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Identification of stable quantitative trait loci for grain yield in rice

Abstract – The objective of this work was to identify the quantitative trait loci (QTLs) associated with grain yield in a rice segregant population (GYP). A population of 245 inbred recombinant rice lines from the 'Epagri 108' (*Oryza sativa* subsp. *indica*) x 'IRAT 122' (*O. sativa* subsp. *japonica*) cross was evaluated at different locations and years and genotyped by single nucletide polymorphism (SNP) markers. A map of 1,592.8 cM was obtained from 9,831 SNPs, identifying 25 QTLs. The following nine SNPs showed stability between the different environments: M1.37719614 and M6.9563117 for GYP; M4.29340056, M5.25588710, M7.29115624, and M12.4534450 for 100-grain weight (HGW); and M1.38398157, M4.28368337, and M7.25991230 for plant height (PH). Six SNPs were not present in the linkage blocks: M6.9563117 and M4.1077080 for GYP; M5.25588710 and M6.8886398 for HGW; and M2.34471005 and M8.5955948 for PH. The M6.9563117 and M5.25588710 SNPs were considered environmentally stable and were not present in the linkage blocks, showing their high potential for use in marker-assisted selection for grain yield in Brazilian rice breeding programs.

Index terms: *Oryza sativa*, DArTseq, genotyping by sequencing, heritability, molecular markers.

Identificação de locos quantitativos estáveis quanto à produtividade de grãos em arroz

Resumo – O objetivo deste trabalho foi identificar locos de caracteres quantitativos (QTLs) associados à produtividade em uma população segregante de arroz (GYP). Uma população de 245 linhagens puras recombinantes de arroz, do cruzamento 'Epagri 108' (*Oryza sativa* subsp. *indica*) x 'IRAT 122' (*O. sativa* subsp. *japonica*), foi avaliada em diferentes locais e anos e genotipada por marcadores de polimorfismo de nucleotídeo único (SNPs). Obteve-se um mapa de 1.592,8 cM a partir de 9.831 SNPs, tendo-se identificado 25 QTLs. Os seguintes nove SNPs apresentaram estabilidade entre os diferentes ambientes: M1.37719614 e M6.9563117 para GYP; M4.29340056, M5.25588710, M7.29115624 e M12.4534450 para peso de 100 grãos (HGW); e M1.38398157, M4.28368337 e M7.25991230 para altura de plantas. Seis SNPs não estavam presentes nos blocos de ligação: M6.9563117 e M4.1077080 para GYP; M5.25588710 e M6.8886398 para HGW; e M2.34471005 e M8.5955948 para altura de plantas. Os SNPs M6.9563117 e M5.25588710 foram considerados ambientalmente estáveis e não estiveram presentes em blocos de ligação, o que indica seu alto potencial para uso na seleção assistida por marcadores de produtividade de grãos, em programas brasileiros de melhoramento de arroz.

Termos para indexação: *Oryza sativa*, DArTseq, genotipagem por sequenciamento, herdabilidade, marcadores moleculares.

Daniany Rodrigues Adorno Silva[1], João Antônio Mendonça[2], Antônio Carlos Centeno Cordeiro[3], Ariano Martins de Magalhães Júnior[4], Rosana Pereira Vianello[2] and Claudio Brondani[2] ✉

[1] Universidade Federal de Goiás, Escola de Agronomia, Rodovia GO-462, Km 0, CEP 74690-900 Goiânia, GO, Brazil. E-mail: daniany.rodrigues@gmail.com

[2] Embrapa Arroz e Feijão, Rodovia GO-462, Km 12, Zona Rural, Caixa Postal 179, CEP 75375-000 Santo Antônio de Goiás, GO, Brazil. E-mail: joao.mendonca@embrapa.br, rosana.vianello@embrapa.br, claudio.brondani@embrapa.br

[3] Embrapa Roraima, Rodovia BR-174, Km 8, CEP 69301-970 Boa Vista, RR, Brazil. E-mail: antonio.cordeiro@embrapa.br

[4] Embrapa Clima Temperado, Rodovia BR-392, Km 78, CEP 96090-575 Pelotas, RS, Brazil. E-mail: ariano.martins@embrapa.br

✉ Corresponding author

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Introduction

In the past, desirable plant architecture was the main selection criterion for obtaining highly productive varieties of rice (*Oryza sativa* L.) breeding (Gaikwad et al., 2014). Although this breeding approach was successful in the late 20th century, it is no longer sufficient for developing high-yielding rice cultivars (Hirano et al., 2017). Currently, the genetic gains in productivity has remained around 1% per year, which may be insufficient to meet the demand for food, due to the growing world population (Breseghello et al., 2011).

