Int.J.Curr.Microbiol.App.Sci (2020) *9*(4): 3216-3224

International Journal of Current Microbiology and Applied Sciences
ISSN: 2319-7706 **Volume 9 Number 4 (2020)**
Journal homepage: http://www.ijcmas.com

Original Research Article https://doi.org/10.20546/ijcmas.2020.904.374

Association Mapping for Important Agronomic Traits in Core Collection of Rice (*Oryza sativa* L.) with SSR Markers

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Keywords

Rice landraces, Cultivated rice, Linear model, Rice breeding

Article Info

Accepted:
30 March 2020
Available Online:
10 April 2020

A B S T R A C T

Mining elite genes within rice landraces is of importance for the improvement of cultivated rice. An association mapping for12 agronomic traits was carried out using a core collection of rice consisting of 100 landraces (Panel 1) with 44 simple sequence repeat (SSR) markers. Our results showed that (1) 76significant (P, 0.05) trait-marker associations were detected using mixed linear model (MLM) within Panel 1 in two years, among which 32% were identical with previously mapped QTLs, and 11 significant associations had.10% explained ratio of genetic variation; (2) A total of seven aforementioned trait-marker associations were verified within Panel 2 and 3 when using a general linear model (GLM) and 55 SSR markers of the 76 significant trait-marker associations. However, non-significant trait-marker association was found to be identical within three panels when using the MLM model; (3) several desirable alleles of the loci which showed significant trait-marker associations were identified. The research provided important information for further mining these elite genes within rice landraces and using them for rice breeding.

Introduction

As a staple cereal crop, rice (*Oryza sativa* L.) feeds more than50% of the world's population and is one of the most important components of human diet in many regions of the world. Thus, genetic improvement of rice for yield is important to the meet food demand of a growing global population. Rice landraces have a greater genetic diversity than elite cultivars (or commercial cultivars). Mining elite genes of rice landraces is of importance for the improvement of cultivated rice. Linkage mapping and association

mapping based linkage disequilibrium (LD) are two main methods for locating genes or QTLs. The major limitations of linkage mapping are that only two alleles at any given locus can be studied in bi-parental crosses and a low mapping resolution, whereas association mapping promises to overcome the limitations of linkage mapping. Association mapping has been widely used in plant research since it was firstly reported in maize.

Population structure may cause false positives in association mapping. To overcome this problem, an approach using a mixed model was proposed for association mapping, which take both population structure (Q) and kinship (K) into account for the reduction of false positives. However, false positive might not be absolutely avoided it required that the significant associations identified within one population should be verified in another population. In this study, an association mapping was performed for 12agronomic traits from the core collection assessed with 44SSR markers. The study aimed to (1) perform association mapping for 12 important agronomic traits in the core collection to identify desirable alleles of the loci which showed significant trait-marker associations for rice breeding.

Materials and Methods

Plant material

Hundred genotypes of rice were taken for this research. The information for each genotype is shown in Table 1.

Phenotyping

All of the germplasm were cultivated at the instructional farm of Indira Gandhi Agricultural University, Raipur, Chhattisgarh (21°16'N latitude and 81°36' E longitude with an altitude of (289.60m)), during the late season (July-November) in wet season (*Kharif*) 2018. The highest temperature was 34.07°C & lowest 27.9°C during the crop development time. The overall average rainfall during crop growing period was (138.69 mm). The highest rainfall received during August month was (39.29 mm).

