



RESEARCH ARTICLE

Genetic analysis of introgression lines of *Oryza rufipogon* for improvement of low phosphorous tolerance in *indica* rice

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Abstract

Soil phosphorus (P) deficiency is one of the major challenges for rice cultivation. The present study was carried out under low soil P condition (available P, < 2 kg ha⁻¹) to study the genetic variability, correlation, path and principal component analysis (PCA) in a set of 40 introgression lines derived from Samba Mahsuri (*Oryza sativa* ssp. *indica*) × *Oryza rufipogon*. High genotypic coefficient of variation and phenotypic coefficient of variation was recorded for productive tillers (PT), seed weight (SW), and grain yield (GY). High heritability coupled with high genetic advance was recorded for plant height (PH), PT, SW, number of spikelets/panicle (SPP), spikelet fertility, and GY. Correlation analysis revealed that grain yield had a significant positive association with PH, PT, panicle length, SPP, and SW. Regression analysis revealed that the grain yield was mainly influenced by PT and SW. This was confirmed by path analysis, wherein PT and SW exerted the highest direct positive effect on grain yield. The PCA revealed that the first two PCs contribute to maximum variability, which together accounted for 60% of the total variability. The traits PT and SW contributed the maximum to load/variance the total variability. Thus, the selection of introgression lines with a greater number of PT and higher SW would be the most appropriate strategy for yield improvement under low soil P condition in rice. Cluster analysis grouped introgression lines along with checks into three clusters. Overall, the study revealed the pattern genetic variability for low P tolerance in the introgression lines. This further helps in designing appropriate breeding strategies for the improvement of rice cultivars for low P tolerance.

Keywords: Nutrition, *Oryza rufipogon*, phosphorous, samba mahsuri, wild rice

Introduction

Grain production is the foundation for global food security and is crucial for feeding the world's population and to meet future food and feed demands. It will, therefore, require a huge output of grain yield in the next decades (Mesterhazy et al. 2020). Globally, wheat, rice and maize are the predominant food crops providing over half of all calories consumed by the entire human population (FAO 2016). Among these, rice is a major staple food crop that provides more than 20% of the world's dietary energy (Fahad et al. 2019; Gadai et al. 2019). Rice production is facing constant threats from many abiotic and biotic factors (Rawte et al. 2021) and therefore, it is critical to increase the productivity levels of rice by combating abiotic and biotic stresses (Roberts and Mattoo 2018).

Among the major nutrients, phosphorus (P) is one of the crucial minerals for growth, development, and other metabolic activities in most crops, including rice. It is also a constituent in essential molecules including nucleic acids and proteins (Raven et al. 2013). Low soil P stress is one of the major constraints on plant growth and yield worldwide

in many crops including rice. According to an estimate, globally about 5.8 billion hectare arable lands are P deficit (Deng et al. 2018), while in India, 49.3 % of soils are deficit in available P, 48.8% of soils have moderate availability of P, and only 1.9% of Indian soils are rich in available P (Hasan

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1996; [Tiwari](#) 2001). Major rice-growing areas are under deficit in available P because rice-growing areas like uplands and acidic soils have high P-fixing ability, resulting in lower P availability in soils and thus lower yields ([Vance](#) et al. 2003). The phosphorous deficiency can be overcome by applying P fertilizer; however, it adds to the production costs and also pollutes water sources due to run-off carrying dissolved fertilizers. Hence, the cost-effective and environmentally safe option is growing rice varieties/genotypes that perform better under low soil P conditions ([Cordell](#) et al. 2009; [Rose](#) and [Wissuwa](#) 2012; [Mahadeva Swamy](#) et al. 2019).

Genetic variability for P deficiency tolerance and P use efficiency traits has been well recognized in different rice genotypes, including landraces and wild species ([Mahadeva Swamy](#) et al. 2019; [Basavaraj](#) et al. 2021). The low soil P tolerance is a naturally occurring trait in wild germplasm and landraces that can be explored to improve phosphorus acquisition efficiency (PAE) and phosphorus usage efficiency (PUE) of elite rice cultivars ([Gamuyao](#) et al. 2012). Several researchers have demonstrated the potential of *O. rufipogon* for P-deficiency tolerance and P uptake efficiency ([Lang](#) and [Buu](#) 2006; [Chen](#) et al. 2011; [Neelam](#) et al. 2017; [Basavaraj](#) et al. 2020, 2021a).

The success of any breeding program depends on a thorough understanding of genetic variability for the traits being improved. Thus, several selection criteria must be used to identify desirable genotypes with a suitable trait combination. Correlation studies measure the relationship between traits under consideration and aid in designing appropriate selection strategies for simultaneous improvement of a group of traits. Furthermore, determining the genetic diversity of a group of genotypes aids in the creation of superior recombinants. On the other hand, principal component analysis (PCA) is a powerful tool that assists in identifying a set of breeding lines that contributes to maximum variability ([Noirot](#) et al. 1996; [Gireesh](#) et al. 2017). Breeding efforts at ICAR-Indian Institute of Rice Research have led to developing a set of BC₂F₂ generation introgression lines. However, these lines have not been characterized at a phenotypic level under low phosphorous stress. The present investigation was thus aimed to (i) assess the genetic variability among the introgression lines under low phosphorous conditions and (ii) to study the traits association for grain yield and related traits under low phosphorous conditions.