One of the main alternatives to increase genetic gain is the use of molecular markers associated with traits of economic importance, to identify superior lines which, in turn, give rise to commercial cultivars with greater productive potential (Xu et al., 2017). Genes that regulate rice grain yield tend to be highly pleiotropic (Xing & Zhang, 2010) and, therefore, allow of an increase of yield that often involves balancing the different phenotypic effects. Genes that control grain yield with pleiotropic effects for other agronomic traits in rice varieties have already been isolated and functionally characterized, such as *Ghd7*, which has also been related to height and flowering period (Weng et al., 2014). Similar pleiotropic effects were also found for the *DTH8* gene (Wei et al., 2010; Yan et al., 2011), *GHD7.1* (Yan et al., 2013), and *HD1* (Zhang et al., 2012). Dwarfism regulation promoted by the *SGDP7* gene has also been observed to decrease grain size, and to increase the number of grains per panicle (Bai et al., 2017; Wing et al., 2018). These studies indicate that working with pleiotropic genes related to productivity is feasible. The identification of molecular markers related to more than one trait, which directly or indirectly affect grain yield, makes it possible to increase the chance of selecting superior genotypes (Budhlakoti et al., 2022).

Advances in statistical models and DNA marker technology, as well as the rapid development of genomic resources, have generated increasingly refined genetic maps and QTL analyses for various traits of interest (Singh et al., 2021). Generally, the size increase of mapping population, combined with a high density of molecular markers, is essential for a good resolution of the genetic map, which means an improvement of the accuracy of QTL mapping (Jangarelli, 2014; Wang et al., 2011).

The objective of this work was to identify stable QTLs associated with grain yield, in a rice segregant population.

Materials and Methods

This work used a segregating population derived from a cross between parents of rice – *Oryza sativa* subsp. *indica* and *O. sativa* subsp. *japonica* –, which were genotyped by thousands of SNP markers and evaluated in three locations. The mapping population consisted of 245 recombinant inbred lines (RILs) from the crossing of 'Epagri 108' (*O. sativa* ssp. indica) x 'IRAT 122' (*O. sativa* ssp. japonica), advanced to the F7 generation by the single seed descent (SSD) method (Janwan et al., 2013). The RILs and their parents were evaluated at three locations of Brazil in different years, as follows: in Goiânia, in the state of Goiás (GO) (2014, 2016, and 2017); in Boa Vista, in the state of Roraima (2014); and in Pelotas, in the state of Rio Grande do Sul (2014) (Table 1).

The experiments were carried out in an irrigated cultivation system in the lattice design, with two replicates. The plots were composed of four lines with 4 m length, totaling a useful area of 1.2 m². The management of the experiments, which were carried out between October and February, followed the instructions described in Soares (2012). The RILs were evaluated for grain yield per plant (GYP, kg ha^{-1}), 100-grain weight (HGW, g), and plant height (PH, mean of 5 plants, cm). The analysis of variance was performed for each environment individually, using a random model for all variables, and joint analysis for locations and years, also estimating the RILs x locations (ME) and RILs x years (MY) interactions. The estimates of the variance components were obtained from the residual maximum likelihood (REML) method, with the application of the best linear unbiased prediction (BLUP) procedure to estimate the associated random effects genetic values (eBLUP) for each trait, each RIL, and their parents, as described by Bueno et al. (2012). Statistical analysis of phenotypic data was performed using the lme4 of the R platform version 3.5.1 package.

