10.29	24,794,707	20,666,240	4,128,467	584	*OsAmy3D*

(Contd.)

MQTL[a]	Chr (LG)[b]	MQTL position (cM)	Weight[c]	Marker Interval[d]	MQTL CI (cM)[e]	No. of projected QTL[f]	CI of projected QTL (cM)[g]	Physical start (bp)[h]	Physical end (bp)[h]	Physical length of MQTL (bp)	No. of candidate genes	Cloned gene[i]
MQTL8.7		97.51	0.08	G56-RM6019	0.18	2	0.295	26,204,324	26,322,207	117,883	20	
MQTL8.8		109.12	0.27	E30441S-RZ572	5.19	8	14.98	20,873,587	27,559,312	6,685,725	978	*OsAmy3D*/*ISA1*
MQTL8.9		118.56	0.05	RM6215-R727	2.61	1	2.63	19,065,746	19,310,989	245,243	31	
MQTL8.10		132.91	0.07	EM18_5-XNpb41	0.12	2	2.04	19,804,465	20,774,073	969,608	135	*OsBADH2*/*fgr*
MQTL9.1	5	63.15	0.38	R3104-R1164	1.61	5	18.31	1,804,037	6,020,349	4,216,312	603	
MQTL9.2		73.22	0.2	RM7038-RZ206	3.81	2	8.29	11,805,788	11,808,914	3,126	1	
MQTL9.3		89.2	0.08	R79-E435SB	4.9	1	4.9	11,805,613	12,899,549	1,093,936	161	
MQTL9.4		102.56	0.17	S15670S-C472	0.91	2	1.3	13,164,154	14,650,175	1,486,021	233	
MQTL9.5		110.02	0.08	R2272-RM24569	0.37	1	2.39	17,092,204	18,788,978	1,696,774	254	*ISA3*
MQTL10.1	6	3.45	0.13	RM474-R10987S	3.92	3	6.78	1,820,074	110,138	1,709,936	263	
MQTL10.2		28.06	0.35	S2083-R2174	4.16	10	27.25	3,012,860	5,490,466	2,477,606	369	
MQTL10.3		44.54	0.18	S13078S-R2825	1.52	3	13.4	16,961,640	17,266,561	304,921	53	*FLO7*
MQTL10.4		57.41	0.14	C11714-RM3510	1.38	4	18.05	15,673,243	19,150,933	3,477,690	506	*Du1*
MQTL10.5		65.31	0.08	R716-RM147	1.19	2	3.91	20,929,638	21,019,533	89,895	18	
MQTL10.6		76.43	0.12	RM228-C405	0.04	3	1.67	22,314,690	23,103,259	788,569	118	
MQTL11.1	4	22.02	0.17	RM1124-RM167	6.64	4	14.39	3,855,192	4,077,273	222,081	30	
MQTL11.2		29.44	0.45	C410-RM4469	3.52	9	10.85	5,419,433	6,260,011	840,578	115	
MQTL11.3		95.51	0.1	C1350-RM2064	0.43	2	0.71	26,437,902	27,487,870	1,049,968	155	
MQTL11.4		106.51	0.24	RM6094-RM144	0.48	5	6.12	28,932,632	28,804,933	127,699	20	
MQTL12.1	5	6.27	0.08	RM415-RM5568	13.17	1	13.17	427,079	712,994	285,915	55	
MQTL12.2		20.91	0.31	RG574-RM19	5.08	4	10.46	1,595,835	2,433,453	837,618	142	
MQTL12.3		33.33	0.15	RM453-RM491	4.25	2	7.00	2,691,369	3,582,936	891,567	133	
MQTL12.4		41.44	0.2	S10043S-S21024S	7.03	3	16.22	15,330,237	19,521,002	4,190,765	561	
MQTL12.5		48.52	0.26	RM511-RM277	0.53	3	17.84	17,401,530	18,319,138	917,608	112	

[a]MQTL, meta-QTL; [b]Chr, chromosome; LG, linkage group; [c]The weight of each meta-QTL (i.e. the mixing proportions in the mixture model; [d]Flanking/closet marker of the CI of the meta-QTL present on the new consensus map; [e]The length of the 95% confidence interval of meta-QTL; [f]Projected QTL for the indicated meta-QTL; [g]The length of the confidence interval of the projected QTL; [h]Physical positions are based on MSU website database (available online: http://rice.plantbiology.msu.edu/); [i]Reported genes related rice quality are based on RiceData of CNRRI (available online: http://www.ricedata.cn/gene/).

QTL using maximum likelihood estimation with consideration of population size and additional QTL information. The 370 of 592 QTL for these traits onto a new consensus map were projected and integrated these QTL into 82 MQTL. Seventy-seven MQTL narrow the confidence intervals compared to projected QTL and several MQTL region of RVA which may contain qualities related gene. Such as *ALK* (Gao *et al.* 2003), *SSIVb* (Toyosawa *et al.* 2016), *Waxy* (Wx) (Tian *et al.* 2009), and so on.

So, meta-analyses can be greatly useful and advantageous for QTL analysis and candidate gene mining. For QTL meta-analysis, collecting data as much as possible are necessary as same as building a QTL mapping population, which may be useful for candidate gene identification in the subsequent study.

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