Materials and methods

Plant material

Samba Mahsuri (*Oryza sativa* ssp. *indica*), an elite rice cultivar in the southern part of India, known for its cooking and eating qualities but sensitive to low soil phosphorus conditions ([Basavaraj](#) et al. 2021b) was used as a female parent and *O. rufipogon* (Acc. IR72046-B-R-3-2-1) as male

were crossed to develop F₁ hybrid. The F₁ was backcrossed to Samba Mahsuri to obtain BC₁F₁ (21 plants). Further, BC₁F₁ plants were backcrossed with the recurrent parent (RP) Samba Mahsuri and obtained 40 plants of BC₂F₁. Plants with the phenotype resembling RP were selected and selfed for two generations to develop a BC₂F₃ population consisting of 40 introgression lines used in the present study.

Screening for low soil P tolerance

The experiment was carried out at ICAR-Indian Institute Rice Research, Hyderabad, India during wet season 2019 (WS 2019, from June to November) and dry season 2019 (DS 2019, from December to May) [hereafter the seasons are represented as WS 2019 and DS 2019, respectively] in a specialized experimental plot of the ICAR-IIRR, Hyderabad. The experimental plot consists of <2 kg/ha available soil phosphorous ([Supplementary Table S1](#)).

Recording of observations

The seeds of 40 introgression lines, parents, and checks viz., Swarna, Ratnachudi, Tanu, Improved Samba Mahsuri (ISM), and Rasi were sown in a nursery bed and 21 days old seedlings from the nursery were uprooted and transplanted to the low soil P plot. Seedlings were spaced at 20 cm × 10 cm in a Randomized Complete Block Design (RCBD) with two replications. No phosphorus fertilizer was applied to the low soil P plot, whereas the recommended dose of phosphorus fertilizer was applied to the normal soil P plot (Phosphorus @ 60 P kg/ha). Other essential nutrients like nitrogen (100 kg/ha) and potash (40 kg/ha) were applied as per recommended agronomic practices to raise a good crop. Observations were recorded on five uniform plants selected randomly in each line and checks for eight quantitative traits namely, days to 50% flowering (DFF), plant height (PH in cm), number of productive tillers/plant (PT), panicle length (PL in cm) and spikelet per panicle (SPP), spikelet fertility (SF in %), seed weight (SW in g); (in some of the lines high sterility was recorded and 1000 seeds were not available, hence, 100 seed weight was taken uniformly for all the lines) and grain yield per plant (GY in g).

Statistical analysis

The mean phenotypic data were used to analyze variance using SAS 9.2 (SAS version 9.2 software package, SAS Institute, Inc.; Cary, NC). In addition, range, phenotypic coefficient of variation (PCV), genotypic coefficient of variation (GCV), heritability (h^2_{bs}), and genetic advance (GA), were computed using the methods of [Johnson](#) et al. (1955). Descriptive statistics were presented in the form of box plots, which depict low, high median quartiles and extremes in the form of outliers. Correlation coefficients were calculated to understand the nature of the association among the traits using R vs4.2. Principal component analysis (PCA), biplots were developed employing Rvs4.2. The introgression lines

were then grouped into low P tolerant and sensitive types through cluster analysis (DARwin6; Perrier and Jacquemoud-Collet 2006) using Euclidean distance, with Unweighted Pair Group Method using Arithmetic means (UPGMA) based on yield and yield-related traits.

Results

The combined analysis of variance (ANOVA) revealed significant differences between the traits considered in the present study (Table 1). The mean performance in introgression lines along with the checks are presented in Supplementary Tables S2 and S3. Early anthesis is the most desirable trait in crop improvement programme including rice. An average of 104 days (d) was recorded for days to 50% anthesis and all the introgression lines were late in flowering than low soil P tolerant check, Rasi. However, a few introgression lines (IL-10, IL-1, IL-4, IL-8, IL-9, IL-12, IL-13, IL-17, IL-18, IL-21, IL-29, IL-34, IL-36, IL-37, IL-38; (101 d) were early flowering than other checks like Swarna (105 d), Ratnachudi (112 d) and recurrent parent Samba Mahsuri (111d). Out of all the introgression lines investigated, IL-10 was most early (<99 d); 24 lines were mid-early (100-104 d) while 15 lines were late flowering (105-115 d). The average plant height of introgression lines was 65.17 cm and ranged from 48.87 cm (IL-8) to 88.87 cm (IL-13). The number of productive tillers per plant was 9.66, the highest and lowest PT was observed in

IL-4 (16.88) and IL-15 (3.88), respectively. The longest panicle length was observed in IL-13 (21.52 cm) and the shortest was IL-8 (13.52 cm), whereas average panicle length was 18.50 cm. The mean value recorded for the number of spikelets/panicle was 143.44, ranging from 85.75 (IL-34) to 333.7 (IL-13). Higher spikelet fertility (98.09%) was recorded in IL-30, whereas the lowest in IL-6 (59.71). Large variation was noticed for 100 seed weight, which varied from 0.3 (IL-8) to 2.84 (IL-13) g with an average of 1.18g. Average grain yield of introgression lines recorded was 13.33g, the highest (19.89g) being of IL-4 and the lowest (2.85g) in IL-10.

Estimation of genetic parameters

Box plots were drawn to depict the amount of genetic variability for eight quantitative traits in the introgression lines of *O. rufipogon* (Fig. 1). The difference between PCV and GCV for all the traits was very less (Table 2). However, slightly higher estimates of PCV observed corresponding GCV estimates for all the traits studied. Low GCV and PCV estimates were recorded for traits such as days to 50% flowering and panicle length (<10%). The moderate magnitude of variability estimates was noticed for plant height and per cent spikelet fertility (11-29%), while it was high for traits such as PT, SW, and GY (>30%). Heritability estimates (h^2_{bs}) were very high (>90%) for all the traits. The high GA was recorded for traits such as PH, PT, SPP, SF (%), SW and GY (>20 %).

