



Full Length Article

Identification of QTLs for Yield-Related Traits using Two Sets of Introgression Lines with a Common Donor Parent in Rice

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Abstract

Rice yield is a complex trait that is the major target in rice breeding program. In the present study, two sets of introgression line populations derived from three parents were used to dissect the genetic basis of yield-related traits, explore the genetic background effect on QTL detection and mine pleiotropic QTL for yield-related traits. Among the three parents, IR75862 was the common donor parent, and Ce258 and Zhongguangxiang1 were two recipient parents. The two introgression line populations were evaluated for yield-related traits in the summer of 2012 at Jingzhou, China. Combined with genotype of the introgression lines, 35 QTLs were detected in all 12 chromosomes except chromosome 5 for eight yield-related traits, including plant height, panicle number per plant, panicle length, filled grain number per panicle, spikelet number per panicle, seed setting rate, thousand grain weight and grain yield per plant, which explained 6.36–36.37% of phenotypic variances. No common QTL was detected in the two backgrounds, and seven chromosome regions on chromosomes 2, 3, 4, 6 and 10 had pleiotropic effects on two or more traits, indicating large genetic background effect on expression of QTLs for yield-related traits. Total of 19 (54%) QTLs including newly identified QTLs, *qGY3*, *qFGN10.2* and *qSN10* with IR75862 alleles increased yield-related traits. Therefore, it's possible to develop new super rice varieties through introgressing or pyramiding the IR75862 alleles at the pleiotropic QTLs (*qPL2.1* and *qPL6.1*) and novel QTLs (*qGY3*, *qFGN10.2* and *qSN10*) into Ce258 and Zhongguangxiang1 by marker-assisted selection. © 2018 Friends Science Publishers

Keywords: Rice; Introgression line; Yield-related trait; Quantitative trait locus; Genetic background

Introduction

Rice (*Oryza sativa* L.) is a very important crop in the world, providing staple food for 60% of the world's people (Kumar *et al.*, 2013). In the past sixty years, rice yield has been sharply increased due to use of semi-dwarfism and heterosis (Zhang, 2007). However, world agriculture faces a big challenge to produce more 70% food for another 2.3 billion people by 2050 (FAO, 2009). The efficient way to solve this problem is to continuously increase rice yield per unit.

Grain yield per plant (GY) consisted of three components including panicle number per plant (PN), filled grain number per panicle (FGN), and 1000 grain weight (TGW), and affected by some other traits, such as plant height (PH), panicle length (PL), spikelet number per panicle (SN), and seed setting rate (SSR). All of them are typical quantitative traits and controlled by multiple genes which distributed on all 12 chromosomes

(<http://archive.gramene.org/qlt/>). Classical genetic research indicated that both genetic (additive effect, dominant effect and epistasis effect) and environment are very important for them (Yu *et al.*, 1997; Xing *et al.*, 2002). With the development of rice functional genomics and molecular marker technology, researchers have mapped many QTLs for them using different populations (Ye *et al.*, 2005; Dong *et al.*, 2009; Fu *et al.*, 2010; Zhang *et al.*, 2010; Wei *et al.*, 2012; Tan *et al.*, 2013; Zhao *et al.*, 2013; Shen *et al.*, 2014). Some of QTLs with large effect were successfully cloned using map-based cloning strategy, including *MOC1* (Li *et al.*, 2003), *D53* (Jiang *et al.*, 2013; Zhou *et al.*, 2013), *Gn1a* (Ashikari *et al.*, 2005), *Ghd7* (Xue *et al.*, 2008), *Ghd7.1* (Yan *et al.*, 2013), *Ghd8/DTH8* (Wei *et al.*, 2010; Yan *et al.*, 2011), *IPAI1/WFP* (Jiao *et al.*, 2010; Miura *et al.*, 2010), *GN2* (Chen *et al.*, 2017), *GNP1* (Wu *et al.*, 2016), *GS3* (Fan *et al.*, 2006; Mao *et al.*, 2010), *GW2* (Song *et al.*, 2007), *qSW5/GW5* (Shomura *et al.*, 2008; Weng *et al.*, 2008),

GS5 (Li *et al.*, 2011), *GW8* (Wang *et al.*, 2012a, b), *TGW6* (Ishimaru *et al.*, 2013), *GL7/ GW7* (Wang *et al.*, 2015a, b), *OsGRF4/ GL2/ GS2* (Che *et al.*, 2015; Duan *et al.*, 2015; Hu *et al.*, 2015; Sun *et al.*, 2016), and most of them are pleiotropic genes, which had large potential values on molecular breeding. Although more and more genes for yield-related traits have been characterized, only a few genes have been successfully used in molecular breeding for increasing rice yield (Wang *et al.*, 2012b). Therefore, identification of more favorable genes/QTLs especially pleiotropic genes affecting yield-related traits from rice germplasms is very important and essential to develop high yield varieties in molecular breeding.

