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Research Article

Genotypic Variation for Phosphorus-use Efficiency Characteristics in Faba Bean (*Vicia faba* L.)

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Abstract

Developing phosphorus-use efficient faba bean (*Vicia faba* L.) genotypes is crucial for ensuring sustainable production in low phosphorus soils. The present study was conducted with the objective of identifying faba bean genotypes that use P efficiently. Twenty genotypes of faba bean in the field and 12 genotypes in the greenhouse were planted under two P fertilizer regimes (0 and recommended, 46 kg/ha). Withholding P fertilizer (0 kg/ha) application has significantly affected the performance of PUE traits; with decreasing effect ranging from 13.8% for grain yield (GY) to 38.6% for biomass phosphorus uptake (BPU) and increasing effect ranging from 5.9% for phosphorus harvest index (PHI) to 305.6% for PUE. Difference among the genotypes for most PUE traits were highly significant ($P<0.01$) under both P fertilizer regimes. Genotypes Moti, Gebelcho, and CS20DK in the field; Hachalu, Gebelcho and Dosha in the greenhouse, were efficient responder (ER) and had statistically higher mean for most PUE traits. Most traits including PUE had moderately high (60-79%) heritability. Biplot analysis showed that PUE, GY, BPU, and PUpE contributed the highest genetic divergence indicating their importance in breeding. Correlation analysis revealed that PUE was positively correlated to most traits including GY. It was shown that PUE and GY were strongly correlated to PUpE than they were to PUtE; suggesting that PUpE was more critical than PUtE for PUE variation. Findings of the study could be used to screen genotypes which have higher PUE and use them for breeding new cultivars better adapted to low P status soils.

Keywords

Phosphorus (P), P Uptake and Utilization Efficiency, Faba Bean, Genotypes

1. Introduction

Faba bean (*Vicia faba* L.) is the fourth most important food legume in the world in terms of area of production, after field pea, chickpea, and lentil [1]. Ethiopia is one of the top five leading producers and consumers of faba bean in the

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world [1]. Its superior nutritional value compared to other grain legumes makes it a good source of protein for many people in Africa, Asia and Latin America, where animal protein is mostly unaffordable [2].

Phosphorus (P) plays an important role in nodule initiation, nitrogen fixation and other biochemical processes [3, 4], and its deficiency often results in serious yield reduction [5-7]. Soil phosphorus deficiency is a major constraint to faba bean production. It is a widespread problem in Ethiopia and other countries in Sub-Saharan Africa (SSA) [8]. Farmers in SSA have limited resources and apply little or no P fertilizers [9, 10], which is mainly due to continuous price increases in phosphorus fertilizer [11]. For instance, Belachew et al. [12] reported that only half of faba bean fields were fertilized in Ethiopia in 2019.

Vance et al., [13] and McBeath et al. [14] reported that even where P fertilizers are applied, 70-90% of the applied P is not available to crops due to fixation in the soil by Fe, Al, and Ca. There are also predicted concerns over the source of P to support agriculture in the future as the world's reserve of phosphate rock could be depleted in the next few decades [15]. Consequently, selection and development of P-efficient' genotypes with greater ability to yield under P-deficient soil conditions should be an important plant breeding goal [16, 17].

Production of P-efficient genotypes would reduce the production costs of P fertilization, minimize environmental pollution and contribute to maintenance of world P resources globally [7, 13]. The cultivation of P-efficient faba bean genotypes would be an important strategy for increasing soil fertility in traditional cropping systems [18] through faba bean-cereal rotation. Phosphorus-use efficient (PUE) genotypes are reported to have higher grain yield due to high P uptake efficiency (PUpE) and/or high P utilization efficiency (PUtE) [16]. P-efficient cultivars showed higher P uptake, dry matter, and grain yield in P-deficient soil via root foraging and P-mining strategies owing to the low mobility of P and relatively high P availability in surface soil layers [6]. Thus, P-use efficient genotypes will contribute to agricultural sustainability by reducing the need to increase soil P status to achieve increased productivity and increasing the efficiency of use of applied P [19].

P-use efficiency has two major components: P uptake and utilization efficiency. P-uptake efficiency is the capacity of plants to uptake P from the soils while P is utilization efficiency is how efficiently the plants utilize the absorbed P [20]. Therefore, different scientists have proposed different criteria of screening genotypes for P-use efficiency under P-deficient conditions, such as total P uptake [21], dry matter produced per unit of P applied [22], and the ratio of physiologically active P to total P uptake [23].