To obtain the SNP markers, two sequencing genotyping methodologies were used: the genotyping-by-sequencing (GBS) (He et al., 2014), conducted at the Beijing Genomics Institute (BGI, China), and

the diversity arrays technology (DArT Pty Ltd., Marrickville, Australia) (Appleby et al., 2009). From the set of identified SNPs, markers that were heterozygous or monomorphic between parents, or that did not present the expected Mendelian segregation (1: 1), were discarded. The genetic map was obtained from the cMConverter software version 1.2.1 (cM Converter, 2022); and the map design and QTL positioning were obtained by the MapChart software version 2.32 (Voorrips, 2002). To calculate the extent of linkage disequilibrium (LD) between SNP markers on chromosomes where QTL was detected, the standard confidence interval method of Gabriel et al. (2002) in the Haploview version 4.2 program was used to obtain a matrix of r^2 values (Gabriel et al., 2002; Barrett et al., 2005). QTL mapping was performed on the R version 3.5.1 computational platform, R/qtl package (Broman & Sen, 2009), using simple (SIM) and composite (CIM) interval mapping, multiple imputation mapping methods and the Haley-Knott's regression, respectively (Haley & Knott, 1992; Sen & Churchill, 2001). The significance level was determined by the logarithm of odds score analysis (LOD score) = 3. For all steps of construction of the QTL mapping model, the genotypic probability condition was calculated using the function calc.genoprob (Sato et al., 2021). The mapping function was Kosambi, the maximum distance used was 1 cM, and the supported genotyping error rate was 0.01. To obtain the significance limit (LODmax) to reject the hypothesis H0: a = 0 (there is no evidence of QTL effect in this position), the permutation test was performed with a value of α=0.05 and 1,000 permutations. Then, the "scantwo" function was used to locate the QTL with smaller effects, besides estimating the interaction between the identified QTL (Lander & Botstein, 1989). The final model was estimated by the multiple QTL method (MQM) based on the results of the CIM and Two-QTL (Broman & Sen, 2009). For the analysis of the QTL x Environment interactions, the values estimated by the eBLUPs in the joint analysis of the RILs were used.

The significant QTL was named according to the method proposed by McCouch et al. (1997), as follows: GYP for grain yield, HGW for 100-grain weight, and PH for plant height. The QTL confidence interval was considered according to the method of Gabriel et al. (2002), by which the marker located closest to the QTL peak is present in the haplotypic block. The largest haplotypic block was delimited in relation to the linkage disequilibrium decay, obtained by the platforms TASSEL version 5 (Bradbury et al., 2007) and R version 3.6.2. The prediction of candidate genes underlying the QTL of interest was performed through the Rice Genome Browser search (Kawahara et al., 2013), and the verification of the effects of SNPs (SNPeff) was performed through the RiceVarMapv2.0 search (RiceVarMapv2.0, 2022). The confirmation of the QTL previously identified for the same region, in the present study, was performed using the Q-TARO database (Yonemaru et al., 2010).

Results and Discussion

The analysis of variance detected highly significant differences, by the f-value test, between the set formed by RILs and their parents for GYP, HGW, and PH, in all environments assessed individually (Table 2). For the annual evaluations, only the experiment carried out in Goiânia, GO, in the second year (Y2) of the experiments, in 2016, showed coefficient of variation (CV) above the average found in the literature (59.27%), which was caused by excess rainfall at harvest (Morais Júnior et al., 2017). The accuracy also showed a good experimental precision for the experiments evaluated individually (values

Table 1. Location of field experiments and average of phenotypic data.

Environment	Location – city, state	Year	Coordinates			GYP	HGW	PH
			Latitude	Longitude	Altitude (m)	(kg ha^{-1})	(g)	(cm)
GO/Y1	Goiânia, GO	2014	16°30'23''S	49°17'00''W	823	9,147.3–2,073.6	3.3–2.4	130.4–79.9
GO/Y2	Goiânia, GO	2016	16°30'23''S	49°17'00''W	823	8,096.3–3,321.8	-	177.4–99.3
GO/Y3	Goiânia, GO	2017	16°30'23''S	49°17'00''W	823	4,7901–1,089.8	-	132.3–91.0
RR	Boa Vista, RR	2014	2°45'26''N	60°43'51''W	83	8,958.1–3,185.0	-	125.8–84.0
RS	Pelotas, RS	2014	31°40'49''S	52°26'23''W	61	9,236.4–2,671.4	3.3–2.3	127.8–79.9

