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Enhancing phosphorus use efficiency in wheat grown on alkaline calcareous soils

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Abstract

Phosphorus (P) use efficiency is crucial for sustainable wheat production, particularly on alkaline calcareous soils. This study investigates the relative importance of two factors; P acquisition efficiency (PAE) and P utilization efficiency (PUtE), in determining P use efficiency (PUE) in wheat. A field trial with ten wheat genotypes was conducted under two P levels (no P application and P application at 110 kg P_2O_5 ha^{-1}). Results revealed significant genetic variability in PUE, PAE, and PUtE among wheat genotypes under varying P availabilities. Genotypes MK-4 and MK-8 exhibited superior PUE, making them ideal candidates for soils with differing P levels. PAE played a more substantial role in influencing PUE, with PUtE contributing less to the variability. The findings underscore the importance of improving PAE, particularly for wheat genotypes grown in P-deficient conditions. Moreover, selecting genotypes with lower grain P concentration can enhance PUtE, contributing to improved PUE. These insights can improve breeding efforts and crop management practices to enhance P use efficiency in wheat, ultimately reducing production costs and fertilizer demand, especially in P-limited alkaline calcareous soils.

Keywords: Alkaline-calcareous soil, P acquisition efficiency, P utilization efficiency, P use efficiency, wheat genotypes.

Introduction

About 30% of the world's cultivated soils are inherently deficient in phosphorus (P) nutrient, therefore, crop production can be sustained only by the regular application of inorganic P fertilizers on these soils (Kochian, 2012). The phosphatic fertilizers are primarily derived from extracted rock phosphate, a finite resource which is anticipated to exhaust by the end of this century (Cordell et al., 2009). Moreover, crops can uptake only 15-20% of the fertilizer P during the year of its application. The remaining P forms insoluble complexes with sesquioxides in acidic soils and with calcium carbonate in alkaline soils and becomes unavailable for plant uptake (Baker et al., 2015). Hence, more attentions are being directed to the efficient utilization of P resources (Cordell et al., 2009).

Crop productivity on P-limited soils can be significantly impacted by breeding for P use efficiency (PUE) and providing farmers with improved crop cultivars, in addition to crop management techniques (Thornton et al., 2014). Analogous to nitrogen use efficiency defined by Moll et al. (1982), PUE can be calculated as grain yield per unit of P supply from soil plus fertilizer, and incorporates both P acquisition efficiency (PAE) and P utilization efficiency (PUtE). Plants can compensate for P deficiency in two ways: either by increasing their P intake from phosphorus-deficient media (PAE) and/or by effectively using the P they already have internally (PUtE) (Karthikeyan et al., 2014). Various morphological, physiological and biochemical traits underlying efficient P acquisition include the modifications in root structure and architecture (Niu et al., 2013), the release of organic acids and phosphatases into the rhizosphere (White et al., 2013) and the overexpression of high-affinity root P transporters (Amtmann and Armengaud, 2009). Higher P utilization is facilitated by effective recycling and reuse of the acquired P (Marschner, 2012), induction of P_i independent metabolic pathways

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(Sulpice et al., 2014), and increased synthesis of P-free cellular macromolecules (Byrne et al., 2011; Lambers et al., 2012).

In Pakistan, the situation is more critical as more than 90% of cultivated soils are P deficient (Memon, 2005). Furthermore, the fertilizer industry in Pakistan is totally dependent on the imports of mined rock phosphate, the raw material for P fertilizers. Therefore, crop production in Pakistan is highly vulnerable to price fluctuation and supply disruption of rock phosphate. In Pakistan, wheat is grown on an area of more than 9.0 million hectares as a staple food grain (Government of Pakistan, 2022), and consumes 2.27 million tons, almost 50% of the annual fertilizer nutrients (4.55 million tons) used by the crops in the country (NFDC, 2019-20). Enhancing P use efficiency in wheat crop alone can significantly lower production costs and future fertilizer requirements. There have been documented genetic differences in wheat for P usage efficiency in the literature (Yaseen and Malhi, 2009a; Abbas et al., 2018a; Irfan et al., 2018). However, there is a dearth of information about the relative significance of PAE and PUtE for wheat P usage efficiency especially in alkaline calcareous soils. According to Wang et al. (2010), when the P supply is enough, PUtE is more significant than PAE. However, under limited P conditions, PAE becomes exceedingly important. Genetic variations in PAE were mainly responsible for the higher P efficiency in low P acidic soil-grown soybean and common bean (Beebe et al., 2006), maize (Bayuelo-Jiménez and Ochoa-Cadavid, 2014), rice (Panigrahy et al., 2009), and potato (Sandaña, 2016). Sandaña and Pinochet (2014) evaluated wheat and pea genotypes in high P fixing acidic soils and ascribed differences in PUE to contrasting PUtE in these crops. According to Manske et al. (2001), P uptake under P-deficient conditions in both acidic and calcareous soil accounted for 71–100% of the variation in wheat grain production, whereas P utilization efficiency in the calcareous soil was more important for grain yield under high P conditions. Conversely, Yang et al. (2022) observed that the genetic variation in PUE of wheat genotypes was primarily explained by PUtE under both high and low P circumstances in a purple lithomorphic soil. These several studies have demonstrated that crop species, environmental factors, and soil P condition can all affect the relative significance of PAE and PUtE. The goal of the current study was to evaluate the differences in PUE amongst wheat genotypes as well as the relative contributions of PAE and PUtE to PUE in the case of both high and low P availability in Pakistan's alkaline calcareous soils. We hypothesized that i) there exists large genetic variations in PAE and PUtE of wheat genotypes, and ii) PAE will be more crucial than PUtE in high P fixing alkaline-calcareous soils. The outcomes of this study will help identify ideal P efficient genotypes for low P input farming systems of Pakistan, and expedite future efforts in wheat breeding and P management.