Significant variations in P-use efficiency have been reported among varieties of many crops including faba bean [24-26]. Furthermore, achieving higher P efficiency is possible through a better understanding of the coordination of P uptake, transport, and remobilization in crops [27, 28]. Hence, screening P-efficient cultivars is very important to ensure sustainable production of the crop in P-deficient soils of Ethiopia. The present study was more comprehensive than similar studies previously conducted for faba bean in Ethiopia as it included higher number of genotypes, number of locations, experiments being conducted at both field and greenhouse and consideration of more number of PUE traits. Consequently, the present study was conducted with the objective of investigating the genotypic variation ~~screening~~ of faba bean genotypes for p-use efficiency.

2. Materials and Methods

2.1. Study Sites and Experimental Design

The study was carried out in 2015 and 2016 under field and greenhouse conditions. The field experiments were conducted under rain-fed condition at Adadi and Holetta, two faba bean growing areas in Ethiopia. The greenhouse experiment was conducted using the soil from Ambo, central Ethiopia. The geographical coordinates, climatic and soil physical and chemical properties of the sites used for the experiments are indicated in Table 1.

Table 1. *General description of the study areas and their soil physico-chemical properties.*

Parameters	Field		Greenhouse
	Adadi	Holetta	Soil
Altitude (masl)	2520	2390	----
Latitude (N)	8.21	9.04	----
Longitude (E)	38.29	38.03	----
Temperature (°C)	8.5-23.5	6.4 -24.4	----
Rainfall (mm)	930.8	760.8	----
Soil type	Vertisol	Nitisol	Vertisol
Soil textural class	Clay	Clay	Clay
% Clay	61.18	46.42	66.58
% Silt	25.34	32.48	15.25
% Sand	12.54	20.17	15.45
pH (H_20)	6.4	7.3	6.79
Available P (ppm)	15.94	23.67	19.92
Total N (%)	0.15	0.18	0.17
K (ppm)	37.35	25.79	31.56
Organic C (%)	1.16	0.738	1.17
CEC (Meq/100g)	25.13	23.05	18.17

Parameters	Field		Greenhouse
	Adadi	Holetta	Soil
EC (μS)	405.63	697.67	--

2.2. Plant Materials and Experimental Method

Twenty faba bean genotypes were used for the field experiments while twelve genotypes were used in the greenhouse. The genotypes included highly commercialized high yielding varieties and most promising breeding lines. The details of the germplasm are presented in Table 2. Seeds of these genotypes were obtained from Holetta Agricultural Research Center. Undamaged, clean and uniform sized seeds of each genotype were used. Soil samples were collected, before planting, from 0-30 cm depth at each location for analysis following the procedure described by [29]. The experimental plots or pots were prepared in pairs in such a way that both are treated in the same way (being a mirror of each other) where one of the pair received phosphorus fertilizer (46 kg/ha P_2O_5) and the second was devoid (0) of the fertilizer. For the field experiment, plots consisted of single rows of 4 m length spaced 0.4 m apart, with seeds planted 0.1 m apart in each row. Two seeds were planted per hill and thinned to one at one week after planting to achieve a plant population of 250,000 plants/ha. For the greenhouse study, each pot (40 cm diameter) was filled with 5 kg of sterilized sand-soil mixture (2:1). Pots were watered to approximately 75% field capacity prior to planting. Four pre-germinated seeds were planted per pot and later thinned to three. Pots were watered daily till maturity. The experimental design was randomized complete block design (RCBD) in both experiments and each treatment was replicated three times.

Table 2. Description of the faba bean genotypes used in the study.

