



Full Length Article

Mapping QTL with Main Effect, Digenic Epistatic and QTL × Environment Interactions of Panicle Related Traits in Rice (*Oryza sativa*)

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Abstract

Panicle related traits are critical agronomic traits which directly associated with grain yield. Although several QTL or genes have been mapped and cloned, we still need to identify new QTL or genes to understand the complex mechanisms of panicle development. In this research, a total of 116 double haploid (DH) population derived from a cross between a *japonica* variety Chunjiang 06 (CJ06) and an *indica* variety Taichung native 1 (TN1) was used to investigate primary branch number (PBN), secondary branch number (SBN), grain number per panicle (GNPP), panicle length (PL), and panicle-neck diameter (PND) under two different environmental conditions. QTL mapping analysis of five panicle related traits was performed by mapmaker/QTL1.1B and QTL Network v2.0 software. A total of 17 main effect QTLs were identified for these traits, which mapped to chromosomes 1, 4, 6, 7 and 8; their *F*-values ranged from 7.9 to 27.7, with a phenotypic variation from 7.81% to 24.22%. Among these QTLs, six loci were novel and two loci contain the known heading date gene, *Hd1* and *Ghd8/DTH8*. Two pairs of epistatic interactions and six QTL-by-environment interactions (QEs) were identified, indicating that panicle related traits are susceptible to environmental influence. These results will facilitate fine mapping and QTL pyramiding for genetically improving grain yield in rice. © 2017 Friends Science Publishers

Keywords: Rice; Panicle related traits; QTL; Epistasis; QEs

Introduction

Food shortage is one of the most serious global problems (Xu *et al.*, 2014). According to the United Nations Food and Agricultural Organization (FAO), approximately 805 million people were chronically undernourished between 2012 and 2014 (FAO, 2014). Rice (*Oryza sativa* L.) is an important staple food for over half of the world population (Fu and Yang, 2012). Achieving increase in rice grain-yield is a permanent topic of concern for over-increasing population (Yuan, 2014). Rice panicles are the main storage of photosynthetic products, which directly associated with grain yield (Ando *et al.*, 2008). Therefore, improvement of panicle related traits has always attracted the attention of breeders. Panicle related traits usually include grain number per panicle (GNPP), panicle length (PL), primary branch number (PBN) and secondary branch number (SBN), etc. Grain number per panicle has shown a largest variation range and was the major objective of improvement in rice high yield breeding (Tian *et al.*, 2006). Several high-yield rice models are most concerned with panicle number (Zhu

et al., 2011). Panicle length is one aspect of panicle architecture and a critical trait for panicle. Panicle length, together with PBN and SBN, determines the grain number per panicle, hence, affecting rice yield (Liu *et al.*, 2016). Panicle neck was the connection between culms and panicle, which played an important role in transporting assimilates from leaves, leaf sheathes and culms to the panicle (Liu *et al.*, 2008a). It was broadly observed that panicle neck diameter (PND) was significantly correlated with PL, GNPP and panicle size (Huang, 1998).

Rice panicle related traits are quantitatively inherited and a great deal of quantitative trait locus (QTL) underlying panicle related traits have been detected using different types of populations, including DH populations (Teng *et al.*, 2001; Yamagishi *et al.*, 2002; Yan *et al.*, 2007; Yun *et al.*, 2016), near-isogenic line (NIL) populations (Zhang *et al.*, 2006; Zhu *et al.*, 2011), recombinant inbred line (RIL) populations (Liu *et al.*, 2008b; Ye *et al.*, 2009; Liu *et al.*, 2010; Peng *et al.*, 2014), introgression line (IL) populations (Tian *et al.*, 2006), and single segment substitution line (SSSL) populations (Ying *et al.*, 2014). Some QTLs identified in

these populations were subsequently fine-mapped or cloned, Such as, *Gn1a*, *DEP1*, *GIF1*, *PROG1*, *Ghd7*, *Ghd8/DTH8* (Ashikari *et al.*, 2005; Jin *et al.*, 2008; Wang *et al.*, 2008; Xue *et al.*, 2008; Huang *et al.*, 2009; Yan *et al.*, 2011).

