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RESEARCH ARTICLE

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Multiple trait contribution towards phosphorus deficiency tolerance at species level in early vegetative stage of rice

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Abstract

Phosphorus deficiency is more pronounced in rice at the early vegetative stages. Compensating rice cultivars with Phosphorus Use Efficiency traits would require identifying the component traits involved and the level of dependence between these traits. This study evaluated four diverse groups of rice, comprising the accessions of improved cultivars, landraces of *Oryza sativa*, representatives of *Oryza nivara* and *Oryza rufipogon* to understand the P uptake and its allocation between shoot and root traits. The results highlighted that traits regulated in a low P tolerant line such as root volume, total root surface area, total dry weight, SPAD value, number of root tips and leaf width. Landraces were found to have higher root volume (3.62cm), shoot dry weight (0.81g), root dry weight (0.25g) and shoot-root P ratio (2.51) as reflected in the group mean. The study also identified accession AC100219 of *O. rufipogon* group which had overall higher shoot P content, root volume, total root length and number of roots tips and may serve as a potential donor.

Keywords: *Oryza* spp., phosphorus use efficiency, rice, SPAD value.

Introduction

Phosphorus (P) is one of the key elements and a pivotal component in the structure of nucleotides, energy transferring inorganic phosphates, involved in cell growth and development, root growth, tillering, flowering and ripening. The element is highly mobile in plant systems and available in the shallow layers of the soil. But even when abundantly present in the soil, its availability to the roots remains scarce as it becomes immobile and inaccessible forming complex with Ca, Fe, and Al in the rhizosphere (Abel et al. 2002) especially in acidic soils where the pH is low (< 6) (Penn and Camberato 2019). Estimates show that around 60% of the rice grown in rainfed conditions in Asia face P deficiency (Culhane et al. 2012). Especially in India, where 90% of its P demand is met from imports making it costly (Swamy et al. 2019). The practice of external P fertilizer application is reliable only up to a certain extent as the rock phosphate reserves are non-renewable and with the current rate of consumption it is set to be exhausted in near future (Anandan et al. 2021a). This calls for an alternative strategy, wherein the external application is controlled and the plant is supplemented with better P use efficiency traits (Pandit et al. 2018; Reddy et al. 2020). However, the hindrances the absence of P efficient traits in most of the modern cultivars of rice (Mahender et al. 2017; Nirubana et al. 2020). For instance, in the sequencing of *Pup1* locus in the Aus variety, Kasalath has revealed that the characteristic 90kb transposon rich indel is missing from the Nipponbare reference genome (Gamuyao et al. 2012). Thus, mining out alleles conferring tolerance in the genotypes expressing them must be the primary effort. Rice is being grown in diverse ecological systems: this has led to diverse adaptive features, with higher degrees of variability between genotypes. Such variations can be exploited especially when we try to improve a trait like abiotic stress tolerance.

Landraces have always been the source of abiotic stress tolerance, may it be the low P tolerance, (Gamuyao et al. 2012), submergence (Bailey-Serres et al. 2010), or heat stress (Prasanth et al. 2017). They have been traditionally cultivated and adapted to tolerate stress and give a stable yield even under a low input environment. Abiotic stress tolerant accessions for soil moisture deficit have been identified in the *O. nivara* L. and *O. rufipogon* L. (Kaur et al. 2018; Luo et al. 2019). A study comprising of 182 accessions of *O. rufipogon* was undertaken for highlighting the P use efficiency traits and the accession IRGC 106506 performed better with respect to root weight and P content in comparison to the positive control, Vandana (Neelam et al. 2017). Screening diverse lines for adaptation to low P traits would require focusing not only on the shoot but also on the root traits. Therefore, various root features along with the shoot morphological traits that would best define a low P tolerant plant have been considered in the present study. This information would improve the basic understanding of the overall response of *Oryza* spp., towards low P stress in the soil during the early vegetative stages. The inclusion of *O. nivara* and *O. rufipogon* in addition to the landraces, improved cultivars would allow us to have a comparative analysis between the four distinct groups and highlight the specific traits regulated under low P stress.

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Materials and methods

Plant materials, experimental design and crop growth conditions

The population for the study included 155 accessions (Supplementary Table S1); 77 improved varieties, 37 landraces, and 41 wild species (22 *O. rufipogon* and 19 *O. nivara*) originating from eight different states of India. Seeds for the experiment were collected from ICAR-National Rice Research Institute (NRRI), Cuttack, Odisha, and Regional Research & Technology Transfer Station (RRTTS), Coastal zone, Bhubaneswar, Orissa University of Agriculture and Technology (OUAT).

Phosphorus stress phenotyping in the microplot

The low P stress for the experiment was created in a microplot facility at NRRI, Cuttack (20°27'09" N, 85°55'57" E, 26 masl). The genotypes were direct seeded in the plots with a spacing of 20cm X 15cm in three replications during June 2019. Soil testing was performed to determine the pH in 1:25 soil-water suspension, available P was determined following the Bray and Kurtz no.1 method, alkaline-KMnO4 extractable nitrogen using a Kelplus-Elite Ex distillation unit (Pelican Equipments, Chennai, India) and 1 N NH4OAc extracted available potassium using a flame photometer (Flame photometer-128, Systronics Limited, India) were measured in the soil samples (Chatterjee et al. 2021). The micro plots were characterised by acidic pH (4.9), low levels of P (<3kg/ha), while nitrogen (295 kg/ha) and potassium (174 kg/ha) levels were in the medium range which was sufficient to grow a crop for 45 days. However, basal recommendation dose (80:0:40 Kg) of N and K were given without any external P fertilizer. The seeds were heat-treated at 50°C for 45 h in a hot air oven to break seed dormancy if present. The average day/night temperature was 33.6/26°C and the relative humidity was 85.9% in bright sunlight of the experiment period. Irrigation was given every alternate day and thinning was done to maintain the population at two seedlings per hill. The chlorophyll content was measured on the 44th day for three plants of each accession with a SPAD meter (SPAD-502, Konica Minolta). Three plants from each genotype were uprooted the next day (45th day) to observe the morphological traits such as shoot length (cm), number of tillers plant^{-1}, number of leaves plant^{-1}, 3rd leaf length (cm) and width (cm), stem thickness (mm), maximum root length (cm) and root shoot length ratio. Other root traits such as total root length (cm), projected root area (cm^2), root surface area (cm^2), average root diameter (mm), root volume (cm^3), and the number of root tips were recorded for each genotype per replication by analyzing them with WinRHIZO Pro 2013e (LA 2400, Regent Instruments INC.) root scanner. The dry weight of shoot and root were recorded in grams after drying the samples in a hot air oven (5-6 days, 60°C). The geometric trait; top view area (mm^2) was calculated utilising Image J software as described by Anandan 1 et al. (2020) and Bhatta et al. (2021). The P quantification was done following the phospho molybdo vanadate colorimetric method with dry powdered 300 mg of the shoot and 90 mg of root sample. The concentration of P in these samples was determined using Systronics, UV Spectrophotometer at 420 nm. The total shoot and root P contents were determined on mgg^{-1} dry weight basis. In order to derive an index value for shoot and root P content, shoot-root P ratio was calculated for ease of categorising genotypes. Additionally, mycorrhiza colonization was also examined following Trypan blue staining method (Koske and Gemma 1989) with minor modifications. The final slides were prepared with atleast 10 root pieces to study under a stereomicroscope and the colonization in the roots were calculated using the formula described by McGonigle et al. (1990). Percentage of colonization = (number of root segments colonized /total number of root segments) x 100.

Statistical analysis

The variation in the sample population due to the P factor was determined using analysis of variance and descriptive statistics in Windostat 7.5 for the 23 traits mentioned above. Principle Component Analysis (PCA) was performed using FactoMine R package (Lê et al. 2008) in R on a matrix of 23 morphometric and geometric traits. Correlation between the traits under low P environment was executed with the corrplot function from the corrplot package in R (version 3.6.3) (Wei and Simko 2016). The K means clustering approach was carried out separately for each group of

genotypes to identify genotypes having similar phenotypic expression and traits that are similar under the P deficiency condition. Similarly, a cluster heat map function (x, scale = "none", dual Scale = FALSE, method = "ward.D2") of the R package made4 (Culhane et al. 2005; Bhatta et al. 2021) was performed for each category of genotypes using 23 traits.