Although many genes were detected to have large effects on grain yield, the application of them on molecular breeding aren't always successful, because of insistence of genetic background between mapping population and breeding population. Many researchers indicated that genetic background has large effect on expression of QTL for panicle and grain size, drought and salt tolerance (Liao *et al.*, 2001; Mei *et al.*, 2006; Xie *et al.*, 2008; Zheng *et al.*, 2011; Cheng *et al.*, 2012; Wang *et al.*, 2013, 2014; Qiu *et al.*, 2015). Although a great number of QTLs for rice yield-related traits have been reported, our understanding of the effect of genetic background on detection of QTL for yield-related traits is very limited, and very few QTL independent from genetic background have been identified. QTL identified in different populations could be compared and common QTLs could be mined in some special mapping populations derived from common parents, such as reciprocal recombinant inbred line (Zhao *et al.*, 2016), reciprocal introgression line (IL) (Wang *et al.*, 2014), two or more introgression lines with common parents (Peng *et al.*, 2014; Qiu *et al.*, 2015).

In our previous study, two sets of IL populations were developed derived from a common donor parent, IR75862-206-2-8-3-B-B-B (IR75862), and two recipient parents, Ce258 and Zhongguangxiang1 (ZGX1) (Qiu *et al.*, 2015). We used these two sets of introgression line populations (ILs) to map QTLs for yield-related traits. The objectives of this study were to (1) illustrate the genetic basis of yield-related traits, (2) dissect genetic background effect on QTL detection and detect QTLs independent from genetic background; (3) identify pleiotropic QTLs for two or more yield-related traits. The results will give us useful information to enhance rice potential in molecular breeding.

Materials and Methods

Plant Materials and Field Experiment

Two sets of IL populations were used in this study. They were derived from IR75862 as common donor parent, and Ce258 and ZGX1 as recipient parents, respectively. IR75862 is a tropical *japonica* glutinous variety with high

zinc and iron concentration introduced from IRRI (Impa *et al.*, 2013). Ce258 is an elite *indica* three-line restorer line with high general combining ability. ZGX1 is an *indica* elite variety with high quality. IR75862 was crossed with Ce258 and ZGX1, respectively and then the F₁ individuals were backcrossed with the recurrent parents for one time. The BC₁F₁ progenies were self-crossed without selections for nine generations to BC₁F₁₀. Ultimately, two sets of introgression lines (ILs) were developed for QTL mapping, each comprising 200 lines in Ce258 background (Ce258-ILs) and ZGX1 background (ZGX1-ILs), respectively.

A total of 403 lines, including 400 ILs and three parents, were planted in the summer season of 2012 on the farm of College of Agriculture, Yangtze University, Jingzhou, China (30.2°N, 112.7°E). Jingzhou is located in the middle of Yangtze River, and is a main production area of rice in China. Seeds were sown on May 10 and transplanted on June 5 with a randomized complete block design. Each IL was planted in three rows and ten individuals in each row at spacing of 20 cm × 20 cm with two replications. All field management followed local farmers' practices.

Trait Measurements

Upon harvest, yield-related traits were measured followed the method described by Wang *et al.* (2012a). GY, PH and PN were measured for five plants in the second row of each IL. PL, FGN, SN and SSR were recorded for three randomly selected panicles from each plant. TGW was measured based on 1000 filled grains.

DNA Extraction and Marker Analysis

Young leaves of about 30 individuals per IL were bulked and used to extract DNA using CTAB method with minor modifications (Murray and Thompson, 1980). Total of 128 and 133 SSR markers evenly distributed on rice genome (<http://archive.gramene.org/markers/>) were selected for genotyping ILs for Ce258-ILs and ZGX1-ILs, respectively. Among them, both two populations have 81 markers (Fig. 2). Marker locations on linkage maps were according to published rice linkage map (Temnykh *et al.*, 2001; McCouch *et al.*, 2002).

Data Analysis

Statistical description and correlations among different traits were analyzed by Statistica 5.5 (Morales, 2001). Inclusive composite interval mapping method (ICIM) in QTL IciMapping 3.2 was used for QTL mapping (Li *et al.*, 2007). The permutation method based on 1000 runs of randomly shuffling the trait values was used to obtain empirical thresholds (Churchill and Doerge, 1994).

Results

Performance of Yield-related Traits in the Two IL Populations

The statistical description of yield-related traits was demonstrated in Table 1. Significant differences were observed between the Ce258/ZGX1 and IR75862 for most of the traits. IR75862 had significantly higher SN and TGW but significantly lower FGN and SSR than those of the two recurrent parents Ce258 and ZGX1. For PH, IR75862 was similar to Ce258 but significantly higher than that of ZGX1. GY of IR75862 was similar to that of ZGX1, and they were higher than Ce258. All above traits exhibited continuous distributions with transgressive segregations in both two IL populations (Table 1; Fig. 1), indicating that all measured traits are typical quantitative traits controlled by multi-genes.