Nurseries were raised and 21 days old seedlings were eventually transplanted in the field. The space between rows and between plants was set to 25 cm and 15 cm, respectively. Thirty plants of each variety were grown in three rows with 10 plants per row. For each block, the five plants in the middle position of the second row of each variety were selected so that the marginal effect was avoided. 12 agronomic traits for these plants were investigated. A randomized complete block design with three replications was used during each season. The space between rows and between plants was set to 20 and 16.5 cm, respectively. Thirty plants of each variety were grown in three rows with 10 plants per row. For each block, the five plants in the middle position of the second row of each variety were selected so that the marginal effect was avoided. 12 agronomic traits for these plants were investigated. Heading date (HD) was recorded as days from sowing to flowering time when 50% of the individuals of one variety started flowering. Plant height (PH), panicle length (PL), flag leaf length (FLL), and flag leaf width (FLW) were measured in centimetres. Number of effective tillers (NT) was counted as effective tillers. For1000-grain weight (1000GW), 100 grains were measured in grams with three replicates and then its average was multiplied by 10. Number of filled grains (NFG) was counted. Biological yield (BY) was recorded as the weight of each of the 5 sun dried plant except root was recorded in grams. The grain (filled) yield (GY) of each of the 5 plants was recorded in (g) after sun drying for five to

eight days after harvesting and averaged. Harvest index (HI) was estimated as the ratio of grain yield to biological yield and the ratio of grain yield and biological yield are expressed in %.

Genotyping

44 SSR markers evenly distributed across the 12 chromosomes**.** Rice genomic DNA was extracted out from each of the landraces of rice using CTAB method. DNA samples isolated from each line were quantified on Nano Drop Spectroscopy (*NANODROP, 2000c)* and the final concentration of DNA was 50 ηg / µl for PCR analysis. The volume of the polymerase chain reaction (PCR) was 10µl in Axygen make 96 well PCR plates. The profile of the PCR program was as follows: 94°C for 5 min followed by 29 cycles of 94°uC for 1 min, 55°C for 1 min, 72°C for1 min with a final extension of 5 minutes at 72°C. PCR products were separated in size by 56% polyacrylamide gel electrophoresis and detected by ethidium bromide. The size of PCR products were detected by BIORAD gel doc XR + System. The length of each allele was compared to the standard bands of the standard marker and scored.

Data analysis

Means and standard deviation (SD) for 12 traits were calculated using MS Excel software. The percentage of phenotypic variation explained by population structure was calculated using a General Linear Model (MLM) with software SPSS 17.0 for Windows (SPSS Inc. Chicago, IL, USA). The broad-sense heritability (H^2) was calculated as$H^2=\sigma^2_g/ (\sigma^2_g + \sigma^2_e)$, where $\sigma^2_g$is the genetic variance, σ^2_e is the environmental variance and correlation coefficients between traits were calculated using the software SPSS. Polymorphism information content (PIC) which measures the extent of polymorphism for marker gene(s) or marker sequence(s)was calculated using the program POWERMARKER V3.25. Software Structure V2.3.1 was used to infer population structure and get Q matrices. During the running, a range of genetic clusters from K= 1 to 15 with the admixture model was examined, and for each K it was replicated 5 times. Each run implemented with a burn-in period of 100,000 steps followed by 100,000 MonteCarlo Markov Chain replicates.

Due to the distribution of L(K) did not show a clear cut off point for the true K, an adhoc measured was used to detect the numbers of subgroup. That runs with the maximum likelihood was applied to subdivide the varieties into different subgroups based on the maximum membership probability. A Q-matrix was obtained from the membership probability of each variety.

The Q-matrix was used for further association mapping. Quantile–quantile plots were generated for observed against expected 2log10 (P) where observed P values were obtained from association mapping and expected P values from the assumption that no associations happened between marker and trait. Association analysis was performed using the software TASSEL (www.maizegenetics.net/tassel). For the mixed linear model (MLM) method, both K and Q matrices were incorporated, whereas for the GLM method, only population structure information (Q-matrix) was used as a covariate.

Significance of associations between loci and traits were determined by their Pvalues (P, 0.05) which were calculated by the statistical models, and the phenotypic variance explained by the significant loci was calculated through analysis of variance (ANOVA). Since MLM method performs

better in controlling spurious associations than GLM method, we first ranked the significant (P,0.05) association from MLM and then compared the significance of these markers (P,0.05) in the permutation based on GLM association tests.