Material and Methods

Description of experimental site, design and treatments

In Rabi 2017-18, a field trial was carried out at the experimental farm of the Nuclear Institute of Agriculture (NIA), Tandojam. Before the start of the experiment, soil was sampled from 20 cm depth and analyzed for various physical and chemical properties. The soil was non-saline (EC_e= 2.1 dS m^{-1}) and alkaline in reaction (pH_e= 8.2) with a clay loam textural class (21.7% sand, 42.2% silt and 36.1% clay). It had 0.69% organic matter, 0.073% Kjeldahl nitrogen and 187 mg kg^{-1} ammonium acetate (NH_4OAc) extractable potassium. The value of P availability index as determined by Olsen (1954) was 8.2 mg kg^{-1}. Split-plot design was used in the experiment, with genotypes assigned to subplots and P levels given to main plots. The treatments were factorial combinations of two P levels [zero/no P application (low P) and P application @110 kg P_2O_5 ha^{-1} (high P)] and 10 wheat genotypes/varieties (MK-1, MK-2, MK-3, MK-4, MK-5, MK-6, MK-7, MK-8, MK-9 and NIA-Sunder). The seed material of genotypes was collected from Plant Breeding and Genetics Division of NIA, Tandojam. Genotypes MK-1 to MK-9 are the advanced wheat lines/future candidate varieties, while NIA-Sundar is released wheat variety and has demonstrated high P efficiency in previous studies (Abbas et al., 2018a,b). There were three replications of each treatment. In low P treatment, P supply was calculated as initial Olsen's P (8.2 mg kg^{-1}) in the upper 20 cm soil layer with soil bulk density of 1.42 g cm^{-3} at planting, while in high P treatment, the projected P supply was the total of Olsen's P and added P (110 kg P_2O_5 ha^{-1} or 48 kg P ha^{-1}) (Valle et al., 2011).

Crop culture

The crop was sown on November 15, 2017. Seeds were sown with the help of dibbler with one seed per hole, maintaining 3 inches plant to plant and 12 inches row to row distance. Five rows (3 m long) of each genotype were sown in each subplot. The main plots received 150 kg nitrogen (N) and 60 kg potash (K_2O) per hectare. These nutrients plus 110 kg P_2O_5 ha^{-1} in high P treatment were incorporated into 20 cm soil with the help of cultivator prior to sowing. The fertilizer sources for N, K and P were urea, sulfate of potash (SOP, 50% K_2O) and triple superphosphate (TSP, 46% P_2O_5). The plots were irrigated with canal water as and when required. The crop was maintained free from weeds and other biotic stresses.

Crop measurements: yield attributes, P analysis and efficiency indices

At crop maturity, five plants of each genotype from each subplot were selected randomly and their plant height was measured with the help of meter rod from the stem base to the top of spike (awns excluded) of the tallest culm and averaged. The number of tillers of the selected plants was counted and spikes form the main tillers were cut with scissor to measure their lengths from first node of rachis to the top of spike excluding awns (Liu et al., 2022). Each spike was threshed with hand to count number of grains per spike. The grains obtained from these spikes were pooled with the rest of produce from the respective experimental unit to obtain the grain yield. To separate the grains and straw, the crop was harvested by hand and threshed. 100-grain weight of randomly sampled hundred kernels was recorded with the help of top-loading digital balance. Grain and straw samples of each genotype from each subplot were oven-dried at 70 °C for 72 hours. After the dry grain and straw samples were finely ground, 0.5 g of the material was digested in 10 mL di-acid mixture of nitric and perchloric acid (Miller, 1998). The phosphorus contents of the digest were measured by spectrophotometer using the method of Chapman and Pratt (1961). By multiplying the dry matter yield by the P concentration, P uptake in grain or straw was determined. P uptake in grain and straw was added together to get the total P uptake. The relative tolerance to P deficiency stress known as the phosphorus stress factor (PSF) was determined by dividing the difference in grain yield at two P levels by the grain yield attained at high P level. Other P efficiency indices e.g. P harvest index (PHI), quotient of P utilization (QPUt), P utilization efficiency (PUtE), P acquisition efficiency (PAE) and P use efficiency (PUE) were calculated by the following formulas of Gill et al. (2004) and Parentoni and Souza Júnior (2008):

