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Article

Locating QTLs Controlling the Yield-Related Traits in Perennial Chinese Rice "Shendao3"

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Abstract This study aimed to explore the genetic information about the yield traits in perennial Chinese rice "Shendao3" and provide a series of theoretical bases for the innovative utilization of perennial Chinese rice germplasm. The F₂ population derived from the cross between perennial Chinese rice "Shendao3" and one annual rice "XiqingzaoB" was developed to identify QTLs' underlying yield-related traits. Fifteen yield traits including plant height, panicle plant⁻¹, and thousand-grain weight were measured for the QTL mapping. The software packages Excel 2010, GraphpadPrism 5.0, and QTL IciMapping 4.10 were used to perform the phenotypic data analysis, construction of molecular map, and QTL mapping, respectively. Results indicated 15 yield-related traits displaying normal distribution and belonging to quantitative trait inheritance. A total of 25 QTLs associated with the yield-related traits and 26 epistatic QTLs were detected on the whole genome except for the 6th and 12th chromosomes. This finding explained phenotypic variance with ranging from 4.21% to 27.30% and 1.15% to 19.30%, respectively. Six pleiotropic QTL (chromosomal regions) underlying two or more yield-related traits were detected on the 1st, 4th, 7th, 8th, and 11th chromosomes, respectively. Among 25 QTLs underlying a single yield-related trait, 11 were primarily identified in the perennial Chinese rice "Shendao3". All QTLs underlying 15 yield-related traits followed the genetic model of additive, dominant, and digenic epistatic of additive by additive, additive by dominant, dominant by additive, and dominant by dominant. This work can serve as a good foundation for yield-related gene mining and its utilization in breeding the perennial Chinese rice "Shendao3".

Keywords perennial Chinese rice "Shendao3", QTLs for yield-related trait; pleiotropic QTLs

1. Introduction

The eternal goal of rice geneticists and breeders is to pursue superior yield-related traits in rice-breeding projects. However, rice yield-related traits are quantitative traits and thus controlled by polygenes, whose genetic basis is complex and affected by environmental and genetic factors. With the rapid development of molecular quantitative genetics, complex quantitative traits are dissected into a single Gregor Mendel factor through molecular-map-based cloning. Determining its genomic position and analyzing its molecular biological function for the genetic improvement and polymerization breeding of quantitative traits has great significance.

QTLs underlying yield-related traits in rice have been extensively studied using a traditional genetic-mapping population (F₂, F_{2:3}, DH, RIL, and BC₁F₂). A total of 2060 QTLs controlling yield-related traits have been detected on the whole genome of rice. Some QTLs controlling yield-related traits including heading date, effective panicle number, grain number per panicle, grain length, and 1000-grain weight were successfully cloned and functionally analyzed. For the heading date of rice for *Hd1* [1], *Hd6* [2], and *Hd3a* [3]. In particular, *Gn1a* is the first QTL control grain number per spike, cloned on the short arm of the first chromosome encoding a cytokinin oxidase dehydrogenase and

degraded cytokinin. Meanwhile, *Gn1a* is a negative regulator that can control the number of spikelets by promoting the number of reproductive organs, thereby achieving the goal of yield control [4]. *Ghd7* located on the 7th chromosome is a pleiotropism gene, which affects plant height, flowering period, spikelet number per panicle, and flag leaf area. It plays an important role in rice-yield increase and ecological adaptability [5]. *GS3* controlling grain length and grain weight is located on the 3rd chromosome, explaining 80%–90% variation of grain weight and grain length in the near-isogenic lines of Minghui 63 and Chuan7 [6]. *GW2* is a major gene on the 2nd chromosome that controls grain width and weight and increases grain-filling rate [7]. *IPA1* is a promoter that binds the protein *OSSPL14*, promotes primary branch differentiation, inhibits tillering, and increases the number and weight of grains per panicle [8,9]. *GW8* is located on the 8th chromosome that encodes a promoter-like SPB-box binding protein *Osspl16*. *Osspl16* promotes glume cell division and grain filling, thereby increasing seed width and grain weight [10]. *LRK1* is located in the leucine-rich receptor kinase gene cluster. *LRK1* overexpression can significantly increase tillers, plant height, grain number, and grain weight per panicle [11]. In summary, the successful isolation and cloning of QTL for yield-related traits in rice have benefited from the innovative utilization of excellent genetic resources. Therefore, a series of unceasing excavation and innovation of rice germplasm resources can promote the transformation and upgrading of the rice-breeding industry.

Perennial Chinese rice can survive the natural cold-winter field environment, sprout from rice tillering node in the following spring, tiller, flower, seed, and be harvested in the following autumn. It is a type of special rice germplasm that can withstand cold and is harvested again at maturity. In agricultural production, if new perennial Chinese rice varieties with "high yield, good quality, and wide adaptability" can be cultivated and commercial released to farmer. Alleviating the negative impact of land wastage on rice production caused by urbanization, industrialization, and even sharp reduction of agricultural population has great practical significance [12]. In 1959, Yan first discovered the overwintering regeneration of rice in the open field in Changsha, Hunan province, and in Yuanjiang and Xiaogan, Hubei Province [13]. Nowadays, rice scientists are focusing on the characteristics of the overwintering germination of perennial rice, especially the yield stability of perennial rice and the genetic expression of yield-related traits such as growth period, tillering, and grain number per panicle in our country. The overwintering male sterile line, overwintering heterosis, combining ability analysis, and breeding of conventional overwintering varieties have also been reported [14–16]. Comparative analysis of the previous studies on perennial rice, the study progress on the genetic basis theory perennial rice and breeding application is still sluggish, mostly staying in the field yield traits investigation and breeding research of the preliminary exploration stage. However, little is known about its deep-seated genetic and molecular mechanism. In particular, the understanding of the genetic loci and their modes of action for the yield-related traits of perennial Chinese rice resources is relatively backward. Aggregating different high-yield genes of perennial rice at the molecular level into the same new perennial rice variety remains difficult. In the present study, perennial Chinese rice "Shendao3#" that can withstand cold tolerance to -1 °C of the daily minimum temperature for one day and 0 °C of the daily minimum temperature for three days in January 2021 throughout the cold-winter season of Chongqing Municipality in China was selected as materials [17]. The F₂ population derived from the cross between "Shendao3#" and "XieqingzaoB" and its molecular genetic map was constructed to map QTLs underlying the yield-related traits. Our results can lay a foundation for further revealing the genetic mechanism of yield-related traits in perennial Chinese rice and its potential utilization in breeding.

2. Materials and Methods

2.1. Plant Materials

Perennial Chinese rice "Shendao3#" was selected as female parent material. It can withstand cold to -1 °C of the daily minimum temperature for one day, 0 °C of the daily minimum temperature for four days and 1 °C of the daily minimum temperature for four days in January 2021 throughout the cold-winter season of Chongqing Municipality, China (<https://lishi.tianqi.com/bishan/202101>). It can

also sprout from rice tillering node in March 2021, tiller, flower, seed and be harvested again, thereby exhibiting perennial characteristics (Figure 1 a-g). However, XieqingzaoB is an inddica maintainer line and sensitive to low temperature. It cannot survive through the natural cold-winter field environment of Chongqing Municipality, China.

