



Mapping QTLs for Agronomic Traits in Rice Under Water Stress Condition Using Iranian Recombinant Inbred Lines Population

Hossein Sabouri^{1*}, Ahmad Reza Dadras², Atefeh Sabouri³ and Mahnaz Katouzi⁴

Received: January 7, 2013 Accepted: August 19, 2013

¹Assistant Prof. of Plant Breeding, Department of Plant Production, College of Agriculture Science and Natural Resources, Gonbad Kavous University, Iran

²PhD Student of Plant Breeding, Guilan University, Iran

³Assistant Prof. of Plant Breeding, Department of Plant Breeding, College of Agriculture Science, University of Guilan, Iran

⁴MSc in Crop Production and MSc Student of Plant Breeding, Gorgan University of Agriculture Science and Natural Resources, Iran

*Corresponding author: E-mail: saboriho@yahoo.com

Abstract

In the current study, a set of 96 recombinant inbred lines (RIL) at F₈, derived from a cross between two varieties, Anbarbu (sensitive to drought stress) and Sepidroud (tolerant to drought stress) were used. The experiment was performed at Gonbad Kavous located in the Golestan province of Iran in 2010–2011 using two augmented designs at normal and stress conditions, separately. The RIL population was assessed for 11 agronomic traits including grain yield, panicle number, panicle length, grain number, grain weight, straw weight and secondary branches number. Linkage map with 135 microsatellite markers was used to map quantitative trait loci (QTLs) for agronomic traits under normal and drought stress conditions. Using the composite interval mapping, a total of 16 QTLs were identified for the studied traits in both conditions. We detected 8 QTLs located on chromosomes 1, 3, 4, 8 and 9 in the non-stress condition. Favorable alleles were contributed by Spidroud for straw weight and grain number. Under drought condition, several QTLs were identified which were located on chromosomes 1, 2, 4, 5, 6, 9 and 10. Among the detected QTLs, 6 explained more than 20% of the phenotype variation.

Keywords: Drought; QTL mapping; Rice

Introduction

Rice (*Oryza sativa* L.) is one of the important staples foods in the world. In Asian countries as well as many African countries it provides the calorific needs of millions of people daily. Also, it is the primary staple in the diet of these countries where overpopulation is becoming a critical issue. In spite of the successful introduction of resistance to biotic/abiotic stresses into a variety of rice cultivars that resulted in improved crop yield, benefits of the 'green revolution' will soon be exhausted due to the population pressure (Yamamoto *et al.* 2009).

In many areas where rice is grown under rainfed condition, drought is one of the main environmental factors that cause a considerable reduction in yield. To reduce the loss of rice yield, new drought tolerant rice varieties are required. In recent decade, molecular markers have been widely used to identify quantitative trait loci (QTL) for important agronomic traits, particularly those that are polygenic in nature (Tanksley 1993). Since drought tolerance is a complex trait controlled by minor and major genes and is dependent on the environment, it is one of the most difficult traits to study and genetic

mechanisms that condition the expression of drought tolerance in rice plants are poorly understood (Lang and Buu 2008).

Identification of the important and stable QTLs for drought tolerance by using of permanent populations should enable the exploitation of these genes in the breeding programs through marker-assisted selection and may lead to the release of new rice varieties with more tolerance to drought. Grain yield in rice represents multiplicative integration of three main components i.e. number of panicles per plant, number of grains per panicle and mean grain weight (Sakamoto and Matsuoka 2008; Xing and Zhang 2010). In recent years, attempts have been made to detect and locate QTLs or polygenes for grain yield and other important agronomical traits in rice (Zhang 2007).

A number of field studies provided information on QTLs linked to grain yield and yield components under managed stress condition, (Babu *et al.* 2003; Lanceras *et al.* 2004; Lafitte *et al.* 2004; Xu *et al.* 2005; Yue *et al.* 2005; Jearakongman 2005). By comparing the coincidence of QTLs for specific drought-resistance traits and QTLs for plant production under drought, it is possible to test whether a particular constitutive or adaptive trait is likely to be useful for improving drought tolerance in the field (Lebreton *et al.* 1995).

Several studies have been conducted under both non-stress and drought-stressed conditions (e.g., Zou *et al.* 2005; Kumar *et al.* 2007), and also under multiple stress regimes (Lanceras *et al.* 2004; Jearakongman, 2005), allowing preliminary assessment of the interaction between QTLs and

drought stress types. Zou *et al.* (2005) reported when the correlation between yield under stress and non-stress conditions was relatively high, only a few cases of QTL-by-environment interaction were detected. In various studies under stress condition, some QTLs for leaf rolling (Champoux *et al.* 1995; Courtois *et al.* 2000; Gomez *et al.* 2005) and leaf drying (Boopathi *et al.* 2005; Yue *et al.* 2006) have been mapped in the adjacency of SSR marker RM215 on chromosome 9. This region harbors also QTLs linked to the integrative traits such as biomass (Lanceras *et al.* 2004; Jearakongman, 2005), number of grains per panicle (Lafitte *et al.* 2004), relative spikelet fertility and delay in flowering time (Yue *et al.* 2005) under stress condition and grain yield under both non-stress and stress conditions (Gomez *et al.* 2005; Xu *et al.* 2005; Jearakongman, 2005). These studies consistently identified regions on chromosomes 1, 4, 8 and 9 that influence a range of drought-resistance traits, yield and yield components under stress condition (Kamoshita *et al.* 2008). Therefore, to increase drought tolerance, it may be more effective to use the potential of specific identified regions by means of molecular marker technology.