Correlations of the Traits in the Two Backgrounds

Correlation coefficients between different traits are given in Table 2. GY were significantly correlated with PN, PL, FGN, SN and SSR but had no correlation with TGW in both backgrounds, suggesting yield more dependent on panicle number and grain number than grain size in the two populations. As expected, TGW had significant negative correlations with PN and FGN in both backgrounds, suggesting there is trade-off among the three component traits. However, FGN was not significantly correlated with PN, suggesting yield could be to some extent improved through simultaneous increase of FGN and PN in the two populations.

There were some inconsistent correlations among the traits in the two populations, such as significant correlations existed between SN and PN, and FGN and PH only in the Ce258-ILs population, while between TGW and PH, TGW and PL and TGW and SSR only in the ZGX1-ILs population.

Identification of QTLs for Yield-related Traits

QTL identification of PH: Three QTLs were identified in the ZGX1-ILs (Table 3; Fig. 1). They were located on chromosome 3, 4 and 11. The phenotypic variations caused by each QTL were around 13.77–23.35%, respectively. Among these QTLs, *qPH11* had the biggest phenotypic variance rate. IR75862 alleles at all three loci increased PH. No QTL for PH was detected in Ce258-ILs, maybe because PH of Ce258 and IR75862 were similar.

QTL identification of PN: Three QTLs were detected in the Ce258-ILs (Table 3; Fig. 1). They were located on chromosome 3, 4 and 8. The QTLs explained 22.86–26.04% of phenotypic variance, respectively. Among these QTLs, *qPN3* had the largest effect, and IR75862 allele at this locus increased PN. No QTL for PN was detected in ZGX1-ILs, probably because of no difference between that of ZGX1 and IR75862.

QTL identification of PL: Six QTLs influencing PL were identified in the two populations, located on chromosome 2, 3, 4 and 6 (Table 3; Fig. 1). Two QTLs were detected in Ce258-ILs and four in ZGX1-ILs, respectively. Each QTL explained 6.36–25.12% of phenotypic variance, respectively. Among them, *qPL2.1* detected in ZGX1-ILs had the largest effect. All positive alleles of QTL came from IR75862 except for *qPL3* and *qPL6.2*.

QTL identification of FGN: A total of five QTLs controlling FGN were detected in the two populations, located on chromosome 2, 3, 4 and 10. One QTL was identified in Ce258-ILs and four in ZGX1-ILs, respectively. Each QTL explained 16.00–22.55% of phenotypic variance, respectively. Among these QTLs, *qFGN4* detected in ZGX1-ILs contributed most. IR75862 alleles decreased FGN at all loci except for *qFGN10.2*.

QTL identification of SN: Three QTLs influencing SN were scanned in the two populations, located on chromosome 2, 8 and 10 (Table 3; Fig. 1). One QTL was identified in Ce258-ILs and two in ZGX1-ILs, respectively, respectively. QTLs explained 15.15–23.07% of phenotypic variance, respectively. Among these QTLs, *qSN2* detected in ZGX1-ILs contributed most. IR75862 alleles increased SN at all loci except for *qSN8*.

QTL identification of SSR: Seven QTLs affecting SSR were found for SSR in the two populations, located on chromosome 2, 3, 4, 7 and 10 (Table 3; Fig. 1). Three QTLs were found in Ce258-ILs and four in ZGX1-ILs, respectively. The QTLs explained up to 36.37% of phenotypic variance, respectively. Among these QTLs, *qSSR10* detected in Ce258-ILs contributed most. IR75862 alleles decreased SSR at all loci.

QTL identification of TGW: Seven QTLs for TGW were mined in the two populations, located on chromosome 1, 3, 6, 9 and 12 (Table 3; Fig. 1). Three QTLs were detected in Ce258-ILs and four in ZGX1-ILs, respectively. The QTLs explained up to 25.64% of phenotypic variance, respectively. *qTGW6* identified in ZGX1-ILs contributed most. IR75862 alleles at all loci increased TGW.

QTL identification of GY: One QTL for GY was identified in Ce258-ILs, located between RM282 and RM156 on chromosome 3 (Table 3; Fig. 1). This QTL explained 30.26% of phenotypic variance. IR75862 alleles increased GY. No QTL for GY was detected in ZGX1-ILs.

QTLs Common Detected in Both Backgrounds

Among total of 35 QTLs identified for yield-related traits in the two ILs, none QTL was consistently detected in both genetic backgrounds, clearly indicating large genetic background effect on expression of QTLs for yield-related traits.