In mid-July 2022, the hybrid combination of "Shendao3[#]/XieqingzaoB" was constructed at the Rice Biotechnology Testing Station of Chongqing Normal University (CQNU), Shapingba district, Chongqing (29°32' N, 106°32' E), China. In late August of the same year, the seed hybrid F₀ was planted at Nanfan breeding bases of the Sichuan Academy of Agricultural Sciences, Yingzhou town, Lingshui County, Hainan Province, China. In late December of the same year, seeds from F₁ plants and F₂ population were collected to construct the molecular-linkage map and identify the QTLs underlying the yield-related traits in perennial Chinese rice "Shendao3[#]".

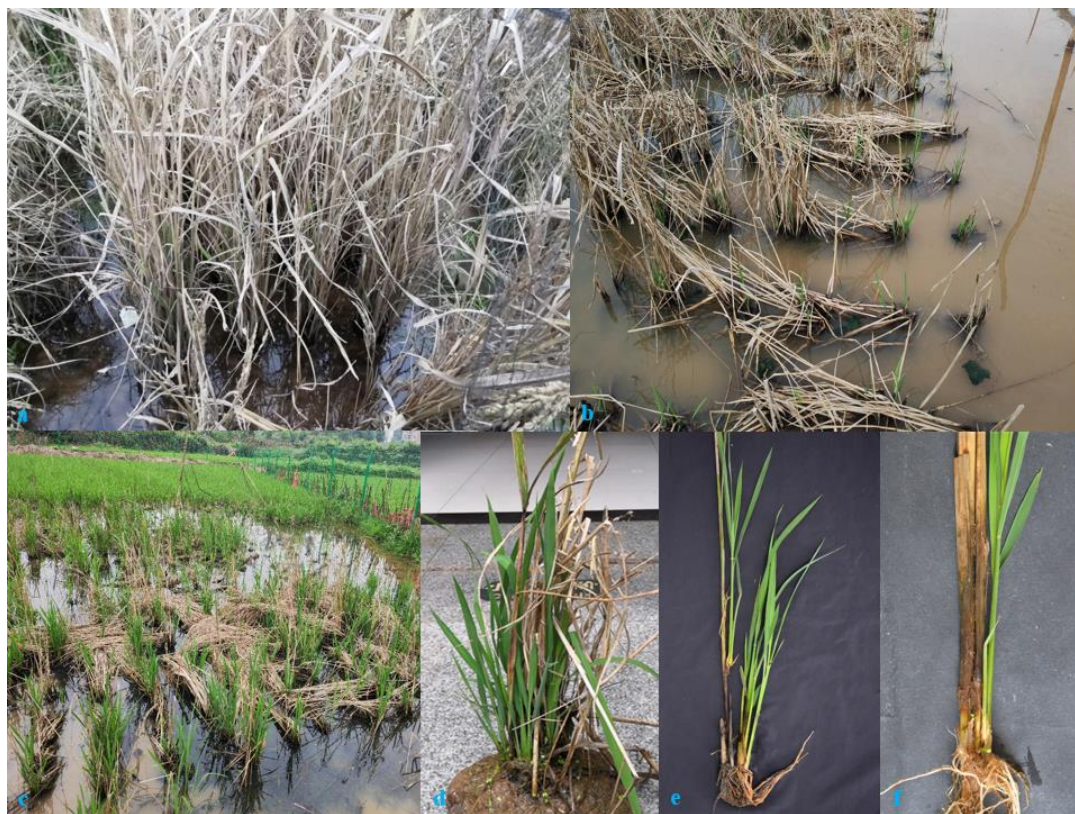


Fig.1 Field performance of perennial Chinese rice "Shendao 3#" at the germination stage

2.2. Phenotyping Experiment

Rice-field experiments were conducted at the Rice Biotechnology Testing Station of CQNU, University Town, Shapingba district, Chongqing (29°32' N, 106°32' E), P. R. China. In March 2022, seeds of F₂ "Shendao3[#]/XieqingzaoB" population and biparents (Shendao3[#] and XieqingzaoB) were sown on 9 March 2022. The 40-day-old seedlings of F₂ "Shendao3[#]/XieqingzaoB" population and biparents (Shendao3[#] and XieqingzaoB) were transplanted into a single row with 10 plants having a 20 cm gap between plants within each row and a 25 cm gap between rows.

A rice special fertilizer 375 kg hm⁻² occupied 70% of the total nutrients, including pure N 150 kg hm⁻², 105 kg hm⁻² P₂O₅, and 120 kg hm⁻² K₂O, was selected as base fertilizer for rice. Rice topdressing fertilizer including pure N 45 kg hm⁻², 31.5 kg hm⁻² P₂O₅, and 36 kg hm⁻² K₂O accounted for only 30% of the total nutrients. Rice topdressing fertilizer and seedling herbicide were applied after two weeks of transplanting. The water-management strategy was adapted in shallow water at the transplanting and tiller stages, and flooding mid-season with drainage-reflooding-moist intermittent irrigation was conducted. Disease, pest, and paddy weed management were performed at different growth stages of rice. At the tiller stage of rice, the leaf of "Shendao3[#]/XieqingzaoB" F₂ individuals and biparents (Shendao3[#] and XieqingzaoB) were sampled to construct a rice molecular linkage map.

2.3. Trait Measurement

Referring to the method of Shen [18], at maturity stage, we sampled five individual plants of biparent “Shendao3# and XieqingzaoB” and 120 F₂ individual plants random for trait measurement. A total of 15 yield-related traits were measured, including plant height (PH, in centimeter), panicle plant⁻¹ (PP), panicle length (PL, in centimeter), fulling grains panicle⁻¹ (FGP), empty grain panicle⁻¹ (EGP), spikelet plant⁻¹ (SP), grain yield major panicle (GYMP, in gram), grain yield plant (GYP, in gram), grain length (GL, in millimeter), grain width (GW, in millimeter), grain thickness (GT, in millimeter), and thousand-grain weight (TGW, in gram). We calculated three derived traits, namely, grain-setting rate (GSR =FGP/SP×100%), grain-setting density (GSD = SP/PL), and length-to-width ratio (LWR=GL/GW). The phenotypic value of single trait in the F₂ plant was used as input data to identify QTLs. The measurement of all traits followed the Standard Evaluation System for Rice (<http://www.Knowledgebank.irri.org/ses/>).

2.4. Data Analysis

All measured trait phenotypic data in the F₂ population and its biparents were inputted into Microsoft Excel 2010. With the same software, analysis of standard derivation (SD) and calculation of mean value and coefficient of variation (CV) were conducted. *GraphPad Prism 5.0* was used to calculate the T-test value and phenotypic correlation coefficient (PCC), as well as draw the histogram.

