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Root Architecture and Genetic Variations Associated with Phosphorus Uptake in Rice

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Abstract: Phosphorus (P) is a finite resource and is a major limiting factor for rice yield on a large area of World's arable land. The main objective of this study was to investigate plant and soil P interaction in P limiting conditions. A P deficient 25/75% subsoil/sand mix was determined using pots in a preliminary experiment as to be used for screening 30 rice genotypes (*Oryza sativa* L.).The experiment was designed using a randomized complete block design to test if shallow and deep-rooted genotypes differ in extracting P present in soil by using rock phosphate in three treatments: when rock P was absent or embedded either in a shallow 10 cm layer or distributed homogenously in soil mix. All treatments were fed with Yoshida's nutrient solution lacking of P (YNS-P). Results indicated that P treatment x genotype interaction was significant on shoot dry weight (SDW). The addition of rock phosphate especially in shallow 10 cm layer greatly stimulated plant growth where SDW of plants grown in homogenous P and shallow P significantly outgrew those in zero P treatment. Both P treatment and genotype affected root dry weight (RDW) and root/shoot ratio significantly. Rice from the aus subgroup grown in zero P treatment accumulated significantly more SDW than indica and japonica genotypes. In zero P treatment, the genotypes Black Gora, Rayada, Kasalath, Azucena, IAC25, Dom Sufid, Aux1Wild type, FR13A and especially Sadu Cho accumulated higher SDW relative to the others.

Keywords: *Oryza sativa*, Phosphorus Deficiency, Shoot Dry Weight, Root/Shoot Ratio

1. Introduction

P deficiency is a major abiotic stress that limits crop productivity on 30−40% of the World's arable land (1). P is limited to plants because of its chemical fixation and low solubility. In most soils, P availability is therefore suboptimal and inadequate for high yield production. P is also expensive and the majority of farmers especially in developing countries cannot afford the rising prices of P fertilizers. So P availability in soil is a matter of concern and invites research attention to find an alternative way for sustainable production and food security for the world's growing population. Soil resources are usually unevenly distributed in space and time and often subject to localized depletion that make root architecture of great importance for plant productivity (2). For example greater nutrient acquisition especially in case of immobile resources such as P has been associated with topsoil foraging (3). Plant residues, remaining roots and P applied as fertilizers constitute the main sources of soil P, most of which is bound by soil particles within the shallow surface layer of the soil. This has made P concentration and availability more at the soil surface than at depth. Therefore, genotypes with a deep rooted system may lose the opportunity to access shallow P and hence root class may be of great importance in terms of P uptake. Root systems are made of a complex array of distinguishable root classes (4; 5). The spatial distribution of root system dictates the nature and function of each root class. Different root classes tap different soil areas, and through their interaction with the surrounding soils are subjected to different external effects. Therefore, they may differ in their capacity for nutrient absorption. For example, adventitious roots with greater intrinsic P influx capacity would benefit the plant as this root class generally forages the topsoil where the greater part of available soil P is located (6; 7; 8). Thus, in considering the limited availability of P, it is imperative to explore the root traits that enable P efficient genotypes to grow well in low and/or stratified availability of P. Most researchers and plant breeders endeavour to evaluate phosphorus use efficiency (PUE) for crop species and genotypes that are promising to

fulfill the economic and agronomic purposes for sustainable agricultural production with low inputs and which offer a more environmentally friendly solution to sustainability. Selection of genotypes with high PUE is essential to sustain productivity with low-inputs. Therefore, exploring the genetic variations of adaptive responses among crop species and genotypes for enhanced P efficiency and soil P acquisition ensures sustainable agricultural production in P-limiting soils. Against this background, this study was designed to screen different rice genotypes aiming at evaluating genotypic differences in P uptake and PUE under P limiting soil. Therefore the objective of this study was to investigate whether the distribution (shallow or homogenous) of P applied as rock phosphate through soil profile affects rice growth and the following hypotheses will be tested;

- Shallow P is more available to rice plants than evenly distributed P.
- Rice genotypes differ in their ability to get P out of soil.
- Shallow rooting genotypes have an advantage over deep rooted varieties when growth is limited by P that is available only in the top of the soil, but not if it is evenly distributed.

2. Material and Methods

2.1. Determination of Plant Available and Totalp in Soil

Available P in the soil was estimated by using acetic acid extraction as described by Allen (9). Five g, in four replicates, of each four air-dried soils were weighed into 250 ml conical flasks then 150 ml of extractant (2.5% v/v acetic acid) was added. The soil samples and blank flasks were shaken for two hours on a rotary shaker, and then allowed to settle overnight. The clear supernatant was then filtered through Whatman No. 40 paper into centrifuge tubes and the first 5–10 ml of filtrate was rejected. P was determined in the remaining filtrate of all samples. P concentration was measured by colorimetric analysis using the automated spectrophotometric flow injection analyzer (FIA). P content was calculated by multiplying soil dry weights with P concentrations. Results are demonstrated in Table 1. The available P in soil can be classified based on Bray P1 test, as defined by Marx et al. (10): < 20 mg kg-1 as low, 20–40 mg kg-1 as medium, 40–100 mg kg-1 as high and > 100 mg kg-1 as excessive. Accordingly, the soil test result for available P in Insch subsoil used in this experiment is 12.24 mg kg-1 indicating that it is low. As for total P in soil, the soil were ground in stainless steel ball mill (Retsch MM200), after being oven dried at 70 °C for 48 hours. 4.5 ml of digest reagent (2.8 ml of concentrated sulphuric acid, 0.08 g of lithium sulphate and 2.33 ml hydrogen peroxide) was added to approximately 0.2 g of oven dried, finely ground sample of each soil and heated to 360 °C for 2 hour to allow digestion. After this time 1 ml of hydrogen peroxide was again added and further digested for an hour. To determine total P in soil, the diluted digest then underwent FIA. Based on the concentration of P present in the soil, total P in soil was determined by multiplying P concentration (mg g-1) in soil with soil dry weight (g).

