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QUANTITATIVE TRAIT LOCI (QTL) ANALYSIS OF GENOMIC REGIONS ASSOCIATED WITH YIELD COMPONENT TRAITS IN A RECOMBINANT INBRED LINE POPULATION OF RICE (ORYZA SATIVA L.)

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ABSTRACT

Six environments across three locations were used to evaluate 144 lines of a rice recombinant inbred line (RIL) population derived from a cross of Kogoni91-1 and IR64. Five traits including days to 50% flowering, plant height, number of grains per panicle, thousand kernels weight and grain yield were recorded. Further, this population was genotyped with 228 single nucleotide polymorphism markers (SNP). Significant differences ($P < 0.001$) were recorded among genotypes for all traits except for GY. Therefore, QTL analyses were performed on the combined phenotype data of the four traits by excluding grain yield. Composite interval mapping (CIM) analysis detected 12 QTLs. Among these, six (*qPH8*, *qPH3*, *qPH2*, *qTKW2*, *qNGP4* and *qNGP8*) are novel and reported for the first time and two are major QTLs, *qPH8* (R^2=16.8) and *qTKW2* (R^2=16.6). These novel QTLs will be suitable for fine mapping and map-based cloning studies. The remaining six had occurrences corresponding to QTLs reported in mapping populations previously. Pyramiding the identified major QTLs could be highly helpful for breeding programs to increase rice grain yield potential. The study confirms that the RIL population used constitutes a prominent source of variability for traits of complex inheritance.

INTRODUCTION

Rice (*Oryza sativa* L.) is a major cereal crop, feeding at least half of the world population. It constitutes a principal source of calories and a staple food in many of the sub-Saharan African (SSA) countries, including Benin and Mali (Atera *et al*., 2011; Maclean *et al*., 2013). Rice grain yield is increasing at a faster rate in SSA than the world average. For example, between 2007 and 2011, the average rice yield in SSA increased by about 30%, which is equivalent to 108 kg ha^{-1} $year^{-1}$ (Seck *et al.*, 2013). Despite such remarkable increase in grain yield, the gap between demand and supply still remains very large due to several abiotic (drought, flood, salinity, cold and iron toxicity) and biotic (blast, rice yellow mottle virus, stem borers and African gall midge) stresses. Hence, self-sufficiency in the region may be achieved either by making more agricultural land available for rice cultivation or increasing rice yield per unit area by growing improved varieties that are stable and high yielding with minimal input requirements. Conventional breeding methods have a proven track record of developing improved germplasm combining a wide range of abiotic and biotic stress resistance. Most traits of interest in breeding are quantitatively inherited, dependent on the cumulative action of many genes or quantitative trait loci (QTL) and their interaction with the environment that can vary among individuals over a given range to produce a continuous distribution of phenotypes (Sham *et al*., 2002). Hence, progress with conventional methods is generally slow, mainly due to the polygenic nature of most traits associated with stress, requiring the simultaneous introgression of several genes or QTLs into one genotype.

Molecular markers can be used to speed up the development and deployment of improved germplasm in one of the following three ways: (i) for quality control analysis, which includes determination of genetic purity, genetic identity among multiple sources of the same cultivar and parent-offspring tests in segregating populations; (ii) for selecting parents for new pedigree starts; and (iii) for tracing the introgression of genes or QTLs of interest using marker-assisted selection (MAS). MAS involves finding a subset of markers that are significantly associated with genes or major effect QTLs (R^2 >15) that regulate the expression of traits of interest in artificially constructed biparental populations, such as F_2s, backcross (BC), doubled haploid lines (DH), recombinant inbred lines (RIL) and near isogenic lines (NIL) (Guo and Ye, 2014).

There are arrays of molecular markers (such as AFLP, RFLP and SSRs) for QTL analysis, but single nucleotide polymorphisms (SNPs) marker are gaining importance in diversity studies because of their high abundance (one SNP being observed per 140 base pair in rice), their ability to

generate polymorphism (Singh *et al*., 2013) and their low cost for genotyping. To date, SNP markers have been used in numerous studies regarding association genetics, genetic variation, linkage mapping, map-based gene isolation, population structure analysis and plant breeding (Konishi *et al.*, 2006; McNally *et al*., 2009; Thomson *et al*., 2012). SNP markers has been used to analyze levels and patterns of genetic diversity in two rice variety subgroups, *indica* and *japonica*(Feltus *et al*., 2004; McNally *et al*., 2009; Wade *et al*., 2015). A SNP map has been used to validate the positions of several cloned genes including GS3 and GW5/qSW5, two major QTLs for grain length and grain width respectively, and OsC1, a QTL for low shattering (Konishi *et al.*, 2006) and pigmentation traits (Yu *et al*., 2011).