Because of the complex relationships among rice panicle traits, genotype-by-environment interactions (GEs) are very important for evaluating the genetic components of panicle related traits (Liu *et al.*, 2008b). Estimation of GEs has been extensively investigated and has provided valuable information for QTL analysis (Ying *et al.*, 2014). Epistasis effect is another important factor that affects genetic variation and phenotypic expression of genes in populations (Li *et al.*, 1997). Epistatic QTL on panicle related traits have also been widely studied (Liu *et al.*, 2008b; Ying *et al.*, 2014).

In this study, a DH population derived from a cross between the *japonica* variety CJ06 and *indica* variety TN1 was used for estimated the effects of main-effect QTL, epistatic QTL and environmental interactions for PBN, SNB, GNPP, PL, and PND under two different conditions. These results will help us to better understand the genetic control of rice panicle related traits and identify the potential target QTL to be manipulated by marker-assisted selection (MAS) in rice panicle related traits breeding programs.

Materials and Methods

Plant Materials

A total 116 DH lines derived from a cross between the *japonica* variety CJ06 and *indica* variety TN1 was developed according to Zeng *et al.* (2009). Uniform seeds of all DH lines and the parents were soaked in distilled water in the dark at 30°C for 2 days and germinated in distilled water at 35°C for 12 h. The germinated seeds were then sown in the seedling nursery in the paddy field. After 25 days, the DH line and parents were transplanted in the experimental farm of the China National Rice Research Institute in Hangzhou (HZ, 119°54' E, 30°04' N) and Hainan (HN, 110°00' E, 18°31' N), during the 2013 and 2014 rice-growing seasons, respectively. The two locations represent two ecological types. The climate of Hangzhou is characterized by high temperature and high humidity and that's Hainan with semi-arid and semi-humid. A randomized complete block design was utilized at both locations, with a planting density of 20 cm × 20 cm. Three replications were growth and each line was planted in six rows with six plants. At each location, field management including irrigation, fertilizer application and pest control, followed normal agricultural practices.

Measurement of Panicle Related Traits

The five panicle related traits were measured at the heading stage (25 day after heading). Six plants in the middle of each plot were used to score the phenotypic data sets. The three

major panicles (the highest three panicle) of each plant were selected to investigate PBN, SBN, GNPP, PL (in cm) and PND (in mm). PBN, SBN and GNPP were recorded by counter. PL was measured by graduated scale. PND was measured at the joint between the panicle and first internode with a digital vernier caliper.

DNA Extraction, PCR Analysis and Sequencing

Genomic DNA was extracted from each plant using the CTAB method (Murray and Thompson, 1980). A total of 227 polymorphism markers including 203 SSR markers based on Gramene database (<http://www.gramene.org/archive>) and 24 STS makers were selected. PCR reaction was performed according to Ren *et al.* (2016). PCR product was subjected to electrophoresis on a 4% agarose gel. To identify the sequence difference of *Hd1* and *Ghd8* between CJ06 and TN1, the DNA segments of *Hd1* and *Ghd8* from two parents were amplified and sequenced.

Data Analysis and QTL Detection

Population distribution and correlation analyses of PBN, SBN, GNPP, PL and PND were performed using the SAS 8.0 software. A total of 227 polymorphism SSR and STS markers covering all 12 chromosomes were selected to construct the genetic linkage map using the mapmaker/Exp3.0b software (Fang *et al.*, 2015). QTLs were detected using the mapmaker/QTL1.1b software. The QTL Network version 2.0 were using to estimated additive effects, genetic parameters and variation percentages and the QTL named followed the system of Khush, 1995; McCouch, 1997.

Results

Phenotypic Variation in the Parents and DH Lines

The panicle related traits of the parents and 116 DH lines are summarized in Table 1. All traits exhibited significant differences between parents under the two different conditions except GNPP in Hangzhou. The performance of panicle related traits for CJ06 were superior to those of TN1 in Hangzhou, while this pattern was reversed in Hainan. It may be due to the sensitivity of photoperiod for *japonica* varieties. The skewness and kurtosis of PBN, GNPP, PL and PND were near zero at least one condition, indicating the phenotypic values of those traits were normally distribution, which indicate that the population was suitable for QTL mapping (Fig. 1 and Table 1).

