

Full Length Article

Differential Performance of Lowland Rice Cultivars for Phosphorus Uptake and Utilization Efficiency under Hydroponic and Soil Conditions

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Abstract

Exploiting the genetic variations in crop plants for enhanced P efficiency seems inevitable for sustaining crop productivity on sub-optimal P supplying agro-ecosystems. However, variation in growth medium used for screening germplasm is a major constraint for poor understanding of the P efficiency mechanisms. In present studies, lowland rice cultivars were evaluated for P utilization efficiency (PUtE) based on shoot dry matter (SDM) and paddy yield under hydroponic and soil conditions. Results revealed that P deficiency significantly reduced SDM, paddy yield and P uptake under both growing environments. Root depth, root-shoot ratio and root dry matter (RDM) was enhanced in all cultivars but at varying rates in response to P deficiency. Rice cultivar Basmati-2000 produced maximum SDM and paddy yield under adequate and deficient P levels. Root DM correlated significantly with SDM (r = 0.72) and shoot P uptake (r = 68) indicating implications of improved root growth for P acquisition under P deficiency. Rice cultivars exhibited wide diversity for PUtE based on SDM and paddy yield. The highest response to P addition was obvious in cultivar KSK-282 under hydroponic and in IR-6 under soil conditions as indicated by their higher stress factors (*i.e.*, 48 and 49%). The results suggested that large variations exist among rice cultivars for biomass production and PUtE under hydroponic and soil conditions signified that special consideration must be paid to growing medium while screening rice for P efficiency. © 2019 Friends Science Publishers

Keywords: Oryza sativa L.; Paddy yield; Root-shoot ratio; Stress factor; Utilization efficiency

Introduction

Phosphorus is a vital constituent for normal plant growth and development and is among the major drivers for global crop productivity (Stewart et al., 2005). It is a typical early-period nutrient whose adequate level in rooting medium must be maintained during early crop growth stage for optimal yields. Its deficiency is reported to limit crop yields on more than 30% of cultivated soils worldwide (Vance et al., 2003). The sustainability of cropping environments demands the maintenance of adequate P level in soil solution through the addition of organic and/or inorganic P sources (Irfan et al., 2016, 2018). The efficiency of added and/or native soil P is seriously low on calcareous soils because only a small portion (10-30%) of applied P is utilized by plants in first growing season (Bertrand et al., 2003). Moreover, the average global P use efficiency for cereal crops is very low and is estimated upto 16% only from 1961 to 2013 (Dhillon *et al.*, 2017). By some estimates, phosphate rock reserves may be depleted by 2050, thus forcing the need for enhanced efficiency of P sources (Vance *et al.*, 2003).

The deficiency of P is a serious concern in alkaline calcareous soils of Mediterranean basin as well as highly weathered soils of tropics and subtropics (Korkmaz *et al.*, 2009). It may precipitate or adsorbed on iron and aluminum oxides in acidic soils or forms secondary minerals of calcium and magnesium, and bound to surfaces of CaCO₃ and clay minerals in alkaline calcareous soils thereby reducing its bio-availability (Yan *et al.*, 2006; Akhtar *et al.*, 2008). The P deficiency is also a serious threat to sustainable productivity in Pakistan where more than 90% arable lands have moderate to severe P deficiency (FAO, 2017). High calcium carbonate contents, high pH and low organic matter coupled with low rainfall are the principal factors for low P availability in Pakistani soils. Although various soils worldwide encompass higher total P reserves,

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but the plant available fraction is often 100-times less than the total P contents (Hinsinger *et al.*, 2011). Therefore, a key challenge to improve P efficiency on arable environments is to raise the bio-availability of native P reserves in soils. Considering the intractable soil nature, much attention has been given on the methods and rates of P application as well as other best management practices to enhance efficiency of P applied. Now the question is how plants can play role in mobilizing the fixed or unavailable soil P fraction in order to satisfy their demands for economically acceptable growth.

A number of morphological, physiological and molecular adaptations have been evolved in plants under P deficiency stress. Considerable variations exist in crop species and even genotypes within same specie for their abilities to sustain plant growth on soils with low P contents (Aziz et al., 2011; Irfan et al., 2017; Abbas et al., 2018a). Several earlier studies illustrated that higher P efficiency may be achieved through altered root system architecture (He et al., 2003), rhizosphere acidification through enhanced carboxylate exudation to mobilize/liberate P from insoluble sources (Dong et al., 2004), symbiotic association with mycorrhizal fungi and application of P solubilizing bacteria (Sial et al., 2017), induction of high affinity phosphate transporters (Yi et al., 2005), reduced tissue P requirement for efficient use (Hammond et al., 2004) and better P remobilization from older and/or non-productive organs to young growing and/or productive organs (Akhtar et al., 2008; Abbas et al., 2018b).