Results

Principal component analysis

The analysis of variance revealed that significant variation ($P < 0.001$) was observed among the genotypes for all 23 traits studied (Supplementary Table S2). Data of 155 genotypes were subjected to principal component analysis (PCA) (Fig. 1). It reduced the data dimensionality and highlighted the traits that contribute the most to the total variance. The analysis revealed six main PCA axes, each having eigenvalues more than one which ensured that each one of these components explained variance more than that of the original variables accounted in the standardized data. This aided in reducing the number of PCs involved in the study. PC1 explained 38.6% of the total variability between the sample genotypes and individual traits. Root volume was the most significant character for PC1 followed by total root surface area, total root projected area, and total dry weight. The genotypes on the higher end of PC1 were the ones that were affected by the low P in soil but still maintained high values for all the traits except for root P, shoot P, root/shoot length, and root/shoot dry weight which were uncorrelated or negatively correlated with rest of the traits. PC2 explained 15.8% of the rest of the variance where SPAD value, number of root tips, and leaf width had a major contribution. The genotypes on the higher end of PC2 maintained high root P content but were not reflected in the shoot P (uncorrelated). The rest four of the PCs had eigenvalues of more than one but their contribution in the variance was below ten percent. Interestingly, the mycorrhizal colony had a positive correlation with PC of 5 and 6. Overall the PCA revealed the heterogeneity between the samples, whereas samples within the group more or less followed a similar trend. This calls for treating the four groups of rice and wild relatives separately.

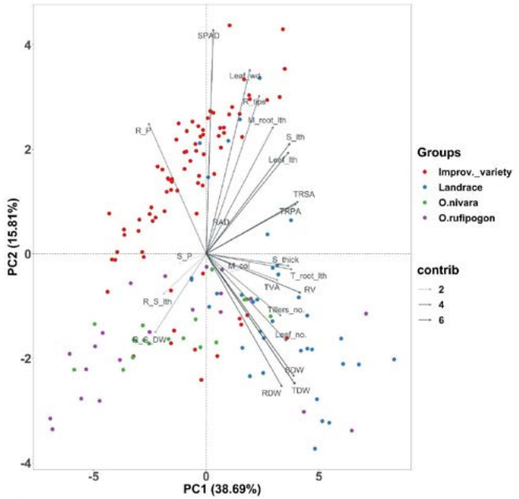

Fig. 1. PCA Biplot graph represents genolypes (Improved, landrace, *O. nivara* and *O. rufipogan*) in two main principal components for traits measured under P deprived condition. The two components explained 38.6% and 15.8% of the variance, respectively. The direction and length of the vector indicate the traits' contribution to the first two components in the PCA. The transparency of the trait vectors represents the contribution to the variance in the dataset, ranging from 2% (lightest) to 6% (darkest)

Descriptive statistics and correlation

The comparative results and spread of the variation (data) of individual group have been represented by the violin graphs in Figs. 2 and 3. The mean value for root volume (3.62 cm^3) was highest in the case of landraces with a CV of 39% (Supplementary Tables S3 – S6). Both shoot dry weight and root dry weight were higher in the landraces with values 0.81 g and 0.25 g respectively (Supplementary Table S3). However, the values for root dry weight were skewed (1.48) and the kurtosis peaked at 2.24. This indicates that few cultivars within the landraces have out-performed the others. Interestingly, the root-shoot dry weight ratio was high in the case of *O. rufipogon* (1.07) (Supplementary Table S4), while the lowest value for this trait was observed in the case of landraces (0.44). The total root length (904.12 cm) and shoot length (26.1 cm) were higher in the case of landraces, however, the root-shoot length ratio was found to be proportionately higher in the case of *O. rufipogon* with a CV of 78% with a minor skewness of 1.1. This shows that *O. rufipogon* has physiologically balanced the proportionate values for both root-shoot dry weight and root-shoot length comparatively. The total P content in root was higher in the case of improved varieties (1.25 mg/g) (Supplementary Table S5), while the highest P content in the shoot was found in *O. rufipogon* (1.36 mg/g). But, the shoot-root P ratio revealed a different picture. The landraces had a value of 2.51, the highest among the four groups indicating its efficiency in uptake and distribution of a major part of its P to the shoots. The four different groups manifested different correlations (Figs. 4a-d) among the traits except a few that were similar in more than one of the groups. Each of the groups' shoot length had a high positive correlation with leaf length. Leaf width was positively correlated with maximum root length in improved varieties and *O. rufipogon* with values 0.70 and 0.66, respectively. Shoot length was negatively correlated to the root-shoot dry weight ratio in all the groups except improved varieties. Total root length was positively correlated with the number of root tips (ranging from 0.55 in

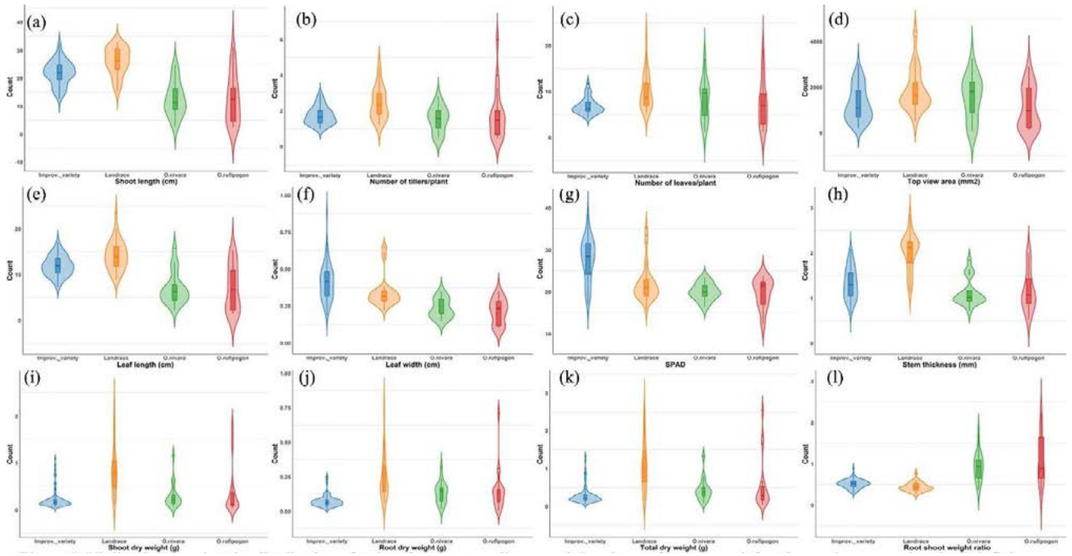

Fig. 2. Violin plot showing the distribution of traits of each group (Improved, landrace, *O. nivara* and *O. rufipogan*) measured under P deficiency. (a) Shoot length, (b) Number of tillers-1, (c) Number of leaves-1, (d) Top view area, (e) Leaf length) (f) Leaf width, (g) SPAD, (h) Stem thickness, (i) Shoot dry weight, (j) Root dry weight, (k) total dry weight and (l) root shoot weight ratio. The upper, median and lower quartiles of boxes (inside violin plot) represent the 75th, 50th and 25th percentiles of the population, respectively. The line extended from both side of the inside box represents the maximum and minimum value of the trait. Dots after the extended line represents outliers. Width of the plot represents frequency

