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DIFFERENTIAL GROWTH RESPONSE, PHOSPHORUS ABSORPTION, TRANSPORT AND UTILIZATION BY WHEAT GENOTYPES UNDER PHOSPHORUS DEFICIENCY

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ABSTRACT

Genotypic differences in phosphorus (P) acquisition and/or utilization can be exploited to enhance the efficiency of P fertilizers and crop productivity on P-deficient soils. Wheat genotypes were evaluated for relative growth rate, P absorption, transport and utilization in a hydroponic study at deficient P (10 μM) and adequate P (200 μM) levels. Phosphorus deficiency drastically reduced dry matter production, P accumulation in root and shoot, relative growth rate (RGR) of shoot, P absorption rate (PAR), and P transport rate of wheat genotypes. However, root- shoot ratio, RGR of root, and P utilization rate (PUR) of shoot and root increased significantly ($P \leq 0.001$) in response to P deficiency. The genotypes SDW-4, SWD-6, YCBW-10 were found superior regarding dry biomass production and relative growth rate of shoot at low P, and therefore can be considered as P-efficient. Strong positive correlation of shoot dry matter with PUR of shoot (r = 0.80, $P \leq 0.001$), while a non-significant relationship with PAR (r = 0.12, $P \leq 0.05$) showed that P utilization was the dominant mechanism for high P efficiency in most of genotypes under P deficiency. The P-efficiency of SDW-6 and YCBW-10 at low P level could be explained by their higher PAR and PUR. However, P utilization appeared to be the main strategy for high P efficiency in SDW-4. The results suggested that wide variations exist among wheat genotypes for mechanisms responsible for P efficiency under low P supply which can be exploited in breeding ventures.

Keywords: absorption rate, relative growth rate, transport rate, utilization rate, wheat genotypes

INTRODUCTION

Phosphorus (P) is the second essential macronutrient after nitrogen required for normal plant growth (Heuer *et al.,* 2017). Despite natural abundance of P in lithosphere, crop production on >30% of world's arable land is constrained by limited P availability (MacDonald *et al.,* 2011). Exceptionally low diffusion rate and substantial fixation of P by soil minerals are the leading causes of lower P bio-availability (Lambers *et al.,* 2015). The P-deficiency in soil is generally ameliorated through the addition of costly mineral phosphatic fertilizers. Nevertheless, low recovery and elevated costs of fertilizers coupled with accelerated depletion of global rock phosphate reserves necessitate the adoption of strategies for efficient and sustainable P use (Vance *et al.,* 2003). In recent years, exploitation of genotypic differences in P absorption and utilization has received considerable attention for improving efficiency of P fertilizers (Richardson *et al.,* 2011). Development of crop cultivars that accumulate and/or utilize P more effectively seems to be the most viable option which can drastically reduce the requirement of P fertilizers in modern agricultural systems (Abbas *et al.,* 2016).

For efficient P acquisition under P limitation, plants may evolve several morphological, physiological and molecular responses such as structural and architectural alterations of roots (Bouain *et al.,* 2016), increased secretion of organic acids, phosphatases and rib nucleases (Vance *et al.,* 2003), and up-regulation of high-affinity P_i transport system (Grün *et al.,* 2018). Efficient internal P use is thought to be conferred by numerous metabolic adjustments like P re-allocation within the plant (Byrne *et al.,* 2011), increased production of P-free polysaccharides within cell (Lambers *et al.,* 2012), and induction of P_i independent metabolic pathways (Sulpice *et al.,* 2014). Despite widespread P deficiency on Pakistani soils, research regarding the improvement of P efficiency in field crops has

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received very less attention (Abbas *et al.,* 2018a). For successful exploitation of such approach, the primary step is to explore the extent of genetic variations among the wheat crop existing germplasm. Among cereals, wheat crop has special importance as it covers the largest cultivated area (~ 9 million hectares) in Pakistan every year and consumes more than 50% of P fertilizers annually (GoP, 2018). Any success regarding improved P acquisition and/or P use in wheat crop can substantially reduce the dependency on commercial P fertilizers. Some recent studies have reported the presence of extensive genetic variations for P acquisition and utilization (Yaseen and Malhi, 2011; Abbas *et al.,* 2016; Abbas *et al.,* 2018 a,b), which can be effectively utilized in the breeding programs destined for improving P efficiency in wheat. We hypothesized that differences in relative growth rate, P absorption, transport and utilization might be the possible adaptive mechanisms contributing towards variations in P efficiency under deficient P supply in wheat germplasm. Hence, the current study was planned to investigate the adaptive mechanisms of wheat genotypes under deficient and adequate P supply.

