



QTLs MAPPING FOR RICE (ORYZA SATIVA SPP.) GRAIN YIELD AND RELATED TRAITS UNDER DROUGHT AND IRRIGATED CONDITIONS

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ABSTRACT

Drought stress is a major limitation to rainfed rice production. Identifying quantitative trait loci (QTLs) with consistent effects on grain yield under drought stress will assist to develop high-yielding rice varieties. Therefore 187 lines from the cross between NERICA3 and NERICA4 were used to identify QTLs for grain yield, flowering date and plant height under control irrigated and drought stress conditions. The F2 progenies were used for genotyping following Genotyping by Sequencing (GBS) method and F3 progenies were phenotyped in irrigated upland and repeated drought stress under a rainout shelter. The experiments were conducted in an Alpha lattice design in both environments. A total of three traits were recorded including grain yield, days to 50% flowering (DF) and plant height (PH). As a result 61 QTLs were identified under both conditions including 55 for PH, three (3) for DF and three (3) for grain yield. The three QTLs identified for grain yield were identified only under drought condition and no QTL found in control irrigated condition. The results provide a good foundation and will be useful for genomics-assisted breeding for selection of drought tolerant genotypes in rice breeding.

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INTRODUCTION

Rice is one of the most important cereal crop in the world and it is the primary food source for more than the half of global population. It contributes to 30 to 50% of the daily caloric intake. It grain contains about 75 to 80% starch, 12% water, 7% protein and some minerals like calcium, magnesium, phosphorus with some traces of iron, copper, zinc and manganese (Fairhurst and Dobermann, 2002; Oko *et al.*, 2012 and Hossain *et al.*, 2015). Among different rice ecosystems, irrigated system occupy about 50% of total rice area and contribute for 75% of global rice production, while the other half of global rice area is occupy by rainfed upland and lowland rice (Zeigler and Barclay, 2008 and Swamy *et al.* 2017).

Despite its importance, rice is severely constrained by several biotic and abiotic factors that reduce rice yield particularly in Africa where the lowest rice yield, around 2.5 t.ha⁻¹ is found, compared to global average yield of about 4.5 t.ha⁻¹. Among the major constraints, abiotic factors particularly drought stress constitutes a serious yield limiting challenge in rice

production. Drought is one of the most important abiotic stresses affecting plant growth and reducing crop productivity, which has been estimated to affect 70% of crop yield (Lanceras *et al.* 2004 and Lang *et al.* 2013). According to Bate *et al.*, (2008) and Wassmann *et al.*, (2009) water deficit will be deteriorated in the years to comes, due to climate change effects and the intensity and frequency of drought are predicted to become worse. Thus, developing new rice varieties combined high yield with greater adaptability to drought is important to reduce climate related risk and offset the reduction of rice yield in rainfed areas.

Breeding based in phenotypic traits has been used a long time with some success (Zhang *et al.*, 2006). However, this approach is time consuming and laborious. In addition, drought tolerance is a complex trait controlled by minor and major genes that are dependent on the environment (Sabouri *et al.*, 2013). Therefore, selection based only on phenotype, would be difficult for such traits (Dashti *et al.*, 2007). Thus, molecular markers can help in identification of quantitative trait loci (QTL) associated with grain yield and its components under drought condition and their indirect selection using marker assisted selection.

QTLs associated to grain yield and its related traits under drought stress condition have been identified and mapped on

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different rice chromosome in several studies (Bernier *et al.* 2007; Kumar *et al.* 2007; Kamoshita *et al.* 2008; Vikram *et al.*, 2011 and Yadaw *et al.*, 2013). Kumar *et al.* (2007) and Bernier *et al.* (2007) detected respectively a major QTLs on chromosome 1 and 12 with consistent effects on grain yield under drought stress condition. It should be noted that most of previous studies were done out of African continent and parental combinations were indica x indica, Indica x Japonica and Japonica x Japonica. However the NERICA type was rarely used.

The present study was conducted at Africa Rice Centre, Ibadan station in Nigeria with the objectives to map consistent QTLs for grain yield and its components in a mapping population developed by crossing a drought susceptible rice variety, NERICA 3, and a drought tolerant variety, NERICA 4, under control and drought stress conditions.

