



Full Length Article

Characterization of Main Effects, Epistatic Effects and Genetic Background Effects on QTL for Yield Related Traits by Two Sets of Reciprocal Introgression Lines in Rice (*Oryza sativa*)

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Abstract

Rice yield is a typical quantitative trait that is hard to improve. In this study, Minghui 63 and 02428 was used to develop reciprocal introgression lines, and they were constructed a high density Bin map by re-sequencing. The reciprocal introgression lines were planted in the summer season of 2014 at Jingzhou, China, and measured ten yield related traits including panicle number per plant, grain number per panicle, 1000–grain weight, yield per plant, heading date, plant height, panicle length, primary branch number per panicle, spikelet number per panicle and seed setting ratio. A total of 24 main-effect QTL and 97 epistatic QTL pairs were detected for yield related traits, explaining 0.9–37.0% of phenotypic variations, and epistatic QTL pairs had larger effect than main-effect QTL. Among them, two main-effect QTL (16.7%) were identified at both genetic backgrounds, indicating large background effect on QTL mapping. Moreover, no epistatic QTL pair was detected at both backgrounds, suggested that they were more sensitive to genetic background than main-effect QTL. A background independent main-effect in 7.3–7.6 Mb on chromosome 9 (qSN9) was validated for spikelet number per panicle by using introgression line, indicating it was genetically true. Our results will give us useful gene resources to improve rice yield in marker-assisted selection. © 2018 Friends Science Publishers

Keywords: Rice; Introgression line; Yield related trait; Main-effect QTL; Epistatic QTL; Genetic background

Introduction

Rice is a very important crop in the world (Kumar *et al.*, 2013). Two green revolutions made rice yield worldwide increase twice and even triple at some areas in the last half century (Zhang, 2007). However, because of sharply increasing of world population, 70% more rice must be produced to meet the needs for dairy, meat consumption and biofuel use (Ray *et al.*, 2012). The agricultural acreage can't be increased, even it has decreased at some areas, so we must increase rice yield per unit to solve these problem.

Rice yield per plant (YD) includes 1000 grain weight (KGW), panicle number per plant (PN) and grain number per panicle (GN), and affected by spikelet number per panicle (SN), seed setting ratio (SSR), primary branch number per panicle (PB), panicle length (PL), heading date (HD) and plant height (PH). They are typical quantitative traits controlled by quantitative trait loci (QTL), and both

gene and epistatic interaction have large effects on all these traits (Xing *et al.*, 2002). Using many different genetic populations, many main-effect QTL and epistatic QTL pairs (E-QTL) were scanned (Ye *et al.*, 2005; Fu *et al.*, 2010; Wei *et al.*, 2012; Zhao *et al.*, 2013; Shen *et al.*, 2014). Among these QTL, some were cloned from rice germplasm (Sasaki *et al.*, 2002; Ashikari *et al.*, 2005; Song *et al.*, 2007; Shomura *et al.*, 2008; Weng *et al.*, 2008; Xue *et al.*, 2008; Jiao *et al.*, 2010; Mao *et al.*, 2010; Miura *et al.*, 2010; Wei *et al.*, 2010; Li *et al.*, 2011; Yan *et al.*, 2011; Hu *et al.*, 2012; Qi *et al.*, 2012; Wang *et al.*, 2012b; Zhang *et al.*, 2012; Ishimaru *et al.*, 2013; Yan *et al.*, 2013; Che *et al.*, 2015; Duan *et al.*, 2015; Hu *et al.*, 2015; Sun *et al.*, 2016; Wu *et al.*, 2016; Bai *et al.*, 2017; Chen *et al.*, 2017). Although almost all above genes have large values in yield molecular breeding, their applications aren't always successful, because their effects diverse in different backgrounds (Wang *et al.*, 2012a),

and epistatic QTL pairs are much more sensitive to background (Qiu *et al.*, 2017).

In this study, Minghui 63 (MH63), an elite *indica* restorer, and 02428, a wide compatible temperate *japonica* variety, were used to develop reciprocal introgression lines (ILs), and they have a high density Bin map. These reciprocal ILs were used to characterize the main-effect QTL, epistatic QTL pairs and genetic background effects on them. Our results will give us useful gene resources to improve rice yield in marker-assisted selection.