MATERIALS AND METHODS

Plant material and experimental setup

Ten wheat genotypes viz., SDW-4, SDW-5, SDW-6, SDW-8, SDW-9, YCBW-3, YCBW-6, YCBW-10, YCBW-18 and YCBW-25 were obtained from Plant Breeding and Genetics Division of Nuclear Institute of Agriculture (NIA), Tandojam- Pakistan. All genotypes were grown in solution culture under a rain protected net-house at NIA, Tandojam (Latitude 25º 25′19.8″ North and Longitude 68º 32′27.8″ East). Seeds of all genotypes were surface-sterilized with 2% solution of sodium hypochlorite for 30 seconds, followed by several washings with distilled water to remove remnants of the disinfectant solution. Disinfected seeds were allowed to germinate on gauze supported on plastic cups filled with distilled water. Seven days old seedlings were shifted to iron tubs containing 200 L nutrient solution (Johnson *et al.,* 1957). The composition of culture solution was 4 m*M* KNO_3, 1 m*M* K_2SO_4, 4 m*M* $Ca(NO_3)_2.4H_2O$, 2 m*M* NH_4NO_3, 50 μM KCl, 1 m*M* $MgSO_4.7H_2O$, 25 μM H_3BO_3, 2 μM $MnSO_4.H_2O$, 0.5 μM H_2MoO_4, 0.5 μM $CuSO_4.5H_2O$, 2 μM $ZnSO_4.7H_2O$, and 50 μM Fe-EDTA. Mono-ammonium phosphate ($NH_4H_2PO_4$) was used to establish P levels i.e., deficient (10 μM P) and adequate (200 μM P) in separate tubs. One seedling of each genotype was transplanted per hole and repeated ten times at each P level. The solution was continuously aerated with an air pump and its pH was daily adjusted at 5 ± 0.5 with hydrochloric acid or sodium hydroxide solution. The culture solution was replaced with fresh solution after every fifth day.

Harvestings and phosphorus assay

Five plants for each genotypes were harvested 21 days after transplanting (DAT) (1st harvest, H_1) and remaining five plants were harvested 35 DAT (2nd harvest, H_2) from both P levels. The plants were rinsed with de-ionized water, air-dried and divided into shoots and roots. The samples were kept in a forced-air oven for 72 hours for drying. After recording dry matter, root and shoot samples were crushed with a mechanical grinder. The samples were digested using di-acid mixture [nitric acid (HNO_3) and perchloric acid ($HClO_4$), 5:1] according to Miller (1998), and P concentration in the digested samples was determined by following the method of Chapman and Pratt (1961) using a spectrophotometer. Plant growth and P-efficiency related characteristics were estimated by the formulae adopted from Elliott and Lauchli (1985). The detail regarding various parameters is given in Table 1.

Statistical analysis

The data pertaining to various growth and P-related parameters were analyzed statistically through the analysis of variance technique, following completely randomized factorial design (Gomez and Gomez, 1984). Genotypic means for various parameters were individually differentiated at each P level using honestly significant difference (HSD) test at 5% probability level. The separate test was suggested by Da Silva and Gabelman (1992) to avoid the heterogeneity of error variances at two P levels. Correlation coefficients (r) among various parameters were determined using the replicated data at low P level.

RESULTS

Plants were harvested 21 (1st harvest, H_1) and 35 DAT (2nd harvest, H_2) to calculate the rate related parameters like relative growth, P absorption, transport and utilization rates in shoot and root. The growth data obtained at both harvests illustrated almost similar trends, therefore, data pertaining to H_2 only are being presented in this paper.