Table 1. Combined analysis of variance for yield and its attributing traits in introgression lines derived from Samba Mahsuri × *O. rufipogon*

Trait	MS_Gen	MS_BlK	MS_Err	MS_Env	MS_GbyE
Days to 50% flowering	101.87	105.27	0.42	46.00	0.000
Plant height	302.09	23.04	0.11	41.95	0.000
Number of productive tillers	32.16	14.30	0.04	26.92	0.000
Panicle length	13.23	16.24	0.16	1.10	0.000
Spikelet per panicle	8526.06	299.23	31.33	20.89	31.39
Spikelet fertility %	561.77	3.33	2.39	0.09	2.36
Seed weight	1.25	0.96	0.005	0.01	0.005
Grain yield per plant	83.60	23.78	0.08	0.71	0.070

MS_Gen, MS_BlK, MS_Err, MS_Env, MS_GbyE, = Mean sum of square due to genotypes, replication (block), error, environment and genotype × environment, respectively

Table 2. Genetic parameters for yield and yield attributing traits under low soil P condition in introgression lines derived from Samba Mahsuri × *O. rufipogon*

Trait	GCV	PCV	h^2_{bs}	Genetic advance as per cent of mean (%)
Days to 50% flowering	4.80	4.84	98.33	9.80
Plant height	13.42	13.48	99.84	27.63
Number of productive tillers per plant	30.50	30.52	99.46	62.67
Panicle length	9.15	9.93	95.15	19.60
Spikelet per panicle	32.03	33.12	97.17	65.20
Spikelet fertility %	14.15	15.39	96.62	28.66
Seed weight	46.87	51.24	96.59	94.90
Grain yield per plant	48.98	50.36	98.23	98.1

GCV = Genotypic coefficient of variation, PCV = Phenotypic coefficient of variation, and h^2_{bs} = heritability in broad sense