Table 1. *Plant available and total P in the sand and subsoil used in the experiment. Mean of 4 replicates ± standard deviation.*

	Available P (µg g^{-1})	Total P (µg g^{-1})
sand	1.95 ± 0.08	12.2 ± 5.9
subsoil	12.24 ± 0.63	814 ± 59

2.2. Determination of Total Phosphorus and Nitrogen (N) in Plant

To determine total P and N in plant, the procedure described above in section2.1. Determination of plant available and total P in soil was used (11). Based on the concentration of each element present in the shoot, total each element in shoot was determined by multiplying element concentration (mg g-1) in shoot with shoot dry weight (g). P use efficiency was calculated by dividing shoot dry weight (g) by total P in shoot (mg).

2.3. Rice Genotype Selection

In a preliminary experiment (data not shown), only one genotype (Azucena) was chosen to be grown. A total of 30 different rice genotypes were used which were mostly obtained from the International Rice Research Institute. Twenty of the genotypes belong to the Oryza SNP set (12): Akihikari, Aswina, Azucena, Bala, Black Gora, CT 9993, Cypress, Dom Sufid, Dular, FR13A, IAC165, IAC25, IR64, Kinandang Patong, Labelle, Lemont, Kasalath, Li-Jiang-Xin-Tuan-Hei-Gu, Moroberekan, N22, Nipponbare, Rayada, Sadu Cho, Sanhuangzhan No 2, Swarna, Tainung 67 and Zhenshan 97. This Oryza SNP panel was selected because they have received extensive genetic (12) and phenotypic (13) studies. Two genotypes are mutants of the Aux1 gene which is known to affect root growth (Aux1Mutant 1 and Aux1Mutant 2) while the genotype called Aux1 Wild type is genotype Zhonghua 11 in which genotype the mutants were made.

2.4. Preparation of Rice Seeds for Germination

Seed of rice cultivars were surface sterilized in 1% sodium hypochlorite for two minutes then washed under running tap water before being soaked in a beaker filled with tap water for 5 minutes. The seeds were placed on wet filter paper in a Petri dish, which was sealed with Para film then kept in an incubator at a temperature of 30 ºC for two days.

2.5. Experimental Design and Growing the Plants

In controlled growth room of the Cruickshank Building at the School of Biological Sciences, University of Aberdeen, UK, a box experiment was conducted during the winter season from January to March 2012. The growth room was supplied with two automatic vents for intake of fresh air and control temperature. The fresh supply of air was continuously circulated by two fans. The light in the room was supplied by fluorescent grow light. A total of 30 rice genotypes were evaluated for their growth response in a mixture of 25 % P-

limited (814 µg g-1dw) Insch subsoil uniformly added to 75 % blast sand (P content = 12.2 µg g-1dw). The experiment was when two levels of rock phosphate treatment were used. The first of the P treatments was by adding 59 mg of phosphorus pentoxide (P2O5) per plant to the soil mixture, achieved by adding 200 mg rock phosphate per plant that was distributed homogenously throughout soil profile (homogenous P). The second treatment was created where the same amount of rock phosphate (200 mg plant-1) was given in a band in the 10 cm surface layer (shallow P), while the control treatment had no P added to the soil mixture (zero P). The experiment was conducted using a randomized complete block design (RCBD) with three replicate blocks (boxes) for each treatment, with two plants of each genotype in each box arranged in two randomized sub-blocks. At the bottom of each box (53 x 33 cm at the top, 49 x 27 cm at the bottom and 39 cm depth), five drainage holes of five mm diameter were introduced then a non-woven fabric (Teram, UK) sheet was placed inside. The Insch subsoil and sand were thoroughly mixed and distributed among clear 60 litre plastic boxes. A total of nine boxes were prepared and a plastic sheet (52 x 32 cm length x width) was place on the soil surface; the plastic sheets had 60 perforations (2 cm diameter) for sowing plants maintaining a 5 x 5 cm distance. A black/white plastic sheet was wrapped around the box to prevent heat gain and light entry. Before sowing, each box was saturated with eight liters of Yoshida's nutrient solution (pH 5.5) (14) without P (YNS-P). Seeds were surface sterilized in diluted bleach (1% Na hypochlorite) before being germinated at 30oC for two days. Two pre-germinated, uniform and healthy seedlings for each genotype were sown in each hole. At the second leaf stage, the seedlings were thinned to one per hole. Each box was watered with four liters of YNS-P, three times a week for the first two weeks and five liters three times a week for another two weeks. In the final week, four liters of nutrient solution a day were supplied until harvested on day 35 so that each plant was supplied with 1.5 liters of YNS-P. To minimize the accumulation of nutrients in the growth medium, each box was watered with six liters of deionizer water once a week. Plants were grown in a controlled condition in a growth room under a 12 hour light regime with a light intensity of approximately 350−400 µmolm-2 s-1 photosynthetically active radiation with 25 ± 2oC at night and 28 ± 2oC in the day. Relative humidity was maintained between 55 and 70% throughout. Weeds were controlled by hand weeding. Plant height was monitored on weekly basis. After 35 days the plants were harvested and the shoot samples were oven-dried for two days at 70oC to constant weight and the SDW was measured. Before analysis, each box was treated as two randomized replicate blocks and the mean for each genotype per box was calculated. The resulting data (one value for each genotype in a box) were treated as a randomized complete block with three replicates. The effect of block on traits was assessed by analysis of variance and data were checked for normality and log transformed when needed by producing residuals of the data then adding these residuals to the mean of these data to produce the corrected data.

3. Results and Discussion

An experiment (data not shown) was conducted to determine a suitable medium for larger screens of rice genotypes in response to P treatments. The 25/75% subsoil/sand mix was selected to be used as a growth medium in the main experiment because this treatment appeared to be the most severely low P treatment that still supported some continued slow growth over the five week period. After this, experiment on the response of 30 rice genotypes were conducted in large storage boxes. The plants were sown in the box maintaining five centimeters between each other in order to minimize the box size that can accommodate a large number of genotypes. There is one limitation with this is that the more the plants grow the more the competition will be. To minimize both the competition among plants and the need for a large box and in the meantime to allow the genetic variations to be expressed, the duration of the experiment conducted here was only five weeks. Nonetheless, it is highly likely that above and below ground competition will be operating in this experiment. Below ground may not be unwelcome since it may emphasize the relative ability of genotypes to access the growth limiting P. Above ground competition is not welcome and it would be useful to verify some of these genotype differences detected here in larger pots where above ground competition could be minimized.