Rice yield is either directly or indirectly affected by various yield related traits, including flowering time, plant height, number of grains per panicle, panicle length and thousand kernels weight (Venu *et al*., 2014; Ying *et al*, 2012). However, the correlation coefficients among these traits is highly variable, ranging from -0.3 to 0.94 (Atif and Khalid, 2013; Bocanski *et al*., 2009; Golam *et al*., 2011; Kishore *et al*., 2015; Rao *et al*., 2014).In another study conducted across four experiments, we found a significant ($p < 0.01$) positive phenotypic correlation between plant height and grain yield (0.66), thousand kernel weight and grain yield (0.58), and plant height and thousand kernel weight (0.54) (Sangare JR, Konaté K.A Cissé Fouseyni Sanni A, 2016. Article submitted for publication,)

Various QTL mapping studies have been conducted in rice (Kwon *et al*., 2011; Lafitte *et al*., 2004; Venuprasad *et al.*, 2012; Xu *et al*., 2015). The proportion of phenotypic variance explained by individual QTL was highly variable, with few QTLs showing large effect (Bernier *et al*., 2007; Kumar *et al*., 2014), while most QTLs generally explained a very small proportion of the phenotypic variance. Most QTLs are also often genetic background specific and remain undetected in crosses from different genetic backgrounds (Price *et al*., 2002; Miura *et al*., 2011). The objectives of the present study were to identify genomic regions associated with flowering, plant height, number of grains per panicle and thousand kernels weight in a RIL population derived from Kogoni91-1 and IR64 evaluated across six experiments executed over two years.

MATERIALS AND METHODS

Plant materials and phenotyping

The mapping population was developed by crossing Kogoni91-1 as the male parent and IR64 as a female parent. The Asian semi-dwarf popular high yielding variety IR64 was released by the International Rice Research Institute (IRRI) in 1985, and has been widely accepted as a high quality rice variety in many countries. Kogoni91-1 is a Malian elite high yielding variety accepted for its good organoleptic quality and it is wide adaption in SSA. F_1 plants were selfed to produce F_2s, which were selfed to produce F_3s. The F_3 plants were later advanced to 144 $F_{3:5}$s (RILs) through the single seed descent method. For each entry, seeds were sown in a seedling bed and seedlings were transplanted to a field 21 days later, with a single plant per hill spaced at 20 × 20 cm. Transplanting was done in an alpha lattice design with two replications in two consecutive growing years (2013-2014 and 2014-2015) at the Africa Rice research field in Cotonou (CTN2013a and CTN2014a; CTN2013b and CTN2014b) and at the Institute of Rural Economy (IER) field station in Longorola (LGL2013 and LGL2014), Mali. The four experiments in Cotonou were conducted from February to May 2013 and from June to September 2014. In Longorola, the field experiments were conducted from August to November 2013 and from July to October 2014. The field experiments in Cotonou were rainfed, with supplementary irrigation whenever needed, while the Longorola experiments were only rainfed. For all experiments, compound fertilizer (NPK 15-15-15) was applied at the rate of 200 kg ha^{-1} at transplanting, followed by 100 kg ha^{-1} urea (46% N) at 15 and 30 days after transplanting. The experiments were kept weed-free by regular hand weeding and bird damage in the field was controlled using bird scares.

For each experiment, we collected data of the following five traits that showed significant differences between the two parents (i) days to 50% flowering (DTF), which is the number of days from sowing up to the day when 50% of the plants from each plot had flowering tillers; (ii) plant height (PH) from the base to the tip of the tallest panicle at physiological maturity; (iii) number of grains per panicle (NGP); and (iv) thousand kernels weight (TKW). All panicles from each plot were harvested at physiological maturity, dried to a moisture content of about 14%, shelled and weighed, and used to estimate grain yield (GY) per hectare.

Genotyping

Genomic DNA was extracted from 2-week-old seedlings by bulking approximately equal leaf tissue of 10 healthy plants per line using the cetyltrimethyl ammonium bromide method (Murray and Thompson, 1980). DNA samples were shipped to LGC Genomics and genotyped using the KASP genotyping platform (LGC GENOMICS, http://www.lgcgroup.com/about-us/#.VyjoevnhDIU May 3, 2016). First, the parents were screened for polymorphism by genotyping them with a set of 2015 SNPs distributed across all the 12 chromosomes.

Statistical analyses

For each trait, the frequency distribution was computed using R3.2.2 software; analysis of variance (ANOVA) was conducted using XLSAT2015.3.01.19790 software and effects declared significant at 5% level. Heritability across all experiments and repeatability in each experiment was estimated using the Breeding Management System (BMS) Version 3.0.8 (2015) (INTEGRATED BREEDING SYSTEM, https://www.integratedbreeding.net/breeding-management-system May 9, 2016)which uses the generalized heritability measure (Cullis et al., 2006).