2.5. Linkage Map and QTL Analysis

We constructed a linkage map containing 112 SSR markers and covering the whole genomic length of 1950.72cM with an average interval of 17.14 cM between markers by using QTL Ici mapping version 4.20 [19]. It was also used to perform QTL analysis for the yield-related traits. Inclusive composite interval mapping (ICIM) for QTL analysis in the F₂ population was performed using IciMapping 4.20 software [19]. The PIN of 0.01 and walking speed of 1 cM were set. An LOD threshold was used as 1000 permutations to advocate QTLs. An LOD score of ≥3.0 was used to declare the significant major QTL. The contribution rate (R²,%) was estimated as the percentage of variance explained by each locus in proportion to the total phenotypic variance. QTL nomenclature followed the principle suggested by McCouch [20]. Digenic epistasis QTLs in the F₂ population were identified by the ICIM-EPI mapping of IciMapping 4.20 version with mapping parameters of 1 cM steps and 0.001 probabilities in a stepwise regression. Genome-wide threshold F-values (F=0.001) were estimated from 1000 permutations to indicate the presence of epistasis [21].

3. Results

3.1. Phenotypic Variation for Yield-Related Traits in the Biparents and F₂ Population

A significant phenotypic difference was observed between Shendao3# and XieqingzaoB for all measured traits, except for EGP, GL, LWR, and TGW (Table 1). It showed a wide T-test value ranging from 0.10 to 13.07. Meanwhile, Shendao3# had significantly higher phenotypic values on PH, FGP, SP, GSR, GSD, GYP, GW, and GT than those of XieqingzaoB. However, XieqingzaoB had significantly higher phenotypic values on PP and PL than those of Shendao3#. All measured traits showed tremendous bidirectional segregation beyond biparents, except for PP, FGP, and GSR, which displayed a wide coefficient of variation ranging from 7.02% for GL to 67.52% for EGP in the F₂ population. It continuously demonstrated normal distribution and belonged to quantitative inheritance (Figure 2), which was suited to QTL mapping.

Table 1. Field performance of yield traits in biparents and "ShenDao3#/XieqingzaoB" F₂ population.

Traits	Parents			F ₂ population		
	Shendao3#	XieqingzaoB	T-test value	Means±SD	Range	CV (%)
PH (cm)	102.80	82.40	13.07**	137.96±16.36	100.00-167.00	9.78
PP	9.80	13.20	3.30*	7.73±2.86	3.00-17.00	37.80

PL (cm)	17.60	22.04	7.89**	28.33±3.15	16.20-34.00	11.78
FGP	157.20	96.60	6.13**	193.29±62.46	27.00-379.00	32.12
EGP	6.20	10.00	1.26	99.02±68.02	12.00-296.00	67.52
SP	163.40	106.60	4.56**	292.32±72.86	143.00-502.00	24.17
GSR (%)	96.25	90.88	2.74*	67.00±0.19	8.36-94.59	27.74
GSD	9.28	4.83	7.85**	10.32±2.25	6.27-17.16	22.07
GYMP (g)	3.99	2.71	6.29**	5.26±1.47	2.32-8.94	27.88
GYP (g)	33.04	24.27	4.43*	34.38±15.84	5.57-88.84	47.17
GL (mm)	10.38	9.80	0.56	10.16±9.49	7.60-10.72	7.02
GW (mm)	3.43	2.58	11.63**	2.87±0.23	2.17-3.71	7.81
LWR	4.01	3.81	0.10	3.56±3.35	2.18-4.54	11.78
GT (mm)	2.31	2.07	6.61**	1.99±0.18	1.17-2.21	8.70
TGW (g)	24.60	26.80	2.42	24.70±0.37	13.50-33.90	15.15

** represent the significant difference at level of 5% and 1% ($\alpha_{0.05}=2.57$; $\alpha_{0.01}=4.03$).

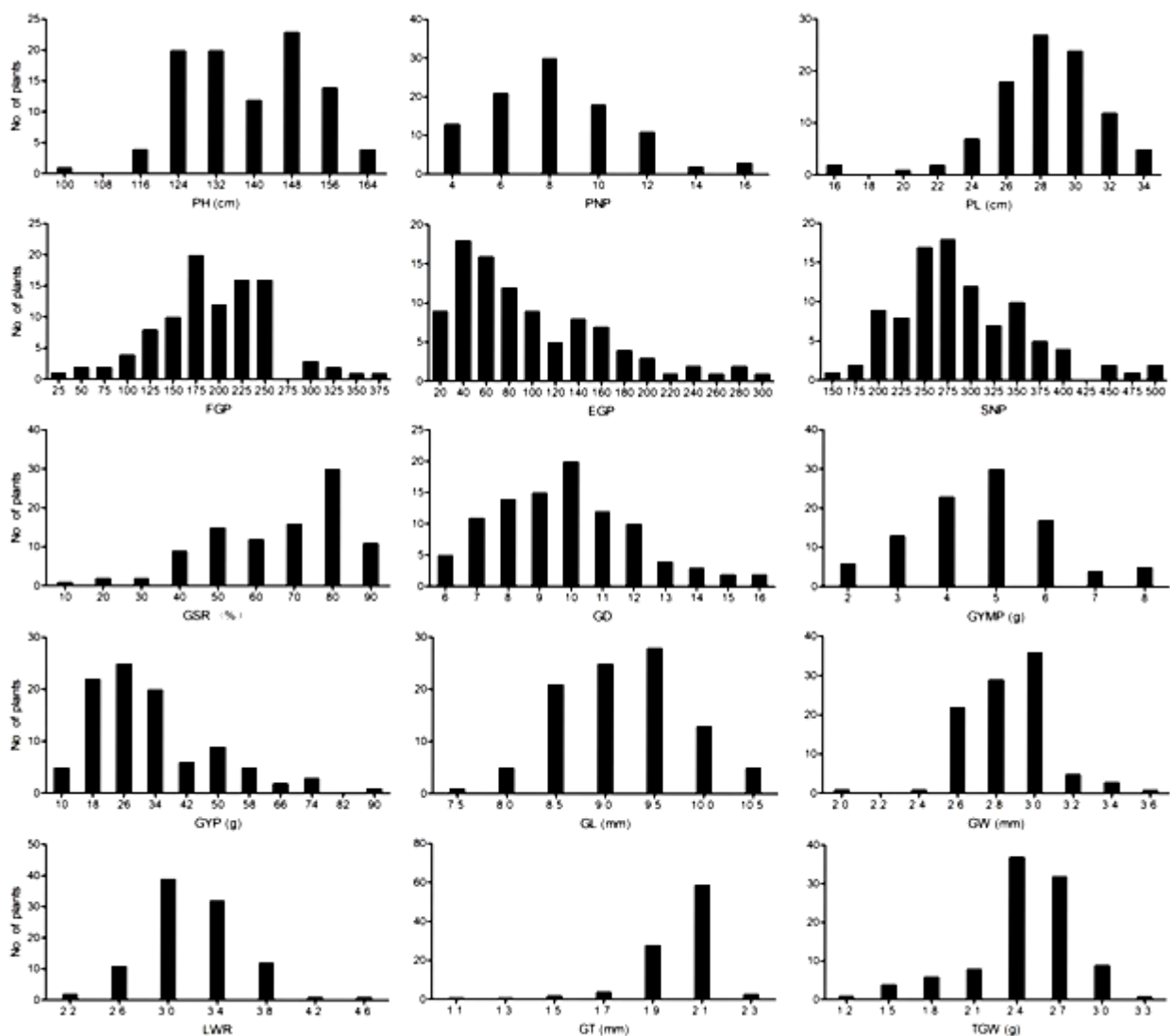


Fig.2 Frequency distribution of the yield traits in the "Shendao3#XieqingzaoB" F₂ population

