

Genome-wide Association Study on Some Agronomic Traits of *Temperate Japonica* Rice

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ABSTRACT

Temperate japonica rice is widely cultivated and plays a very important role in food security. Understanding the genetics of important agronomic traits is essential for developing high yield varieties. In this study, we selected 191 temperate japonica accessions from the 3000 sequenced accessions of three thousand rice genome project (3K-RGP), and planted in the field in Yunnan province of China. The plant height (PH), panicle length (PL), number of spikelets per panicle (SPP), grain density (GD), awn length (AL), grain length (GL), grain length and width ratio (GLWR, L/W), grain thickness (GT), grain width (GW) and thousand-grain weight (TGW) were measured. The results showed wide range of variations for the measured traits. Twenty-five quantitative traits loci (QTLs) were identified for 10 measured traits by genome-wide association analysis (GWAS). Some of the QTLs are located in the known gene regions, and some new QTLs were identified. This study provided useful information for future gene validation and marker assisted selection for some important agronomic traits of *temperate japonica* rice.

Key words – plant height, grain size, grain weight, yield component, quantitative trait locus

1. Introduction

Temperate japonica rice occupies 20% of the rice cultivation area worldwide, mainly distributed in high altitude and high latitude areas. With its high yield and high grain quality, *temperate japonica* rice plays a very important role in world food security and high-end consumption.

Germplasm with good agronomic traits is essential for plant breeding. Rice yield was greatly increased by using semi-dwarf gene (*sd1*) to reduce the plant height, however, some other genes control plant height exist in rice and potentially could be used in rice breeding (Bai et al., 2011). Rice yield components include number of panicles per given area, the number of spikelets per panicle, the percent of filled grains per panicle, and the weight of each grain (Yoshida 1981). Among them, panicle size and grain size (weight) are very important for increasing rice yield.

Recent development of high density markers such as SNPs enables identification of trait-marker association through association mapping, and GWAS for many important agronomic traits have been reported (Zhao et al. 2011; Huang et al. 2010; Huang et al. 2012). With the collaboration among the Chinese Academy of Agricultural Sciences (CAAS), the Beijing Genomics Institute (BGI) and the International Rice Research Institute (IRRI), 3000 rice accessions of known diversity were systematically sequenced (Li et al. 2014). After alignment with the reference genome (Nipponbare), around 18.9

million SNPs were identified. This database provided valuable information for understanding the genetic mechanism of useful traits in these diversity accessions. Thus, we evaluated some important agronomic traits of the temperate japonica accessions from 3K RGP which had been fully sequenced. The objectives of this study were to identify accessions with useful agronomic traits and SNPs associated with these traits, and to identify potential candidate genes for the promising QTLs.

2. Materials and methods

2.1 Plant materials

The 3K Rice Genomes Project sequenced 3,000 rice genomes with an average sequencing depth of 14x. The dataset includes publicly available genome sequences derived from 3,000 accessions of rice with global representation (from 89 countries) of genetic and functional diversity (Li et al. 2014). Phylogenetic analyses based on SNP data confirmed differentiation of the *O. sativa* gene pool into 5 varietal groups – *indica*, *aus/boro*, *basmati/sadri*, *tropical japonica* and *temperate japonica* (The3KRGP 2014). There were 203 accessions in the *temperate japonica* group. We requested all the sequenced *temperate japonica* accessions, however, seed availability was limited to 191 accessions, and these were used in this study.

2.2 Investigation of agronomic traits

The seeds of selected accessions were treated at 50 °C for 5 days in an oven to break seed dormancy, and then sown in wet seeding-bed in the field in Yuanjiang city (102°E, 23°59'N, 401m ASL) of Yunnan province, China. Seeding was done on January 18 and transplanting was done on March 2. Crop management was the same as the local farms. At maturity, plant height (PH) and panicle length (PL) of 5 plants were measured, and five panicles were harvested for the following measurements: awn length (AL), number of empty and filled grains of each panicle, grain length (GL), grain width (GW), grain thickness (GT) and thousand-grain weight (TGW). All the traits were measured with 5 replications. Number of spikelet per panicle (SPP) was calculated as: empty grains + filled grains. Grain length and width ratio (GLWR) was calculated as: grain length / grain width. Grain density (GD) was calculated as: number of grains per panicle / panicle length.