MATERIALS AND METHODS

Study area

The phenotyping study was carried out in 2013 at Ikenne, a substation of the International Institute of Tropical Agriculture (IITA) based in Nigeria. Ikenne is located in Nigeria at 6°52' N latitude, and 3°43' E longitude of about 70 m above mean sea level. The soil type is clay loamy with pH range of 4.5 - 5.4 and annual rainfall of 1300 to 1500 mm.

Mapping population

NERICA3, a drought susceptible rice variety was used as a female parent to cross with NERICA4, a drought tolerant variety. F₂ population comprising of 187 individual and their parents were used to identify and map QTLs for grain yield and its components under control and drought stress conditions. The F₂ progenies and their descendant F₃ were used respectively for genotyping and phenotyping, respectively. The population was developed at Africa Rice Ibadan station and phenotyped under rainout shelter at Ikenne's research station.

Phenotyping under drought and control conditions

Trials management

The whole F₃ populations were evaluated under control and drought stress conditions. Under each condition the trial was conducted in alpha lattice designs with two replications. The elementary plots were two-rows of 2 m length. Four seeds were sown per hill, spaced by 20 × 20 cm and thinned to two plants after emergence. Spacing between rows was 20 cm. Fertilizer was applied at the rate of 50-50-50 kg NPK ha⁻¹ (as basal treatment) at 10 days after sowing. Plots were maintained weed-free during the trials by hand-weeding. Sprinkler irrigation was provided once in 3 days for 4 hours duration for the first 7 weeks. As top dress, 40 kg/ha⁻¹ of urea 46-0-0 was applied at 49 days after sowing in each plot. After the top dressing fertilizer application, the whole experiment was irrigated once and thereafter the water stress was immediately imposed in the stress environments. Irrigation was withheld until soil water tension (measured by tensiometer installed in the fields) reached about -75 KPa at 15 cm and -60 KPa at 30 cm soil depth. Trials were then re-irrigated until soil was saturated in the root zone. The stress cycle was then repeated. This irrigation regime resulted in stress levels that caused leaf rolling and tip drying at the end of each drought cycle. The

repeated cycles of stress ensured that all entries experienced stress during the sensitive stage of 15 days around flowering.

Traits measurements

Data of three traits were collected including days to 50% flowering (DF), plant height (PH) and grain yield (GY) in both trials. Days to 50% flowering was recorded when the panicle was exerted in approximately 50% of the plants in a plot and plant height were recorded during maturity period. Grains from each plot were harvested, dried at moisture content of 14%, and weighed.

Genotyping

Young leaf samples of 187 F_{2,3} progenies from NERICA3 X NERICA4 and the two parents were collected and were kept at -20°C in a freeze for conservation. Genomic DNA was extracted in IITA Central biotechnology laboratory in 2015 using the Qiagen plex DNeasy kit as per the Qiagen fresh leaf tissue 96 – plex protocol protocol (www.qiagen.com/KB/DNeasy96Plant). Quality and quantity of DNA was checked by running aliquots of DNA samples on 2% agarose gel. Concentration of isolated DNA was estimated based on the band brightness and thickness compared with those of the reference λ DNA. DNA was then normalized and shipped to Genomic Diversity Facility, Cornell University Institute of Biotechnology (<http://www.biotech.cornell.edu/brc/genomic-diversity-facility>) for genotyping following Genotyping by Sequencing (GBS) method. Genomic DNA library was constructed following the method of Elshire *et al.* (2011). 288-plex sequencing using the Illumina HiSeq sequencer, and SNP calling based on the Nipponbare reference genome MSU release 7 (Kawahara *et al.* 2013). A total of 5,290 SNPs markers distributed throughout the rice genome were used for this study. The data of segregating markers (861) were then used to perform QTLs analysis.

Statistical analysis

Phenotyping analysis

Phenotypic data recorded for days to flowering (DF), plant height (PH) and grain yield (GY) from F₃ progenies and their parents, were subjected to statistical analysis. Analysis of variance (ANOVA) was performed to access the genotype effect using GenStat 15th edition software (Payne *et al.*, 2011). In order to assess and quantify the genetic variability among F₃ progenies. Phenotypic and genotypic coefficients of variance were estimated according to Burton (1952). The heritability in broad sense was estimated using the formula given by Johnson *et al.* (1955).

$$GCV = \frac{\sqrt{Vg}}{X} 100$$

$$PCV = \frac{\sqrt{Vp}}{X} 100$$

Where GCV= genotypic coefficient of variability; PCV= phenotypic coefficient of variability; \sqrt{Vg} = genotypic standard deviation; \sqrt{Vp} = phenotypic standard deviation and X= general mean of the character

$$H^2 = \frac{Vg}{Vp} 100$$

Heritability in broad sense (H^2) was computed as the ratio of genetic variance (V_g) to the total phenotypic variance (V_p).