3.2. Trait Correlations

Altogether 61 significant correlation pairs for 15 yield-related traits were estimated in the F₂ population (Table 2). In the F₂ population, 46 significantly positive correlation pairs and 15 significantly negative correlation pairs exhibiting a wide absolute value ranging from 0 to 1.00 were

calculated for all measured traits. PL showed significantly positive correlation with PH, PP, FGP, EGP, SP, GYMP, GYP, GL, and LWR, respectively. Correlation coefficients (*r*) ranged from 0.19 to 0.44. GYP showed significantly positive correlation with PH, PP, PL, FGP, SP, GSR, GSD, GYMP and TGW, respectively. Correlation coefficients (*r*) ranged from 0.24 to 0.80. PL and GYP were regarded as some of the most important determinants in the yield-related traits of perennial Chinese rice. GW showed a significantly positive correlation only with PH, EGP, and GSD, with correlation coefficients (*r*) ranging from 0.16 to 0.24. GW determined the field performance of the three yield-related traits. TGW showed significantly negative correlation with EGP, SP, GSD, and GW, with correlation coefficients (*r*) ranging from -0.15 to -0.38. It was negatively correlated with the other four measured traits. GW showed a significantly negative correlation with EGP, GSR, GYMP, and GW, with correlation coefficients (*r*) ranging from -0.15 to -0.27. It was negatively correlated with the other four measured traits. PH showed a significantly negative correlation only with GSR, with a correlation coefficient of -0.21. In summary, the yield-related trait in perennial Chinese rice "Shendao3#" was a very complex character. It showed complex correlations among all measured traits directly or indirectly determined the formation of yield traits.

Table 2. Correlation coefficients (*r*) among fifteen yield-related traits in the "Shendao3#/XieqingzaoB" F₂ population.

Traits	PH	PP	PL	FGP	EGP	SP	GSR	GSD	GYM P	GYP	GL	GW	LWR	GT	TG W
PH	1.00														
PP	0.33**	1.00													
PL	0.37**	0.25**	1.00												
FGP	0.04	0.12	0.20**	1.00											
EGP	0.28**	0.10	0.29**	-	1.00										
				0.37**											
SP	0.30**	0.20**	0.44**	0.52**	0.60**	1.00									
GSR	-	-0.02	-0.13	0.68**	-	-	1.00								
	0.21**			0.90**	0.24**										
GSD	0.14	0.11	-0.03	0.47**	0.52**	0.88**	-0.20*	1.00							
GYM P	0.15*	0.20**	0.30**	0.78**	-0.23*	0.45**	0.47**	0.34**	1.00						
GYP	0.33**	0.80**	0.35**	0.51**	-0.09	0.36**	0.26**	0.21**	0.60**	1.00					
GL	0.08	0.15*	0.19*	-0.06	0.23**	0.16*	-0.15*	0.07	0.02	0.09	1.00				
GW	0.16*	0.09	-0.14	-	0.24**	0.09	-	0.18*	-0.17*	-0.06	-0.03	1.00			
				0.20**			0.27**								
LWR	0.07	0.14	0.20*	-0.04	0.20**	0.15*	-0.13	0.05	0.03	0.09	1.00**	-0.11	1.00		
GT	-0.01	0.02	0.07	-0.11	-0.10	-0.19*	-0.00	-	0.14	0.07	0.01	0.12	0.00	1.00	
								0.25**							
TGW	-0.02	0.17*	0.13	-0.05	-	-	0.15*	-	0.25**	0.24**	-0.05	-0.15*	-0.03	0.47**	1.00
					0.27**	0.29**		0.38**							

** represent the significant difference at level of 5% and 1% ($\alpha_{0.05}=0.146$; $\alpha_{0.01}=0.191$).

3.3. QTLs for Yield-Related Traits

A total of 25 QTLs affecting 15 yield traits were detected on the 1st , 2nd, 3rd, 4th, 5th, 7th, 8th, 9th, 10th, and 11th chromosomes, respectively. LOD values ranged from 3.00 to 6.06, which explained a wide phenotypic variation ranging from 4.21% for *qGW2a* to 27.30% for *qPH1* (Figure 3; Table 3). For PH, only one QTL *qPH1* was detected on the 1st chromosome and explained a phenotypic variation of 27.30%. Moreover, the Shendao3# allele increased PH at *qPH1* genetic loci. For the number of panicle plant⁻¹, four QTLs (*qPP1*, *qPP3*, *qPP7* and *qPP11*) were detected on the 1st, 3rd, 7th, and 11th chromosomes, respectively, which explained the phenotypic variation ranging from 7.33% to 10.82%. Among them, Shendao3# alleles increased the number of panicle plant⁻¹ at *qPP1*, *qPP3*, and

qPP11 but XieqingzaoB allele increased PP at *qPP7*. For panicle length, three QTLs (*qPL1*, *qPL2*, and *qPL11*) were detected on the 1st, 2nd, and 11th chromosomes, respectively. It explained the phenotypic variation ranging from 6.07% to 8.23%, XieqingzaoB allele increased PL at *qPL1* but Shendao3# alleles increased PL at *qPL2*, and *qPL11*. For the grain yield plant⁻¹, four QTLs (*qGYP7*, *qGYP9*, *qGYP10a*, and *qGYP10b*) were detected on the 7th, 9th, and 10th chromosomes, respectively. It explained the phenotypic variation ranging from 5.16% to 9.07%, XieqingzaoB allele increased GYP at *qGYP7*, but Shendao3# alleles increased GYP at *qGYP9*, *qGYP10a*, and *qGYP10b*, respectively. For spikelet plant⁻¹, grain thickness, and empty grain panicle⁻¹, three QTLs (*qSP1*, *qGT5*, and *qEGP8*) were detected on the 1st, 5th, and 8th chromosomes, respectively. It explained 25.56%, 9.30%, and 14.32% of the phenotypic variation, respectively, XieqingzaoB allele increased EGP at *qEGP8* but Shendao3# alleles increased SP at *qSP1* and GT at *qGT5*. For grain-setting rate, two QTLs (*qGSR4* and *qGSR8*) were detected on the 4th and 8th chromosomes, which explained 4.61% and 5.40% of the phenotypic variation, respectively, Shendao3# allele increased GSR at *qGSR4* but XieqingzaoB allele increased GSR at *qGSR8*. For grain-setting density, two QTLs (*qGSD1* and *qGSD2*) were detected on the 1st and 2nd chromosome, which explained 14.11% and 20.65% of the phenotypic variation, respectively, Shendao3# alleles increased GSD at *qGSD1* and *qGSD2*. For thousand-grain weight, two QTLs (*qTGW1* and *qTGW4*) were detected on the 1st and 4th chromosomes, which explained 4.76% and 5.08% of the phenotypic variation, respectively, Shendao3# alleles increased TGW at *qTGW1* and *qTGW4*. For grain width, four QTLs (*qGW2a*, *qGW2b*, *qGW11a*, and *qGW11b*) were detected on the 2nd and 11th chromosomes, which explained the phenotypic variation ranging from 4.76% to 5.08%. Shendao3# alleles increased GW at *qGW2a*, *qGW2b*, *qGW11a*, and *qGW11b*, respectively.