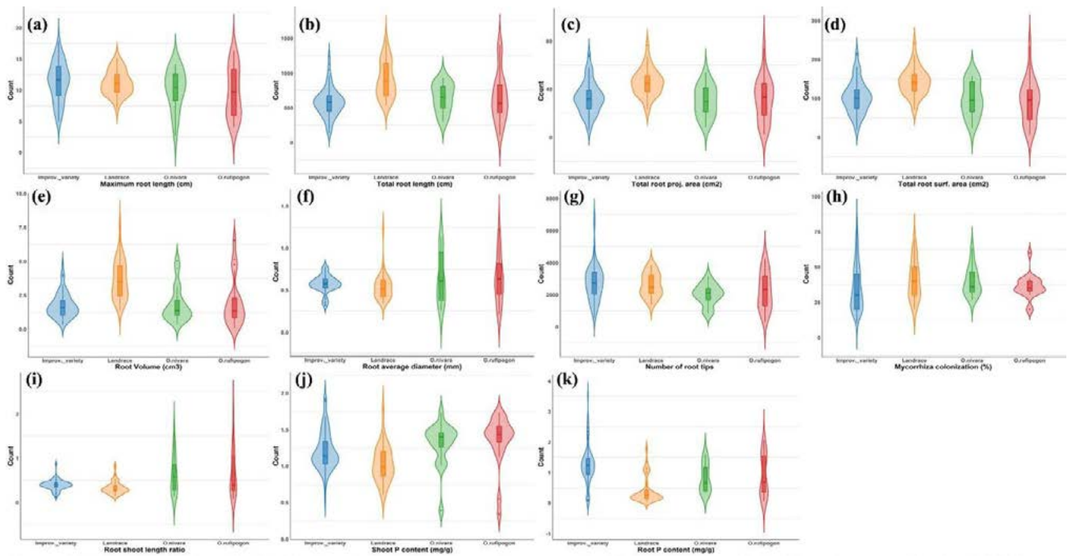

Fig. 3. Violin plot showing the distribution of traits of each group (Improved, Landrace, *O. nivara* and *O. rufipogan*) measured under P deficiency. (a) Max. root length, (b) Total root length, (c) Total root projected area, (d) Total root surface area, (e) Root volume, (f) Root avarage diameter, (g) Number of root tips, (h) *Mycorrhiza* colonization, (i) Root shoot length ratio, (j) Shoot P content and (k) Root P content. The upper, median and lower quartiles of boxes (inside violin plot) represent the 75th, 50th and 25th percentiles of the population, respectively. The line extended from both side of the inside box represents the maximum and minimum value of the trait. Dots after the extended line represents outliers. Width of the plot represents frequency

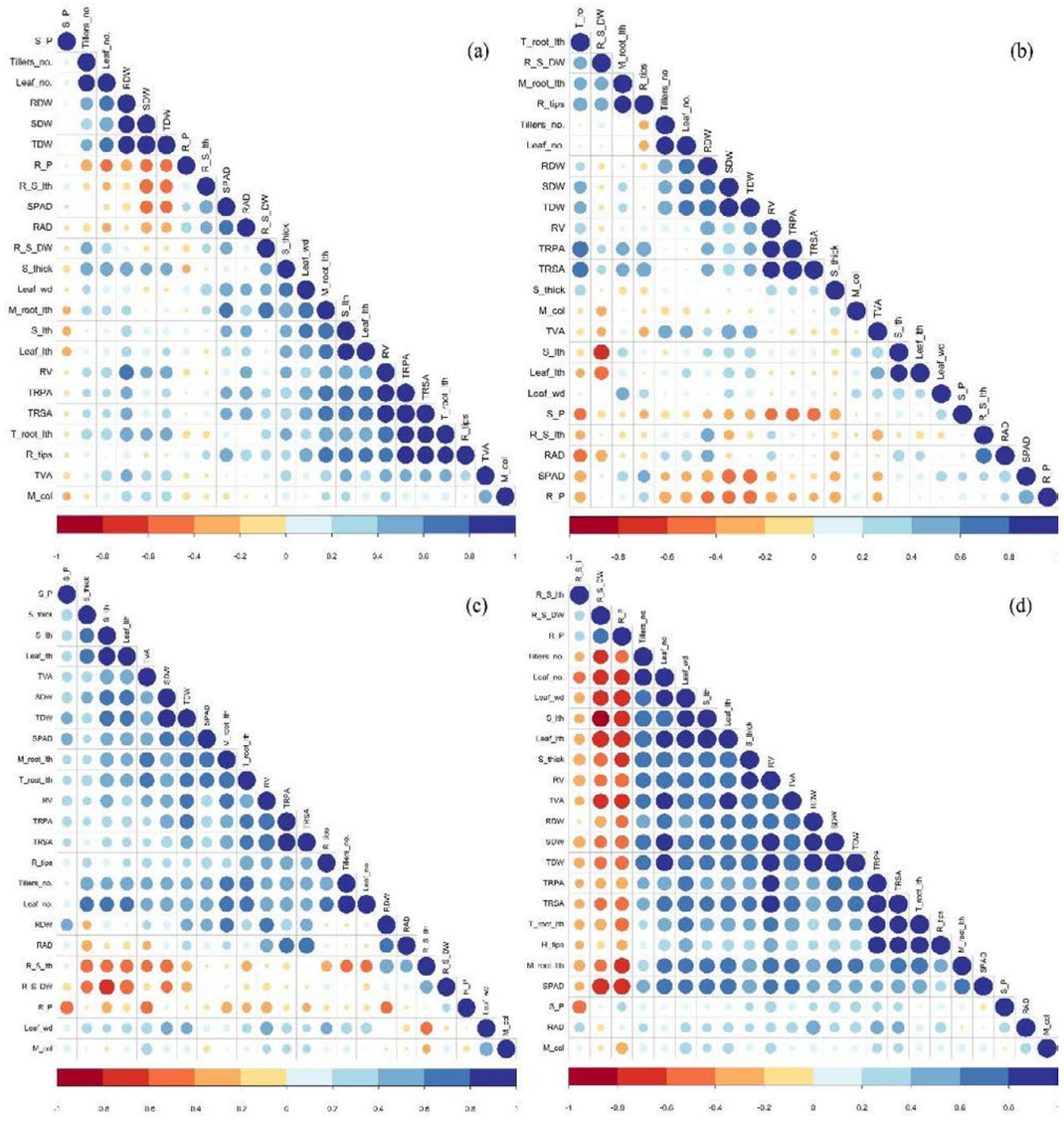

Fig. 4. Pearson correlation matrix among the 23 traits measured under P deficiency, (a) improved genotypes, (b) landrace, (c) *O. nivara* and (d) *O. rufipogan*. The colour denotes the sort of correlation, where 1 represents complete positive correlation (dark blue) and -1 represents complete negative correlation (dark red) between two traits. Large circle denotes strong and small circle denotes weaker correlation

landraces to 0.87 in *O. rufipogon*). The P content in root and shoot had no significant relation except in *O. nivara*, where they were negatively correlated (-0.50).

K means cluster analysis

The sample cultivars were subjected to K means cluster analysis to highlight the underlying trend and the subgroups they form taking into account the multiple variable traits in the study. Improved varieties, landraces, *O. rufipogon*, and *O. nivara* were analyzed separately and these four groups show distinct patterns of trait expressions. The clusters displaying high mean indicate that their representative cultivars have fared well under P deficient conditions for that specific trait.

Improved varieties had the highest number of samples that were grouped into four clusters based on their respective trait expressions. Cluster 2 with 17 genotypes had higher mean values for most of the traits, comparatively. However, the shoot P content was higher in cluster 3, a desirable trait for low P tolerance. Cluster 1 had higher expression in the case of dry matter accumulation. The heat map for improved varieties also highlighted the representatives of Cluster 2 with the maximum amount of correlation for multiple of the traits (Supplementary Fig. S1.a). The heatmap identified few genotypes like Bhanja, Keshari, and Improved Lalat that had a high expression for all traits except for shoot P and root P accumulation. However, Gajapati had a better accumulation of shoot and root P but lacked superiority in other traits. Landraces were categorized into three clusters based on their trait expressions. Cluster 1 and 3 had high mean values for a different set of traits followed by Cluster 2 under the low P environment. Cluster 2 had a high mean characteristically for root traits. The hierarchical heat map conformed with k-mean cluster analysis (Supplementary Fig. S1.b). *O. nivara* was grouped into two clusters where all the morphological trait means were high for cluster 2 except for root P content which was high in cluster 1. *O. nivara* displayed higher trait correlation with shoot P for most of its representative cultivars, especially AC100142, AC100123, AC100117 and AC100285 (Supplementary Fig. S2.a). Especially, AC100142 stood out and had higher correlation with most of the traits as revealed by the heatmap. *O. rufipogon* was grouped into three clusters and clearly, the mean value for cluster 2 was the highest. This cluster had three genotypes that also had higher intensity for most of the traits in the K mean and heat map (Supplementary Fig.S2.b). Accessions like AC100062, AC100219, and AC100219(A) were having high trait correlation for most of the traits shoot P content as inferred from the heat map.