SN	Genotype	Pedigree	Year of Release	1000 seed weight	Altitude Range (masl)	Yield (t/ha)	
						Research Station	Farmer Field
1	Lalo	Selale Kasim 89-4	2002	325	2600-3000	3.6	--
2	Dagim	Girar Jarso 89-8	2002	299	2600-3000	3.5	--
3	CS20DK	CS20DK	1977	476	2300-3000	2.0-4.0	1.5-3.0
4	Obse	CS20DK x ILB4427	2007	821	1800-3001	2.5-6.1	2.1-3.5
5	Gebelcho	ILB4726 x Tesfa	2006	797	1800-3001	2.5-4.4	2.0-3.0
6	Holetta-2	BPL 1802-2	2000	506	2300-3000	2.0-5.0	1.5-3.5
7	Hachalu	EH00102-4-1	2010	890	1900-2800	3.2-4.5	2.4-3.5
8	Wayu	Wayu 89-5	2002	312	2100-2700	1.8-3.2	1.0-2.3
9	Selale	Selale Kasim 91-13	2002	346	2100-2700	2.2-3.3	1.0-2.3
10	Didea	EH01048-1	2014	700	1800-2800	3.5-4.6	2.0-4.4
11	Gora	EK01024-1-2	2013	980	1800-2800	3.0-5.0	2.0-4.0
12	Dosha	Coll 155/00-3	2009	704	1800-3000	2.8-6.2	2.3-3.9
13	Walki	Bulga-70 x ILB4615	2008	676	1900-2800	2.4-5.2	2.0-4.2
14	NC58	NC58	1978	449	1800-3000	2.0-4.0	1.5-3.5
15	Moti	ILB4432 x Kuse 2-27-33	2006	781	1800-3000	2.8-5.1	2.3-3.5
16	Tumsa	Tesfa x ILB 4726	2010	737	1800-3000	2.5-6.9	2.0-3.8
17	EH06088-1	Advanced breeding lines	--	--	--	--	--
18	EH07015-7	Advanced breeding lines	--	--	--	--	--
19	EH06022-4	Advanced breeding lines	--	--	--	--	--
20	EH06006-6	Advanced breeding lines	--	--	--	--	--

2.3. Data Collection

2.3.1. Phosphorus Use Efficiency Traits

1. Shoot and grain phosphorus (P) concentrations were estimated by the methods described by Chapman and Pratt (1961). Shoot and grain phosphorus concentrations were read on a spectrophotometer at absorbance values of 420 nm. A standard curve was constructed to calculate the shoot and grain P concentrations of the test genotypes.
2. Plant P uptake was calculated for shoot, grain and total biomass [17, 30, 31] as follows: Shoot P uptake (SPU) = Shoot P concentration x Shoot dry weight; Grain P uptake (GPU) = Grain P concentration x Grain Yield; and Biomass P uptake, (BPU) = SPU + GPU.
3. Phosphorus-use efficiency (PUE) was calculated as P-utilization efficiency (PUtE) x P-uptake efficiency (PUpE) [32, 33]. PUtE was in turn calculated as Grain yield/P uptake. PUpE was estimated as P-uptake/ available P. Available P was estimated as the sum of P availability at sowing and P from fertilization.
4. Phosphorus harvest index (PHI,%), was calculated as (GPU/ BPU) x 100.
5. Apparent P-fertilizer recovery (APFR,%) was calculated as [(BPU+ - BPU-)/ P applied] x100, where BPU+ and BPU- are biomass phosphorus uptake under P fertilized and unfertilized trial respectively.
6. Phosphorus Agronomic efficiency (PAE) was calculated as (GY+ - GY-)/ P applied to treated plants, where GY+ and GY-; are grain yield under P fertilized and unfertilized trial respectively.
7. Phosphorus Physiological efficiency (PPE,%) was computed as (GY+ - GY-)/ (BPU+ - BPU-) x 100.
8. Phosphorus efficiency ratio (PER,%) was calculated as the ratio of shoot dry matter weight under low soil P to shoot dry matter weight under adequate P supply; (SDW-/ SDW+) x 100 [34].
9. Shoot dry weight (SDW) and grain yield (GY, g/plant) were estimated from five plants per plot and three plants per pot for field and greenhouse experiments, respectively.
10. Relative reduction (RR,%) of trait's performance under P unfertilized trial as compared to their performance under P-fertilized trial is calculated as; RR = 1- (performance of trait under P unfertilized / performance of trait under P fertilized trial) x 100. It is used to evaluate the sensitivity of the traits to reduced phosphorus amount in the soil.

2.3.2. Classification of Genotypes into Phosphorus-use Efficiency Groups

The genotypes were classified into phosphorus-use efficiency groups based on grain yield and phosphorus utilization efficiency. Using both traits as a means of categorization, four phosphorus efficiency classes are obtained [35-37] viz. (i) inefficient, non-responder (INR); (ii) efficient, non- responder (ENR); (iii) inefficient, responder (IR); and (iv) efficient, responder (ER). In this method, an efficient genotype performs better than the mean performance of other genotypes under low phosphorus; while a responder genotype performs better than the mean performance of other genotypes under high phosphorus. INR genotypes perform lower than the mean performance of other genotypes under low and high phosphorus, respectively.