Phosphorus efficient cultivars may play an important role in enhancing crop productivity in 21st century, primarily because of restricted soil resources for cultivating crops, costly inorganic P fertilizers and increasing environmental concerns globally (Fageria et al., 2008; Nourgholipour et al., 2017). In low-input cropping systems, adaptation of P efficient crop plants is crucial for sustaining productivity and utilizing P sources efficiently (Ozturk et al., 2005). Identification of P efficient cultivars from existing germplasm to manage low P soil environments is among the viable approaches and the most realistic solution as genetic variations for P efficiency among cultivars of various crops is well documented in the literature (Gunes et al., 2006; Korkmaz et al., 2009; Aziz et al., 2011; Akhtar et al., 2016; Irfan et al., 2017; Nourgholipour et al., 2017; Abbas et al., 2018a). Mechanisms responsible for P efficiency can differ from specie to specie and even among plants within same specie (Ozturk et al., 2005). Variation in environment used for screening crop germplasm is among the main reasons for poor understanding of P efficiency mechanisms. The information regarding the effect of growth medium i.e., solution culture or soil on P efficiency among genotypes is exceptionally diminutive. According to Hayes et al. (2004), screening of wheat cultivars for P efficiency in solution culture is less reliable, because cultivars behave differentially under soil conditions. Therefore, present studies were conducted to evaluate rice cultivars for biomass and paddy production, P uptake and utilization efficiency under hydroponic and soil conditions.

Materials and Methods

Plant Material

Seeds of four rice cultivars (Basmati-2000, KSK-282, KSK-434 and IR-6) used in the hydroponic and pot studies were obtained from Rice Research Institute, Kala Shah Kaku – Pakistan. Both studies were carried out under natural conditions of a rain-protected wire house at Institute of Soil and Environmental Sciences, University of Agriculture, Faisalabad – Pakistan (latitude 31° 02 – 31° 45 North; longitude 72° 50–73° 22 East).

Hydroponic Study

For rice nursery, seeds were surface sterilized with sodium hypochlorite solution (3%) followed by thorough washing with distilled water. Seeds were sown in polythene lined metal trays with two inches layer of pre-washed river bed sand. Two weeks old uniform seedlings were shifted to plastic tubs having 25 liters of modified Johnson's nutrient solution. Prior to seedling transplanting, root systems of the plants were carefully rinsed with distilled water to remove adhering sand. The composition of full-strength nutrient solution (pH 5.5) was 5.0 mM N, 3.5 mM K, 1.5 mM Ca, 0.5 mM Mg, 2.15 mM S, 50 µM Cl, 0.5 µM Mo, 25.0 µM B, 0.5 μ M Cu, 2.0 μ M Mn, 2.0 μ M Zn and 50.0 μ M Fe as Fe-EDTA. The seedlings were supported by foam plugs in the holes of thermopole sheet fixed at the top of plastic tubs. The seedlings of rice cultivars were arranged following two factor completely randomized design with six replications. Rice plants were allowed to grow at two P levels *i.e.*, deficient P (20 μ M Pi) and adequate P (200 μ M Pi). The P levels were maintained using potassium dihydrogen phosphate (KH₂PO₄) as P source. The pH of the solution was maintained at 5.5 \pm 0.2 and after every five days nutrition solution was renewed with fresh solution in order to ensure continuous supply of nutrients. Plants were harvested on 45 days after transplanting, washed with distilled water and subsequently roots were separated from shoots. After air drying, plant material was oven dried at 70°C for 48 h and stored under desiccation until recording of dry weights.

