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RESEARCH ARTICLE

Allelic distribution and association of key gene-specific markers with rice (*Oryza sativa* L.) yield under acidic soil

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Abstract

Rice blast disease and soil acidity-related phosphorus deficiency are the major issues observed in rice-growing ecosystems across the world, especially in the North Eastern Hill (NEH) region of India. The present study aimed to check the allelic distribution of major genes for blast resistance, low P tolerance, grain yield and their association with increasing yield under acidic soils in NEH region. A set of 75 genotypes, including parental lines, advanced breeding lines and landraces, were evaluated and a significant association of *SPIKE* allele (Type-5) with spikelets per panicle, grain yield per panicle and plot yield was recorded. Gn1a-InDel3 allele was significantly associated with increased spikelets and grain number per panicle. The gene *PSTOL1* showed a significant association with tiller number at 30 and 60 days after transplanting but not with plot yield. The genotypes carrying desirable alleles for *Pi9, Pi2* and *Pi-ta* recorded lower disease scores but none of them were significantly associated with blast resistance. The study also identified advanced breeding lines ULRC24-48-5-1, ULRC24-57-1-1-1, ULRC24-49-5-1-1, ULRC24-99-3-1-1, ULRC26-11-2-1-1 and ULRC26-1-1-1 carrying six to eight favorable allelic combinations with high plot yield under acidic soil conditions. These lines can be used as potential donors for enhancing genetic gain under low input acidic soil conditions.

Keywords: Blast resistance, low P tolerance, haplotype, yield gain, acid soils.

Introduction

An ever-increasing human population and fast-changing climatic conditions call for accelerated development of climate-resilient crop varieties with enhanced tolerance to abiotic and biotic stresses. North Eastern Region (NER) of India is a center of diversity for rice and is home to thousands of landraces, which in spite of being low-yielding, are preferred by the local consumers for their desirable grain qualities. Most of the breeding programmes focus on developing high-yielding varieties and seldom on increasing the yield of specialty rice (colored, aromatic rice) by incorporating minor alleles which contribute to yield gain. Globally nearly 30 to 40% of potential arable land is acidic and left unused due to adverse soil conditions like soil acidity and it is associated with nutrient deficiencies and mineral toxicities (Zhu and Shen 2023). Reduced availability of P causes poor plant growth, low productive tillers, spikelet sterility, poor root growth, and ultimately adversely affects yield. P starvation tolerance 1 (*PSTOL1*) is one such locus identified from Pup1 (Phosphorous Uptake 1) QTL imparts low P tolerance in rice (Gamuyao et al. 2012). Introgression of *PSTOL1* locus showed increased biomass, tiller number and yield up to 30% in low P condition (Wissuwa et al. 2005; Vigueria et al. 2016; Tyagi et al. 2021). Till now, *PSTOL1* is the only gene being successfully used in marker-assisted breeding programs (Chitrameenal et al. 2018). However, its effect varies according to genetic background (Wissuwa et al. 2016). Novel haplotypes for *PSTOL1* from the genotypes adapted to acidic soil conditions are also reported (Yumnam et al. 2017) and validated under low land acid soil conditions (Bhutia et al. 2021).

Apart from soil conditions, biotic stress like blast disease also causes yield loss upto 30 to 50% in southeast Asian

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countries (Suprapta et al. 2012). To date, more than 100 R genes are reported and 31 R genes are cloned (Ning et al. 2020). Among them, *Pi1, Pi2, Pi9, Pigm, Pi21* and *Pi54* are reported to impart broad-spectrum resistance (Thakur et al. 2015; Ning et al. 2020) and *Pib, Pi-km, Pi12* confer race-specific resistance (Yang et al. 2008). Some major genes like *Piz, Pi-ta, Pi54, Pi5, Pb1* have been used for developing durable blast resistance in different genetic backgrounds like Pusa basmati1, PB1121, PB6 and PRR78 (Singh et al. 2012; Khanna et al. 2015a; Ellur et al. 2016) under lowland ecosystem.

Yield is a complex quantitative trait governed by several genes. Nearly 87 key genes associated with grain yield were reported based on haplotype analysis by Abbai et al. 2019. Among the several genes *SPIKE* (*SPIKELET NUMBER*) (Fujita et al. 2013); *Gn1a* (Ashikari et al. 2005); *SCM2* (*STRONG CULM2*) (Ookawa et al. 2010); *DEP1* (*DENSE and ERRECT PANICLE1*) (Huang et al. 2009); *OsSPL14* (Miura et al. 2010; Jiao et al. 2010); *Gs5* (Li et al. 2011); *TGW6* (Ishimaru et al. 2013) are widely used in breeding programs as the markers for desirable alleles of these genes are reported (Kim et al. 2016). Identification of superior haplotypes for traits of importance in a particular agroecosystem is one of the first steps in achieving genetic gain. Therefore, the present study was undertaken to find the allelic status of validated genes reported for blast resistance, low P tolerance and yield in the parents and advanced breeding lines involved in the breeding pipeline. Effective gene combinations for lowland acidic soil were also identified.

Materials and methods

Plant materials and phenotyping

A total of 75 genotypes, including 21 rice parental genotypes and 54 advanced breeding lines (ABLs) developed at the College of Post Graduate Studies in Agricultural Sciences (CPGSAS), Central Agricultural University (CAU), Imphal, three landraces (two of them are GI protected) from Manipur, Assam, Arunachal Pradesh, and thirteen released varieties (Supplementary Table S1) were used in the present study. The materials were evaluated under lowland acidic soil conditions (pH- 5.6) during *kharif* 2019 and 2020 for leaf blast resistance and yield traits. Young seedlings (25 days old) were transplanted in plots of $1m^2$ per genotype with 20 cm row-to-row and 15 cm plant-to-plant spacing. Field management was done as reported previously (Bhutia et al. 2021).

Data were recorded randomly on ten plants from each genotype. All the 21 parental lines and 54 advanced breeding lines were evaluated for twelve yield and related traits like tiller number at 30 DAT (DAT-days after transplanting) (TN30), tiller number at 60 DAT (TN60), number of panicles per plant (NP), panicle length (cm) (PL), spikelets per panicle (SPP), filled grains per panicle (FGPP), spikelet fertility percentage (SF%), 100 seed weight (g) (SW), Plot Yield (g) (PY), length and breadth ratio (mm) (L: B ratio), leaf blast score and shoot P content. Leaf blast disease score was recorded three times at fifteen days intervals before initiation of flowering under natural field conditions. The relative humidity (75–90%) and temperature (25–28°C) of this region naturally favor the blast disease. The disease scoring was done using the 0 to 9 scale as per the standard evaluation system (SES). The genotypes scored as resistant (0–3 score), moderately resistant (4–6 score) and susceptible (7–9 score) based on the disease incidence (IRRI, 2013). Shoot P content was estimated by using the vanadate molybdate colorimetric method as previously described in Yumnam et al. (2017). The shoot phosphorous use efficiency (PUE) is the amount (g) of biomass produced per unit P (g DM/mg P) (Rose and Wissuwa, 2012).

Genotyping

Healthy young leaves (30DAT) were collected from plants grown in field conditions and genomic DNA was extracted using sodium dodecyl sulfate (SDS) method (Dellaporta et al. 1983). The parental genotypes were screened using 22 previously reported gene-specific/linked SSR and InDel markers for blast resistance, low P tolerance and yield traits (Supplementary Table S2). A subset of nine polymorphic markers that are associated with respective phenotypes among parents are considered important for blast resistance and yield under acidic soil were used for genotyping the 54 advanced breeding lines. Polymerase chain reaction (PCR) was performed to investigate the allelic status of reported markers for blast resistance, low P tolerance and grain yield (Kim et al. 2016; Singh et al. 2015; Li et al. 2008; Tian et al. 2016; Chin et al. 2011). Amplified PCR products were resolved in 2.5% agarose gel made with 0.5X TBE buffer. Gels were stained in ethidium bromide (10mg/ml) and visualized under UV light.