2.4. Data Analysis

Data were checked for homogeneity of variance and transformed, where applicable, before statistical analysis. An individual site and combined analysis of variance were performed using SAS 9.3 [38]. Variance components were calculated using mixed models;

$$\rho_{ijk} = \mu + g_i + l_j + (gl)_{ij} + (r/l)_{jk} + e_{ijk} \tag{1}$$

Where ρ_{ijk} = phenotypic observation on variety i in replicate k at location j (i = 1...g, j = 1...L, and k = 1...r) and g, l and r = number of genotypes, locations and replications, respectively, μ = grand mean, g_i = the effect of genotype i, l_j = the effect of location j, $(gl)_{ij}$ = the interaction effect between genotype and location, $(r/l)_{jk}$ = the effect of replicate k within location j and e_{ijk} = error. Multiple mean comparisons were performed using Duncan's New Multiple Range Test at 0.05 level of probability. Genetic relationships among individuals were assessed by multivariate principal component analysis (PCA) and Genotype by trait (GT) biplot using Minitab19 software. Relative reduction (RR) of the agronomic performance of the genotypes on phosphorus untreated plot relative to their performance on phosphorus treated plot was calculated as, RR = 1- (performance without P/ performance with P). Broad sense heritability (h^2) was calculated as: $h^2 = \sigma^2 g / [\sigma^2 g + \sigma^2 gl/L + \sigma^2 e / (RL)]$; where $\sigma^2 p$, $\sigma^2 g$, $\sigma^2 gl$, and $\sigma^2 e$ are phenotypic, genotypic, genotype by location interaction, and error variances, respectively. L = number of locations, R = number of replications. Pearson's correlation coefficients were estimated using the PROC CANCORR subprogram of SAS.

3. Results

3.1. Effect of Phosphorus Application Levels on the Phosphorus Use Efficiency Traits

Mean performance of the phosphorus use efficiency traits under P-fertilized and P-unfertilized treatments in the field and greenhouse and their relative reductions are presented in

Table 3. In both the field and greenhouse conditions, the mean performances of the traits were significantly affected (positively and negatively) by the level of P application.

In the field, traits which were negatively affected by withholding P fertilizer were shoot P concentration (SP), grain phosphorus concentration (GP) and biomass phosphorus uptake (BPU) and were reduced by 28.5, 27.9, and 36.6%, respectively. In contrary, mean values of phosphorus harvest index (PHI), phosphorus utilization efficiency (PUtE), phosphorus uptake efficiency (PUpE), and phosphorus use efficiency (PUE) were lower on P-fertilized than on P-unfertilized treatment with respective RR of -5.9, -34.9, -101.5 and -175.0%. Similar trends of the effect of P fertilization levels on the performances of the traits were observed for the greenhouse experiment. Three traits viz. SP, GP and BPU under P-fertilized were increased compared to P-unfertilized treatment by 25.3, 17.6, and 37.3% respectively, PHI, PUtE, PUpE and PUE under P-fertilized compared to P-unfertilized treatment were reduced by 6.5, 29.2, 223.5 and 305.6% respectively (Table 3).

3.2. Effect of Genotypes on the Performance of Phosphorus Use Efficiency Traits

The faba bean genotypes were highly significantly ($P<0.05$) different for plant (shoot and grain) phosphorus concentration, on all experimental variants, except for grain phosphorus concentration under P-unfertilized trials (Table 3). In the field, shoot phosphorus concentration (in g/kg) of genotypes was highest for Hachalu, Tumsa, Didea, Dosha and Moti under the phosphorus fertilized trial; and EH06022-4, Walki, Hachalu, Dosha and Moti under the P-unfertilized trial. Grain phosphorus concentration (in g/kg) of the genotypes ranged from 3.93 for Walki to 4.50 for Didea for phosphorus fertilized field trial; and the value of the trait ranged from 2.87 for Walki to 3.12 for Dagim for the P unfertilized field trial (Table 4). In the greenhouse, Moti, Walki and ILB4358 had the highest shoot phosphorus for the P fertilized trial; while Tumsa, Moti and Walki were the top performers for the P-unfertilized trial. Selale, Didea, and Obse with 3.49, 3.47 and 3.40 g/kg, respectively, had the highest grain phosphorus concentration (Table 5).

