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ORIGINAL PAPER

H. W. Mei · J. L. Xu · Z. K. Li · X. Q. Yu · L. B. Guo
Y. P. Wang · C. S. Ying · L. J. Luo

QTLs influencing panicle size detected in two reciprocal introgressive line (IL) populations in rice (*Oryza sativa* L.)

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Abstract Two sets of reciprocal introgression line (IL) populations, i.e., ILs with Lemont as recurrent parent (IL_LT) and ILs with Teqing as recurrent parent (IL_TQ), were developed and evaluated for traits representing panicle size, including primary branch number (PBN), secondary branch number (SBN), and spikelet number per panicle (SNP). Together with the regression to recurrent parent by advanced backcross, transgressive segregations were observed for all traits. Correlation and regression analysis showed that SBN had much higher contribution to SNP than PBN. It was confirmed by the QTL analysis that many common loci were detected between SBN and SNP, in comparison with single common locus between PBN and SNP. One and three main effect QTLs (M-QTLs) were detected for PBN in IL_LT and IL_TQ, respectively. Six M-QTLs per trait per populations were associated with SBN and SNP. Less number and lower contribution of epistasis were detected in IL populations in comparison with mapping result from F_2 or RI population. There were only four QTLs in fourteen loci (near 30%) commonly detected in both reciprocal IL populations implying the large impact of genetic background on QTLs expression.

Keywords Introgressive lines (ILs) · Reciprocal populations · Panicle architecture · Quantitative trait locus · Epistasis · *Oryza sativa* L

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H. W. Mei and J. L. Xu contributed equally to this work.

H. W. Mei · X. Q. Yu · L. J. Luo (✉)
Shanghai Agrobiological Gene Center, 2901 Beidi Road, 201106 Shanghai, China
E-mail: lijun@sagc.org.cn
Tel.: +86-021-62200490
Fax: +86-021-62204010

J. L. Xu · Z. K. Li
Institute of Crop Sciences, Chinese Academy of Agricultural Sciences, 12 South Zhongguancun St., 100081 Beijing, China

L. B. Guo · Y. P. Wang · C. S. Ying
China National Rice Research Institute, 359 Tiyuchang Road, 310006 Hangzhou, China

Z. K. Li
Plant Breeding, Genetics and Biotechnology Division, International Rice Research Institute, DAPO Box 7777, Metro Manila, Philippines

Introduction

Understanding of genetic bases of grain yield as a complex trait is valuable in rice improvement and then in food security of the world. However, direct analysis of grain yield did not give ideal results, mainly because final yield was influenced by too many processions and factors. In addition, selection on grain yield itself requires strict field trials of breeding lines in advanced generations. In many characters contributed to grain yield, i.e., yield components, breeding programs designed for different eco-regions have uniquely favored combinations and emphasis. It will be helpful to make proper dissection and focused studies on yield components, instead of yield itself as a whole. Panicle structure, as an important factor of sink size, had been studied by many researchers (Kato and Takeda 1996; Peng et al. 1999; Cui et al. 2002, 2003; Xu et al. 2004).

The QTL approaches had been developed based on molecular markers (Paterson et al. 1988, 1991; Lander and Botstein 1989) and successfully used to learn the genetic basis of complex traits for decades. Compared to a great deal of publications on QTL mapping, there are only a few QTLs that had been confirmed by map-based cloning and transformation (Alpert and Tanksley 1996; Frary et al. 2000; Yano et al. 2000). Intended contribution of QTL to crop genetic improvement was not as noticeable as predicted. One of the main reasons was that most QTL analysis was conducted in a population with genome-wide segregation. Wide variance in genetic background caused the uncertainty of mapping result even with some algorithm to control the genetic background like composite interval mapping. AB-QTL was

suggested to locate quantitative trait loci in an advanced backcross population and to give a more reliable implication for genetic improvement, mainly by getting profit from more precise estimation of genetic effect under a relatively uniform and probably elite background (Tanksley and Nelson 1996).

Overlapping of chromosomal segments in introgression lines (ILs) was a powerful strategy to map QTL more precisely in a spot of genome and to validate QTL mapped in early generation or in genome-wide segregating populations (Paterson et al. 1990; Eshed et al. 1992). Based on near isogenic lines covering target QTL (QTL-NIL), several QTLs had been isolated via map-based cloning (Frary et al. 2000; Yano et al. 2000; Kojima et al. 2002). Besides the successful application of ILs for regional fine mapping, this approach also showed some merit in whole genome QTL screening by construction of populations with introgressive segments covering whole linkage map in tomato (Eshed and Zamir 1994a, b, 1995). In rice, a set of QTL-NILs was developed focusing on several QTLs influencing heading date (*Hd1*∼*Hd7*; Yamamoto et al. 1998, 2000). More powerful detecting of QTLs was reported, i.e., giving more loci (*Hd6* and *Hd7*) than in F_2 and finding authentic epistasis between QTLs (*Hd6* vs. *Hd2*).