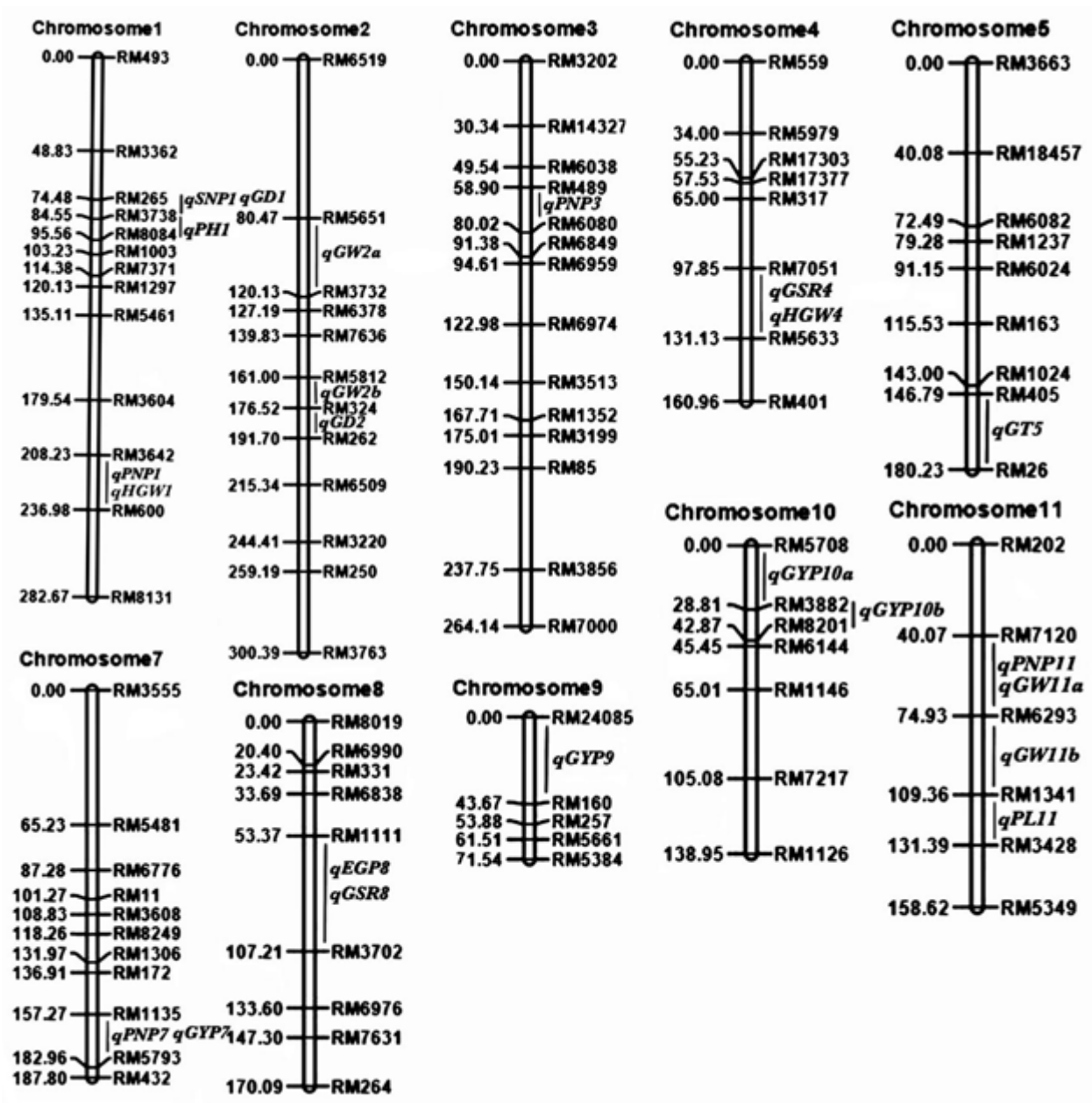


Fig.3 QTL for the yield-related traits detected in the "Shendao3#'/XieqingzaoB'F2 population

Table 3. QTLs underlying the yield-related traits in perennial Chinese rice "Shendao3#".

Trait	QTL	Chromosome	Genomic Position	Marker interval	LOD	Additive	Dominant	R ² (%)	Derived
PH	<i>qPH1</i>	1	34902085-37261443	RM3738-RM8084	6.06	9.93	7.21	27.30	Shendao3#
PP	<i>qPP1</i>	1	9463544-24866202	RM3642-RM600	3.06	-3.02	-4.80	8.06	XieqingzaoB
	<i>qPP3</i>	3	4333680-13933574	RM489-RM6080	3.02	3.84	-5.56	7.33	Shendao3#
	<i>qPP7</i>	7	16932001-17489638	RM1135-RM5793	5.23	-3.58	-6.52	10.82	XieqingzaoB
	<i>qPP11</i>	11	11763775-2888052	RM7120-RM6293	4.28	-3.04	-5.09	8.53	XieqingzaoB
PL	<i>qPL1</i>	1	27925715-32774365	RM3642-RM600	3.00	6.05	4.19	6.07	Shendao3#
	<i>qPL2</i>	2	13481661-19677083	RM250-RM3763	4.67	-6.67	3.94	8.05	XieqingzaoB
	<i>qPL11</i>	11	1124242-4773752	RM1341-RM3428	3.96	-3.11	5.53	8.23	XieqingzaoB
EGP	<i>qEGP8</i>	8	35196573-37261443	RM1111-RM3702	3.10	49.48	-132.62	14.32	Shendao3#
SP	<i>qSP1</i>	1	13059580-24116775	RM265-RM3738	5.52	48.12	33.14	26.56	Shendao3#
GSR	<i>qGSR4</i>	4	11389704-20800963	RM7051-RM5633	3.88	0.02	-0.32	4.61	Shendao3#
	<i>qGSR8</i>	8	16932001-17489638	RM1111-RM3702	5.90	-0.17	0.46	5.40	XieqingzaoB
GSD	<i>qGSD1</i>	1	10811135-19788247	RM265-RM3738	4.53	0.47	1.82	14.11	Shendao3#
	<i>qGSD2</i>	2	2722348-14527760	RM324-RM262	5.25	1.49	-3.80	20.65	Shendao3#
GYP	<i>qGYP7</i>	7	2722348-13761888	RM1135-RM5793	3.32	-14.32	-23.54	7.25	XieqingzaoB
	<i>qGYP9</i>	9	4407860-23568212	RM24085-RM160	3.41	21.40	-14.19	5.79	Shendao3#
	<i>qGYP10a</i>	10	11389704-15894177	RM5708-RM3882	4.24	17.86	-13.64	9.07	Shendao3#
	<i>qGYP10b</i>	10	19677083-28788052	RM3882-RM8201	3.74	19.60	-23.56	5.16	Shendao3#
GW	<i>qGW2a</i>	2	3073406-27342022	RM5651-RM3732	3.04	0.34	-0.37	4.21	Shendao3#
	<i>qGW2b</i>	2	11389704-15894177	RM5812-RM324	4.07	0.28	-0.26	5.38	Shendao3#
	<i>qGW11a</i>	11	11763775-28788053	RM7120-RM6293	3.82	0.27	-0.35	5.34	Shendao3#
	<i>qGW11b</i>	11	19677083-28788052	RM6293-RM1341	3.46	0.28	-0.35	5.03	Shendao3#
GT	<i>qGT5</i>	5	3073406-27342022	RM405-RM26	3.98	-0.16	0.28	9.30	XieqingzaoB
TGW	<i>qTGW1</i>	1	9463544-24866202	RM3642-RM600	4.15	0.44	0.32	4.76	Shendao3#
	<i>qTGW4</i>	4	13059580-24116775	RM7051-RM5633	4.43	0.38	0.57	5.08	Shendao3#