Results and Discussion

Phenotypic data

The range for days to 50% flowering varied from 75.00 days (R-RF 75) to 118.00 days (Danwar) with the overall mean of 96.15 days. Four categories for days to 50% flowering (table 4.4) were reported i.e. early (91- 90days), medium (91-110days), late (111-130days) and very late (> 131days). The coefficient of variation was 10.92%. The range for plant height varied from 75.01 cm (Bagri) to 271.45cm (Hanuman Langur) with the overall mean of 130.49 cm. The coefficient of variation of plant height was 19.74%.The range for leaf length varied from 22.30 cm (Bisni-I) to 76.61 cm (Roti) with the overall mean of 47.55 cm.

The coefficient of variation was 29.42%.The range for leaf width varied from 0.78 cm (JeeraPhool) to 2.01 cm (R-RF 75) with the overall mean of 1.26 cm. For flag leaf width, the coefficient of variation was 16.80%. It ranged from2.10cm (HathiPanjara) to 13.40cm (Bagri) with the overall mean of 5.83. The coefficient of variation was 35.15%.

Four category of panicle length was found i.e. Very short (< 16 cm), Short (16-20 cm), Medium (21-25 cm) and Long (26-30 cm) (Table 4.5). The maximum and minimum panicle length were found 29.67 cm (Dokraemechha) and 18.51 cm (Koto), respectively, with the overall mean of 24.65 cm. Highest panicle length was found 29.67 cm in Dokraemechha followed by 29.05 cm in BhatanPhool-I and 28.84 cm in Shyam Jira – I and 28.62 cm in BhainsaPunchhi. The coefficient of variation was 10.09%. 1000-grain weight ranged from 7.70 g to 43.45 g with an average weight of 22.31g. The maximum 1000-seed weight recorded in Dokra-Dokri (43.45 g) followed by HathiPanjara (42.31 g) and Chiko (40.96 g). The minimum 1000-seed weight recorded in Ram Jira (7.70 g).

The coefficient of variation was 37.98%. Number of filled grains ranged from 25.45 to 531.45 with an average of 141.18. The maximum 1000-seed weight recorded in JouPhool (531.45) followed by Ram Jira (381.12). The minimum 1000-seed weight recorded in Bhejari (25.45). The coefficient of variation was 60.40%. Number of unfilled grains ranged from 9.74 to 220.00 with an average of 33.61. The maximum 1000-seed weight recorded in Bhejari (220.00). The minimum 1000-seed weight recorded in Koto (9.73). The coefficient of variation was 85.20%.

Total number of grains ranged from 57.42 to 606.49 with an average weight of 174.80. The maximum 1000-seed weight recorded in JouPhool (606.49). The minimum 1000-seed weight recorded in Koto (57.42). The coefficient of variation was 32.01%. The mean performance of biological yield was 295.63g. It showed variation from 72.08 to 774.04 g. The maximum biological yield was recorded in Lanji (774.04 g) followed by SindorSenga (654.88 g) and the minimum were recorded in Luchai-A (72.08 g).

The coefficient of variation was 13.63%. Harvest index was found to vary from 1.27% to 18.72% with an overall mean of 6.37%. The maximum harvest index was recorded in PadariDhan (18.72%). The minimum harvest index was recorded in Koto (1.27%). The coefficient of variation was 43.22%.The range

for grain yield (g) varied from 4.07 g to 29.66 g with a mean value of 15.66 g. The highest grain yield (g) was recorded in BailaAankhi (29.66 g) followed by SuaPankhi (29.60 g) and BawatiChudi (29.19 g). The minimum grain yield (g) was recorded in Koto (4.07 g). The coefficient of variation was 37.24%.

Heritability estimates provide the information regarding the amount of transmissible genetic variation to total variation and determine genetic improvement and response to selection. Thus, heritability is the heritable portion of the phenotypic variance. It is a good index of the transformation of characters from parents to their offspring (Falconer, 1981). Heritability and genetic advance are important selection parameters. Heritability estimates along with genetic advance are normally more helpful in predicting the grain under selection than heritability estimates alone.