In this study, two reciprocal IL populations were developed via random backcross and evaluated for a series of agronomic characteristics. QTL mapping of three traits contributing to panicle size and analysis of effect from genetic background were reported in this paper.

Materials and methods

Reciprocal IL populations

As outstanding rice varieties, "Lemont" from US and "Teqing" from China were used as two parents to develop reciprocal ILs. For ILs with Lemont background (IL_LT), 100 individuals were selected randomly from Lemont/Teqing F_2 population and backcrossed to Lemont. As the derived BC generations would be segregating, they were planted in BC families. More than one individual different from the recurrent parent or randomly selected individuals from each family backcrossed to Lemont continuously up to BC_3 or BC_4 generations. Stable lines were developed after more than two times of selfing. The procedure for developing ILs with Teqing background (IL_TQ) is similar but using Teqing as the recurrent parent. Total 494 lines were used in this study, including 217 ILs from IL_LT, 275 ILs from IL_TQ and two parents.

Field experiment and trait recording

All materials were grown in a randomized complete block design with three replications in Hangzhou, China. The germinated seeds were sown in seedling nursery on May 25, 2000. Seedlings were transplanted to paddy fields on June 20 with single plant per hill spaced at 20×25 cm. Each plot included five rows with seven plants per row.

Three representative plants were sampled from five plants in the middle of the third row in each plot according the uniformity by optical observation. Primary branch number (PBN) and secondary branch number (SBN) were recorded for three randomly selected panicles from each plant. Grain number (GRN) and sterile spikelet number (SSN) were measured for each plant. Total spikelet number per panicle (SNP) was calculated as follows: SNP = (GRN + SSN)/PNN.

Frequency distribution, phenotypic correlation and linear regression analysis were conducted in two reciprocal introgressive populations by using S-Plus 6 for Windows (Insightful Corporation 2001).

Genotyping, linkage map and QTL analysis

Total 160 markers, including 157 SSRs and three morphological markers (*Ph*, *gl-1* and *C*), were used to survey the genotypes of ILs. Linkage maps were constructed separately in each IL population by MapManager QTX 18 (Manly and Olson 1999).

Main-effect QTL (M-QTL) and digenic epistatic QTL (E-QTL) mappings were conducted by using QTLMapper V1.0 (Wang et al. 1999). A significant level of $P < 0.005$ were used to select markers and to declare putative QTL. M-QTLs were named following the popular nomenclature (McCouch et al. 1997) but using alphabetic order for QTLs on same chromosome.

Results

Transgressive segregation of introgressive populations

It was observed that introgressive populations had wide ranges of segregation, i.e., there were transgressive segregations for all traits (Fig. 1). If the phenotypic values of two parents had a large difference, like SBN and SNP, the peak values of reciprocal sets of ILs separated largely with a small proportion of overlapping between frequency distributions. For traits having less parental difference like PBN, peak values had small difference and density curves overlapped for a large amount in two reciprocal populations. By comparison between two cases described above, striking transgressive variances were observed in traits with smaller parental difference. When two parents performed more differently, the peak values were significantly shifted to the side of donor parent from the expected regression to recurrent parent. This part of offset represented the effects of substitution of donor alleles to recipient alleles in average.

Table 1 showed phenotypic correlation coefficients in IL_LT (below diagonal) and in IL_TQ (above diagonal) populations. There were striking positive correlation