$$\text{PSF (\%)} = \frac{\text{Grain yield at high P (kg ha}^{-1}\text{)} - \text{Grain yield at low P (kg ha}^{-1}\text{)}}{\text{Grain yield at high P (kg ha}^{-1}\text{)}} \times 100$$

$$\text{PHI (kg kg}^{-1}\text{)} = \frac{\text{P uptake in grain (kg ha}^{-1}\text{)}}{\text{Total P uptake (kg ha}^{-1}\text{)}}$$

$$\text{QPUt (kg kg}^{-1}\text{)} = \frac{\text{Grain yield (kg ha}^{-1}\text{)}}{\text{P uptake in grain (kg ha}^{-1}\text{)}}$$

$$\text{PUtE (kg kg}^{-1}\text{)} = \frac{\text{Grain yield (kg ha}^{-1}\text{)}}{\text{Total P uptake (kg ha}^{-1}\text{)}}$$

$$\text{PAE (kg kg}^{-1}\text{)} = \frac{\text{Total P uptake (kg ha}^{-1}\text{)}}{\text{P supply (kg ha}^{-1}\text{)}}$$

$$\text{PUE (kg kg}^{-1}\text{)} = \text{PUtE} \times \text{PAE}$$

According to Moll et al. (1982), the relative significance of PAE and PUtE in the P usage efficiency was investigated. This methodology determines the relative contribution of two experimentally obtained variables (e.g. PAE and PUtE) to a third variable (e.g. PUE), which is derived by multiplying PAE and PUtE. An additive relationship [log PUE (Y) = log PAE (X_1) + log PUtE (X_2)] was created by applying a logarithmic modification to the multiplicative relationship (PUE = PAE × PUtE). The relative importance of PAE over PUE was a function of the product of two quantities: a) the coefficient of correlation between variable (X_1) and (Y) or r_{X1Y}, and b) the ratio of the standard deviation of X_1 and Y (S_{X1}/S_Y). Similarly, the relative contribution to the P utilization efficiency (PUtE) of the P harvest index (PHI) and the quotient of P utilization (QPUt) was found.

Statistical analysis

Analysis of variance (ANOVA) was used to analyze the data regarding different growth, yield, and P-related characteristics for the split-plot design. Tukey's honestly significant difference (HSD) approach was used to separate the treatment means at the 5% probability level (Gomez and Gomez, 1984).

Results

Growth and yield related attributes

Wheat genotypes (G) differed significantly ($P < 0.05$) for plant height, tiller count plant^{-1}, spike length, number of grains spike^{-1}and 100-grain weight at each phosphorus (P) level (Table 1). However, P levels and P × G interactions could not produce significant effect on the above mentioned attributes except no. of grains spike^{-1}. Mean plant height varied between 86.78 (MK-5) to 105.89 cm (MK-2) at deficient P and between 88.89 (MK-6) to 105.3 cm (MK-7) at adequate soil P level (Table 2). Across the two P levels, MK-2 exhibited the highest while MK-5 revealed the lowest plant height. Tiller count plant^{-1} increased from 7.72 at deficient P to 8.23 at high P, although non-significantly. However, genotypes produced significant variations for tiller count, with MK-5 and MK-3 producing maximum and minimum tillers per plant, respectively across both P levels (Table 2). Likewise, spike length increased from 12.81 cm at deficient P to 13.0 cm at high P supply. The longer spikes were produced by MK-3 at both P levels while MK-6 produced shorter spikes (Table 2). Increasing P level from deficient to sufficient range resulted in higher number of grains per spike (from 68.17 to 73.03). Averaged across two P levels, genotypes MK-3 and MK-7 produced the highest number of grains per spike while MK-1 exhibited the lowest value. Phosphorus application could not significantly (P > 0.05) increase the 100-grain weight of wheat genotypes. Genotype MK-3 and MK-8 exhibited the lowest and the highest 100-grain weight, respectively, at both P levels (Table 2).

Table 1. Means and mean squares of phosphorus level (P), genotype (G) and P × G interaction for various traits of wheat genotypes at low (0 kg P_2O_5 ha^{-1}) and high P (110 kg P_2O_5 ha^{-1}) level.