Statistical analysis

The experiments were conducted using an augmented design with four blocks and five checks. Block-adjusted means of data collected on ten plants of each genotype were used for further analysis. Correlation among traits was estimated using the Metan package (Olivoto and Col Lucio 2020) in RStudio. The molecular data and mean phenotypic data were used for performing a t-test to understand the marker-trait association using RStudio. The P values less than 0.05 ($p < 0.05$) were considered significant.

Results and discussion

Blast disease and soil acidity are severe in the north-eastern region of India, which adversely affects rice productivity. Breeding for stress-tolerant/resistant varieties provides the best alternative way to enhance yield. Identification, validation, introgression and consolidation of desirable genes/alleles into elite varieties involved in the breeding pipeline will serve this purpose.

Variation for key phenotypic traits under acidic soil

Significant variation for the twelve traits (as mentioned in the materials and methods section) was observed in the 21 parental lines and 54 ABLs (Fig. 1). Correlation analysis between the traits revealed a positive significant correlation of TN60 with TN30 (r = 0.89), NP (r = 0.46) and PY (r = 0.48). Similarly, PL was significantly correlated with SW (r = 0.56), LB ratio (r = 0.61), PY (r = 0.52), and FGPP correlated with SPP (p = 0.67). SW positive significantly correlated with PL (r = 0.56), PY correlated with NP (r = 0.52) (Fig. 1).

Genotyping of parental lines for the genes reported for blast resistance, low P tolerance and yield

About 21 parental lines were genotyped for fourteen blast resistance genes to check the allelic distribution of key genes among the parents. Six blast genes (*Piz, Pi1, Pi20(t), qPbm11, Pi12, Piz5*) were observed to be fixed for the respective desirable alleles in the parental lines. The parents carried differential alleles for eight blast resistance genes, namely, *Pi-k^m, Pi5, Pi-ta, Pi2, Pb1, Pi38, Pib* and *Pi9* (Fig. 2) which were located on chromosomes 6, 9, 11 and 12, respectively. The frequency of desirable allele was 85.71% for *Pi2* and *Pb1*, 80.95% for *Pi-ta* gene and 71.43% for *Pi38*. Genes *Pib, Pi-k^m* and *Pi5* linked with marker Pibdom, Ckm-2 and JJ803 showed a desirable allele frequency of 61.9, 47.6, and 42.8%,

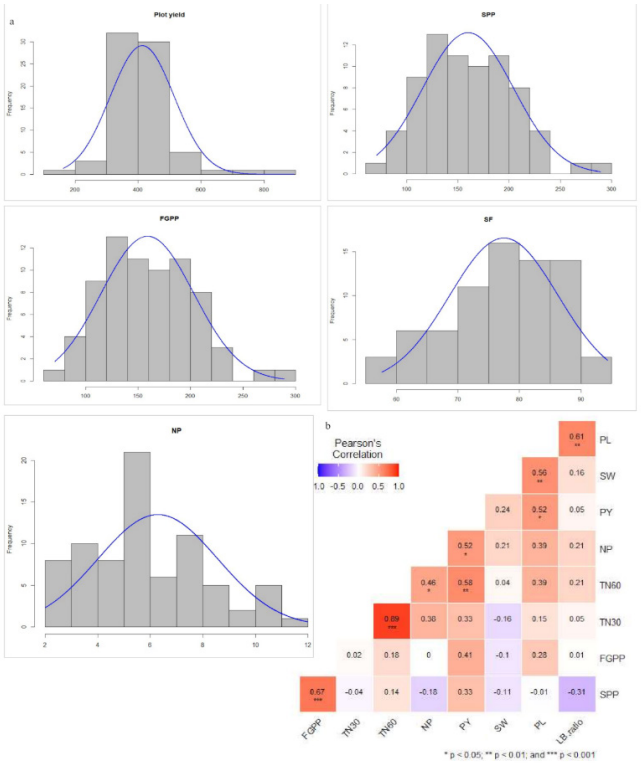

Fig. 1. A) Phenotypic variations observed for yield-related traits and B) Correlation between nine yield-related traits evaluated under low land conditions. TN 30 – Tiller number at 30 days; TN 60- tiller number at 60 days; PL- panicle length; NP- number of panicles; SF – spikelet fertility; GW- 100-grain weight; SPP- Spikelet per panicle; FGPP- filled grain per panicle; PY-Plot yield; LB ratio- length and breadth ratio

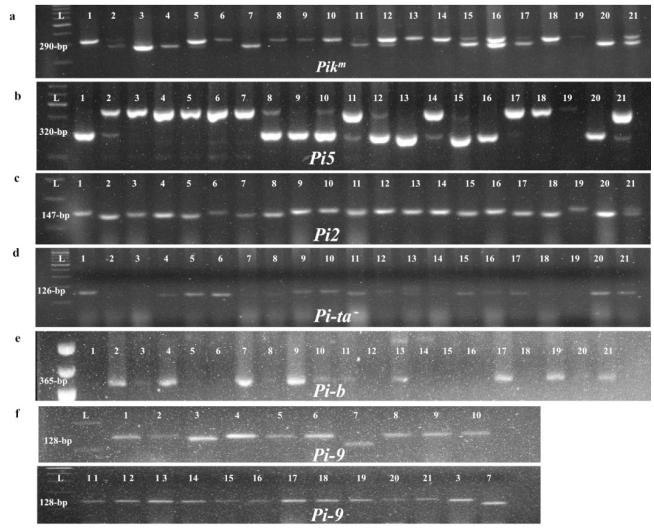

Fig. 2. Allelic status for blast resistance genes *Pik^m, Pi5, Pi2, Pi-ta, Pib* and Pi9 based on markers CKM-2, JJ 803, RM7311, RM247, Pibdom, and Pi9-Pro, respectively. The desirable allele size is given on the left side of each gel. L denotes 100 bp ladder (gene ruler). The numbers on the top correspond to sl.no. of the rice genotypes in Supplementary Table S1

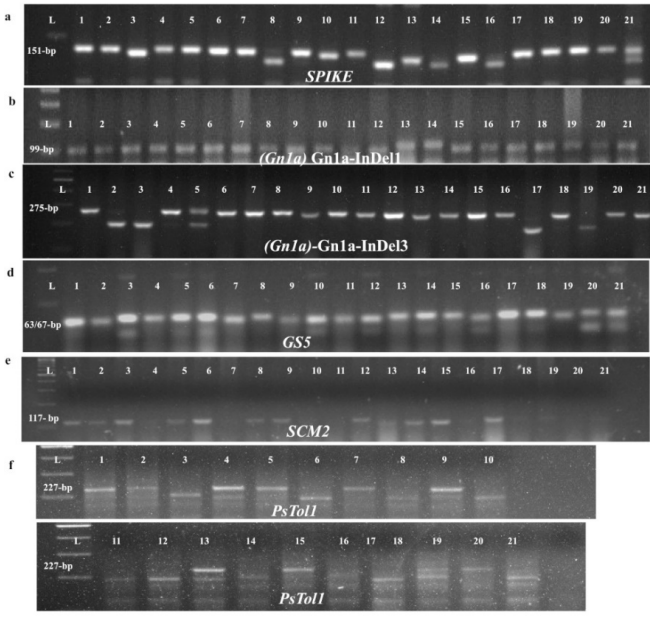

Fig. 3. Allelic status of grain yield-related genes and low P tolerance gene based on markers SPIKE-indel3, Gn1a-indel1 and Gn1a-indel3, GS5-indel1, SCM2-indel1 and K46-2, respectively. The desirable allele size is given on the left side of each gel. L- denotes 100 bp ladder (gene ruler). The numbers on the top correspond to sl.no. of the rice genotypes in Supplementary Table S1

respectively. Marker Pi9-Pro with expected amplicon size of 128-bp showed a desirable allele frequency of 4.76% for the gene *Pi9*. The parental genotypes IR64, Shasharang, VL40387, and CAUS105 possessed a combination of twelve R genes, while BLM9 that had least disease score, carried thirteen R genes. On the other hand, three landraces, Chakhaopoireiton, Mang Meikri and Joha, carried eight and