Discussion

To expedite understanding of the heterogeneous population, the sampled cultivars were studied in four different groups. This made the study focus on the diversity within and between groups rather than just highlighting a few tolerant lines from all the groups together. The P deficiency symptoms, in general, are so pronounced that studying morphological characters can itself sketch a clear picture like the type of root, root length, root volume, SPAD, leaf width, shoot P, and root P content can be regarded as indicative traits (Anandan 2 et al. 2021b) that can determine the adaptability of a genotype.

The descriptive statistics have highlighted landraces to be the best group that survived a low P environment. The mean performance (for traits like shoot length, tiller numbers, root volume, total root surface area, root dry weight, total root length, and shoot-root P) of the group is suggestive of the fact that most of the landraces were well adapted to face the low levels of P in their respective places of origin. It is known that more than 90% of India falls into the category of low to medium levels of P in the soil (Tiwari 2001) and landraces are adapted more to manures than synthetic fertilizers. Only from the mid of 21st century, farmers were driven towards high-input agriculture and ideally designed improved varieties. Thus, it is expected from the landraces to perform better in a low P stress environment comparatively. For other traits like leaf width, shoot P, and dry weight accumulation, landraces performed at par or higher than the other three groups.

Narrowing of the leaf is a sign of P deficiency in rice plants (Chen et al. 2014) and leaf width had the highest mean in the case of improved varieties. The correlation analysis indicated a positive correlation between the leaf width and root length and this is in agreement with Anandan et al. (2021b). In a P deficient soil, higher root development helps in mining greater amount of P, ensuring unhindered supply to the shoot and leaves (Panda et al. 2021). The total root length and number of root tips had a positive correlation between all four sample groups. This shows that the plants under low P have developed newer roots (for mining shallow depth) for maximum P acquisition (Vejchasarn et al. 2016). The measure of root and shoot P in the samples revealed an interesting fact. High P content in the roots does not always correspond to low P tolerance. There are examples from this study where the root P is high but the same is not reflected in the shoot. The lack of association between root and shoot P is also highlighted in the correlation analysis, showing an absence of correlation (or even negative in case *O. nivara*). Thus, it was decided to go for a simple ratio of shoot P to that of root P, creating an index for comparing P levels both above and below the ground. This index using group means was as high as 2.51 in case of landraces, the lowest was in improved varieties (0.97).

The clusters formed using K means analysis has helped in revealing the subgroups within each sample population expressing specific traits with higher magnitude in response to low levels of P in the soil. It is appropriate to mention here that we were able to appreciate the differences between the clusters formed by k means and the hierarchical grouping of the heat map. The former clustered genotypes having similar magnitude of trait expression into one whereas the latter considered the correlation of individual traits with the respective genotypes and then grouped them in different branches. The hierarchical heat map (Supplementary Figs. S1 and S2) was found to be more versatile in representing multiple traits and genotypes in a single illustration.

A few genotypes were sorted out that had the combination of some of the desirable traits for a low P tolerant plant, these were scattered across the four different groups (Fig. 5). The most important trait in such a study is

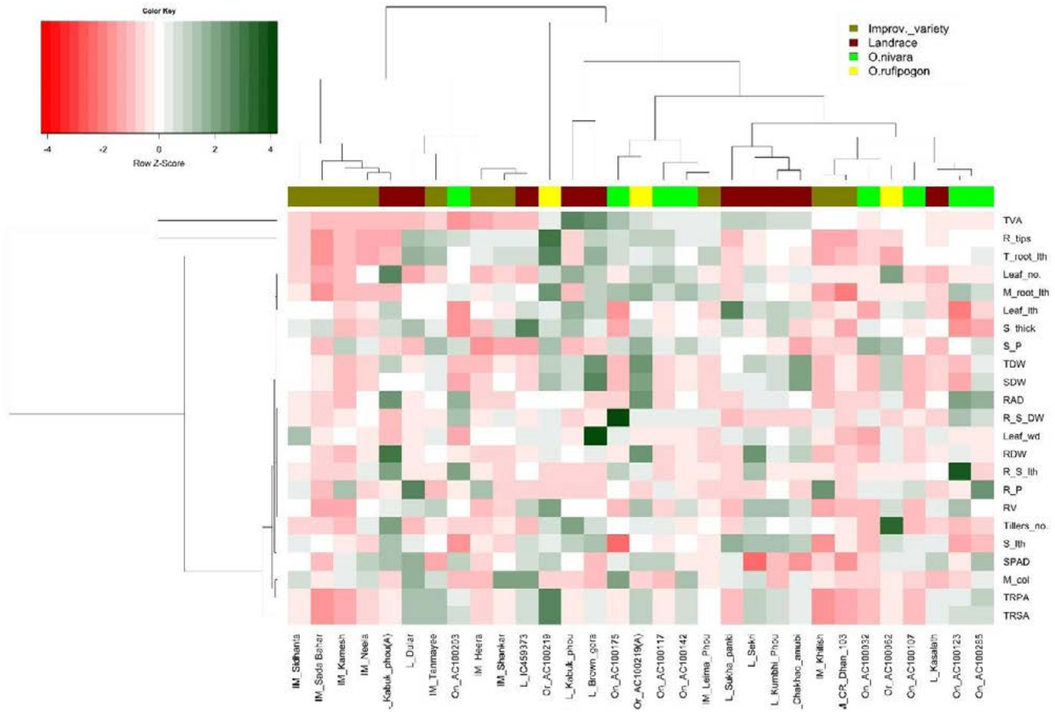

Fig. 5. Hierarchical clustering and heat map of selected rice genotypes and low P tolerance related traits. Each column represents an accession and each row represents a trait. Genotypes divide into two main clusters. Both upper and lower clusters are divided into two sub-clusters. The colour spectrum (legend) illustrates the Z-score across the range of –4 to +4. A Z-score of '0' indicates that the trait value is identical to the mean, and values greater than the mean are categorized into +4 (green) and *vice versa* (red)

the ultimate accumulation of P in the shoot and roots. It was observed that, on an average shoot P was high in *O. rufipogon* group (1.36 mg/g) but looking at the individual cultivars, we found the highest shoot P content was in the members of improved varieties (Bhatta et al. 2021) such as Suphala (1.37 mg/g) and Sarathi (1.45 mg/g). Interestingly, in the improved varieties, the corresponding root P was also high (1.25 mg/g) (Fig. 1; Supplementary Table S6) suggesting that the nutrient allocation from the root to the shoot was not efficient. On the contrary, the members with relatively high shoot P content in *O. rufipogon* displayed proper P allocation between the root and shoot. The shoot and root biomass accumulation as reflected by their dry weight was highest in landraces while the cultivars from the two groups of wild species did not fare well in this regard. The morphology of the root is another important yardstick to measure the tolerance to a low P environment (Bhatta et al. 2021). Root volume and total root length were high in the case of landraces with respect to the group mean. Moreover, AC100219 (*O. rufipogon*) had one of the highest figures for root volume and total root length apart from few superior representatives of the landraces. As P in soil is limited to the shallow layers, deeper roots are not desirable, thus it is apt to look for a cultivar with a higher value for both root volume and number of root tips. Besides, the positive correlation between the total root length and number of root tips supports the notion that plants under P stress do not need longer roots rather a higher number of shallow roots/lateral roots (Panda et al. 2021).The highest expressions for each of these traits were seen in AC100219 of *O. rufipogon*. Each group (*O. nivara*) had displayed a positive correlation between root dry weight and shoot dry weight indicating a synergistic relationship between the underground and above the ground traits. This finding supports the argument that screening for low P condition in rice suggest equal emphasis should be given for the shoot as well as the root morphological features. The highlighted tolerant genotypes can be further studied to dissect the genetic basis of their tolerant trait manifestation and the effect on yield under a low P environment through molecular approaches.