Table 1. The detail of various plant growth and P-efficiency related parameters

Parameter	Formula	Comments
P uptake (mg plant^{-1})	P concentration (mg g^{-1}) ×Dry matter (g plant^{-1})	---
Total P uptake (mg plant^{-1})	Shoot P uptake + Root P uptake	---
Relative growth rate (RGR, mg g^{-1}day^{-1})	$\frac{\ln DM_2 - \ln DM_1}{t_2 - t_1}$	Where DM_1 and DM_2 represents dry matter at time interval t_1 and t_2
P absorption rate (PAR, µM P g^{-1} RDM day^{-1})	$\frac{TP_2 - TP_1}{RDM_2 - RDM_1} \times RGRR$	Where TP_1 and TP_2 represent total P uptake, and RDM_1 and RDM_2 are the root dry matter at H_1 and H_2, respectively. The RGRR denotes the relative root growth rate.
P transport rate (PTR, µM P g^{-1} SDM day^{-1})	$\frac{P_2 - P_1}{SDM_2 - SDM_1} \times RGRS$	Where P_1 and P_2 represent P uptake in shoot and SDM_1 and SDM_2 are the shoot dry matter at H_1 and H_2, respectively. The RGRS denotes the relative shoot growth rate.
P utilization rate (PUR, mg DM mg^{-1} P day^{-1})	$\frac{DM_2 - DM_1}{P_2 - P_1} \times RGR$	Where P_1 and P_2 are P uptake in shoot or root, and DM_1 and DM_2 are shoot or root dry matter at H_1 and H_2, respectively. The RGR is the relative growth rate of shoot or root.

Table 2. Dry matter, root-shoot ratio and relative growth rate of wheat genotypes grown in solution culture at deficient P (10 μM) and adequate P (200 μM) levels

Genotypes	Dry matter (g plant^{-1})						Root - shoot ratio		Relative growth rate (mg g^{-1} day^{-1})			
	Shoot		Root		Total				Shoot		Root	
	$P_{10\ \mu M}$	$P_{200\ \mu M}$	$P_{10\ \mu M}$	$P_{200\ \mu M}$	$P_{10\ \mu M}$	$P_{200\ \mu M}$	$P_{10\ \mu M}$	$P_{200\ \mu M}$	$P_{10\ \mu M}$	$P_{200\ \mu M}$	$P_{10\ \mu M}$	$P_{200\ \mu M}$
SDW-4	0.61 a	4.41 a	0.65 ab	0.75 ab	1.26 ab	5.16 a	1.08bcd	0.17 cd	86.07abc	122.94 a	76.92 ab	67.39 a
SDW-5	0.41 d	4.32 a	0.49cde	0.77 a	0.89 cd	5.08 ab	1.18 bc	0.18bcd	48.81 e	121.31 ab	40.07 d	62.72 ab
SDW-6	0.59 ab	3.69 ab	0.74 a	0.64abc	1.32 a	4.33bcd	1.26 ab	0.17 cd	96.34 a	109.35 ae	84.89 ab	50.35 ab
SDW-8	0.43 cd	2.57 c	0.61abc	0.56 cd	1.04abc	3.13 e	1.43a	0.22 ab	73.68 bc	94.23 de	81.81 ab	56.40 ab
SDW-9	0.39 d	2.48 c	0.36 ef	0.62 bc	0.75 d	3.10 e	0.91 d	0.25 a	50.78 de	95.30 cde	47.97 cd	65.84 ab
YCBW-3	0.52abc	3.35 bc	0.46def	0.46 d	0.99bcd	3.81cde	0.88 de	0.14 d	67.10cde	117.04abc	64.97 bc	50.88 ab
YCBW-6	0.43 cd	3.03 bc	0.41def	0.55 cd	0.84 cd	3.58 de	0.96 cd	0.18bcd	67.40cde	107.97ae	69.53 b	58.79 ab
YCBW-10	0.54 ab	3.72 ab	0.53bcd	0.68abc	1.07abc	4.39abc	0.98 cd	0.18bcd	88.77 ab	115.78 ad	90.02 a	68.11 a
YCBW-18	0.51 bc	2.79 bc	0.34 f	0.56 cd	0.85 cd	3.35 e	0.65 e	0.20 bc	70.72 bc	89.72 e	70.70 ab	48.46 b
YCBW-25	0.52abc	3.06 bc	0.50 cd	0.64abc	1.02bcd	3.70cde	0.95 cd	0.21abc	69.50bcd	99.41 be	74.59 ab	54.50 ab
$HSD_{0.05}$	0.10	0.94	0.14	0.15	0.29	0.81	0.24	0.05	19.54	22.16	20.08	18.13
F values for analysis of variance												
P level (P)	2498***		77.02***		3214***		488***		363***		45.43***	
Genotypes (G)	16.04***		20.11***		27.37***		3.34**		13.01***		8.67***	
P × G	12.94***		10.06***		16.37***		3.35**		9.00***		11.09***	
$HSD_{0.05}$ = honestly significant difference at 5% probability level; ** = Significant at $P \leq 0.01$; *** = Significant at $P \leq 0.001$												