3.4. Pleiotropic QTLs for Yield Traits

The chromosomal locations of all QTLs identified in the F₂ population revealed six genomic regions on the 1st, 4th, 7th, 8th, and 11th chromosomes where clustered QTLs affected two yield traits (Figure 3; Table 4). For the 1st chromosome, two QTL (*qSP1* and *qGSD1*) genomic regions underlying spikelet panicle⁻¹ and grain-setting density were flanked repeatedly by RM265 and RM3738 on the 1st chromosome. The Shendao3[#] alleles increased SP at *qSP1* and GSD at *qGSD1*. Two QTL (*qPP1* and *qPL1*) genomic regions affecting panicle plant⁻¹ and panicle length were flanked repeatedly by RM3642 and RM600 on the 1st chromosome. The Shendao3[#] allele increased PP at *qPP1*, and XieqingzaoB allele increased PL at *qPL1*. For the 4th chromosome, two QTL (*qGSR4* and *qTGW4*) genomic regions were flanked repeatedly by RM7051 and RM5633 controlling grain-setting rate and thousand-grain weight. The Shendao3[#] allele increased GSR at *qGSR4* and TGW at *qTGW4*. For the 7th chromosome, two QTL (*qPP7* and *qGYP7*) genomic regions were flanked repeatedly by RM1135 and RM5793 and repeatedly affected panicle plant⁻¹ and grain yield plant⁻¹, respectively. The XieqingzaoB allele increased PP at *qPP7* and GYP at *qGYP7*. For the 8th chromosome, two QTL (*qEGP8* and *qGSR8*) genomic regions were flanked repeatedly by RM1111 and RM3702, which were affected simultaneously empty grain panicle⁻¹ and grain-setting rate. The Shendao3[#] allele increased EGP at *qEGP8*, and XieqingzaoB allele increased GSR at *qGSR8*. For the 11th chromosome, two QTL (*qPP11* and *qGW11a*) genomic regions were flanked repeatedly by RM7120 and RM6293 and affected simultaneously the number panicle plant⁻¹ and grain width. The XieqingzaoB allele increased PP at *qPP11*, and the Shendao3[#] allele increased GW at *qGW11a*. For the pleiotropic QTLs that controlled two or more yield-related traits, they were located repeatedly at the same marker interval. Thus, pleiotropic QTLs should be given more attention in future rice genetic and breeding projects. It's twice as efficient that multi-yield traits will be synchronous improved through one yield trait was genetically improved in the future rice genetic and breeding project.

Table 4. Pleiotropic QTLs underlying the yield-related traits in perennial Chinese rice "Shendao3[#]".

Traits	QTL	Chromosome	Marker interval	LOD value	Additive	Dominant	R ² (%)
SP	<i>qSP1</i>	1	RM265-RM3738	5.52	48.12	33.14	26.56
GSD	<i>qGSD1</i>	1	RM265-RM3738	4.53	0.47	1.82	14.11
PP	<i>qPP1</i>	1	RM3642-RM600	3.06	-3.02	-4.80	8.06
PL	<i>qPL1</i>	1	RM3642-RM600	3.00	6.05	4.19	6.07
GSR	<i>qGSR4</i>	4	RM7051-RM5633	3.88	0.02	-0.32	4.61
TGW	<i>qTGW4</i>	4	RM7051-RM5633	4.43	0.38	0.57	5.08
PP	<i>qPP7</i>	7	RM1135-RM5793	5.23	-3.58	-6.52	10.82
GYP	<i>qGYP7</i>	7	RM1135-RM5793	3.32	-14.32	-23.54	7.25
EGP	<i>qEGP8</i>	8	RM1111-RM3702	3.10	49.48	-132.62	14.32
GSR	<i>qGSR8</i>	8	RM1111-RM3702	5.90	-0.17	0.46	5.40
PP	<i>qPP11</i>	11	RM7120-RM6293	4.28	-3.04	-5.09	8.53
GW	<i>qGW11a</i>	11	RM7120-RM6293	3.82	0.27	-0.35	5.34

3.5. Digenic Epistatic QTLs for Yield-Related Traits

A total of 26 epistatic QTL pairs for 15 yield traits were detected on the whole genome of rice, except for the 6th and 11th chromosomes in the F₂ population. It accounted for an extensive phenotypic variation ranging from 1.15% to 19.30%, with wide-ranging LODs from 5.01 to 8.74 (Table 5). Among them, eight epistatic QTL pairs were found for GSR, six for SP, five for GYP, for PL, and one each for PH, EGP, GW, and GT. For all epistatic QTL pairs exhibiting four interaction patterns including additive-additive, additive-dominant, dominant-additive, and dominant-dominant were identified in the F₂ population. A total of 11 out of 24 genomic regions of the QTLs interacted repeatedly with two or more marker intervals. For example, the genomic interval RM3642-RM600 underlying PP and PL on the 1st chromosome interacted with the genomic interval RM6519-RM5651