Correlation Analyses of Panicle Related Traits

Correlation analyses of five panicle related traits were performed as shown in Table 2. PBN, SBN, GNPP and PL showed significantly positive correlations between each

Table 1: Statistical analysis of panicle related traits by two parents and their DH population

Year	Traits	Parents (Mean \pm SD)			DH population			
		CJ06	TN1	P value	Means \pm SD	Range	Skewness	Kurtosis
Hangzhou	PBN	13.3 \pm 0.5	12.8 \pm 0.9	0.007	12.7 \pm 2.3	8.9–20.0	1.03	1.99
	SBN	23.3 \pm 1.8	16.0 \pm 2.7	0.035	18.0 \pm 9.3	3.9–45.4	0.93	1.08
	GNPP	147.9 \pm 6.3	122.5 \pm 12.8	0.132	121.4 \pm 34.7	59.8–222.6	0.53	0.22
	PL(cm)	24.7 \pm 0.8	25.5 \pm 1.5	<0.0001	21.2 \pm 3.0	15.5–27.9	0.07	-0.23
	PND (mm)	2.3 \pm 0.1	2.01 \pm 0.1	<0.0001	1.9 \pm 0.3	1.4–2.6	0.25	-0.36
Hainan	PBN	9.9 \pm 0.8	12.0 \pm 0.6	<0.0001	11.9 \pm 2.2	6.5–17.8	-0.07	0.19
	SBN	16.1 \pm 2.0	24.3 \pm 5.5	<0.0001	18.6 \pm 6.9	7.3–43.3	1.00	1.38
	GNPP	93.0 \pm 9.8	148.2 \pm 19.2	<0.0001	114.8 \pm 29.1	55.0–207.3	0.64	0.74
	PL(cm)	17.7 \pm 1.2	23.1 \pm 0.8	<0.0001	18.5 \pm 1.9	14.6–23.1	0.23	-0.73
	PND (mm)	1.9 \pm 0.1	2.2 \pm 0.1	0.0022	2.0 \pm 0.2	1.5–2.6	0.32	0.05

Data are presented as the average \pm standard deviation (SD). PBN: Primary branch number; SBN: Secondary branch number; GNPP: Grain number per panicle; PL: Panicle length; PND: Panicle-neck diameter

other in both Hangzhou and Hainan. Secondary branch number exhibited a highly significant correlation with GNPP with correlation coefficients reaching up to 0.925 in Hangzhou and 0.879 in Hainan, indicating that SBN was the most important contributor to GNPP. The next strongest correlations were between PBN and GNPP, which were 0.607 in Hangzhou and 0.719 in Hainan. Similarly, plant length also exhibited a highly significant correlation with PBN, SBN and GNPP under the two different conditions. Panicle neck diameter displayed a highly significant correlation with PBN, SBN and GNPP, with the coefficients of 0.586, 0.620, and 0.653 in Hainan, respectively. Nevertheless, there was no significant correlation between PND and other panicle related traits in Hangzhou.

Main-effect QTLs in DH Population

A total of 17 main-effect QTLs, including 4 for SBN, 3 for PBN, 2 for GNPP, 4 for PL and 4 for PND, were identified on chromosomes 1, 4, 6, 7 and 8 under two different conditions (Fig. 2 and Table 3). The *F*-values of these main-effect QTLs ranged from 7.9 to 27.7, with the additive heritability ranging from 7.81% to 24.22%.