Materials and Methods

Plant Materials and Field Experiments

Two sets of reciprocal ILs were developed from Minghui 63 (MH63) and 02428. MH63 is an elite *indica* restorer, the male parent of the widely adapted hybrid variety Shanyou 63. 02428 is a wide compatible temperate *japonica* variety. The yield of MH63 is much higher than 02428. MH63 was crossed with 02428, and the F_1 was backcrossed with two recipient parents for two times, respectively. The BC_2F_1 individuals were then self-crossed for seven generations by single seed descent method to BC_2F_8 generation. Ultimately, two reciprocal ILs were developed with 424 lines (including 198 lines at 02428 background (02428-ILs) and 226 lines at MH63 background (MH63-ILs)). A high density Bin map containing 4568 Bins was constructed in the two ILs by re-sequencing. The genotype of reciprocal ILs was described in Qiu *et al.* (2017).

All the 424 reciprocal ILs and parents were grown at Jingzhou (30.18°N, 112.15°E) in China in 2014. Jingzhou is a main production area of *indica/japonica* mix-cultivating area in China. They were planted following the protocol described in Qiu *et al.* (2017).

Trait Evaluation

From heading to mature, yield related traits were measured as described in Wang *et al.* (2012a). HD was evaluated for all plants in each plot. Three individuals in the middle of each IL were selected to evaluate for PH, PN and YD. PL, PB, GN, SN and SSR were measured for main panicle from each plant. 1000 filled grains were used to measure KGW.

Data Analysis

Statistica 5.5 was used to analyze statistical description, correlations between different traits and analysis of variance (Morales, 2001). IciMapping ver. 4.0 software (Li *et al.*, 2007) was used for detecting Main-effect QTL (M-QTL) and digenic epistatic QTL (E-QTL). Default thresholds of LOD for M-QTL and E-QTL were set as 2.5 and 5.0, respectively.

Validation of a Novel Important M-QTL for SN

The region of 7.3–7.6 Mb on chromosome 9 (*qSN9*) was detected for SN at both MH63 and 02428 backgrounds. To confirm *qSN9*, one IL, DQ071, was selected from MH63-ILs. DQ071 and MH63 were also planted at Jingzhou in 2016 following the method described above. Eight individuals were selected to measure SN. They were tested for difference using t-test threshold of P was 0.01.

Results

Performance of Yield Related Traits of Reciprocal ILs and their Parents

The yield related traits of reciprocal ILs and their parents were demonstrated in Table 1 and Fig. 1. All traits exhibited significant differences between MH63 and 02428 except SN. YD of MH63 was much higher than that of 02428. Besides, MH63 had higher HD, PH, PN, PL, GN, SSR and KGW but lower PB than 02428. The IL progenies presented phenotypic trends of their recurrent parents, and they were continuously distributed at both genetic backgrounds (Table 1 and Fig. 1).

Correlations between different traits are listed in Table 2. YD was positively correlated with all traits and reached to significant, indicating that plants with longer HD and PL, higher PH, SSR and KGW, more PN, PB, GN and SN would have higher YD. Three yield component traits (PN, GN and KGW) showed significantly negative correlations with each other at both backgrounds, suggesting there is trade-off among them. In the two ILs, there were some inconsistent correlations, such as significant correlations existed between HD and PB, SSR, KGW, between PB and PH, SSR only in the MH63-ILs, while between HD and PN only in the 02428-ILs.

M-QTL for Yield Related Traits

Nineteen QTL were identified in MH63-ILs, including seven for HD, four for PL, two for each of PH and KGW, one for each of PN, PB, SN and SSR, distributed on chromosomes 2, 3, 4, 5, 6, 8, 9, 11 and 12 and accounting for 3.2–37.0% of phenotypic variance (Table 3 and Fig. 2). The 02428 alleles at *qHD2*, *qHD4*, *qHD12* and *qPB9* increased trait values. *qPB9* and *qSN9* were co-located in the region of 7.3–7.6 Mb on chromosome 9; *qHD9* and *qPH9* were mapped together at 11.8–14.0 Mb on chromosome 9. Five QTL were detected in 02428-ILs, including two for KGW, one for each of HD, PH, SN, distributed on chromosomes 3, 4, 5, 7 and 9 (Table 3 and Fig. 2). The MH63 alleles at all QTL were associated with increase of trait values. *qKGW4* had the largest phenotypic variance rate (13.5%).