Traits	Low P Mean	High P Mean	Mean square P (df:1)	Mean square G (df:9)	Mean square P×G (df:9)
Plant height (cm)	95.99	96.88	11.97 ns	203.39***	5.03 ns
No. of tillers $plant^{-1}$	7.72	8.33	5.61 ns	9.19***	0.551 ns
Spike length (cm)	12.81	13.13	1.56 ns	6.89***	0.12 ns
No. of grains $spike^{-1}$	68.17	74.03	516.27***	251.71***	15.64 ns
100-grain weight (g)	4.22	4.26	0.03 ns	0.66***	0.01 ns
Grain yield (t ha^{-1})	4.55	4.83	1.17*	1.92***	0.14**
Straw yield (t ha^{-1})	7.99	8.33	1.71 ns	7.62***	1.38***
Total yield (grain + straw) (t ha^{-1})	12.55	13.16	5.56 ns	14.52***	1.76**
Grain P concentration (mg g^{-1})	3.05	2.99	0.04 ns	0.35**	0.03 ns
Straw P concentration (mg g^{-1})	0.56	0.63	0.06 ns	0.07*	0.01 ns
Grain P uptake (kg ha^{-1})	13.79	14.41	5.61 ns	14.42***	1.88*
Straw P uptake (kg ha^{-1})	4.52	5.15	5.86***	5.39***	0.97*
Total P uptake (kg ha^{-1})	18.32	19.56	22.85 ns	24.13***	4.00*
P stress factor (%)	5.64	-	-	86.99***	-
P harvest index (kg kg^{-1})	0.76	0.74	0.01 ns	0.01***	0.001 ns
Quotient of P utilization (kg kg^{-1})	331.64	336.54	360.44 ns	3991.41***	282.05 ns
P utilization efficiency (kg kg^{-1})	250.54	247.12	176 ns	1996***	427*
P acquisition efficiency (kg kg^{-1})	0.79	0.27	3.93**	0.02***	0.01***
P use efficiency (kg kg^{-1})	195.61	67.81	244865***	1521***	440 ns

* = Significant at $P < 0.05$, ** = Significant at $P < 0.01$, *** = Significant at $P < 0.001$, ns = non-significant at $P > 0.05$

Table 2. Performance of wheat genotypes for plant height, tiller count $plant^{-1}$, spike length, no. of grains $spike^{-1}$ and 100-grain weight at low (0 kg P_2O_5 ha^{-1}) and high P (110 kg P_2O_5 ha^{-1}) level.

Genotypes	Plant height (cm)		Tillers count $plant^{-1}$		Spike length (cm)		No. of grains $spike^{-1}$		100-grain weight (g)	
	Low P	High P	Low P	High P	Low P	High P	Low P	High P	Low P	High P
MK-1	96.28	96.44	7.44	8.22	13.28	13.50	64.33	74.33	4.34	4.37
MK-2	105.89	104.33	6.78	7.33	13.17	13.33	65.33	72.33	4.48	4.33
MK-3	88.78	88.89	6.22	6.56	11.00	11.17	63.67	65.33	3.69	3.71
MK-4	97.78	98.11	9.78	11.56	14.22	14.78	79.00	89.67	4.49	4.57
MK-5	86.78	90.00	8.22	8.00	12.83	13.06	65.00	70.67	4.07	4.19
MK-6	89.44	89.67	7.56	7.67	11.89	12.94	66.00	69.00	3.96	4.02
MK-7	100.50	105.33	7.11	7.33	11.22	11.50	60.67	67.33	3.85	3.97
MK-8	96.44	97.22	8.89	9.33	13.78	13.89	77.67	81.33	4.81	4.78
MK-9	99.50	99.28	6.67	8.11	13.44	13.72	68.67	77.00	4.43	4.58
NIA-Sunder	98.50	99.56	8.56	9.22	13.28	13.44	71.33	73.33	4.08	4.12
$HSD_{0.05}$, P	-		-		-		0.79		-	
$HSD_{0.05}$, G	5.91		1.81		1.08		5.96		0.34	
$HSD_{0.05}$, P × G	-		-		-		-		-	

$HSD_{0.05}$ = Honestly Significant Difference at 5% probability level, P = phosphorus levels, G = genotypes, P × G = interaction between phosphorus levels and genotypes

Grain, straw and total yield

The main and interaction effects of P and G had a significant ($P < 0.05$) impact on the grain yield of wheat genotypes (Table 1). Grain yield increased, on average, from 4.55 t ha^{-1} with deficient P to 4.83 t ha^{-1} (6 % increase) at adequate P supply across all genotypes. The genotype MK-4 and MK-8 produced the highest grain yield while MK-3 and MK-7 produced the lowest grain yield at both P levels. Phosphorus levels could not significantly ($P < 0.05$) influence straw and total yield of wheat genotypes; however, genotypic response for straw yield was variable at each P level. Across the two P levels, MK-4 showed the highest straw as well as total yield while MK-3 exhibited the lowest straw and total yield (Table 3).

Table 3. Performance of wheat genotypes for grain, straw and total yield, and phosphorus stress factor (PSF) at low (0 kg P_2O_5 ha^{-1}) and high P (110 kg P_2O_5 ha^{-1}) level.