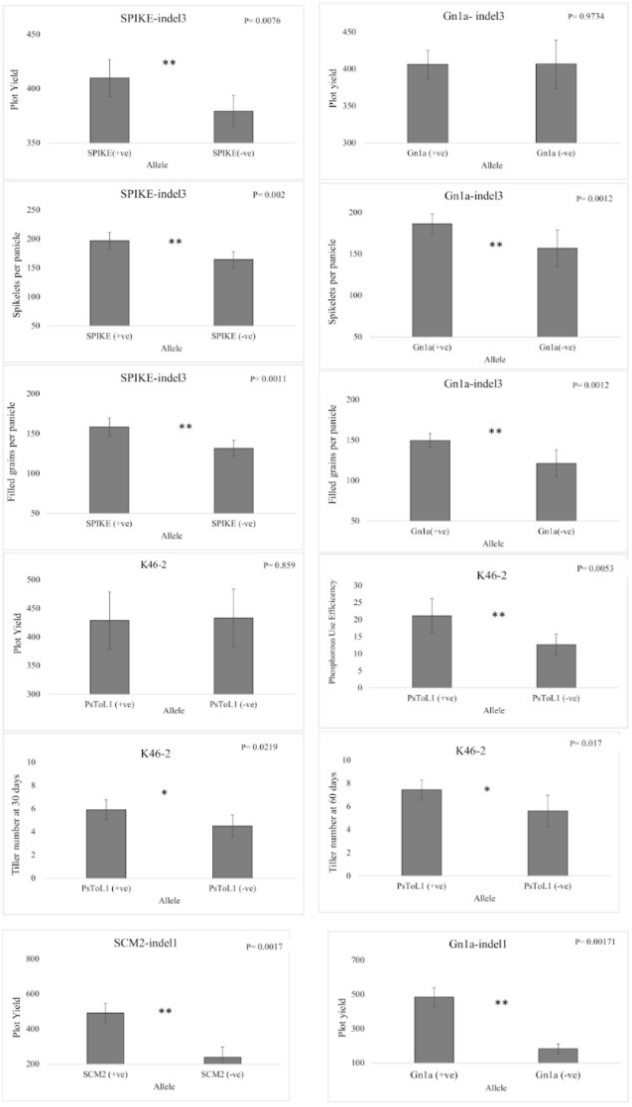

Fig. 4. Test of association of markers SPIKE-indel3, Gn1a-indel3, K46-2, SCM2-indel1, Gn1a-indel1 with important phenotypic traits in terms of mean phenotypic differences between two marker allelic classes in genotypes evaluated under low land conditions. *- Significant difference between alleles for a trait at 5% level of significance. **- Significant difference between alleles for a trait at 1% level of significance

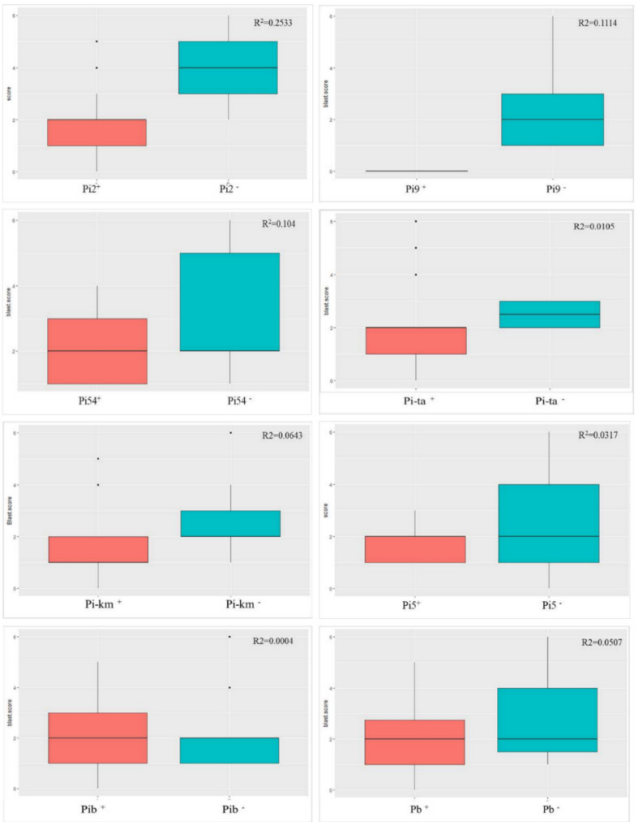

Fig. 5. Box plots representing leaf blast score variation for two allelic groups of genes *Pi9, Pi2, Pi54, Pi-ta, Pi-km, Pi5, Pib, Pb1* observed using markers Pi9-Pro, RM7311, RM224, RM247, CKM-2, JJ803, Pibdom, and Pb3810 respectively along with R^2value in the top corner

ten R genes, respectively displayed a moderately resistant reaction. With the exception of Kasalath which carried 12 R genes and showed a moderately resistant response, the genotypes carrying higher number of R genes showed higher resistance response to blast disease. This is concurrent with the reports of Yadav et al. (2019) and Wu et al. (2015). With the identification of multiple blast resistance genes, several breeding efforts have been made to introgress these genes into elite susceptible varieties, and a series of improved lines were developed in the past (Swathi et al. 2019; Chukwu et al.2020). However, the single gene resistance can be broken down rapidly in a few years due to the dynamic and diverse races of *M. oryzae* and it was already shown that a combination of blast resistance genes can provide enhanced resistance in a different background (Jiang et al. 2019). The present study also showed that presence or absence of a single gene was not significantly affecting resistance, and therefore it is important to assemble a suitable haplotype of desirable alleles across multiple major resistance genes to achieve durable resistance.

Similarly, K46-2, a dominant marker, reported for the gene *PSTOL1,* was present in 52.38% of the parental lines (Fig. 3). For yield related gene *SCM2,* the desirable amplicon size of 117-bp for SCM2-indel1 marker had a frequency of 85.71%. All the lines except joha, mang meikri and PB1121 carried the *SCM2*-Habataki type allele, which is allelic to *APO1 (ABERRANT PANICLE ORGANIZATION1)*. A 20-bp deletion in the promoter region of *SPIKE* gene leading to a desirable allele with 151-bp amplicon size was found with a frequency of 19% in the parents. For the *SPIKE* gene, two alleles were observed in the parental lines, yield a positive *NAL1*-japonica allele (Type-5) was found only in CAUS103, CAUS110, Shasharang and Mang Meikri. The marker GS5-indel1 associated with grain size gene (*GS5*) produced 63-bp (MG- medium grain allele) and 67-bp (WG or NG- wide or narrow grain allele) amplicons with the frequency of 42.85% and 57.14%, respectively. Eight lines carrying the medium