Figure 1 shows representative boxes of three treatments (zero P, shallow P and homogenous P) as they display differences in shoot growth between treatments. In shallow P treatment, plants exhibit healthy growth with wide, long and light green coloured leaves while zero P treatment-grown plants are shorter with narrower and dark green coloured leaves, thin stem and reduced numbers of tillers. As for plant growth in homogenous P, it was somewhat between the other two treatments. P addition greatly stimulated growth in both treatments (homogenous P and shallow P). For example SDW increased by 1.9 times in homogenous P and 2.9 times in shallow P treatment compared to that in zero P treatment (Table 2).

When P was applied as rock phosphate either homogenously or as a shallow layer of 10 cm depth, It was expected that whether homogenously or in shallow layer the addition of rock phosphate to the soil profile would increase total plant mass. It was also expected that the partitioning of carbon between roots and shoots will be one of the most important mechanisms that determines plant performance in P limiting conditions and that the relative performance of genotypes might differ depending on the distribution of P throughout soil profile. The results reported here are consistent with these predictions. Plant growth was greatly stimulated by the addition of rock phosphate where SDW in both homogenous P and shallow P increased by 1.9 and 2.9 times compared to that in zero P treatment, where for SDW, general linear model of ANOVA revealed that there was a significant genotype by P treatment interaction (P=0.014)

with both factors had a significant (P<0.001) effect. This pattern of the significant genotype by treatment interaction and effect was also observed for number of tillers at day 35 with R2 value at about 71%. There was more tillering in shallow, then homogenous and finally zero P treatment. The significant genotype by P treatment interaction for SDW supports the hypothesis that rice genotypes differ in their ability to get P out of soil. There were very strong correlations (Table 3) between SDW and total P uptake within each treatment indicative of an important role for P in plant growth in this experiment. Of course, the correlations could reflect an important role of plant growth in obtaining P, but distinguishing the cause and effect here will be very difficult. The significant (P<0.001, F=41.62, R2=19%) increase in SDW of shallow P compared to homogenous P treatment supports the hypothesis that shallow P is more available to rice plants than evenly distributed P. Thus shallow rooting genotypes should have a greater advantage over deep rooted genotypes when growth is limited by P that is available only in the top of the soil.

Both shoot length and RDW were affected significantly (P<0.001) by P treatment and genotype but no significant interaction between these two factors was found. R2 value for both factors was 62% in RDW and 86% in shoot length. As for RDW, it increased by 1.4 in homogenous P and 1.8 times in shallow P treatment compared to that in zero P treatment. Most importantly, as can be clearly seen in the bar chart (Figure 2), all genotypes in zero P had higher root/shoot ratio than homogenous P and in the latter there was more root/shoot ratio than in shallow P treatment. Two way ANOVA revealed a significant (P<0.001) interaction for root/shoot ratio with both P treatment and genotype had a significant (P<0.001) effect.

In zero P treatment, the subgroup effect was significant (P<0.001, F=9.21) on SDW and on average, aus subgroup had 1.2 and 1.4 fold more SDW than indicas and Japonicas respectively, which suggest that for the genotypes used in this study, aus subgroup are more tolerant to P deficiency than indicas and Japonicas(Table 2). On the other hand, the SDW of both indicas and Japonicas increased by 55% in shallow P treatment relative to homogenous P treatment while the increase of aus genotypes was only 50%. This indicates that genotypes belonged to aus subgroup had less shallow roots than either indicias or Japonicas and is in consistent with what is known about aus subgroup as deep rooted genotypes (15). It can be suggested that both Indicas and Japonicas had a greater ability to take up shallow P in soil than aus subgroup while the latter may had more P efficiency when grown in P deficient conditions. Figure 3 demonstrates plotted data of SDW in shallow P vs SDW in zero P treatment. By examining this plot, a general statement can be made that two main categories of genotypes can be considered according to their P treatment response. A first category of genotypes that falls below the line that are relatively tolerant for P deficiency especially those belong to aus subgroup (Black Gora, Rayada, Kasalath and FR13A) and the Aux1Wild type, which were notable by having a higher SDW in zero P treatment than predicted by their SDW in shallow P treatment. On the other hand, all genotypes occupied their position above the line are responsive to P in shallow layer (category two). The indica genotype Sadu Cho seems to be substantially superior to all genotypes in all treatments. In homogenous P treatment, RDW for genotypes belonging to both aus and indica was slightly above the average by 5.6% and 8.9% respectively.

Table 4 shows results from the analysis of variance for the data recorded from root scanning. The rock phosphate treatment and genotype had a significant (P<0.001) effect upon root surface area and volume but not on root length or root tips and there were no interactions for all traits measured. A significant (P<0.001 and P=0.005) effect for P treatment on specific root length [root length (m)/RDW (g)] and average diameter respectively were found. The specific root length decreased by 18.2% in shallow P while in zero P increased by 75.5% compared to that in homogenous P treatment. Likewise, the average diameter in shallow P increased by 17% while in zero P decreased by 7.3% compared to that in homogenous P treatment.

P concentration in eleven selected rice genotypes was measured. When the mean of SDW and plant P status were tested for correlation using the Pearson correlation coefficient, it was found that within each treatment there is very strong correlation between SDW and total P uptake. r=0.941, 0.951 and 0.875 in homogenous, shallow and zero P treatment respectively (Table 3). Table 5 demonstrates the output of analysis of variance for P status in eleven genotypes. There were massive genotype and treatment effects (P<0.001) on P concentration but no interaction was found. In general, [P] increased in shallow P by 1.5 times while it decreased by half in zero P compared to homogenous P treatment. Kasalath and to some extent black Gora has low [P] in the rock P treatments. [P] of Aux1Mutant1 and Aux1Mutant 2 is lower than Aux1wild type except in shallow P where trend is reversed, but unfortunately only the treatment effect is significant when just these three genotypes were used. For both total P in shoot and PUE [SDW (g)/total P in shoot (mg)], a significant (P<0.05) interaction was found with both P treatment and genotype affecting both traits in a highly significant (P<0.001) manner. On average, genotypes in shallow P treatment absorbed only 2.2 times more P than in homogenous P and 9.1 times more than the zero P treatment respectively. Azucena and IAC25 have high P per plant except in low P treatment. When SDW is plotted against PUE, there is a trend for the high mass plants to have high P efficiency and vice versa (Figure 4). The two genotypes Azucena and IAC25, which belong to Japonica subspecies, occupied their position as having higher SDW and higher P efficiency than the rest while Aux1 Mutant1, Aux1 Mutant2 and Nipponbare are the lowest in both SDW and P efficiency. The genotype Aux1Wild type had a low P efficiency but a high mass especially in homogenous P and zero P treatments. Using Pearson correlation coefficient the RDW was found to be correlated significantly (r=0.868, P=0.001 and r=0.883, P<0.001) with total P in shoot in both homogenous P and

shallow P treatments respectively while in zero P treatment do not. This can clearly be seen in Figure 5.

