Electronic Journal of Plant Breeding, 8(3): 892-899 (September 2017) DOI: 10.5958/0975-928X.2017.00148.X
ISSN 0975-928X

**Research Article**

# Identification of elite lines and consistent markers linked to yield and yield components in rice (*Oryza sativa* L.) using association mapping

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(Received: 20 July 2017; Revised: 31 Aug 2017; Accepted: 01 Sep 2017)

## Abstract

Genetic variation is the foundation of crop improvement. Identifying donors for yield and yield components will help to develop high yielding cultivars. Yield being a complex trait, understanding its molecular genetics may hasten breeding for high yield. Identifying molecular markers associated with yield traits will improve efficiency of breeding. Forty-nine diverse rice genotypes were evaluated for yield and yield components under irrigated conditions in three separate field trials at Paddy Breeding Station, Coimbatore during February – June, 2014, August – December, 2014 and 2015. Significant variation for yield and yield-related traits was noticed among the genotypes. IR58821 and IR52561 gave consistently higher yield in three and two trials, respectively. Association mapping detected a total of 46 markers associated with growth and yield traits. PSM432, PSM371A and PSM167 were consistently associated with yield and harvest index. IR58821 and IR52561 and markers consistently associated with yield traits may help to develop improved rice cultivars through marker assisted breeding.

## Keywords

Rice, Diverse germplasm, Yield, SSRs and Association mapping

## Introduction

The demographic increase in the population which is estimated to reach 9 billion by 2050 is a major concern for global food security, placing enormous demands on agriculture and natural resources. Rice is the most important staple crop, feeding more than half of the world's population. However, there is no major increase in rice productivity since 1990s due to its narrow genetic base and less genetic diversity of germplasm used in rice breeding programs (Xuan *et al*., 2010). Thus, to feed the increasing world population with limited arable land and declining natural resources, it is important to increase rice productivity during the next two-three decades by improving yield and yield-related traits. Increasing parental genetic diversity can significantly improve rice yield through increased variation in breeding process. Diverse germplasm can play a significant role in expanding the genetic base of cultivated rice varieties. The crosses between parents with maximum genetic divergence are generally the most responsive for genetic improvement**.** Diverse germplasm helps in broadening the genetic base, identifying recombinants and therefore, giving chance to breeders in selecting lines with favourable alleles.

We used 49 rice genotypes from different geographical regions which included several lines known for their specific adaptation to marginal environments. For example, cultivar, FR 13A is the flood tolerant donor of the submergence tolerance gene, *Sub1* (Xu *et al.,* 2006). Dular is a rice cultivar that has drought resistance associated with greater root length and root density (Henry *et al.,* 2011). Rayada also has a large root length and high root density (Henry *et al.,* 2011). Black Gora is a rice cultivar with high seedling vigour (Redoña and Mackill, 1996) and deep roots (Shrestha *et al.,* 2014). N22 is heat tolerant (Jagadish *et al*., 2008). Besides the diverse set also include local landraces, Nootripathu, Norungan and Kallurundaikar, which have been selected over generations by farmers for drought adaptation in rainfed production environment and are important repositories of genetic variability. This diverse panel has been recently used in association studies discovering markers linked to phenology, plant production and root traits under drought in target populations of environment (TPE) in this laboratory (Deshmukh *et al.*, 2017).

The grain yield and yield-related traits are often complex in nature regulated by multiple genes. If the amount and distribution of favourable genes are unknown, it is difficult to apply the diverse rice germplasm in traditional breeding. In addition, there are interactions between genes underlying yield and related traits and growing environments. It is important to identify favourable yield related alleles/loci utilizing these diverse rice germplasms in specific ecological environment (Ya-Fang *et al.,* 2015).