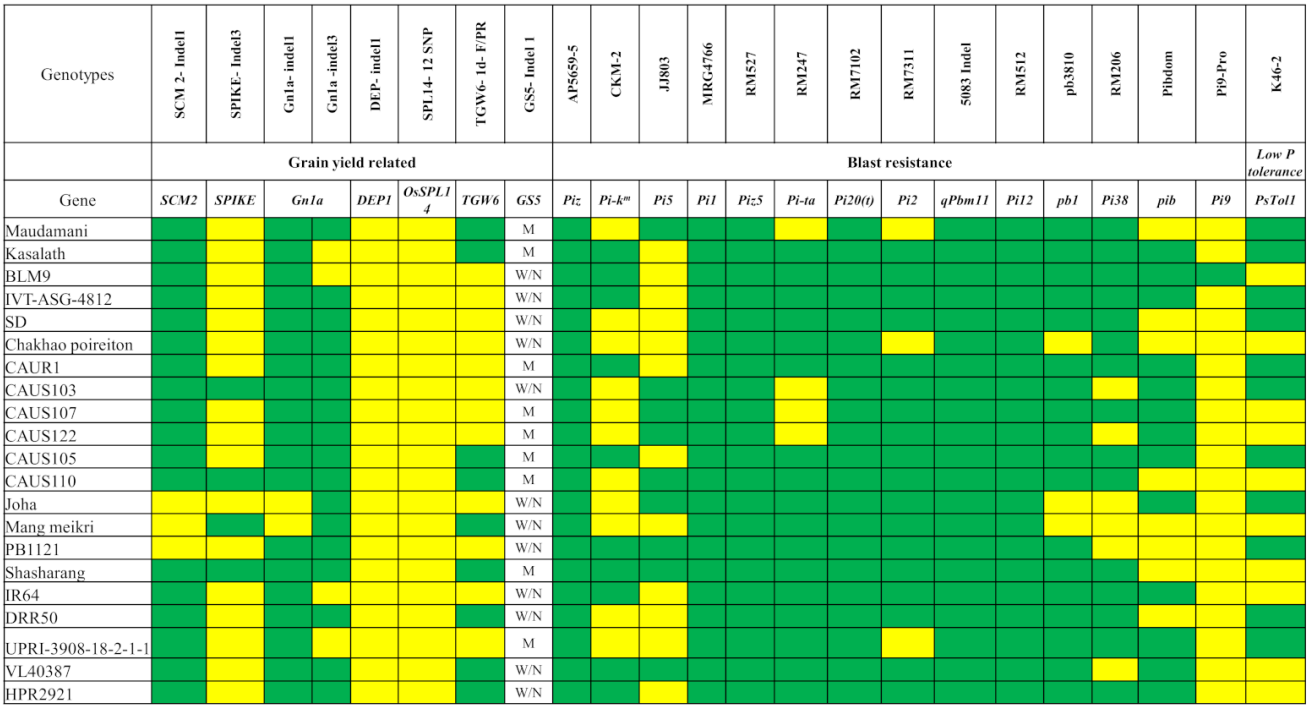

Fig. 6. Allelic status of all the genes selected for blast resistance, Low P tolerance and yield-related genes across the parental genotypes. Green colour denotes the positive/desirable allele; Yellow colour denotes the negative allele. W/N = Wide/narrow grain; M = Medium grain

grain type allele showed higher yield compared with lines carry W/N grain type allele. The presence of desirable *Gn1a* allele was determined by two markers namely Gn1a-indel1 and Gn1a-indel3. A 16-bp deletion in the 5'UTR region with an amplicon size of 99-bp is the desirable allele reported for the Gn1a-indel1 marker. A 70-bp deletion near 3'UTR region is reported as the desirable allele (275-bp) for Gn1a-indel3 marker. The desirable allele frequency of 90.47% and 80.95% was observed for Gn1a-indel1 and Gn1a-indel3 markers, respectively. Three haplotypes (Type-1, Type-2, Type-3) have been reported for the gene *Gn1a* by kim et al. 2016. The positive *Gn1a*-Habataki type allele (Type-3) was observed in all the lines except Joha and Mang Meikri for Gn1a-indel1 marker. But this marker is not effective in introducing the Type-3 allele into the Type-2 background. Gn1a-indel3 marker that detects a 70-bp polymorphism in the 3¢UTR was found useful in introducing the *Gn1a* allele in Type-2 background as well.*TGW6* is a single exon gene and the loss of function allele carries 1-bp deletion in CDS with the desirable allele at 388-bp for marker TGW6-1d-F/PR and 42.85% of parents carried the desirable allele for *TGW6* gene. Whereas *DEP1* and *OsSPL14* were absent among the parents suggests the donors carrying the respective alleles need to be incorporated in the breeding programme. Thus, among theparental genotypes, CAUS103 had positive alleles for *SCM2*, *SPIKE*, *Gn1a*, W/N grain type, while CAUS110 and Shasharang carried positive alleles for *SCM2*, *SPIKE, Gn1a, TGW6*, and M grain type recorded the highest yield per plant.

Marker trait association

Significant difference for grain yield per plant between two allelic classes was observed for markers SCM2-indel1, Gn1a- indel1, Gn1a- indel3, SPIKE- indel3 and K46-2 (Fig. 4), indicating association of the markers with grain yield. A significant association was observed for SCM2-indel1 with PY (p = 0.0017). SPIKE- indel3 with PY (p = 0.0076), SPP (p = 0.002) and FGPP (p= 0.0011). Gn1a-indel3 is significantly associated with SPP (p = 0.0012), and FGPP (p = 0.0012). Gn1a-indel1 showed significant association with PY (p = 0.0017) and K46-2 was found to be associated with TN30 (p = 0.0219) and TN60 (p = 0.017) and phosphorous use efficiency (p = 0.0053). With respect to blast resistance genes, genotypes carrying desirable alleles for *Pi2, Pi9* and *Pita* had lower mean disease scores as compared to parents lacking them (Fig. 5). However, none of the fourteen individual blast resistance genes were significantly associated with leaf blast score.

Among the yield genes, *SPIKE* reported a significant association with plot yield and among the four lines carrying the desirable *SPIKE*allele, three lines recorded a higher single plant yield. The consistent effect of *SPIKE* gene for increasing yield under low fertile conditions has been reported earlier (Fujita et al. 2013; Takai et al. 2017; Takai et al. 2019). Based on the results and previous reports, the *SPIKE* gene can be a potential target and needs to be selected in the breeding pipeline to increase yield. On the other hand, the traditional local variety Joha lacks a desirable allele for the above-mentioned yield genes (Fig. 6) reflected in poor yield,

Table 1. Identified haplotypes for blast resistance, low P tolerance and yield in advanced breeding lines

S. No.	ULRC lines	Gene combination (s)
1	6*7-3-1-1-1, 24-48-5-1 and 36-300	*SPIKE, Gn1a, Pi54, Pi-ta, PsTol1, Os02g08018, OsMLO8 and OsWD40-2*
2	2*11-2-1 and 24-57-1-1-1	*SPIKE, Gn1a, Pi54, PsTol1, Os02g08018, OsMLO8 and OsWD40-2*
3	6*7-2-1-1, 24-49-5-1-1, 26-1-1-1, 26-11-2-1-1, 34-17, 34-178, 34-30, 34-354-2 and 35-SSD-5	*Gn1a, Pi54, Pi-ta, PsTol1, Os02g08018, OsMLO8* and *OsWD40-2*
4	4*4-1-5-1 and 24-99-3-1-1	*SPIKE, Gn1a, Pi54, Pi-ta, PsTol1, Os02g08018 and OsWD40-2*
5	4-2-5-1-1-1, 6*7-5-1-1, 29-8-2-1and 29-50-2-1-1	*SPIKE, Gn1a, Pi54, Pi-ta, Os02g08018, OsMLO8 and OsWD40-2*
6	26-1-1-1, 34-248, 34-354-1, 34-97 and 35-SSD-2	*Gn1a, Pi54, PsTol1, Os02g08018, OsMLO8* and *OsWD40-2*
7	6*7-3-3-1 and 36-285	*Gn1a, Pi54, Pi-ta, Os02g08018* and *OsWD40-2*
8	24-119-5-1-1, 24-49-4-1-1, 36-1 and 36-175	*Pi54, Pi-ta, Os02g08018, OsMLO8* and *OsWD40-2*
9	6*7-3-3-31 and 29-8-3-1-1	*Gn1a, Pi54, Pi-ta* and *Os02g08018*

whereas Chakhaopoireiton possesses *Gn1a* and *SCM2* but it is highly prone to leaf and neck blast infection leading to low yield. Interestingly, the landrace Mang Meikri carries *SPIKE* gene but is low-yielding. The different genetic backgrounds between genotypes and GXE interaction might reduce the efficiency of a gene. It may be essential to consider the genetic background for the future use of *SPIKE* gene, as also suggested by Takai et al. 2017. As it was already known, yield is a quantitative traits. The presence of a single gene may not be effective in increasing the yield, especially in stress conditions. Identification of superior haplotypes across loci for yield along with blast resistance and low P tolerance provide the opportunity for yield gain in rice.