Improvement in the mean genotypic value of selected plants over the parental population is known as genetic advance. It is the measure of genetic gain under selection. The success of genetic advance under selection depends on genetic variability, heritability and selection intensity. In the present investigation heritability in broad sense and genetic advance were calculated for 33 yield and quality characters under study and is presented in Table4.3.

Highest estimate of heritability was found for biological yield (99.47 %) followed by days to flowering (98.69%), grain yield (98.09%), thousand grain weight (98.63%), harvest index (97.66%), flag leaf width (95.34%), flag leaf length (89.35%) and total number of grains (62.91%). Rest of the traits was found to have moderate heritability. It clearly indicates that most likely the heritability is due to additive gene effects and selection may be effective. These findings are in agreement with findings of Choudhary *et al.*, 2004; Satheeshkumar and Saravanan, 2012; Sravan *et al.*, 2012 and Khare *et al.*, 2016.

Molecular characterization

Genetic associations among 100 accessions were analysed, based on phenotypic variation of yield traits with the help of 44 SSR markers covering all the chromosomes. A total of 217 alleles were amplified and the number of alleles per locus generated by each marker ranged from 3 to 11 alleles with an average number of 4.93 alleles per locus. Maximum number of alleles (11) was amplified by marker RM 164 marker. The PIC value across markers ranged from 0.24 to 0.85 with an average of 0.66. Maximum PIC value was observed on chromosome 1 (RM 164 = 0.85) followed by RM 248 of chromosome 7 (0.84) and RM 474 of chromosome 1 (0.82).

Population structure analysis

The Bayesion model-based Structure v2.3.4 program was used to infer population structure of rice genotypes. The 100 lines were divided into two sub groups (Fig 4.4 and 4.5) based on the result of Structure Harvester, as delta K kinship was highest at K=2. With population inferred ancestry (Q) = 0.80, 48 lines were assigned to subgroup POP1, rest 48 lines were assigned to subgroup POP2 and four lines namely, R RF 75 (49); KadamPhool (50); AmaJhopa (51) and KoudiDhull (52) were assigned to admixture (AD) which has less than <0.80 inferred ancestry (Fig 4.5). Courtois *et al.*, (2012) has successfully detected two subgroups in their study population and assigned rice varieties into two groups with few admixture lines. Our results are also in conformity with the findings of Borba (2010) suggesting that using structure analysis, the accessions were sub divided into two panels. Likewise, the

association of yield traits with SSR markers was undertaken with MLM model, with markers and sub population as fixed factors, and kinship matrix as random factor.

Marker-trait association

Association analysis between SSR markers and thirteen agronomic and yield attributing traits was carried out using MLM model over the 100 rice germplasm lines. Eleven SSR markers were found to be tightly linked with the panicle length trait. These markers covered the entire linkage groups except chromosome # 2, 5, 7, 8 and 11.

Apart from this, 4 markers each for days to flowering followed by, plant height and total number of grains, 7 markers for flag leaf length, 5 markers both for flag leaf width and biological yield, 3 markers for number of tillers, harvest index and thousand grain weight, 6 markers for number of filled grains and 2 markers each for number of unfilled grains and grain yield were found to be significantly association with the traits at 0.05 threshold level of significance. However, these were significantly associated with all the yield traits (Table 4.11) at the FDR correction level in the entire population. For days to flowering, lowest phenotypic variation (17.08%) by RM 208 whereas highest phenotypic variation was explained by marker RM 338 (22.68 %) followed by RM 307 (21.05 %) and RM 287 (18.89 %) which was significantly associated with the trait.