Table 1: Statistical descriptions of yield-related traits in two sets of ILs populations derived from a common donor, IR75862, and two recipient parents, Ce258 and ZGX1

	Ce258 (P ₁)	ZGX1 (P ₂)	IR75862 (P ₃)	P ₁ -P ₃	P ₂ -P ₃	Ce258-ILs			ZGX1-ILs		
						Mean ± SD	Range	CV (%)	Mean ± SD	Range	CV (%)
PH	115.33	101.17	119.40	-4.07	-18.23**	113.78±5.83	93.67-129.00	5.13	104.46±6.22	89.10-128.42	5.95
PN	15.33	18.33	17.17	-1.84	1.16	13.87±2.67	5.00-24.83	19.95	18.17±3.13	8.67-29.35	17.24
PL	28.97	26.29	26.44	2.53	-0.15	28.24±1.67	19.83-33.70	5.91	26.18±1.28	22.13-33.17	4.88
FGN	170.17	192.00	148.67	21.5*	43.33**	163.70±25.45	63.33-242.50	15.55	185.12±23.63	90.50-247.83	12.77
SN	201.17	223.92	243.08	-41.91**	-19.16*	212.03±30.18	79.67-305.58	14.24	228.50±24.35	145.00-327.50	10.66
SSR	84.59	85.65	63.86	20.73**	21.79**	77.37±7.36	43.26-87.98	9.51	81.02±6.26	48.79-89.68	7.72
TGW	23.43	20.62	26.36	-2.93**	-5.74***	24.69±1.75	18.20-31.98	7.10	18.22±2.34	15.25-28.85	12.83
GY	61.14	72.57	71.70	-10.56**	0.87	53.19±14.22	16.08-129.76	26.25	60.74±12.90	23.51-108.32	21.23

* and **, represent significant levels at P≤0.05 and 0.01, respectively; ZGX1, Zhongguangxiang 1; SD, Standard deviation; CV, Coefficient of Variation; Ce258-ILs, introgression lines at Ce258 background; ZGX1-ILs, introgression lines at Zhongguangxiang 1 background; PH: plant height, PN: panicle number per plant, PL: panicle length, FGN: filled grain number per panicle, SN: spikelet number per panicle, SSR: seed setting rate, TGW: thousand grain weight, GY: grain yield per plant

Table 2: Correlation coefficients of yield-related traits in two sets of ILs populations derived from the crosses between IR75862 and Ce258 or ZGX1

Characteristics	PH	PN	PL	FGN	SN	SSR	TGW	GY
PH		-0.13	0.51**	-0.1	0.11	-0.31**	0.51**	0.08
PN	0.17*		-0.12	0.11	0.07	0.07	-0.25**	0.75**
PL	0.31**	0.13		0.22**	0.40**	-0.22**	0.54**	0.29**
FGN	0.22**	0.14	0.53**		0.79**	0.60**	-0.39**	0.53**
SN	0.33**	0.15*	0.55**	0.78**		-0.02	-0.06	0.52**
SSR	-0.11	-0.01	0.02	0.45**	-0.2**		-0.58**	0.16*
TGW	0.09	-0.16*	0.01	-0.14*	-0.21**	0.07		0.05
GY	0.26**	0.81**	0.39**	0.62**	0.49**	0.27**	0.02	

Note: Data under and above the diagonal are correlation coefficients in Ce258-ILs and ZGX1-ILs, respectively. * and **, represent significant levels at P≤0.05 and 0.01, respectively; ZGX1, Zhongguangxiang 1; Ce258-ILs, introgression lines at Ce258 background; ZGX1-ILs, introgression lines at Zhongguangxiang 1 background; PH: plant height, PN: panicle number per plant, PL: panicle length, FGN: filled grain number per panicle, SN: spikelet number per panicle, SSR: seed setting rate, TGW: thousand grain weight, GY: grain yield per plant

Discussion

Genetic Background Effect on QTL Detection of Yield-related Traits

A lot of evidences indicated that effect of genetic background on QTL mapping is very large. The QTL effects in different backgrounds were diverse when different recipient parents were used (Yousef and Juvik, 2002). It was reported that below twenty percent of the QTLs for panicle size, resistance to drought and salt were detected in reciprocal ILs (Mei *et al.*, 2006; Xie *et al.*, 2008; Cheng *et al.*, 2012; Wang *et al.*, 2014; Qiu *et al.*, 2015). Till now, very little researches reported genetic background effect on QTL expression for yield-related traits. It's uncertain whether it will be successful when a QTL is applied in molecular breeding for increasing yield potential, because no one knows if the QTL still works in a different genetic background. In this study, none QTL out of 35 QTLs for yield-related traits was identified in the both ILs. It was fully demonstrated that genetic background had very large effect on QTL detection for yield-related traits, and expressions of QTL for yield-related traits were diverse when genetic background changed. Therefore, if QTL mapping information is wanted to apply to rice molecular breeding for yield-related traits, much attention should be paid. It is essential for an

integration of QTL mapping with molecular breeding in the same genetic background.