At present, the identification of diverse sources of genes has become crucial to increase the yield potential of rice. Recent advances in next generation sequencing and molecular marker technology has been extensively used in studying genetic diversity. One way to identify alleles/genes for various qualitative and quantitative traits has been through use of various types of molecular markers. Genotyping of rice breeding lines with simple sequence repeat (SSR) markers is done in molecular genetics studies. Using SSR markers, researchers performed association studies on yield-related traits in different geographic collections of diverse rice varieties (Zhang *et al.*, 2014). The extremely dense genetic markers have provided the potential for discovering genes underlying phenotypic diversity (Rietveld *et al.*, 2013) comparable to low density markers, where the distance between the identified loci and target genes remains large, affecting their subsequent utilization in breeding (Ya-Fang *et al.*, 2015). Genome wide association studies (GWAS) is cost effective and time saving approach for identifying genomic regions linked to traits of interest in plants since broad genetic resources can be scanned for marker-trait associations (Barabaschi *et al.*, 2016). It enables researchers to exploit natural diversity using modern genetic technologies and locate valuable genes in the genome.

With this background, in the present study, we studied marker-trait associations for yield related traits under irrigated conditions using GWAS to identify novel alleles using diverse rice lines for application in breeding for yield improvement in rice.

## Materials and methods

*Phenotyping:* Field trials were conducted in experimental fields of the University at Paddy Breeding Station, Tamil Nadu Agricultural University, Coimbatore. The 49 rice genotypes were evaluated for yield and related traits during February – June, 2014 (Trial 1), August – December, 2014 (Trial 2) and August – December, 2015 (Trial 3). Twenty-one day old seedlings were transplanted with a spacing of 20 x 10 cm. The plots were surface irrigated to field capacity once in every four days. NPK fertilizers were applied at the rate of 100:50:50 kg ha$^{-1}$.

Data on days to 50 per cent flowering, plant height, number of productive tillers, panicle length, number of grains per panicle and yield per plant were collected following standard evaluation system for rice (IRRI, 1996). All the plants in each plot were harvested at maturity and grain yield (GY) and straw yield (SY) were recorded after sun drying. Total above ground biomass was computed by summing grain and straw yields. Harvest index (HI) was calculated as the ratio of grain weight to total above ground biomass for each germplasm.

*Genotypic analysis:* Genetic diversity analysis and population structure of these diverse rice were studied previously in our laboratory at Centre for Plant Molecular Biology and Biotechnology, TNAU, Coimbatore and reported earlier (Deshmukh *et al.*, 2017). Briefly, genomic DNA was isolated by CTAB procedure following Gawel and Jarret (1991). Rice lines were genotyped using 1403 SSR markers selected from across the genome by polymerase chain reaction (PCR). Information on primer sequences and PCR amplification conditions for each set of primers are available in public database (www.gramene.org/markers).

*Marker-trait associations:* Marker-trait association was carried out using TASSEL [Trait Analysis by aSSociation, Evolution and Linkage] version 3.0 software (Bradbury *et al.*, 2007) considering gross level population structure (Q) in GLM analysis. The Q + K (kinship) model was used in the MLM analysis with P3D algorithm. It has been reported that the Q + K model reduces the false positive associations (Lu *et al.*, 2015). Hence, the results of MLM are reported in the study.

## Results and Discussion

*Variation in yield traits:* Considerable variation in yield and yield related traits was observed among the rice genotypes in all the trials. The mean and range values of yield and yield components for the three trials are presented (Table 1). IR58821 (5183 kg ha$^{-1}$), Apo (5233 kg ha$^{-1}$) and the landrace, Pokkali (4986 kg ha$^{-1}$) recorded higher yield in trial 1, 2 and 3, respectively (Table 2). In all the three trials, IR58821 consistently gave higher yield and total biomass. IR52561 has recorded significantly higher yield in trial 1 and 3 and total biomass in all three trials. IR58821 and IR52561 differ for a range of drought resistance traits *viz.* gross root morphology, root penetration index, root pulling force and osmotic adjustment (Babu *et al.*, 2001). IR58821 has high root penetration index and thicker roots, while IR52561 has low root penetration index and thinner roots (Biji *et al.*, 2008). IR58821 had higher deep root mass under anaerobic flooded conditions (Azhiri-Sigari *et al.*, 2000). IR58821 reported to be contributing favourable alleles for drought resistance and yield traits in a study using a mapping population derived from the cross IR58821xIR52561 (Manickavelu *et al.*, 2006). IR58821 is known to have a deep and thick root system under well-watered conditions and higher water extraction from sub soils (Kamoshita *et al.*, 2000).