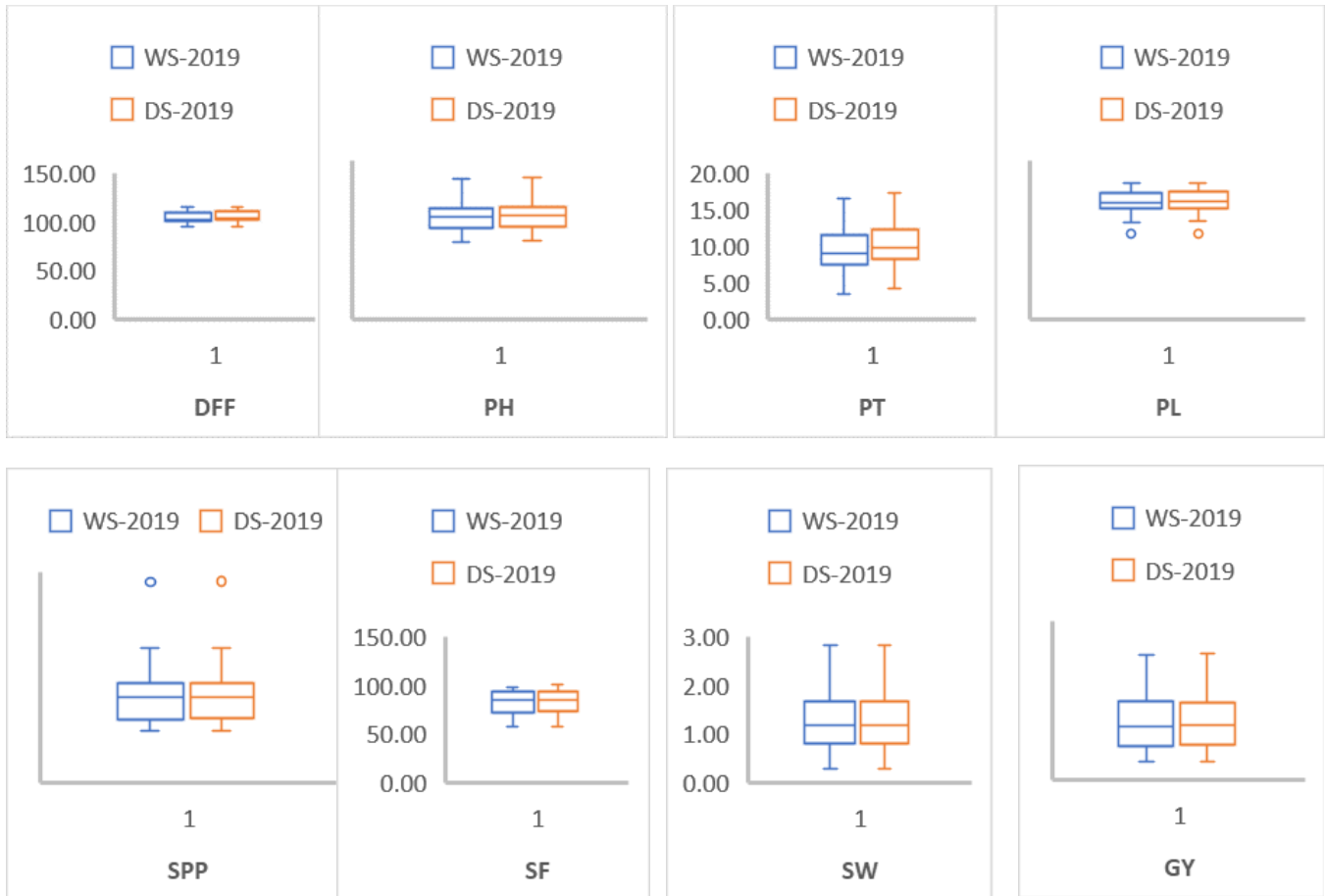


Fig. 1. Box plots depicting variation of introgression lines for yield and yield-related traits under low soil phosphorous conditions. The upper, median and lower quartiles represent the 75th, 50th and 25th percentiles of the genotypes, respectively. The vertical lines represent the variation in the population. Dots represent the outliers (Transgressive segregants)

Table 3. Correlation coefficients for yield and yield attributing traits under low soil P condition in introgression lines

Traits	DFF	PH	PT	PL	SPP	SF	SW	GY
DFF	1	0.220	-0.147	0.053	0.052	-0.151	0.087	0.012
PH		1	0.199	0.647**	0.652**	-0.197	0.697**	0.450**
PT			1	0.154	0.116	0.109	0.135	0.740**
PL				1	0.473**	0.056	0.563**	0.404**
SPP					1	0.074	0.776**	0.424**
SF						1	0.177	0.067
SW							1	0.526**
GY								1

DFF = Days to 50% flowering, PH = Plant height, PT = Number of productive tillers per plant, PL = Panicle length, SPP = Spikelet per panicle, SF = Spikelet fertility in per cent, SW = Seed weight and GY = Grain yield

Correlation, regression and path coefficient analysis

Results of the correlation indicated that GY had a significant and positive association with PH ($r=0.450^{**}$), PT ($r=0.740^{**}$), PL ($r=0.404^{**}$), SPP ($r=0.424^{**}$) and SW ($r=0.526^{**}$), while non-significant positive association were observed with DFF ($r=0.012$) and per cent SF ($r=0.067$) (Table 3 and Fig. 2).

The grain yield was influenced mainly the number of productive tillers and seed weight (Table 6). The regression equation for GY is as follows:

$$Y (GY)=1.170 (PT)+ (3.016) SW.$$

Results indicated that with an increase in each productive tiller, there is an increase of 1.17 g of GY; with an increase in every 1 g of SW, there is an increase of 3.01 g of GY. The coefficient of determination tells us that the extent of variation in the dependent variable is attributed to the independent variable, which gave a value of $R^2= 0.676$, indicating 67.60% variation in the yield trait caused by other independent traits.

The path coefficient analysis indicated that PT exerted the highest direct positive effect on GY (0.723), followed

by SW (0.390) (Table 4). In contrast, traits such as PT and SF exerted a negative direct effect on GY. The high positive indirect effects on GY were of SPP via SW (0.295) and SPP via PL (0.211).

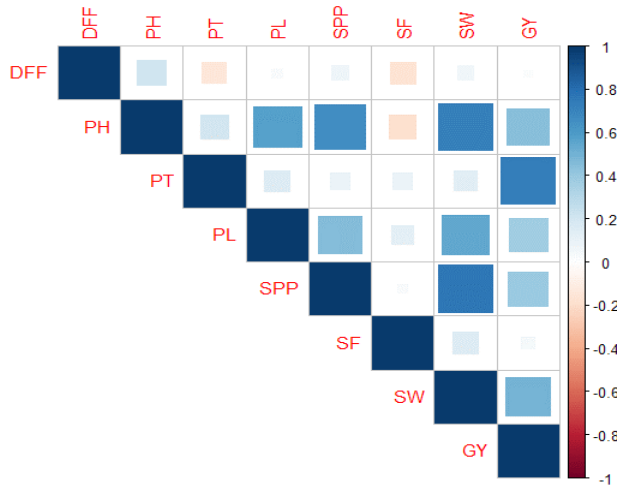


Fig. 2. Correlogram depicting association between grain yield and its component traits under low soil phosphorous condition (Box indicates significance of association, while size of box represents strength of association)

Principal component and cluster analysis

The results of PCA showed that a total of eight principal components were obtained (PCs), of which PC1 and PC2 were the most informative components with eigenvalues 3.34 and 1.49, respectively. PC1 and PC2 together explained 60.37% of the total variability (Table 5). According to PC1 the SW (22.57), PH (22.51) and SPP (19.53) contributed the maximum to PC1, while PT (43.22), GY (14.86), and DFF contributed maximum variability in PC2 (Fig.3). Among the 40 introgression lines and six checks, PC scores ranged from 0.01 (IL-18) to 12.61 (IL-13), whereas, in PC2, it varied from 0.003 (Samba Mahsuri) to 12.36 (IL-13). Six introgression lines, namely, IL-6, IL-7, IL-8, IL-13, IL-36, and IL-40 in PC1 and four introgression lines (IL-4, IL-13, IL-24 and IL-30) in PC2 were found to be associated with the highest genetic variation

Table 4. Path coefficients for yield and its attributing traits in introgression lines

Traits	DFF	PH	PT	PL	SPP	SF	SW	GY
DFF	0.080	-0.035	-0.092	0.009	0.002	0.020	0.033	0.456
PH	0.018	-0.156	0.142	0.099	0.018	0.023	0.294	0.168
PT	-0.010	-0.031	0.723	0.021	0.002	-0.009	0.033	0.064
PL	0.005	-0.093	0.089	0.168	0.013	-0.015	0.211	0.548
SPP	0.007	-0.106	0.045	0.079	0.028	0.004	0.295	0.205
SF	-0.013	0.029	0.051	0.020	-0.001	-0.128	0.050	0.049
SW	0.007	-0.118	0.061	0.091	0.021	-0.017	0.390	0.688

Residual-0.30, Diagonal and bold values are direct effect and remaining are indirect effect.