Linkage groups were established using LOD scores ranging between 3 and 15, and recombination frequency of 0.30. The order of the SNPs on each chromosome was determined using the Kosambi mapping function. $\chi 2$ analyses and linkage mapping were performed using JoinMap version 4.0 (Van Ooijen, 2006). A whole genome scan with composite interval mapping (CIM) was conducted using the PLABQTL software, version 1.2 (Utz and Melchinger, 2003) using the following options: a minimum LOD score of 3.0, a walking distance of 2 cM, automatic cofactor selection, model to determine additive effect at individual QTL and additive × additive epistatic interactions, and F-to-Enter value of ten.

Additive effect is half the difference between the genotypic values of the two parental homozygotes; the sign of the additive effect of each QTL was used to identify the parental origin of the favorable alleles. Genetic maps and QTL graphs were drawn using MapChart v2.1 (Voorrips 2002). Each QTL was named with a prefix q, followed by three letters representing the trait name, and chromosome number.

RESULTS

Phenotypic data

A wide variation was observed in the performance of the RILs for all four traits, which varied from 62 to 112 days for flowering, from 57 to 153 cm in height, from 22 to 145 grains per panicle, from 20 to 100 g for thousand kernels weight and from 0.4 to 7 $T.ha^{-1}$.the performance of the RIL and their two parents are presented in Table 1,on average across the six experiments, each line was about 91 cm tall, needed 93 days to reach 50% flowering, produced 55 grains per panicle with a thousand kernel weight of 27 g and produced 6 $T.ha^{-1}$ (Table 1). Analysis of variance performed on the combined data of the six experiments showed significant ($p < 0.0001$) differences among genotypes for all traits except grain yield (Table 1). The mean phenotype data of all five traits showed continuous variation and normal or approximately normal distribution (Fig 1). Broad sense heritability across the combined data of all six experiments was highly variable depending on trait complexity and varied from 0.19 for grains yield to 0.91 for days to flowering (Table 1).

The phenotypic correlation analysis revealed significant positive correlation between plant height and all other traits studied excepted thousand kernels weight. The only negative correlation was observed between NGP and TKW. Grain yield (GY) showed significant correlation with days to 50% flowering and plant height (Table 2)

Linkage and QTL mapping

Of the 2015 SNPs initially used for genotyping the two parents, only 244 (12.1%) were polymorphic between the two parents (Kogoni91-1 and IR64). These SNPs were used to genotype the mapping population.Table 3 shows summary of the distribution of the 244 polymorph SNPs across 12 chromosomes and the map length for each chromosome. The number of polymorphic SNPs varied from 12 on chromosomes 7 and 9 to 28 on chromosome 12, with an average of 20 SNPs per chromosome. Map length varied from 71 cM on chromosome 9 to 169 cM on chromosome 1, and the total map length across all 12 chromosomes was 1392 cM. Map distance between adjacent markers of each chromosome varied from 0.10 to 29.9 cM, with an overall mean of 6.4 cM. Most adjacent SNPs had a map distance that varied from 2.5 and 7.5 cM (Table 3).

Since ANOVA of the combined data from the six experiments showed significant ($p < 0.05$) differences among genotypes for all traits except grain yield, QTL analyses were performed on the phenotype data of the other four traits.

Table 1 Agronomic performance of 144 rice recombinant inbred lines (RIL) and their two parents Kogoni91-1 and IR64; and broad sense heritability for yield and 4 yield-related traits obtained by combined analysis over 6 experiments conductedat Cotonou and Longorola locations.

Trait	Kogoni91-1	IR64	RILs				Prob	H^2
			Mean	S.D	Max	Min		
DTF	88.91	91.57	93.01	3.64	103.12	84.41	***	0.91
PHT	87.66	82.30	91.15	4.13	109.86	83.20	***	0.77
NGP	60.67	57.38	54.87	8.47	90.36	47.27	***	0.65
TKW	30.30	25.39	27.36	1.48	31.50	24.08	***	0.85
GY	7.33	6.22	6.27	0.52	7.95	4.97	ns	0.19

DTF: days to 50% flowering (days), PH: plant height (cm), NGP: number of grains per panicle, TKW: thousand kernels weight (g), GY: grain yield (Tha^{-1}), SD: Standard Deviation, ***: significant at 1%, ns: not significant, Prob: Probability, H^2 Broad sense heritability