Apo, having higher yield in trial 2, is tolerant to many stresses, especially drought and is reported to give high yield under drought/aerobic conditions characteristic of upland, rainfed lowlands as well as well-watered areas (Calingacion *et al.*, 2017) subjected to periodic water deficits. Apo has inherent potential for higher yields under non-stress conditions (Venuprasad *et al.*, 2007) due to profuse tillering, intermediate height, higher number of productive tillers, dense panicles and higher HI. The higher yield of Apo with continuous flooded conditions was also reported earlier (Kumar *et al.*, 2017). The landrace, Pokkali is an excellent source of salt tolerance and contributed major QTL, *Saltol1*, associated with Na/K ratio and salinity tolerance (Bonilla *et al*., 2002). The yield potential of these lines with adaptation to various stress environments will help developing cultivars with increasing rice yields even in marginal environments and sustaining global food security. Rayada showed less number of productive tillers in all the trials and higher harvest index in trial 1 and 3, while Dular recorded lower harvest index in trial 1 and 2. The average spikelet fertility ranged from 73 (trial 3) to 85% (trial 1) consistent with earlier observations of spikelet fertility ranging from 64 to 89% in rice (Yan *et al.*, 2010).

The landrace, Kallurundaikar (50 kg ha$^{-1}$ in trial 1) and the japonica ecotype, Zhenshan (792 kg ha$^{-1}$ in trial 2) and (347 kg ha$^{-1}$ in trial 3) recorded lower yields among the accessions. Zhenshan had shorter panicle length, 16.5 and 13.3 cm in trial 1 and 3, respectively. Panicle length is one aspect of panicle architecture and is usually measured as a yield-related trait together with spikelet number and density and seed setting rate which determines the grain number per panicle, hence yield increase in rice (Liu *et al.*, 2016). Considerable variation of panicle length within subspecies was reported earlier in rice (Jambhulkar and Bose, 2014).

*Marker-trait associations:* Marker-trait analysis identified significant markers associated ($P < 0.05$) with yield traits in all the trials. MLM analysis revealed association of 109, 108 and 157 markers for yield and yield traits in trial 1, 2 and 3, respectively (data not shown). Among them, 46 markers are associated traits in two out of the three trials (Supplementary table 1). Several marker regions showed pleiotropic effect for grain yield and yield components. For instance, PSM371A (Chr 1), RM6650 (Chr 2), PSM 432 (Chr 7) and RM5405 (Chr 7) were associated with grain yield in trial 1. PSM432 and PSM371A were also associated with grain yield in trial 2 and trial 3, respectively. PSM371A was also associated with harvest index (HI) and days to fifty percent flowering (DFF) in trial 3. Zhao *et al.*, (2016) reported association of PSM371A with yield traits in rice. RM6650 was associated with straw yield (SY) and total biomass (TBM) in trial 1 and trial 3. RM6650 was also associated with number of tillers (NTT) and productive tillers (NPT) in trial 3. RM5405 was associated with GY in trial 1 and panicle length (PL) and spikelet fertility (SF) in trial 2. This marker was earlier reported for heading date (*HD*7) in rice (Ding *et al.*, 2015).

RM318 (Chr 2) was associated with GY and TBM in trial 2 and plant height (PH) in trial 2 and 3. Zou *et al.*, (2005) reported association of RM318 with PL under irrigated and SF and 1000 grain weight under water stress conditions in rice. PSM412 (Chr 11) and RM12 (Chr 12) were associated with GY in trial 3. PSM412 was also associated with SF in trial 2 and HI in trial 3. RM12 was associated with PH and SY in both trial 2 and 3. RM12 was earlier reported for PH (Yu *et al.*, 2002), yield and spikelet density (Liu *et al.*, 2011) and grain quality traits in rice (Verma *et al.*, 2015).

Four markers were detected in all the three trials (Table 3). For instance, PSM167 was associated with DFF in trial 1, HI, NTT and NPT in trial 2 and 3, and SF in trial 3. RM3376 was associated with DFF and GY in trial 1, NTT and NPT in trial 2, HI and SF in trial 3. PSM340 was associated with HI in trial 1, GY in trial 2 and PH in all the three trials. Linkage of plant height and yield QTLs under drought has been recently discussed (Vikram *et al.*, 2016). RM1303 was associated with SY in trial 1 and TBM in trial 1 and trial 2 and NPT in trial 3. Hence these markers consistently detected for plant height (PSM340), biomass (RM1303) and HI (PSM167) may be useful for early selection.