Table 1: Statistical descriptions of yield related traits in two sets of reciprocal ILs derived from MH63 and 02428

Trait	Parents			MH63-ILs			02428-ILs		
	MH63	02428	MH63-02428	Mean±SD	Range	CV (%)	Mean±SD	Range	CV (%)
HD(d)	92.9	84.7	8.2**	92.5±3.4	77.5–107.0	3.7	85.4±6.2	75.0–107.5	7.2
PH(cm)	112.8	85.0	27.8**	111.1±8.7	75.1–134.6	7.8	93.8±15.2	62.7–134.7	16.2
PN	8.9	4.4	4.5**	7.0±1.6	2.9–11.3	23.1	6.4±1.9	2.5–12.3	28.9
PL(cm)	27.6	23.2	4.3**	25.9±2.3	19.6–32.1	9.0	24.3±2.3	19.1–31.6	9.6
PB	13.6	14.9	-1.3*	12.8±1.4	9.7–16.3	10.7	14.5±2.1	5.7–19.3	14.6
GN	155.1	131.6	23.5*	129.0±34.5	70.7–244.3	26.8	156.8±48.5	30.7–266.3	30.9
SN	184.8	182.4	2.4	165.6±35.8	84.3–293.7	21.6	208.4±51.8	64.5–327.0	24.9
SSR(%)	84.0	72.2	11.8**	77.4±9.3	49.8–94.7	12.0	75.0±11.0	47.3–94.9	14.7
KGW(g)	27.5	18.6	8.9**	27.8±2.6	20.7–34.9	9.4	22.6±3.6	14.8–37.9	16.1
YD(g)	30.0	8.4	21.6**	19.6±7.0	3.4–39.9	35.6	16.5±7.4	2.9–41.9	45.2

* and ** represent significant levels at P≤0.05 and 0.01, respectively; MH63, Minghui63; SD, standard deviation; CV, Coefficient of variation; MH63-ILs, introgression lines at Minghui63 background; 02428-ILs, introgression lines at 02428 background; HD, heading date; PH: plant height, PN: panicle number per plant, PL: panicle length, PB: primary branch number per panicle, GN: grain number per panicle, SN: spikelet number per panicle, SSR: seed setting ratio, KGW: 1000-grain weight, YD: rice yield per plant

Table 2: Correlation coefficients of yield related traits in two sets of reciprocal ILs derived from MH63 and 02428

	HD(d)	PH (cm)	PN	PL(cm)	PB	GN	SN	SSR (%)	KGW(g)	YD(g)
HD(d)		0.24**	0.30**	0.07	0.02	-0.06	-0.09	0.08	0.12	0.21**
PH(cm)	0.43**		0.23**	0.34**	0.08	0.28**	0.20**	0.30**	0.15*	0.37**
PN	0.11	0.16*		0.30**	0.02	-0.20**	0.06	-0.33**	-0.31**	0.77**
PL(cm)	0.09	0.41**	-0.36**		0.54**	0.59**	0.54**	0.34**	0.09	0.54**
PB	0.22**	0.43**	0.05	0.44**		0.59**	0.67**	0.13	-0.08	0.26**
GN	0.09	0.49**	-0.19**	0.48**	0.71**		0.87**	0.62**	-0.15*	0.57**
SN	0.04	0.41**	0.01	0.37**	0.72**	0.89**		0.17**	-0.25**	0.38**
SSR(%)	0.15*	0.39**	-0.39**	0.27**	0.27**	0.61**	0.28**		0.15	0.55**
KGW(g)	0.26**	0.38**	-0.16*	0.11	0.10	-0.17*	-0.18*	0.03		0.32**
YD(g)	0.19**	0.46**	0.66**	0.45**	0.67**	0.67**	0.49**	0.61**	0.35**	

Data under and above the diagonal are correlation coefficients in MH63-ILs and 02428-ILs, respectively. * and ** represent significant levels at P≤0.05 and 0.01, respectively; MH63, Minghui63; MH63-ILs, introgression lines at Minghui63 background; 02428-ILs, introgression lines at 02428 background; HD, heading date; PH: plant height, PN: panicle number per plant, PL: panicle length, PB: primary branch number per panicle, GN: grain number per panicle, SN: spikelet number per panicle, SSR: seed setting ratio, KGW: 1000-grain weight, YD: rice yield per plant