Highly significant ($P<0.05$) variation was observed among genotypes performance for biomass phosphorus uptake (BPU, mg/plant) (Table 3). It ranged from 101.3 mg/plant for EH06088-1 to 126.6 mg/plant for Hachalu under P-fertilized field; while it ranged from 61.6 EH06088-1 to 78.5 mg/plant for Moti under P unfertilized field trial (Figure 1). Genotypes Hachalu, Didea, Dosha, Tumsa, and Moti under P-fertilized field trial; Moti, Dosha, Walki, Tumsa and Hachalu under P-unfertilized field trial had the highest amount of BPU. For the greenhouse trial, Hachalu, Dosha and Moti were the best performing genotypes; under both fertilized and unfertilized trial. Averaged over genotypes, BPU in the field was 1.3 times more than the value obtained in the greenhouse owing to the higher plant P concentration, grain yield and shoot dry weight of the genotypes in the field.

Phosphorus harvest index (PHI) (proportion of P exported via grains) of the faba bean genotypes was significantly different ($p<0.05$) from one another, under P-fertilized field and -unfertilized greenhouse trials (Table 3). In the field, EH06088-1, Lalo and CS20DK had the highest PHI under P-fertilized treatment, while EH06088-1, Lalo and Holetta-2 were the genotypes with the highest PHI under P-unfertilized treatment (Table 4). In the greenhouse condition, genotypes Moti, Dosha and Gebelcho had the highest PHI under both P-fertilized and P-unfertilized treatments (Table 5).

The tested faba bean genotypes were highly significantly ($P<0.05$) different from one another in their phosphorus utilization efficiency (PUtE) performance, except for the unfertilized field trial (Table 3). EH06088-1, Lalo, Gebelcho, and CS20DK were the top performing genotypes for fertilized field trial (Table 4). Gebelcho, Dosha, and Moti were the best performing genotypes under P fertilized and unfertilized greenhouse trial, respectively, as appeared in the bracket (Table 5). The PUtE performance of the genotypes was higher for phosphorus unfertilized than fertilized trial; and was higher at greenhouse than field (Table 3).

Analysis of variance showed that highly significant ($P< 0.05$) variation was observed among faba bean genotypes for phosphorus uptake efficiency (PUpE) performance; at both field and greenhouse under both P fertilizer levels (Table 3). Hachalu, Didea, Dosha, Gebelcho and Moti, under P fertilized trial; Moti, Tumsa, Dosha, Walki and Hachalu under P unfertilized trial, were the best performing genotypes for PUpE. At greenhouse, Hachalu, Didea, Dosha and Moti were the best performing genotypes for the trait (Table 4).

Phosphorus use efficiency (PUE) performance of the faba bean genotypes was highly significantly varied for all variants of the treatments (Table 3). PUE of the genotypes ranged from 47 for Selale to 53.68 for Gebelcho under P fertilized field; while it ranged from 129.24 for EH06088-1 to 151.23 for Moti under P unfertilized field. Gebelcho, Hachalu, Dosha, Moti and CS20DK, under P fertilized field trial; Moti, Dosha, Gebelcho, Walki and Tumsa under P unfertilized trial were PUE efficient genotypes. At greenhouse condition, Moti, Dosha, Hachalu and Gebelcho had higher PUE, under both fertilized and unfertilized trials (Figure 1).

PUE performance of the genotypes was by far greater on P unfertilized than P fertilized trial. To put it more clearly, mean PUE performance on unfertilized field was 2.75 times the performance on fertilized field; while it was 4 times, on average, greater with unfertilized greenhouse than fertilized greenhouse trial. This is mostly due to reduction in the amount of total available phosphorus, which is a denominator term in the estimation of PUE, for unfertilized trial which ultimately yielded higher PUE values. Likewise, the faba bean genotypes had higher PUE at Holetta than Adadi. This is due to higher PUtE performance observed at Holetta than Adadi. Genotypes performance of PUE at Greenhouse was also higher than that at field, which is most probably attributed for high PUtE values associated with greenhouse trials.