Pot Study

Bulk soil (15 cm surface layer) was collected from research area of Institute of Soil and Environmental Sciences, University of Agriculture, Faisalabad – Pakistan. A composite sample of collected soil was air dried and grinded to pass 2 mm sieve. After sieving, a uniform portion of soil was analyzed for basic physico-chemical characteristics. Briefly, the soil of the experimental site was clay loam in texture characterized by alkaline in reaction, high in available potassium while low in organic matter, nitrogen and available phosphorus (Table 1). Plastic pots inner lined with polythene sheet were filled with seven kg of

Soil characteristics	Unit	Value	Reference/Method
pH _s	-	7.76	U.S. Salinity Laboratory Staff (1954)
ECe	dS m ⁻¹	2.12	~
Organic Matter	%	0.71	Nelson and Sommers (1982)
Kjeldahl Nitrogen	%	0.04	Jackson (1962)
Available Phosphorus	mg kg ⁻¹	5.30	U.S. Salinity Laboratory Staff (1954)
Available Potassium	mg kg ⁻¹	160	~
Saturation Percentage	%	24.30	~
Sand	%	29.35	Bouyoucos (1962)
Silt	%	31.20	~
Clay	%	39.45	~
Textural Class	-	Clay loam	~

 Table 1: Selected physico-chemical characteristics of soil used in pot experiment

 $pH_{s}\!=\!pH$ of saturated paste; EC_{e} = electrical conductivity of saturated paste extract

thoroughly mixed soil. The experiment was planned following two factor completely randomized design with three repeats. The plants were grown at two P levels i.e., deficient P (without external P addition or only native soil P *i.e.*, 5.30 mg kg⁻¹) and adequate P (P addition at 50 mg kg⁻¹) soil) (Doberman and Fairhurst, 2000). Each pot was also supplied with 30 mg K_2O kg⁻¹ soil along with 70 mg N kg⁻¹ soil. Required quantity of P according to treatments and K was added at the time of pot filling. However, N was applied in three equivalent splits. After filling the pots with soil, canal water was applied from the top of the pots till soil saturation. The pots were kept for two days to allow the soil to settle. Seeds of rice cultivars (same as studied in hydroponic experiment) were sown in nursery trays having similar soil. On the emergence of 3^{rd} leaf, three uniform and healthy seedlings of each cultivar were transplanted to each pot. A water layer (1-2 cm) on soil surface was maintained during the entire crop period. At maturity plants were harvested, threshed manually to separate paddy from straw. After recording yield and related attributes, plant material was oven dried at 70°C till further analysis.

Phosphorus Assay and Estimation of P-efficiency Characteristics

Oven dried plant material from both studies (root, shoot, paddy, straw) was grinded to pass through a 0.42 mm screen using Wiley's mill (IKA Werke, Wilmington, USA) fitted with stainless steel blades. Samples (0.3 g each) were wet digested using 10 mL of di-acid mixture [nitric acid and perchloric acid (5:1, v/v)]. The total P concentration in digested samples was determined following yellow color method as described by Chapman and Pratt (1961) by reading light absorption at 470 nm wavelength using spectrophotometer (Shimadzu UV-VIS 1201, Shimadzu Co. Kyoto, Japan).

Phosphorus efficiency and related parameters were estimated to find relationship between P supply and growth performance of rice cultivars such as P uptake (Zhang *et al.*, 2007), P stress factor (Hunt, 1978), root efficiency ratio (Jones *et al.*, 1989) and P utilization efficiency (Hammond *et al.*, 2009).

• Phosphorus uptake (PU)

 $PU(mg plant^{-1}) = P \text{ concentration } (mg g^{-1})$ × Root or shoot dry matter(g plant^{-1}) $PU (mg pot^{-1}) = P \text{ concentration } (mg g^{-1})$

× Paddy or straw yield (g pot⁻¹)

• Phosphorus stress factor (PSF)

$$PSF(\%) = \frac{Dry matter_{adequate P} - Dry matter_{deficient P}}{Dry matter_{adequate P}} \times 100$$

• Root efficiency ratio (RER)

RER (mg P in shoot g^{-1} RDM) = $\frac{\text{Shoot P uptake (mg plant}^{-1})}{\text{RDM (g plant}^{-1})}$

"Where RDM is root dry matter"

• Phosphorus utilization efficiency (PUtE)

PUtE (g SDM g⁻¹ P) =
$$\frac{\text{SDM}_{\text{adequate P}} - \text{SDM}_{\text{deficient P}}}{\text{SPU}_{\text{adequate P}} - \text{SPU}_{\text{deficient P}}} \times 1000$$

PUtE (g PY g⁻¹ P) = $\frac{\text{PY}_{\text{adequate P}} - \text{PY}_{\text{deficient P}}}{\text{PPU}_{\text{adequate P}} - \text{PPU}_{\text{deficient P}}} \times 1000$

"Where SDM is shoot dry matter (g plant⁻¹), SPU is shoot P uptake (mg plant⁻¹), PY is paddy yield (g pot⁻¹) and PPU is paddy P uptake (mg pot⁻¹)".