Genotyping of advanced breeding lines

On the basis of parental genotyping data, the markers that showed significant association with yield were selected and evaluated in the 54 advanced breeding lines. For yield Gn1a-indel1, Gn1a-indel3 and SPIKE-indel3 markers, and for low P tolerance K46-2 and 3 more markers (PR9-2, RM12557, HvSSR 02-14), which showed significant association with yield traits in the previous studies (Bhutia et al. 2021) were used. Since none of the blast markers were significantly associated with leaf blast score among the parental lines, two genes *Pi54* and *Pi-ta* reported earlier to confer durable resistance (Khanna et al. 2015b; Jia et al. 2016) were chosen to screen on the advanced breeding lines. Genotyping of advanced breeding lines showed a variation in allelic distribution for all the markers evaluated except Gn1a-indel1. The desirable allele for Gn1a-indel1 was already fixed among the 54 advanced breeding lines. Whereas, for other genes, the desirable/significant allele frequency was observed highest for RM12557 (27.54%), which is a genetic marker for *Os02g08018* gene. While the lowest was observed for yield marker SPIKE-indel3 (10.26%).

Identification of desirable haplotype combinations in ABLs for blast resistance, low P tolerance and grain yield

Haplotype analysis was done on advanced breeding lines based on eight markers, excluding Gn1a-indel1. Three genotypes ULRC6*7-3-1-1-1, ULRC24-48-5-1, and ULRC36-300 carry all the desired alleles for the eight genes evaluated for blast resistance, low P tolerance and yield (Table 1). A total of nine haplotype combinations were observed among the advanced breeding lines. Sixteen genotypes had desirable haplotypes for seven genes. Eleven genotypes carry desirable haplotypes for six genes. Five genes were fixed in a total of twelve genotypes, while nine genotypes possessed desirable haplotypes for four genes. All the advanced breeding lines used in the study had a minimum of three genes fixed for the respective desirable allele. Our study identified superior haplotypes, indicating that ABLs carrying desirable alleles for genes *SPIKE, Gn1a* and *Os02g08018* showed the highest yield. For instance, we identified four ULRC24 lines (Kasalath x Shasharang), namely ULRC24-48-5-1, ULRC24-57-1-1-1, ULRC24-49-5-1-1 and ULRC24-99-3-1-1 having the highest number of favorable alleles (7-8) and a higher yield of 400-500g/m^2 was observed. Similarly, two ULRC26 lines (Kasalath X BORO paddy), i.e., ULRC26-11-2-1-1 and ULRC26-1-1-1, had a combination of 7 and 6 favorable alleles, respectively with high yield among the 52 ABLs. Based on the result, the above-mentioned lines can be used as parents in breeding programs for blast resistance, low P tolerance, and yield under lowland acidic conditions or can be nominated for multilocational trials.

Supplementary material

Supplementary Tables S1 and S2 can be accessed at www.isgpb.org

Authors' contribution

Conceptualization of research (MR); Designing of the experiments (MR, MP, SA); Contribution of experimental materials (MR, WT); Execution of field/lab experiments and data collection (MP, SA, LK, JB); Analysis of data and interpretation (MP, MR); Preparation of the manuscript (MP, MR, WT).

References

Abbai R., Singh V.K, Nachimuthu V.V., Sinha P., Selvaraj R., Vipparla A.K., Singh A.K., Singh U.M., Varshney R.K. and Kumar A. 2019. Haplotype analysis of key genes governing grain yield and quality traits across 3K RG panel reveals scope for the development of tailor-made rice with enhanced genetic gains. Plant Biotechnol. J., **17**(8): 1612-1622.

Ashikari M., Sakakibara H., Lin S., Yamamoto T., Takashi T., Nishimura A., Angeles E.R., Qian Q., Kitano H. and Matsuoka M. 2005. Cytokinin oxidase regulates rice grain production. Sci., **309**(5735): 741-745.

Bhutia K.L., Nongbri E.L., Sharma T.O., Rai M. and Tyagi W. 2021. A 1.84-Mb region on rice chromosome 2 carrying *SPL4,SPL5* and *MLO8* genes is associated with higher yield under phosphorus-deficient acidic soil. J. App. Genet., **62**(2): 207-222.

Chin J.H., Gamuyao R., Dalid C., Bustamam M., Prasetiyono J., Moeljopawiro S., Wissuwa M. and Heuer S. 2011. Developing rice with high yield under phosphorus deficiency: Pup1 sequence to application. Plant Physiol., **156**(3): 1202-16.

Chithrameenal K., Alagarasan G., Raveendran M., Robin S., Meena S., Ramanathan A. and Ramalingam J. 2018. Genetic enhancement of phosphorus starvation tolerance through marker assisted introgression of *OsPSTOL1* gene in rice genotypes harbouring bacterial blight and blast resistance. PLoS One, **13**(9): e0204144.

Chukwu S.C., Rafii M.Y., Ramlee S.I., Ismail S.I., Oladosu Y., Kolapo K., Musa I., Halidu J., Muhammad I. and Ahmed M. 2020. Marker-assisted introgression of multiple resistance genes confers broad spectrum resistance against bacterial leaf blight and blast diseases in Putra-1 rice variety. Agronomy, **10**(1): 42.

Dellaporta S.L., Wood J. and Hicks J.B. 1983. A plant DNA minipreparation: version II. Plant Mol. Biol. Rep., **1**: 19–21.

Ellur R.K., Khanna A., Yadav A., Pathania S., Rajashekara H., Singh V.K., Gopala Krishnan S., Bhowmick P.K., Nagarajan M., Vinod K.K., Prakash G., Mondal K.K., Singh N.K., Prabhu K.V. and Singh A.K. 2016. Improvement of basmati rice varieties for resistance to blast and bacterial blight diseases using marker assisted backcross breeding. Plant Sci., **242**: 330–341.

Fujita D., Trijatmiko K.R., Tagle A.G., Sapasap M.V., Koide Y., Sasaki K., Tsakirpaloglou N., Gannaban R.B., Nishimura T., Yanagihara S. and Fukuta Y. 2013. NAL1 allele from a rice landrace greatly increases yield in modern indica cultivars. Proc. National Academy Sci., **110**(51): 20431-20436.

Gamuyao R., Chin J., Pariasca-Tanaka J., Pesaresi P., Catausan S., et al. 2012. The protein kinase Pstol1 from traditional rice confers tolerance of phosphorus deficiency. Nature, **488**: 535–39.

Huang X., Qian Q., Liu Z., Sun H., He S., Luo D., Xia G., Chu C., Li J. and Fu X. 2009. Natural variation at the DEP1 locus enhances grain yield in rice. Nature Genet., **41**(4): 494-497.