Both P treatment and genotype significantly affected root mass. RDW in shallow P and homogenous P was significantly more than that in zero P. These results are consistent with Drew (16) and Drew and Saker (17). The authors studied the relationship between growth and nutrient supply and found that if nutrients such as nitrate, ammonium and phosphate are differentially available to parts of the root system, the part with the greater supply grows more. The effect of P treatment on specific root length [root length (m)/RDW (g)] was significant where the specific root length in shallow P decreased by 18.2% while in zero P increased by 75.5% compared to that in homogenous P treatment. This means that P deficiency reduced root diameter of plant (the less P available in soil is, the finer the root will be). Indeed, P treatment was found to have a significant effect on average diameter of the root (Table 4). This finding is in consistent with results presented by Fitter (18) and Hill et al. (19) who showed that many species adjusting to low P conditions concurrently increase specific root length to achieve longer or more branched roots per unit of root mass. It is logical to predict that all the treatments used in this experiment would alter the partitioning between roots and shoots. Genotypes with shallow roots would be expected to benefit from P in shallow layers of the soil. Under edaphic stress, especially when facing P deficiency, roots must explore a large volume of soil. Under low P conditions, the plant therefore allocates more photosynthates towards the roots than to shoots (20; 5). The significant effect of genotype and P treatment on both SDW and RDW was reflected in an effect on root/shoot ratio, where all genotypes had significantly higher root/shoot ratio in zero P, then homogenous P and the lower root/shoot ratio was in shallow P treatment. This clearly demonstrates the effect of P stress on all genotypes in zero P that make the plant allocate more metabolites towards the roots in order to access limited soil P by exploring more soil volume. On the other hand, the closely embedded rock phosphate in the shallow P treatment allow the plants to take up more P and consequently allocate less carbon (metabolites) in the root than plants grown in both homogenous P and zero P treatments.

4. Conclusion

Evidence presented here indicates that rice genotypes interact strongly with P added in rock phosphate experiment for almost all growth parameters and P uptake indicating that they differ significantly in their ability for P uptake and growth under low P. This study gave evidence that shallow rooting genotypes have the opportunity to grow better than deep rooted genotypes when growth is limited by P that is available only in the top of the soil. From a practical perspective, genotypes like Black Gora, Rayada, Kasalath, Azucena, IAC25, Dom Sufid, Aux1Wildtype, FR13A and especially Sadu Cho are outstanding as they perform well in these screens including when soil P is very low. These genotypes can be used in breeding programs and should attract more research attention to find more about mechanisms behind their superiority for P uptake and PUE.

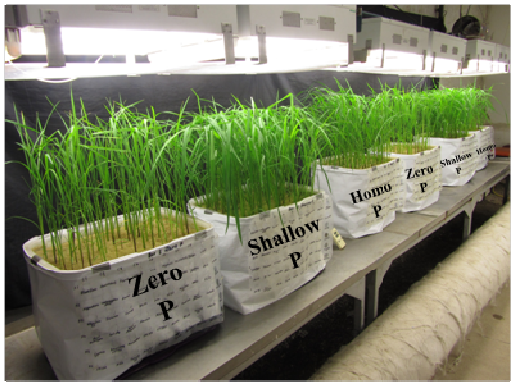


Figure 1. *Growing rice genotypes in plastic boxes in the growth room.*

Table 2. *Analysis of variance and average parameters of plant growth parameters for 29 rice genotypes grown in a 25/75% subsoil/sand mix either with (homogenous P or shallow P) or without rock phosphate (zero P) as a control. Mean = 6.*

		Shoot length day 35 (cm)			SDW (mg)		
Genotypes	Subgroup	Homo	Shallow	Zero	Homo	Shallow	Zero
FR 13A	*aus*	67.6	74.7	60.3	724	995	380
Rayada	*aus*	72.6	80	60.1	529	791	304
Kasalath	*aus*	63.1	70.9	56.5	439	758	301
Black Gora	*aus*	61.5	66.8	56	476	758	273
Dular	*aus*	63.9	72.2	54.4	466	735	241
N22	*aus*	64.4	72.8	51.3	386	508	229
aus mean		65.5	72.9	56.4	503	758	288
Sadu Cho	IND	65.7	71.5	55	954	1569	414
Aswina	IND	72.3	80.6	62	495	688	287
Bala	IND	63.6	72.1	49.9	469	792	246
Kinandang Patong	IND	59	65	49	517	651	233
IR 64	IND	50.6	59.2	46.2	505	760	212
Zhenshan 97	IND	51.9	57.3	45.4	267	595	211
Swarna	IND	51.5	57	42.6	386	443	194
Sanhuangzhan No 2	IND	47.3	50.3	41.2	311	565	193
indica mean		57.7	64.1	48.9	488	758	249
Azucena	TRJ	74.9	80.4	58.8	733	1034	328
IAC 25	TRJ	73.4	81.7	56	657	1127	327
IAC 165	TRJ	62.8	70.4	51.4	442	742	238