Statistical Analysis

The collected data regarding plant growth, biomass production, P uptake and efficiency related characteristics of rice cultivars under adequate and deficient P supply was statistically analyzed employing computer software STATISTIX 8.1 (Analytical Software, Inc., Tallahassee, FL, USA) following the methods of Steel *et al.* (1997). A two factor completely randomized design was used for analysis of variance. Graphical presentation of data and correlation coefficients among various parameters was carried out using Microsoft Excel (Redmond, WA, USA). Significant differences among treatment means were separated using least significant difference test at $P \leq 0.05$ and presented with standard errors.

Results

Hydroponic Study

The tested lowland rice cultivars varied significantly ($P \le 0.05$) for root depth, root dry matter (RDM), shoot dry matter (SDM) and root-shoot ratio (RSR) under adequate and deficient P supply in solution culture (Table 2 and Fig. 1). The average root depth and RDM was recorded relatively higher in all cultivars under P deficiency than with adequate P nutrition. Root depth ranged from 33.2 cm (KSK-434) to 36.0 cm (IR-6)

under P deficiency. Averaged over all cultivars, RDM was enhanced from 3.04 g plant⁻¹ at adequate P to 3.52 g plant⁻¹ under P deficient supply. Rice cultivar Basmati-2000 produced higher RDM (5.58 *vs.* 4.36 g plant⁻¹) under P deficiency and adequate P supply, respectively. Shoot DM varied from 5.25 to 9.08 g plant⁻¹, with mean value of 6.52 g plant⁻¹ in response to P deficiency and 8.46 to 13.84 g plant⁻¹ , with mean value of 10.54 g plant⁻¹ at sufficient P level. Cultivars also differed considerably for RSR in both P treatments. The RSR was enhanced in P deficient plants compared with those having adequate P supply and ranged from 0.45 in IR-6 to 0.63 in Basmati-2000.

Phosphorus levels and rice cultivars had also significant ($P \le 0.05$) main and interactive effects for root and shoot P uptake when grown in solution culture (Table 2 and Fig. 2). Low P resulted in invariable decline in P uptake by the tested cultivars. However, the extent of reduction was comparatively lower in roots than aboveground plant parts. Averaged over cultivars, root and shoot P uptake was about 2 and 3 fold lower under P deficiency, respectively than plants having adequate P supply. Root P uptake in plants under P deficiency varied from 3.79 mg plant⁻¹ in IR-6 to 5.78 mg plant⁻¹ in Basmati-2000. Shoot P uptake ranged from 36.46 to 51.67 mg plant⁻¹, with mean value of 45.67mg plant⁻¹ at adequate P supply and 14.08 to 21.59 mg plant⁻¹ ¹, with average of 16.93 mg plant⁻¹ under P deficiency. The root efficiency ratio (RER) of tested rice cultivars was considerably influenced by P treatments and increased almost 3 fold under adequate P than with P deficiency (Table 2). The RER ranged from 3.91 to 6.45 and 12.47 to 21.37 mg P g⁻¹ RDM under deficient and adequate P, respectively. Rice cultivars also differed significantly for P utilization efficiency (PUtE) in solution culture. The maximum value of PUtE (172.2 g SDM g⁻¹ P) was noted in Basmati-2000 while minimum (128.8 g SDM g^{-1} P) was observed in KSK-282, with average value of 144.7 g SDM g^{-1} P among the tested cultivars (Fig. 4).

Pot Study

Rice cultivars and P levels had significant effects on panicle length, paddy yield and straw yield when grown in soil conditions (Table 3 and Fig. 3). Maximum panicle length under P deficiency was observed in Basmati-2000 (12.0 cm) while minimum was observed in IR-6 (10.0 cm). At adequate P, Basmati-2000 also produced higher panicle length of 15.7 cm and KSK-282 produced minimum panicle length (13.3 cm). Phosphorus deficiency stress in soil exhibited variable effects on paddy and straw yield. Averaged over all cultivars, paddy yield was reduced almost 1.6 fold in response to P deficiency compared to plants with adequate P nutrition (12.1 vs. 19.4 g pot⁻¹). The highest paddy yield was recorded in cultivar Basmati-2000 (17.2 vs. 23.3 g pot⁻¹) under deficient and adequate P supply, respectively. Cultivar IR-6 produced minimum paddy yield (9.0 g pot⁻¹) with P deficiency while KSK-434 showed minimum paddy yield (16.0 g pot⁻¹) with adequate P supply. Basmti-2000 produced highest straw yield (33.6 vs. 40.0 g pot⁻¹) while KSK-282 produced minimum straw yield (24.4 vs. 31.5 g pot⁻¹) with and without P deficiency.