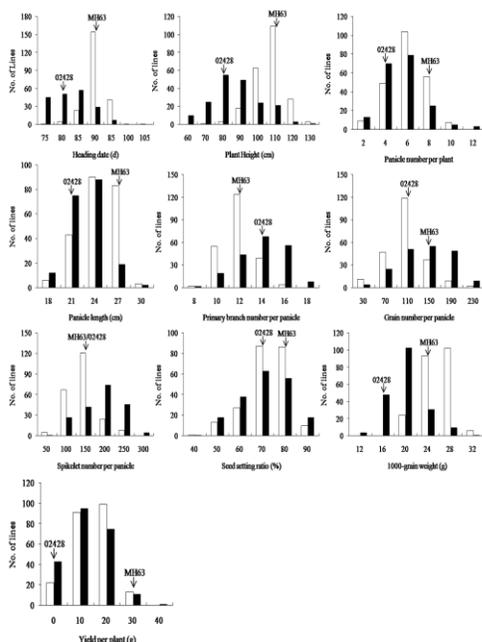


Fig. 1: Frequency distributions of ten yield related traits in two sets of reciprocal ILs derived from MH63 and 02428. White and black bars represent introgression line populations with MH63 and 02428 backgrounds, respectively; MH63, Minghui 63

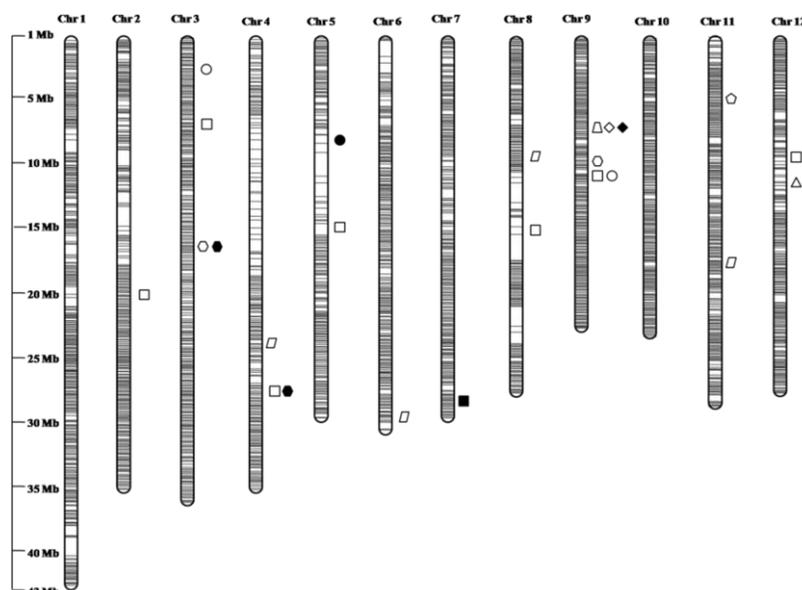


Fig. 2: Genome distribution of M-QTL for yield related traits in two sets of reciprocal ILs derived from MH63 and 02428
 □ ○ △ ▢ ▹ ▸ ◇ ◊ ◻ represent M-QTL for HD, PH, PN, PL, PB, SN, SSR and KGW in MH63-ILs, and ■ ● ◆ ● represent M-QTL for HD, PH, SN and KGW in 02428-ILs; MH63, Minghui63; MH63-ILs, introgression lines at Minghui63 background; 02428-ILs, introgression lines at 02428 background; M-QTL, main effect quantitative trait locus; HD, heading date; PH: plant height, PN: panicle number per plant, PL: panicle length, PB: primary branch number per panicle, SN: spikelet number per panicle, SSR: seed setting ratio, KGW: 1000-grain weight

Among 24 yield related traits QTL, only 2 QTL (16.7%) were consistently detected at both genetic backgrounds, clearly indicating the expression of QTL was largely affected by genetic background.

E-QTL Underlying Yield Related Traits

In MH63-ILs, 15, 6, 7, 12, 8, 4 and 3 digenic epistatic QTL pairs for DH, PH, PL, PB, SN, SSR and KGW were detected (Table 4). One pair occurred between two M-QTL, 14 pairs between one M-QTL and one locus, and the rest between two loci without main effect. 23 pairs improved yield related traits. No E-QTL was found to control two or more traits. In 02428-ILs, 9, 14, 15, 1 and 3 E-QTL pairs for DH, PH, PL, PB, and SSR were identified (Table 4). 11 were between one M-QTL and one locus, the rest between two loci without main effect. 38 E-QTL enhanced yield related traits. Two pairs were detected for both HD and PH, accounting for 1.6–7.9% of phenotypic variances. Two E-QTL detected for both PH and PL, explaining up to 6.8% of phenotypic variances. One E-QTL were detected for HD, PH and PL, explaining 1.5, 5.2, 4.2% of phenotypic variances, respectively. None E-QTL was detected at both backgrounds.