The objectives of the present study were as follows: Evaluation and characterization of drought tolerance of recombinant inbred lines, determining the number and effects of individual QTLs controlling drought tolerance, along with identifying molecular markers closely linked to the resistance QTLs that may be useful for cloning the genes and for improving drought tolerance in rice breeding programs such as marker assisted selection and comparing of detected major QTLs

in this research with the results of other previous reports.

Material and Methods

Mapping population and phenotyping

A mapping population consisted of 96 recombinant inbred lines (RIL) was developed from a cross between Anbarbu (ANB), an *Indica* traditional variety, and Spidroud (SPD), an *Indica* improved variety. The RILs were evaluated at non-stress and stress conditions. Drought stress was imposed from the around maximum tillering stage by withholding irrigation at the paddy field. The experiment was performed at Gonbad Kavous located in the Golestan province of Iran in 2010–2011 using two augment designs at normal and stress conditions, separately. The RIL population was assessed for 11 agronomic traits including grain yield, panicle number, panicle length, grain number, grain weight, straw weight and secondary branches number.

Genotyping and QTL mapping

Genomic DNA was extracted from the young leaf tissue following cetyl trimethyl ammonium bromide (CTAB) method (Saghai Maroof *et al.* 1994). The 520 pairs of SSR primer pairs (based on the sequences obtained from McCouch *et al.* 2002, Temnykh *et al.* 1999, Chen *et al.* 1997 and Causse *et al.* 1994) were screened for polymorphism between parental lines.

Polymerase chain reaction (PCR) was carried out in a total volume of 10 μ l per reaction containing 2 μ l of template DNA, 0.4 μ l of forward and reverse primers each of 10 pmol concentration, 0.6 μ l dNTPs (2mM), 0.12 μ l Taq

polymerase (5U/ μ l), 0.48 μ l of MgCl₂ (50mM), 1 μ l 10x PCR buffer and 5 μ l sterile nanopure H₂O. The PCR reaction conditions were set as follows: initial denaturation at 94°C for 5 min, followed by 35 cycles of denaturation at 94°C for 30s, primer annealing at 55 or 60°C for 30s with most of the primers while some were adjusted, extension at 72°C for 2 min, with final extension at 72°C for 5min. The PCR products were separated on 6% polyacrylamide gel electrophoresis (PAGE) (19:1 acrylamide: bisacrylamide) and visualized by silver staining method (Xu *et al.* 2002). A SSR linkage map of the RIL population was constructed using QTXb17 Mapmanager (Manly and Olson 1999), and genetic distances (cM) were calculated from recombination values using the Kosambi mapping function (Kosambi 1944). Assignment of linkage groups to the respective chromosomes was done based on the rice maps developed by the Cornell University (Causse *et al.* 1994; Chen *et al.* 1997; Temnykh *et al.* 1999; McCouch *et al.* 2002) and the rice genome program (Harushima *et al.* 1998).

QTL mapping was performed using composite interval mapping (CIM) of WinQTL Cartographer (Wang *et al.* 2005) adopting the Model 6 as well keeping a threshold of LR>11 for testing the hypothesis of QTL presence. A walk speed of 0.5 cM and the forward regression method were selected in the CIM procedure.

Results and Discussion

Linkage map construction

Out of 365 SSR markers, 135 markers distributed on 12 chromosomes were polymorphic between ANB and SPD parental lines and were evenly

used for genotyping of the RIL population. The resulting linkage map covered 1397.7 cM of rice genome with an average distance of 10.35 cM between two markers (Figure 1). All of the 135 microsatellite loci involved in the construction of the genetic map were tested for segregation distortion. Distortion was detected using the χ^2 -test for goodness of fit to expected allelic frequency of 1:1.

Phenotypic analysis

Frequency distribution of RILs and their parents for most of the studied traits showed continuous variation and transgressive segregation as some RILs showed lower values than their parents for the studied traits, whereas some others showed higher values than the parents, suggesting the involvement of multiple genes with quantitative inheritance (Figure 1). Descriptive statistics of RILs in two conditions are shown in Table 1. The correlation coefficients among the traits were given in Table 2. Significant positive correlations were observed between some of the studied traits under two conditions. Grain yield was significantly correlated with panicle number, panicle length, grain number, grain weight, straw weight in the non-stress condition. Correlations of grain number with panicle number and panicle length, and straw weight with panicle number, panicle length and grain number were significant in the non-stress condition ($P < 0.01$). In the

drought condition, grain yield was significantly correlated with panicle number and straw weight. Also, the correlations between grain number and panicle length, between straw weight and panicle length were highly significant ($P < 0.01$).

Identification of QTL for traits under different conditions

Four major QTLs (on chromosomes 4, 8 and 9 with two QTLs) and four minor QTLs (on chromosomes 1, 3 and 4 with two QTLs) were identified for agronomic traits under non-stress condition (Table 3, Figures 2 & 3). QTLs for agronomic traits under non-stress conditions were contributed from both parents and favorable alleles contributed from the donor parent (SPD) for high panicle number. The additive effects of the QTLs related to panicle number and grain number were 5.147 and 26.969 respectively. Also, direction of phenotypic effect of major QTL for straw weight on chromosome 9 was toward SPD (Table 3). The additive effect of this QTL was 32.32 grams. Two major QTLs (on chromosomes 5 and 9) and six minor QTLs (on chromosomes 1, 2, 4, 6 with two QTLs, and 10) were identified for traits under drought stress condition (see Table 3 and Figures 2 & 3). Similarly, in the non-stress condition, both parents had alleles in the detected QTLs.