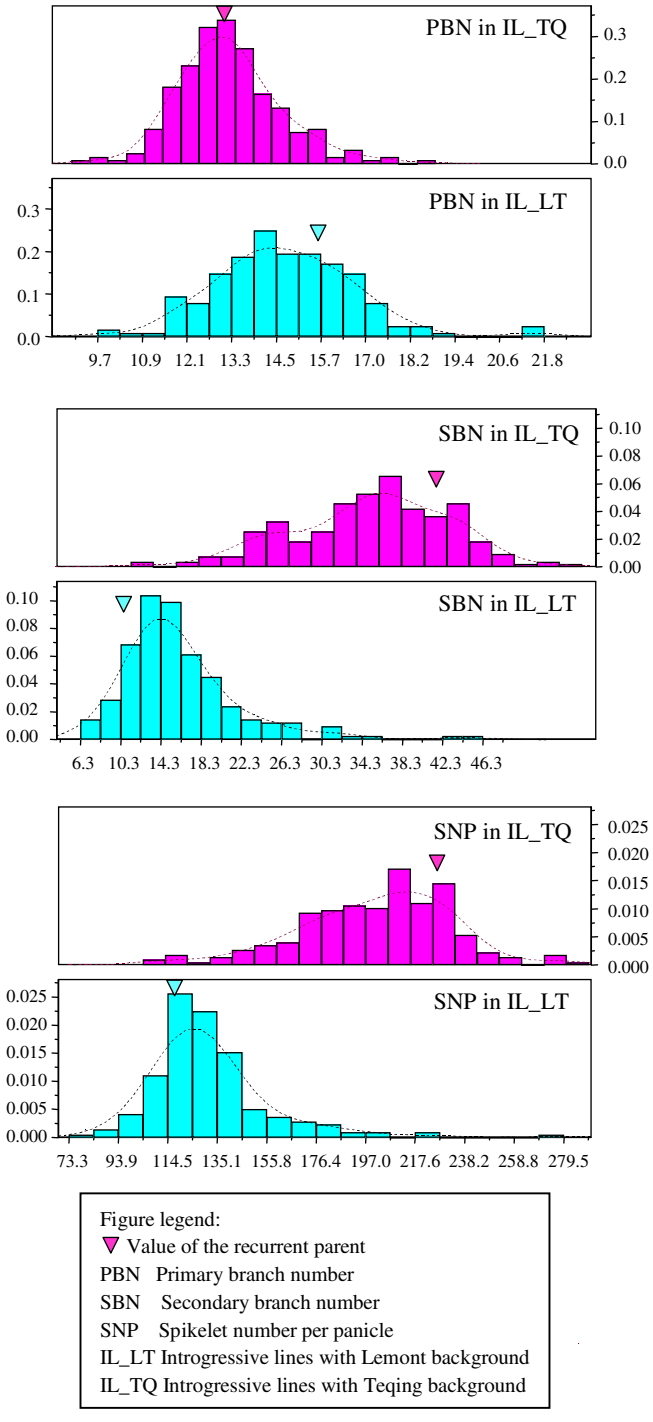

Fig. 1 Frequency distribution of three panicle traits, primary branch number (PBN), secondary branch number (SBN) and spikelet number panicle (SNP), found in two reciprocal introgressive line (IL) populations between Lemont and Teqing

coefficients between SBN and SNP. The multiple R^2 values of SBN reached 80.14% in IL_LT and 81.58% in IL_TQ. PBN had highly significant correlation with SBN and SNP. But PBN had a quite low contribution to SBN and SNP ($R^2 < 30\%$). Negative or low correlations were observed between SNP and some other panicle traits like panicle number, panicle length (data not shown). It was found that secondary branch number (SBN) is the most important contributor to SNP.

Table 1 Correlation coefficients between three panicle traits, primary branch number (PBN), secondary branch number (SBN) and spikelet number per panicle (SNP) in two reciprocal introgressive line (IL) populations between Lemont and Teqing

	PBN	SBN	SNP
PBN		0.3002***	0.4499***
SBN	0.2583***		0.9032***
SNP	0.5182***	0.8952***	

Data under and above the diagonal are correlation coefficients in IL_LT and IL_TQ populations, respectively
***Indicates $P < 0.001$

Linkage maps constructed in reciprocal IL populations

In IL_LT population, the linkage map spanned 1,516 cM with an average distance of 10.2 cM between two adjacent markers. In IL_TQ population, the linkage map spanned 1,677 cM with an average distance of 11.3 cM between two adjacent markers (Fig. 2). The linkage maps in this study covered 79.1~87.5% of total length of the linkage map (1,916.5 cM, with 95 common markers) constructed in the RIL population from the same cross (Xu et al. 2004).

Figure 2 showed significant difference in both marker orders and genetic distances between the linkage maps constructed in reciprocal IL populations. There were 19 chromosome regions where marker orders were inverted, including a large inversion on chr. 6 and small inversions on all chromosomes. Most putative inversions were supported by at least 3 LOD while about half of them happened in or near telomeric or centromeric regions (data not shown).

Segregation distortions were observed for 85 and 40 markers in IL_LT and IL_TQ. Among them, Teqing alleles were favored at 79 and 23 loci, respectively.