Validation of M-QTL (*qSN9*) for SN

As mentioned above, two M-QTL (*qKGW3* and *qSN9*) was detected at both backgrounds. *qKGW3* was located in 16.2–17.2 Mb on chromosome 3, and there is a cloned gene (*GS3*) for grain weight in this region; *qSN9* was located in 7.3–7.6 Mb on chromosome 9, and it was a novel QTL.

Table 3: M-QTL affecting yield related traits in two sets of reciprocal ILs derived from MH63 and 02428

Background	Trait ¹	QTL	Chr.	Position (Mb)	LOD	A ²	R ² (%) ³	
MH63	HD	<i>qHD2</i>	2	19.8–20.4	11.5	3.1	7.3	
		<i>qHD3</i>	3	7.0–8.0	12.7	-2.1	7.5	
		<i>qHD4</i>	4	27.0–27.9	9.1	3.1	5.1	
		<i>qHD5</i>	5	14.1–16.1	12.9	-2.5	3.3	
		<i>qHD8</i>	8	14.9–17.4	3.0	-4.2	4.1	
		<i>qHD9</i>	9	11.8–14.0	15.6	-2.1	7.3	
	PH	<i>qHD12</i>	12	9.4–10.5	3.5	1.5	8.1	
		<i>qPH3</i>	3	2.1–3.1	2.8	-8.7	8.5	
		<i>qPH9</i>	9	11.8–14.0	2.6	-10.2	11.2	
	PN	PL	<i>qPN12</i>	12	11.2–12.8	2.6	-1.2	7.1
			<i>qPL4</i>	4	24.5–25.2	3.0	-1.1	3.2
	PB	SN	<i>qPL6</i>	6	29.9–30.8	5.0	-1.0	5.4
			<i>qPL8</i>	8	9.8–10.2	10.4	-1.8	7.1
			<i>qPL11</i>	11	17.1–17.8	2.5	-1.4	3.7
	SSR	KGW	<i>qPB9</i>	9	7.3–7.6	5.1	1.7	13.7
<i>qSN9</i>			9	7.3–7.6	2.7	-26.5	12.0	
<i>qSSR11</i>			11	5.0–5.5	9.6	-11.9	37.0	
02428	KGW	<i>qKGW3</i>	3	16.2–17.2	5.1	-0.5	11.2	
		<i>qKGW9</i>	9	10.0–10.2	7.7	-5.5	24.5	
		HD	<i>qHD7</i>	7	28.8–29.5	3.1	1.5	6.3
		PH	<i>qPH5</i>	5	8.8–9.1	3.2	5.1	5.0
SN	KGW	<i>qSN9</i>	9	7.3–7.6	3.3	18.3	6.6	
		<i>qKGW3</i>	3	16.2–17.2	3.8	0.3	5.3	
		<i>qKGW4</i>	4	27.4–27.6	5.9	1.5	13.5	

¹ HD, heading date; PH: plant height, PN: panicle number per plant, PL: panicle length, PB: primary branch number per panicle, SN: spikelet number per panicle, SSR: seed setting ratio, KGW: 1000-grain weight; QTL, quantitative trait locus; Chr., chromosome; MH63, Minghui63; ² A, additive effect; the additive effects were estimated by the substitution the MH63 allele by the 02428 allele in MH63-ILs and 02428 allele by the MH63 allele in 02428-ILs; ³ R², Phenotypic variation explained by the QTL

Table 4: Digenic epistatic QTL pairs (E-QTL) affecting yield related traits in two sets of reciprocal ILs derived from MH63 and 02428