2.3 Genome sequence data

The core SNP V2.1 of the selected 191 *temperate japonica* rice accessions were downloaded from the SNP-seek system (<http://www.oryzasnp.org/iric-portal/>) (Alexandrov et al. 2015) and used for data analysis.

2.4 Data analysis

For the phenotypic data of measured traits, the mean values of five replications were calculated and used for genome-wide association study. Basic statistical information of the traits and correlations among different traits were calculated by using MINITAB V14.0 (Minitab Inc.).

The core SNP of the selected 191 accessions included 365,710 SNPs. However, some accessions did not heading because of photoperiod sensitivity, only 160 accessions with phenotyping data were used for GWAS using the Trait Analysis by Association Evolution and Linkage (TASSEL) program version 5.2.18 (Bradbury et al. 2007). The SNP sites were filtered at a maximum count of 144 of the 160 remaining accessions, which accounts for sites in which 90% of the accessions have a call and a minimum frequency of 0.05 for the minor allele. The above criteria resulted in 54,124 filtered sites. Finally 160 accessions with 54,124 SNPs were used for making cladogram tree with neighbor-joining and generating kinship matrix with centered IBS (default). A united data file with the genotype and phenotype of the lines was created by using union join. The united file along with kinship matrix was used to analyze marker-trait associations using a mixed linear model (MLM). The compression level was set to optimum

level, and variance component estimation was set to P3D. The criteria for claiming a QTL was $p < 1 \times 10^{-4}$ ($-\log_{10}$ p-value > 4.0) and marker $R^2 > 0.1$. The identified QTLs were named using the CGSNL nomenclature (McCouch and CGSNL 2008). A promising QTL was considered when many SNPs (> 10) with significant p value were lined up near the peak of the QTL. The chromosomes and QTL regions of the promising QTLs were re-analyzed using general linear model (GLM) with 1000 times permutation.

3. Results

3.1 Phenotypic variation among the accessions

There are wide range of variations among the measured traits (Table 1). Most of the traits are normally distributed with skewness and kurtosis less than 2.0, except awn length, because there are only 27 accessions with awn. There are 37 accessions had high values for one or more of the measured traits (Table 2). The plant height of this set of *temperate japonica* accessions is relatively short, only 3 accessions had plant height over 120 cm, and the maximum plant height is 135.6 cm (Rubi from Portugal). The panicle size of these accessions are relatively small with maximum value of 26 cm in length (Hong Pi Nuo and Duan Shen Zi from China) and 240 spikelets per panicle (C722323 from Taiwan). Many accessions with big grains were identified, for example, IBO400 from Portugal had grain length of 10.2 mm, grain width of 4.0 mm, and thousand-grain weight of 40.8 g. These accessions with big panicle and big grains are important genetic resources for developing high yield rice varieties.

Table 1. Basic statistics of the measured traits

Traits ¹	Mean	StDev	Minimum	Maximum	Skewness	Kurtosis
AL(mm)	0.6	1.5	0.0	7.5	2.6	6.0
GD(grain/cm)	5.8	1.9	2.4	12.0	0.8	0.6
GL(mm)	8.3	0.9	6.8	11.4	1.1	0.7
GLWR	2.3	0.3	1.8	3.4	1.4	1.7
SPP	108.6	40.1	43.0	239.8	0.7	0.1
GT(mm)	2.4	0.2	2.1	2.8	0.1	-0.5
GW(mm)	3.7	0.3	3.0	4.5	0.2	-0.1
PH(cm)	92.6	14.8	61.0	135.6	0.2	-0.3
PL(cm)	18.6	2.7	11.9	26.0	0.1	0.0
TGW(g)	27.9	4.0	19.6	40.8	0.5	0.4