Paddy, straw and total (paddy + straw) P uptake by rice cultivars grown under deficient and adequate P nutrition is depicted in Fig. 3. Significant effects of cultivars, P levels and $C \times P$ interactions were observed on P uptake by paddy and straw (Table 3). As expected, average P uptake by both straw and paddy was about two-fold higher in plants when P supply was increased from deficient to adequate levels.

Table 2: Analysis of variance for the combine effect of phosphorus levels and rice cultivars on various parameters of rice plants grown under hydroponic conditions

Source of variation	DF	RD	RDM	SDM	RSR	RPU	SPU	TPU	RER	
Phosphorus levels (P)	1	96.3**	2.79*	194.1**	0.78**	343.1**	9913.3**	13945.5**	1630.5**	
Cultivars (C)	3	16.3 ns	15.94**	46.9**	0.04*	31.4**	229.7**	368.0**	93.9**	
$P \times C$	3	5.6 ns	0.84 ns	3.1 ns	0.02 ns	8.1 ns	138.3*	133.2*	56.8*	
Error	40	7.0	0.49	2.4	0.01	3.8	43.8	44.5	17.5	
Total	47									

DF = degree of freedom; RD = root depth; RDM = root dry matter; SDM = shoot dry matter; RSR = root-shoot ratio; RPU = root P uptake; SPU = shoot P uptake; TPU = total (root + shoot) P uptake; RER = root efficiency ratio

** = significant at $P \le 0.01$; * = significant at $P \le 0.05$; ns = non-significant at $P \ge 0.05$

Table 3: Analysis of variance for the combine effect of phosphorus levels and rice cultivars on various parameters of rice plants grown under soil conditions

Source of variation	DF	PL	PY	STY	PPU	STPU	TPU	
Phosphorus levels (P)	1	88.55**	318.28**	225.71**	13691.4**	11668.4**	50639.7**	
Cultivars (C)	3	4.10 ns	66.77**	90.72**	718.7**	161.0**	1549.9**	
$P \times C$	3	1.59 ns	3.97 ns	1.96 ns	179.6**	64.1**	36.0 ns	
Error	16	1.72	1.80	3.33	8.8	9.0	18.4	
Total	23							

DF = degree of freedom; PL = panicle length; PY = paddy yield; STY = straw yield; PPU = paddy P uptake; STPU = straw P uptake; TPU = total (paddy + straw) P uptake

** = significant at $P \le 0.01$; ns = non-significant at $P \ge 0.05$



Fig. 1: (a) Root depth, (b) root dry matter, (c) shoot dry matter and (d) root-shoot ratio of rice cultivars grown hydroponically under adequate (*dark bars*) and deficient (*grey bars*) P levels. Values are means of six replicates. Bars not sharing same letter(s) are significantly different from each other at $P \le 0.05$.



Fig. 2: (a) Root P uptake, (b) shoot P uptake, (c) total P uptake and (d) root efficiency ratio of rice cultivars grown hydroponically under adequate (*dark bars*) and deficient (*grey bars*) P levels. Values are means of six replicates. Bars not sharing identical letter(s) are significantly different from each other at $P \le 0.05$.

Maximum P uptake in paddy was estimated in Basmati-2000 under both adequate (105.68 mg pot⁻¹) and deficient P (70.15 mg pot⁻¹) levels. The values of straw P uptake ranged from 33.13 to 38.03 mg pot⁻¹, with a mean value of 35.21 mg pot⁻¹ at deficient P level, while 71.42 to 90.83 mg pot⁻¹, with average value of 79.31 mg pot⁻¹ at adequate P level among the tested cultivars. Similarly, total P uptake varied from 69.08 – 108.17 mg pot⁻¹ and 163.67 – 196.51 mg pot⁻¹ when P level was changed from low P to high P in soil. Cultivars performed differentially for P utilization