IRRI, (2013)- SES (Rice standard evaluation system). https://www.clrri.org/ver2/uploads/SES_5th_edition.pdf.

Ishimaru K., Hirotsu N., Madoka Y., Murakami N., Hara N., Onodera H., Kashiwagi T., Ujiie K., Shimizu B.I., Onishi A. and Miyagawa, H. 2013. Loss of function of the IAA-glucose hydrolase gene TGW6 enhances rice grain weight and increases yield. Nature Genet., **45**(6): 707-711.

Jia Y., Zhou E., Lee S. and Bianco T. 2016. Coevolutionary dynamics of rice blast resistance gene *Pi-ta* and Magnaporthe oryzae avirulence gene *AVR-Pita 1*. Phytopathology, **106**: 676–683.

Jiang H., Li Z., Liu J., Shen Z., Gao G., Zhang Q. and He Y. 2019. Development and evaluation of improved lines with broad-spectrum resistance to rice blast using nine resistance genes. Rice, **12**(1): 1-11.

Jiao Y., Wang Y., Xue D., Wang J., Yan M., Liu G., Dong G., Zeng D., Lu Z., Zhu X., Qian Q. and Li J. 2010. Regulation of OsSPL14 by OsmiR156 defines ideal plant architecture in rice. Nat. Genet., **42**(6): 541–544.

Khanna A., Sharma V., Ellur R.K., Shikari A.B., Gopala Krishnan S., Singh U.D., Prakash G., Sharma T.R., Rathour R., Variar M. and Prashanthi S.K. 2015b. Development and evaluation of near-isogenic lines for major blast resistance gene (s) in Basmati rice. Theor. Appl. Genet., **128**(7): 1243-59.

Khanna A., Sharma V., Ellur R.K., Shikari A.B., Krishnan S.G., Singh U.D., Prakash G., Sharma T. R., Rathour R., Variar M. and Prashanthi S.K. 2015a. Marker assisted pyramiding of major blast resistance genes *Pi9* and *Pita* in the genetic background of an elite Basmati rice variety, Pusa Basmati 1. Indian J. Genet. Plant Breed., **75**(4): 417-25.

Kim S.R., Ramos J., Ashikari M., Virk P.S., Torres E.A., Nissila E., Hechanova S.L., Mauleon R. and Jena K.K. 2016. Development and validation of allele-specific SNP/indel markers for eight yield-enhancing genes using whole-genome sequencing strategy to increase yield potential of rice, *Oryza sativa* L. Rice, **9**(1): 1-17.

Li W., Lei C., Cheng Z., Jia Y., Huang D., Wang J., Wang J., Zhang X., Su N., Guo X., Zhai H. and Wan J. 2008. Identification of SSR markers for a broad-spectrum blast resistance gene Pi20(t) for marker-assisted breeding. Mol. Breeding., **22**: 141-149.

Li Y., Fan C., Xing Y., Jiang Y., Luo L., Sun L., Shao D., Xu C., Li X., Xiao J. and He Y. 2011. Natural variation in GS5 plays an important role in regulating grain size and yield in rice. Nature Genet., **43**(12): 1266-1269.

Miura K., Ikeda M., Matsubara A., Song X.J., Ito M., Asano K., Matsuoka M., Kitano H. and Ashikari M. 2010. OsSPL14 promotes panicle branching and higher grain productivity in rice. Nature genetics, **42**(6): 545-549.

Ning X., Yunyu W. and Aihong L. 2020. Strategy for use of rice blast resistance genes in rice molecular breeding. Rice Sci., **27**(4): 263-277.

Olivoto T. and Col Lúcio A.D. 2020. metan: An R package for multi-environment trial analysis. Methods in Ecology and Evolution, **11**(6): 783-789.

Ookawa T., Hobo T., Yano M., Murata K., Ando T., Miura H., Asano K., Ochiai Y., Ikeda M., Nishitani R., Ebitani T., Ozaki H., Angeles E. R., Hirasawa T. and Matsuoka M. 2010. New approach for rice improvement using a pleiotropic QTL gene for lodging resistance and yield. Nat. Comms., **1**: 132.

Rose T.J. and Wissuwa M. 2012. Rethinking internal phosphorus utilization efficiency: a new approach is needed to improve PUE in grain crops. Adv. Agron., **116**: 185-217. https://doi.org/10.1016 /B978-0-12-394277-7.00005-1.

Singh A.K., Singh P.K., Arya M., Singh N.K. and Singh U.S. 2015. Molecular screening of blast resistance genes in rice using SSR markers. The Plant Pathol. J., **31**(1): 12.

Singh H., Deshmukh R.K., Singh A., Singh A.K., Gaikwad K., Sharma T.R., Mohapatra T. and Singh N.K. 2010. Highly variable SSR markers suitable for rice genotyping using agarose gels. Mol. Breed., **25**(2): 359-364.

Singh V.K., Singh A., Singh S.P., Ellur R.K., Choudhary V., Sarkel S., Singh D., Krishnan S.G., Nagarajan M., Vinod K.K. and Singh U.D. 2012. Incorporation of blast resistance into "PRR78", an elite Basmati rice restorer line, through marker assisted backcross breeding. Field Crops Res., **128**: 8-16.

Suprapta D.N. and Khalimi K. 2012. Potential of microbial antagonists as biocontrol agents against plant fungal pathogens. J. Int. Society of Southeast Asian Agril. Sci., **18**(2): 1-8.

Swathi G., Durga Rani C.V., Md J., Madhav M.S., Vanisree S., Anuradha C., Kumar N.R., Kumar N., Kumari K.A., Bhogadhi S.C. and Ramprasad E. 2019. Marker-assisted introgression of the major bacterial blight resistance genes, *Xa21* and *xa13*, and blast resistance gene, *Pi54*, into the popular rice variety, JGL1798. Mol.Breed., **39**(4): 1-2.

Takai T., Adachi S., Fujita D., Arai-Sanoh Y., Okamura M., Kondo M. and Kobayashi N. 2017. Effects of yield-related QTLs SPIKE and GPS in two indica rice genetic backgrounds. Plant Prod. Sci., **20**(4): 467-476.

Takai T., Fujita D., Lumanglas P., Simon E.V., Sasaki K., Ishimaru T., Asai H. and Kobayashi N. 2019. SPIKE, a quantitative-trait locus, increases rice grain yield under low-yield conditions. Euphytica, **215**(6): 10.

Thakur S., Singh P.K., Das A., Rathour R., Variar M., Prashanthi S.K., Singh A.K., Singh U.D., Chand D., Singh N.K. and Sharma T.R. 2015. Extensive sequence variation in rice blast resistance gene Pi54 makes it broad spectrum in nature. Front Plant Sci., **6**: 345.

Tian D., Chen Z., Chen Z., Zhou Y., Wang Z., Wang F. and Chen S. 2016. Allele-specific marker-based assessment revealed that the rice blast resistance genes Pi2 and Pi9 have not been widely deployed in Chinese indica rice cultivars. Rice, **9**(1): 1-1.

Tyagi W., Nongbri E.N. and Rai M. 2021. Harnessing Tolerance to Low Phosphorus in Rice: Recent Progress and Future Perspectives. In: Hossain M.A., Hassan L., Kumar A., Henry R. (eds). Molecular Breeding for Rice Abiotic Stress Tolerance and Nutritional Quality, 215-233. ISBN:9781119633174.

Vigueira C.C., Small L.L. and Olsen K.M. 2016. Long-term balancing selection at the phosphorus starvation tolerance 1 (*PSTOL1*) locus in wild, domesticated and weedy rice (*Oryza*). BMC Plant Biol., **16**: 101.

Wissuwa M. 2005. Combining a modelling with a genetic approach in establishing associations between genetic and physiological effects in relation to phosphorus uptake. Plant Soil, **269**: 57–68.