Main effect QTL influencing panicle size

Table 2 showed QTLs affecting panicle traits detected in two reciprocal introgressive populations. In IL_LT population, there were one QTL for PBN on chr. 4; six QTLs for SBN on chr. 1, 2, 2, 3, 8 and 9; six QTLs for SNP on chr. 1, 1, 3, 4, 8 and 9. For all loci, the additive effect of allele from the recurrent parent Lemont increased phenotypic values of PBN, but decreased that of SBN and SNP, except *qSNP-4b* on chr. 4 having positive effect on SNP.

In IL_TQ population, there were three QTLs for PBN on chr. 1, 4 and 10; six QTLs for SBN on chr. 1, 2, 2, 3, 5 and 11; six QTLs for SNP on chr. 4, 7, 8, 9, 10 and 11. The contribution rate of single locus varied from 6.83 to 28.27%. Introgressive allele from Lemont

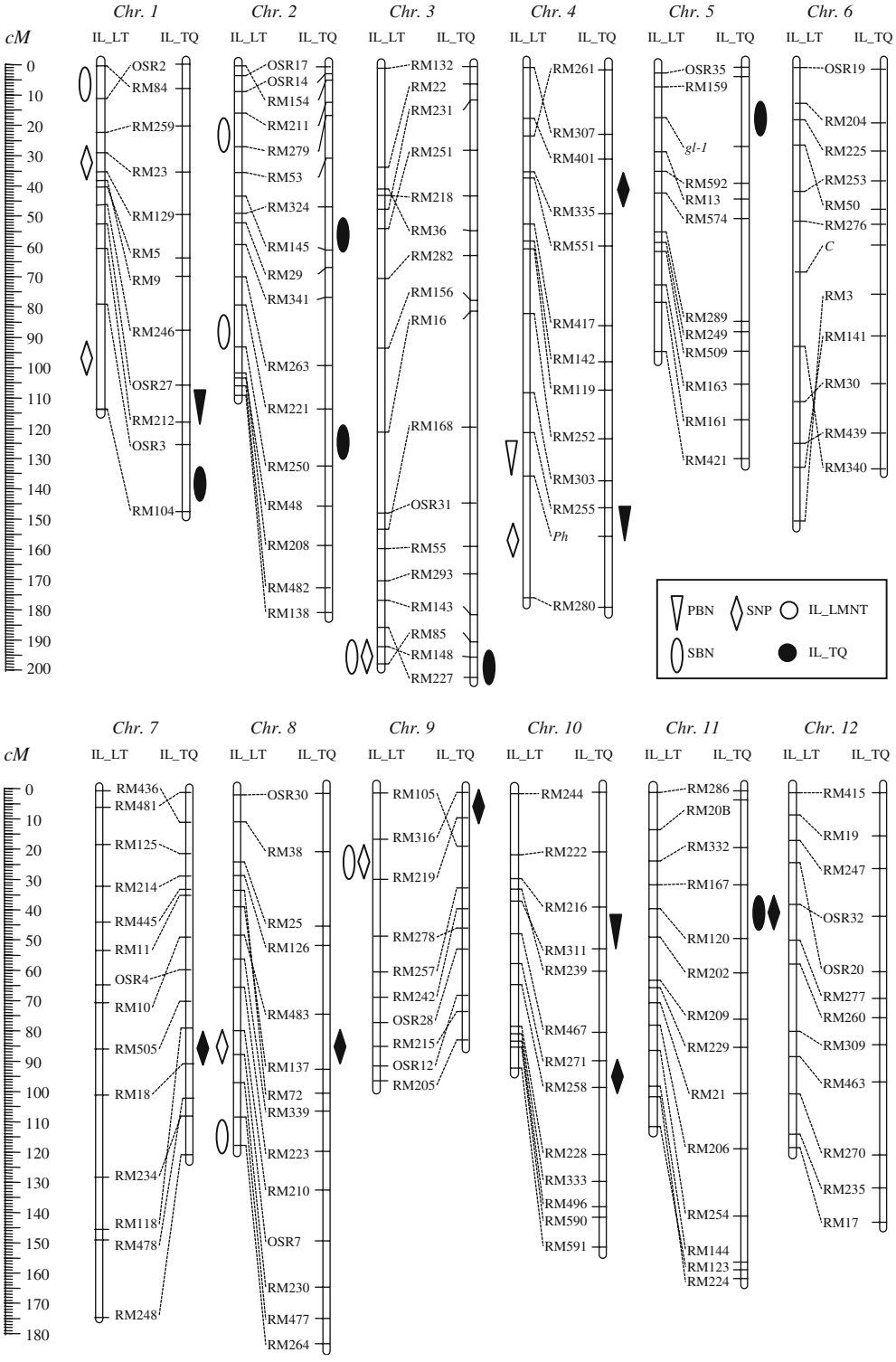

Fig. 2 Chromosomal locations of main effect QTLs influencing three panicle traits, PBN, SBN and SNP, detected in two reciprocal IL populations between Lemont and Teqing