Fig. 3: (a) Panicle length, (b) paddy yield, (c) straw yield, (d) paddy P uptake, (e) straw P uptake and (f) total P uptake of rice cultivars grown in soil under adequate (*dark bars*) and deficient (*grey bars*) P levels. Values are means of three replicates. Bars not sharing identical letter(s) are significantly different from each other at two P levels (LSD test, $P \le 0.05$)

efficiency (PUtE) regarding paddy production at two P supplies in soil (Fig. 4). Maximum PUtE was calculated in KSK-282 (193.3 g PY g^{-1} P) followed by Basmati-2000 (173.6 g PY g^{-1} P), IR-6 (140.8 g PY g^{-1} P) and KSK-434 (115.2 g PY g^{-1} P).

Phosphorus Stress Factor (PSF)

The data regarding PSF for SDM and paddy yield is depicted in Fig. 5. The tested rice cultivars differed substantially for PSF for SDM in solution culture with average value of 38.4 percent. Maximum value of PSF was noted in KSK-282 (47.7%) while minimum was observed in KSK-434 (31.1%), with mean value of 38.4%. Rice cultivars also performed differentially with respect to PSF for paddy yield in soil conditions and it ranged between 26.2% in Basmati-2000 to 49.0% in IR-6, with average value of 38.1%.

Discussion

The results of present studies showed that wide variations exist in lowland rice cultivars in relation to the efficiency with which they acquire P from deficient medium, as well as their response to P application. The genetic differences for P efficiency characteristics in rice

Table 4: Correlations (r) for various parameters of rice cultivars with shoot dry matter (hydroponic study) and paddy yield (pot study) at adequate and deficient P levels

	Parameter	Adequate P	Deficient P
Shoot dry matter (g plant ⁻¹)	Root depth (cm)	0.10 ns	0.22 ns
	Root dry matter (g plant ⁻¹)	0.47 *	0.72 **
	Root: shoot ratio	-0.26 ns	-0.20 ns
	Root P uptake (mg plant ⁻¹)	0.34 ns	0.44 *
	Shoot P uptake (mg plant ¹)	0.78 ***	0.92 ***
	Root efficiency ratio (mg	0.04 ns	-0.05 ns
	P in shoot g ⁻¹ RDM)		
Paddy yield (g pot ⁻¹)	Panicle length (cm)	0.11 ns	0.52 *
	Straw yield (g pot ⁻¹)	0.62 *	0.57 *
	Biological yield (g pot ⁻¹)	0.87 ***	0.88 ***
	Paddy P uptake (mg pot ⁻¹)	0.78 **	0.97 ***
	Straw P uptake (mg pot ⁻¹)	0.76 **	0.47 ns
	Total P uptake (mg pot ⁻¹)	0.83 ***	0.94 ***

*** = significant at $P \le 0.001$; ** = significant at $P \le 0.01$; * = significant at $P \le 0.05$; ns = non-significant at $P \ge 0.05$



Fig. 4: Phosphorus utilization efficiency (PUtE) based on shoot dry matter (hydroponic study) and paddy yield (pot study) of rice cultivars calculated at two P supplies. Values are means of six (shoot dry matter) and three (paddy yield) replicates. Bars not sharing identical letter(s) are significantly different from each other (LSD test, $P \le 0.05$)

crop have also been reported in earlier investigations (Aziz et al., 2005; Fageria, 2014; Vandamme et al., 2015). Phosphorus uptake in shoot and paddy of tested cultivars was higher under adequate P compared with low P which associated with enhanced SDM or paddy yield. According to Baligar et al. (1998), more P uptake in plants growing at high P compared with those at low P supply is due to greater root fine hairs density resulting in better ability for P uptake. It was also obvious from the results that high yielding cultivar Basmati-2000 had maximum P uptake in paddy and low yielding cultivar IR-6 had lowest paddy P uptake under P deficiency. This fact was further supported by the positive and significant ($P \le 0.01$) correlation between paddy yield and P uptake at low (r = 0.97) and high P (r =0.78) (Table 4). Fageria (2014) also reported the significant increase in P uptake in shoot and grains of rice genotypes at high P level.