Table 1. Descriptive statistics of Iranian rice recombinant in bred lines developed from the Anbarbu and Spidroud cross under non-stress and drought stress conditions

	Biomass	Plant height	Grain yield	Panicle number	Straw weight	Panicle length	Filled grain number	Unfilled grain number	Grain number	Grain weight	Branches number
Mean±SE	264.35±8.53	109.02±1.98	74.39±2.75	26.17±1.14	155.79±6.35	27.55±0.31	112.42±5.40	111.73±8.38	194.90±6.49	3.00±0.14	10.86±0.24
	152.92±5.84	86.45±2.02	64.17±1.99	34.69±1.49	54.11±3.29	26.27±0.22	92.21±5.00	137.54±5.52	54.31±4.49	2.32±0.12	9.2188
Median	252.6350	106.5000	72.2100	26.0000	153.1700	28.5000	115.0000	95.0000	172.5000	3.0100	11.0000
	140.0000	87.0000	64.9800	34.5000	43.1250	26.0000	89.5000	123.5000	40.0000	2.1500	8.5000
Mode	137.57	112.00	35.36	27.00	67.21	29.50	116.00	150.00	125.00	4.80	10.00
	110.00	87.00	58.25	19.00	0.04	24.00	0.00	107.00	88.00	0.00	8.00
Variance	7000.111	378.103	730.806	125.263	3873.156	9.339	2809.321	6749.395	4053.454	1.906	5.655
	3278.931	395.037	381.600	215.245	1041.570	4.899	2408.299	2932.735	1939.122	1.448	7.478
Skewness	0.182	0.308	0.268	0.398	0.344	-1.400	0.119	1.143	0.734	0.428	0.524
	0.351	0.322	0.475	0.345	1.080	0.267	1.334	0.943	0.977	0.931	0.759
Kurtosis	-0.865	-0.955	-0.479	-0.307	-0.497	2.029	-0.212	0.866	-0.050	1.355	-0.225
	0.012	-0.135	0.261	-0.724	0.809	-0.132	3.564	0.717	0.063	1.969	0.224
Range	377.08	70.50	119.87	51.00	283.29	15.00	233.00	362.00	285.00	8.13	10.00
	284.00	102.50	95.64	57.00	147.47	11.00	258.00	276.00	171.00	5.85	14.00
Minimum	103.99	76.00	23.87	5.00	45.35	17.00	10.00	11.00	105.00	0.20	7.00
	11.00	39.50	23.07	11.00	0.04	21.00	0.00	5.00	10.00	0.00	2.00
Maximum	481.07	146.50	143.74	56.00	328.64	32.00	243.00	373.00	390.00	8.33	17.00
	295.00	142.00	118.71	68.00	147.50	32.00	258.00	281.00	181.00	5.85	16.00

Table 2. Correlation coefficients among agronomic traits of Iranian rice recombinant inbred lines under non-stress (first row) and drought stress (second row) conditions, respectively

	Biomass	Plant height	Grain yield	Panicle number	Straw weight	Panicle length	filled grain number	unfilled grain number	Grain number	Grain weight	Branches number	
Biomass	1											
Plant height	0.298**	1										
Grain yield	0.442**		1									
Panicle number	0.764**	-0.068		1								
Straw weight	0.646**	-0.094			1							
Panicle length	0.714**	.057	.856**			1						
filled grain number	-0.034	-0.433**	0.313**				1					
unfilled grain number	0.933**	0.435**	0.521**	0.531**				1				
Grain number	0.737**	0.625**	0.409**	-0.106					1			
Grain weight	0.260*	0.436**	0.085	0.129	0.294**					1		
Branches number	0.400**	0.677**	0.097	-0.137	0.533**						1	
	-0.405**	-0.263**	-0.091	-0.266**	-0.495**		1					
	0.367**	-0.065	0.285**	-0.222**	0.096			1				
	-0.007	-0.149	-0.181	-0.211*	0.064		-0.179		1			
	0.361**	0.192	0.206*	-0.537**	0.317**		0.547**			1		
	-0.156	-0.111	-0.435**	-0.602**	0.004		0.023	0.334**			1	
	-0.197	0.065	-0.246*	-0.278**	-0.176		0.060	-0.090	0.116		1	
	-0.405**	-0.077	-0.252*	-0.365**	-0.384**		-0.008	0.663**	0.096	0.249*	1	
	0.414**	0.068	0.287**	-0.339**	0.182		0.940**	0.545**		-0.062	1	
	-0.045	-0.101	-0.324**	-0.483**	0.088		-0.144	0.003	0.298**	0.770**	0.013	1
	0.373**	0.199	0.302**	-0.499**	0.259*		0.274**	0.494**	0.833**	0.140	0.538**	1

*, ** Significant at 0.05 and 0.01 probability level, respectively (2-tailed)

A total of 16 QTLs were identified with significant effects on agronomical traits under two conditions. Seven out of 16 QTLs were contributed from high yielding donor parent (SPD) and nine from ANB. Of these, four, two and two QTLs affected panicle length under stress condition, straw weight and grain weight in non-stress condition, respectively, and eight QTLs affected other traits, one QTL for each trait. Totally five QTLs affected panicle length under two different conditions, including one on chromosomes 3 under normal condition, four on chromosomes 5, 6, 9 and 10 under drought condition. According to these results, there were no coincidences between the chromosomal location of QTLs for traits under non-stress and QTLs for traits under stress condition. Six QTLs with sharp effects were detected in this study, but no QTLs across conditions were mapped in this

research. For all of the characters, the majority of the QTLs detected had high effects, explaining more than 20% of the phenotypic variation.