QTL analysis

Genotypic data obtained and the phenotypic data for three traits including days to flowering (DF), plant height (PH) and grain yield (GY) under control and drought stress conditions were used for QTL analysis using QTL IciMapping V.4.1 software (Meng *et al.* 2015). Inclusive Composite Interval Mapping (ICIM) method was performed to detect QTL-marker for grain yield and its components under control and water stress conditions. LOD value of 4.0 was selected as the minimum to declare the presence of a QTL in a given genomic region. Additive effects (Add) and percentage of phenotypic variance explained (PVE) of QTLs detected were also estimated.

RESULTS

Phenotypic analysis of parents and population

Under irrigated and drought stress conditions, the parents, NERICA3 and NERICA4 showed significant differences in respect of all the traits studied (Table 1). NERICA4 showed higher mean values than NERICA3 for plant height (PH) and grain yield irrespective to the water regime, whereas NERICA3 is late flowering (DF) than NERICA4 in both condition. In the global F3's population, there was a reduction in days to flowering, plant height and grain yield under drought stress condition compared with control condition indicating the effect of drought stress on plant growth. The genetic parameters estimated under drought stress revealed low (<10%) to high (>20%) phenotypic values (PCV) and genotypic coefficient of variation (GCV). GCV was 3.41% for plant height and 48.84% for grain yield, and PCV was 5.09% and 60.86% for plant height and grain yield, respectively. In addition, PCV estimates were higher than their corresponding GCV for all traits studies. Broad-sense heritability (H^2) estimates under drought stress condition showed high heritability 78.31% and 64.41% for days to flowering (DF) and grain yield, respectively. Plant height recorded medium heritability (44.88%).

Identification of QTLs under drought and normal

irrigated conditions

QTLs for plant height (PH)

Fifty five QTLs for plant height (PH) were identified and mapped to the eleven rice chromosomes excepted in chromosome 7 (Table 2 and Figure 1). Fourteen QTLs were identified under control condition only with their additive effect ranged from -3.90 to 5.62 recorded with *qPH-1-1* (chromosome 1) and *qPH-5-1* (chromosome 5); and their proportions of total phenotypic variances explained (R^2 %) were ranged from 0.32% to 2.40% showed with *qPH-10-1* (chromosome 10) and *qPH-5-1* (chromosome 5), respectively. Thirty seven QTLs were detected only under drought stress condition; their additive effect varied from -4.61 (*qPH-9-5* mapped in chromosome 9) to 4.73 (*qPH-8-9* and *qPH-8-10* mapped in chromosome 8). In addition their phenotypic variance explained were ranged from 0.75% (*qPH-9-1*, *qPH-9-3* and *qPH-9-4*) to 1.01 (*qPH-3-3*). Based on the differential behaviors, plant height QTLs identified in this study could be classified into three types. Type I included 14 QTLs mapped in

chromosomes 1; 2; 3; 4; 5; 8; 10; 11 and 12 which were expressed only under control irrigated condition. Favorable alleles for almost of these QTLs were from susceptible parent (NERICA3) except *qPH-5-1* mapped in chromosome 5 which showed positive additive effect. Type II included 37 QTLs, which expressed only in drought stress condition but not under control condition, suggesting they were apparently induced by stress. Almost of these QTLs recorded positive additive effect except ten QTLs (*qPH-2-3*, *qPH-3-5*, *qPH-4-2*, *qPH-4-3*, *qPH-5-3*, *qPH-6-5*, *qPH-6-6*, *qPH-9-1*, *qPH-9-5* and *qPH-12-2*) which showed negative additive effect. All of the QTLs mapped in chromosome 9 were identified only under drought stress condition. Type III included four QTLs *qPH-2-5*, *qPH-6-5*, *qPH-6-6* and *qPH-8-1* which were detectable under both conditions. Among these common QTLs, positive alleles of *qPH-6-5* and *qPH-6-6* were from NERICA3 under drought stress condition and were from NERICA4 under control condition; those of *qPH-2-5* and *qPH-8-1* were from NERICA4 under stress condition and were from NERICA3 in control condition.