¹Traits: AL = awn length, GD = grain density, GL = grain length, GLWR = grain length and width ratio (L/W), SPP = number of spikelets per panicle, GT = grain thickness, GW = grain width, PH = plant height, PL = panicle length, TGW = thousand-grain weight

Table 2. Accessions with high values (highlighted) for the measured traits

Accession	Origin	AL(cm)	GD	GL(mm)	GLWR	SPP	GT(mm)	GW(mm)	PH(cm)	PL(cm)	TGW(g)
S102	United States	0.0	4.5	8.3	2.0	74.8	2.6	4.1	75.5	16.8	31.4
SAGRES	Portugal	0.0	4.2	10.4	2.6	87.8	2.2	4.0	107.6	21.4	32.1
AUZGUSTA	Hungary	0.0	3.2	11.0	3.4	54.0	2.4	3.3	89.8	17.1	35.0
CAPATAZ	Spain	0.0	4.2	8.7	2.2	65.8	2.7	4.0	87.4	15.6	30.8
CHIPKA	Bulgaria	0.0	7.1	8.3	2.0	135.4	2.6	4.2	111.4	19.0	31.8
CT58	Colombia	0.0	5.9	10.4	3.6	117.6	2.0	2.9	94.4	20.0	23.3

GIOVANNI MARCHETTI	Italy	0.0	5.1	8.2	2.0	81.0	2.5	4.1	76.4	16.1	31.9
IBO400	Portugal	0.0	6.5	10.2	2.5	165.2	2.6	4.0	82.8	25.3	40.8
ITALPATNA 48	Italy	0.0	7.7	10.3	3.2	160.6	2.1	3.2	94.8	21.0	27.7
JUBILIENI	Bulgaria	0.0	11.0	8.3	2.1	177.6	2.4	4.0	80.2	16.2	27.5
OPALE	Italy	0.0	8.6	10.5	3.6	166.0	2.1	2.9	95.8	19.4	24.3
OTA	Portugal	0.0	9.7	8.7	2.4	219.6	2.4	3.6	116.4	22.8	27.5
PLOVDIV 24	Bulgaria	0.0	5.8	8.3	2.0	86.2	2.7	4.1	85.0	14.8	32.5
RUBI	Portugal	0.0	9.1	9.8	2.8	219.6	2.4	3.4	135.6	24.2	28.7
RUBINO	Italy	0.0	10.8	8.8	2.2	153.8	2.5	4.1	89.6	14.3	32.1
SALOIO	Portugal	0.0	4.2	8.9	2.2	89.4	2.3	4.1	89.6	21.3	34.2
SANGHAI	China	0.0	6.9	7.4	1.8	129.4	2.7	4.1	107.2	18.7	26.2
SUPER	Portugal	0.0	5.3	11.4	3.2	105.6	2.5	3.6	119.4	19.9	37.8
T 757	India	6.6	6.2	8.9	2.2	142.2	2.6	4.2	119.2	22.8	36.3
TOPAZIO	Portugal	0.0	5.7	8.0	1.9	100.0	2.5	4.1	87.2	17.7	29.8
ULLAL	Spain	0.0	11.7	8.1	1.9	177.4	2.1	3.4	68.2	15.0	25.0
VALTEJO	Portugal	0.0	5.9	8.4	1.9	113.4	2.8	4.5	108.2	19.4	36.4
DELTA	France	0.0	6.2	11.0	3.0	123.0	2.2	3.6	100.2	19.7	37.2
81A32	China	0.0	8.6	8.1	2.1	181.2	2.7	3.8	104.2	21.0	28.7
GITANO	Italy	0.0	7.1	10.6	3.1	144.4	2.4	3.4	100.2	20.4	33.5
KALIN	Bulgaria	0.0	5.8	7.7	1.8	86.8	2.7	4.3	74.8	15.1	31.8
SANT ANDREA	Italy	0.0	7.5	9.9	2.3	135.8	2.5	4.2	107.0	18.2	35.6
SZANISZLO 2	Hungary	7.5	3.0	9.4	2.3	58.4	2.6	4.1	102.4	19.5	40.5
H305-84	Hungary	0.0	4.8	10.6	3.4	88.8	2.3	3.1	82.2	18.7	28.9
HONG PI NUO	China	4.9	5.3	7.8	2.2	136.4	2.2	3.5	122.2	25.9	20.4
SI WAN 14	China	0.0	8.9	7.6	1.8	188.0	2.8	4.1	96.0	21.2	27.2
C722323	Chinese Taipei	0.0	12.0	7.2	2.0	239.8	2.3	3.5	96.6	20.0	23.0
DUAN SHEN ZI	China	2.6	5.5	7.9	2.1	141.4	2.6	3.8	98.2	26.0	27.5
K113	India	0.0	8.3	8.5	2.8	204.0	2.0	3.1	98.8	24.7	22.3
MA SHE 8	China	0.0	9.7	7.4	1.8	186.6	2.3	4.2	68.2	19.2	26.5
NOINJO	Korea	4.5	5.1	7.1	1.9	84.4	2.7	3.8	94.8	16.6	24.7
TAICHUNG 188	Chinese Taipei	0.0	3.3	7.7	2.1	60.6	2.7	3.6	84.2	18.3	28.8