Although, genetic improvement with regards to PUE is highly challenging one due to several reasons including incomplete understanding of control of P uptake, appropriate phenotyping, variable soil properties across the cultivable land, gene interactions under variable environments and conduct of large scale trials (Bovill et al. 2013). There are several reports of the traits result in substantial improvement in P nutrition under controlled conditions like pot study in laboratories, screening under hydroponics fail to show similar advantages in field soil. To understand the genetics of PUE, relatively a few studies have identified QTLs in the crop species. Generally, the process has been to measure traits of interest such as biomass production and shoot P concentration under both limiting and non-limiting P conditions (Bovill et al. 2013; Bhatta et al. 2021) and the QTLs have been detected for these traits. However, it has been also noticed that QTLs for biomass and yield often co-locate with QTLs for P uptake and/or P utilisation efficiency, for example, in wheat (Su et al. 2009) and rice (Wissuwa et al. 1998). They further argued that it is because of the correlation between biomass production and shoot P uptake is often extremely high, however, it would be difficult to improve both the traits simultaneously (Bovill et al. 2013). A few authors have attempted to overcome this issue by assessing relative yield, and detecting QTLs for relative yield. Yang et al. (2010), in a study assessing the relationship between QTLs for root traits and P uptake in Brassica napus, found that QTLs for P uptake and biomass production were linked. The present study has identified lines that can be used in identification of QTLs responsible for low P tolerance and also serve as a source of breeding material for developing low P tolerant rice cultivars through classical breeding approach. It is also suggested that the advances made in molecular and genomic tools combining traditional science of plant breeding may facilitate to study the genetic differences in PUE, bringing P-efficient crops.

Authors' contribution

Conceptualization of research (AA, SP); Designing of the experiments (AA); Contribution of experimental materials (BCP, DB); Execution of field/lab experiments and data collection (SP, BB); Analysis of data and interpretation (AA, SP); Preparation of the manuscript (SP, AA).

Supplementary materials

Six Supplementary tables and two figures are supplied.

Declaration

The authors declare no conflict of interest.

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Supplementary Table S1. List of accessions of different *Oryza* spp. used for evaluating in P deprived soil

S.No.	Genotype	Species/Landrace/ Iimproved	S.No.	Genotype	Species/Landrace/ Improved	S.No.	Genotype	Species/Landrace/ Improved
1	Dular	Landrace	**26**	AC100295	*O. rufipogon*	**51**	AC100117	*O. nivara*
2	Kasalath	Landrace	**27**	AC100296	*O. nivara*	**52**	Sekri	Landrace
3	IC459373	Landrace	**28**	AC100285	*O. nivara*	**53**	Longmanabi(A)	Landrace
4	CR Dhan 801	Improved variety	**29**	AC100203	*O. nivara*	**54**	Sukhapnki	Landrace
5	AC100281	*O. rufipogon*	**30**	AC100219	*O. rufipogon*	**55**	Lalat MAS	Improved variety
6	AC100062	*O. rufipogon*	**31**	Kabuk Phou	Landrace	**56**	Meher	Improved variety
7	AC100326	*O. rufipogon*	**32**	Chakhao Aubi	Landrace	**57**	Rajeswari	Improved variety
8	AC100035	*O. rufipogon*	**33**	Kumbhi Phou	Landrace	**58**	Subhadra	Improved variety
9	AC100142	*O. nivara*	**34**	Akhiyaturfa	Landrace	**59**	Asutosh	Improved variety
10	AC100021	*O. nivara*	**35**	Leimaphou	Landrace	**60**	Hiranmayee	Improved variety
11	AC100032	*O. nivara*	**36**	Longmanabi	Landrace	**61**	Pratap	Improved variety
12	AC100284	*O. rufipogon*	**37**	CR Dhan 103	Improved variety	**62**	Lalitagiri	Improved variety
13	AC100329	*O. nivara*	**38**	Khitish	Improved variety	**63**	Mrunalini	Improved variety
14	AC100193	*O. rufipogon*	**39**	Sadabahar	Improved variety	**64**	Pradeep	Improved variety
15	AC100042	*O. rufipogon*	**40**	Neela	Improved variety	**65**	Pathara	Improved variety
16	AC100015	*O. rufipogon*	**41**	Abhishek	Improved variety	**66**	Pratibha	Improved variety
17	AC100282	*O. rufipogon*	**42**	Harishankar	Landrace	**67**	Ranidhan	Improved variety
18	AC100010	*O. nivara*	**43**	Kamesh	Improved variety	**68**	Suphala	Improved variety
19	AC100006	*O. rufipogon*	**44**	Phalguni	Improved variety	**69**	Sarathi	Improved variety
20	AC100293	*O. nivara*	**45**	Kowni	Landrace	**70**	Manaswini	Improved variety
21	AC100189	*O. rufipogon*	**46**	AC100175	O. nivara	**71**	Uphar	Improved variety
22	AC100328	*O. nivara*	**47**	AC100142(A)	O. nivara	**72**	Ramchandi	Improved variety
23	AC100309	*O. rufipogon*	**48**	ASD16	Improved variety	**73**	Sebati	Improved variety
24	AC100107	*O. nivara*	**49**	Poongar	Landrace	**74**	Vandana	Improved variety
25	AC100301	*O. nivara*	**50**	AC100135	O. rufipogon	**75**	Sneha	Improved variety
76	Ramba	Improved variety	**103**	Badami	Improved variety	**130**	Chakhao(A)	Landrace
77	Pooja	Improved variety	**104**	Prachi	Improved variety	**131**	Chakhao Aubi(A)	Landrace
78	Mahanadi	Improved variety	**105**	Gajapati	Improved variety	**132**	Chakhao Poreition	Landrace
79	Annapurna	Improved variety	**106**	Pratikshya	Improved variety	**133**	IC418443	Landrace
80	Vanaprabha	Improved variety	**107**	Bhanja	Improved variety	**134**	IC450521	Landrace
81	Jagannath	Improved variety	**108**	Kharavela	Improved variety	**135**	IC544887	Landrace
82	Udayagiri	Improved variety	**109**	Shankar	Improved variety	**136**	Kabuk phou(A)	Landrace
83	Samanta	Improved variety	**110**	Keshari	Improved variety	**137**	Kaliabhat	Landrace
84	Birupa	Improved variety	**111**	Anjali	Improved variety	**138**	Kaliabhat(A)	Landrace
85	Rudra	Improved variety	**112**	Gouri	Improved variety	**139**	Manipuri black	Landrace
86	Ghanteswari	Improved variety	**113**	Konark	Improved variety	**140**	Manipuri black(A)	Landrace
87	Bhubana	Improved variety	**114**	Nilagiri	Improved variety	**141**	Mummy hunger	Landrace
88	Tanmayee	Improved variety	**115**	Mahalaxmi	Improved variety	**142**	Baman Phou	Landrace
89	Sabitree	Improved variety	**116**	Heera	Improved variety	**143**	Bulu harana	Landrace
90	Daya	Improved variety	**117**	Khandagiri	Improved variety	**144**	Gini	Landrace
91	Bhoi	Improved variety	**118**	Hema	Improved variety	**145**	AC100062(A)	*O. rufipogon*
92	Parijat	Improved variety	**119**	Manika	Improved variety	**146**	AC100133	*O. rufipogon*
93	Kalinga 3	Improved variety	**120**	Annada	Improved variety	**147**	AC100169	*O. rufipogon*
94	Indarbati	Improved variety	**121**	CR Dhan 40	Improved variety	**148**	AC100170	*O. rufipogon*
95	Sidhanta	Improved variety	**122**	IR36	Improved variety	**149**	AC100209	*O. rufipogon*
96	Urbasi	Improved variety	**123**	A. kuruvai	Landrace	**150**	AC100219(A)	*O. rufipogon*
97	Jagabandhu	Improved variety	**124**	A. kuruvai(A)	Landrace	**151**	AC100281(A)	*O. rufipogon*
98	Jajati	Improved variety	**125**	H24	Landrace	**152**	AC100032(A)	*O. nivara*
99	Kanchan	Improved variety	**126**	Black puttu	Landrace	**153**	AC100121	*O. nivara*
100	Tejaswini	Improved variety	**127**	Brown gora	Landrace	**154**	AC100123	*O. nivara*
101	Hasanta	Improved variety	**128**	Burma black	Landrace	**155**	AC100283	*O. nivara*
102	Surendra	Improved variety	**129**	Chakhao	Landrace			