Comparison of QTLs among Different Populations and Novel QTLs Detected in this Study

In this study, 35 QTLs were detected for yield-related traits using two sets of IL populations with the same donor parent. Some QTLs were in the same or near regions with those previously reported. *qPH3* flanked by markers of RM293 and RM571, *qPH4* flanked by markers of RM349 and RM127 and *qPH11* between RM332 and RM167 for PH were mapped in the same regions or near *QPh3b*, *QPh3c*, *QPh11*, respectively (Zhang *et al.*, 2013). *qPN3* flanked by markers of RM51 and RM5488 and *qPN8* between RM284 and RM80 for PN were mapped in the adjacent regions harboring *QPN3a* and *QPN8*, respectively (Ishimaru *et al.*, 2001; Zhang *et al.*, 2013). *qPL2.1*, *qPL3* and *qPL4* located in the region of RM109-RM110, RM411-RM565 and RM349-RM127 for PL were mapped together with QTL in the region of RZ123-RZ446 (Xiao *et al.*, 1996), *qPLT3-3* (Hittalmani *et al.*, 2003) and QTL in the region of XBpb331-XNpb235 (Kobayashi *et al.*, 2003) for PL, respectively. *qFGN3* and *qFGN4* located in the region of RM85-RM227 RM119-RM273 for FGN were mapped near *qSPP3* (Zhang *et al.*, 2009) and the cloned gene *NAL1* (Fujita *et al.*, 2013), respectively. *qSN8* located in the region

Table 3: QTLs affecting yield-related traits in two sets of ILs populations derived from crosses between IR75862 and Ce258 or ZGX1

Background	Trait ¹	QTL	Chr.	Marker interval	LOD	A ²	R ² (%) ³	
Ce258	PN	<i>qPN3</i>	3	RM251-RM5488	6.34	6.26	26.04	
		<i>qPN4</i>	4	RM119-RM273	4.86	-5.15	24.95	
		<i>qPN8</i>	8	RM284-RM80	4.81	-4.23	22.86	
	PL	<i>qPL2.2</i>	2	RM112-RM250	2.61	1.36	6.36	
		<i>qPL3</i>	3	RM411-RM565	2.54	-3.54	16.45	
	FGN	<i>qFGN10.1</i>	10	RM467-RM3773	3.45	-26.30	18.56	
	SN	<i>qSN10</i>	10	RM467-RM3773	3.08	28.72	17.62	
	SSR	<i>qSSR3.1</i>	3	RM411-RM565	2.67	-6.89	17.71	
		<i>qSSR4.1</i>	4	RM335-RM1155	3.19	-5.71	35.62	
		<i>qSSR10</i>	10	RM467-RM3773	4.31	-10.97	36.37	
	TGW	<i>qTGW1.1</i>	1	RM3234-RM243	3.74	0.84	11.70	
		<i>qTGW3.1</i>	3	RM231-RM1324	3.42	0.84	12.52	
		<i>qTGW12</i>	12	RM4-RM247	7.27	1.59	20.65	
	GY	<i>qGY3</i>	3	RM282-RM156	4.38	3.44	30.26	
	ZGX1	PH	<i>qPH3</i>	3	RM293-RM571	2.66	5.70	13.77
			<i>qPH4</i>	4	RM349-RM127	4.02	6.62	15.93
			<i>qPH11</i>	11	RM332-RM167	6.37	4.82	23.35
PL		<i>qPL2.1</i>	2	RM109-RM110	12.47	2.01	25.12	
		<i>qPL4</i>	4	RM349-RM127	3.58	1.00	11.97	
		<i>qPL6.1</i>	6	RM136-RM527	4.44	1.16	14.29	
		<i>qPL6.2</i>	6	RM3-RM162	7.48	-1.73	25.08	
FGN		<i>qFGN2</i>	2	RM573-RM318	3.30	-27.17	16.00	
		<i>qFGN3</i>	3	RM85-RM227	3.91	-25.20	22.23	
		<i>qFGN4</i>	4	RM119-RM273	3.40	-28.49	22.55	
		<i>qFGN10.2</i>	10	RM258-RM228	2.84	38.25	19.75	
SN		<i>qSN2</i>	2	RM110-RM211	3.74	48.69	23.07	
		<i>qSN8</i>	8	RM72-RM331	2.93	-39.67	15.15	
SSR		<i>qSSR2</i>	2	RM573-RM318	4.59	-12.37	22.48	
		<i>qSSR3.2</i>	3	RM571-RM148	5.35	-11.69	22.02	
		<i>qSSR4.2</i>	4	RM349-RM127	6.00	-13.35	22.42	
		<i>qSSR7</i>	7	RM125-RM542	4.75	-11.97	21.96	
TGW	<i>qTGW1.2</i>	1	RM488-RM473	9.72	1.97	17.90		
	<i>qTGW3.2</i>	3	RM571-RM148	8.84	1.97	16.73		
	<i>qTGW6</i>	6	RM276-RM136	13.70	1.83	25.64		
	<i>qTGW9</i>	9	RM316-RM105	4.56	1.41	14.28		