Genotypes	Grain yield (t ha^{-1})		Straw yield (t ha^{-1})		Total yield (t ha^{-1})		PSF (%)
	Low P	High P	Low P	High P	Low P	High P	
MK-1	4.80	4.89	8.36	9.47	13.16	14.35	1.71
MK-2	4.69	4.79	8.92	8.30	13.61	13.09	2.02
MK-3	3.55	4.04	5.95	6.05	9.50	10.09	13.04
MK-4	5.05	6.10	9.00	10.28	14.05	16.38	17.08
MK-5	4.45	4.56	6.96	7.23	11.41	11.80	2.25
MK-6	4.20	4.47	8.10	6.55	12.30	11.03	6.07
MK-7	3.90	4.13	8.30	8.85	12.20	12.99	5.62
MK-8	5.48	5.48	8.49	8.19	14.00	13.68	0.06
MK-9	4.78	5.00	7.16	8.19	11.94	13.19	4.20
NIA-Sunder	4.64	4.86	8.66	10.13	13.33	14.99	4.34
$HSD_{0.05}$, P	0.23		-		-		-
$HSD_{0.05}$, G	0.39		0.82		1.37		6.18
$HSD_{0.05}$, P × G	0.63		1.31		2.19		3.68

$HSD_{0.05}$ = Honestly Significant Difference at 5% probability level, P = phosphorus levels, G = genotypes, P × G = interaction between phosphorus levels and genotypes

The term "phosphorus stress factor" (PSF) describes the wheat genotypes' relative tolerance to P deprivation. Table 3 shows that it differed considerably ($P < 0.05$) amongst wheat genotypes. The PSF showed a wide genetic variability in wheat genotypes for grain yield in response to elevated P levels, ranging from 0.06 to 17.08 %. Because genotype MK-8's PSF value was less than one, it did not respond to a high P level. Higher PSF values, however, indicate that MK-3 and MK-4 are highly P responsive (Table 3).

Phosphorus concentration and uptake

Wheat genotypes differed significantly in P concentration present in grain and straw at each P level (Table 1). There was no discernible increase in P concentration in either grain or straw with a higher P level. As P increased, the concentration of P in the grain actually slightly reduced, demonstrating the dilution effect of yield increase on grain P concentration. The P concentration in grain and straw of wheat genotypes, respectively, ranged from 2.76 to 3.43 mg kg^{-1} and 0.41 to 0.72 mg kg^{-1}, in the absence of P fertilization. Application of P at the rate of 110 kg P_2O_5 ha^{-1} caused variations in grain P concentration ranging from 2.80 to 3.21 mg kg^{-1} and straw P concentration from 0.52 to 0.80 mg kg^{-1} (Table 4).

Table 4. Phosphorus concentration and uptake in grain and straw of wheat genotypes grown at low (0 kg P_2O_5 ha^{-1}) and high P (110 kg P_2O_5 ha^{-1}) level.

Genotypes	P concentration (mg g^{-1})				P uptake (kg ha^{-1})					
	Grain		Straw		Grain		Straw		Total	
	Low P	High P	Low P	High P	Low P	High P	Low P	High P	Low P	High P
MK-1	2.89	3.02	0.68	0.64	13.96	14.70	5.69	6.02	19.65	20.72
MK-2	2.76	2.80	0.64	0.75	12.98	13.40	5.70	6.32	18.69	19.72
MK-3	3.43	3.47	0.41	0.64	12.19	14.02	2.46	3.89	14.64	17.91
MK-4	2.94	2.88	0.55	0.54	14.81	17.62	4.98	5.57	19.79	23.19
MK-5	3.36	3.18	0.68	0.65	15.00	14.53	4.75	4.74	19.75	19.27
MK-6	3.43	3.21	0.72	0.80	14.46	14.39	5.84	5.21	20.33	19.61
MK-7	2.81	2.70	0.45	0.67	10.85	11.14	3.75	5.89	14.61	17.03
MK-8	3.03	2.90	0.62	0.64	16.76	15.85	5.26	5.22	22.02	21.08
MK-9	2.82	2.96	0.42	0.52	13.38	14.78	3.00	4.23	16.38	19.00
NIA-Sunder	2.96	2.82	0.45	0.43	13.57	13.66	3.80	4.38	17.38	18.05
$HSD_{0.05}$, P	-		-		-		0.03		-	
$HSD_{0.05}$, G	0.59		0.31		1.69		1.13		2.29	
$HSD_{0.05}$, P ×G	-		-		2.72		1.81		-	

$HSD_{0.05}$ = Honestly Significant Difference at 5% probability level, P = phosphorus levels, G = genotypes, P × G = interaction between phosphorus levels and genotypes