Table 3. Mean, relative reduction (RR) and mean squares of the phosphorus use efficiency traits.

Trait	Field						Greenhouse				
Trait	Mean	RR (%)	MS_G	MS_{GL}	h^2 (%)	CV (%)	Mean	RR (%)	MS_G	h^2 (%)	CV (%)
	With Phosphorus										
SP (g/kg)	3.20	---	0.11**	0.035ns	68.5	8.5	2.72	---	0.03**	78.5	4.5
GP (g/kg)	4.12	---	0.11**	0.003ns	75.0	5.3	3.32	---	0.04**	78.7	4.2
BPU (mg/p)	114.7	---	0.00**	0.001ns	79.6	17.1	85.2	---	0.00**	80.2	5.3
PHI (%)	46.9	---	18.20**	3.87ns	78.1	12.1	50.6	---	13.89**	71.7	5.8
PUtE (g/g)	143.6	---	155.82*	35.36ns	70.9	15.9	152.7	---	249.1**	82.2	6.8
PUpE (g/g)	0.36	---	0.00**	0.000ns	83.0	14.9	0.34	---	0.00**	79.1	5.3
PUE (g/g)	50.0	---	20.77**	7.29ns	64.9	5.8	52.1	---	54.35**	84.6	8.8
PAE (%)	10.1	---	21.68**	23.71**	11.2	24.6	12.3	---	8.56ns	39.3	18.7
PPE (%)	55.5	---	377.30*	471.4*	18.3	28.9	77.6	---	394.36*	62.7	19.6
APFR (%)	19.1	---	22.09**	8.78*	60.2	25.2	15.9	---	3.64ns	47.1	9.9
GY (g/p)	14.6	---	1.752**	0.620**	64.5	5.7	12.6	---	1.318***	78.8	6.7
Trait	Without Phosphorus										
SP (g/kg)	2.29	28.5	0.05*	0.009ns	77.1	9.3	2.03	25.3	0.03**	77.9	5.7
GP (g/kg)	2.97	27.9	0.04ns	0.019ns	74.7	6.5	2.73	17.6	0.01ns	67.2	3.1
BPU (mg/p)	70.5	38.6	0.00**	0.000ns	78.8	14.8	53.4	37.2	0.00**	76.8	5.8
PHI (%)	49.7	-5.9	21.87*	10.04ns	60.0	9.2	53.9	-6.5	19.58**	64.6	5.7
PUtE (g/g)	193.7	-34.9	258.3ns	69.38ns	63.3	13.0	197.3	-29.2	393.2**	76.6	6.7
PUpE (g/g)	0.72	-101.2	0.01**	0.001ns	84.1	9.0	1.07	-223.5	0.01**	87.3	5.8
PUE (g/g)	137.6	-175.2	159.5**	59.84ns	62.5	8.2	211.2	-305.6	1132.0*	82.8	9.8
GY (g/p)	13.0	13.8	1.351**	0.399*	70.5	5.9	10.6	18.9	1.017**	76.7	7.0

Note: SP, Shoot phosphorus concentration; GP, Grain phosphorus concentration; BPU, Biomass phosphorus uptake; PHI, Phosphorus Harvest Index; PUtE, Phosphorus utilization efficiency; PUpE, Phosphorus uptake efficiency, PUE, Phosphorus use efficiency; PAE, Phosphorus agronomic efficiency; PPE, Phosphorus physiological efficiency; APFR, Apparent phosphorus fertilizer recovery; GY, Grain yield; h^2, heritability; CV, coefficient of variation.

Grain yield (GY, g/plant) of the genotypes, at field, ranged from 13.7 g/plant for Selale to 15.7 g/plant for Gebelcho under P-fertilized trial; while it ranged from 11.8 g/plant for EH06088-1 to 13.8 g/plant for Moti under P-fertilized trial (Table 4). In the greenhouse, under both P levels, the highest GWP was observed for Moti (14.6 and 11.9 g/plant); while it was lowest for Tumsa (11.4 and 9.2 g/plant) (Table 5). Among the genotypes, Moti and Dosha showed consistently higher GY at both field and in the greenhouse under the two P levels; indicating the stability of the genotypes across different environmental conditions.