¹ PH: plant height, PN: panicle number per plant, PL: panicle length, FGN: filled grain number per panicle, SN: spikelet number per panicle, SSR: seed setting rate, TGW: thousand grain weight, GY: grain yield per plant; QTL, quantitative trait locus; Chr., chromosome; ZGX1, Zhongguangxiang 1; ² A, additive effect; the additive effect is the effect associated with substitution of Ce258 and ZGX1 alleles by the corresponding IR75862 alleles; ³ R², Phenotypic variation explained by the QTL

of RM72-RM331 on chromosome 8 controlling SN was mapped near the *IPAI/WFP* (Jiao *et al.*, 2010; Miura *et al.*, 2010). *qSSR2* flanked by RM573 and RM318 on chromosome 2, *qSSR3.1* flanked by markers RM411 and RM565, which controlled SSR, were mapped in the adjacent regions with *qFLn2-1* and *qFLl3-1* (Wei *et al.*, 2012). *qSSR4.2* in the region of RM349-RM127 on chromosome 4 was mapped together with *qSSR4* (Zhao *et al.*, 2013). *qTGW1.1* located in the region of RM3234-RM243, *qTGW1.2* in the region of RM488-RM473 on chromosome 1, *qTGW3.1* in the region of RM231-RM1324 and *qTGW3.2* in the region of RM571-RM148 on chromosome 3 for TGW were mapped in the same regions or near *kgw1.1*, *kgw1.2*, *kgw3.1* and *kgw3.2*, respectively (Fu *et al.*, 2010). *qTGW6*, *qTGW9* and *qTGW12* in the region of RM276-RM136, RM316-RM105 and RM4-RM247 were mapped together with *gw6* (Dong *et al.*, 2009), *qGW9-1* (Li *et al.*, 2009) and *qKW12* (Ye *et al.*, 2005), respectively. Whether the

above QTLs identified in this study and the reported grain shape QTLs/genes are the same genes will need to be further clarified after fine mapping and cloning of the QTLs.

Based on above comparative mapping, eleven QTLs for yield components were found to be newly identified in the present study. Phenotypic variations explained by most QTLs were above 15%, and they had large additive effects. For instance, the Ce258 alleles at *qPN4*, *qFGN10.1*, *qSSR4.1* and *qSSR10* can increase 5.15 panicles, 26.30 filled grains, 5.71 and 10.97% SSR, respectively. The ZGX1 allele at *qFGN2*, *qSSR3.2* and *qSSR7* can increase 27.17 filled grains, 11.69 and 11.97% SSR, respectively. The IR75862 alleles at *qSN2*, *qSN10*, *qFGN10.2* and *qGY3* can increase 48.69 and 28.72 spikelets, 38.25 filled grains and 3.44 g grain yield, respectively. Fine mapping and cloning of above new QTLs will facilitate understanding genetic basis of rice yield.