increased PBN for more cases, and also decreased the phenotypic values of other two traits (i.e., SBN and SNP), being highly coherent with the cases in IL_LT.

Two QTLs on chr. 3 and 9 in IL_LT, but only one QTL on chr.11 in IL_TQ were commonly detected for SBN and SNP (Fig. 2). Among these QTLs, *qSBN-9* had the highest contribution rate to SBN ($h^2 = 40.50\%$) and had very large effect on SNP (*qSNP-9*, $h^2 = 31.18\%$) in IL_LT; *qSBN-3b* and q*SNP-3* had contribution rates higher than 10% for both traits in IL_LT; *qSBN-11* and *qSNP-11* had contribution rate higher than 10% for both traits in IL_TQ. These commonly detected QTLs with large contribution rates could partially explain the highly positive correlation between SBN and SNP.

Table 2 Main effect QTLs influencing three panicle traits, primary branch number (PBN), secondary branch number (SBN) and spikelet number per panicle (SNP), isolated in two reciprocal introgressive line (IL) populations between Lemont and Teqing

Trait	Chr.	QTL	Interval	LOD	A[a]	h^2 (%)[b]
Introgressive lines with Lemont background (IL_LT)						
PBN	4	*qPBN-4*	RM255-*Ph*	7.04	1.16	32.87
SBN	1	*qSBN-1a*	RM84–OSR2	5.92	−4.60	10.85
	2	*qSBN-2a*	RM211–RM279	4.04	−3.19	5.21
	2	*qSBN-2c*	RM221–RM250	2.65	−3.27	5.46
	3	*qSBN-3b*	RM148–RM85	14.27	−5.19	13.81
	8	*qSBN-8*	RM477–RM264	7.64	−4.05	8.39
	9	*qSBN-9*	RM219–RM316	7.05	−8.90	40.50
SNP	1	*qSNP-1a*	RM23–RM129	4.74	−29.74	24.14
	1	*qSNP-1b*	OSR3–RM104	6.26	−16.19	7.16
	3	*qSNP-3*	RM148–RM85	14.73	−22.28	13.55
	4	*qSNP-4b*	*Ph*-RM280	2.37	7.44	1.51
	8	*qSNP-8*	RM210–OSR7	3.95	−12.60	4.33
	9	*qSNP-9*	RM219–RM316	5.43	−33.80	31.18
Introgressive lines with Teqing background (IL_TQ)						
PBN	1	*qPBN-1*	OSR27–RM212	2.19	0.52**	7.84
	4	*qPBN-4*	RM255–*Ph*	4.79	0.98	28.27
	10	*qPBN-10*	RM216–RM311	2.72	−0.52	7.92
SBN	1	*qSBN-1b*	OSR3–RM104	7.26	−6.80	15.45
	2	*qSBN-2b*	RM145–RM324	6.57	−6.23	12.95
	2	*qSBN-2c*	RM221–RM250	5.98	−6.07	12.32
	3	*qSBN-3a*	RM148–RM227	8.08	−5.71	10.90
	5	*qSBN-5*	RM159– *gl-1*	7.49	−4.98	8.29
	11	*qSBN-11*	RM167–RM120	8.25	−5.99	11.99
SNP	4	*qSNP-4a*	RM401–RM335	16.68	−27.56	16.07
	7	*qSNP-7*	RM18–RM118	7.14	−34.60	25.34
	8	*qSNP-8*	RM483–RM137	5.84	−21.61	9.89
	9	*qSNP-9*	RM316–RM219	2.02	−17.96**	6.83
	10	*qSNP-10*	RM271–RM258	6.49	−22.31	10.54
	11	*qSNP-11*	RM167–RM120	10.77	−25.19	13.43

**Indicates $P < 0.01$, while all other loci were declared at significant level of $P < 0.005$ based on t test
[a] A represents the additive effect, estimated as the substitution effect of Teqing allele by Lemont allele
[b] h^2(%) represents contribution rate estimated as percentage of total phenotypic variance explained by each QTL