To sum up, the SSR markers viz., PSM432 and PSM371A are consistently linked to yield traits across trials and the four high yielding genotypes *viz.* IR58821, IR52561, Apo and Pokkali were identified as a good donors and can be used as better parents while formulating breeding for development of climate smart high yielding rice cultivars. Functional analysis and validation of genes underlying these genomic regions will help hastening breeding for yield increase in rice. Hence, association studies is a useful tool to identify novel alleles for high yield using diverse germplasm, thus saving time and resources required for conventional QTL mapping using biparental population with narrow genetic variation. While conventional linkage analysis works on an experimental population derived from a cross of bi-parents divergent for trait of interest, association mapping applies to collections of samples of much wider germplasm base. Providing the intrinsic nature of exploiting historical recombination events, association mapping offers increased mapping resolution to polymorphism at sequence level and should therefore enhance the efficiency of gene discovery and facilitate marker assisted selection (MAS) in plant breeding (Moose and Mumm, 2008).

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**Table 1. Mean and range values of phenology and yield traits for 49 rice lines under irrigated conditions.**

| Traits | Trial | Mean | Range | SD |
|---|---|---|---|---|
| **Days to 50% flowering** | 1 | 81.64 | 63.0 - 110.0 | 11.5 |
| | 2 | 84.94 | 68.0 - 98.0 | 7.0 |
| | 3 | 92.65 | 81.0 -105.0 | 6.5 |
| **Plant Height (cm)** | 1 | 99.40 | 62.7 - 138.3 | 15.1 |
| | 2 | 109.44 | 80.7 - 135.7 | 16.0 |
| | 3 | 104.90 | 53.1 - 160.0 | 21.6 |
| **Number of Tillers/plant** | 1 | 12.97 | 7.3 - 21.3 | 3.1 |
| | 2 | 12.43 | 8.7 - 17.3 | 1.8 |
| | 3 | 13.49 | 6.0 - 26.3 | 4.1 |
| **Number of Productive tillers/plant** | 1 | 12.53 | 7.3 - 21.3 | 2.9 |
| | 2 | 11.63 | 8.0 - 16.0 | 1.8 |
| | 3 | 11.74 | 5.0 - 21.7 | 3.5 |
| **Spikelet Fertility (%)** | 1 | 85.28 | 58.8 - 96.0 | 8.6 |
| | 2 | 82.32 | 67.6 - 94.4 | 6.2 |
| | 3 | 72.45 | 31.7 - 91.9 | 11.8 |
| **Panicle Length (cm)** | 1 | 21.83 | 16.5 - 26.5 | 2.5 |
| | 2 | 23.19 | 17.4 - 28.9 | 2.6 |
| | 3 | 21.51 | 13.3 - 27.0 | 3.2 |
| **Grain yield (kg ha$^{-1}$)** | 1 | 2217.75 | 50.0 - 5183.3 | 1381.5 |
| | 2 | 2512.50 | 791.7 - 5233.3 | 1064.3 |
| | 3 | 2184.49 | 347.2 - 4986.1 | 1015.6 |
| **Straw Yield (kg ha$^{-1}$)** | 1 | 6755.25 | 1233.3 - 12666.7 | 3086.9 |
| | 2 | 3620.94 | 750.0 - 7200.0 | 1565.3 |
| | 3 | 4419.08 | 833.3 - 9152.8 | 1872.1 |
| **Total Biomass (kg ha$^{-1}$)** | 1 | 8973.01 | 1633.3 - 17850.0 | 3865.8 |
| | 2 | 6133.44 | 1883.3 - 10191.7 | 2277.7 |
| | 3 | 6591.67 | 1180.6 -13729.2 | 2569.7 |
| **Harvest Index** | 1 | 0.25 | 0.01 -0.43 | 0.11 |
| | 2 | 0.41 | 0.15 - 0.60 | 0.10 |
| | 3 | 0.33 | 0.07 - 0.47 | 0.08 |

Trial 1: Feb., – June 2014, Trial 2: Aug., – Dec., 2014 and Trial 3: Aug., - Dec., 2015