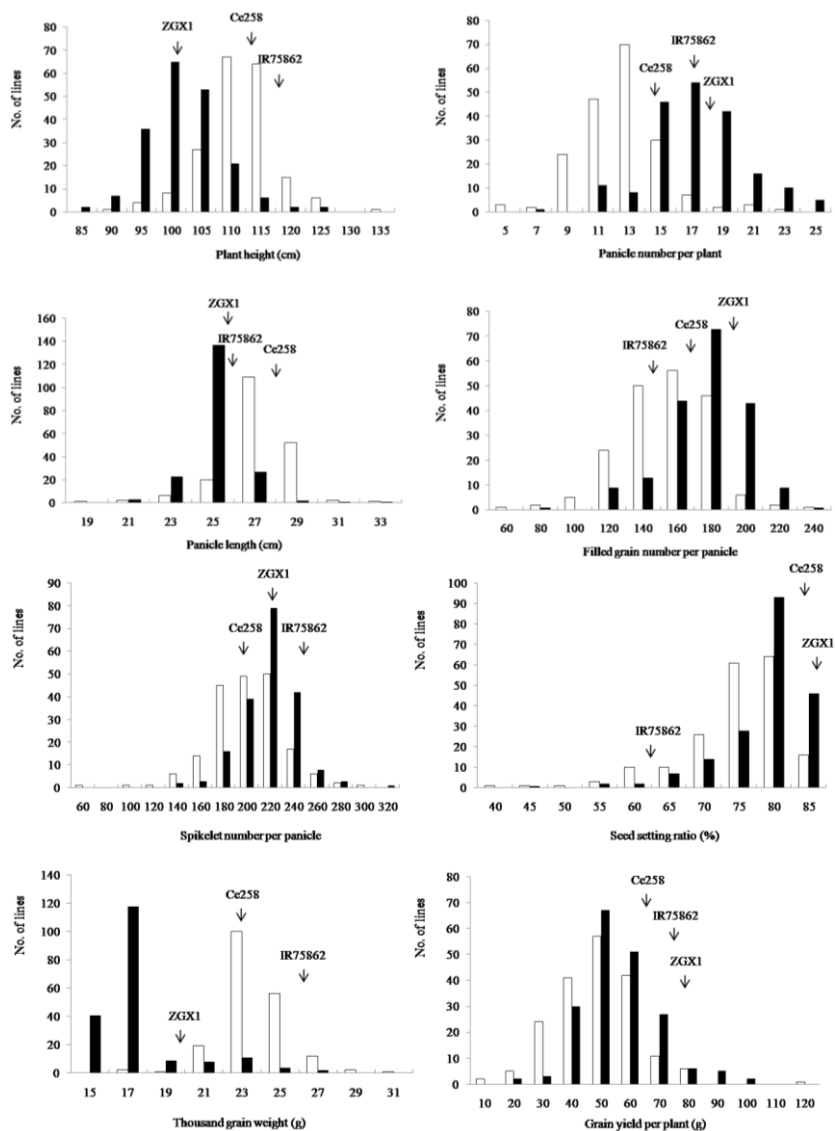


Fig. 1: Frequency distributions of eight yield-related traits in the two sets of IL populations using a common donor IR75862 introgressed separately into two recipients used as female parents, Ce258 and ZGX1. White and black bars represent IL populations with Ce258 and ZGX1 backgrounds, respectively
ZGX1, Zhongguangxiang 1

Pleiotropic QTLs and QTL Clusters in this Study

One QTL or QTL clusters controlling two or more traits are very common in plants. For example, *Ghd7* (Xue *et al.*, 2008), *Ghd7.1* (Yan *et al.*, 2013) and *Ghd8/DTH8* (Wei *et al.*, 2010; Yan *et al.*, 2011) simultaneously control heading date, PH and SN. *GW2* (Song *et al.*, 2007), *qSW5/GW5* (Shomura *et al.*, 2008; Weng *et al.*, 2008), *GS5* (Li *et al.*, 2011), *GW8* (Wang *et al.*, 2012b) control grain width and weight, and *GS3* and *qSS7* had pleiotropic effects on grain length and width (Fan *et al.*, 2006; Qiu *et al.*, 2012). Wang *et al.* (2012a) detected nine QTL clusters affecting two or more plant type and yield traits.

In this study, seven regions on chromosomes 2, 3, 4, 6 and 10 had pleiotropic effects on two or more traits. For instance, both *qFGN2* and *qSSR2* were in the region of RM573-RM318, probably being a same QTL having pleiotropic effects on FGN and SSR with same direction of gene effect. Similarly, *qPL3* and *qSSR3.1* in RM411-RM565 region have pleiotropic effects on PL and SSR with same direction of gene effect. The QTLs *qPH4*, *qPL4* and *qSSR4.2* in the region of RM349-RM127 on chromosome 4 had pleiotropic effects on PH, PL and SSR. The direction of gene effect of *qSSR4.2* is opposite to that of *qPH4* and *qPL4*. The QTLs *qFGN10.1*, *qSN10* and *qSSR10* in the region of RM467-RM3773 on