Background	Trait ¹	Region1			Region2			LOD	AA ³	R ² (%) ⁴	
		Chr.	Position (Mb)	M-QTL ²	Chr.	Position (Mb)	M-QTL				
MH63	HD	1	3.5-4.0		6	29.9-30.8		5.4	-2.7	1.9	
		1	3.5-4.0		7	10.5-15.3		6.0	-2.7	1.9	
		1	25.0-26.1		5	8.9-13.0		6.2	4.4	4.3	
		1	25.0-26.1		11	8.1-8.9		11.0	2.4	4.1	
		1	37.4-37.8		2	20.7-22.4		7.9	-1.0	2.0	
		3	7.0-8.0	<i>qHD3</i>	9	11.8-14.0	<i>qHD9</i>	7.0	1.3	1.5	
		3	18.2-20.0		5	17.4-18.2		5.9	-1.4	1.2	
		3	34.9-35.4		4	7.1-11.4		10.4	-1.2	3.4	
		4	7.1-11.4		7	1.2-1.8		8.1	-3.0	4.9	
		4	7.1-11.4		6	24.5-25.8		5.1	1.3	3.0	
	6	29.9-30.8		8	4.6-5.8		10.9	-1.0	4.7		
	7	10.5-15.3		9	4.2-6.1		9.5	-2.5	5.4		
	7	10.5-15.3		10	6.2-7.1		7.8	-1.7	2.0		
	7	9.8-10.2		12	19.8-20.8		10.4	-2.0	2.1		
	9	11.8-14.0	<i>qHD9</i>	10	6.2-7.1		11.1	-1.1	4.0		
	PH	1	41.2-41.4		8	6.2-7.0		8.7	-1.2	1.9	
		3	6.2-6.5		5	0.9-1.5		8.9	-4.7	0.9	
		3	6.2-6.5		8	6.2-7.0		8.1	5.9	2.2	
		5	14.1-16.1		8	6.2-7.0		8.2	-7.7	1.4	
		7	2.3-2.9		8	6.2-7.0		8.2	-1.4	4.0	
		9	11.8-14.0	<i>qPH9</i>	11	0-0.3		8.7	9.7	8.3	
		PL	8	9.8-10.2	<i>qPL8</i>	2	8.9-10.2		8.9	0.2	10.7
			8	9.8-10.2	<i>qPL8</i>	4	27.0-27.9		8.9	1.8	12.2
			8	9.8-10.2	<i>qPL8</i>	5	3.4-4.3		8.2	2.3	5.8
	8		9.8-10.2	<i>qPL8</i>	6	0.3-2.4		8.0	0.4	7.7	
	8		9.8-10.2	<i>qPL8</i>	10	17.2-18.0		10.8	-1.9	12.1	
	8		9.8-10.2	<i>qPL8</i>	11	27.2-28.8		8.4	-2.4	6.6	
	PB	8	9.8-10.2	<i>qPL8</i>	12	1.0-1.4		9.6	1.4	6.9	
		1	9.8-10.4		2	20.7-22.4		7.7	0.5	1.8	
		1	9.8-10.4		3	7.0-8.0		5.7	-1.6	2.5	
		1	11.2-11.3		8	14.9-17.4		5.1	1.4	2.6	
		2	20.7-22.4		2	24.8-25.1		7.4	0.5	2.5	
		3	2.1-3.1		3	3.4-3.9		6.3	0.0	2.6	
		4	7.1-11.4		6	23.7-23.9		8.4	-0.3	1.2	
		4	7.1-11.4		7	26.1-26.4		6.2	-0.3	2.2	
		5	0.9-1.5		9	11.8-14.0		6.3	1.6	1.7	
		6	10.9-11.7		6	17.7-19.6		5.3	0.1	1.7	
		6	22.4-22.8		11	6.2-7.0		8.5	-1.8	5.5	
		8	15.0-17.4		8	19.8-20.1		6.3	1.8	3.5	
		9	11.8-14.0		11	2.0-2.6		7.3	1.2	3.1	
		SN	1	28.6-28.9		11	18.4-18.9		8.1	-8.8	2.7
			1	41.2-41.4		4	1.1-2.8		7.9	-10.3	5.8
	1		42.5-42.6		12	26.2-26.4		7.2	6.8	1.8	
	3		7.0-8.0		11	18.4-18.9		7.5	36.2	3.1	
	4		0-0.2		4	15.9-17.1		7.4	-7.2	10.9	
	5		8.5-13.0		11	20.0-20.5		7.0	-4.1	2.7	
	5		8.5-13.0		12	26.2-26.4		7.6	-13.8	8.0	
	11		18.4-18.9		12	26.2-26.4		8.3	-10.5	3.0	
	SSR		1	27.4-27.7		11	23.2-24.2		6.9	-5.2	6.1
			6	8.7-8.8		12	26.2-26.4		5.3	-3.3	1.4
11		5.0-5.5	<i>qSSR11</i>	11	21.2-21.3		16.6	17.4	16.9		
11		5.0-5.5	<i>qSSR11</i>	12	14.2-17.0		20.7	10.2	9.4		
KGW	9	10.0-10.2	<i>qKGW9</i>	1	0-1.6		5.8	-1.6	7.6		
	9	10.0-10.2	<i>qKGW9</i>	7	6.2-7.3		7.6	-0.6	17.6		
	9	10.0-10.2	<i>qKGW9</i>	12	26.2-26.4		7.4	-1.6	5.7		
02428	HD	1	0-0.6		4	9.7-11.4		7.7	3.0	1.6	
		1	42.2-43.0		5	7.9-13.9		6.3	2.9	1.7	
		3	27.4-27.6		5	7.9-13.9		6.9	-2.3	1.9	
		4	17.1-17.7		5	7.9-13.9		8.5	1.1	1.6	
		5	7.9-13.9		6	25.0-25.1		7.4	1.2	9.6	
		5	7.9-13.9		8	10.0-10.1		8.0	2.4	2.9	
		5	7.9-13.9		9	12.4-12.6		7.2	1.2	1.5	
	5	7.9-13.9		11	20.0-20.5		7.6	1.7	1.6		
	7	26.6-27.8	<i>qHD7</i>	11	20.0-20.5		7.2	1.7	7.6		
	PH	1	39.2-40.5		5	7.9-13.9	<i>qPH5</i>	8.2	1.8	6.8	
		1	42.2-43.0		12	24.8-25.2		6.9	2.0	4.7	
		2	22.4-22.6		5	7.9-13.9	<i>qPH5</i>	6.6	0.8	3.9	
		3	10.0-10.1		5	7.9-13.9	<i>qPH5</i>	5.7	1.2	7.4	
		4	4.8-5.1		7	26.6-27.8		5.9	1.7	6.2	
		4	4.8-5.1		8	10.6-13.5		5.2	2.2	5.3	
		4	17.1-17.7		5	7.9-13.9	<i>qPH5</i>	7.5	8.3	7.1	
		5	7.9-13.9	<i>qPH5</i>	6	22.4-22.7		8.3	1.2	5.7	
		5	7.9-13.9	<i>qPH5</i>	7	4.8-5.2		5.6	-2.8	3.7	
		5	7.9-13.9	<i>qPH5</i>	8	10.0-10.1		10.8	1.1	7.9	