Only genotypic and G × P factors significantly impacted the P absorption in grain (Table 1). On an average, P uptake in grain increased from 13.80 (without P) to 14.41 kg ha^{-1}(with P addition). Among various genotypes, MK-8 and MK-4 were the highest accumulator of P in grain while MK-7 accumulated the least P in grain, when averaged across two P levels. Phosphorus uptake in straw increased significantly (14% over control/no P) when adequate P was added into soil. Genotypes varied substantially for straw P uptake, with MK-2 and

MK-3 accumulating the highest and the lowest P in straw, respectively. Overall, it ranged from 2.46 to 5.84 kg ha^{-1} at deficient P level and from 3.89 to 6.32 kg ha^{-1} under high P treatment (Table 4). The amount of total P uptake increased, though non-significantly, from 18.32 kg ha^{-1} under P deficiency to 19.56 kg ha^{-1} in P-treated soil. Overall, it ranged from 14.61 to 22.02 kg ha^{-1} at deficient P level and from 17.03 to 23.19 kg ha^{-1} under P adequacy (Table 4).

Phosphorus use efficiency and its components

The phosphorus harvest index (PHI) shows the amount of P that has accumulated in grain in relation to the overall amount of P at crop harvest (grain + straw). While genotypes showed significant diversity for P allocation to grains at both P levels, the PHI was not significantly ($P < 0.05$) impacted by P levels (Table 1). The PHI varied from 65.44 to 78.51% at high P and from 69.71 to 83.16% at low P. According to Table 5's PHI values, wheat genotypes assigned the majority of the P reserves to grain.

The capacity of a crop to yield grain per unit of P collected in the above-ground portions is determined by the quotient of P utilization (QPUt). Table 1 shows that there was no significant ($P > 0.05$) impact of the P levels and G × P interactions on the QPUt. At both P levels, however, genotypic effects were more noticeable. QPUt ranged in magnitude from 289 to 372 kg kg^{-1} at high P treatment and from 291 to 362 kg kg^{-1} at low P treatment. MK-3 and MK-7 showed the lowest and greatest values of QPUt, respectively, when averaged over both P levels (Table 5).

Table 5. Phosphorus use efficiency and its components of wheat genotypes at low (0 kg P_2O_5 ha^{-1}) and high P (110 kg P_2O_5 ha^{-1}) level.

Genotypes	P harvest index (kg kg^{-1})		Quotient of P utilization (kg kg^{-1})		P utilization efficiency (kg kg^{-1})		P acquisition efficiency (kg kg^{-1})		P use efficiency (kg kg^{-1})	
	Low P	High P	Low P	High P	Low P	High P	Low P	High P	Low P	High P
MK-1	0.72	0.71	344	333	245	236	0.84	0.29	207	69
MK-2	0.70	0.70	362	358	252	244	0.80	0.28	202	67
MK-3	0.83	0.79	293	289	243	226	0.63	0.25	152	57
MK-4	0.75	0.76	341	346	257	264	0.85	0.33	217	86
MK-5	0.76	0.76	298	314	226	237	0.85	0.27	191	64
MK-6	0.72	0.73	291	311	207	228	0.87	0.28	180	63
MK-7	0.74	0.65	360	372	267	243	0.63	0.24	167	58
MK-8	0.76	0.75	328	347	249	261	0.95	0.30	235	77
MK-9	0.82	0.78	358	338	292	263	0.70	0.27	205	70
NIA-Sunder	0.79	0.76	342	356	267	270	0.75	0.25	199	68
$HSD_{0.05}$, P	-		-		-		0.07		2.12	
$HSD_{0.05}$, G	0.08		23.75		24.82		0.07		29.87	
$HSD_{0.05}$, P×G	-		-		39.74		0.12		-	

$HSD_{0.05}$ = Honestly Significant Difference at 5% probability level, P = phosphorus levels, G = genotypes, P × G = interaction between phosphorus levels and genotypes

Phosphorus rates could not produce significant effects on P utilization efficiency (PUtE), though, genotypes and G × P interactions significantly ($P < 0.05$) influenced PUtE (Table 1). Under low P treatment, the PUtE ranged from 207 to 292 kg grain yield kg^{-1} total P uptake, whereas under high P treatment, it ranged from 226 to 270 kg grain yield kg^{-1} total P uptake (Table 5). Averaging across P rates, the genotype MK-9 was highly efficient in P utilization, while MK-6 showed the lowest PUtE (Table 5). Phosphorus acquisition efficiency (PAE) and P use efficiency (PUE) were significantly ($P < 0.05$) affected by P rates, genotypes and G × P interactions (Table 1). The PAE decreased by 78% under high P treatment. It varied between 1.19 and 1.79 kg total P uptake kg^{-1} P supply under no/zero P application, and between 0.28 and 0.38 kg total P uptake kg^{-1} P supply in P treated soil (Table 5). Genotype MK-8 showed the highest PAE, while MK-7 and MK-3 showed the lowest PAE when evaluated across both P levels. It is interesting to note that with P deprivation, more variations in PUtE and PAE were seen among wheat genotypes. When P @ 110 kg P_2O_5 ha^{-1} was given to the soil, phosphorus use efficiency (PUE), the product of PUtE and PAE, dropped from 378 to 81 kg grain yield kg^{-1} P supply (79% decrease). Table 5 shows that its ranges were 289-446 kg grain yield kg^{-1} P supply at low P and 67-101 kg grain yield kg^{-1} P supply at high P. MK-8 and MK-4 had the highest PUE when averaging across P levels, while MK-3 and MK-7 had the lowest PUE.