Table 3. Phosphorus concentration and uptake in shoot and root of wheat genotypes grown in solution culture at deficient P (10 μM) and adequate P (200 μM) levels

Genotypes	Phosphorus concentration (mg P g^{-1})				Phosphorus uptake (mg P plant^{-1})					
	Shoot		Root		Shoot		Root		Total	
	$P_{10\ \mu M}$	$P_{200\ \mu M}$	$P_{10\ \mu M}$	$P_{200\ \mu M}$	$P_{10\ \mu M}$	$P_{200\ \mu M}$	$P_{10\ \mu M}$	$P_{200\ \mu M}$	$P_{10\ \mu M}$	$P_{200\ \mu M}$
SDW-4	1.34 b	2.29 e	1.40 c	5.25 ab	0.81 b	10.09 bc	0.91 bc	3.92 a	1.72 bc	14.02 abc
SDW-5	1.24 b	2.94 bcd	2.03 b	5.00 ab	0.49 e	12.71 a	0.87 c	3.87 a	1.36 de	16.57 a
SDW-6	2.04 a	3.10 b	1.68 c	4.94 abc	1.12 a	11.49 ab	1.18 ab	3.13 bc	2.30 a	14.62 ab
SDW-8	1.96 a	3.13 b	2.10 b	5.10 ab	0.80 b	7.99 de	1.25 a	2.84 cde	2.05 ab	10.83 c
SDW-9	1.39 b	3.04 bc	2.51 a	4.84 abc	0.55 de	7.53 e	0.89 c	2.96 bcd	1.44 cde	10.49 c
YCBW-3	1.35 b	2.64 cde	1.59 c	4.98 ab	0.70 bc	8.84 cde	0.73 cd	2.32 de	1.43 cde	11.16 bc
YCBW-6	1.42 b	2.96 bcd	1.38 c	4.01 c	0.61 cd	8.93 cde	0.57 d	2.18 e	1.17 e	11.12 bc
YCBW-10	1.34 b	2.56 de	1.46 c	4.50 bc	0.72 bc	9.49 b-e	0.77 cd	3.00 bc	1.48 cde	12.49 bc
YCBW-18	1.25 b	3.57 a	2.09 b	5.53 a	0.64 cd	9.94 bcd	0.71 cd	3.11 bc	1.35 de	13.06 abc
YCBW-25	1.51 b	2.86 bcd	1.62 c	5.51 a	0.77 b	8.73 cde	0.79 cd	3.56 ab	1.56 cd	12.30 bc
$HSD_{0.05}$	0.34	0.43	0.34	0.93	0.12	2.06	0.29	0.67	0.36	3.65
F values for analysis of variance										
P level (P)	1686***		2481***		4856***		2533***		2279***	
Genotypes (G)	20.93***		11.14***		15.93***		22.99***		7.64***	
P × G	13.33***		5.99***		15.08***		16.10***		6.85***	
$HSD_{0.05}$ = honestly significant difference at 5% probability level; *** = Significant at $P < 0.001$										

Table 4. Phosphorus absorption, transport and utilization rate of wheat genotypes grown in solution culture at deficient P (10 μM) and adequate P (200 μM) levels