and the genomic interval RM8019-RM6990 on the 8th chromosome. The genomic interval RM250-RM3763 underlying PL and GW on the 2nd chromosome interacted with the interval RM1352-RM3199 on the 3rd chromosome and the genomic interval RM559-RM5979 on the 4th chromosome. The genomic interval RM7051-RM5633 underlying GSR on the 4th chromosome interacted with the genomic interval RM7637-RM5812 on the 2nd chromosome and the genomic interval RM317-RM7051 underlying both GSR and GW on the 4th chromosome, the genomic interval RM24085-RM160 on the 9th chromosome. The genomic interval RM1135-RM5793 underlying PP and GYP on the 7th chromosome interacted with the interval RM3555-RM5481 on the 7th chromosome, the genomic interval RM1111-RM3702 on the 8th chromosome, and the genomic interval RM202-RM7120 on the 11th chromosome. The genomic interval RM1111-RM3702 underlying EGP and GSR on the 8th chromosome interacted with the genomic interval RM5793-RM432 on the 7th chromosome, the genomic interval RM1135-RM5793 underlying PP and GYP on the 7th chromosome, the genomic interval RM257-RM5661 and RM24085-RM160 on the 9th chromosome, and the genomic interval RM5708-RM3882 on the 10th chromosome. the genomic interval RM202-RM7120 and RM6293-RM1341 on the 11th chromosome. The genomic interval RM24085-RM160 underlying GYP on the 9th chromosome interacted with the genomic interval RM7051-RM5633 underlying GSR on the 4th chromosome and the genomic interval RM1111-RM3702 underlying GSR on the 8th chromosome. The genomic interval RM5708-RM3882 underlying GYP on the 10th chromosome interacted with the interval RM85-RM3856 underlying PP on the 3rd chromosome, the genomic interval RM317-RM7051 underlying GSR on the 4th chromosome, and the genomic interval RM1111-RM3702 underlying GSR on the 8th chromosome. the genomic interval RM202-RM7120 on the 8th chromosome. The genomic interval RM202-RM7120 on the 11th chromosome interacted with the interval RM3738-RM8084 underlying PH on the 1st chromosome, the genomic interval RM1135-RM5793 underlying PP and GYP on the 7th chromosome. And the genomic interval RM5708-RM3882 underlying GYP on the 10th chromosome. the genomic interval RM405-RM26 underlying GT on the 5th chromosome. the genomic interval RM7120-RM6293 on the 11th chromosome interacted with the genomic interval RM559-RM5979 underlying GSR on the 4th chromosome and the genomic interval RM24085-RM160 underlying GYP on the 9th chromosome. The remaining 11 epistatic QTL pairs involved only one interaction pair.

Table 5. Epistatic QTL underlying the yield-related traits in perennial Chinese rice "Shendao3#".

Traits	Chr ^a	Marker interval	Chr ^a	Marker interval	LOD value	Add ^b	Add	Dom ^c	Dom	Add×Add	Add×Dom	Dom×Add	Dom×Dom	R ² (%) ^d
PH	1	RM3738-RM8084	11	RM202-RM7120	5.01	4.82	-8.37	0.49	-28.13	8.08	-21.17	-5.63	30.51	19.3
PNP	1	RM3642-RM600	2	RM6519-RM5651	7.08	-1.97	1.90	-3.21	1.56	-3.38	3.30	0.42	-0.59	2.21
	3	RM3513-RM1352	5	RM405-RM26	5.03	0.91	-1.03	3.50	1.48	-0.7	-2.76	5.63	-7.37	1.49
	3	RM85-RM3856	10	RM5708-RM3882	6.40	-0.34	1.58	4.55	0.98	-1.78	2.01	2.20	-8.64	1.98
	7	RM3555-RM5481	7	RM1135-RM5793	6.13	-3.07	-1.71	-2.01	-6.46	0.69	2.89	1.55	4.18	2.19
	7	RM5793-RM432	8	RM1111-RM3702	5.08	0.41	0.36	0.67	1.55	0.39	-5.50	4.95	-6.19	1.61
	7	RM1135-RM5793	11	RM202-RM7120	6.84	0.55	-2.71	-1.06	3.88	0.89	-4.19	3.52	-7.08	2.2
PL	1	RM3642-RM600	8	RM8019-RM6990	5.48	-4.58	-3.57	-2.01	-2.00	-2.56	6.12	1.03	7.14	6.28
	2	RM250-RM3763	3	RM1352-RM3199	5.10	-5.30	0.77	4.32	6.97	1.58	5.93	-1.27	-9.50	4.94
	2	RM7637-RM5812	4	RM7051-RM5633	5.49	0.91	0.34	3.40	3.33	-2.59	-3.69	-0.77	-5.13	5.13
EGP	8	RM1111-RM3702	9	RM257-RM5661	5.11	7.29	-9.84	-88.52	-27.85	-52.25	-51.59	45.48	-29.79	1.74
GSR	4	RM317-RM7051	4	RM7051-RM5633	5.94	-0.01	0.07	0.07	-0.10	0.04	-0.36	0.09	-0.14	1.53
	4	RM5633-RM401	8	RM1111-RM3702	7.42	0.07	0.00	-0.33	0.21	-0.006	-0.04	-0.15	0.34	1.45
	4	RM7051-RM5633	9	RM24085-RM160	5.69	0.00	0.02	-0.41	-0.13	0.02	0.13	-0.10	0.56	1.24
	4	RM317-RM7051	10	RM5708-RM3882	7.22	0.12	0.15	0.09	0.12	-0.22	-0.03	0.02	-0.38	1.49
	4	RM559-RM5979	11	RM7120-RM6293	6.72	-0.03	0.02	0.00	-0.24	0.24	-0.22	-0.12	0.47	1.54
	8	RM1111-RM3702	9	RM24085-RM160	5.32	-0.04	0.16	-0.12	-0.09	0.04	0.16	-0.43	0.34	1.30
GYP	8	RM1111-RM3702	10	RM5708-RM3882	7.95	-0.06	0.20	0.28	-0.01	0.18	0.18	-0.17	-0.01	1.50
	8	RM1111-RM3702	11	RM6293-RM1341	6.80	-0.05	0.16	0.26	-0.06	0.19	0.12	-0.13	0.07	1.52
	7	RM3555-RM5481	7	RM1135-RM5793	7.01	14.80	-1.74	17.34	-5.76	0.78	-25.40	21.76	-22.25	2.28
	7	RM1135-RM5793	8	RM1111-RM3702	5.68	1.06	-18.79	-18.91	-8.21	-8.94	8.78	8.10	6.61	2.52
	7	RM1135-RM5793	11	RM202-RM7120	5.87	-2.54	-3.60	-3.50	12.75	-12.47	24.77	7.82	-26.83	2.28
	9	RM24085-RM160	11	RM7120-RM6293	5.31	9.01	-13.95	11.16	-14.50	-12.05	-4.57	10.83	-2.13	2.36
	10	RM5708-RM3882	11	RM202-RM7120	5.40	7.41	-13.27	1.72	15.35	-2.44	18.95	20.25	-31.15	2.94
	2	RM250-RM3763	4	RM559-RM5979	6.25	0.12	-0.01	0.46	0.28	0.18	-0.003	0.34	-0.79	2.49
GT	5	RM405-RM26	11	RM202-RM7120	8.74	-0.04	0.11	0.17	-0.25	0.15	0.18	-0.10	0.26	2.65

^aChromosome. ^bAdditive effect. ^cDominant effect. ^dR² the total phenotypic variation explained by single epistatic QTL pairs.

4. Discussion

The cardinal goal of any study on the genetics mechanism of quantitatively inherited traits is to identify the major QTLs hidden in different rice germplasm resources and finally mine the interest gene for rice molecular breeding [22]. In this study, perennial Chinese rice "Shendao3#" was selected as plant material to identify QTLs underlying yield-related traits and thus lay a good foundation for the molecular-design breeding of yield-related genes in perennial Chinese rice.