Wissuwa M., Kretzschmar T. and Rose T.J. 2016. From promise to application: root traits for enhanced nutrient capture in rice breeding. Journal of Experimental Botany, **67**(12): 3605-15.

Wu Y.Y., Xiao N., Yu L., Pan C.H., Li Y.H., Zhang X.X., Liu G.Q., Dai Z.Y., Pan X.B. and Li A.H. 2015. Combination patterns of major R genes determine the level of resistance to the *M. oryzae* in rice (*Oryza sativa* L.). PLoS One, **10**(6): e0126130.

Yadav M.K., Aravindan S., Ngangkham U., Raghu S., Prabhukarthikeyan S.R., Keerthana U., Marndi B.C., Adak T., Munda S., Deshmukh R. and Pramesh D. 2019. Blast resistance in Indian rice landraces: Genetic dissection by gene specific markers. PLoS One, **14**(1): e0211061.

Yang J.Y., Chen S., Zeng L.X., Li Y.L., Chuan-ying Li, and Zhu X.Y. 2008. Race specificity of major rice blast resistance genes to *Magnaporthe grisea* isolates collected from indica rice in Guangdong, China. Rice Sci., **15**: 311–318.

Yumnam J.S., Rai M. and Tyagi W. 2017. Allele mining across two low-P tolerant genes PSTOL1 and PupK20-2 reveals novel haplotypes in rice genotypes adapted to acidic soils. Plant Genetic Resources, **15**(3): 221-229.

Zhu X.F. and Shen R.F. 2023. Towards sustainable use of acidic soils: Deciphering aluminum-resistant mechanisms in plants. Fundamental Res., https://doi.org/10.1016/j.fmre.2023.03.004.

Supplementary Table S1. A list of parental genotypes and advanced breeding lines used in the present study along with their plot yield under low land acidic soil conditions

S.No.	Genotypes/ Lines	Source of collection	Landrace/variety	Ecosystem	Features	Yield (g/m2)
1	Maudhmani	NRRI, Cuttack	Variety	Irrigated low land	High yielding variety	455.7
2	Kasalath	IRRI, Philipines	Variety	Low land	Donor for *PsTol1*	537
3	BLM 9	NRRI, Cuttack	Variety	Low land	Donor for *Pi9*	579.9
4	IVT-ASG-4812	AICRP	Variety	Low land	High yielding elite breeding line	540.9
5	Sabhagidhan	NRRI, Cuttack	Variety	Rainfed upland and lowland	Multiple stress tolerant variety	474.6
6	ChakhaoPoirieton	ICAR-RC for NER, Manipur	Landrace	Low land	GI tagged, Purple rice of manipur with medicinal and economic value	293.1
7	CAU R1	CAU, Imphal	Variety	Low land	High yielding variety	519.6
8	CAU S 103	CPGS, CAU, Imphal	Elite breeding line	Low land	High yielding elite breeding line with amylose content ~20%,	708
9	CAU-R 107	CPGS, CAU, Imphal	Variety	Low land	Elite breeding line with high zinc content and resistant to blast	558.6
10	CAU S 122	CPGS, CAU, Imphal	Elite breeding line	Low land	High yielding early maturing line	465
11	CAU-R 105	CPGS, CAU, Imphal	Variety	Low land	High yielding elite breeding line with amylose content ~20%	498.3
12	CAU S 110	CPGS, CAU, Imphal	Elite breeding line	Low land	high yielding medium duration line	594.6
13	Joha	AAU,Jorhat, Assam	Landrace	Low land	GI tagged, Aromatic, Low yielding, Landrace of Assam	162
14	Mang meikri	ICAR-RC for NER, Arunachal Pradesh	Landrace	Low land	Red rice, Low yielding, Landrace of Arunachal Pradesh	204
15	PB1121	Pusa, Newdelhi	Variety	Irrigated low land	Extra-long slender basmati variety	352.2
16	Shasharang	ICAR-NEH	Variety	Rainfed lowland	Red rice, HYV of Meghalaya.	681.9
17	IR64	IRRI, Philipines	Variety	Low land	High yielding variety	385.5
18	DRR 50	IIRR, Hyderabad	Variety	Low land	Drought tolerance, submergence tolerance	387.9
19	UPRI- 3908-18-2-1-1	Pantnagar	Variety	Low land	Long slender grain, resistance to blast	473.4
20	VL40387	Uttarakhand	Variety	Low land	Long slender grain, resistance to blast	344.7
21	HPR2921	Himachal	Variety	Low land	Long slender grain, resistance to blast	354.9
22	ULRC 2 *11-2-1	CPGS, CAU, Imphal	Advanced Breeding line	Low land	(Shahsarng X SahbhagiDhan)X (Paijong X PAU 201)	430

23	ULRC 2*6-1-2-1	CPGS, CAU, Imphal	Advanced Breeding line	Low land	(Shahsarng X Sahbhagi Dhan) x (Shahsarng X PAU 201)	330
24	ULRC 4*4-1-5-1	CPGS, CAU, Imphal	Advanced Breeding line	Low land	Shahsarng X Priya	440
25	ULRC 4*4-1-1-1	CPGS, CAU, Imphal	Advanced Breeding line	Low land		360
26	ULRC 4-2-5-1-1	CPGS, CAU, Imphal	Advanced Breeding line	Low land		360
27	ULRC 5-4-3-1-1-1	CPGS, CAU, Imphal	Advanced Breeding line	Low land	Shasharang X CAUR1	350
28	ULRC 5-7-7-1-1	CPGS, CAU, Imphal	Advanced Breeding line	Low land		430
29	ULRC 6*7-6-1-1	CPGS, CAU, Imphal	Advanced Breeding line	Low land	(Shasharang X PAU201) X (Shasharang X IR64)	390
30	ULRC 6*7-2-1-1	CPGS, CAU, Imphal	Advanced Breeding line	Low land		370
31	ULRC 6*7-3-1-1-1	CPGS, CAU, Imphal	Advanced Breeding line	Low land		420
32	ULRC 6*7-3-3-1	CPGS, CAU, Imphal	Advanced Breeding line	Low land		410
33	ULRC 6*7-5-1-1	CPGS, CAU, Imphal	Advanced Breeding line	Low land		410
34	ULRC 10-4-1-1-1	CPGS, CAU, Imphal	Advanced Breeding line	Low land	IR64 X PAU201	340
35	ULRC 12-2-1-1-1	CPGS, CAU, Imphal	Advanced Breeding line	Low land	IR64 X Priya	420
36	ULRC 24-119-5-1-1	CPGS, CAU, Imphal	Advanced Breeding line	Low land	Kasalath X Shasharang	370
37	ULRC 24-119-5-1-2	CPGS, CAU, Imphal	Advanced Breeding line	Low land		410
38	ULRC 24-21-2-1-1	CPGS, CAU, Imphal	Advanced Breeding line	Low land		420
39	ULRC 24-26-4-1-1	CPGS, CAU, Imphal	Advanced Breeding line	Low land		400
40	ULRC 24-45-3-1-1	CPGS, CAU, Imphal	Advanced Breeding line	Low land		430
41	ULRC 24-48-1-1-1	CPGS, CAU, Imphal	Advanced Breeding line	Low land		350
42	ULRC 24-48-1-1-1-4	CPGS, CAU, Imphal	Advanced Breeding line	Low land		430
43	ULRC 24-48-5-1	CPGS, CAU, Imphal	Advanced Breeding line	Low land		360
44	ULRC 24-49-5-1-1	CPGS, CAU, Imphal	Advanced Breeding line	Low land		360
45	ULRC 24-49-4-1-1	CPGS, CAU, Imphal	Advanced Breeding line	Low land		410
46	ULRC 24-57-1-1-1	CPGS, CAU, Imphal	Advanced Breeding line	Low land		500
47	ULRC 24-99-3-1-1	CPGS, CAU, Imphal	Advanced Breeding line	Low land		420