		Shoot length day 35 (cm)			SDW (mg)		
Cypress	TRJ	57	65.4	48.4	334	538	199
Moroberekan	TRJ	65.6	73.7	53.4	442	693	251
Lemont	TRJ	60.7	67.7	45.1	360	498	170
Labelle	TRJ	50.2	54.7	42.6	297	492	151
Li-Jiang-Xin-Tuan-Hei-Gu	TEJ	67.5	70.7	57.2	523	784	263
Nipponbare	TEJ	57.6	62.4	45.8	446	523	183
Tainung 67	TEJ	49.4	65.2	45.2	278	411	172
Akihikari	TEJ	53.1	59.5	38.9	152	380	138
Japonica mean	-	61.1	68.3	49.3	424	657	220
Aux1 Wild type	-	62.1	65.7	53.5	568	752	297
Aux1Mutant 1	-	56.1	65.1	45.9	351	616	177
Aux1Mutant 2	-	43.3	55.1	40.5	245	348	149
Dom Sufid	*aromatic**	67.9	78.4	56.5	655	925	312
Mean		60.6	67.8	50.7	463	705	245
#ANOVA		F	*P*		F	*P*	
T (2)		381.03	0.000		235.82	0.000	
G (28)		30.89	0.000		11.54	0.000	
TxG (56)		1.14	0.258		1.57	0.014	
R^2		86.06%			75.40%		

Table 2. *Continue.*

		Number of tillers day 35			RDW (mg)			Root/shoot ratio		
Genotypes	Subgroup	Homo	Shallow	Zero	Homo	Shallow	Zero	Homo	Shallow	Zero
FR 13A	*aus*	1	2	0	225	230	148	0.31	0.23	0.41
Rayada	*aus*	1.6	2.33	1.25	195	181	155	0.37	0.27	0.51
Kasalath	*aus*	0.83	1.83	1	118	151	44	0.30	0.25	0.32
Black Gora	*aus*	0.83	1.17	0	130	133	137	0.34	0.27	0.44
Dular	*aus*	0.5	1.83	0	189	219	120	0.37	0.27	0.51
N22	*aus*	1	1.5	0	144	214	119	0.51	0.37	0.61
aus mean		1.0	1.8	0.4	167	188	120	0.37	0.28	0.46
Sadu Cho	IND	2.83	4	1	279	410	196	0.28	0.23	0.51
Aswina	IND	1.25	1.67	0.5	172	238	167	0.38	0.31	0.53
Bala	IND	1.5	2.17	0.33	136	222	106	0.34	0.30	0.44
Kinandang Patong	IND	0.67	1.17	0	222	221	121	0.45	0.34	0.58
IR 64	IND	1.83	3.33	1	154	212	70	0.31	0.24	0.34
Zhenshan 97	IND	1	1.67	0	164	233	120	0.43	0.34	0.56
Swarna	IND	1.33	1.67	0	135	148	57	0.38	0.30	0.39
Sanhuangzhan No 2	IND	1.33	2.5	0.33	113	163	79	0.33	0.28	0.50
indica mean		1.5	2.3	0.4	172	231	115	0.37	0.29	0.52
Azucena	TRJ	0.67	1.83	0	229	344	128	0.36	0.27	0.37
IAC 25	TRJ	0.67	1.67	0	192	244	140	0.34	0.24	0.42
IAC 165	TRJ	0	1.17	0	187	239	130	0.40	0.36	0.57
Cypress	TRJ	1	1.33	0	168	141	110	0.42	0.28	0.48
Moroberekan	TRJ	0.33	1.17	0	191	217	128	0.44	0.26	0.49
Lemont	TRJ	0.2	1	0	142	216	110	0.44	0.33	0.66
Labelle	TRJ	0	0.33	0	129	211	80	0.37	0.32	0.52
Li-Jiang-Xin-Tuan-Hei-Gu	TEJ	2	2.6	0	133	375	135	0.33	0.23	0.53
Nipponbare	TEJ	1.5	2	0	117	87	47	0.26	0.19	0.27
Tainung 67	TEJ	0.8	1.17	0	106	123	56	0.33	0.31	0.35
Akihikari	TEJ	0.2	1.6	0	70	116	73	0.33	0.30	0.43
Japonica mean	-	0.67	1.44	0.00	151	210	103	0.37	0.28	0.46
Aux1 Wild type	-	2	2.17	0.5	143	198	166	0.29	0.29	0.54
Aux1Mutant 1	-	1.67	2	0	107	165	85	0.34	0.27	0.53
Aux1Mutant 2	-	0.5	1.33	0	83	121	119	0.42	0.30	0.83
Dom Sufid	*aromatic**	1.33	1.83	0	206	203	142	0.36	0.27	0.53
Mean		1.04	1.79	0.21	158	206	113	0.36	0.28	0.49
#ANOVA		F	*P*		F	*P*		F	*P*	
T (2)		207.50	0.000		58.42	0.000		41.24	0.000	
G (28)		7.79	0.000		6.55	0.000		7.41	0.000	
TxG (56)		1.45	0.035		1.10	0.345		2.20	0.000	
R^2		70.74%			62.10%			38.92%		

ANOVA output and R^2; T, rock phosphate treatment; G, genotype (29); degrees of freedom between brackets. The factors and interactions in bold are significant.