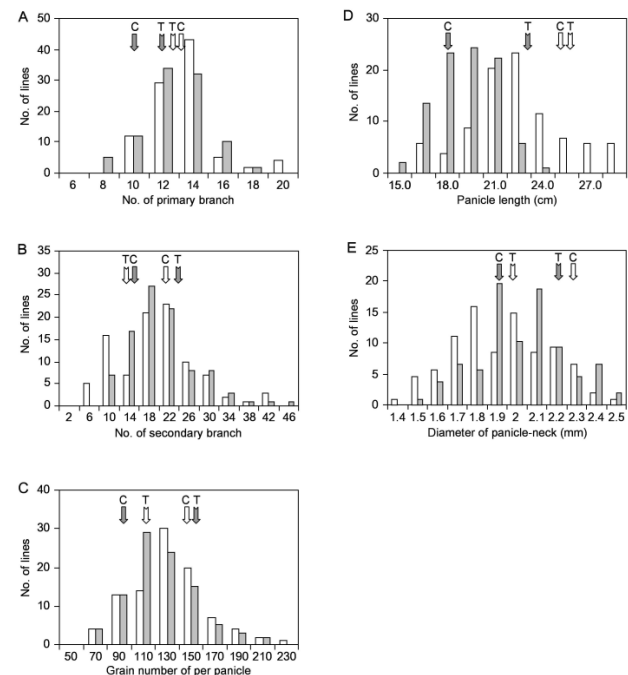
For PBN, two and one QTLs were identified on chromosomes 1, 7 and 6 in Hangzhou and Hainan, respectively, each with additive effects ranging from 0.72 to 1.04 and explaining from 11.3% to 24.5% of phenotypic variance (Table 3). Two QTLs for SBN were identified on chromosomes 4 and 6 in Hangzhou, each explaining 24.2% and 15.5% of phenotypic variance, with the favorable alleles derived from CJ06 and TN1, respectively. However, no corresponding SBN QTLs were detected in Hainan; other QTLs related to SBN were mapped to chromosomes 4 and 8 in Hainan, explaining 18.1% and 19.9% of phenotypic variance, respectively. Two QTLs for GNPP were identified on chromosomes 4 and 6. *qGNPP4h* was located on chromosomes 4 only in Hangzhou, the allele from CJ06 increased GNPP by 20, explaining 19.20% of the phenotypic variance. The other QTL, *qGNPP6n*, was located on chromosome 6, but only in Hainan. The allele from TN1 increased GNPP and explained 16.3% of the phenotypic variance.

Four QTLs for PL were located on chromosomes 6

Table 2: Trait correlations for panicle related traits from a DH population derived from the cross of CJ06/TN1 observed in Hangzhou (upper) and Hainan (lower)

Trait	PBN	SBN	GNPP	PL
SBN	0.316**			
	0.483**			
GNPP	0.607**	0.925**		
	0.719**	0.879**		
PL	0.354**	0.455**	0.546**	
	0.367**	0.333**	0.508**	
PND	-0.028	-0.167	-0.162	-0.097
	0.586**	0.620**	0.653**	0.178

**Significant at the level of 1%

**Fig. 1:** Frequency distribution of PBN, SBN, GNPP, PL and PND in the DH population

The empty columns and arrows indicate the rice grown in Hangzhou in 2013. The gray columns and arrows indicate the rice grown in Hainan in 2014. Arrows with a smooth end indicate CJ06, and arrows with a notched end indicate TN1. The capital C and T indicate CJ06 and TN1, respectively

Table 3: QTLs for panicle related traits in the DH population of CJ06 and TN1

Trait	Locus	Chr.	Marker Interval	F-value	Additive effect (A)	H ² (A)%
<i>Hangzhou</i>						
PBN	<i>qPBN1h</i>	1	RM5389-RM1198	8.8	0.98	15.2
	<i>qPBN7h</i>	7	RM1279-RM505	7.9	1.04	17.0
SBN	<i>qSBN4h</i>	4	SSIII-1-RM3306	27.7	4.41	24.2
	<i>qSBN6h</i>	6	RM6836-RM527	27.0	-3.53	15.5
GNPP	<i>qGNPP4h</i>	4	SSIII-1-RM3306	18.2	20.11	19.2
PL	<i>qPL6h</i>	6	RM6836-RM527	11.1	-1.08	12.8
	<i>qPL6</i>	6	RM528-RM340	14.5	-1.43	22.6
	<i>qPL8h</i>	8	RM310-SSIII-2	8.7	-0.84	7.8
PND	<i>qPND6h</i>	6	RM528-RM340	8.7	-0.09	12.0
	<i>qPND8</i>	8	RM1376-RM4085	23.3	-0.11	18.7
<i>Hainan</i>						
PBN	<i>qPBN6n</i>	6	RM6836-RM527	12.4	-0.72	11.3
SBN	<i>qSBN4n</i>	4	RM401-RM16874	11.3	3.31	18.1
	<i>qSBN8n</i>	8	RM4085-RM310	22.3	-3.47	19.9
GNPP	<i>qGNPP6n</i>	6	RM6836-RM527	12.1	-12.05	16.3
PL	<i>qPL6</i>	6	RM528-RM340	13.2	-0.57	18.9
PND	<i>qPND4n</i>	4	RM401-RM16874	13.8	0.10	14.3
	<i>qPND8</i>	8	RM1376-RM4085	15.3	-0.11	17.7