Kamoshita *et al.* (2008) reviewed many reports related to QTL mapping of drought tolerance in rice and found regions on chromosomes 1, 4, 8 and 9 that influence a range of drought-resistance traits including yield and yield components under stress consistently identified by these studies. In this research, a total of eight QTLs were detected under drought condition, of which three QTLs located on chromosomes 1, 4 and 9. These QTLs were related to straw weight, secondary branches and panicle length, respectively. The positions of the QTLs are shown in Table 3 and Figure 2. The major QTL of qPL-9, explaining more than 20% of the panicle length variation could be regarded as effective QTL and comparable with previous reports. The positions of qPL-9, RM8206 and

RM7038 as its flanking markers were 26.0, 30.3 and 29.01 cM, respectively. Therefore, RM7038 is closely linked to the QTL. On the other hand, RM7038 was approximately in the vicinity of RM215 which is also reported by several researches (Champoux *et al.* 1995; Courtois *et al.* 2000; Lanceras *et al.* 2004; Gomez *et al.* 2005; Boopathi *et al.* 2005; Yue *et al.* 2006). It seems that qPL-9 in the present genetic background is in concordance with the QTLs detected in the above mentioned studies and may be used in the marker assisted selection programs. Also one major QTL, qPLS-5, was identified for panicle length under stress condition that explained about 31.68% of the phenotypic variance. If this QTL is approved, it can significantly affect the panicle length. More resolution of the regions on these chromosomes would be useful in fine-mapping of QTLs for panicle length in rice. Furthermore, qGNN-8 and qGNS-2 were detected for grain number under non-stress stress condition with additive effect of 26.97 and 21.09 directed from SPD alleles, respectively. These QTLs explained about 25 and 14.8% of the phenotypic variance of grain number at non-stress and drought stress conditions, respectively. Considering the important effect of

grain number on final yield, linkage map should be saturated at these region and after QTL validation it can be used in the marker assisted selection program. It is possible to produce a variety with increased grain yield under drought condition by pyramiding the positive alleles from different sources through MAS.

Generally the more common goal of QTL mapping is the use of QTL in MAS to transfer genomic regions associated with drought tolerance from a tolerant source to an elite but drought susceptible genotype, thus augmenting and improving the outcomes of phenotypic selection. Johnson (2004) and Ribaut *et al.* (1997) described the transfer of five QTL from donor line Ac7643 into the drought susceptible recipient line CML 247. The transferred fragments included 12% of the genome containing these QTL and a further 7% lying outside of these regions (Johnson, 2004). These results provide information for further functional analysis of water stress tolerance genes in rice. In fact, the molecular markers linked to QTLs for the traits related to water stress tolerance might be useful after fine mapping for indirect selection of these traits by MAS.

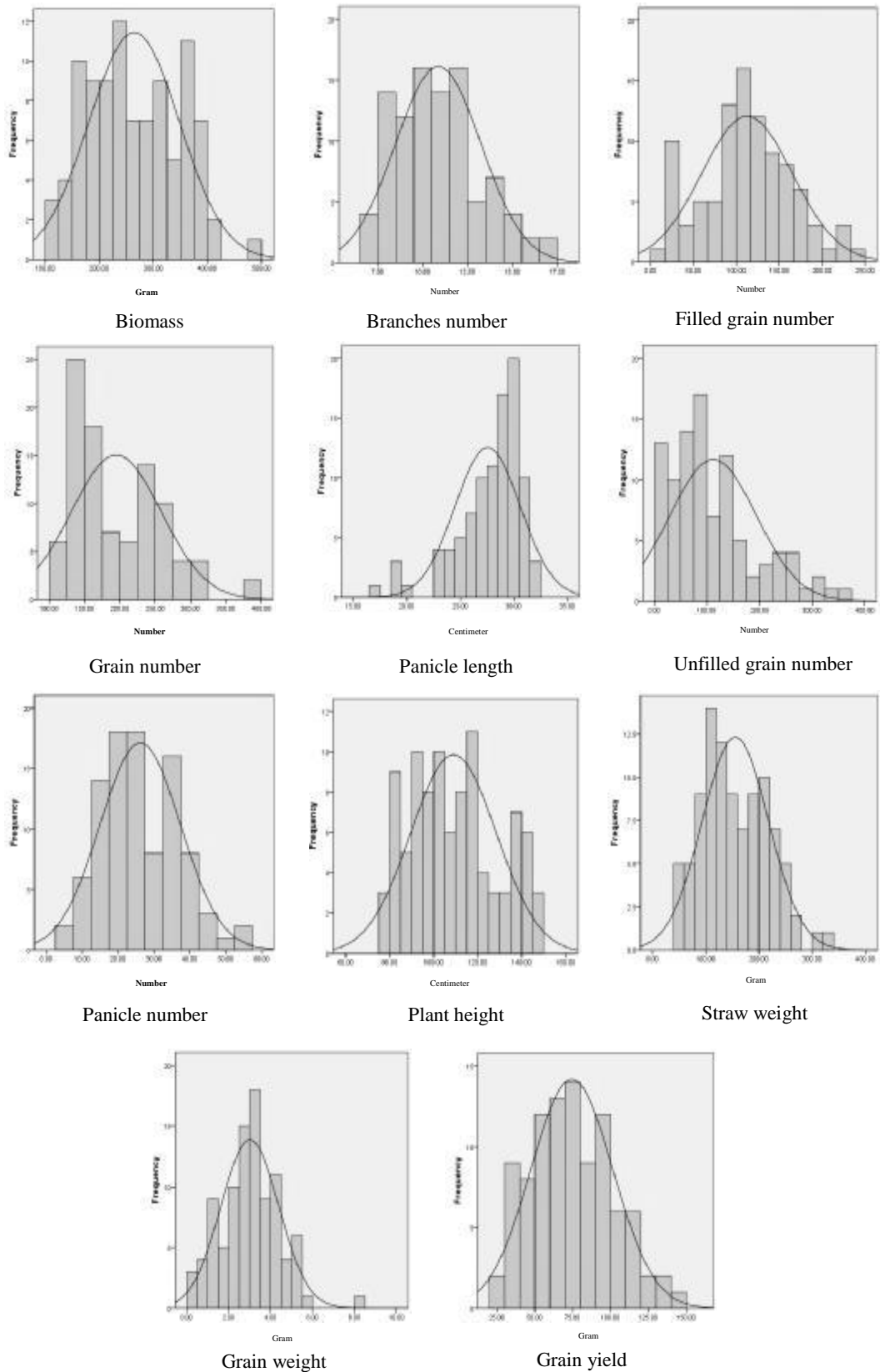


Figure 1. Phenotypic distribution of the studied traits in Iranian rice recombinant inbred lines in non-stress condition