3.2 Correlation among measured traits

In the used subset of temperate japonica, plant height was correlated with panicle length and number of spikelets per panicle, tall plants have longer panicle and more spikelets on the panicle (Table 3). More spikelets on the panicle also means higher grain density. Awn length was not correlated with other traits, except a weak correlation with plant height. For grain size, grain length and width were not correlated, but grain length, width and thickness are all correlated grain length/width ratio and thousand-grain weight.

Table 3. Correlations among the measured traits

	AL	GD	GL	GLWR	SPP	GT	GW	PH	PL
GD	-0.115 ^{ns 1}								
GL	-0.032 ^{ns}	0.050 ^{ns}							
GLWR	-0.091 ^{ns}	-0.001 ^{ns}	0.851 ^{***}						
SPP	-0.074 ^{ns}	0.903 ^{***}	0.030 ^{ns}	0.008 ^{ns}					
GT	0.109 ^{ns}	-0.210 ^{**}	-0.206 ^{**}	-0.443 ^{***}	-0.180 [*]				
GW	0.109 ^{ns}	0.007 ^{ns}	-0.095 ^{ns}	-0.572 ^{***}	-0.037 ^{ns}	0.610 ^{***}			
PH	0.265 ^{**}	0.141 ^{ns}	0.087 ^{ns}	0.063 ^{ns}	0.408 ^{***}	-0.027 ^{ns}	-0.001 ^{ns}		
PL	0.075 ^{ns}	0.124 ^{ns}	0.009 ^{ns}	0.038 ^{ns}	0.518 ^{***}	-0.087 ^{ns}	-0.089 ^{ns}	0.701 ^{***}	
TGW	0.066 ^{ns}	-0.111 ^{ns}	0.712 ^{***}	0.351 ^{***}	-0.130 ^{ns}	0.286 ^{***}	0.446 ^{***}	0.025 ^{ns}	-0.058 ^{ns}

¹ns = not significant, * p<0.05, **p<0.01, *** p<0.0005

3.3 Trait-marker association of the measured traits

By genome-wide association analysis using 54,124 SNPs, twenty-five QTLs were identified for 10 measured traits (Table 4). In some of the QTL regions, many SNPs with low p values were lined up. These QTLs were very promising for the traits, and some of the SNPs are very close to known genes. Examples of QTL for grain length and grain width are showing in Figure 1.