QTLs for day to flowering (DF) and grain yield

Several QTLs were associated to days to flowering and grain yield under both conditions (Table 3 and Figures 2 and 3). Three QTLs were identified for days to flowering and mapped on chromosomes 1; 9 and 12 (Table 3 and Figure 2). Among these QTLs, *qDF-1* and *qDF-9* were identified under control condition, their additive effects were respectively of 0.58 and 0.07 and their contribution to phenotypic variation (R^2 %) were respectively of 3.42% and 7.15%. Only one QTL (*qDF-12*) was identified for days to flowering under stress condition (Figure 2) and the positive alleles were from tolerant parent NERICA4.

A total of three QTLs also were identified for grain yield mapped on chromosomes 1 and 12. These three QTLs were identified only under drought stress condition (Table 3 and Figure 3). The two QTLs, *qYield-1-1* and *qYield-12-2*, showed negative additive effects of -10.10 and -4.02, respectively, indicating that their favorable alleles were from susceptible parent NERICA3. The major QTL, *qYield-12-1*, was identified for grain yield on chromosome 12 located at 45.97 cM between S12_954678-S12 and S12_2437220, LOD score of 5.56 with 11.43% phenotypic variation explained (R^2 %). This QTL pinpointed positive additive effects (7.62), indicating that allele at this locus increase grain yield under drought stress condition and come from tolerant parent NERICA4.

DISCUSSION

Phenotyping analysis

Drought stress is the major abiotic stress limiting rice production. Developing rice varieties with high grain yield under drought stress condition is necessary to increase rainfed rice production. In the present study, both the parents have been found to differ in their response to the induced drought stress. Susceptible parent NERICA3 showed significant low response in respect of grain yield. This result is in agreement with the findings of Cui *et al.* (2008); Srividhya *et al.* (2011) and Ahmadikhah and Marufinia, (2016) who have reported that water deficit contribute to inhibit grain yield in rice. Analyses of variance showed significant difference between genotypes for all traits studies under drought stress condition, indicating differential response of genotypes under water stress

Table 1 Trial means, range and broad-sense heritability for days to flowering, plant height and grain yield under control and drought stress conditions for the two parents (Nerica 3 and Nerica 4) and the F3's population

Traits	Treatments	N4	N3	F3 population		Fproba	GCV	PCV	H ² %
				range	Mean				
DF	control	45.5	46.25	46 – 58	55.27	**	6.61	7.47	78.31
	stress	52.62	59.12	46 – 79	53.05				
PH	control	107.75	103.5	126 – 146	129.33	**	3.41	5.09	44.88
	stress	114.5	104.6	65.33 – 126	101				
Yield	control	179.57	132.287	25.85 – 207.6	105.12	**	48.84	60.86	64.41
	stress	174.9	69.82	3.3 – 197	54.36				

DF: days to flowering, PH: plant height, N4: Nerica4, N3: Nerica3, GCV: genotypic coefficient of variance, PCV: phenotypic coefficient of variance, H²%; heritability in broad sense

Table 2 QTLs for plant height under control and drought stress conditions identified from the NERICA3 X /NERICA4 population