Lowest phenotypic variation in plant height was observed by RM 212 of C# 1 (12.07%) whereas highest variance was seen in C# 3 with RM 338 (23.94 %) followed by RM 105 (C#9) and RM 348 (C#4) (28.92%).The total phenotypic variation for flag leaf length was observed lowest in RM 105 (8.31%) and highest in RM 431 (18.63%) whereas in case of flag leaf width, it ranged from RM 235 (20.18%) to RM 247 (32.58%).RM338 of C#3 (11.05%) exhibited lowest and RM 348 (24.89%) showed highest followed by RM 510 (22.14 %) for number of tillers and RM 105 of C# 9 (10.96 %) lowest and RM 269 (22.89%) phenotypic variation in panicle length. There were two markers, namely RM 283 and 431 from linkage group 1, RM 55 and RM 338 from linkage group 3, RM 124 and RM 307 from C# 4, RM 553 and RM 105 of linkage group 9 and RM 269 (C#10) and RM 235 (C#12) were found to have tight linkage with the trait i.e., panicle length.

Five SSR markers namely, RM 133 (C#6), RM 536 (C#11), RM 312 (C#1), RM 474 (C#10) and RM 11 (C#7) were to have tight association with biological yield, the phenotypic variance ranging from 4.2% (RM 11) to 25.68% (RM 133).For grain yield two primers, RM 208 (C#2) and RM 247 (C#12) and for harvest index, RM 133 (C#6), RM 208 (C#2) and RM 271 (C#10) were found to be significantly associated with the above traits.

Three markers viz., RM 474, RM 247 and RM 316 were significantly associated with thousand grain weight, likewise, six markers showed tightly linked response with number of filled grains. Similarly, RM 316 and RM 433 for number of unfilled grains and four markers, RM 474, RM 413, RM 536 and RM 248 showed significant and tight linkage with total number of grains.

Agrama *et al.*, 2006 conveyed that to make advances in rice breeding it is essential to understand the relatedness and ancestry of introduced rice accessions and identify SSR markers associated with agronomically important phenotypic traits, for example yield. Identification of a candidate gene for panicle length in trice through association mapping is an important trait for improving panicle architecture and grain yield in rice.

Using the MLM model, RM 338 of chromosome #3 was found to have significant association with days to flowering, plant height, flag leaf width, number of tillers and panicle length.RM 208 of linkage group 2 showed relationship with days to flowering, grain yield and harvest index. For grain yield, thousand grain weight and number of filled grains and flag leaf width RM 247 of chromosome 12 showed significant association and RM 133 (C#6) for biological yield, harvest index and panicle length.

Similar results were reported by Liu *et al.*, 2016. The research provided important information for further mining these elite genes within rice landraces and using them for rice breeding. RM 287 and RM 447 were found to have significant association with flag leaf length and thousand grain weights, respectively. Zhang *et al.*, 2014 also reported same marker with the above traits. In our material, panicle length showed association with RM 283 of chromosome 1, Rabaei *et al.*, 2015 reported a QTL named *qPL-1* responsible of panicle length between flanking markers RM 283 –RM 8132. Likewise another QTL for panicle length was found on C#4 named qpl4.1 between flanking markers RM 131-RM 124 as reported by Jia *et al.*, 2019. In our germplasm accessions, RM 124 also showed significant association with the trait.

The results have clearly shown that structures association mapping in one of the feasible options to identify major effect QTLs for yield traits in rice. These marker-trait associations could be further validated and used in marker assisted breeding for improving particular trait in any rice variety and can be further confirmed in new set of population as well as in bi-parental mapping population.