Table 4. QTLs for the measured traits

Trait	QTL	Chr	Peak Position	Start ¹	End	Interval Kb	SNPs	F	p	Marker R ²
AL	qAL4.1 ²	4	5931328	5631302	6090535	459.2	18	29.01	2.62E-07	0.1959
AL	qAL7.1	7	27027178	26977651	27045622	68.0	10	19.42	1.94E-05	0.12228
AL	qAL8.1	8	23713738	23713738	24000142	286.4	4	21.19	8.71E-06	0.14099
AL	qAL9.1	9	6088466	6070925	6091731	20.8	4	24.15	2.28E-06	0.16696
AL	qAL11.1	11	6486497	6486497	6649863	163.4	10	24.52	1.92E-06	0.15546
AL	qAL11.2	11	28934599	27658829	29002814	1344.0	10	28.37	3.52E-07	0.1823
GD	qGD4.1	4	31423289	30628864	32573729	1944.9	31	16.54	7.63E-05	0.11062
GL	qGL2.1	2	17224213	17210947	17370306	159.4	7	16.75	6.77E-05	0.10537
GL	qGL3.1	3	16059274	14808674	20798278	5989.6	128	21.50	5.65E-09	0.26259
GL	qGL7.1	7	19996900	19270569	20119165	848.6	9	10.00	8.25E-05	0.12808
GL	qGL9.1	9	13674942	13653700	13739140	85.4	5	19.65	1.75E-05	0.12343
GLWR	qGLWR3.1	3	15682213	14808364	21206289	6397.9	218	34.08	3.09E-08	0.21738
GLWR	qGLWR5.1	5	5376147	4888896	6827210	1938.3	19	28.37	3.54E-07	0.1833
GLWR	qGLWR12.1	12	4931837	4676401	4969516	293.1	6	21.54	7.31E-06	0.13983
SPP	qSPP6.1	6	8249567	8249567	8343156	93.6	3	17.80	4.18E-05	0.11297
SPP	qSPP8.1	8	26771958	26737405	26847846	110.4	16	15.24	1.41E-04	0.10139
GT	qGT5.1	5	5537507	5492140	5552097	60.0	13	19.17	2.22E-05	0.12273
GT	qGT9.1	9	21330199	21316108	21359117	43.0	5	17.55	4.72E-05	0.12197
GW	qGW5.1	5	5501574	4753735	6248041	1494.3	96	33.34	4.14E-08	0.21337
PH	qPH6.1	6	10844177	7996136	10877302	2881.2	16	18.06	3.67E-05	0.11457
PL	qPL6.1	6	10844177	8158663	10877302	2718.6	12	20.03	1.46E-05	0.12598
TGW	qTGW7.1	7	20368732	20084856	20614036	529.2	16	20.13	1.42E-05	0.12907
TGW	qTGW9.1	9	14400854	13674942	14602303	927.4	9	22.90	4.01E-06	0.14569

TGW	qTGW11.1	11	10666281	10658208	10666281	8.1	3	19.31	2.06E-05	0.12699
TGW	qTGW12.1	12	246253	246253	634468	388.2	4	16.78	6.72E-05	0.10958

¹The QTL interval is the chromosomal region with SNPs showing p values less than 1×10^{-4}

²Highlighted QTLs are the most promising QTLs with low p values and large number of significant SNPs in the QTL interval.