QTLs	Ch	Position	marker interval	LOD	control		stress	
					R ² %	Add	R ² %	Add
qPH-1-1	1	1316.45	S1_6492975 – S1_7245656	4.94	0.94	-3.90		
qPH-1-2	1	211.45	S1_2371246 – S1_2890241	9.27			0.95	4.71
qPH-1-3	1	823.45	S1_4852728 – S1_4979038	11.07			0.94	4.70
qPH-1-4	1	884.45	S1_4979038 – S1_4979046	7.19			0.92	3.30
qPH-1-5	1	1207.45	S1_5781984 – S1_6217168	9.22			0.95	4.72
qPH-1-6	1	12418.45	S1_34834808 – S1_34949558	6.35			0.92	3.32
qPH-1-7	1	12438.45	S1_34949558 – S1_35016706	6.35			0.92	3.32
qPH-2-1	2	7.48	S2_348477 – S2_790040	8.90	0.91	-3.79		
qPH-2-2	2	25.48	S2_841537 – S2_841539	8.59	0.92	-3.87		
qPH-2-3	2	22.48	S2_841537 – S2_841539	6.61			0.77	-4.22
qPH-2-4	2	73.48	S2_1764567 – S2_2404722	10.81			0.93	4.68
qPH-2-5	2	795.48	S2_6278855 – S2_6550284	6.70	0.96	-3.75	0.98	4.61
qPH-3-1	3	840.52	S3_8747428 – S3_10367805	6.11	0.89	-3.86		
qPH-3-2	3	234.52	S3_3833833 – S3_4136216	5.38			0.90	3.64
qPH-3-3	3	438.52	S3_5442750 – S3_6162276	6.64			1.01	4.59
qPH-3-4	3	1210.52	S3_12119078 – S3_12236280	6.67			0.93	4.67
qPH-3-5	3	1231.52	S3_12236280 – S3_12788569	5.16			0.75	-4.17
qPH-4-1	4	5631.23	S4_21337508 – S4_21845412	7.12	0.90	-3.79		
qPH-4-2	4	10532.23	S4_26227453 – S4_26309776	8.92			0.94	-4.71
qPH-4-3	4	10557.23	S4_26309776 – S4_26309780	7.92			0.94	-4.71
qPH-4-4	4	17917.23	S4_35027625 – S4_35027627	6.83			0.75	4.16
qPH-5-1	5	1902.41	S5_14855174 – S5_14855176	13.33	2.40	5.62		
qPH-5-2	5	881.41	S5_9802816 – S5_10772598	4.49			0.92	3.27
qPH-5-3	5	3264.41	S5_17215523 – S5_17215529	5.84			0.78	-4.14
qPH-6-1	6	43.32	S6_2133744 – S6_2234638	12.36			0.94	4.66
qPH-6-2	6	58.32	S6_2234638 – S6_3947314	11.22			0.96	4.64
qPH-6-3	6	177.32	S6_5036280 – S6_5038191	6.77			0.93	3.25
qPH-6-4	6	895.32	S6_7921641 – S6_8187015	7.35			0.92	3.29
qPH-6-5	6	6239.32	S6_29148653 – S6_30069929	9.70	0.90	3.86	0.99	-4.74
qPH-6-6	6	6274.32	S6_30069929 – S6_30785062	10.19	0.90	3.86	0.99	-4.74
qPH-8-1	8	515.77	S8_4834100 – S8_5066310	12.10	0.87	-3.84	0.96	4.64
qPH-8-2	8	5006.77	S8_23761736 – S8_24056070	5.02	0.93	-3.78		
qPH-8-3	8	5034.77	S8_24056070 – S8_24906814	5.03	0.93	-3.78		
qPH-8-4	8	7419.77	S8_27912087 – S8_28126604	10.06	0.88	-3.80		
qPH-8-5	8	7425.77	S8_28126604 – S8_28173582	10.04	0.89	-3.80		
qPH-8-6	8	533.77	S8_5066310 – S8_5753624	11.48			0.96	4.64
qPH-8-7	8	1574.77	S8_14284283 – S8_17321570	7.85			0.92	3.30
qPH-8-8	8	1588.77	S8_17321570 – S8_17321571	7.84			0.91	3.30
qPH-8-9	8	3601.77	S8_22477705 – S8_23353847	10.15			0.95	4.73
qPH-8-10	8	3610.77	S8_23353847 – S8_23411919	10.14			0.95	4.73
qPH-9-1	9	10.16	S9_422846 – S9_756767	6.07			0.75	-4.21
qPH-9-2	9	271.16	S9_6538236 – S9_7342589	8.38			0.94	4.71
qPH-9-3	9	5396.16	S9_20933240 – S9_21321668	8.08			0.75	4.20
qPH-9-4	9	5399.16	S9_21321668 – S9_22188617	8.08			0.75	4.20
qPH-9-5	9	5402.16	S9_21321668 – S9_22188617	11.42			0.95	-4.61
qPH-10-1	10	5190.08	S10_19014035 – S10_19530679	4.07	0.32	-0.57		
qPH-10-2	10	7325.08	S10_22469404 – S10_22541201	12.39			0.95	4.62
qPH-11-1	11	2948.48	S11_18626048 – S11_18827168	5.83	0.87	-3.83		
qPH-11-2	11	2970.48	S11_18827168 – S11_19048709	5.79	0.87	-3.83		
qPH-11-3	11	115.48	S11_2333320 – S11_2457740	8.63			1.00	4.60
qPH-11-4	11	135.48	S11_2457740 – S11_2462765	9.24			0.95	4.65
qPH-11-5	11	164.48	S11_2462765 – S11_2672234	11.16			0.95	4.70
qPH-11-6	11	189.48	S11_2672234 – S11_3707207	9.66			0.95	4.71
qPH-12-1	12	189.97	S12_2549538 – S12_3009662	7.81	0.90	-3.80		
qPH-12-2	12	7389.97	S12_25689428 – S12_26208429	8.10			0.76	-4.26