**Table 2. Yield and yield components of 49 rice lines under irrigated conditions across seasons**

| Accession | Grain yield (kg ha$^{-1}$) | | | Biomass (kg ha$^{-1}$) | | | Harvest index | | |
|---|---|---|---|---|---|---|---|---|---|
| | Trial 1 | Trial 2 | Trial 3 | Trial 1 | Trial 2 | Trial 3 | Trial 1 | Trial 2 | Trial 3 |
| Akihikari | 2367 | 892 | 917 | 7542 | 3008 | 3236 | 0.31 | 0.30 | 0.28 |
| Anna 4 | 1467 | 850 | 1785 | 10633 | 3067 | 3882 | 0.14 | 0.28 | 0.46 |
| APO | 3600 | 5233 | 2201 | 9200 | 9092 | 7090 | 0.39 | 0.58 | 0.31 |
| Aswina | 3800 | 3008 | 1701 | 12300 | 5142 | 5188 | 0.31 | 0.59 | 0.33 |
| Azucena | 725 | 2392 | 2875 | 8825 | 6350 | 7431 | 0.08 | 0.38 | 0.39 |
| Bala | 2917 | 2317 | 1236 | 7250 | 4483 | 4944 | 0.40 | 0.52 | 0.25 |
| Blackgora | 1583 | 1467 | 1917 | 5083 | 3725 | 5653 | 0.31 | 0.39 | 0.34 |
| CO39 | 400 | 2300 | 2924 | 1633 | 5267 | 6451 | 0.24 | 0.44 | 0.45 |
| CPMBIR20AYT70 | 1358 | 2633 | 2201 | 4458 | 5117 | 6729 | 0.30 | 0.51 | 0.33 |
| CT9993 | 2908 | 2058 | 1243 | 8908 | 5600 | 5229 | 0.33 | 0.37 | 0.24 |
| Dom sufid | 600 | 2742 | 2414 | 4100 | 8375 | 9206 | 0.15 | 0.33 | 0.26 |
| Dular | 2717 | 3242 | 2965 | 6317 | 5433 | 6771 | 0.43 | 0.60 | 0.44 |
| FR13A | - | 1133 | 2340 | - | 1883 | - | - | 0.60 | - |
| IAC165 | 3533 | 4950 | 2069 | 11033 | 10192 | 5639 | 0.32 | 0.49 | 0.37 |
| IR1552 | 2033 | 2292 | 1368 | 8467 | 5392 | 4563 | 0.24 | 0.43 | 0.30 |
| IR20 | 2583 | 2433 | 2146 | 8000 | 6067 | 7410 | 0.32 | 0.40 | 0.29 |
| IR20/CT9993 NIL-212 | 4217 | 2542 | 1208 | 11883 | 4842 | 4958 | 0.35 | 0.52 | 0.24 |
| IR20/CT9993 NIL-297 | 2158 | 2317 | 1903 | 10458 | 5500 | 7111 | 0.21 | 0.42 | 0.27 |
| IR52561 | 4067 | 3042 | 4743 | 15767 | 9625 | 11813 | 0.26 | 0.32 | 0.40 |
| IR58821 | 5183 | 4500 | 3431 | 17850 | 10000 | 11931 | 0.29 | 0.45 | 0.29 |
| IR62266 | 2950 | 2208 | 958 | 10625 | 5008 | 3667 | 0.28 | 0.44 | 0.26 |
| IR64 | 4367 | 2733 | 1507 | 13867 | 5700 | 4007 | 0.31 | 0.48 | 0.38 |
| IR-80013 PVS2 | 4775 | 1375 | 2576 | 11608 | 5000 | - | 0.41 | 0.28 | - |
| IR-83895 AYT56 | 3467 | 3367 | 3007 | 12933 | 6367 | 7951 | 0.27 | 0.53 | 0.38 |
| IR-84887 PVS4 | 3142 | 875 | 3021 | 8642 | 2825 | 6438 | 0.36 | 0.31 | 0.47 |
| IR-84894 PVS8 | 2667 | 3508 | 2313 | 9250 | 6975 | 5729 | 0.29 | 0.50 | 0.40 |
| IRAT109 | 1033 | 2475 | 792 | 13533 | 5033 | 3458 | 0.08 | 0.49 | 0.23 |
| Kalinga III | 1850 | 2233 | 1840 | 10850 | 6400 | 5743 | 0.17 | 0.35 | 0.32 |