Genotypes	P absorption rate (µM P g^{-1} RDM day^{-1})		P transport rate (µM P g^{-1} SDM day^{-1})		P utilization rate (mg DM mg^{-1} P day^{-1})			
					Shoot		Root	
	$P_{10\ \mu M}$	$P_{200\ \mu M}$	$P_{10\ \mu M}$	$P_{200\ \mu M}$	$P_{10\ \mu M}$	$P_{200\ \mu M}$	$P_{10\ \mu M}$	$P_{200\ \mu M}$
SDW-4	5.78 bc	36.37 bcd	3.49 cd	6.47 c	61.21 ab	38.58 a	46.87 ab	10.91 ab
SDW-5	4.64 c	46.56 a	1.86 e	9.42 a	40.40 cd	32.77 ab	26.92 cd	11.15 ab
SDW-6	9.70 a	39.82 ab	6.60 a	8.59 ab	57.39 ab	27.85 d-e	51.75 ab	8.46 c
SDW-8	9.90 a	32.77 bcd	4.57 b	7.11 bc	40.37 cd	24.37 de	41.28 bc	9.79 abc
SDW-9	7.03 bc	30.45 d	2.03 e	6.61 bc	34.49 d	24.54 cde	21.57 d	12.02 a
YCBW-3	5.94 bc	38.39 bc	2.53 de	7.19 bc	46.08 bcd	32.67 abc	39.05 bc	8.03 c
YCBW-6	5.94 bc	35.96 bcd	3.20 cd	7.74 abc	49.56 a-d	28.53 bcd	44.96 ab	11.66 ab
YCBW-10	7.79 ab	31.48 cd	3.77 bc	6.27 c	65.69 a	31.95 a-d	58.08 a	11.92 a
YCBW-18	9.83 a	35.91 bcd	2.82 cde	7.75 abc	56.37 abc	20.32 e	36.35 bcd	8.01 c
YCBW-25	7.39 ab	35.36 bcd	3.64 bc	7.12 bc	49.31 a-d	28.18 b-e	43.38 ab	9.39 bc
$HSD_{0.05}$	2.53	7.84	1.07	1.99	16.52	8.13	15.49	2.34
F values for analysis of variance								
P level (P)	2961**		868***		339***		1029***	
Genotypes (G)	6.33***		16.72***		12.37***		12.67***	
P × G	11.41***		14.82***		7.17***		13.41***	

$HSD_{0.05}$ = honestly significant difference at 5% probability level; ** = Significant at $P \leq 0.01$; *** = Significant at $P \leq 0.001$

Table 5. Correlation matrix among various growth and P-related parameters of wheat genotypes at deficient P (10 μM) level

Parameters	SDW	RDW	RSR	RGRS			RGRS	SPUP	PAR	PTR	PUR
RDW	0.53**										
RSR	−0.03 ns	0.70***									
RGRS	0.78***	0.61***	0.08 ns								
RGRR	0.61***	0.53**	0.23 ns	0.81***							
SPUP	0.64***	0.76***	0.35 ns	0.79***	0.68***						
RPUP	0.10 ns	0.69***	0.71***	0.23 ns	0.27 ns	0.54**					
TPUP	0.35 ns	0.79***	0.57**	0.52**	0.48**	0.84***	0.85***				
PAR	0.12 ns	0.14 ns	−0.02 ns	0.44*	0.51**	0.53**	0.38*	0.57**			
PTR	0.44*	0.73***	0.39*	0.76***	0.69***	0.92***	0.55**	0.81***	0.28 ns		
PURS	0.80***	0.30 ns	−0.20 ns	0.83***	0.63***	0.40*	−0.17 ns	0.07 ns	0.15 ns	0.37*	
PURR	0.61***	0.57***	0.19 ns	0.77***	0.87***	0.57***	0.10 ns	0.36 ns	0.25 ns	0.61***	0.68***

SDW = shoot dry weight; RDW = root dry weight; RSR = root-shoot ratio; RGRS = relative growth rate of shoot; RGRR = relative growth rate of root; SPUP = shoot P uptake; RPUP = root P uptake; TPUP = total P uptake; PAR = P absorption rate; PTR = P transport rate; PURS = P utilization rate in shoot; PURR = P utilization rate in root; ns = non-significant at $P \geq 0.05$; * = Significant at $P \leq 0.05$; ** = Significant at $P \leq 0.01$; *** = Significant at $P \leq 0.001$ (n = 50)