States: GO, Goiás; RR, Roraima; RS, Rio Grande do Sul. Y1, 2014; Y2, 2016; Y3, 2017; GYP, plant grain yield; HGW, 100-grain weight; PH, plant height.

above 0.7), except for the traits GYP and PH for GO/Y2, which showed relatively low accuracy (0.49 and 0.75, respectively). High heritability values were also observed for all traits (values above 0.7), except for the GO/Y2 experiment for traits GYP and PH (0.24 and 0.57, respectively). The correlation analysis was positive and significant between GYP and HGW, with values of 0.2 and 0.3 for the environments Goiânia, year 1 (GO/Y1) (2014), and RS, respectively. GYP correlated with PH moderately, with values of 0.2 and 0.3 for the environments GO/Y1 and RR, respectively. There was a positive correlation for GYP and PH in 2014 (year 1) and 2017 (year 3) in the GO environment, with 0.3 and 0.2 estimated correlation, respectively.

Table 2. Analysis of variance, estimates of variance components, coefficient of variation, accuracy, and heritability of rice plant grain yield (GYP), 100-grain weight (HGW), and plant height (PH).

Component [(1)]	Location[(2)]	GYP	HGW	PH
F-value	GO/Y1	34.1***	198.2***	88.26***
	GO/Y2	4.4**	–	8.74***
	GO/Y3	3.8***	–	8.2***
	RR	60.5***	–	92.86***
	RS	33.9***	184.9***	86.8***
	ME	13.2**	–	19.3**
	MY	6.06*	–	61.18***
σ^2_G	GO/Y1	2,996,945	0.047	400.8
	GO/Y2	1,144,844	–	188.19
	GO/Y3	695,880	–	195.48
	RR	2,346,000	–	223.3
	RS	2,275,011	0.039	157.2
	ME	2,480,000	–	150.8
	MY	965,300	–	1.38e-5
σ^2_P	GO/Y1	3,354,160	0.055	423.9
	GO/Y2	4,841,642	–	327.8
	GO/Y3	901,627,5	–	249.49
	RR	2,607,450	–	236.4
	RS	3,154,293	0.053	205.8
	ME	3,176,300	–	360.01
	MY	1,459,496	–	23.85
CV (%)	GO/Y1	15.73	4.38	5.96
	GO/Y2	59.27	–	13.94
	GO/Y3	21.45	–	8.95
	RR	11.05	–	5.34
	RS	25.12	5.66	9.69
AC	GO/Y1	0.94	0.92	0.97
	GO/Y2	0.49	–	0.75
	GO/Y3	0.88	–	0.88
	RR	0.95	–	0.97
	RS	0.85	0.86	0.87
H^2	GO/Y1	0.89	0.85	0.94
	GO/Y2	0.24	–	0.57
	GO/Y3	0.77	–	0.78
	RR	0.90	–	0.94
	RS	0.72	0.74	0.76

[(1)]σ^2_G, genotypic variance; σ^2_P, phenotypic variance; CV, coefficient of variation; AC, accuracy; H^2, heritability. [(2)]GO/Y1, Goiânia 2014; GO/Y2, Goiânia 2016; GO/Y3, Goiânia 2017; RR, Boa Vista; RS, Pelotas; ME, joint analysis between locations; MY, joint analysis between years. Analysis of variance: *, **, ***Significant at 5%, 1%, and 0.1% probability.

The molecular characterization of the 245 RILs and the two parents by GBS and DArTseq methodologies resulted in the identification of 12,283 SNPs distributed in the 12 rice chromosomes and, after discarding heterozygous, monomorphic, or distorted segregation markers (markers did not show the expected Mendelian segregation of 1:1), 9,831 polymorphic SNPs remained (Table 3). From these markers, a genetic map of 1,592.08 cM size was generated, with an average distance between markers of 0.19 cM, and an average physical density of one SNP every 44.8 kbp. This size is in accordance with the size of the map used in recent works on rice, that is, the current literature indicates that this is the physical size of the map suitable for performing QTL analysis (Yadav et al., 2019; Zhang et al., 2020). Multiple interval mapping identified 21 QTLs considering the three traits and three locations, and seven QTLs showed environmental interaction (Table 4), distributed in all rice chromosomes, except for chromosome 2. Considering the different years, 14 QTLs were identified for GYP and PH, and four QTLs showed annual interaction (Table 5).