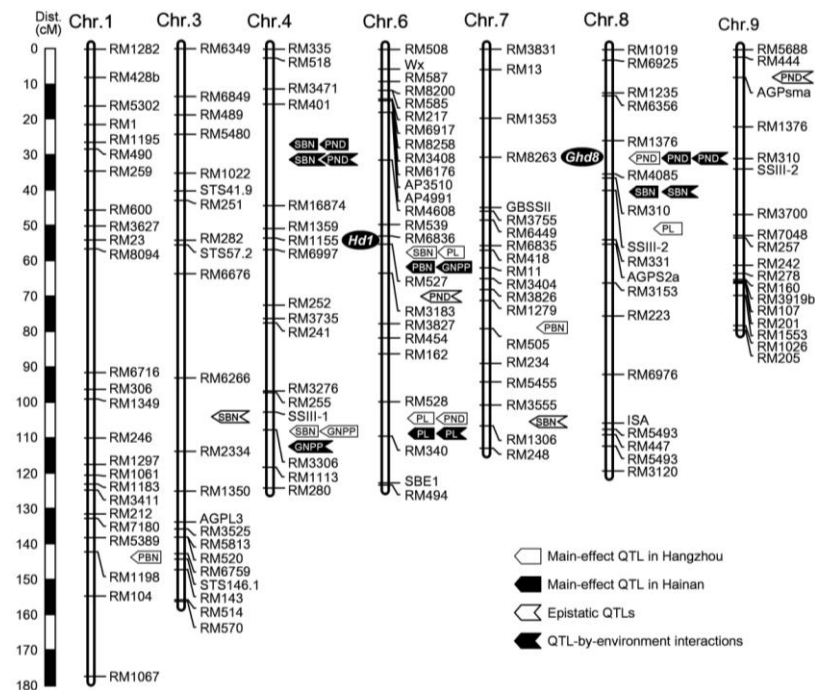


Fig. 2: Locations of main effect and epistatic QTLs for PBN, SBN, GNPP, PL and PND on the linkage map. Open arrows indicate QTLs identified in Hangzhou. Solid arrows indicate QTLs identified in Hainan. Empty arrows with the same notched ends indicate the pairs of epistatic interaction QTLs. Solid arrows with the same notched end indicate QTL-by-environment interactions. The bar on the left indicates the genetic distance on the linkage map. The markers starting with “RM” are SSR markers and all others are STS markers

and 8 under both conditions. All the QTLs that increased PL were derived from TN1, which is consistent with increased PL in TN1 relative to CJ06. *qPL6* was mapped on chromosome 6 between RM528 and RM340 in both Hangzhou and Hainan, explaining 22.6% and 18.9% of variation, respectively. *qPL6h* and *qPL8h* were identified only in Hangzhou, which explained the variation of 12.8% and 7.8%, respectively. The interval of RM1376-RM4085

on chromosome 8 was a major locus affecting PND and explained 18.7% and 17.7% of the variation in Hangzhou and Hainan, respectively.