Biomass production

Data related to shoot dry matter (SDM), root dry matter (RDM), total dry matter (TDM), and root-shoot ratio (RSR) are shown in Table 2. The highly significant effects of P levels, genotypes as well as their interactions were observed on all the above mentioned parameters. Genotypes revealed substantial variations for SDM at both P levels. The SDM ranged between 0.39 to 0.61 g $plant^{-1}$ under P deficiency and 2.48 to 4.41 g $plant^{-1}$ at adequate P supply. Averaged across all genotypes, the SDM at adequate P was almost seven folds higher than at deficient P level. The genotype SDW-6 produced the highest RDM of 0.74 g $plant^{-1}$ and it was statistically at par with that of SDW-4 and SDW-8, while SDW-9 and YCBW-18 produced the lowest values of RDM in response to P deficiency. The RDM recorded 22% increase when genotypes were grown in adequate P supply and it varied between 0.46 g $plant^{-1}$ in YCBW-3 to 0.77 g $plant^{-1}$ in SDW-5. Genotypes also varied considerably for TDM at each P level. The genotypes SDW-4, SDW-6, SDW-8 and YCBW-10 produced the highest and statistically identical TDM, while genotype SDW-9 produced the lowest TDM at deficient P level. Under adequate P nutrition, genotypes SDW-4, SDW-5 and YCBW-10 performed better for TDM production over the rest of genotypes. Averaged over all genotypes, adequate P level produced 4 fold higher TDW than at deficient P level. Under P deficiency, genotypes SDW-8 and SDW-6 produced the highest as well as statistically at par RSR (1.43 and 1.26), while genotypes YCBW-3 andYCBW-18 exhibited the lowest RSR (0.88 and 0.65). Averaged over all genotypes, the RSR decreased by 88% as P supply was increased from 10 to 200 μM in the rooting medium (Table 2).

Relative growth rate (RGR)

The RGR refers to the production of dry biomass (shoot or root) per unit time. Wheat genotypes showed significant differences for RGR of shoot at deficient and adequate P levels (Table 2). Genotypes with higher RGR are believed to have better adaptation to stress conditions. At

low P level, genotypes SDW-6, YCBW-10 and SDW-4 showed higher shoot RGR of 96.34, 88.77 and 86.07 mg g^{-1} day^{-1}, respectively and were statistically identical to each other. The lowest RGR for shoot (48.81 mg g^{-1} day^{-1}) was recorded in genotype SDW-5. The mean RGR of shoot increased by 49% when genotypes were supplied with adequate P level and it varied between 89.72 mg g^{-1} day^{-1} in genotype YCBW-18 to 122.94 mg g^{-1} day^{-1} in genotype SDW-4.The tested genotypes also revealed marked differences for relative growth rate of root at both P levels, however, these differences were more pronounced at deficient P level (Table 2). The RGR for root varied between 40.07 to 90.02 mg g^{-1} day^{-1} at low P and from 48.46 to 68.11 mg g^{-1} day^{-1} at adequate P level. Overall, the RGR for root decreased by 17% when P supply was enhanced from 10 to 200 μM in solution culture.

Phosphorus accumulation

The P levels, genotypes and their interaction significantly influenced the P accumulation in shoot and root (Table 3). The P concentration [P] in shoot (averaged across all genotypes) was almost 2-fold lower at deficient P than at adequate P level. The genotypes SDW-6 and SDW-8 showed the highest [P] in shoot (2.04 and 1.96 mg g^{-1}) at deficient P level. The genotypes revealed more pronounced differences in shoot [P] when grown with adequate P level. The genotype YCBW-18 showed the highest (3.57 mg g^{-1}) and genotype SDW-4 showed the lowest (2.29 mg g^{-1}) [P] in shoot at adequate P level. The root [P] was drastically reduced from 4.97 to 1.79 mg g^{-1} as a result of induced P deficiency. The root [P] ranged between 1.38 to 2.51 mg g^{-1} at 10 μM P and 4.10 to 5.51 mg g^{-1} at 200 μM P. Shoot P uptake revealed significant differences among wheat genotypes at each P level (Table 3). The highest shoot P uptake (1.12 mg $plant^{-1}$) was noticed in SDW-6 while the lowest (0.49 and 0.55 mg P $plant^{-1}$) was recorded in SWD-5 and SWD-9 when grown at deficient P level. The magnitude of root P uptake varied between 0.57 to 1.25 mg $plant^{-1}$ under P deficiency, and between 2.18 to 3.92 mg $plant^{-1}$ at high P level. Change in solution P from 10 to 200 μM resulted in 3.5 fold increase in root P uptake (Table 3). The P uptake by roots of wheat genotypes was invariably higher than shoot P uptake at deficient P. The total P uptake coincided consistently with shoot P uptake. At deficient P, SDW-6 and SDW-8 with total P uptake of 2.30 and 2.05 mg $plant^{-1}$ were statistically superior to the rest of genotypes. Higher P level resulted in 8 fold higher total P uptake and its magnitude ranged between 10.49 mg $plant^{-1}$ in genotype SDW-9 to 16.57 mg $plant^{-1}$ in genotype SDW-5.