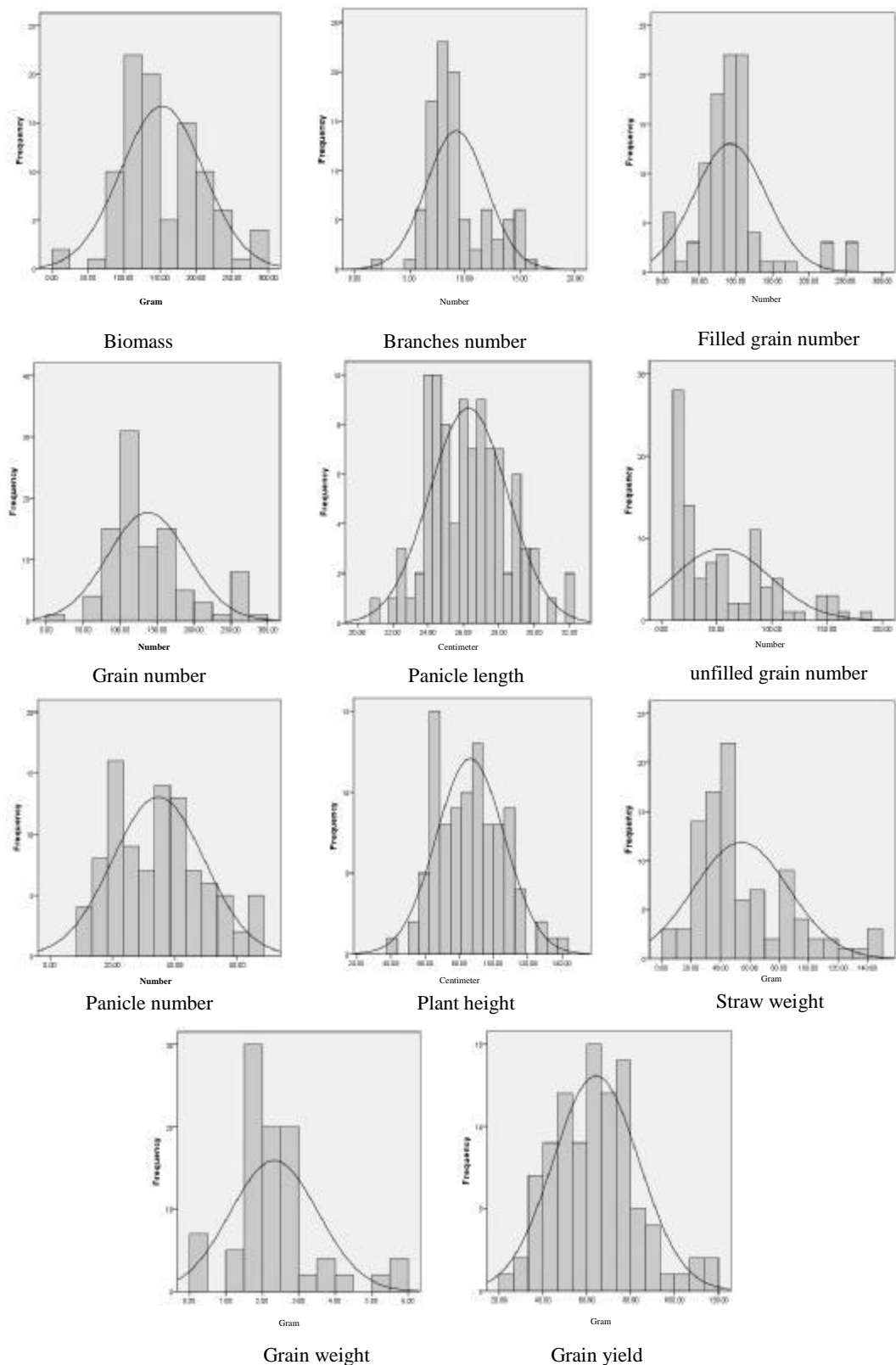


Figure 2. Phenotypic distribution of the studied traits in Iranian rice recombinant inbred lines under drought condition