As shown in figure 2, grain yield and phosphorus use efficiency of the genotypes showed a very strong collinearity for all test conditions. This was also observed in the biplot (figure 3) which showed highly strong and positive correlation between the two traits. Accordingly, Gebelcho, Hachalu, Moti, Dosha, Holetta-2 and Walki had the highest GY and PUE under both P levels at field; while Wayu, Holetta-2, Didea, Dagim, Gebelcho, and Obse had the highest GY and PUE under both P levels at greenhouse (Figure 3).

The performance of the genotypes with respect to apparent phosphorus fertilizer recovery (APFR) was highly significantly (P< 0.05) different for the field trial, but not for the greenhouse trial (Table 3). The highest APFR was recorded for Hachalu, Didea, Wayu and Gebelcho. APFR of the genotypes at Adadi was highest for Hachalu and Wayu; while genotypes Didea and Wayu performed best at Holetta (Table 6). Generally, the APFR performance of the genotypes was better at Adadi than at Holetta.

Phosphorus agronomic efficiency (PAE) indicates the ability of plants to use P fertilizer to produce grain yield. For field experiment, genotypes were highly significantly (P< 0.001) varied for PAE; whereas there was no significant variation among genotypes for greenhouse experiment (Table 3). Hachalu and Gebelcho out-performed other genotypes with PAE value of 15.55 and 13.51%, respectively. Genotype Hachalu followed by Gebelcho were the best performing genotypes with respect to Phosphorus agronomic efficiency at Adadi; while Hachalu and Didea were the best performing genotypes at Holetta. However, genotypes had comparable performance of PAE at both Holetta and Adadi (Table 6).

Analysis of variance showed that there was highly significant variation among genotypes for phosphorus physiological efficiency (PPE), at both field and greenhouse (Table 3). At field condition, Hachalu and EH06088-1 with 72.36% and 72.28% respectively were the highest performing genotypes for PPE. Hachalu and EH06022 were the highest performing genotypes for PPE at Holetta. Performance for the parameter at Adadi was highest for EH06088-1 and Gebelcho (Table 6). Generally, PPE performance of the genotypes was higher at Holetta than at Adadi; because biomass phosphorus uptake was higher at Adadi than at Holetta. For greenhouse trial, Walki, Wayu and Obse genotypes had the highest PPE value.

3.3. Heritability of the Phosphorus Use Efficiency Traits

In the field, heritability values of the phosphorus use efficiency traits ranged from 11.2% for phosphorus agronomic efficiency (PAE) to 83.0% for phosphorus uptake efficiency (PUpE) for the P-fertilized treatment, while the heritability for P-unfertilized treatment ranged from 60.0% for phosphorus harvest index (PHI) to 84.1% for PUpE (Table 6). For P fertilized treatment in the greenhouse, heritability of the traits ranged from 39.3% for PAE to 84.6% for PUE, while the range was from 64.6% for PUtE to 87.28% for PUpE for P-unfertilized treatment (Table 6).

On the basis of the criteria provided by Singh, (2000), in both field and greenhouse, only few traits had very high (≥80%) heritability (PUpE on P+ and P- in the field; PUtE and PUE on P+ and P- in the greenhouse; BPU on P+ in the greenhouse) and low (<40%) heritability (PAE in both field and greenhouse, and PPE in the field). Most PUE traits were found to have comparable values of heritability in the field and greenhouse, indicating repeatability of the results.

Table 4. *Plant phosphorus concentrations and PUE characteristics of faba bean genotypes on P fertilized and unfertilized field trial.*