Digenic epistatic QTL influencing panicle size

Mapping results from digenic model were listed in Table 3. In IL_LT population, there were six QTL pairs for SBN, and three pairs for SNP. Among them, all QTL pairs involved the intervals having main effects. Four QTL pairs involved one locus having main effects while other five QTL pairs expressed epistatic effect between two intervals both having main effects. Most digenic epistasis had low contribution rate. The total contribution rate of epistasis were 18.33% for SNP and 23.6% for SBN, in contrast with the high contribution rates of main effect QTLs in total (72.16% for SBN and 77.85% for SNP). All epistatic QTL pairs had positive *AAij*, implying that recombinant type interactions decreased the trait performance. No QTL pair was detected to have significant epistasis for PBN.

In IL_TQ population, there was one QTL pair for each of PBN and SBN, four pairs for SNP having significant epistatic effect. Among them, two QTL pairs did not involve the intervals having main effect. Four QTL pairs involved one locus with significant main effect. It is similar to the result in IL_LT that contribution rates of QTL pairs (h^2_{AA}) were low in total (6.34∼29.05%) in comparison with the high contribution rates of main effect QTL in total (h^2_A, 64.66∼87.51%). Most epistatic QTL pairs had negative effect (*AAij*), except one in SNP, implying that recombinant type interactions had positive effect in Teqing background.

Effect of pleiotropy and genetic background on QTL expression

Several intervals were shared by QTLs for SBN and SNP (Fig. 2). The interval OSR3-RM104 on chr. 1 hosted *qSNP-1b* in IL_LT *and qSBN-1b* in IL_TQ; RM148-RM85 on chr. 3 hosted *qSBN-3b* and *qSNP-3* in IL_LT; RM219-RM316 on chr. 9 hosted *qSBN-9* in IL_LT and *qSNP-9* in both populations; RM167-RM120 on chr. 11 hosted *qSBN-11* and *qSNP-11* in IL_TQ. QTLs located on same interval contributed in same direction to all phenotypic performance implying pleiotropic effect for SBN and SNP.

QTL expression was strikingly affected by the genetic background, i.e., the recurrent parental genomes in this study. There were only a few loci commonly detected in both introgressive populations. Three main effect QTLs were located in same marker interval (*qSBN-2c*, *qPBN-4* and *qSNP-9*) and one in near intervals (*qSBN-3a*/*b*), i.e.,

Table 3 Digenic epistasis influencing three panicle traits, primary branch number (PBN), secondary branch number (SBN) and spikelet number per panicle (SNP), detected in two reciprocal introgressive line (IL) populations between Lemont and Teqing

Trait	Int i[a]	Int name i	Int j	Int name j	LOD	Ai[b]	h^2 (%)	Aj[b]	h^2 (%)	AAij[c]	h^2 (%)	h^2_A (%)[d]	h^2_{AA} (%)[d]
Introgressive lines with Lemont background (IL_LT)													
SBN	1–1	RM84–OSR2	5–1	OSR35–RM159	8.48	−8.47	11.89	−5.23	4.53	4.87**	3.94	72.16	23.6
	2–4	RM211–RM279	3–8	RM156–RM16	9.42	−6.77	7.60	−4.25	2.99	5.55	5.11		
	2–13	RM250–RM208	4–10	RM303–RM255	8.62	−7.57	9.50	−4.95	4.07	7.06	8.26		
	3–16	RM148–RM85	4–6	RM417–RM142	18.52	−8.14	11.00			3.36	1.87		
	7–13	RM118–RM248	11–11	RM254–RM123	7.87	−5.00	4.14			3.47**	2.00		
	8–13	RM477–RM264	9–2	RM316–RM105	15.96	−6.39	6.77	−6.25	6.47	3.82	2.42		
SNP	1–3	RM259–RM23	3–2	RM22–RM231	12.29	−34.84	9.72	−26.56	5.65	34.56	9.56	77.85	18.33
	1–11	OSR3–RM104	11–13	RM144–RM224	8.73	−34.36	9.45			21.12	3.57		
	4–12	*Ph*–RM280	6–1	OSR19–RM204	8.73			−32.79	8.61	23.05	4.25		
Introgressive lines with Teqing background (IL_TQ)													
PBN	7–3	RM125–RM214	11–1	RM20B–RM286	5.65					−0.71**	6.34	71.93	6.34
SBN	3–3	RM132–RM36	7–12	RM118–RM478	11.29	−13.09	18.65			−8.15	7.24	87.51	7.24
SNP	7–2	RM481–RM125	11–6	RM202–RM209	5.50					17.22	2.35	64.66	29.05
	7–12	RM118–RM478	11–2	RM286–RM332	9.20			−49.02	19.06	−31.01	7.63		
	7–12	RM118–RM478	12–4	OSR20–OSR32	6.54			−42.20	14.12	−38.05	11.48		
	7–13	RM478–RM248	11–2	RM286–RM332	7.99			−43.10	14.73	−30.93	7.59		