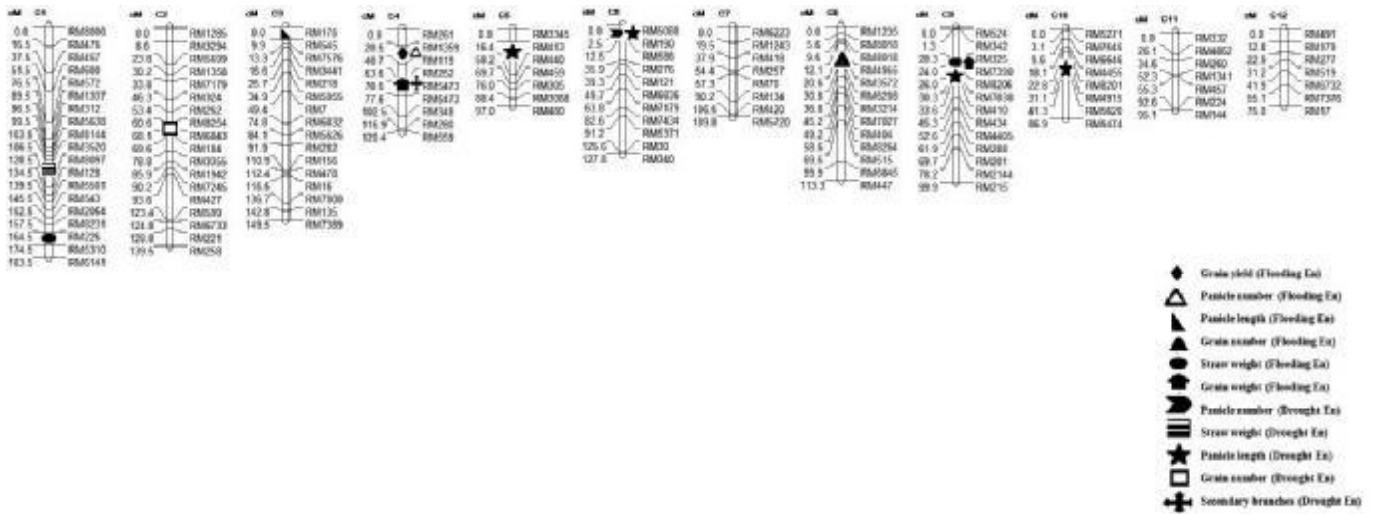
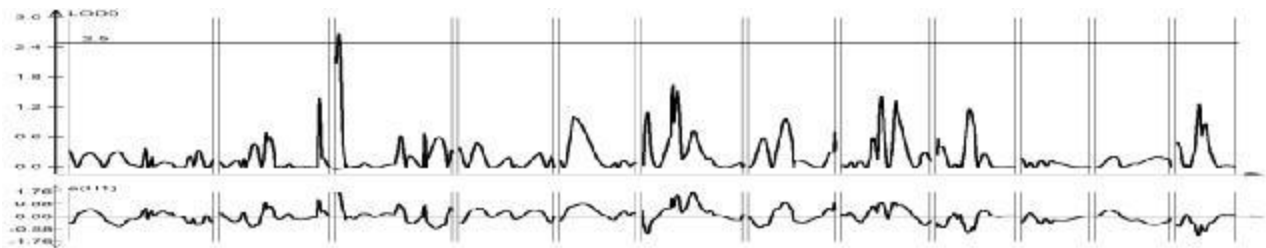


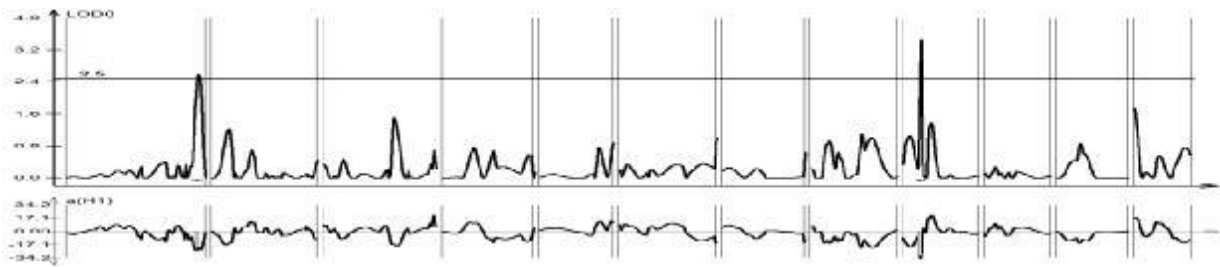
Figure 3. Mapping of QTLs for grain yield, panicle number, panicle length, grain number, straw weight and grain weight under control condition and panicle number, straw weight, panicle length, grain number and secondary branches under drought stress condition using Iranian RIL population derived from the cross between Anbarbu and Spidroud varieties. Significance threshold for composite interval mapping was determined at LR=11



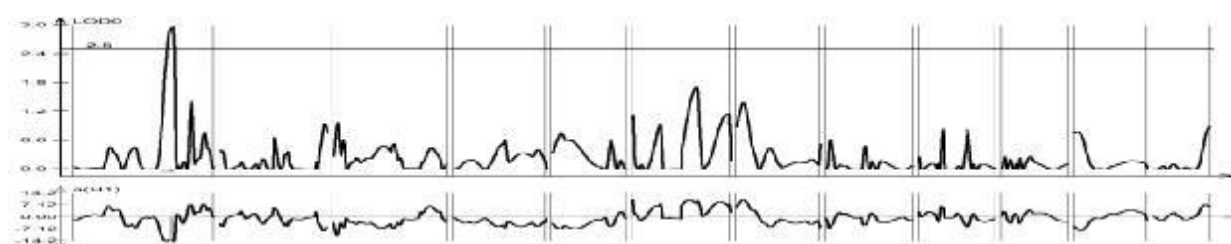
a. Panicle length in non-stress condition



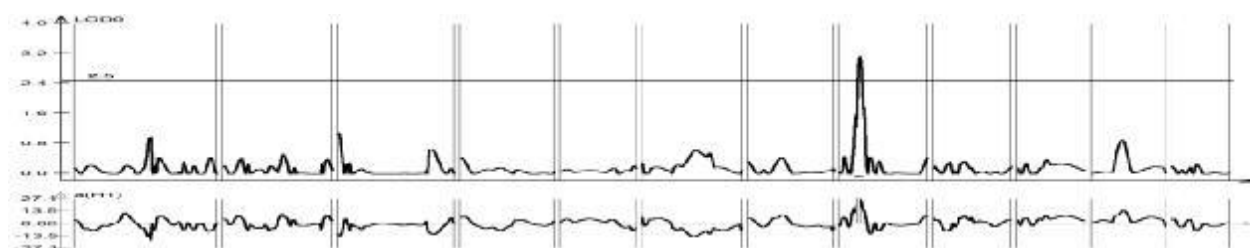
b. Panicle length in drought condition



c. Straw weight in non-stress condition



d. Straw weight in drought condition



e. Grain number in non-stress condition

Figure 4. Majors QTL detected for rice traits

Table 3. Putative QTLs for the RIL population derived from ANB × SPD cross under normal and water stress conditions. QTLs are named by abbreviations plus chromosomal number