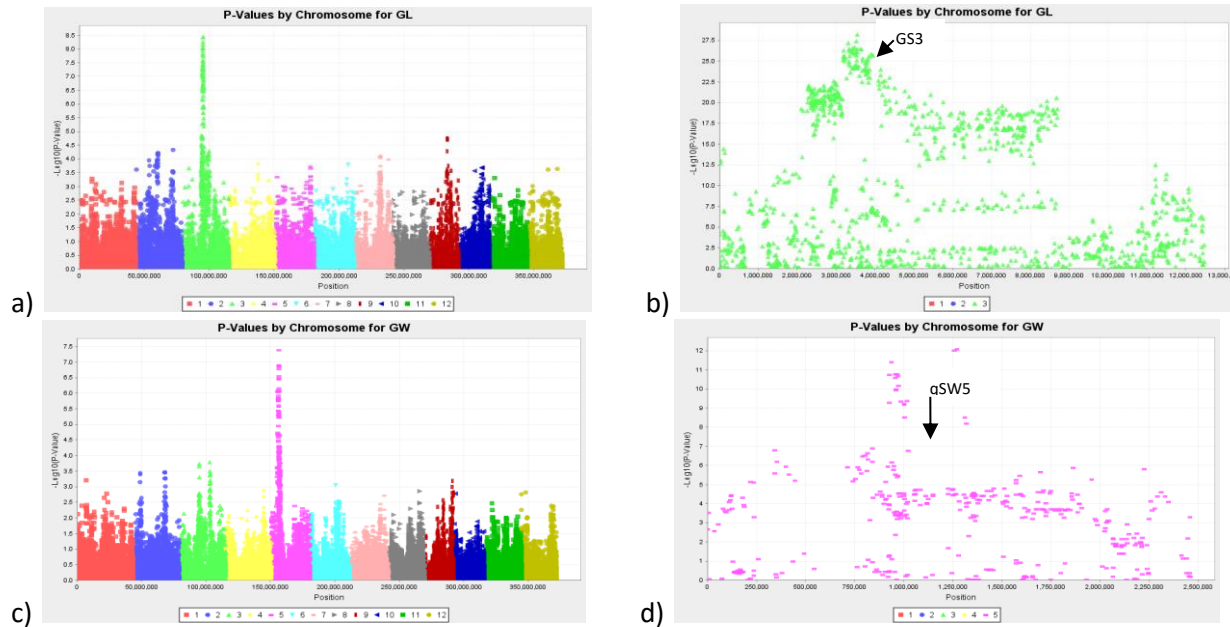


Figure 1. a) QTL for grain length (qGL3.1) identified by using MLM in TASSEL; b) detailed position of the QTL on chromosome 3 (by GLM); c) QTL for grain width (qGW5.1); d) detailed position of the QTL on chromosome 5. Arrows show the position of known grain length gene GS3 (Os03g40740) and grain width gene qSW5 (Os05g10540).

4. Discussion

In modern rice breeding, new plant type with short stem, less tillers, big panicle and big grain is an important way to improve yield. Therefore it is important to identify genetic resources with these excellent traits and use them in the breeding programs. In the present study, we evaluated a subset of 160 *temperate japonica* from the 3,000 sequenced rice accessions, and found that all the accessions are relatively short (only 3 accessions had plant height over 120 cm), and more than 30 accessions had big panicles and/or big grains (Table 2). These accessions are very important resources for improve rice yield. However, with the high grain quality desired in the market, we still need to analyze the grain quality of these accessions and look for high quality accessions for our breeding programs.

Among the measured traits, awn length was not correlated with other traits, except a weak correlation with plant height. This is possibly because the accessions with awn are usually traditional tall varieties, and plants with awn was discharged during selection for short high-yield varieties. Grain length was not correlated with grain width, it is possible to develop varieties with different grain shape (length/width ratio) for different markets. The plant height was correlated with panicle length and

number of spikelets per panicle, thus it is important to select relatively tall (about 100 cm) plants with strong stem and big panicles in breeding programs.

In rice breeding programs, semi-dwarf gene *sd1* is the most widely used source for short plant. However, *sd1* gene was not identified in the *temperate japonica* accessions used in this study. Possibly the *sd1* alleles in these temperate japonica accessions are different from those from *indica* or other subgroups. On the other hand, a QTL controlling plant height was identified on chromosome 6. QTLs *qPH6.1*, *qSPP8.1*, and *qTGW9.1* are located in similar regions of the previously reported QTLs (Bai et al., 2011), while the highly significant SNPs in *qGL3.1* and *qGW5.1* are very close to the cloned grain length gene *GS3* (Mao et al., 2010) and grain width gene *SW5* (Shomura et al., 2008). Therefore, these QTLs are promising for the related traits, and the SNPs near the peak positions of the QTLs could be directly used for marker assisted selection in rice breeding programs.

5. Conclusions

The selected temperate japonica accessions with big panicles and big grains are important resources for improve yield of new varieties. Since the sequence information of these accessions are already available, SNPs closely linked to the QTLs controlling important agronomic traits were also identified in this study, it is easier to develop breeding populations using the *temperate japonica* accessions evaluated in this study, and use related SNP markers for selection for the target traits. This will greatly improve the selection efficiency for increasing rice yield. This study also provided useful information for further validation of the genes underlining the QTLs.

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