The identified QTLs showed only additive effects, which is interesting, since the alleles with positive effects tend to be maintained throughout the breeding generations (Beissinger et al., 2018). Epistatic interactions were not significant, which is important from the point of view of using these identified SNPs in a marker-assisted selection strategy, as the effects of one QTL are independent of the effects of other loci (Bocianowski, 2013).

The QTLs identified for GYP were unique for each location (Table 4). Considering all QTLs detected, just *qGYP6* was common between years (in this case, Y1 and Y3, for the GO environment) (Table 5). Specific significant QTLs were identified for the GO/Y1 environment (*qGYP1.1*, *qGYP1.2*, *qGYP3.1*, *qGYP3.2*, *qGYP4*, and *qGYP11*), GO/A2 (q*GYP2*), and GO/Y3 (*qGYP9.2*). The specific QTL for RR location was

qGYP10, and for RS was *qGYP9.1*. These results mean that a marker-assisted selection (MAS) strategy should be targeted to specific sites, decreasing the chance of successful use of markers for multiple sites, as noted by Hasan et al. (2021).

The proportions of phenotypic variance explained by the individual QTLs ranged between 2.7 and 25.2%. The QTL model explained 56% of the phenotypic variance for yield in GO/Y1, 7% in GO/Y2, 30% in GO/Y3, 19% in RR, and 7% in RS. Despite the high phenotypic variance observed for the grain yield trait, these values should be viewed with caution, as they are specific to the population and environment studied (Wang et al., 2020). For HGW trait, six significant QTLs were identified for GO/Y1 (*qHGW1*, *qHGW5*, *qHGW6*, *qHGW10*, *qHGW12.1*, and *qHGW12.2*) (Table 4). Among them, *qHGW12.1* was also identified in the RS environment, which may be interesting for the MAS, after additional studies that should be carried out to confirm the importance of this QTL for these two environments. As HGW is one of the components of rice grain yield (Dou et al., 2016), and it has greater heritability than the GYP trait, it may be an alternative for MAS. For PH, four significant QTLs were identified, with the QTL *qPH1* occurring in all environments (Table 4). The QTL *qPH1* stood out for its high LOD (66) and R^2 (69%), and it is the only one identified in the three experimental years, in the three locations, and in the environmental joint analysis. The linkage block to which *qPH1* belongs is 689 kbp, with 111 genes, and it is close to QTL *qGYP1.2* (block with 562 kbp and 93 genes). Lei et al. (2018) also identified a QTL cluster for grain yield, height, and tillering, in the same region of chromosome 1, which makes it a priority target for developing molecular markers for assisted selection in rice. The study by Tanger et al. (2017) involving the crossing between the two cultivars of the Indica group ('IR64' x 'Aswina') also identified the QTLs *qGYP1.2* and *qPH1*. Hua et al. (2002) and Xing et al. (2002) previously associated the QTL *qGYP1.2* to increased grain yield in rice. Two QTLs related to plant height – *qPH4* (GO/Y1 environment and joint analysis) and *qPH7* (year 1 and joint analysis) – showed stability. The QTL *qPH4* (R^2=2%) is found in a 745 kbp linkage block containing 54 genes. This region was previously related to plant height in rice with the genes *dwarf1* and *dwarf17* (Kudo et al., 2012; Umehara et al., 2008). The QTL *qPH7* (R^2=3%) is found in a 607 kbp linkage block with 63 genes, and it was not previously related to plant height, but to traits such as panicle number, grain size, dormancy, spikelet fertility and tolerance to abiotic stress (Abe et al., 2010; Ni et al., 2014).