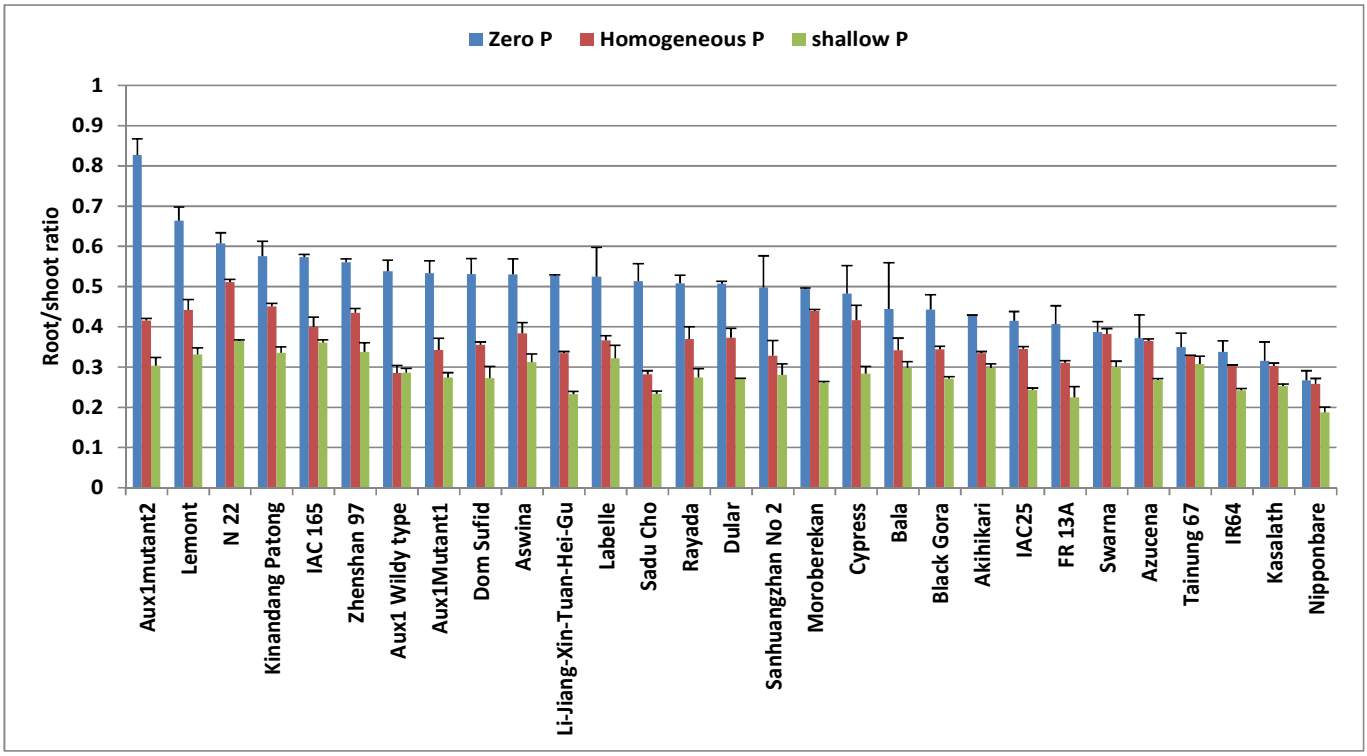


Figure 2. *Root/shoot ratio of rice genotypes grown in a 25/75% subsoil/sand mix either with (homogenous P and shallow P, red and green respectively) or without rock phosphate (zero P, blue). n = 6, Bar = s.e.*

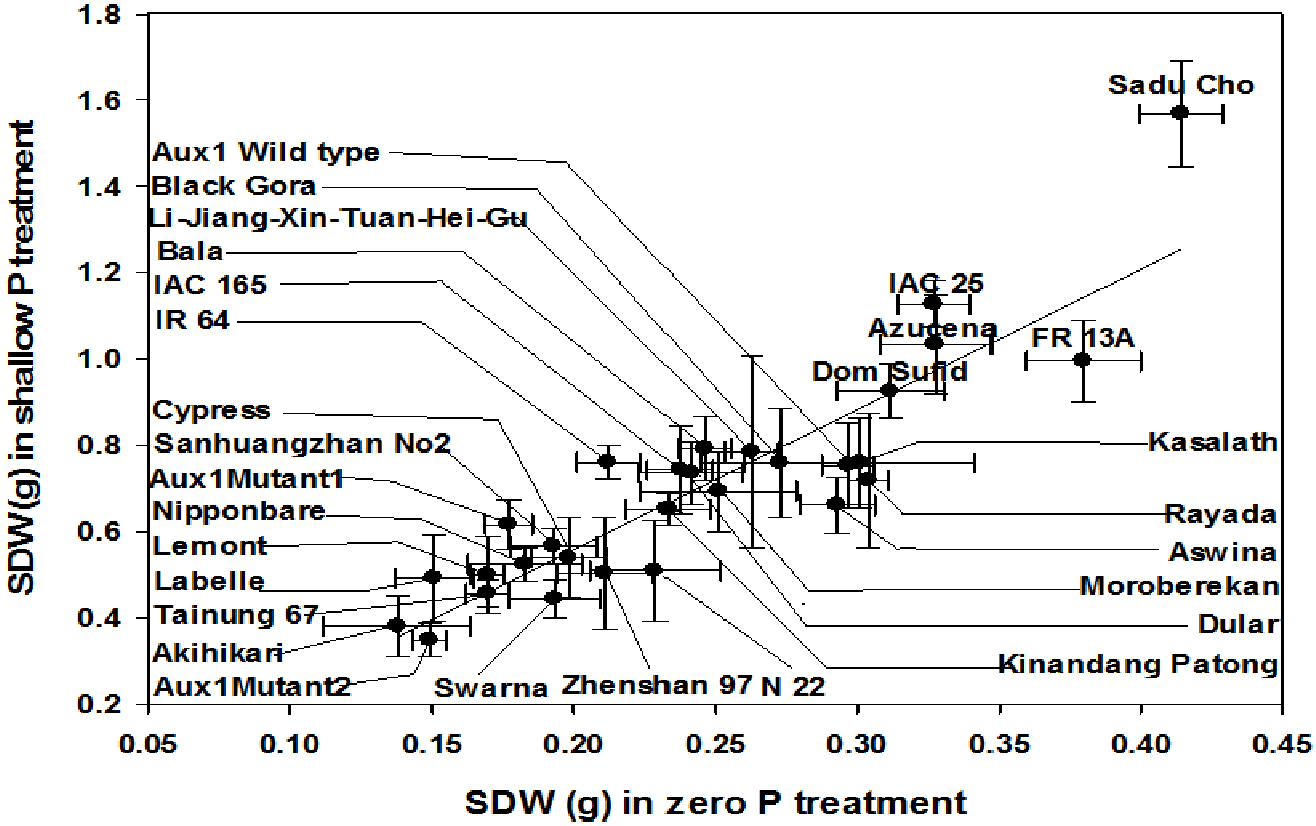


Figure 3. *Scatter plot for SDW in zero P versus shallow P treatment. Bars are standard errors.*

Table 3. *Correlation coefficients between SDW, total P, P concentration in shoot and P use efficiency within each treatment of rock P experiment. n=11.*

		SDW			P use efficiency			P conc. in shoot		
		Homo	Shallow	Zero	Homo	Shallow	Zero	Homo	Shallow	Zero
Total P in shoot	Homo	0.941***	0.785**	0.678*	-0.329 ns	0.297 ns	0.049 ns	-0.136 ns	0.049 ns	-0.136 ns
	Shallow	0.923***	0.951***	0.779**	-0.023 ns	-0.086 ns	-0.275 ns	-0.542 ns	-0.275 ns	-0.542 ns
	Zero	0.693*	0.662*	0.875***	0.257 ns	-0.205 ns	-0.441 ns	-0.032 ns	-0.441 ns	-0.032 ns
P concentration in shoot	Homo	-0.041 ns	-0.244 ns	-0.389 ns	-0.994 ***	-0.864***	-0.569 ns			
	Shallow	-0.389 ns	-0.549 ns	-0.698*	-0.907***	-0.991***	-0.500 ns			
	Zero	-0.451 ns	-0.584 ns	-0.504 ns	-0.620*	-0.544 ns	-0.993***			
P use efficiency	Homo	0.003 ns	0.195 ns	0.383 ns						
	Shallow	0.288 ns	0.458 ns	0.640*						
	Zero	0.501 ns	0.630*	0.553 ns						

*, **, *** Significant at P=0.05, P=0.01, and P=0.001, respectively; ns, not significant.