Phosphorus absorption, transport and utilization rate

Phosphorus levels, genotypes and their interaction had significant ($P \leq 0.001$) effects on P absorption, transport and utilization rate (Table 4).The P absorption rate (PAR) measures the amount of P uptaken per unit of root dry matter in unit time and is considered an index of root uptake efficiency. In this study, root weight was used to calculate PAR, however, root length and root volume can also be used. The PAR exhibited substantial variations at both P levels and its extent varied between 4.64 to 9.90μM P g^{-1} RDM day^{-1} under P deficiency, and between 30.45 to 46.56 μM P g^{-1} RDM day^{-1} at adequate P. Averaged across wheat genotypes, PAR increased five-fold by increasing external P supply from 10 to 200 μM. Substantial differences were observed among genotypes for PTR to shoot at both levels. At low P level, the highest PTR (6.60 μM P g^{-1} SDM day^{-1}) was noted for genotype SDW-6, while the lowest for SWD-5 (1.86 μM P g^{-1} SDM day^{-1}) and SDW-9 (2.03 μM P g^{-1} SDM day^{-1}). The PTR varied between 6.27 to 9.42 μM P g^{-1} SDM day^{-1} at adequate P level (Table 4).The PUR describes the rate of shoot or root dry matter yield per unit of P absorbed in a particular tissue. The PUR in shoot and root decreased invariably among all genotypes with increase of P in solution. The PUR in roots showed more reduction (75%) than in shoots (42%) with adequate P nutrition. In shoot, PUR varied from 34.49 to 65.69 mg SDM mg^{-1} P day^{-1} with P deficiency, and from 20.32 to 38.58 mg SDM mg^{-1} P day^{-1} at adequate P level. Wide genotypic variations for PUR in roots were observed and its extent ranged from 21.57 to 51.75 mg RDM mg^{-1} P day^{-1} at deficient P and from 8.01 to 12.02 mg RDM mg^{-1} P day^{-1} at adequate P supply.

DISCUSSION

The goal of efficient nutrient use can be accomplished by improving the acquisition and/or utilization efficiency of the nutrient. In case of P, both approaches are possible (Wang *et al.,* 2010). Nonetheless, the traits involved in P acquisition or utilization must show sufficient genetic variability and heritability for the successful selection and genetic improvement. Production of shoot dry matter correlates well

with ultimate economic yield and can be helpful in assessing adaptability of genotypes to P deficiency at a seedling stage (Yaseen and Malhi, 2011; Irfan *et al*., 2017). The results of the current experiment revealed that wheat genotypes considerably differed in SDM yield. Significant interactive effects of genotypes and P levels on SDM production (Table 2) clearly indicated differential growth response of wheat genotypes to different P regimes. Such types of interactions are important for the development of P efficient cultivars (Aziz *et al.,* 2005). Positive correlation of SDM with RDM (r = 0.52, $P \leq 0.01$), shoot P uptake (r = 0.64, $P \leq 0.01$) and P utilization rate (r = 0.80, $P \leq 0.001$) (Table 5) indicated the role of these parameters in maximizing SDM production under deficient P condition. The SDM had a non-significant relationship with PAR (r = 0.12, $P \leq 0.05$) (Table 5), illustrating that P utilization was the key mechanism for their efficiency in producing maximum biomass at low P supply in the growth medium. The RGR of shoot was also calculated to avoid any discrepancy in ranking of genotypes for P-efficiency due to variability in the initial size of the seedlings at the time of transplanting. However, in this study both parameters were strongly associated (r = 0.78, $P \leq 0.001$), which evidenced that genotypes (e.g. SDW-4, SDW-6, YCBW-10) having high SDM after 35 DAT also exhibited higher RGR of shoot.