A total of 25 QTLs underlying the 15 yield-related traits were detected on the whole genome except for the 6th and 11th chromosomes. Among them, six major QTLs can explain more than 10% of phenotypic variation. Six pleiotropic QTL genomic regions controlling two or more yield-related traits were detected on the 1st, 4th, 7th, 8th, and 11th chromosomes, respectively. All QTLs followed the genetic model of additive, dominant and epistatic effect of additive by additive, additive by dominant, dominant by additive, and dominant by dominant in the "Shendao3#/XieqingzaoB" combination. However, the remaining 13 QTL genomic regions such as *qPP3*, *qPL2*, *qPL11*, *qGYP9*, *qGYP10a*, and *qGYP10b* were detected for only a single yield trait. Among the 25 QTLs, 14 were located the same genomic region and even cloned. Accordingly, we searched their alignment QTLs identified in the same chromosomal region through the publicly available QTL database (www.gramene.org) published by previous researchers. For *qPH1* underlying PH, it has been previously reported in the Yangdao6/Lvhan1# RIL population [23]. For *qPP1* related to PP, it has been previously detected on the 1st chromosome in the Zhongjiazao17/D50 F₂ population [24]. For *qPP3* related to PP, it has been detected on the 3rd chromosome in the Zhaiyeqin8/Jingxi17 DH population [25]. For *qPP11* related to PP, it has been detected on the 11th chromosome in the *Oryza sativa*×*Oryza rufipogon* BC₂F₂ population [26]. For *qPL1* related to PL, it has been detected on the 1st chromosome in the Zhongjiazao17/D50 DH population [27]. For *qPL2* related to PL, it has been detected on the 2nd chromosome in the *O. rufipogon*/Jefferson BC₂F₂ population [28]. For *qPL11* related to PL, it has been detected on the 11th chromosome in the Lemont/Teqing RIL population [29]. For *qGSR4* underlying GSR, it has been previously reported in the two populations of Zhaiyeqin8/Jingxi17 DH [25,30] and Zhongjiazao17 /D50 F₂ [24]. For *qGSR8* related to GSR, it has been detected on the 8th chromosome in the Nipponbare/Zhongjiazao17 RIL population [31]. For *qGW2a* and *qGW2b* related to the GW, it has been detected on the 2nd chromosome in the Nipponbare/Zhongjiazao17 RIL population [31]. For *qGW11a* related to GW, it has been detected on the 11th chromosome in the *O. sativa*/*O. glaberrima* DH population [32]. For *qGW11b* related to GW, it has been detected on the 11th chromosome in the IR64/Azucena DH population [33]. For *qGT5* related to GW, it has been detected on the 11th chromosome in the four populations of Tesanai2/CB F₂ and F_{2:3} [34], *O. rufipogon*/V20A BCF₂ [35], and *Oryza rufipogon* Griff/Guichao2 ILs [36].

However, 11 QTLs associated with the yield-related were primarily mapped in the "Shendao3#/XieqingzaoB" combination. Among them, for *qPP7* related to the number of panicle per plant and *qGYP7* underlying the grain yield plant⁻¹, XieqingzaoB alleles increased PP at *qPP7* and increased GYP at *qGYP7*. For the remaining nine QTLs related with the yield-related traits, the Shendao3# alleles increased EGP at *qEGP8*, SP at *qSP1*, GSD at *qGSD1* and *qGSD2*, GYP at *qGYP9*, *qGYP10a*, and *qGYP10b*, and TGW at *qTGW1* and *qTGW4*, respectively. Nine newly discovered QTLs (*qEGP8*, *qSP1*, *qGSD1*, *qGSD2*, *qGYP9*, *qGYP10a*, *qGYP10b*, *qTGW1*, and *qTGW4*) underlying the yield-related traits might exhibit a unique genetic model of the perennial Chinese rice "Shendao3#". They may also provide a novel genetic resource for perennial Chinese rice varieties' breeding. Therefore, special efforts should be devoted to fine mapping these newly discovered QTLs and studying their positional cloning for perennial Chinese rice-molecular breeding.

Six QTL chromosomal regions associated with two or more yield-related traits were detected repeatedly in the "Shendao3#/XieqingzaoB" F₂ population. For example, the *qPP1* and *qPL1* were flanked repeatedly at the marker interval of RM1135-RM57930 on the 1st chromosome, and *qPP7* and *qGYP7* were detected repeatedly at the marker interval of RM1135-RM57930 on the 7th chromosome. Similarly, the clustered distribution of QTL has also been reported in previous studies [37–39]. Consequently, paying more attention to pleiotropic QTLs (chromosome regions) in future rice genetic

and breeding projects is necessary. It's twice as efficient that multi-yield traits will be synchronous improved through one yield trait was genetically improved in the future rice genetic and breeding project.

5. Conclusion

Perennial Chinese rice "Shendao3#" was selected as parental materia. The F₂ population of "Shendao3#/XieqingzaoB" was constructed to identify QTLs associated with 15 yield-related traits. A total of 25 QTLs and 26 epistatic QTLs were detected on the whole genome, except for the 6th and 12th chromosomes. It explained phenotypic variation ranging from 4.21% to 27.30% and 1.15% to 19.30%. Six pleiotropic QTLs (chromosomal regions) associated with two or more yield-related traits were detected repeatedly in the "Shendao3#/XieqingzaoB" F₂ population. Among 24 QTLs, 11 were associated with yield-related traits and were primarily mapped in the "Shendao3#/XieqingzaoB" combination. All QTLs associated with 15 yield-related traits followed the genetic model of additive, dominant, and digenic epistatic of additive by additive, additive by dominant, dominant by additive, and dominant by dominant. This study laid a good foundation for yield-related gene mining and its utilization in breeding perennial Chinese rice "Shendao3#".

Author Contributions: YSL carried out the supervision, data curation, writing-original draft and funding acquisition; JYG provided perennial rice seeds; YXY carried out the agronomic trait investigation and QTL analysis; TSP carried out the agronomic trait investigation and the DNA extraction; JYL carried out the agronomic trait investigation and PCR amplification; LT carried out the agronomic trait investigation; ML and WBW carried out data curation; XJQ carried out the field experiments. All authors have reviewed and approved the final manuscript.

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Abbreviations

QTL: quantitative trait locus; SSR: single sequence repeat; PH: plant height; PP: panicle plant⁻¹; PL: panicle length; FGP: fulling grains panicle⁻¹; EGP: empty grain panicle⁻¹; SP: spikelet plant⁻¹; GYMP: grain yield major panicle; GYP: grain yield plant; GL: grain length; GW: grain width; GT: grain thickness; TGW: thousand-grain weight; GSR: grain-setting rate; GSD: grain-setting density; LWR: length-to-width ratio; SD: standard derivation; CV: coefficient of variation; PCC: phenotypic correlation coefficient; ICIM: Inclusive composite interval mapping.

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