The SNP markers associated with the linkage blocks M1.37719614 (*qGYP1.2*), M12.4534450 (*qHGW12.1*), M1.38398157 (*qPH1*), M4.28368337 (*qPH4*), and M7.25991230 (*qPH7*) would be indicated for the development and validation of

Table 3. Number of single nucleotide polymorphism (SNP) markers obtained from genotyping-by-sequencing (GBS) methodology and the diversity arrays technology DArTseq of rice recombinant inbred lines.

Chromosome	Total SNP markers	Total filtered SNP markers	Total distance (Mbp)	Total distance (cM)	Average distance between SNPs (cM)	Average Density of SNPs (kbp/SNP)
1	1,962	1,875	43	203.86	0.11	23
2	1,493	1,432	36	175.13	0.12	25
3	833	730	36	194.58	0.27	50
4	1,061	538	35	130.59	0.24	65
5	1,209	966	28	120.41	0.12	29
6	920	397	27	114.08	0.29	69
7	639	590	29	155.62	0.26	49
8	617	571	28	117.31	0.21	49
9	731	316	23	92.38	0.29	72
10	565	506	23	92.99	0.18	46
11	990	822	29	94.26	0.11	35
12	1,263	1,088	27	100.87	0.09	25
Total	12,283	9,831	364	1,592.08	0.19*	44.8*

Mbp: megabase pairs; kbp: kilobase pairs; cM, centimorgan.

Table 4. Quantitative trait loci (QTLs) identified, considering the three experimental locations.

Trait[1]	QTL	LD interval[2] (bp)	Gene number	SNP marker	GO/Y1[3]				RR				RS				ME			
					LOD	Pos	Add	R^2	LOD	Pos	Add	R^2	LOD	Pos	Add	R^2	LOD	Pos	Add	R^2
GYP	*qGYP1.1*	20608740..21083225	66	M1.20784324	5	77.8	-303.2	5	-	-	-	-	-	-	-	-	-	-	-	-
	qGYP1.2	37362221..37925006	93	M1.37719614	14	165.8	-489.4	13	-	-	-	-	-	-	-	-	4	164.2	36	7
	qGYP3.1	3447267..3447286	-	M3.3447267	6	25	-297.6	5	-	-	-	-	-	-	-	-	-	-	-	-
	qGYP3.2	35670223..36412933	125	M3.35771748	4	189.1	265.4	3	-	-	-	-	-	-	-	-	-	-	-	-
	qGYP4	–	-	M4.1077080	5	8	270.8	4	-	-	-	-	-	-	-	-	-	-	-	-
	qGYP6	–	-	M6.9563117	24	47	-722.2	25	-	-	-	-	-	-	-	-	6	52.6	-44	9
	qGYP9.1	15703948..15951147	29	M9.15873858	-	-	-	-	-	-	-	-	3	51	-451.6	7	-	-	-	-
	qGYP10	17304937..17318753	2	M10.17304937	-	-	-	-	3	53.2	-307.1	6	-	-	-	-	-	-	-	-
	qGYP11	4937420..5439040	84	M11.5245849	3	31.4	-223.8	3	-	-	-	-	-	-	-	-	-	-	-	-
	TOTAL				44			56	10			19	3			7	10			18
HGW	*qHGW1*	1724593..2297175	90	M1.2078044	3	12.2	0.03	4	-	-	-	-	-	-	-	-	-	-	-	-
	qHGW4	28680378..29442097	92	M4.29340056	-	-	-	-	-	-	-	-	-	-	-	-	5	98.1	0.005	7
	qHGW5	–	-	M5.25588710	7	101.1	-0.05	9	-	-	-	-	-	-	-	-	4	107.7	0.005	7
	qHGW6	–	-	M6.8886398	3	49	-0.03	4	-	-	-	-	-	-	-	-	-	-	-	-
	qHGW7	28858818..29586014	109	M7.29115624	-	-	-	-	-	-	-	-	-	-	-	-	3	153.3	0.005	5
	qHGW10	17440110..17905986	55	M10.17759332	4	55.8	-0.03	5	-	-	-	-	-	-	-	-	-	-	-	-
	qHGW12.1	4254605..4668537	55	M12.4534450	5	31.6	0.04	7	-	-	-	-	3	32	-0.05	8	-	-	-	-
	qHGW12.2	25842248..26273116	56	M12.25886429	4	92.8	0.03	4	-	-	-	-	-	-	-	-	-	-	-	-
	TOTAL				24			36					3			8	11			19
PH	*qPH1*	38000079..38689259	111	M1.38398157	66	168	-9.1	69	10	170	-3.2	18	10	159	4.96	23	53	168	-7	62
	qPH4	27916117..28661996	103	M4.28368337	3	97	-1.4	2	-	-	-	-	-	-	-	-	4	93	1	2
	qPH7	25660807..26268775	104	M7.25991230	6	153	-1.7	3	-	-	-	-	-	-	-	-	-	-	-	-
	qPH8	–	2	M8.5955948	-	-	-	-	3	42	-1.8	6	-	-	-	-	-	-	-	-
	TOTAL				68			72	13			24	10			23	53			63