Traits	QTL	Chr.	Flanking markers	Position	Peak LR	a ^a	PEV ^b	Dpe ^c
Non stress condition								
Grain yield	qGYN-4	4	RM1359–RM119	40.61	13.93	-9.553	11.57	ANB
Panicle number	qPNN-4	4	RM1359–RM119	36.61	14.76	5.147	20.32	SPD
Panicle length	qPLN-4	3	RM175–RM545	3.01	12.32	1.652	18.81	ANB
Grain number	qGNN-8	8	RM3572–RM6208	25.61	14.34	26.969	25.00	SPD
Straw weight	qSWN-1	1	RM226–RM5310	173.51	12.02	-21.461	11.09	ANB
	qSWN-9	9	RM325–RM7390	23.31	16.02	32.320	22.84	SPD
Grain weight	qSWN-4	4	RM252–RM5473	64.61	13.85	-0.920	14.16	SPD
	qSWN-9	9	RM325–RM7390	23.31	18.76	-1.106	20.57	SPD
Drought stress condition								
Panicle number	qPNS-6	6	RM5088–RM190	0.01	12.51	-5.792	9.81	ANB
Straw weight	qSWS-1	1	RM3520–RM8097	126.51	13.65	13.824	17.40	SPD
Panicle length	qPLS-5	5	RM413–RM440	31.41	14.79	1.267	31.68	ANB
	qPLS-6	6	RM5088–RM190	0.01	14.07	0.901	10.07	ANB
	qPLS-9	9	RM8263–RM7038	29.01	16.98	1.029	20.73	ANB
	qPLS-10	10	RM4915–RM5620	41.11	11.64	0.663	8.57	ANB
Grain number	qGNS-2	2	RM8254–RM6843	63.61	14.58	21.098	14.78	SPD
Secondary branches	qSBS-4	4	RM252–RM5473	69.61	13.21	-1.141	14.75	ANB

^a Additive effect, ^b Percentage of total phenotypic variance explained by the QTL, ^c Direction of phenotypic effect, ANB and SPD indicate Anbarbu and Spidroud cultivars, respectively

References

- Babu RC, Nguyen BD, Chamarek V, Shanmugasundaram P, Chezian P and Jeyaprakash P, 2003. Genetic analysis of drought resistance in rice by molecular markers: association between secondary traits and field performance. *Crop Science* 43: 1457–1469.
- Boopathi NM, Chezian P, Jeyaprakash P, Kumar, S, Gomez M, Suresh R, Atlin, G, Subudhi PK, Shanmugasundaram P and Babu RC, 2005. QTL mapping of drought–resistance traits using Indica rice (*Oryza sativa* L.) lines adapted to target population of environment. In: Proceedings of the 2nd International Conference on Integrated Approaches to Sustain and Improve Plant Production under Drought Stress, September 24–28, University of Rome, La Sapienza, Rome, Italy, P6.05.
- Capell T, Bassie L and Christou P, 2004. Modulation of the polyamine biosynthetic pathway in transgenic rice confers tolerance to drought stress. *PNAS* 101: 9909–9914.
- Causse MA, Fulton TM, Cho YG, Ahn SN, Chunwongse J, Wu K, Xiao J, Yu Z, Ronald PC, Harrington SE, Second G, McCouch SR and Tanksley SD, 1994. Saturated molecular map of the rice genome based on an interspecific backcross population. *Genetics* 138: 1251–1274.
- Champoux MC, Wang G, Sarkarung S, Mackill DJ, O’Toole JC and Huang N, 1995. Locating genes associated for root morphology and drought avoidance in rice via linkage to molecular markers. *Theoretical and Applied Genetics* 90: 969–981.
- Chen X, Temnykh S, Xu Y, Cho YG and McCouch SR, 1997. Development of a microsatellite framework map providing genome–wide coverage in rice (*Oryza sativa* L.). *Theoretical and Applied Genetics* 95: 553–567.
- Courtois B, McLaren GM and Sinha PK, 2000. Mapping QTLs associated with drought avoidance in upland rice. *Molecular Breeding* 6: 55–66.
- Gomez M, Babu RC, Shanmugasundaram P, Satheesh Kumar R, Suresh R, Biji KR, Boopathi NM, Jeyaprakash P, Gurumurthy S and Price AH, 2005. QTL mapping and marker assisted selection for drought tolerance in rice (*Oryza sativa* L.). In: Proceedings of the 2nd International Conference on Integrated Approaches to Sustain and Improve Plant Production under Drought Stress, September 24–28, University of Rome, La Sapienza, Rome, Italy, P6.19.
- Harushima Y, Yano M, Shomura A, Sato M, Shimano T, Kuboki Y, Yamamoto T, Lin SY, Antonio BA, Parco A, Kajiya H, Huang N, Yamamoto K, Nagamura Y, Kurata N, Khush GS and Sasaki T, 1998. A high density rice genetic linkage map with 2,275 markers using a single F₂ population. *Genetics* 148: 479–494.
- Jearakongman S, 2005. Validation and discovery of quantitative trait loci for drought tolerance in backcross introgression lines in rice (*Oryza sativa* L.) cultivar IR64. PhD Thesis, Kasetsart University, p. 95.
- Johnson R, 2004. Marker-assisted selection. *Plant Breed Reviews* 24: 239–309.
- Kamoshita A, Chandra Babu R, Manikanda Boopathi N and Fukai S, 2008. Phenotypic and genotypic analysis of drought resistance traits for development of rice cultivars adapted to rainfed environments. *Field Crops Research* 109: 1–23.
- Kumar R, Venuprasad R and Atlin GN, 2007. Genetic analysis of rainfed lowland rice drought tolerance under naturally occurring stress in eastern India: heritability and QTL effects. *Field Crops Research* 103: 42–52.
- Lanceras JC, Pantuwan G, Jongdee B and Toojinda T, 2004. Quantitative trait loci associated with drought tolerance at reproductive stage in rice. *Plant Physiology* 135: 384–399.
- Lafitte HR, Price AH and Courtois B, 2004. Yield response to water deficit in an upland rice mapping population: associations among traits and genetic markers. *Theoretical and Applied Genetics* 109: 1237–1246.
- Lanceras JC, Pantuwan G, Jongdee B and Toojinda T, 2004. Quantitative trait loci associated with drought tolerance at reproductive stage in rice. *Plant Physiology* 135: 384–399.
- Lanceras JC, Pantuwan G, Jongdee B and Toojinda, T, 2004. Quantitative trait loci associated with drought tolerance at reproductive stage in rice. *Plant Physiology* 135: 384–399.
- Lang NT and Buu BC, 2008. Fine mapping for drought tolerance in rice (*Oryza sativa* L.). *Omonrice* 16: 9–15.
- Lebreton C, LazicJancic V, Steed A and Pekic S, 1995. Identification of QTL for drought responses in maize and their use in testing causal relationships between traits. *Journal of Experimental Botany* 46: 853–865.
- Manly KF and Olson JM, 1999. Overview of QTL mapping software and introduction to Map Manager QTX. *Mammalian Genome* 10: 327–334.
- McCouch SR, Teytelman L, Xu Y, Lobos K, Clare K and Walton M, 2002. Development of 2243 new SSR markers for rice by the international rice microsatellite initiative. *DNA Research* 9: 199–207.
- O’Toole JC and Namuco OS, 1983. Role of panicle exertion in water stress induced sterility. *Crop Science* 23(6): 1093–1097.
- Pantuwan G, Fukai S, Cooper M, Rajatasereekul S and O’Toole JC, 2002. Yield response of rice (*Oryza sativa* L.) genotypes to drought under rainfed lowlands. 3. Plant factors contributing to drought resistance. *Field Crops Research* 73: 181–200.