Digenic Epistatic QTLs and QEs in the DH Population

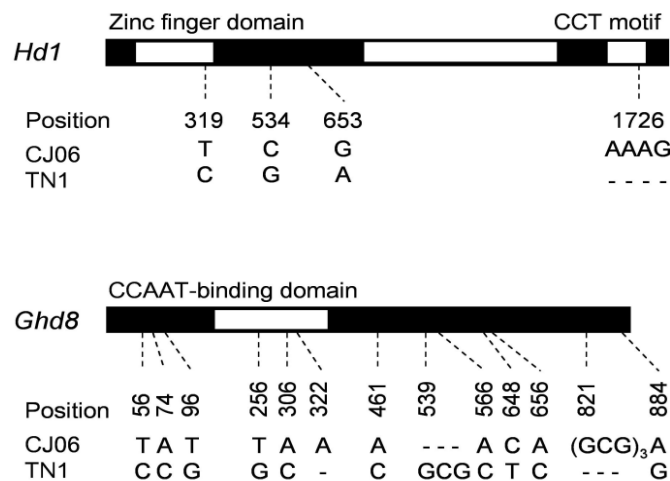
To further investigate the genetic basis of panicle related traits, the digenic epistatic effects of PBN, SBN, GNPP, PL,

Table 4: Epistasis effect for panicle related traits in DH population of CJ06 and TN1

Trait	Chr.	Marker interval	Chr.	Marker interval	F-value	Epistasis (AA)	H ² (AA) (%)
SBN	3	RM6266-RM2334	7	RM3555-RM1306	13.9	2.5872	9.97
PND	6	RM527-RM3183	9	RM444-AGPsm	5.85	0.0523	3.87

Table 5: Environment interactions of putative QTLs for panicle related traits in DH population

Traits	Chr.	Interval	F-value	A	H ² _A (%)	AE ₁	H ² _{AE1} (%)	AE ₂	H ² _{AE2} (%)
SBN	4	RM401-RM16874	18.8	2.93	12.8	0.0713	12.77	-0.0708	12.77
	8	RM4085-RM310	21.3	-3.14	14.7	0	14.70	0	14.70
GNPP	4	SSIII-1-RM3306	9.9	12.73	11.9	5.5953	13.24	-5.6157	13.26
PL	6	RM528-RM340	14.8	-1.25	21.8	-0.5511	26.07	0.547	26.00
PND	4	RM401-RM16874	11.9	0.11	17.7	-0.0001	17.66	0.0001	17.66
	8	RM1376-RM4085	18.6	-0.11	17.5	-0.0001	17.54	0.0001	17.54

**Fig. 3:** Arrangement in *Hd1* and *Ghd8* between CJ06 and TN1

and PND were estimated. Two pairs of epistatic interactions were detected for SBN and NPD, which explained 9.97% and 3.87% of the phenotypic variation, respectively (Table 4 and Fig. 2). However, no significant epistasis was detected for PBN, GNPP and PL, which indicates that the main-effect QTLs were the primary genetic basis of those traits. To some extent, environment factors may significantly influence panicle-related traits. In this study, a total of 6 QEs were detected for panicle related traits except for PBN, including 2 for SBN, 1 for GNPP, 1 for PL and 2 for PND, with the phenotypic variation ranging from 12.77% to 26.00% (Table 5 and Fig. 2).

Comparative Genetic Analysis for QTLs and Heading Date Related Genes

Panicle related traits QTL were commonly co-identified with heading date (Liu et al., 2016). Thus, we further integrated the heading date related genes and QTL mapping in this study. Two heading date-related genes, namely *Hd1* and *Ghd8/DTH8* were integrated with panicle-related QTLs (Fig. 2). *Hd1* is located in the interval for *qSBN6h*, *qPL6h*, *qPBN6n* and *qGNPP6n* between RM6838 and RM527 on

chromosome 6. *Hd1* encode a zinc-finger type transcriptional activator with CCT domain, which can promotes flowering under SD (Yano et al., 2000). The loss of *Hd1* results in greater biomass in most *indica* under short-day (Yano et al., 2000). Similarly, *Ghd8/DTH8*, which simultaneously regulates grain yield, heading date, and plant height, was integrated with *qPND8* between RM1376 and RM4085 on chromosome 8 (Yan et al., 2011). We further compare the sequence of *Hd1* and *Ghd8* between the two parents, some deletion, insertion and non-synonymous change were identified between CJ06 and TN1 (Fig. 3).