[1]GYP, grain yield per plant; HGW, hundred-grain weight; PH, plant height. [2]LD, block in linkage disequilibrium. [3]GO, Goiás state; Y1, 2014; RR, Roraima state; RS, Rio Grande do Sul state; ME, joint analysis between locations. LOD, logarithm of odds score; Pos, position of the QTL in the genetic map (cM); Add, additive effect (negative sign means allele inherited from parent 'Epagri 108'); R^2, percentage of phenotypic variation explained by individual QTL.

Table 5. Quantitative trait loci (QTLs) identified considering the three years of experiments.

Trait[1]	QTL	LD interval[2] (bp)	Gene number	SNP marker	Y1 (2014)				Y2 (2016)				Y3 (2017)				MY[3]			
					LOD	Pos	Add	R^2	LOD	Pos	Add	R^2	LOD	Pos	Add	R^2	LOD	Pos	Add	R^2
GYP	*qGYP1.1*	20608740..21083225	66	M1.20784324	5	77.8	-303.2	5	-	-	-	-	-	-	-	-	-	-	-	-
	qGYP1.2	37362221..37925006	93	M1.37719614	14	165.8	-489.4	13	-	-	-	-	-	-	-	-	5	165.8	-173.1	13
	qGYP2	23548832..2528326	258	M2.23548832	-	-	-	-	2	108.2	147.4	7	-	-	-	-	-	-	-	-
	qGYP3.1	3447267..3447286	-	M3.3447267	6	25	-297.6	5	-	-	-	-	-	-	-	-	-	-	-	-
	qGYP3.2	35670223..36412933	125	M3.35771748	4	189.1	265.4	3	-	-	-	-	-	-	-	-	-	-	-	-
	qGYP4	–	-	M4.1077080	5	8	270.8	4	-	-	-	-	-	-	-	-	-	-	-	-
	qGYP6	–	-	M6.9563117	24	47	-722.2	25	-	-	-	-	8	52.6	-353.7	20	9	47	-239.9	22
	qGYP9.2	21782549..22925474	210	M9.22544728	-	-	-	-	-	-	-	-	3	91.8	-217.9	9	-	-	-	-
	qGYP11	4937420..5439040	84	M11.5245849	3	31.4	-223.8	3	-	-	-	-	-	-	-	-	-	-	-	-
	TOTAL				44			56	2			7	10			30	14			38
Hd	*qPH1*	38000079..38689259	111	M1.38398054	66	168	-9.1	69	18	167.8	-7.7	46	46	167.8	-10.6	77	48	167.8	-13.7	80
	qPH2	–	-	M2.34471005	-	-	-	-	-	-	-	-	4	167.7	-1.8	3	-	-	-	-
	qPH3	33433409..33550772	20	M3.33466106	-	-	-	-	-	-	-	-	3	175.8	1.5	2	-	-	-	-
	qPH4	27916117..28661996	103	M4.28368337	3	97	-1.4	2	-	-	-	-	-	-	-	-	-	-	-	-
	qPH7	25660807..26268775	104	M7.25991230	6	153	-1.8	3	-	-	-	-	-	-	-	-	3	133.3	-1.5	2
	Total				68			72	18			46	46			79	49			81