Table 6 displays the relative significance of the P use efficiency components: acquisition and utilization, based on the methodology of Moll et al. (1982). According to the data, 83.1 and 16.6% of the genotypic variability for PUE at low P treatment was explained by PAE and PUtE, respectively. PUtE accounts for 37.6% of the variability in P use efficiency seen in P fertilized soil, while PAE contributed 62.9% of this variability. The correlation coefficients and the ratio of the variability found between PUE and its constituents, PAE and PUtE,

(Table 6) provide more insight into these interactions. In P deficient circumstances, the high correlation between PAE and PUE (r = 0.751) and their substantial standard deviation ratio (1.107) account for 83.1% of the variability in PUE. Due to a lower correlation (r = 0.221) between these two variables and a smaller variability for PUtE (0.751), PUtE at low soil P only explained 16.6% of the variability found in PUE. Similar pattern was noted at the high P level.

The PUtE of the genotypes was also decomposed into two components: quotient of P utilization (QPUt) and P harvest index (PHI). Wheat genotypes exhibited more variability for QPUt than PHI which was confirmed by the higher ratio of standard deviation of QPUt and PUtE at both low and high P environments (Table 6). The QPUt accounted for the largest fraction of the variability observed in the genotypes for PUtE at low P (72.5%) and at high P environments (111.2%), due to a higher correlation coefficient of QPUt with PUtE and also to a larger ratio of standard deviation between QPUt and this trait (Table 6).

Table 6. Relative contribution of the components traits (X_i) to the variation of resultant trait (Y) according to Moll et al. (1982).

Resultant trait (Y)	Component trait (X_i)	Low P			High P		
		Contribution of X_i to Y	r_{xiy}	Sx_i/S_y	Contribution of X_i to Y	r_{xiy}	Sx_i/S_y
P use efficiency	P utilization efficiency	0.166	0.221	0.751	0.377	0.715	0.526
	P acquisition efficiency	0.831	0.751	1.107	0.629	0.864	0.729
P utilization efficiency	Quotient of P utilization	0.725	0.798	0.908	1.112	0.754	1.476
	P harvest index	0.258	0.431	0.598	-0.130	-0.121	1.079

r_{xiy} is the coefficient of correlation between the components trait (X_i) and the resultant trait (Y), while Sx_i/S_y is the ratio between standard deviation of X_i and Y.

Discussion

Selection of crop genotypes that adapt well to situations of contrasting P availability is an efficacious strategy for sustainable P use. A genotype is considered ideal if it yields higher under P deficiency and responds well to P application (van de Wiel et al., 2016). The primary goal of evaluating germplasm under low P conditions is to increase PAE, and genotypes chosen in this manner frequently have low yield potential and P fertilization responsiveness. High input conditions are ideal for expressing yield potential (Sandaña, 2016). Therefore, selection under various P supply conditions can lead to improvements in both PAE and PUtE in the given species. This purpose is effectively covered by the current study.

Grain yield of wheat genotypes varied significantly at both P levels. Genotypes MK-3 and MK-4 with PSF > 10% were highly responsive to P fertilization (Table 3). However, grain yield of MK-8 was not affected by P deficiency as its phosphorus stress factor was less than 1. Such genotypes have the ability to sustain growth and development even in low P conditions (Abbas et al., 2018a). According to Yaseen and Malhi (2009b), modern wheat cultivars can yield more than their predecessors, even though P application rates are lower. As demonstrated by their high grain and total P uptake under low P treatment, genotypes like MK-8, which are less sensitive to P deprivation, translocate more P towards grain (Table 3). Our claim was reinforced by the notable positive correlation between grain yield and both grain P absorption ($r > 0.73$, $P < 0.001$) and total P uptake ($r > 0.72$, $P < 0.001$) at both P levels.