| Kallurundaikar | 50 | 2817 | 2583 | 6617 | 5017 | 8514 | 0.01 | 0.56 | 0.30 |
| KinandangPatong | 1375 | 2758 | 2167 | 12375 | 6258 | 7028 | 0.11 | 0.44 | 0.31 |
| Labelle | 4200 | 3375 | 2931 | 15933 | 8858 | 7569 | 0.26 | 0.38 | 0.39 |
| LTH* | - | - | - | - | - | - | - | - | - |
| M202 | 1400 | 3383 | 2153 | 9233 | 9772 | 7806 | 0.15 | 0.35 | 0.28 |
| Minghui | 3475 | 3733 | 4576 | 11808 | 9850 | 13729 | 0.29 | 0.38 | 0.33 |
| Moroberekan | 633 | 908 | 1778 | 4033 | 2667 | 8528 | 0.16 | 0.34 | 0.21 |
| N22 | 283 | 1108 | 740 | 2742 | 2608 | 2282 | 0.10 | 0.42 | 0.32 |
| NIL10 | 2933 | 2858 | 2646 | 11033 | 10058 | 6840 | 0.27 | 0.28 | 0.39 |
| Nipponbare | 1067 | 1967 | 1563 | 5867 | 6900 | 10507 | 0.18 | 0.29 | 0.15 |
| Nootripathu | 308 | 1408 | 1215 | 3083 | 7008 | 3715 | 0.10 | 0.20 | 0.33 |
| Norungan | 367 | 3142 | 2917 | 12200 | 7667 | 6736 | 0.03 | 0.41 | 0.43 |
| PM04022 | 1108 | 1892 | 1111 | 5075 | 4467 | 3194 | 0.22 | 0.42 | 0.35 |
| PMK 3 | 267 | 3317 | 2424 | 7592 | 8383 | 6257 | 0.04 | 0.40 | 0.39 |
| Pokkali | 1683 | 2575 | 4986 | 12517 | 6308 | 10917 | 0.13 | 0.41 | 0.46 |
| Rayada | - | 933 | 556 | - | 6333 | 8417 | - | 0.15 | 0.07 |
| R-RF-65PVS1 | 2500 | 1842 | 3000 | 5833 | 3958 | 8014 | 0.43 | 0.47 | 0.37 |
| Saducho | 3067 | 3592 | 2028 | 11275 | 7283 | 6083 | 0.27 | 0.49 | 0.33 |
| SHZ2* | 2875 | 3833 | 3160 | 9050 | 7367 | 7799 | 0.32 | 0.52 | 0.41 |
| Tainung 67 | 825 | 3250 | 2375 | 2833 | 9550 | 5875 | 0.29 | 0.34 | 0.40 |
| Zhenshan | 1133 | 792 | 347 | 2642 | 2625 | 1181 | 0.43 | 0.30 | 0.29 |

Trial 1: Feb., – June 2014, Trial 2: Aug., – Dec., 2014 and Trial 3: Aug., - Dec., 2015
LTH: Li-jiang-Xin-Tuan-Hei-Gu, SHZ2: Shan-Huang Zhan-2, - Data not available,

**Table 3. Consistent marker-trait associations in 49 diverse rice accessions across trials conducted under irrigated conditions**

| Marker | Chr. | Traits | | |
|---|---|---|---|---|
| | | Trial 1 | Trial 2 | Trial 3 |
| PSM167 | 10 | DFF | HI, NPT, NTT | HI, NPT, NTT, SF |
| RM3376 | 8 | DFF, GY | NPT, NTT | HI SF |
| RM1303 | 2 | SY, TBM | TBM | NPT |
| PSM340 | 9 | HI, PH | GY, PH | PH |

Trial 1: Feb., – June 2014, Trial 2: Aug., – Dec., 2014 and Trial 3: Aug., - Dec., 2015
DFF: Days to 50% flowering, PH: Plant Height, NTT: No. of total tillers, NPT: No. of productive tillers, SF: Spikelet Fertility, GY: Grain yield, SY: Stray yield, TBM: Total Biomass, HI: Harvest Index.