GYP, grain yield per plant; HGW; hundred-grain weight; PH,: plant height. [2]LD, block in linkage disequilibrium. [3]MY, joint analysis between years. LOD, logarithm of odds score; Pos, position of the QTL in the genetic map (cM); Add, additive effect (negative sign means allele inherited from parent 'Epagri 108'); R^2, percentage of phenotypic variation explained by individual QTL.

markers for assisted selection, since they were considered stable in the present study. However, this marker:trait relation can be lost because of crossing-over, as they are located in linkage blocks and co-segregate with dozens of potentially causal genes. The alternative is to select SNP markers with high R^2 values and that are not present in linkage blocks, such as M4.1077080 (*qGYP4*), M6.9563117 (*qGYP6*), M5.25588710 (*qHGW5*), M6.8886398 (*qHGW6*), M2.34471005 (*qPH2*), and M8.5955948 (*qPH8*). The marker M4.1077080 (*qGYP4*) is located between the genes *LOC_Os04g02780* (amidase family protein) and *LOC_Os04g02790* (unannotated expressed protein). According to the RiceVarMap database (RiceVarMapv2.0, 2022), the gene *LOC_Os04g02780* modifies the expression of 28 genes (the SNP can act as a modifier, changing their respective expression levels), and it is involved in 6 metabolic pathways (KEGG and MetaCyc Pathways), which indicates its important role in the general metabolism of rice. The marker M6.8886398 (*qHGW6*) is located between the genes *LOC_Os06g15680* (cytochrome P450) and *LOC_Os06g15700* (unannotated expressed protein). Cytochrome P450 is a superfamily of enzymes that function as monooxygenases and with the biosynthesis of various endogenous molecules, such as antibiotics, essential secondary metabolites, fatty acids, conjugates, signaling molecules, lipid degradation, hormones, among others (Naveed et al., 2018). The SNP marker M2.34471005 (*qPH2*) is located between the genes *LOC_Os02g56310* (phosphoenolpyruvate carboxylase kinase 2) and *LOC_Os02g56320* (starch synthase 4). The second gene was also predicted to target microRNAs encoding APETALA2 type transcription factors, which are often associated with genes responsible for the genetic control of the stress response, plant growth, and development (Ma et al., 2020). SNP M8.5955948 (qPH8) is located in an intron of the *LOC_Os08g10250* gene (*SHR5* receptor-like kinase, RLK). The plant's RLK gene family is involved in several processes related to development, responses to plant biotic and abiotic stresses, and symbiosis (Liu et al., 2017). The *SHR5* gene has been previously linked to signal transduction involved in the establishment of beneficial endophytic plant-bacteria interaction in sugarcane (Vinagre et al., 2006). The potential alteration in the expression of the above genes by the modifier SNPs may have been the

reason for their association with the genetic control of the evaluated traits, which makes them candidates for use in assisted selection.

The SNP M6.9563117 of the QTL *qGYP6* stands out for its identification in GO/Y1, GO/Y3, MY, and ME, as well as for not being located in a linkage block and for showing a high LOD score (24) and additivity (722 kg ha^{-1}). The SNP M5.25588710 of the QTL *qHGW5* is not present in a linkage block, and it is located between the genes *LOC_Os06g16630* (unannotated gene) and *LOC_Os06g16640* (carboxy-terminal peptidase). This genomic region was previously related to the increase of grain yield in rice (Hua et al., 2002; Cui et al., 2003), in addition to other traits, such as plant height and tillering, grain weight, flowering, and resistance, or tolerance to abiotic stresses. Therefore, the SNPs M6.9563117 and M5.25588710 are strong candidates to be used in marker-assisted selection of Brazilian rice breeding programs. The use of few SNP markers for a quantitative trait, such as grain yield, means a significant reduction of the genotyping cost, which allows of the screening of many genotypes. The selected accessions can then be used to conduct smaller and more precise experiments. The validation of the SNPs associated with traits identified in this work is an essential activity to enable the effective use of these markers in breeding programs (Kikuchi et al., 2017), and it will be the next step of the selected SNP markers before being incorporated into the marker-assisted selection routine.

Conclusion

The SNPs M6.9563117 and M5.25588710 are candidates to be used in marker-assisted selection for grain yield in Brazilian rice (*Oryza sativa*) breeding programs.

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