Supplementary Table S2. Analysis of variance of 23 traits in P deprived soil

Traits	MS (Treatment)	F ratio	Probability	Mean	CD 5%
Shoot length (cm)	101.29	6.40	<0.001	19.97	5.54
Tillers plant^{-1}	1.28	3.60	<0.001	1.86	0.82
Leaf number plant^{-1}	29.75	8.79	<0.001	8.30	2.56
Leaf length (cm)	31.92	6.98	<0.001	11.05	2.97
Leaf width (cm)	0.03	5.70	<0.001	0.34	0.10
Stem thickness (mm)	0.42	3.72	<0.001	1.35	0.46
Max. root length (cm)	19.66	2.61	<0.001	10.54	3.82
SPAD	71.32	3.29	<0.001	38.28	6.47
Shoot dry weight (g)	0.28	20.21	<0.001	35.98	0.16
Root dry weight (g)	0.10	6.85	<0.001	20.05	0.17
Total dry weight (g)	0.66	16.72	<0.001	56.62	0.27
Root shoot length ratio	0.22	13.08	<0.001	0.62	0.18
Total root length (cm)	149981.20	21.47	<0.001	671.66	116.35
Total root proj. area (cm^2)	434.26	11.42	<0.001	34.64	8.58
Total root surf. area (cm^2)	3949.07	11.35	<0.001	107.74	25.96
Root avg. diam. (mm)	0.12	7.05	<0.001	0.75	0.18
Root Volume (cm^3)	4.36	10.28	<0.001	2.03	0.90
Root tips	1700945.00	7.38	<0.001	2268.67	668.27
Root Shoot dry wt. ratio	0.28	6.13	<0.001	0.59	0.29
Top view area (mm^2)	1649071.00	25.11	<0.001	1480.70	356.73
Mycorrhiza coloni. (%)	541.23	259.88	<0.001	40.99	2.00
Shoot P (mg g^{-1})	0.17	201.29	<0.001	1.18	0.04
Root P (mg g^{-1})	0.88	872.82	<0.001	0.94	0.04

Supplementary Table S3. Descriptive statistics in thirty-seven landrace rice genotypes under P deprived soil

Traits	Mean	SD mean	SE of ness	Skew-	Kurtosis	CV	Min. quartile (Q1)	1st	Median quartile (Q3)	3rd	Max.
Shoot length (cm)	26.10	4.86	0.80	-0.55	-0.59	0.19	15.20	23.18	26.18	30.50	33.02
Tillers plant^{-1}	2.42	0.89	0.15	0.64	-0.22	0.37	1.17	1.83	2.33	3.00	4.50
Leaf number plant^{-1}	10.07	3.99	0.66	1.14	1.30	0.40	5.00	7.00	8.67	11.83	22.35
Leaf length	14.21	3.19	0.52	0.62	0.59	0.22	8.92	11.88	13.98	16.07	23.40
Leaf width	0.34	0.11	0.02	2.03	3.55	0.31	0.22	0.28	0.32	0.35	0.65
Stem thickness	2.02	0.40	0.07	-0.58	-0.03	0.20	1.11	1.78	2.12	2.25	2.84
Max. root length	11.19	1.95	0.32	0.22	-0.60	0.17	7.12	9.63	11.07	12.50	15.17
SPAD	21.85	4.26	0.70	1.76	3.18	0.20	15.73	19.02	21.08	22.92	35.33
Shoot dry weight	0.81	0.50	0.08	0.97	0.88	0.62	0.13	0.47	0.78	1.04	2.24
Root dry weight	0.25	0.17	0.03	1.48	2.24	0.69	0.05	0.14	0.18	0.33	0.78
Total dry weight	1.06	0.63	0.10	0.71	-0.05	0.59	0.19	0.65	0.98	1.47	2.57
Root shoot length ratio	0.33	0.14	0.02	1.45	2.95	0.42	0.14	0.25	0.29	0.38	0.81
Total root length	904.12	259.39	42.64	0.46	-0.85	0.29	533.30	668.52	885.83	1137.97	1479.65
Total root proj. area	45.50	11.43	1.88	0.42	0.58	0.25	23.11	37.90	44.88	51.44	76.69
Total root surf. area	142.94	35.92	5.91	0.42	0.58	0.25	72.61	119.08	141.01	161.59	240.92
Root avg. diam.	0.54	0.16	0.03	2.35	9.00	0.29	0.34	0.42	0.52	0.62	1.23
Root Volume	3.62	1.42	0.23	0.65	0.15	0.39	1.37	2.45	3.47	4.68	7.65
Root tips	2622.89	726.21	119.39	0.12	-1.06	0.28	1353.00	2075.00	2481.00	3202.00	3868.00
Root Shoot dry wt. ratio	0.44	0.10	0.02	0.93	1.31	0.24	0.27	0.37	0.43	0.52	0.77
Top view area	1878.11	919.60	151.18	1.13	1.13	0.49	505.00	1258.00	1618.00	2190.00	4471.00
Mycorrhiza coloni.	40.61	13.62	2.24	0.43	-0.74	0.34	20.00	30.00	40.00	50.00	70.00
Shoot P	1.03	0.25	0.04	0.68	1.09	0.24	0.61	0.86	0.99	1.20	1.78
Root P	0.41	0.43	0.07	1.70	2.06	1.03	0.05	0.15	0.25	0.43	1.78

SD = Standard deviation, Min. = Minimum, Max. = Maximum; CV = Coefficient of variation

Supplementary Table S4. Descriptive statistics in twenty-two Oryza rufipogon genotypes under P deprived soil

Traits	Mean	SD mean	SE of ness	Skew-	Kurtosis	CV	Min. quartile (Q1)	1st	Median quartile (Q3)	3rd	Max.
Shoot length (cm)	12.64	8.83	1.93	0.61	-0.70	0.70	2.55	4.50	12.45	16.62	31.15
Tillers plant^{-1}	1.76	1.38	0.30	1.71	3.47	0.78	0.50	0.67	1.50	2.00	6.00
Leaf number plant^{-1}	7.38	5.14	1.12	0.80	0.00	0.70	1.18	2.94	7.06	9.50	19.33
Leaf length	6.95	4.95	1.08	0.38	-1.43	0.71	1.55	2.25	6.72	10.92	15.25
Leaf width	0.21	0.08	0.02	-0.12	-1.26	0.40	0.10	0.12	0.23	0.28	0.35
Stem thickness	1.16	0.44	0.10	0.74	-0.36	0.38	0.53	0.88	1.07	1.43	2.00
Max. root length	9.62	3.99	0.87	0.24	-1.42	0.42	4.10	5.91	9.68	13.35	16.30
SPAD	19.76	3.45	0.75	-0.89	-0.11	0.17	12.10	17.00	21.55	22.30	23.78
Shoot dry weight	0.38	0.52	0.11	2.01	2.97	1.37	0.04	0.10	0.12	0.38	1.83
Root dry weight	0.15	0.15	0.03	2.74	9.55	1.01	0.01	0.07	0.14	0.16	0.71
Total dry weight	0.53	0.66	0.14	2.15	4.01	1.24	0.05	0.18	0.29	0.53	2.54
Root shoot length ratio	0.66	0.51	0.11	1.10	0.64	0.78	0.10	0.26	0.40	1.06	2.00
Total root length	657.50	357.31	77.97	0.69	0.05	0.54	101.65	429.17	568.76	828.76	1405.07
Total root proj. area	31.52	18.05	3.94	0.30	0.02	0.57	2.32	18.70	33.22	44.82	74.44
Total root surf. area	92.39	55.48	12.11	0.56	0.61	0.60	7.29	45.61	96.03	122.03	233.85
Root avg. diam.	0.63	0.29	0.06	0.43	-0.42	0.45	0.22	0.45	0.63	0.81	1.24
Root Volume	1.97	1.78	0.39	1.32	1.01	0.90	0.08	0.83	1.33	2.27	6.53
Root tips	2231.57	1166.39	254.53	0.23	-1.06	0.52	319.00	1298.00	2344.00	3175.00	4261.00
Root Shoot dry wt. ratio	1.07	0.58	0.13	0.69	-0.65	0.54	0.26	0.66	0.89	1.64	2.22
Top view area	1092.05	921.12	201.01	0.48	-1.28	0.84	145.00	218.00	970.00	1976.00	2913.00
Mycorrhiza coloni.	35.82	8.22	1.79	0.67	3.52	0.23	20.00	33.20	35.00	40.00	60.00
Shoot P	1.36	0.34	0.08	-1.98	4.11	0.25	0.34	1.33	1.43	1.55	1.73
Root P	0.91	0.69	0.15	0.33	-1.61	0.75	0.06	0.36	0.70	1.55	2.07