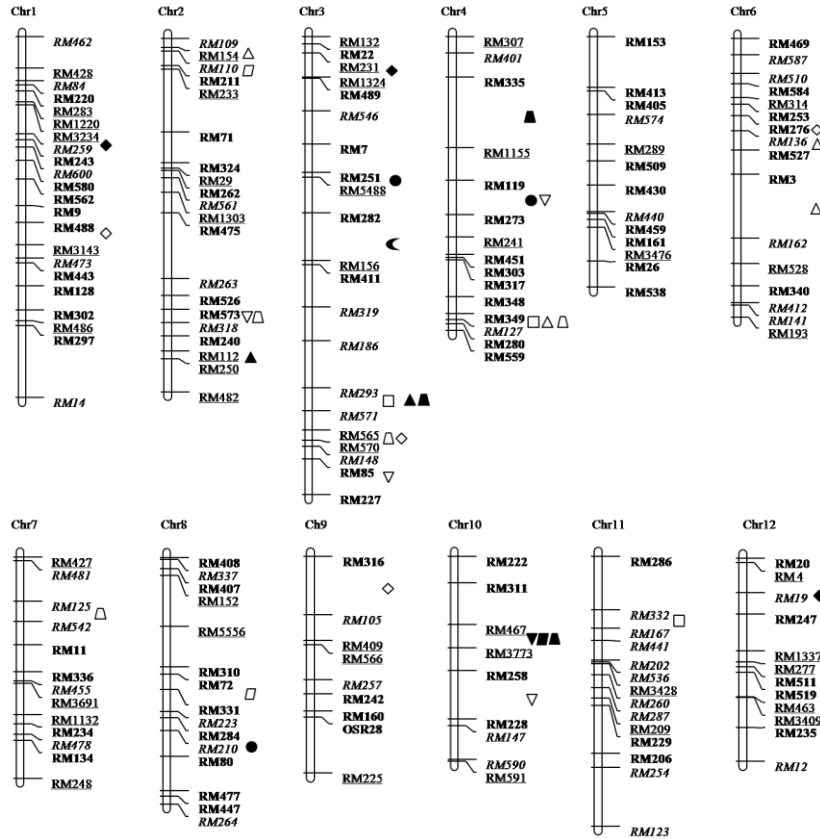


Fig. 2: Linkage maps and locations of QTLs affecting PH, PN, PL, FGN, SN, SSR, TGW and GY identified in two set of IL populations derived from the crosses between IR75862 and Ce258/ZGX1. ■ ● ▲ ▼ ▽ ▹ ◆ ◀ represent QTLs for PH, PN, PL, FGN, SN, SSR, TGW and GY in Ce258-ILs, and □ ○ △ ▽ ▹ ◇ ◀ represent QTLs for PH, PN, PL, FGN, SN, SSR, TGW and GY in ZGX1-ILs. Underline stand for markers in Ce258-ILs only, italic font stands for markers in ZGX1-ILs only, overstriking font stand for markers in two ILs common
 ZGX1, Zhongguangxiang1; Ce258-ILs, introgression lines at Ce258 background; ZGX1-ILs, introgression lines at Zhongguangxiang 1 background; PH: plant height, PN: panicle number per plant, PL: panicle length, FGN: filled grain number per panicle, SN: spikelet number per panicle, SSR: seed setting rate, TGW: thousand grain weight, GY: grain yield per plant

chromosome 10 had pleiotropic effects on PH, PL and SSR, in which direction of gene effect of *qSN10* is opposite to that of *qFGN10.1* and *qSSR10*.

Besides, some QTLs were identified in the adjacent regions. *qPH3*, *qFGN3*, *qSSR3.2* and *qTGW3.2* were in the adjacent regions on chromosome 3, simultaneously controlling PH, FGN, SSR and TGW. Thus, we suppose that some tightly linked genes in a chromosome block control a series of yield-related traits. Similarly, two tightly linked genes in a block on chromosome 2 control PL and SN due to adjacent QTLs, *qPL2.1* and *qSN2*. Two tightly linked genes in a block on chromosome 6 control PL and TGW due to adjacent QTLs, *qPL6.1* and *qKGW6*. These QTL clusters may be responsible for high correlations among the related traits.

The pleiotropic QTLs and QTL clusters were very valuable gene resources in molecular breeding to increase rice yield (Wang *et al.*, 2012a). Breeders can introgressing only one locus to enhance more yield-related traits instead

of pyramiding two or more locus, which needs more labour, time and money, and has higher risk of failure. However, some pleiotropic QTLs and QTL clusters had negative effects, which was unpopular. For instance, The QTLs *qPH4*, *qPL4* and *qSSR4.2* in the region of RM349-RM127 on chromosome 4 had pleiotropic effects on PH, PL, and SSR, in which the direction of gene effect of *qSSR4.2* is opposite to that of *qPH4* and *qPL4*. The region of RM467-RM3773 on chromosome 10 controls FGN, SSR and SN. The direction of gene effect on SN is opposite to that on FGN and SSR. Researcher can't simultaneously improve these three traits. Breeder should avoid using these gene recourses in high-yield breeding.

Implications for Molecular Breeding

Improving rice yield potential is undoubtedly the first goal of most rice breeding programs. However, yield-related traits are typical quantitative traits controlled by multi-

genes, how to efficiently select for high yield in breeding populations remains a large challenge. Fortunately, rice has a large number of germplasms, which are gene carriers with all kinds of alleles (Xing and Zhang, 2012). Identification and use of QTL especially pleiotropic QTLs and QTL clusters in rice molecular breeding can greatly speed up breeding proceeding. In the present study, 19 (54%) QTLs from the donor parent, IR75862 can increase yield-related traits. Among favorable alleles, IR75862 at *qPL2.1* and *qPL6.1* could improve SN and TGW due to pleiotropic effect or tight linkage, thus resulting in increase of grain yield. So, it's possible to develop new super rice varieties through introgressing and/ or pyramiding the IR75862 alleles at the pleiotropic QTLs (*qPL2.1* and *qPL6.1*) or new QTLs (*qGY3*, *qFGN10.2* and *qSN10*) into Ce258 and ZGX1 by molecular-assistant selection.

Acknowledgments

This work was supported by the National Natural Science Foundation of China (31261140369, 31371248), the Key Special Project on Molecular Design Breeding for Rice (2016YFD0101801) from the Chinese Ministry of Science & Technology, scientific research plan project of education department of Hubei (Q20151303), open funds of Hubei Collaborative Innovation Center for Grain Industry (2015MS008, LXT-16-01, LXT-17-08), National Key Laboratory of Crop Genetic Improvement (ZK201603), the Yangtze Youth Fund (2015cqn56), the Yangtze Fund for Youth Teams of Science and Technology Innovation (2015cqt02), Engineering Research Center of Ecology and Agricultural Use of Wetland, Ministry of Education, China (KF201508), and Hubei Key Laboratory of Food Crop Germplasm and Genetic Improvement (2014lzzj04).

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(Received 19 September 2016; Accepted 04 January 2017)