**Represents significant level at $P \leq 0.01$, while all other additive effect estimates were significant at $P \leq 0.005$

[a] Interval locations labeled as "chr. interval"

[b] *Ai* and *Aj* represent the additive effect of interval *i* and *j*, estimated as the substitution effect of Teqing allele by Lemont allele

[c] *AAij* represents the epistatic effect between interval *i* and *j* as defined by Mather and Jinks (1982)

[d] Total contributions of M-QTL and E-QTL were estimated in the same digenic model and presented as the explained percentage of total variation

near 30% of total M-QTL in each IL populations. These loci had same directions of additive effects in reciprocal populations (Table 2). There were no epistatic QTL pairs exactly between two same intervals detected in both populations (Table 3).

Discussion

Genetic components explaining transgressive segregation and introgressive impact

The frequency distributions of all traits showed wide range of variance and transgressive segregation (Fig. 1). The introgressive Teqing genome in IL_LT was 11.4% and introgressive Lemont genome in IL_TQ was 9.0% (data not shown). The results indicated that partial recombinant populations from advanced BC progenies, compared to whole genome segregation lines like RILs or DHLs, still possessed adequate variance. During the development of materials in this study, BC or selfing progenies were picked randomly or by the visual difference from the recurrent parent. It was quite different from BC breeding practice where a selection pressure was imposed to make the breeding lines to regress to the recurrent parents quickly.

The transgressive segregation, especially the ILs exceeding the donor parent, showed strong genetic interaction, i.e., the epistasis or complementary effect between alleles from donor parent and recurrent parent. As a result of partial segregating populations, there was a low power in detecting epistatic QTLs (Table 3, see details below). It was observed that the direction of main effect QTLs were consistent in most panicle traits (Table 2). In IL_LT as an example, a Lemont allele for PBN had positive effects while those for SBN and SNP had negative effects, but *qSNP-4b* had positive effect from Lemont that might come from the derived effect of *qPBN-4* detected in adjacent intervals. This result showed a possibility to combine the positive effects in PBN and SBN from two parents to achieve higher SNP. It was frequently detected that a few positive alleles came from weak parent in RIL or DH populations. More consistent QTL directions detected in IL populations worth further study in the purpose to understand the genetic effect of introgressive alleles into new genomic background.

On average, introgressive impact of donor genomic components could be estimated by the deviation of peak value or means of ILs from the performance of the recurrent parent (Fig. 1). For a trait with higher performance in donor parent than in recurrent parent, randomly introgressive components may cause the derived ILs perform better or worse than the recurrent parent, but a positive genetic gain can be obtained in population level. In QTL analysis, more positive alleles came from the high-value parent. So there was a positive profit after balanced with the negative alleles. As the additive effects were estimated from the substitution effect of alleles from two parents, and the introgressive segments covered the whole donor genome (data not shown), introgressive impact estimated in this study partially expressed the advance of genome of one parent beyond that of another parent as a whole.

Relative importance of traits contributing to panicle size and grain yield

Spikelet number per panicle (SNP) is an important characteristic in panicle architecture as it determined the panicle size together with spikelet fertility. Regression analysis showed highest contribution of SBN to SNP ($R^2 = 80.14\%$ in IL_LT and $R^2 = 81.58\%$ in IL_TQ), whereas panicle length (data not shown) and PBN ($R^2 = 26.85\%$ in IL_LT and $R^2 = 20.24\%$ in IL_TQ) had low contribution to SNP. Weak negative impact of panicle number to all other panicle size traits was observed (data not shown). As contributors to grain yield per plant (data not shown), SNP and SBN were more important ($R^2 = 50.08\%$ for SNP, $R^2 = 52.84\%$ for SBN) than all other traits. As two parents had a large difference in SBN, panicle size and grain yield were largely determined by SBN in their progenies. This was also observed in RI population from the same cross (Xu et al. 2004) and some other populations or varieties (Cui et al. 2002; Yamagishi et al. 2003, 2004).