Fig. 5: Phosphorus stress factor (percent reduction in biomass due to P deficiency) for shoot dry matter (hydroponic study) and paddy yield (pot study) of rice cultivars grown under adequate and deficient P levels. Values are means of six (shoot dry matter) and three (paddy yield) replicates. Bars not sharing identical letter(s) are significantly different from each other (LSD test, $P \le 0.05$)



Fig. 6: Relationship of P utilization efficiency with (a) shoot dry matter in hydroponic and (b) paddy yield in soil conditions under adequate and deficient P levels. Each plotted point represents the individual value of samples taken from replicated treatments

Under P deficiency, photosynthates transportation form shoots towards roots increases thereby enhancing rootshoot ratio (RSR) of the plants (Marschner, 1995). Higher RSR at low P is well reported because roots had to explore larger volume of soil in order to absorb more P (Aziz *et al.*, 2005; Lambers *et al.*, 2010). In present study, RSR was increased under P deficiency and noted comparatively higher in P efficient cultivars than in-efficient cultivars (Fig. 1) which might be one of the promising mechanisms to increase P uptake in plants with more root dry matter (RDM). Moreover, a significant correlation ($P \le 0.01$) of RDM with SDM (r = 0.72) and shoot P uptake (r = 0.68) suggested the major role of below ground plant parts in P acquisition under P deficiency. The higher P uptake is one of the responsible mechanisms for P efficiency which promotes the development of larger root systems thereby improving plant access to soil P (Nourgholipour *et al.*, 2017).

Cultivars performed differentially for PUtE in relation to low P under hydroponic and soil conditions. The PUtE based on SDM production ranged from 128.8 to 172.2 g SDM g⁻¹ P in hydroponic while PUtE based on paddy yield varied from 115.2 to 193.3 g PY g⁻¹ P in pot study. The extensive variation in P efficiency among rice genotypes have also been indicated by Aziz et al. (2005) and Fageria (2014). The PUtE showed 70% variability in SDM production and 64% variability in paddy yield under P deficiency (Fig. 6). The variation in PUtE of rice cultivars may be associated with their differential P uptake ability and root efficiency ratio (RER). The RER is the indication of P uptake by shoot per unit of root DM which explains the potential of a genotype to acquire P from rooting environment. Yaseen and Malhi (2009) have reported a positive correlation of SDM with RER and suggested that RER can be used for selecting genotypes for more DM production and enhanced P use efficiency. A positive and significant correlation ($P \le 0.01$) of SDM production with root biomass (r = 0.72), root P uptake (r = 0.44) and shoot P uptake (r = 0.92) in tested rice cultivars illustrated that these were the main traits responsible for maximizing SDM under P deficiency. Fageria et al. (2004) reported the improvement in SDM of rice genotypes with the addition of P and found significant relationship with grain yield.

Biomass production is influenced by environmental factors. A genotype producing more dry matter in controlled conditions may not produce higher grain yield in field conditions because of the altered growing medium (Hayashi, 1995). In current studies, the highest response to P addition was observed in cultivar KSK-282 under hydroponic and in IR-6 under soil conditions as indicated by their higher stress factors (i.e., 48 and 49%). Percent reduction in dry matter or paddy production due to P deficiency in the rooting medium can be described by the P stress factor. It facilitates to demark a line between P responsive and non-responsive cultivars and also explain comparative ability of a cultivar to produce biomass with P addition (Aziz et al., 2011; Irfan et al., 2017; Abbas et al., 2018a). Rice cultivars exhibited wide diversity for PUtE based on SDM and paddy yield. The patterns of PUtE and P deficiency tolerance among rice cultivars were not same when grown under hydroponic and soil conditions. The results suggested that rooting environment influence greatly

on P efficiency traits in rice plants. Thus, particular attention must be paid to growth conditions while screening germplasm for P efficiency.

Conclusion

The lowland rice cultivars exhibited wide diversity for P uptake and utilization efficiency under altered growing environment. Phosphorus deficiency significantly reduced biomass production and P uptake in all rice cultivars. A significant interaction between cultivars and P supply was found for most of the parameters studied as some cultivars were responsive to P application while others were not. The cultivar Basmati-2000 concurrently having higher P uptake, utilization efficiency and paddy yield supports the idea that exploiting natural variations between crop plants instead of specific gene manipulation is the most preferred tool for selecting plants for more P uptake under P deficiency. The efficient and responsive cultivars (i.e., Basmati-2000) can be the potential cultivars for growing on soils with varying P contents. Moreover, higher RSR, PUtE and lower PSF were the important parameters responsible for enhanced P efficiency in efficient cultivars which can be exploited to identify/select cultivars for more biomass production and P efficiency.

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