Table 5. Eigen values, contribution of variability and factor loading for the principal component axis in introgression lines

Eigenvalue	PC 1	PC 2	PC 3	PC 4	PC 5	PC 6	PC 7	PC 8
	3.34	1.49	1.17	0.82	0.57	0.27	0.24	0.11
Variability (%)	41.73	18.64	14.58	10.25	7.11	3.33	2.99	1.37
Cumulative %	41.73	60.37	74.95	85.20	92.31	95.64	98.63	100.00
Days to 50% flowering	0.60	17.45	17.19	62.81	0.14	0.71	0.23	0.88
Plant height	22.51	4.46	1.65	1.34	0.31	41.03	7.18	21.52
Number of productive tillers	4.49	43.22	10.61	0.80	0.04	1.50	21.64	17.69
Panicle length	15.40	0.45	4.69	0.12	71.24	5.85	0.09	2.16
Spikelet per panicle	19.53	4.13	1.99	3.11	17.82	35.02	17.86	0.55
Spikelet fertility %	0.04	8.86	50.86	30.69	1.48	1.50	1.59	4.97
Seed weight	22.57	1.97	5.19	0.07	8.66	7.60	21.00	32.94
Grain yield per plant	14.86	19.46	7.83	1.07	0.31	6.78	30.41	19.29

Table 6. Stepwise regression analysis of grain yield and other traits in introgression lines

Variable	Estimates	Standard error	Partial R ²	Model R ²
Intercept	-4.517	1.050		
PT	1.102	0.097	0.686	0.676
SW	3.016	0.491	0.370	

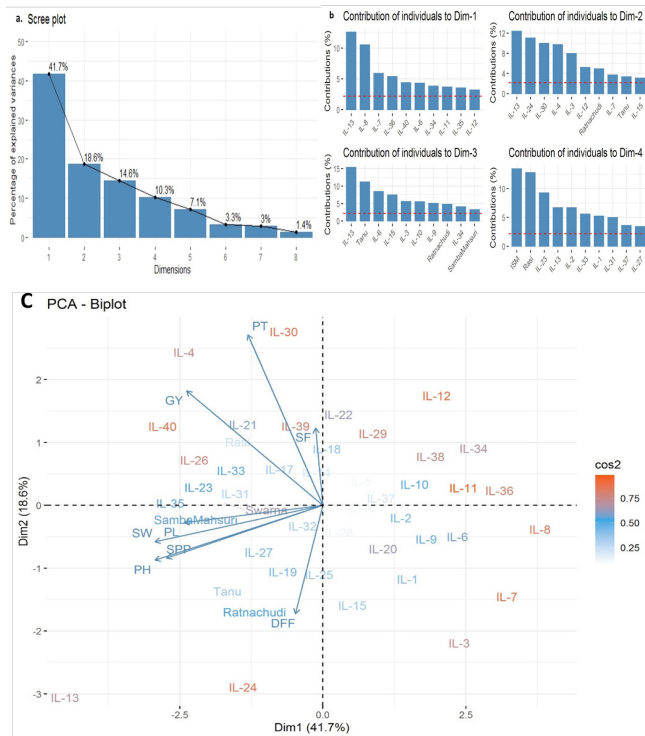


Fig. 3. (a) Scree Plot depicting the contribution of 8 principal components, (b) PCA-Biplots explaining the contribution of 8 traits to the total variation in the 40 introgression lines and 6 checks and (c) Contribution of introgression lines and checks to individual Principal components

(Figs. 3a and 3b). Based on Euclidean distance, the clustering was carried out following the Unweighted Pair Group Method using Arithmetic means (UPGMA) to group the introgression lines and checks considering yield and yield-related traits under low soil P stress. The introgression lines and checks were grouped into three clusters (Fig. 4). Cluster I was the largest, comprising 26 genotypes (19 introgression lines and 7 checks), cluster II had three introgression lines (IL-22, IL-29, IL-5), while cluster III contained 18 introgression lines.

Discussion

During domestication and selection, several of the beneficial alleles were lost. About 50-60% of alleles of wild rice are lost in the present-day rice varieties which were present previously (Deng et al. 2018). Hence, renewed interest was gained in exploring wild relatives in the research programs as pre-breeding for diversification of primary gene pool for various useful traits. *Oryza rufipogon*, an ancestor of cultivated rice was explored for genetic enhancement of many agronomically important traits such as yield (Xiao et al. 1998; Basavaraj et al. 2020; 2021a), biotic and stress tolerance (Utami et al. 2008; Neelam et al. 2017; Basavaraj et al. 2021b) and several other trait improvements. Earlier studies (Chen et al. 2011; Deng et al. 2018) unveiled the potential of *O. rufipogon* as a source for the P-deficiency tolerance traits/genes in rice.