R²%; percentage of phenotypic variation explained; Add: additive effect; ch: chromosome

Table 3 QTLs for day to flowering and grain yield under control and drought stress condition identified from the NERICA3 X NERICA4 population

Traits	QTLs	Ch	Pos	marker interval	LOD	control		stress	
						R ² %	Add	R ² %	Add
DF	qDF-1	1	3795.45	S1_18851659 – S1_20944779	4.85	3.42	0.58		
	qDF-9	9	2.16	S9_115892 – S9_422846	7.20	7.15	0.07		
	qDF-12	12	748.97	S12_11184941 – S12_11184955	4.04			3.77	0.98
Yield	qYield-1-1	1	3228.45	S1_16597122–S1_17228464	4.15			7.18	-10.10
	qYield-12-1	12	45.97	S12_954678–S12_2437220	5.56			11.43	7.62
	qYield-12-2	12	295.97	S12_3088091–S12_3228903	4.13			7.36	-4.02

R²%: percentage of phenotypic variation explained; Add: additive effect; ch: chromosome; pos: position; DF: days to 50% flowering; Yield: grain yield

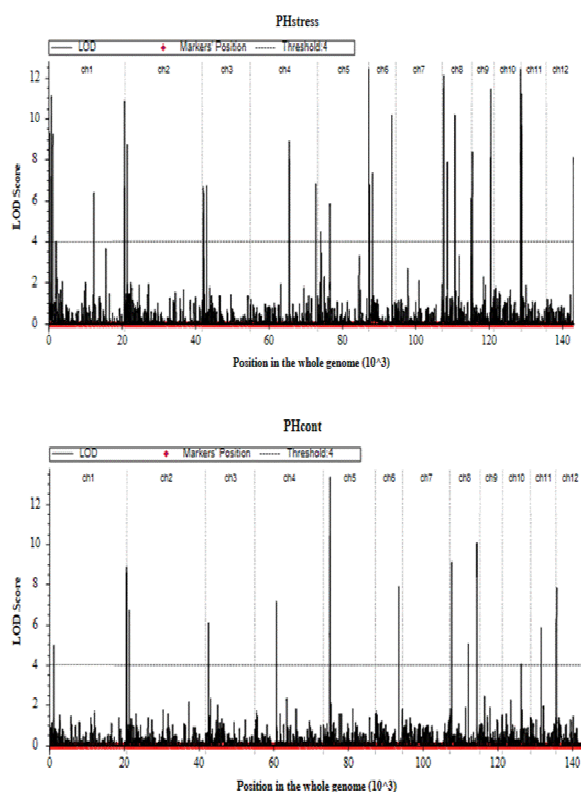


Figure 1 LOD profile of QTLs for plant height under control and drought stress conditions

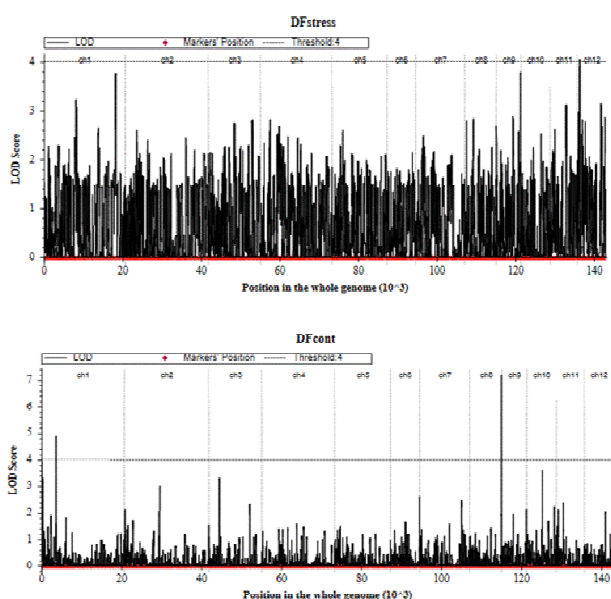


Figure 2 LOD profile of QTLs for days to flowering under control and drought stress conditions