By choosing genotypes with greater P utilization quotient (QPUt) and P harvest index (PHI), grain output can be increased through higher PUtE (Sandaña and Pinochet, 2014). QPUt corresponds exactly to the reciprocal of the grain P concentration and is equal to the grain yield divided by the quantity of P absorbed in the grain (grain yield multiplied by grain P concentration). The P utilization efficiency, therefore, increases with decreasing grain P concentration (Parentoni and Souza Júnior, 2008). Selection of wheat genotypes with low grain P concentration will support sustainable land usage (Korkmaz et al., 2009). In this experimentation, grain P concentration was negatively related with PUtE at low P ($r = -0.53$, $P < 0.01$) and high P ($r = -0.45$, $P < 0.05$) which infers that selecting for lower grain P concentration may help in evolving cultivars with increased PUtE (Gemenet et al., 2015). However, there is a limit to the approach of P concentration reduction in grain. For nutritional purposes and seed vigor, the grain must have a minimal amount of P (White and Veneklaas, 2012). Increased P translocation into the grains - the PHI- can increase P utilization efficiency without lowering grain P content. Our research findings demonstrated that wheat grain at both P levels gathered more than 73% of the total P (Table 4), indicating a narrow space for breeding for greater PHI. If P absorption efficiency is not increased, selecting for high grain production under these conditions will further lower grain P concentration due to the dilution effect (Rose et al., 2011). Because variations in the P harvest index appear to have little bearing on the PUtE of the wheat genotypes under varying P conditions, selection strategies aimed at increasing wheat P utilization efficiency in alkaline calcareous soils should concentrate on lowering grain P concentration (Yaseen and Malhi, 2009a).

Important genetic variability in PAE was observed in the present study (Table 5). The PAE had strong positive relationship with total P uptake (r > 0.90, $P < 0.001$), and the total P uptake was related to grain (r > 0.72, $P < 0.001$) and total yield (r > 0.50, $P < 0.05$) at both P levels. Thus, PAE can be improved by selecting genotypes with higher grain and/or total yield (Yaseen and Malhi, 2009b). Differential P uptake by wheat genotypes having comparable yield indicates important genotypic differences in PAE (Table 4). Wheat genotypes with greater PAE (e.g. MK-8) under both P conditions require lower soil P threshold values for fertilizer response than genotypes with low PAE (MK-3 and MK-7) (Irfan et al., 2018). In low input cropping systems, cultivating genotypes with high PAE would significantly boost productivity. Conversely, in high input systems, these genotypes would lessen the wasteful use of P fertilizers and environmental issues related to P losses to water bodies (Manschadi et al., 2014; Ruark et al., 2014). The improved P acquisition by crop can be attributed to several mechanisms, i.e. root structural and architectural modifications (Niu et al., 2013), up-regulation of high-affinity root P transporters (Amtmann and Armengaud, 2009), mycorrhizal associations (Smith and Read, 2010), and enhanced carboxylate exudations into rhizosphere (White et al., 2013). Root characteristics were not examined in this investigation. Thus, more research on PAE and associated root properties can help choose cultivars with better qualities related to uptake of P.

Our research shows that when it comes to determining grain yield and PUE in wheat genotypes, PAE is more important than PUtE. According to our findings, PAE had a two-fold greater significance at high P conditions and an approximately five-fold greater significance at low P conditions in explaining the genetic variability for PUE (Table 6). Our results were consistent with those of Manske et al. (2001), who found that P acquisition in low and high P acidic soil accounted for > 85% of the variability in wheat PUE. The findings of Parentoni and Souza Júnior (2008) also substantiate our results. Contrarily, McDonald et al. (2015) reported higher contribution of P utilisation to the genetic variability in grain yield of wheat genotypes grown under diverse soil and environmental conditions. These contrasting results indicate the influence of soil type, P status and environmental conditions (Parentoni and Souza Júnior, 2008; Wang et al., 2010). Therefore, mechanisms associated to P acquisition efficiency rather than P internal utilization should receive more focus in physiological research on P use efficiency of the test genotypes in our study (Rose and Wissuwa, 2012). Future breeding initiatives should prioritize root structural and architectural traits due to the paramount significance of P acquisition in high P-fixing alkaline calcareous soil conditions. The data reported in this study show that there exist sufficient variations among wheat genotypes for PUE which can be exploited for wheat improvement. Moreover, it was revealed that MK-4 and MK-8 were the best wheat genotypes in terms of PUE under contrasting P availabilities.

Conclusion

The current study showed that when several genotypes were cultivated in field conditions with both low and high P supplies, there was significant genetic variability among wheat genotypes for PUE, PAE, PUtE, and the related characteristics. It was shown that the genotypes MK-4 and MK-8 were the best fits for soils with different levels of P availability. Furthermore, the PAE of wheat genotypes was primarily responsible for PUE discrepancies. By choosing genotypes with lower grain P concentration, it is possible to boost P utilization efficiency by placing more weight on the quotient of utilization than the P harvest index. These results highlight the necessity of screening vast genetic pools on various soil types with variable P supply. This will provide a window of opportunity for conventional breeding to increase PUE in wheat production systems. Furthermore, by modifying P fertilization in accordance with cultivar sensitivity to P deprivation (tolerant vs. sensitive genotypes), this information will be helpful for P management, which will ultimately lower production costs and fertilizer requirements especially in P-limited alkaline calcareous soils.

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