SD = Standard deviation, Min. = Minimum, Max. = Maximum; CV = Coefficient of variation

Supplementary Table S5. Descriptive statistics in seventy-seven improved rice varieties under P deprive soil

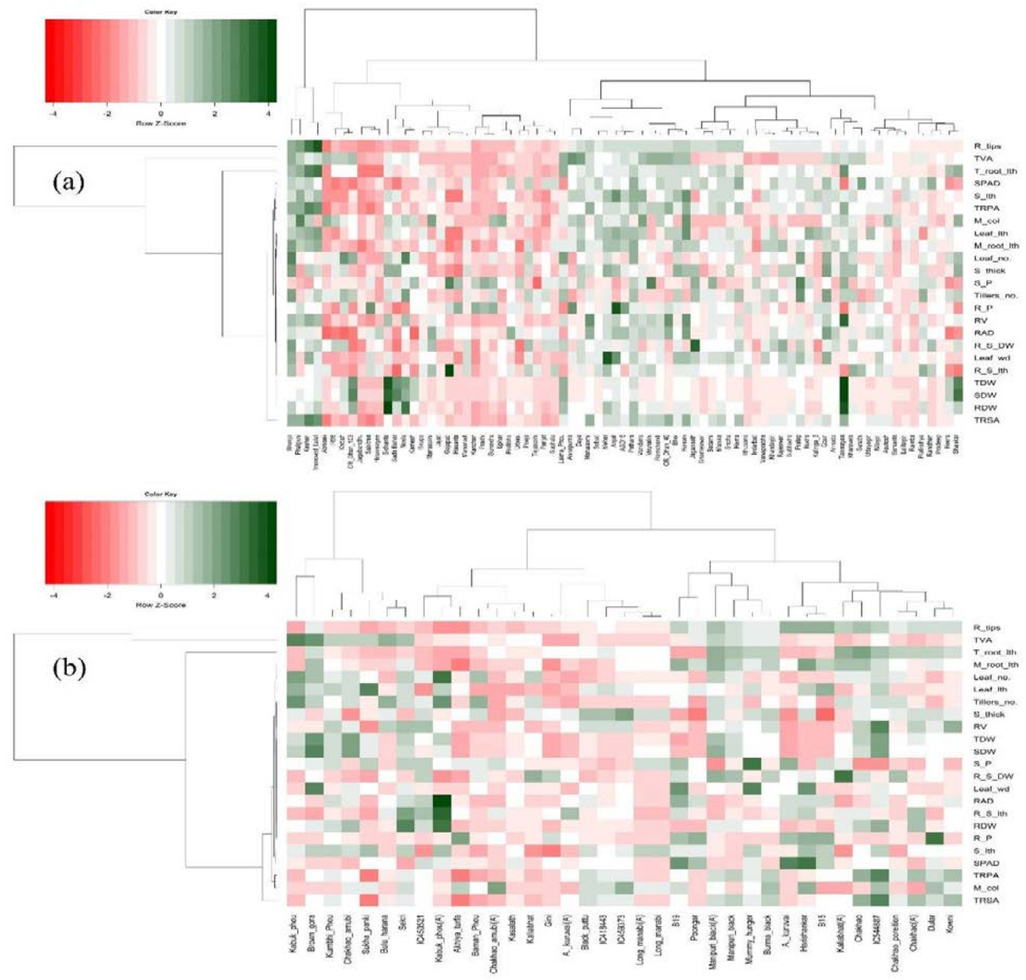
Traits	Mean	SD mean	SE of ness	Skew-	Kurtosis	CV	Min. quartile (Q1)	1st	Median quartile (Q3)	3rd	Max.
Shoot length (cm)	21.89	4.33	0.49	-0.07	-0.30	0.20	12.38	19.53	22.02	24.92	32.00
Tillers plant^{-1}	1.74	0.50	0.06	0.62	-0.31	0.29	1.00	1.33	1.67	2.00	3.00
Leaf number plant^{-1}	6.83	1.76	0.20	1.03	0.64	0.26	4.17	5.67	6.33	7.67	11.83
Leaf length	11.94	2.22	0.25	0.18	-0.45	0.19	7.33	10.42	11.95	13.52	17.15
Leaf width	0.41	0.12	0.01	0.86	1.92	0.30	0.18	0.32	0.42	0.48	0.88
Stem thickness	1.33	0.35	0.04	0.26	-0.80	0.26	0.65	1.05	1.30	1.56	2.08
Max. root length	11.35	3.14	0.36	-0.20	-0.60	0.28	4.90	9.15	11.65	13.83	17.92
SPAD	27.75	5.02	0.57	-0.37	-0.53	0.18	16.93	24.22	28.50	31.58	38.28
Shoot dry weight	0.22	0.20	0.02	2.67	7.15	0.91	0.05	0.12	0.16	0.22	1.09
Root dry weight	0.07	0.04	0.00	2.13	6.15	0.57	0.02	0.05	0.07	0.08	0.25
Total dry weight	0.30	0.24	0.03	2.59	7.05	0.81	0.07	0.17	0.23	0.31	1.33
Root shoot length ratio	0.39	0.11	0.01	0.61	3.35	0.29	0.13	0.34	0.39	0.45	0.87
Total root length	575.66	208.06	23.71	0.54	1.16	0.36	134.02	451.55	584.38	677.45	1242.59
Total root proj. area	32.92	13.40	1.53	0.44	0.15	0.41	6.30	23.63	31.77	38.93	68.72
Total root surf. area	103.41	42.10	4.80	0.44	0.15	0.41	19.78	74.24	99.82	122.31	215.89
Root avg. diam.	0.57	0.10	0.01	-0.48	0.61	0.18	0.32	0.53	0.57	0.63	0.78
Root Volume	1.72	0.90	0.10	1.05	1.28	0.52	0.31	1.02	1.56	2.11	4.75
Root tips	2738.83	1130.22	128.80	0.87	2.36	0.41	535.00	2038.00	2737.00	3400.00	6846.00
Root Shoot dry wt. ratio	0.52	0.11	0.01	0.32	1.26	0.20	0.28	0.45	0.52	0.59	0.89
Top view area	1279.23	751.33	85.62	0.52	-0.81	0.59	225.00	696.00	1101.00	1859.00	3055.00
Mycorrhiza coloni.	35.38	16.09	1.83	0.85	-0.05	0.45	10.00	20.00	30.00	45.00	80.00
Shoot P	1.21	0.26	0.03	0.71	0.67	0.22	0.57	1.03	1.14	1.34	1.92
Root P	1.25	0.62	0.07	0.78	2.25	0.49	0.06	0.94	1.22	1.46	3.52

SD = Standard deviation, Min. = Minimum, Max. = Maximum; CV = Coefficient of variation