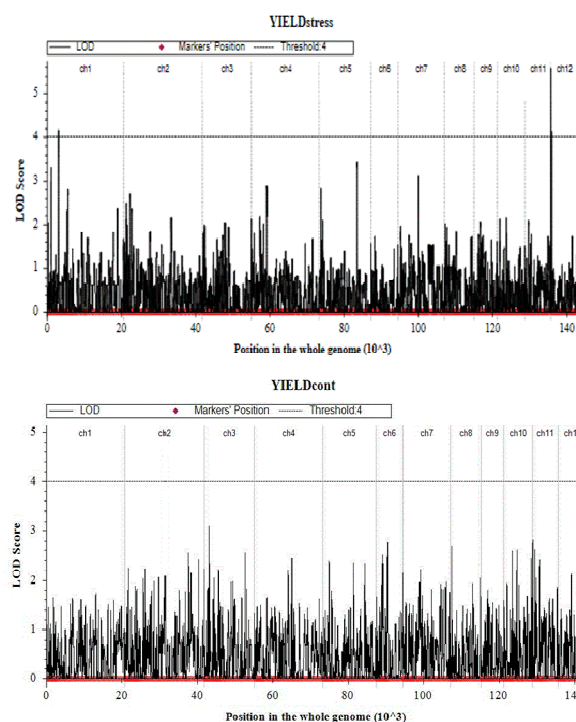


Figure 3 LOD profile of QTLs for grain yield under control and drought stress conditions

condition. Similar results were early reported by Mall *et al.*, (2012) and Verma *et al.* (2014). Grain yield recorded high phenotypic (PCV) and genotypic (GCV) coefficient of variations estimates indicating the importance of this trait in evaluation and selection of superior genotypes, whereas days to flowering and plant height showed lowest PCV and GCV under stress condition indicating that selection directly based on these traits would not be much rewarding. These results are in agreement with those of Pandey *et al.*,(2012), Uday Kumar *et al.* (2017) and Garg *et al.* (2017). Broad sense Heritability for days to flowering and grain yield were found to be higher under drought stress condition indicating a high response to selection in these traits. Similar results were early reported by Rafii *et al.*, (2014); Konaté *et al.* (2016); Uday Kumar *et al.* (2017) and Garg *et al.* (2017).

Genotyping analysis and QTLs identification

Out of the 5,290 SNPs markers genotyped in NERICA3 X NERICA4F_{2:3} population, 861 (16.25%) were found to be polymorphic. The number of markers varied on different chromosomes. Genotypic data from these polymorphic markers and field based phenotypic data of plant height (PH), days to flowering (DF) and grain yield were used conjointly to perform QTL analysis followed Inclusive Composite Interval

Mapping method. In this study, a total of 61 QTLs were identified included 55 QTLs associated to plant height, three (3) QTLs associated to days to flowering and as well three (3) other QTLs associated to grain yield. Sixteen (16) QTLs were found to be involved only under the control condition (qPH-1-1; qPH-2-1; qPH-2-2; qPH-3-1; qPH-4-1; qPH-5-1; qPH-8-2; qPH-8-3; qPH-8-4; qPH-8-5; qPH-10-1; qPH-11-1; qPH-11-2; qPH-12-1; qDF-1; qDF-9) and forty one (41) QTLs were found to be involved only under drought stress condition, including 37 QTLs associated to plant height, one QTLs associated to days to flowering (qDF-12) and three (03) QTLs associated to grain yield (qYield-1-1; qYield-12-1 and qYield-12-2).