- Ribaut JM, Jiang C, Gonzalez de Leon, D, Edmeades GO and Hoisington DA, 1997. Identification of quantitative trait loci under drought conditions in tropical maize: Part 2. Yield components and marker-assisted selection strategies. *Theoretical and Applied Genetics* 94: 887–896
- Saghai Maroof MA, Biyashev RM, Yang GP, Zhang Q and Allard RW, 1994. Extraordinarily polymorphic microsatellite DNA in barely species diversity, chromosomal location, and population dynamics. *Proceedings of the National Academy of Sciences, USA* 91: 5466–5570.
- Sakamoto T and Matsuoka M, 2008. Identifying and exploiting grain yield genes in rice. *Current Opinion Plant Biology* 11:209–214.
- Tanksley SD, 1993. Mapping polygenes. *Annual Review of Genetics* 27: 205–233.
- Temnykh S, Park WD, Ayres N, Cartinhour S, Hauck N, Lipovich L, Cho YG, Ishii T and McCouch SR, 2000. Mapping and genome organization of microsatellite sequences in rice (*Oryza sativa* L.). *Theoretical and Applied Genetics* 100: 697–712.
- Wang S, Basten CJ and Zeng ZB (2005) Windows QTL Cartographer 2.5. Department of Statistics, NCSU, Raleigh, NC. <http://statgen.ncsu.edu/qtlcart/WQTLCart.htm>.
- Xing Y and Zhang Q, 2010. Genetic and molecular bases of rice yield. *Annual Review of Plant Biology* 61: 421–442.
- Xu JL, Lafitte HR, Gao YM, Fu BY, Torres R and Li ZK, 2005. QTLs for drought escape and tolerance identified in a set of random introgression lines of rice. *Theoretical and Applied Genetics* 111: 1642–1650.
- Xu SB, Tao YF, Yang ZQ and Chu JY, 2002. A simple and rapid method used for silver staining and gel preservation. *Hereditas* 24: 335–336.
- Yamamoto T, Yonemaru J and Yano M, 2009. Towards the understanding of complex traits in rice: substantially or superficially? *DNA Research* 16: 141–154.
- Yue B, Xiong L, Xue W, Xing Y, Luo L and Xu C, 2005. Genetic analysis for drought resistance of rice at reproductive stage in field with different types of soil. *Theoretical and Applied Genetics* 111: 1127–1136.
- Yue B, Xue W, Xiong L, Yu Z, Luo L, Cui K, Jin D, Xing Y and Zhang Q, 2006. Genetic basis of drought resistance at reproductive stage in rice: separation of drought resistance from drought avoidance. *Genetics* 172: 1213–1228.
- Zhang Q, 2007. Strategies for developing green super rice. *Proceedings of the National Academy of Sciences USA* 104: 16402–16409.
- Zou GH, Mei HW, Liu HY, Liu GL, Hu SP, Yu XQ, Li MS, Wu JH and Luo LJ, 2005. Grain yield responses to moisture regimes in a rice population: association among traits and genetic markers. *Theoretical and Applied Genetics* 112: 106–113.