Plants invest more into roots by redirecting assimilates from shoots to roots under P deficiency, resulting in higher root - shoot ratios (Marschner, 1995). Drastic reductions in leaf area under P deficiency are thought to result in lower leaf demand for photosynthates, leading to accelerated translocation thereof to roots (Yaseen and Malhi, 2011). In current study, higher RSR were observed at deficient P level (Table 2), as roots had to explore more volume to acquire P. Significant positive correlation of RSR with shoot P uptake (r = 0.37, $P \leq 0.05$) and total P uptake (r = 0.57, $P \leq 0.01$) at low P level signifies the role of RSR in plant acclimation to P stress. Root DM of plants also correlated significantly with shoot P uptake (r = 0.76, $P \leq 0.01$) and total P uptake (r = 0.79,$P \leq 0.01$). This suggested that higher P uptake in wheat genotypes was associated with larger root system under conditions of low P availability. The significance of extensive root systems becomes more pronounced in soil where P supply is mostly diffusion limited. These findings of our study supported a number of earlier studies (Yaseen and Malhi, 2011; Abbas *et al.,* 2016; Abbas *et al.,* 2018a).

The plants under P deficiency have tendency to retain more P in their roots than shoots, a well-known acclimation to P deficiency (Akhtar *et al.,* 2015; Abbas *et al.,* 2016). In this experiment, the partitioning of P simply followed the separation pattern of dry matter between the roots and shoots. The genotypes grown with adequate P retained 24% of total absorbed P in their roots than plants under deficient P supply, which retained 55% of their total P contents in roots (Table 3).

In the present experiment, P absorption rate (PAR) during 21 to 35 DAT increased significantly with increasing P supply (Table 4). These findings are in line with the results reported by Yaseen and Malhi (2011) and Abbadi (2017) who observed many fold increase in PAR of wheat cultivars in response to high P levels. Contrarily, Akhtar *et al.* (2015) reported an increase in PAR of wheat cultivars under P deficient supply. Significant correlations (r> 0.50, $P \leq 0.01$) were observed for PAR with shoot and total P uptake of P deficient genotypes which pointed out that the genotypes with relatively higher P absorption rate per unit root dry matter were more tolerant to P deficiency stress. The genotype SDW-6, with highest PAR value at deficient P level, accumulated highest shoot as well as total P contents which might have triggered its higher biomass production. This genotype also had higher P transport as well utilization rate (Table 4). In this way, the higher P efficiency of this genotype can be explained by both efficient P absorption and utilization. In contrast, genotype SDW-4, which produced SDM and TDM statistically at par with that of SDW-6, had PAR value lower than most of genotypes. This genotype had higher rate of P utilization in shoot and root which appeared to be the main strategy for high P efficiency in this genotype. These findings suggest different mechanisms employed by genotypes for efficient P use under P deficiency which can be exploited in breeding programs.

Phosphorus transport rate (PTR) is considered as an estimate of PAR independent of root physical characteristics (Elliot and Lauchli, 1985). It was evident from the strong positive correlation between PAR and PTR (r = 0.61, $P \leq 0.001$) at low P stress. The PTR was also strongly associated with shoot P uptake (r = 0.92, $P \leq 0.001$) (Table 5) indicating that genotypes with higher PTR were able to tolerate low P stress and might be a better choice for

growing in P stress environment. A positive and significant correlation (r = 0.76, $P \leq 0.001$) among PTR and RGR of shoot indicates that higher PTR of genotypes might have been triggered by their shoot RGR at deficient P supply. The P utilization rate (PUR) in shoots and roots were positively correlated (r = 0.68, $P \leq 0.001$), indicating that genotypes efficient in utilizing P in shoots were also efficient in utilizing P in roots. Strong correlation between PUR and RGR of shoot (r = 0.83, $P \leq 0.001$) pointed out that genotypes (e.g. SDW-4, SDW-6, YCBW-10) with higher RGR of shoot were able to efficiently utilize the accumulated P in shoots.

CONCLUSION

The findings of present study suggested that wheat genotypes varied significantly for biomass production, relative growth rate, P absorption, transport and utilization at adequate and deficient P levels. Genotypes SDW-4, SDW-6, YCBW-10 performed better regarding biomass yield and relative growth rate of shoot at deficient P level. Phosphorus utilization appeared to be the dominant mechanism for high biomass production in most of genotypes under P deficiency. The P efficiency of SDW-6 and YCBW-10 at low P level was conferred by both higher P absorption and utilization rate. However, P utilization was the main mechanism for high P efficiency in genotype SDW-4.

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