48	ULRC 26-1-1-1	CPGS, CAU, Imphal	Advanced Breeding line	Low land	Kasalath X Boro Paddy	410
49	ULRC 26-11-2-1-1	CPGS, CAU, Imphal	Advanced Breeding line	Low land		430
50	ULEC 26-1-2-2-1	CPGS, CAU, Imphal	Advanced Breeding line	Low land		430
51	ULRC 29-1-2-1	CPGS, CAU, Imphal	Advanced Breeding line	Low land	SMS X Shasharang	370
52	ULRC 29-15-1-1	CPGS, CAU, Imphal	Advanced Breeding line	Low land		400
53	ULRC 29-50-2-1-1	CPGS, CAU, Imphal	Advanced Breeding line	Low land		400
54	ULRC 29-8-2-1	CPGS, CAU, Imphal	Advanced Breeding line	Low land		440
55	ULRC 29-8-3-1-1	CPGS, CAU, Imphal	Advanced Breeding line	Low land		420
56	ULRC 29-8-4-1	CPGS, CAU, Imphal	Advanced Breeding line	Low land		450
57	ULRC 34-134	CPGS, CAU, Imphal	Advanced Breeding line	Low land	Sabhagidhan X ChakhaoPoireiton	320
58	ULRC 34-17	CPGS, CAU, Imphal	Advanced Breeding line	Low land		nil
59	ULRC 34-178	CPGS, CAU, Imphal	Advanced Breeding line	Low land		330
60	ULRC 34-234	CPGS, CAU, Imphal	Advanced Breeding line	Low land		300
61	ULRC 34-248	CPGS, CAU, Imphal	Advanced Breeding line	Low land		370
62	ULRC 34-30	CPGS, CAU, Imphal	Advanced Breeding line	Low land		360
63	ULRC 34-348	CPGS, CAU, Imphal	Advanced Breeding line	Low land		360
64	ULRC 34-354-1	CPGS, CAU, Imphal	Advanced Breeding line	Low land		440
65	ULRC 34-354-2	CPGS, CAU, Imphal	Advanced Breeding line	Low land		nil
66	ULRC 34-97	CPGS, CAU, Imphal	Advanced Breeding line	Low land		350
67	ULRC 35-SSD-2	CPGS, CAU, Imphal	Advanced Breeding line	Low land	Kasalath X Sabhagidhan	330
68	ULRC 35-SSD-5	CPGS, CAU, Imphal	Advanced Breeding line	Low land		330
69	ULRC 36-1	CPGS, CAU, Imphal	Advanced Breeding line	Low land	Shasharang X KMR3	430
70	ULRC 36-175	CPGS, CAU, Imphal	Advanced Breeding line	Low land		340
71	ULRC 36-181	CPGS, CAU, Imphal	Advanced Breeding line	Low land		410
72	ULRC 36-184	CPGS, CAU, Imphal	Advanced Breeding line	Low land		380

73	ULRC 36-285	CPGS, CAU, Imphal	Advanced Breeding line	Low land	410
74	ULRC 36-299	CPGS, CAU, Imphal	Advanced Breeding line	Low land	360
75	ULRC 36-300	CPGS, CAU, Imphal	Advanced Breeding line	Low land	400

Supplementary Table S2. The details of markers used for blast resistance, low p tolerance and yield traits in the present study

S.No	Gene	Marker Name	Trait	Chromosome	Desirable allele Size (bp)	Sequence	References
1	*SCM2*	SCM2- indel1	Yield	6	117	F : GGAAATGATGAACACTGTCCA	Kim et al. 2016
						R: GTTTGTCTCAGCTCTGATCTG	
2	*SPIKE*	SPIKE- indel3		4	151	F: GGAGAGACATGGACGGCT	
						R: TGGTGGCGATCATGCTGC	
3	*Gn1a*	Gn1a-indel1		1	99	F: GCCACCTTGTCCCTTCTACA	
						R: TGCCATCCTGACCTGCTCT	
		Gn1a -indel3			275	F : GATCTAGATGCTCCAAAGTCC	
						R : CTGTACGTACGTGCACGTAG	
4	*DEP1*	DEP- indel1 (F/R/625F)		9	406	F: GCAAGTGCTCACCCAAGTG	
						R: GTTCGAACTTAATCAAAGGCCT	
5	*OsSPL14*	SPL 14-12 SNP (AR/F)		8	302	F: GTTCAGAAGCTTTACGTTGGA	
						R: GCTGGGTTGACAGAAGAGATAT	
6	*TGW6*	TGW6-1d-F/PR		6	388	F: GCCAACTGATCAGACTGAG	
						R: CGTGGGGAGAGTCGATtCG	
7	*GS5*	GS5- indel1		5	63/67	F: CTAACTCCCATGGAATTACTAG	
						R: GGAAAGCGAAACTGATTGACA	
8	*Piz*	AP5659-5	Blast resistance	6	279	F:CTCCTTCAGCTGCTCCTC	Singh et al. 2015; Li et al. 2008
						R:TGATGACTTCCAAACGGTAG	
9	*Piz5*	RM527			233	F: GGACCCGCGTTTTCCACGTGTAA	
						R: AGGAATCTATTGCTAAGCATGAC	
10	*Pi-km*	CKM-2		11	290	F:CAGTAGCTGTGTCTCAGAACTATG	
						R:AAGGTACCTCTTTTCGGCCAG	
11	*Pi5*	JJ803		9	320	F: AAGTGAGCATCCAGTGCCTAATGA	
						R:AGCCGGTGCTCATAACACGTATTA	
12	*Pi1*	MRG4766		2	110	F: ATTGCTGCAAAGTGGGAGAC	
						R:AAGTGGAGGCAGTTCACCAC	
13	*Pi-ta*	RM247		12	126	F: AGCAGGTTATAAGCTAGGCC	
						R:CTACCAACAAGTTCATCAAA	
14	*Pi 20(t)*	RM7102		12	180	F: TTGAGAGCGTTTTTAGGAG	
						R: TCGGTTTACTTGGTTACTCG	

15	*Pi2/Pi9*	RM7311		6	147	F: AGTGGTCGTTGAACTCGGAG R: TCGTGGCGCCTTTAATCTC	
16	*qPbm11*	5083 indel		11	380	F: TTCAGTCACCTCACAAGGCA R: TGCCTCACCAATCACATACG	
17	*Pi12*	RM512		12	214	F: CTGCCTTTCTTACCCCCTTC R: AACCCCTCGCTGGATTCTAG	
18	*Pb1*	Pb3810		11	105	F: TCTACGAGAGTTACAGCTTCTCC R:GAGTTGCATGGTACACCTAGCC	
20	*Pib*	Pibdom		2	365	F:GAACAATGCCCAAACTTGAGA R:GGGTCCACATGTCAGTGAGC	
21	*Pi9*	9Pro		6	128	F: TGATTATGTTTTTTATGTGGGG R: ATTAGTGAGATCCATTGTTCC	Tian et al. 2016
22	*PSTOL1*	K46-2	low P tolerance	12	227	F: AGGAAGATGGTTGTCGTTGG R: TTCACACCAAACAGTGTTGTC	Chin et al. 2011 Singh et al. 2010
22	*OsMLO8*	HvSSR02-14		2		F: CTTTGAGATTGATCGAGAGG R:ACGGAATGAGCAGTATCTGT	
23	*Os02g 08018*	RM12557		2		F: AGCACCACCTCCTCGAACTCC R: CAACCCTACCTTGCTTCTTCTTGC	Bhutia et al. 2021