Table 4: Continued

Table 4: Continued

	5	7.9-13.9	<i>qPH5</i>	9	12.4-12.6	6.7	1.9	5.2
	5	7.9-13.9	<i>qPH5</i>	10	19.8-20.0	7.2	1.3	5.7
	5	7.9-13.9	<i>qPH5</i>	11	17.5-17.6	6.8	1.6	5.1
	7	26.6-27.8		12	24.8-25.2	5.1	2.5	5.2
PL	1	7.2-8.4		6	4.8-5.1	5.4	0.3	4.1
	1	7.2-8.4		12	24.8-25.2	5.8	1.5	5.6
	1	9.6-10.2		11	20.0-20.5	5.9	0.4	4.3
	1	34.9-35.3		7	26.6-27.8	5.0	0.4	6.2
	1	39.2-40.5		5	7.9-13.9	5.8	0.9	3.7
	2	12.3-13.0		5	7.9-13.9	5.8	-0.2	4.7
	3	25.0-25.2		5	7.9-13.9	6.9	-0.3	3.1
	4	12.4-14.1		5	7.9-13.9	5.7	0.6	5.9
	5	7.9-13.9		6	19.9-20.1	5.6	1.3	2.2
	5	7.9-13.9		9	12.4-12.6	5.7	0.3	4.2
	5	7.9-13.9		12	24.8-25.2	5.0	0.6	3.2
	6	4.8-5.1		7	26.6-27.8	5.1	0.3	3.2
	7	26.6-27.8		10	10.0-10.1	5.1	0.6	3.0
	7	26.6-27.8		11	24.8-25.2	7.8	0.3	1.1
	7	26.6-27.8		12	24.8-25.2	5.7	0.4	4.2
PB	7	10.0-10.2		7	11.5-12.9	5.2	2.0	18.1
SSR	4	4.8-5.1		5	7.9-13.9	6.6	6.8	14.3
	5	7.9-13.9		5	7.9-13.9	5.7	7.4	23.0
	7	26.6-27.8		11	7.5-7.6	5.4	3.2	4.0

¹HD, heading date; PH: plant height, PL: panicle length, PB: primary branch number per panicle, SN: spikelet number per panicle, SSR: seed setting ratio, KGW: 1000-grain weight; QTL, quantitative trait locus; Chr., chromosome; MH63, Minghui63; ² M-QTL, main effect QTL listed in Table 3; ³ AA, additive interaction effect; positive value represents E-QTL enhanced trait value, while negative value indicates E-QTL decreased traits value; ⁴R², Phenotypic variation explained by the QTL

To validate *qSN9*, one IL from MH63-ILs (DQ071) was selected and further measured its SN. The percentage of recurrent parent genome of DQ071 was 97.46%, and it harbored two 02428 introgression segments distributed on 22.0-24.5 Mb on chromosome 4 and 0-9.4 Mb on chromosome 9. DQ071 had 128.2 spikelets per panicle, and was significantly lower than MH63 which had 168.8 spikelets per panicle (Fig. 3), suggesting *qSN9* was a real QTL for SN.