Discussion

Rice is an essential staple crop in the world that feeds more than over three billion people worldwide (Zhu et al., 2011). Over the past decades, the use of the semi-dwarf breeding and hybrid breeding has significantly contributed to the improvement of rice yield. However, rice yield level has been at a standstill in recently 10 years (Yan et al., 2009). Panicle related traits are the most important traits for rice yields and ideal plant breeding. Therefore, understanding

the genetic mechanism of panicle related traits is important for genetic improvement rice cultivars with a high-yield. Previous studies demonstrated that panicle related traits are typical quantitative trait controlled by multiple genes and easily influenced by environmental (Liu *et al.*, 2016). A number of QTLs for panicle related traits were detected by different segregating populations, such as DH populations, RILs or near-isogenic lines (Teng *et al.*, 2001; Zhang *et al.*, 2006; Peng *et al.*, 2014; Yun *et al.*, 2016). Although numerous QTL for panicle related traits have been mapped or cloned, we still need to identify new QTL or genes to understand the complex mechanisms of panicle development. In this study, rice panicle related traits including GNPP, PL, PBN, SBN and PND in DH population were investigated under two conditions. Seventeen main-effect QTLs, two pairs of epistatic interactions and six QEs were detected. The results should be helpful for improving panicle related traits and QTL pyramiding in rice.

A number of QTLs affecting panicle related traits have been mapped previously. Yamagishi *et al.* (2002) found two QTLs for PBN and SBN on chromosome 6 and 7, which were closed to *qSBN6h* and *qPBN7h* in our study. Liu *et al.* (2008a) identified 3 QTLs for SBN and 7 QTLs for PBN using a RIL population from the cross ZS97B/IRAT109, and two of them were anchored to the intervals of *qSBN4h* and *qPBN6n*. Two QTLs for GNPP on chromosome 4 and 6, *qGNPP4h* and *qGNPP6n*, were also detected by Deshmukh *et al.* (2010) and Ying *et al.* (2014), respectively. Moreover, the *qPL6* on the flanking of RM528-RM340 on chromosome 6 was also found by Xing *et al.* (2001). Compared with previous studies, a novel major QTL for PBN, *qPBN8n*, was detected only in Hainan, which explained 19.9% of the phenotypic variance. In addition, we identified four QTLs for PND on chromosome 4, 6 and 8 under two different condition, the loci of them were all different with Liu *et al.* (2008a) reported. One possible explanation was the different genetic background between parents or different environment conditions.

Genotype \times environment interactions are very important to the expression of QTL. In our study, ten and seven main-effect QTLs for panicle-related traits were identified in Hangzhou and Hainan, respectively. However, just two QTLs for PL and PND were detected in both conditions. Eight QTLs were only detected in Hangzhou, and five QTLs were just found in Hainan. The results revealed that the expression of QTL for panicle related traits were susceptible to environment. It was agreement with the previous reported by Ying *et al.* (2014).

Rice is a short-day plant, the short photoperiods conducted its heading and consequently impacted growth duration and the grain-yield in different latitudinal region. In our study, we found that some QTL for panicle-related traits were co-located on the flanking carrying with heading date, such as, *qSBN6h* and *qPBN6n* were anchored on the same flanking contained *Hd1*, the interval with *qSBN8n* was close to *Ghd8/DTH8* on the short arm of chromosome 8. The

sequence analysis of *Hd1* and *Ghd8/DTH8* revealed that many difference involving single base-pair substitutions and insertions and/or deletions between CJ06 and TN1 were found (Fig. 3). Thus, we speculated that the sequence difference maybe results in variance of heading date and causing the different performance of panicle-related traits.

Conclusion

The result in this study showed significant implications on grain-yield improvement programs of rice. To some panicle-related traits, the attention should also be considered the effects from genotype \times environment interactions. The QEs effects make the utilization of some favorable allele difficulty. Otherwise, some environment-specific QTLs also could be applied with MAS under the corresponding specific region. For example, the allele of *Ghd8* form CJ06 significantly delays heading date in Hangzhou, which simultaneously increased the grain-yield under natural LD conditions.

Acknowledgements

This research was supported by grants from the National Natural Science Foundation of China (Grant Nos. 91435105 and 31171531), the State Key Basic Research Program (Grant No. 2013CBA01403), and the Ministry of Agriculture of China for Transgenic Research (Grant No. 2013ZX08009003-001).

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(Received 07 November 2016; Accepted 03 April 2017)