Table 4. *ANOVA output and average of root parameters of eight selected rice genotypes grown in a 25/75% subsoil/sand mix either with (homogenous P or shallow P) or without rock phosphate (zero P) as a control. Mean = 6.*

	Root length (m)			Specific root length (m g^{-1})			Root surface area (cm^2)		
Genotype	Homo	Shallow	Zero	Homo	Shallow	Zero	Homo	Shallow	Zero
Azucena	38.6	38.4	21.1	169	111	172	499	590	333
Bala	25.2	25.7	19.1	185	116	189	310	429	281
Black Gora	19.8	19.2	37.8	152	149	276	261	285	317
Dular	26.8	24.9	30.9	142	117	243	341	368	259
IAC 25	27.3	27.7	29.5	142	114	219	350	433	256
IR 64	28.1	26.9	18.6	182	127	269	345	409	253
Kasalath	16.6	23.1	12.2	141	156	304	225	316	168
Nipponbare	18.2	12.9	26.6	156	152	560	224	181	181
Mean	25.1	24.8	24.5	159	130	279	319	376	256
ANOVA#	F	*P*		F	*P*		F	*P*	
T (2)	0.02	0.980		13.78	0.000		17.81	0.000	
G (7)	1.99	0.099		1.63	0.175		12.77	0.000	
T x G (14)	1.32	0.268		1.34	0.258		1.60	0.150	
R^2	16.67%			42.46%			72.59%		

Table 4. *Continue.*

	Root volume (cm^3)			Average diameter (mm)			Root tips (divided by 1000)		
Genotype	Homo	Shallow	Zero	Homo	Shallow	Zero	Homo	Shallow	Zero
Azucena	5.1	7.2	4.2	0.41	0.49	0.49	14.2	14.2	9.1
Bala	3.0	5.7	3.3	0.39	0.53	0.47	14.4	13.6	11.1
Black Gora	2.7	3.4	2.7	0.42	0.47	0.33	11.5	10.6	34.6
Dular	3.4	4.4	1.9	0.40	0.47	0.31	10.7	10.8	25.3
IAC 25	3.6	5.4	2.0	0.41	0.50	0.32	10.4	11.2	27.5
IR 64	3.4	5.0	2.7	0.39	0.48	0.43	11.1	10.3	7.7
Kasalath	2.4	3.4	1.9	0.43	0.43	0.44	7.3	11.4	5.3
Nipponbare	2.2	2.0	1.3	0.39	0.44	0.27	10.3	7.2	22.4
Mean	3.2	4.6	2.5	0.41	0.48	0.38	11.2	11.2	17.8
ANOVA#	F	*P*		F	*P*		F	*P*	
T (2)	22.23	0.000		6.81	0.005		2.01	0.156	
G (7)	9.12	0.000		1.17	0.355		0.64	0.716	
T x G (14)	0.93	0.543		0.83	0.635		0.78	0.683	
R^2	67.66%			18.13%			0.00%		

ANOVA output and R^2; T, rock phosphate treatment; G, genotype; degrees of freedom between brackets. *P* value in bold is significant.

Table 5. *ANOVA output and average of P element status in shoot of eleven rice genotypes grown in a 25/75% subsoil/sand mix either with (homogenous P or shallow P) or without rock phosphate (zero P) as a control. Mean = 6.*

	Shoot P concentration (µg g^{-1})			Total P in shoot (µg)			P use efficiency (PUE)		
Genotype	Homo	Shallow	Zero	Homo	Shallow	Zero	Homo	Shallow	Zero
Aux1 wild type	1968	2612	1039	1116	2024	309	0.51	0.39	0.98
Aux1Mutant1	1860	2745	996	651	1693	175	0.54	0.37	1.03
Aux1Mutant2	1834	2928	903	454	1031	121	0.55	0.34	1.14
Azucena	1761	2584	733	1294	2689	231	0.57	0.39	1.39
Bala	1750	2548	795	830	2027	194	0.57	0.40	1.28
Black Gora	1449	2227	773	695	1623	214	0.71	0.46	1.30
Dular	1867	2808	861	870	2062	208	0.54	0.36	1.17
IAC 25	1702	2421	764	1116	2733	248	0.59	0.42	1.34

	Shoot P concentration (µg g^{-1})			Total P in shoot (µg)			P use efficiency (PUE)		
IR 64	1719	2508	889	877	1899	189	0.59	0.40	1.15
Kasalath	1352	2171	801	600	1671	248	0.75	0.47	1.28
Nipponbare	1862	2787	909	804	1464	164	0.54	0.36	1.11
Mean	1739	2576	860	846	1902	209	0.59	0.40	1.20
ANOVA#	F		P	F		P	F		P
T (2)	874.17		0.000	337.43		0.000	869.00		0.000
G (10)	8.16		0.000	8.07		0.000	6.92		0.000
T x G (20)	1.39		0.133	2.48		0.001	1.95		0.012
R2	90.30%			79.85%			90.19%		

Element content in shoot = element concentration in shoot (mg g^{-1}) x SDW (g).
PUE = SDW (g)/P in shoot (mg).
P value in bold is significant.