Discussion

Yield related traits are controlled by genetic components and affected by environments, and genetic components are composed by gene effect and epistatic interaction. Many researches indicated that main effects and epistatic interaction effects were both important for heterosis (Yu *et al.*, 1997), yield related traits (Xing *et al.*, 2002), panicle size (Mei *et al.*, 2006), grain shape (Yan *et al.*, 2014) and reproductive isolation (Li *et al.*, 2017). As there was no heterozygous genotype in the two reciprocal introgression lines in this study, only additive effects and additive by additive interaction effects could be detected. The number of E-QTL was much more than M-QTL, and most E-QTL (72.7% and 73.8% at MH63 and 02428 backgrounds, respectively) were detected with two loci without main effects. Moreover, total phenotypic variance rate of E-QTL was similar or even much larger than M-QTL for most traits (46.5% vs. 42.7% for HD, 62.0% vs. 19.4% for PL, 31.1% vs. 13.7% for PB, 38.2% vs. 12.0% for SN and 38.2% vs. 12.0% for SN at MH63 background, 30.0% vs. 6.3% for HD and 84.2% vs. 5.0% for PH at 02428 background). Thus, we concluded that E-QTL has much larger effect for yield related traits than M-QTL.

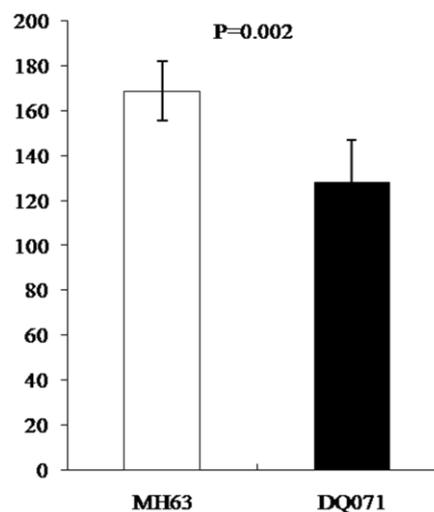


Fig. 3: Difference of spikelet number per panicle (SN) between an introgression line (DQ071) harboring *qSN9* and MH63

In many previous reports, effect of genetic background on QTL mapping is very large. Below twenty percent of the QTL for panicle size (Mei *et al.*, 2006), resistance to drought (Cheng *et al.*, 2012) and salt (Qiu *et al.*, 2015) and appearance quality (Qiu *et al.*, 2017) were commonly detected at multiple genetic backgrounds in reciprocal ILs or ILs with common parents. In this study, two of 24 M-QTL (16.7%) for yield related traits were identified at both backgrounds, which was in agreement with previous studies and suggested large genetic background effect on QTL expression.

In addition, epistatic QTL pair was much more

sensitive to genetic background (Qiu *et al.*, 2017), and no E-QTL was detected at both backgrounds in this work. If a QTL is wanted to apply in molecular breeding program to improve rice yield, genetic background shouldn't be changed.

Nowadays, improving rice yield is more and more difficult, because yield related traits are typical quantitative traits controlled by multi-genes and affected by environment. In the present study, 2 (16.7%) QTL distributed on 16.2–17.2 Mb on chromosome 3 for KGW (*qKGW3*) and 7.3–7.6 Mb on chromosome 9 (*qSN9*) were detected at both genetic backgrounds. MH63 allele at both QTL enhanced trait values. There is a cloned gene (*GS3*) in the region of *qKGW3* for grain length and grain weight. A C-A mutant of *GS3* make rice grain longer and heavier (Fan *et al.*, 2006). MH63 belongs to A allele and 02428 belongs to C allele (Lu *et al.*, 2013), thus *GS3* is the possible cause underlying *qKGW3* for KGW. The *qSN9* contained no cloned SN genes in its candidate region, so it was a new region.

Conclusion

Validation of *qSN9* by an introgression line indicated it was a true region for SN. Pyramiding of favorable alleles (MH63 alleles) at these two QTL will be most likely to improve yield by marker-assisted selection.

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