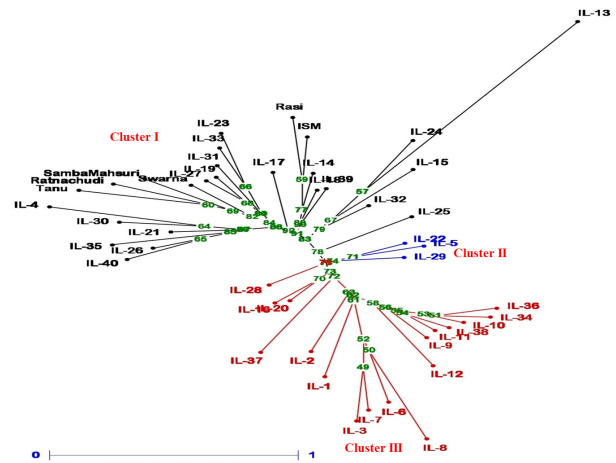


Fig. 4. Clustering of introgression lines and checks following Euclidean distance, with Unweighted Pair Group Method using Arithmetic means (UPGMA) based on yield and yield related traits

Genetic variability is a measure of the differences among the individuals of the plant population. It arises due to either differences in their genetic constitution or the environment in which they are grown. The existence of genetic variability is a prerequisite for the success of the plant breeding program, as it offers an opportunity for a breeder to choose the best recombinants from a diverse group of materials. Hence, insight into the magnitude of genetic variability present in a population is of paramount importance to a plant breeder for starting a judicious plant breeding program. In the present study, phenotyping of 40 introgression lines derived from Samba Mahsuri and *O. rufipogon* (Acc. IR72046-B-R-3-2-1) revealed the presence of adequate genetic variation and transgressive sergeants among introgression lines for yield-related traits under low soil P conditions. High magnitudes of PCV and GCV were recorded for traits viz., PT, SPP, SW and GY compared to other traits studied, direct selection *per se* for these traits would be rewarding. Furthermore, a very slight difference between PCV and GCV estimates was observed for all the traits, indicating that there was less influence of environmental factors on the trait expression. Similar such inferences were drawn by Basavaraj et al. (2020). Thus, selection based on phenotype can be effective for the improvement of these traits. Heritability estimates assist in the improvement of traits in a set of breeding materials under consideration as they are a good index of the transmission of characters from parents to offspring. Johnson et al. (1955) advocated that heritability estimates coupled with genetic advance are more beneficial in predicting genetic gain under selection than heritability estimates alone since high heritability does not always indicate high genetic gain. High heritability coupled with high genetic advance was observed for the traits such as PT, SPP, SW, and GY, indicating the preponderance of additive genetic variance, which enables the selection of promising

lines. Transgressive segregation was reported for the PT, SPP, SW, and GY indicating the contribution of valuable alleles from the wild parent. Present results align with reports of Xiao et al. (1998) and Basavaraj et al. (2020; 2021a) for transgressive segregation in *rufipogon*-derived lines for yield and its related traits. The expression of favorable alleles in wild *Oryza* is frequently concealed by detrimental alleles. However, improved phenotypic expression can be achieved when such desirable alleles are instilled into elite cultivar backgrounds. The superior performance of some ILs over recurrent parent for yield and its related traits under low soil P condition is mainly due to the accumulation of favorable alleles from both parents as well as due to favorable interactions between disparate alleles (Xiao et al. 1998).

Correlation analysis provides insight into the association between grain yield and other traits and helps plant breeders to plan suitable selection strategies in the concurrent improvement of an amalgamation of traits (Dixit and Dubey 1984). In our study grain yield per plant was positively significantly correlated with traits; PH, PT, PL, SPP, and SW. Thus, direct selection for these traits could be ideal criteria for higher grain yield under low soil P conditions. Interestingly, trait SF had a positive but non-significant association with grain yield, in contrast to the general observation of a positive significant association between grain yield and spikelet fertility. Similar to the present findings, Jambhulkar and Bose (2014) and Ronghua et al. (2019) also observed a significant positive correlation between GY and PH. In addition, significant positive correlations between the pair of traits PH and PL and PL and SPP, a common trend was also reported by Ishwarya Lakshmi et al. (2019) and Basavaraj et al. (2020).

Regression analysis revealed that GY was mainly under the influence of PT and SW. In addition, path coefficient analysis also revealed that the direct highest positive effect on yield was exerted by PT and SW. Hence direct selection for these traits may result in higher genetic grain under low soil P condition. PCs explained the variability which could not be attributed to the other factors. In the present study, genetic variability was mainly explained by the first two PCs which accounted for 60.37% of the variance, while Anchor 1 et al. (2021) reported a similar amount of cumulative variance with four major PCs. Selection of traits via the traits that contribute to maximum variability through two major PCs would be rewarding. Traits such as SW, SPP, PH in PC1, while, traits GY, PT and DFF in PC2 accounted for a major portion of variation. Four introgression lines (IL-13, IL-8, IL-7 and IL-36) in PC1 and two (IL-13 and IL-24) in PC2 are contributed to the maximum genetic variability. Hence, utilizing these introgression lines as donor parents in breeding for low phosphorous tolerance rice would be rewarding.

Cluster analysis grouped introgression lines and checks into three clusters based on yield and yield-related traits under low soil P condition. Cluster I comprised of 26

genotypes (19 introgression lines and 7 check genotypes) indicating their close relatedness. Cluster II had three introgression lines (IL-22, IL-29, IL-5), while, cluster III contained 18 introgression lines. Cluster I had introgression lines that had better performance for traits like number of productive tillers and high seed weight and high yield. Selection of introgression lines from this cluster in a breeding program for developing low P tolerant rice cultivars would be beneficial.