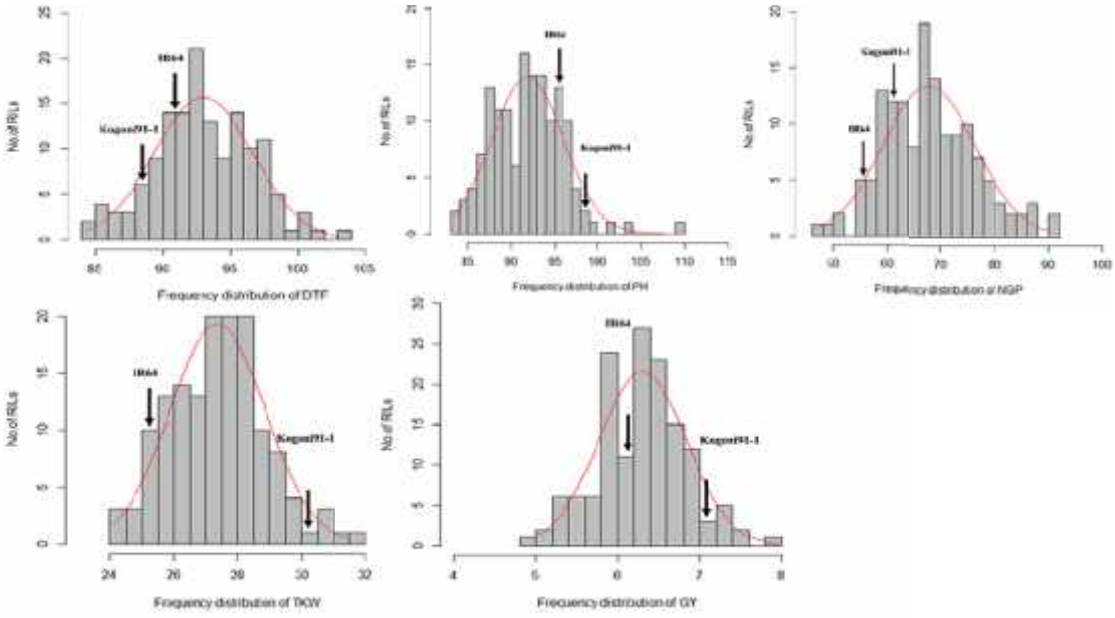

Figure 1 Phenotypic variation of Kogoni91-1 x IR64 derived recombinant inbred lines (RILs) for yield and four yield related-traits evaluated in six experiments conducted at Cotonou and Longorola locations;Parental trait means are indicated by arrows

Table 2 Phenotypic correlations testing the relationships among four yield related-traits evaluated in Kogoni91-1 x IR64 recombinant inbred lines (RILs) evaluated in six experiments conducted at Cotonou and Longorola locations

Variables	DTF	PHT	NGP	TKW	GY
DTF	1				
PHT	0.455**	1			
NGP	0.022	0.225**	1		
TKW	0.003	0.160	-0.311**	1	
GY	0.200**	0.193*	0.037	0.115	1

DTF: days to 50% flowering (days), PH: plant height (cm), NGP: number of grains per panicle, TKW: thousand kernels weight (g), *: significant at 5 and 1%

QTLs for PH, three QTLs for NGP and three QTLs for TKW. The two QTLs for DTF mapped at the tip of chromosome 3 (*qDTF3*) and at 26 cM on chromosome 6 (*qDTF6*) and explained 10.9 and 13.6% of the phenotypic variation, respectively (Fig 2). Together they accounted for 24.5% of the phenotypic variance for DTF across the six experiments. For both *qDTF3* and *qDTF6*, the favorable alleles originated from IR64; RILs homozygous to the IR64 alleles at the two flanking markers for *qDTF3* and q*DTF6* flowered about 2.5 and 4.5 days earlier, respectively, than those lines that were homozygous to the Kogoni91-1 alleles.