The QTLs for yield, day to flowering and plant height differ under the control and stress conditions. Thus, 37 seven QTLs were induced by drought stress. Similar results were early reported by Xuet *et al.* (2005); Venuprasad *et al.* (2012); Xing *et al.* (2014) and Verma *et al.* (2014). QTLs induced only on stress condition may be due to mechanisms of rice stress response. Thus the difference in gene expression between the two environments could be due to different QTLs or different alleles of the same QTL or a set of QTLs being responsible for the expression of the target traits under control and drought stress conditions (Xing *et al.* 2014). Only four (04) QTLs (qPH-2-5; qPH-6-5; qPH-6-6 and qPH-8-1) were identified in both conditions suggesting that a small proportion of QTLs appear in different environments. These results are in agreement with those of Xuet *et al.* (2005) and Xing *et al.* (2014). In addition these QTLs had effects in opposite direction under control and drought stress condition, indicating that they are affecting by drought. Percentage of phenotypic variation explained ($R^2\%$) were generally very low ($<5\%$) for almost QTLs identified except qDF-9; qYield-1-1; qYield-12-1 and qYield-12-2, indicating minor effect QTLs. Small-effect QTLs for complex traits such as yield under drought condition were also identified in rice by Bernier *et al.* (2007); Zhou *et al.* (2011) and Dixit *et al.*, (2012), in maize by Ribaut *et al.* (1997) and in groundnut by Faye *et al.* (2015). According to Collar *et al.* (2005), only qYield-12-1 associated to grain yield which recorded $R^2\%$ more than 10% could be considered like major QTL.

Most of QTLs identified for plant height under drought stress were reported in previous studies. Thus, qPH-9-1; qPH-9-2 and qPH-9-5 were early identified in the same position by Jiang (2011) and Xing *et al.* (2014). Using RIL population from a cross between indica rice Teqing and japonica rice Lemont, Xu *et al.* (2005) has identified 14 QTLs associated to plant height under stress condition. 12 of these QTLs located in chromosome 1; 2; 3; 4; 5; 6; 8; 9; 10; 11 and 12 were also mapped in the same region in this study. Six QTLs identified for plant height in this study including qPH-1-2; qPH-1-3; qPH-1-6; qPH-2-4; qPH-8-6 and qPH-9-5 were also reported previously in the same region by Prince *et al.* (2014). All the three QTLs (qDF-1; qDF-9 and qDF-12) identified for days to flowering (DF) under drought stress condition in this study were also identified by previous studies (Li *et al.* 2003; Chakraborty and Zeng, 2011 and Lang *et al.* 2013). A total of three QTLs were mapped in chromosome 1 and 12 for grain yield only under drought stress condition, indicating that these QTLs are induced by drought. The QTLs qYield-1-1 ; qYield-12-1 and qYield-12-2 were early mapped in the same region by previous researchers (Kumar *et al.*, 2007; Bernier *et al.*,

2007; Srividhya *et al.* 2011 ; Dixit *et al.*, 2012; Trijatmiko *et al.* 2014; Verma *et al.* 2014; Swamy *et al.* 2017). qYield-1-1 and qYield-12-1 were early reported by Kumar *et al.*, (2007); Bernier *et al.*, (2007); Bernier (2008); Gomez *et al.*, (2010); Vikram *et al.*, (2011); Dixit *et al.*, (2012) Mishra *et al.*, (2013) Yadav *et al.*, (2013), and Verma *et al.* (2014), which contribute significantly for grain yield under drought stress condition. These two QTLs are considered like major QTLs with a consistent effect on grain yield under drought in rice (Bernier *et al.* 2008; Vikram *et al.* 2011 and Mishra *et al.* 2013). The other QTL for grain yield, qYield-12-2, identified on chromosome 12 under drought stress condition seems to be a new QTL and can be designate as qYield-12-2. However its recorded negative additive effect indicating that the favorable allele is from susceptible parent NERICA3. Sometimes, the desirable allele of a QTL may be present in poor parent.

CONCLUSION

This study provided much more contribution on the genetic basis of drought tolerance in rice. A total of 61 QTL were identified for the plant height, days to flowering and grain yield with alleles from both parents contributing to increased trait values. Several genetic regions were associated with more than one trait, indicating possible linked and/or pleiotropic effects. Major QTLs for grain yield under drought stress condition were identified on chromosome 1 and 12 and can be useful in marker assisted breeding for drought tolerance in rice. In addition several new QTLs were also identified for plant height and days to 50% flowering under control and drought stress conditions and need to be confirmed in the future.

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