Supplementary materials

Supplementary Tables S1 to S3 having analysed data are presented.

Authors' contribution

Conceptualization of research (MSA, CG, RMS, PS); Designing of the experiments (BPS, MCA, BM); Contribution of experimental materials (CG, MSA); Execution of field/lab experiments and data collection (BPS, BM, MCA, VGI); Analysis of data and interpretation (BPS, BM, MCA, VGI); Preparation of the manuscript (BPS, BM, MCA, VGI).

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Supplementary Table S1. Soil nitrogen, phosphorous, potassium and pH status of the experimental plot during 2019-20

Nutrients	Low Soil P plot (P ₀)		P ₂₀		P ₄₀		Normal Soil P plot (P ₆₀)	
	Content	Remarks	Content	Remarks	Content	Remarks	Content	Remarks
Nitrogen	0.1ppm	very low	0.3ppm	Low	0.3ppm	Low	0.3ppm	Low
Phosphorous	<2kg/ha	very low	<5kg/ha	Very low	5-10kg/ha	Low	20 kg/ha	Normal
Potassium	100Kg/ha	low	100Kg/ha	Low	100Kg/ha	Low	200Kg/ha	Medium
pH	7.4	Neutral	7.2	Neutral	7.4	Neutral	7.4	Neutral

Supplementary Table S2. Mean performance of introgression lines under low soil phosphorus condition during WS2019

Genotype	DFF	PH	PT	PL	SPP	SF	SW	GY
Swarna	105.50	70.50	12.50	19.23	193.50	72.69	1.69	10.65
Ratnachudi	112.50	78.00	7.50	17.13	210.50	66.94	1.37	11.68
Tanu	113.00	80.76	8.50	18.84	110.50	57.22	1.70	13.32
ISM	97.00	70.30	10.50	19.23	146.50	59.28	1.17	11.93
Rasi	94.50	75.20	10.50	18.26	118.50	68.03	1.85	14.07
Samba Mahsuri	111.00	78.90	13.50	18.58	165.50	77.79	1.80	11.77
IL-1	100.50	56.40	5.50	16.45	154.00	71.76	1.68	2.89
IL-2	111.50	59.40	8.50	15.95	104.00	91.32	0.94	6.49
IL-3	114.50	57.40	5.50	17.45	121.00	60.40	0.41	3.14
IL-4	100.50	63.40	16.50	18.75	223.00	83.08	1.28	19.80
IL-5	105.50	60.40	9.50	20.45	101.00	97.17	0.93	8.26
IL-6	107.50	55.40	9.50	15.45	99.00	59.61	0.33	5.83
IL-7	109.50	51.40	4.50	17.45	86.00	71.32	0.39	2.90
IL-8	100.50	48.40	5.50	13.45	90.00	72.65	0.30	4.22
IL-9	100.50	58.40	5.50	17.45	118.00	94.15	1.12	4.43
IL-10	99.50	54.40	8.50	18.45	102.00	97.20	0.95	2.79
IL-11	102.50	55.40	8.50	16.45	88.00	86.12	0.59	5.63
IL-12	100.50	55.40	12.50	15.35	89.00	88.61	0.47	8.16
IL-13	100.50	88.40	4.50	21.45	333.00	90.24	2.84	5.10
IL-14	101.50	69.40	11.50	18.35	162.00	71.30	0.82	12.13
IL-15	101.50	62.60	3.50	19.95	142.00	90.88	1.22	3.40
IL-16	109.50	63.40	10.50	16.45	141.00	81.39	1.12	8.04
IL-17	100.50	69.40	9.50	17.45	185.00	90.34	1.63	11.50
IL-18	100.50	63.30	9.50	18.65	146.00	79.96	1.04	13.18
IL-19	109.50	67.30	7.50	19.45	163.00	93.99	1.70	8.58
IL-20	107.50	61.90	8.50	17.45	141.00	76.32	0.86	7.52
IL-21	100.50	68.80	10.50	20.55	133.00	94.85	1.42	13.40
IL-22	104.50	62.40	11.50	18.45	105.00	95.33	0.82	10.73
IL-23	112.50	70.50	10.50	20.45	149.00	94.07	1.91	15.74
IL-24	110.50	72.40	4.50	21.45	178.00	75.09	1.66	5.15
IL-25	110.50	67.40	7.50	19.95	136.00	70.91	0.70	8.35
IL-26	102.50	70.90	12.50	21.45	156.00	79.97	1.59	13.71
IL-27	111.50	67.50	8.50	17.95	163.00	87.11	1.86	9.78
IL-28	103.50	70.40	8.50	17.95	124.00	88.66	1.17	5.94
IL-29	100.50	57.40	11.50	18.65	132.00	84.73	0.77	9.84
IL-30	101.50	60.40	13.50	18.45	154.00	95.74	1.14	18.02
IL-31	110.50	67.40	11.50	17.45	187.00	94.26	1.51	13.12
IL-32	102.50	68.40	8.50	20.45	169.00	82.16	1.23	7.72
IL-33	110.50	76.40	12.50	20.45	153.00	93.57	1.25	12.27
IL-34	100.50	50.40	8.50	18.45	85.00	97.80	0.58	3.67
IL-35	107.50	62.40	8.50	20.95	204.00	88.12	1.68	18.54
IL-36	100.50	50.40	6.50	16.45	92.00	95.74	0.57	4.61
IL-37	100.50	65.40	10.50	19.95	90.00	66.90	0.30	5.43
IL-38	100.50	56.40	8.50	15.65	108.00	93.57	0.84	5.60
IL-39	101.50	66.40	12.50	18.45	164.00	83.46	1.20	11.59
IL-40	102.50	69.40	12.50	20.45	168.00	86.24	2.22	16.01
Average	104.62	64.697	9.283	18.420	143.109	82.566	1.182	9.274
Min	94.50	48.395	3.500	13.445	85.000	57.219	0.295	2.790
Max	114.500	88.39	16.50	21.44	33.00	97.79	2.83	19.80
CV	9.82	13.43	10.55	9.88	12.27	14.28	147.07	13.08