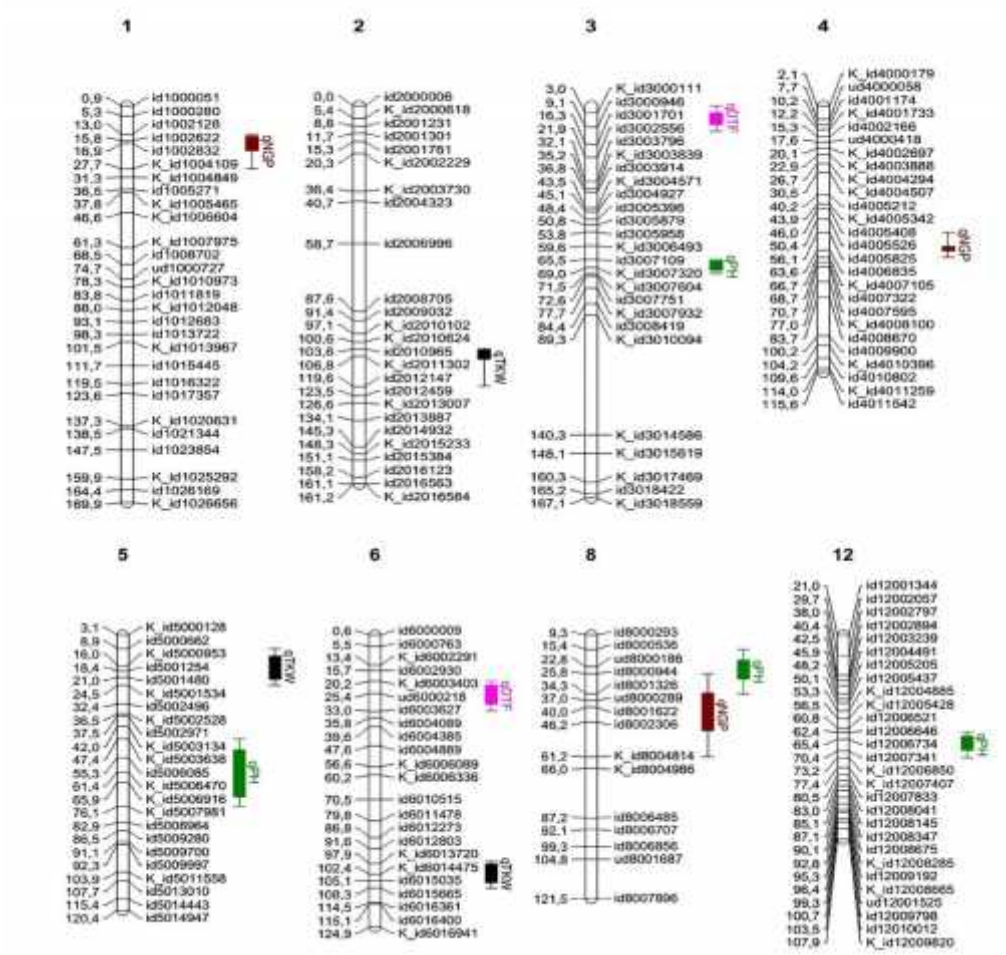

Figure 2 Genetic linkage map and QTLs for four yield related-trait identified on eight chromosomes in Kogoni91-1 x IR64 recombinant inbred lines (RIL) population.

Table 3 Distribution of the polymorphic SNP markers between the two rice RIL parents, Kogoni91-1 and IR64, and overview of map length and inter-marker interval in each of the 12 chromosomes

Chromosome	Total map length (cM)	Number. of polymorphic SNPs	Distance between adjacent markers (cM)	Distance between adjacent SNPs (range in cM)
1	169.0	28	6.3	1.1-14.7
2	161.1	25	6.7	0.1-28.9
3	164.0	25	5.3	1.1-12.3
4	113.5	26	5.2	1.6-16.6
5	117.4	23	5.9	1-14.7
6	124.3	23	5.6	0.7-10.3
7	95.3	12	5.0	0.9-20
8	112.2	15	8.6	2.7-21.2
9	71.7	12	8.7	1.3-22.5
10	79.9	13	6.5	1.3-27.9
11	96.9	14	7.5	1.6-29.9
12	86.9	28	3.2	1.2-8.7
Total	1392.1	244	6.2	0.1-29.9

Composite interval mapping (CIM) identified a total of 12 QTLs (Table 4), which includes two QTLs for DFT, four

Table 4 Summary of rice QTLs identified in the combined data of six experiments conducted at Cotonou and Longorola locations.

QTL	Trait	Chromosome	Position (cM)	Left marker	Right marker	Confidence interval (cM)	LOD	R^2 (%)	Additive effect	Origin of favorable allele
qDTF3	DTF	3	0	K_id3000111	id3002556	0-8	4.2	13.6	-2.3	IR64
qDTF6	DTF	6	26	ud6000218	id6003627	22-30	3.6	10.9	-4.5	IR64
qPH3	PH	3	68	K_id3007320	K_id3007604	66-70	3.6	10.9	-0.9	IR64
qPH5	PH	5	66	K_id5006470	K_id5007981	52-72	7.1	20.2	-4.4	Kogoni91-1
qPH8	PH	8	26	id8001326	ud8000289	20-28	5.7	16.8	-1.9	IR64
qPH12	PH	12	66	id12008145	id12008347	64-70	3.8	11.3	-2.5	Kogoni91-1
qNGP1	NGP	1	16	id1002622	id1002832	14-22	5.0	14.7	7.1	Kogoni91-1
qNGP4	NGP	4	62	id4006835	K_id4007105	56-64	4.9	14.4	7.1	Kogoni91-1
qNGP8	NGP	8	38	id8002306	K_id8004986	34-50	3.9	11.6	4.6	Kogoni91-1
qTKW2	TKW	2	112	K_id2011302	id2012147	104-108	5.7	16.6	0.9	Kogoni91-1
qTKW5	TKW	5	16	K_id5000953	id5001480	déc-22	3.8	11.5	1.3	IR64
qTKW6	TKW	6	102	K_id6014475	id6015035	98-106	3.6	11.1	1.1	Kogoni91-1

DTF: days to 50% flowering, PH: plant height, NGP: number of grains per panicle, TKW: thousand kernels weight, R^2: the percentage of phenotypic variance explained by the QTL, LOD: score *logarithm* (base 10) *of Odds*