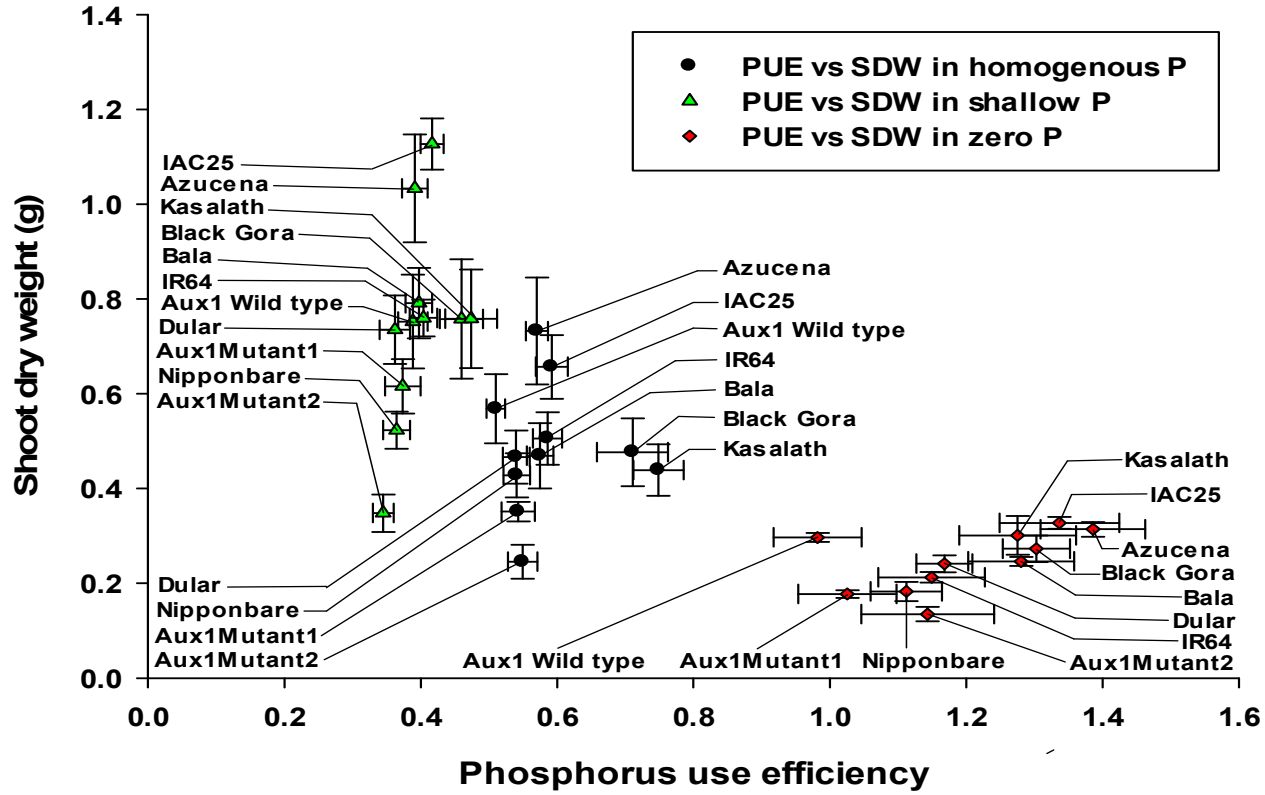
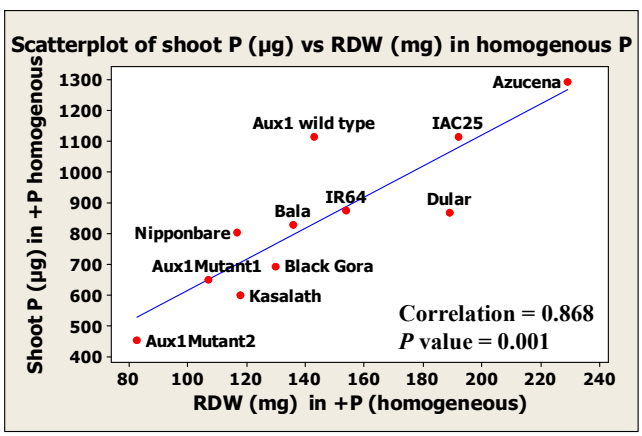
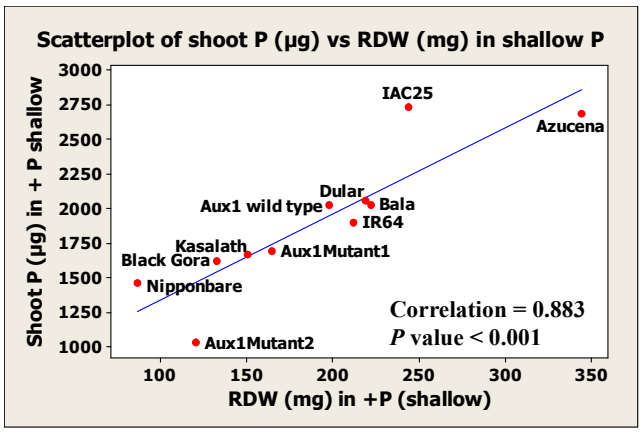


Figure 4. *Scatter plot for SDW versus P use efficiency [shoot dry weight (g)/P in shoot (mg)] in homogenous P, shallow P and zero P treatment. Bars are standard errors.*





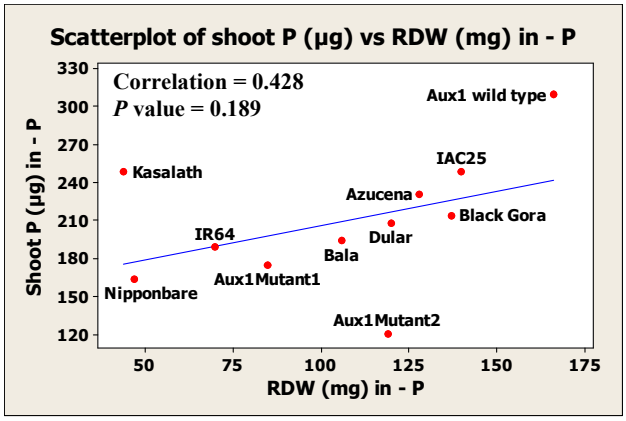


Figure 5. *Scatter plot of total P in shoot of eleven genotypes plotted against RDW in each of three treatments (homogenous P, shallow P and zero P) of rock phosphate experiment. The Pearson correlation coefficient and P-value for each graph are shown.*

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