Supplementary Table S3. Mean performance of introgression lines under low soil phosphorus condition during DS2019

Genotype	DFF	PH	PT	PL	SPP	SF	SW	GY
Swarna	106.50	71.46	13.27	19.38	195.00	72.90	1.69	10.78
Ratnachudi	113.50	78.96	8.27	17.28	212.00	67.15	1.37	11.81
Tanu	114.00	81.72	9.27	18.99	112.00	57.43	1.70	13.45
ISM	98.00	71.26	11.27	19.38	148.00	59.49	1.17	12.06
Rasi	95.50	76.16	11.27	18.41	120.00	68.24	1.85	14.20
Samba Mahsuri	112.00	79.86	14.27	18.73	167.00	78.00	1.80	11.90
IL-1	101.50	57.35	6.27	16.60	155.50	71.97	1.68	3.02
IL-2	112.50	60.35	9.27	16.10	105.50	91.53	0.94	6.62
IL-3	115.50	58.35	6.27	17.60	122.50	60.61	0.41	3.27
IL-4	101.50	64.35	17.27	18.90	224.50	74.54	1.28	19.99
IL-5	106.50	61.35	10.27	20.60	102.50	97.38	0.93	8.39
IL-6	108.50	56.35	10.27	15.60	100.50	59.82	0.33	5.96
IL-7	110.50	52.35	5.27	17.60	87.50	71.53	0.39	3.03
IL-8	101.50	49.35	6.27	13.60	91.50	72.86	0.30	4.35
IL-9	101.50	59.35	6.27	17.60	119.50	94.36	1.12	4.56
IL-10	100.50	55.35	9.27	18.60	103.50	97.41	0.95	2.92
IL-11	103.50	56.35	9.27	16.60	89.50	86.33	0.59	5.76
IL-12	101.50	56.35	13.27	15.50	90.50	88.82	0.47	8.29
IL-13	101.50	89.35	5.27	21.60	334.50	90.45	2.84	5.23
IL-14	102.50	70.35	12.27	18.50	163.50	71.51	0.82	12.26
IL-15	102.50	63.55	4.27	20.10	143.50	91.09	1.22	3.53
IL-16	110.50	64.35	11.27	16.60	142.50	81.60	1.12	8.17
IL-17	101.50	70.35	10.27	17.60	186.50	90.55	1.63	11.63
IL-18	101.50	64.25	10.27	18.80	147.50	80.17	1.04	13.31
IL-19	110.50	68.25	8.27	19.60	164.50	94.20	1.70	8.71
IL-20	108.50	62.85	9.27	17.60	142.50	76.53	0.86	7.65
IL-21	101.50	69.75	11.27	20.70	134.50	95.06	1.42	13.53
IL-22	105.50	63.35	12.27	18.60	106.50	95.54	0.82	10.86
IL-23	113.50	71.45	11.27	20.60	150.50	94.28	1.91	15.87
IL-24	111.50	73.35	5.27	21.60	179.50	75.30	1.66	5.28
IL-25	111.50	68.35	8.27	20.10	137.50	71.12	0.70	8.48
IL-26	103.50	71.85	13.27	21.60	157.50	80.18	1.59	13.84
IL-27	112.50	68.45	9.27	18.10	164.50	87.32	1.86	9.91
IL-28	104.50	71.35	9.27	18.10	125.50	88.87	1.17	6.07
IL-29	101.50	58.35	12.27	18.80	133.50	84.94	0.77	9.97
IL-30	102.50	61.35	14.27	18.60	117.50	100.45	1.14	19.14
IL-31	111.50	68.35	12.27	17.60	188.50	94.47	1.51	11.77
IL-32	103.50	69.35	9.27	20.60	170.50	82.37	1.23	7.85
IL-33	111.50	77.35	13.27	20.60	154.50	93.78	1.25	12.40
IL-34	101.50	51.35	9.27	18.60	86.50	98.01	0.58	3.80
IL-35	108.50	63.35	9.27	21.10	205.50	85.02	1.68	19.05
IL-36	101.50	51.35	7.27	16.60	93.50	95.95	0.57	4.74
IL-37	101.50	66.35	11.27	20.10	91.50	67.11	0.30	5.56
IL-38	101.50	57.35	9.27	15.80	109.50	93.78	0.84	5.73
IL-39	102.50	67.35	13.27	18.60	165.50	83.67	1.20	11.72
IL-40	103.50	70.35	13.27	20.60	169.50	86.45	2.22	16.14
Average	105.62	65.65	10.05	18.58	143.78	82.61	1.18	9.40
Min	95.5	49.35	4.265	13.6	86.5	57.42	0.29	23.91
Max	115.5	89.35	17.265	21.6	334.5	100.44	2.83	19.98
CV	4.78	13.24	12.22	9.79	12.21	14.48	14.5	14.90