The four QTLs for PH mapped at 68 cM on chromosome 3 (*qPH3*), at 66 cM on chromosome 5 (*qPH5*), at 26 cM on chromosome 8 (*qPH8*) and at 66 cM on chromosome 12 (*qPH12*) (Fig 2). Each QTL explained between 10.9 and 20.2% of the phenotypic variance and together accounted for 59.2%. The favorable alleles for *qPH3* and *qPH8* originated from IR64, while those of *qPH5* and *qPH12* originated from Kogoni91-1. The lines that were homozygous to IR64 alleles at flanking markers for *qPH3* and *qPH8* were 0.9 and 1.9 cm shorter than those lines that were homozygous to Kogoni91-1 alleles. In the same way, the lines that were homozygous to Kogoni91-1 alleles at the flanking markers for *qPH5* and *qPH12* were about 4.4 and 2.5 cm shorter than those lines that were homozygous for the IR64 alleles.

For NGP, there were three QTLs on chromosomes 1 at 16 cM (*qNGP1*), chromosome 4 at 62 cM (*qNGP4*) and chromosome 8 at 38 cM (*qNGP8*) (Fig 2). Each QTL explained between 11.6 and 14.7% of the phenotypic variance for NGP and together accounted for 40.7% of the variance. The favorable alleles for all three QTLs associated with NGP originated from Kogoni91-1, with lines that were homozygous to the favorable alleles at the two flanking markers of each QTL showing between 4.6 and 7.1 more grains per panicle than those that were homozygous for the unfavorable alleles from the IR64 parent.

The three QTLs for TKW were located on chromosome 2 at 112 cM (*qTKW2*), chromosome 5 at 16 cM (*qTKW5*) and chromosome 6 at 102 cM (*qTKW6*) (Fig 2). Each QTL for TKW individually explained between 11.1 and 16.6% of the phenotypic variance and together accounted for 39.2%. The favorable allele for *qTKW5* originated from IR64 and all lines that were homozygous to the IR64 alleles at the two flanking markers had a TKW that was 1.3 g higher than those lines that were homozygous for the Kogoni91-1 alleles. Kogoni91-1 contributed the favorable alleles for *qNGP2* and *qNGP6*, with lines homozygous to the Kogoni91-1 alleles at the two flanking markers of each QTL on average showing a TKW approximately 1 g higher than those lines that were homozygous for the IR64 alleles.

DISCUSSION

Discovering genomic regions affecting yield or yield related traits, is of paramount importance to increase the agricultural productivity needed to feed the world's growing population.

The first step in identifying these genetic regions is QTL analyses (Verbyla *et al.*, 2014). The main factors influencing QTL identification include population size, marker density and the parental genetic diversity. Of them, parental genetic diversity is the key factor because it controls the phenotypic variation in a population and largely determines the number of markers available for map construction (Tan *et al*., 2013). Here the Philippine high-yielding elite variety IR64 and the Malian elite variety Kogoni91-1 were included as female and male parent respectively because of their extreme differences in origin, for their genetic background and for their morpho-physiological traits. IR64 is a mega variety widely cultivated in many countries in Asia due to its high yield, desirable quality traits and acceptable tolerance for major biotic stresses; however, it is sensitive to many African environmental constraints such as drought (Manneh *et al*., 2007; Sandhu *et al.*, 2014) while Kogoni91-1 is known as a high yield variety which is adapted to many difficult African environmental conditions particularly rainfed conditions in Mali. The parental genetic diversity translated by the polymorphism rate was relatively low (12.1%) and the genetic map constructed based on this polymorphism had a length of 1392.1 cM. This low polymorphism and consequently the relative low density of linkage map could be explained by the fact that we used two parents from the same variety group. Indeed, the density of the linkage map for an inter-subgroup population is much highest than that of an intra-subgroup population (Tan *et al.*, 2013; Wang *et al.*, 2011; Xing *et al*., 2002). It is important to notice that although the polymorphism rate observed was low, our study focused only on the phenotypic traits that highly discriminated the two parents.

Choosing an appropriate mapping population is critical for the success of any QTL mapping project (Djedatin *et al.*, 2011; Semagn *et al.*, 2010). Here we used a popular RIL population because it can be planted repeatedly in different seasons or environments and hence it is possible to take into account environmental effects and experimental error as recommended by (Bai *et al.*, 2012). Hence the approach we followed in our study enabled the identification of 12 QTLs for DTF, PH, NGP and TKW, six expressed with a large effect (16.6 to 20.2%). IR64 alleles contributed to five QTLs: two related to DTF, two to PH and one to TKW; the remaining seven alleles come from the male parent Kogoni91-1. This shows that the two parents used to develop the

mapping population evaluated in this study contains favorable alleles for breeding.