Table.1 List of germplasm accessions

S. No.	Name	S. No.	Name	S. No.	Name	S. No.	Name
1	Bagri	26	Kanak	51	Amajhopa	76	Ram Jira
2	Hardichudi	27	Mehapal	52	Koudidhull	77	Bhejari
3	Koto	28	TebarooMundaria	53	Saupankhi	78	Danwar
4	Kotte (II)	29	Padaridhan IV	54	DokraDokri	79	Karhani
5	Sathadhan	30	Budhiyawako	55	Parmal	80	Chiko
6	Karhani	31	BD kankaribija	56	Dokraemechha	81	FarsaPhool
7	Kohaka	32	Bawatichudi	57	Roti	82	BailaAankhi
8	Luchai(A)	33	Kalajira	58	Khatiapati	83	Bokra Mundi
9	AngurGuchcha	34	Sonapan	59	Hathipanjra	84	HunumanLangur
10	Basigal(ii)	35	Bakal	60	CR-1014	85	JalPonga
11	Bhejari	36	Cross 116	61	Elayachi	86	Banda
12	Bhulau	37	Deshilaldhan	62	Tulsimanjari	87	Lanji
13	Bodi	38	IR 42253	63	Shyam jira-1	88	Raja Bangla
14	PeeleeLuchai	39	Lalmati	64	LoktiMachhi	89	BhainsaMundariya
15	TulsiPhool	40	Laloo-14	65	Muni Bhog	90	NariyalChudi
16	Silipat	41	Jhitpiti	66	JouPhool	91	Kating
17	Unknown	42	WR99	67	BhainsaPunchhi	92	Bhamasur
18	AmaDhul	43	E-1702	68	Bhanta Phool-1	93	Paltu
19	Baisur	44	Chaptigurmatia	69	Lahsun Bhog	94	Sindursenga
20	Bylao	45	Elayachi	70	Ichchawati	95	Swarna
21	AsamChudi	46	Bisni-I	71	Laxmi Bhog	96	MTU-1010
22	Bhaniya	47	Moroberekan	72	Tulsi Mala	97	IR64
23	FarsaPhool	48	Nagina-22	73	Jou Phool-2	98	R-RF-75
24	Jalle	49	R-RF-75	74	JeeraPhool	99	IGKV R1
25	Kanak Jira	50	KadamPhool	75	TulsiMongra	100	Danteshwari

Table.2 Descriptive statistics, percentage of phenotypic variation explained by population structure (R^2), and heritability in broad sense (h^2) for 12 agronomic traits

Genetic Parameters	Mean±SD	Range	h^2 (%)	R^2	CV(%)
DTF (Days)	96.15±10.50	75.00-118.00	98.69		10.92
PH (cm)	130.49±25.76	75.01-271.45	47.98		19.74
FLL (cm)	47.55±13.99	22.30-76.61	89.35		29.42
FLW (cm)	1.26±0.21	0.78-2.01	95.34		16.80
NT	5.83±2.05	2.10-13.40	91.98		35.15
PL (cm)	24.65±2.49	18.31-29.67	47.99		10.09
TGW (g)	22.31±8.47	7.70-43.45	98.63		37.98
NFG	141.18±85.27	25.45-531.45	60.29		60.40
NUFG	33.61±28.64	9.73-220.00	46.60		85.20
TNG	174.80±55.97	57.42-606.49	62.91		32.01
BYP (g)	295.63±40.31	72.08-774.04	99.47		13.63
HI (%)	6.37±2.61	1.27-18.72	97.66		43.22
GYP (g)	15.66±5.83	4.07-29.66	98.09		37.24

The 100 lines were divided into two sub groups based on the result of Structure Harvester, as delta K kinship was highest at K=2. With population inferred ancestry (Q) = 0.80, 48 lines were assigned to subgroup POP1, rest 48 lines were assigned to subgroup POP2 and four lines namely, R RF 75 (49); KadamPhool (50); AmaJhopa (51) and KoudiDhull (52) were assigned to admixture (AD) which has less than <0.80 inferred ancestry. Eleven SSR markers were found to be tightly linked with the panicle length trait. These markers covered the entire linkage groups except chromosome # 2, 5, 7, 8 and11. Using the MLM model, for grain yield RM 208 and RM 247 were found to be associated for the trait.

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How to cite this article:

Ritu R. Saxena, Sujit Roy, Suman Rawte, Parmeshwar K. Sahu, Ravi R. Saxena and Verulkar, S. B. 2020. Association Mapping for Important Agronomic Traits in Core Collection of Rice (*Oryza sativa* L.) with SSR Markers. *Int.J.Curr.Microbiol.App.Sci.* 9(04): 3216-3224.
doi: https://doi.org/10.20546/ijcmas.2020.904.374