Epistasis between genetic background and introgressive alleles

To understand the epistasis between putative QTL and its genetic background, algorisms of one-dimensional genome search were proposed by Jannink and Jansen (2001) and Boer et al. (2002). This approach not only avoided the difficulty in two-dimensional searches covering the whole genome, but also resolved epistasis of high orders. The authors emphasized that the detection of QTL-by-background interaction was valuable for marker-assisted selection of target QTLs.

In an advanced backcross population, QTLs are estimated with the lines having similar genetic background from the recurrent parent. Therefore, the QTL-by-background interaction can be revealed by comparing mapping results from two reciprocal IL populations. In this study, strong interaction between genetic background and introgressive donor alleles was observed as only a low number of M-QTLs, and no epistatic QTL pairs were commonly detected in both introgressive populations (Tables 2, 3).

Because of lower resolution of epistatic QTLs, less contribution was observed from epistasis in proportion to main effect QTL compared with regular populations like RILs and DHLs (See next section for details). Mixed effect from epistatic loci acted as an epistatic genetic background from recurrent genome. As an objective of a research network of International Rice Molecular Breeding Program (Yu et al. 2003), a series of IL populations with more than ten recurrent parents will be developed by introgression of chromosomal segments from a common set of about 100 donor lines. With these coming materials, QTL-by-background interactions might be well addressed.

QTL identification in different kinds of populations and via different mapping strategies

In F_2 or RIL population with similar size from the same cross, E-QTLs were found to have higher contribution rate than M-QTLs for more traits, especially for QTLs influencing heterosis isolated in RILs and their testcross or backcross hybrids (Li et al. 1995, 1997a, b, 2001; Luo et al. 2001; Mei et al. 2003, 2005). In this study, less epistatic QTL pairs (2.5 pairs per trait per population) and lower contribution rate from epistatic QTLs (Table 3) were observed. It was mainly caused by higher power in detecting main effect QTL and lower power in isolation of epistasis since the epistatic loci detected in whole genome segregating populations like F_2 or RILs would be detected as main effect QTLs in ILs as one of the interacting loci was fixed (Li et al. 1997a).

Xu et al. (2004) carried out QTL analysis for SNP and its related traits using RIL population from the same cross in International Rice Research Institute, Philippines. A total of ten QTLs for PBN, eight QTLs for SBN and eight QTLs for SNP were mapped on 15 regions of 9 rice chromosomes. Low numbers of QTLs among them were commonly detected in this study. QTLs detected in one or both of IL populations in same or adjacent intervals as in RILs include: two loci for PBN (*qPBN-1* and *qPBN-4*); two QTLs for SBN (*qSBN-2b* and *qSBN-3a/b*; and two QTL for SNP (*qSNP-3* and *qSNP-4b*). Besides the influence from large difference in environment during the field experiments, it can be explained by the QTL-by-background interaction and by the over-sensitive to the control of genetic background.

Compared with the composite interval mapping result shown in this paper, more markers or intervals were significantly associated with target trait via ANOVA or interval mapping without genetic background control (data not shown). Composite or multiple interval mapping was recognized as a more reliable approach, which could detect less number of loci and also reduce the risk of Type I Error (Belknap et al. 1996). But genetic background control might cause Type II Error, especially between two markers with similar LOD values. Selecting one marker into the model for background control will exclude another marker and vice versa. For example, markers at both ends of chr. 3 were associated with SBN and SNP by ANOVA and interval mapping (data not shown), but putative QTLs were declared only at the bottom after controlling the genetic background in this study. QTL analysis might be more sensitive to background control in advanced BC population than F_2 or RILs because lower number of recombinants is available. And the background genetic variance has already been reduced along BC procedures. So background control might not be as necessary in IL populations as in genome-wide segregating populations. Without controlling the genetic background, the number of detected loci would be doubled or tripled.

There is a shortage of BC population with high generation caused by the low copy numbers of donor

alleles or chromosome segments available in the population. The freedom degree is quite low for introgressive allele in some loci. This will result in following consequences in this study: (1) less epistasis was detected because proper individual occupying different recombinants were not available; (2) The discrepancy between mapping results in reciprocal introgressive populations was probably caused by the weak cover of donor segment in one population, rather than caused by foreground-by-background interaction; 3) Mapping result may be excessively influenced by a few lines with extreme phenotypes. This will cause some risk of error in field trials with larger amount of lines and small plot size. So the genetic effects estimated here required further confirm by conducting more reliable field trial with fewer selected ILs and with larger plot area.

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