A QTL can be considered as major when the phenotypic variance explained by the QTL is more than 15% (Echeverry-Solarte *et al.*, 2015). Hence, in our study, three major QTLs (R^2 ranging from 16.6 to 20.2 %) were identified. The flanking markers of these robust and stable QTLs can be used for marker assisted transfer into varieties for yield improvement through these four yield-related traits. The other nine QTLs showed minor effects (LOD ranging from 3.6 to 3.8 and R^2 ranging from 10.9 to 14.7%). This included *qDTF6*, *qPH3*, *qPH12*, *qNGP8*, *qTKW5* and *qTKW6*. Despite their minor effect,these QTLs will be useful as they will help in improvement of yield in a cumulative manner as suggested by (Marathi *et al*., 2012). Additionally the study of these QTL may allow a better understanding of the genetic regulation of the traits.

The correlation analysis was carried out to understand how the traits influenced each other. Significant phenotypic correlation was observed between plant height and days to 50% flowering. As expected, since in grasses vegetative growth is always followed by flowering (also called heading), there was highly significant relation between PH and DTF. It is commonly accepted that correlations between traits are attributed to the effect of pleiotropy or very close linkage of genes. Despite the significant correlation observed between the traits in this study, we found no overlapped or closely linked QTLs affecting two or more of these traits together. Therefore this significant correlation can be attributed to the effect of undetected QTLs rather than pleiotropy or linkage of the genes.

QTLs identified in this study in relation to already identified ones

Because DTF, PH, TKW and NGP are important components of rice grain yield, the discovery of QTLs and genes related to these component traits and their cloning are important for rice breeding programs. To date, numerous QTLs and genes for these traits have been cloned and studied deeply. Most of these published QTLs have been curated from the literature and are currently available in the gramene database *(GRAMENE QTL Database,* http://archive.gramene.org/qtl/ , *May 3, 2016)*.To understand if the genomic regions associated to the four yield components traits evaluated in this study had been identified and cloned previously, we compared the QTL positions in the present study with those reported earlier. Six of the 12 QTLs identified in this study have similar chromosomal locations with QTLs from different mapping experiments and different genetic backgrounds. The remaining six were identified for the first time.

For example, *qTKW6* which was identified and located at the position 102 cM, shared the same chromosomic regions with the gene *GW6* identified and cloned more recently between 98.6 and 109.5 cM in a population ofbackcrossed inbred lines derived from a cross of Kasalath (an *indica* variety) with Nipponbare (a *japonica* variety) (Song *et al.*, 2015). *GW6* has two loci (*GW6a* and *GW6b*) that impacted grain weight equally,by enlarging spikelet hulls via increasing cell number and accelerating grain fillingin rice (Song *et al*., 2015). Other previous studies identified and located the gene *GW6* in the region between 57.1 and 116.9 cM (Li *et al*., 1997; Xing *et al*., 2002; Ishimaru *et al*., 2013). However, (Ngu *et al.*, 2014) using NILs derived from crossing *Oryza rufipogon*accession IRGC105491 and *O. sativa* cultivar MR219, identified and fine-mapped *qGW6* on the short arm of chromosome 6 between RM19268 and RM19271 which is different from the position found in our study, suggesting that this QTL is affected by the genetic background. Furthermore the chromosomic region of *qTKW6* in our study has been found to affect rice grain yield and plant height in backcross populations developed from crossing IR55419-04/2 and TDK1 (Dixit *et al.*, 2014).Hong *et al*. (2003), using the public rice SSR genetic map (McCouch *et al*., 2002; Temnykh *et al.*, 2000, 2001) mapped two major genes related to grain shape and weight Dwarf1 (D1) and D2 between 16-31cM and 0-27cM on chromosome 1 and 5 respectively. The chromosomic region where *qTKW5* was located (12-22cM) in this study coincided with the chromosomic region of D1 (16 and 31cM). D1, also known as the rice heterotrimeric G protein alpha submit (RGA1) (Huang *et al.*, 2013), is the first gene cloned that has substantial effects on seed-size regulation (Ashikari *et al.*, 1999; Fujisawa *et al.*, 1999).

The *qNGP1* detected between 14 and 22 cM does not share chromosomic region with other QTLs/genes related to grain number but it is in same confidence interval (0-27cM) of the cloned gene D2 related to grain shape and weight (Hong *et al.*, 2003). It could be that D2 gene has a pleiotropic effect on number of grains per panicle.