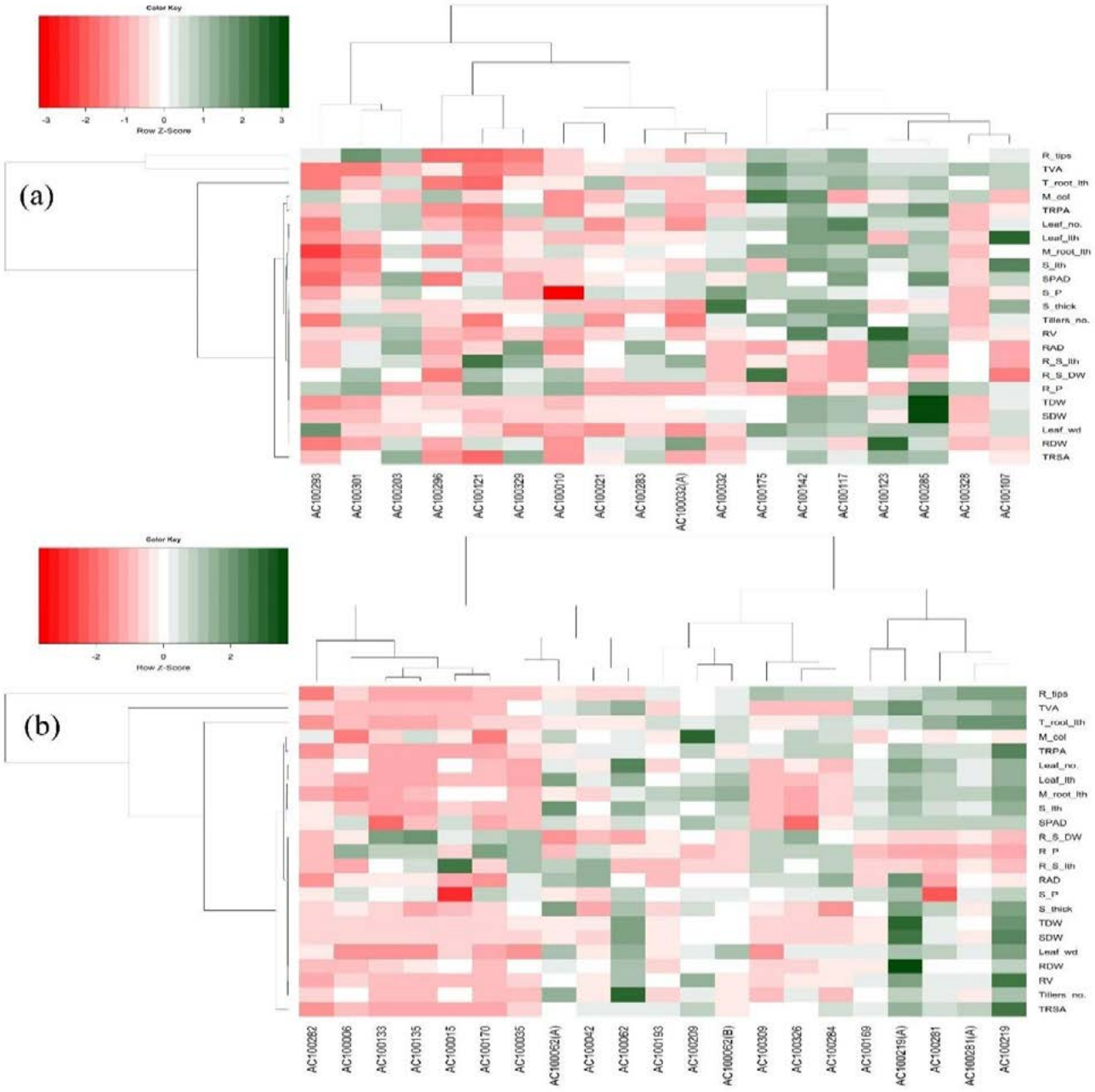
Supplementary Table S6. Descriptive statistics in nineteen Oryza nivara genotypes under P deprive soil

Traits	Mean	SD mean	SE of ness	Skew-	Kurtosis	CV	Min. quartile (Q1)	1st	Median quartile (Q3)	3rd	Max.
Shoot length (cm)	12.56	6.16	1.45	0.46	-0.41	0.49	2.80	8.75	11.40	16.75	24.83
Tillers plant^{-1}	1.54	0.71	0.17	-0.11	-0.83	0.46	0.50	1.00	1.59	2.00	2.83
Leaf number plant^{-1}	8.14	4.46	1.05	0.26	-0.54	0.55	1.18	4.71	9.67	10.59	17.33
Leaf length	7.04	3.55	0.84	1.14	0.83	0.50	2.25	4.33	6.25	7.80	15.75
Leaf width	0.23	0.06	0.02	0.38	-1.15	0.28	0.15	0.20	0.20	0.30	0.35
Stem thickness	1.13	0.30	0.07	1.16	0.47	0.27	0.71	0.93	1.02	1.18	1.84
Max. root length	10.13	3.28	0.77	-0.76	0.03	0.32	2.67	7.95	10.52	12.81	14.17
SPAD	20.02	1.99	0.47	-0.02	-0.52	0.10	16.30	18.90	19.95	21.72	23.45
Shoot dry weight	0.30	0.27	0.06	2.20	5.54	0.90	0.07	0.13	0.22	0.34	1.16
Root dry weight	0.13	0.08	0.02	0.68	0.73	0.56	0.02	0.07	0.15	0.17	0.32
Total dry weight	0.43	0.29	0.07	1.77	4.27	0.68	0.09	0.28	0.38	0.52	1.33
Root shoot length ratio	0.63	0.44	0.10	0.81	-0.24	0.69	0.15	0.28	0.56	0.88	1.62
Total root length	648.38	203.17	47.89	-0.35	-1.13	0.31	302.91	490.70	649.35	813.41	928.16
Total root proj. area	30.09	12.94	3.05	0.05	-0.95	0.43	8.66	21.11	29.67	41.05	54.05
Total root surf. area	97.92	43.79	10.32	-0.01	-1.19	0.45	23.35	62.03	95.24	146.66	158.66
Root avg. diam.	0.64	0.30	0.07	0.53	-1.19	0.47	0.26	0.37	0.61	1.02	1.14
Root Volume	1.82	1.32	0.31	1.37	1.19	0.72	0.37	1.02	1.37	2.14	5.05
Root tips	2007.56	646.00	152.26	-0.36	-0.31	0.32	842.00	1636.00	2098.00	2490.00	3145.00
Root Shoot dry wt. ratio	0.92	0.33	0.08	0.43	0.53	0.36	0.38	0.63	0.94	1.10	1.72
Top view area	1539.94	950.46	224.03	-0.23	-0.90	0.62	106.00	832.00	1810.00	2306.00	3239.00
Mycorrhiza coloni.	39.81	10.03	2.36	0.93	0.29	0.25	26.60	32.00	36.00	47.00	63.40
Shoot P	1.31	0.30	0.07	-1.78	4.57	0.23	0.39	1.26	1.40	1.46	1.74
Root P	0.83	0.47	0.11	0.49	-1.43	0.56	0.37	0.39	0.68	1.17	1.61

SD = Standard deviation, Min. = Minimum, Max. = Maximum; CV = Coefficient of variation



Supplementary Fig. S1. Hierarchical clustering and heat map of rice genotypes and low P tolerance related traits. Each column represents an accession and each row represents a trait. a) improved genotypes. Genotypes are divided into two main clusters. Lower cluster is further divided into four sub-clusters and b) landrace. Genotypes divide into two main clusters. Upper cluster is further divided into two and lower cluster in divided into four subclusters. The colour spectrum (legend) illustrates the Z-score across the range of "4 to 4. A Z-score of '0'indicates that the trait value is identical to the mean, and values greater than the mean are categorized into +4 (green) and *vice versa* (red).



Supplementary Fig. S2. Hierarchical clustering and heat map of rice genotypes and low P tolerance related traits. Each column represents an accession and each row represents a trait. a) *O. nivara*. Genotypes are divided into two main clusters. Both upper and lower clusters are divided into two sub-clusters and b) *O. rufipogon*. Genotypes divide into two main clusters. Both upper and lower clusters are divided into two sub-clusters. The colour spectrum (legend) illustrates the Z-score across the range of –4 to +4. A Z-score of '0' indicates that the trait value is identical to the mean, and values greater than the mean are categorized into +4 (green) and *vice versa* (red)