QTL qDTF6 was identified by our analysis in the confidence interval between 22 and 30 cM which is not far from the region where the gene Hd3 related to heading date was originally detected (Yano *et al*., 1997).The gene Hd3 has been found to be located between 10.4 and 16 cM by many studies (Yamamoto *et al.*, 1998; Yano *et al*., 2001; Kojima *et al.*, 2002). An analysis of advanced backcross progeny and NILs revealed two distinct genes, Hd3a and Hd3b, in the Hd3 region with the Kasalath allele of Hd3a promoting heading under short-day (SD) conditions while the Kasalath allele of Hd3b causes late heading under long-day (LD) and natural field conditions (Monna *et al*., 2002). Photoperiod is an important environmental signal which determines flowering time in many plants. It is well known that in rice, flowering is earlier under SD conditions (Vega-Sánchez *et al.*, 2008). When rice is in SD conditions, Hd1 activates flowering by up-regulating Hd3a which causes early heading (Izawa *et al.*, 2002; Hayama *et al.*, 2003; Hayama and Coupland, 2004). In contrast, Hd1 represses flowering by down-regulating Hd3a expression under LD conditions (Kojima et al., 2002). Even though we did not identify any QTLs near the position of Hd1, the delay of flowering by 5 days promoted by the presence of qDTF6 in the region of gene Hd3, suggests that qDTF6 may have the same locus as Hd3a. The effect of Hd1 is not detected because of its weakness, probably due to the photoperiod insensitivity of IR64 which contributed an allele to the QTL. Hence it not surprising that the qDTF6 expressed with minor effect (LOD=3.6; R2=10.9) because of the undetectable effects of gene Hd1. These results are consistent with studies in which Hd3 has been detected with minor effect and only when the phenotypic effect of Hd1 and Hd2 has been removed from the analysis (Yamamoto *et al*., 1998; Yano *et al*., 1997).

We identified the qDTF3 between 0-8cM, which is the same region where was identified a QTL named Ehd4 involved in early heading in diverses rice species including *O.sativa , O.*

rufipogon, *O. nivara*(Gao *et al*., 2013andHori *et al*., 2015).Ehd4 encodes a novel CCCH (C-X7-C-X5-C-X3-H)-type zinc finger protein and it acts as a critical regulator promoting flowering under both SD and LD, particularly under LDs. Mutation in Ehd4 causes a never-flowering phenotype under natural long-day conditions (NLDs)(Gao *et al*., 2013). Wang *et al*. (2011) identified the *qHD-3* related to heading date at 3.7cM in the 93-11/ Nipponbare background; Lin *et al*. (2011) identified the *Qhd3* in 6 and 10 cM explaining 15.4 and 35.74% of the phenotypic variation in TK8/IR1545-339 and Nipponbare/IR1545-339 populations, respectively. Previously, several works identified QTLs affecting flowering times in many genetic backgrounds; comparison of the chromosomal regions of *qDTF3* and these other QTLs suggest that *qDTF3* is the same locus as *QHD3a*(Li *et al*., 1995), *dth3*(Xiao *et al.*, 1996),*dth3.1*(Xiao *et al.*, 1998), *DTH3*(Hori *et al.*, 2015), Hd9 (Lin *et al.*, 2002; Yano *et al.*, 2001). However Lin *et al.*, (2002); Yamamoto *et al.*, (2000) and Yano *et al.*, (2001)detected *Hd9* only in advanced backcross progeny, such as BC_3F_2 or BC_4F_2 but not in F_2 or BC_1F_5 which is contrary to our findings that detected qDTF3 in the position of Hd9 in the RIL population. Our results are supported by those from *Lei and Chen, (2010) and Mei et al. (2005)*who, using RIL population derived from crossing between indica rice Lemont and japonica rice Teqing, detected a QTL related to heading with large effect in the Hd9 region.

The major QTL, *qPH5* identified between 52-72cM coincided with the chromosomic position of the *Qph5* identified between 61 and 85cM in a F2 population derived from TK8/IR1545-339 crosses (Lin *et al.*, 2011).

The comparison of QTLs identified in this study to those mapped in previous studies provided additional information about the natural variation of DTF, PHT, NGP and TKW during evolution and breeding. However, it is important to note that it is still difficult to clarify with certainty the relationship between QTLs identified by our investigation and those already identified because the experimental material and conditions we used were different.

To the best of our knowledge, this is the first time that QTLs related to PHT, NGP and TKW are identified at the positions of the*qPH8*, *qPH3*, *qPH12*, *qTKW2*, *qNGP4* and *qNGP8*. An attempt was also made in this study to specially estimate the allelic contribution of the parent Kogoni91-1 which is a target of QTL analysis for the first time. Compared with the IR64, we found that Kogoni91-1 alleles contributed new QTLs with higher negative and positive effect suggesting the existence of favorable alleles in this genotype which would be useful and should be studied in depth for deployment in breeding programs.

CONCLUSION

In conclusion, the present study identified 12 QTLs affecting flowering date, plant height, number of grains per panicle and thousand kernel weight with small and large positive and negative effects. Our study both confirmed some previously identified QTLs and cloned genes for yield-related traits in rice and detected some novel QTLs, confirming the presence of novel favorable alleles for yield component traits in the population used. Pyramiding these novel major QTLs with those previously identified should help in enhancing rice yield potential. The flanking markers for the different major QTLs are suitable for use in marker assisted selection.

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