Genotypes	With Phosphorus						Without Phosphorus					
	SP (g/kg)	GP (g/kg)	PHI (%)	PUtE (g/g)	PUpE (g/g)	GY (g/p)	SP (g/kg)	GP (g/kg)	PHI (%)	PUtE (g/g)	PUpE (g/g)	GY (g/p)
Lalo	3.09b-d	3.98cd	49.15ab	150.88ab	0.33ef	14.3b-e	2.05c	2.91a	53.26a	207.81a	0.65ef	12.25b-d
Dagim	3.20bc	4.37ab	47.60bc	139.81a-c	0.36a-e	14.5a-e	2.25a-c	3.12a	50.47a	190.33ab	0.73a-e	12.53b-d
EH06088-1	2.84d	4.11b-d	53.01a	156.52a	0.32f	14.2c-e	2.09bc	2.94a	54.12a	203.42ab	0.64f	11.80d
CS20DK	3.02cd	4.14b-d	48.78a-c	147.57a-c	0.35b-f	14.8a-e	2.27a-c	2.95a	50.45a	197.84ab	0.70b-f	12.64b-d
Obse	3.21bc	4.15b-d	47.76a-c	144.24a-c	0.36b-e	14.7a-e	2.29a-c	2.98a	48.91a	188.69ab	0.72a-e	12.37b-d
Gebelcho	3.09b-d	4.07b-d	47.06bc	150.59ab	0.37a-d	15.7a	2.23a-c	2.96a	49.53a	200.30ab	0.72a-f	12.96a-d
Holetta-2	3.13b-d	3.96c-d	46.97bc	148.39a-c	0.34c-f	14.7a-e	2.25a-c	2.93a	52.44a	203.91ab	0.69b-e	12.64b-d
Hachalu	3.56a	4.06b-d	44.46bc	139.89a-c	0.40a	15.6ab	2.40a-c	2.98a	47.80a	184.50ab	0.75a-d	12.53b-d
Wayu	3.26a-c	4.15b-d	46.35bc	138.98bc	0.36a-e	14.3a-e	2.27a-c	2.89a	50.83a	197.76ab	0.67d-f	11.99cd
Selale	3.12b-d	4.06b-d	47.67bc	144.56a-c	0.33d-f	13.7e	2.25a-c	2.96a	51.94a	197.27ab	0.70b-f	12.49b-d
Didea	3.33ab	4.50a	46.62bc	132.33c	0.39ab	14.6a-e	2.32a-c	2.92a	47.52a	190.45ab	0.74a-d	12.77a-d
Gora	3.09b-d	4.10b-d	46.25bc	144.69a-c	0.35b-f	14.4a-e	2.23a-c	2.96a	47.57a	192.09ab	0.74a-d	12.86a-d
Dosha	3.32a-c	4.13b-d	45.20bc	141.63a-c	0.38a-c	15.2a-d	2.38a-c	2.99a	47.65a	191.41ab	0.77ab	13.27ab

Genotypes	With Phosphorus						Without Phosphorus					
	SP (g/kg)	GP (g/kg)	PHI (%)	PUtE (g/g)	PUpE (g/g)	GY (g/p)	SP (g/kg)	GP (g/kg)	PHI (%)	PUtE (g/g)	PUpE (g/g)	GY (g/p)
EH07015-7	3.14b-d	4.19a-d	47.26bc	138.39bc	0.36a-e	14.3a-e	2.30a-c	2.98a	48.37a	188.34ab	0.72a-e	12.49b-d
EH06022-4	3.14b-d	4.14b-d	46.85bc	140.55a-c	0.34c-f	13.8de	2.44a	3.09a	48.39a	177.57b	0.74a-d	12.01cd
Walki	3.27a-c	3.93d	43.80c	142.82a-c	0.36a-e	14.8a-e	2.43ab	2.87a	46.62a	189.58ab	0.76a-c	13.03a-c
NC58	3.32a-c	4.05cd	47.64bc	143.84a-c	0.35b-f	14.1c-e	2.24a-c	2.90a	51.62a	198.47ab	0.68c-f	12.27b-d
Moti	3.32a-c	3.99cd	44.13bc	144.79a-c	0.37a-c	15.4a-c	2.38a-c	3.00a	48.53a	193.74ab	0.79a	13.84a
Tumsa	3.37ab	4.26a-c	45.54bc	137.83bc	0.37a-c	14.7a-e	2.36a-c	3.14a	48.99a	185.99ab	0.77ab	12.87a-d
EH06006-6	3.23a-c	4.00cd	45.94bc	141.89a-c	0.35b-f	14.1c-e	2.37a-c	2.84a	48.04a	194.06ab	0.70b-f	12.23b-d
Mean	3.20	4.12	46.94	143.61	0.36	14.6	2.29	2.96	49.65	193.68	0.72	12.6
CV	11.21	8.15	12.55	9.47	8.75	7.21	9.34	6.5	9.22	13.01	9.03	5.89

Means followed by different letters within a column are significantly different at P < 0.05.
SP, Shoot phosphorus concentration; GP, Grain phosphorus concentration; PHI, Phosphorus Harvest Index; PUtE, Phosphorus utilization efficiency; PUpE, Phosphorus uptake efficiency, GY, Grain yield.

Table 5. *Plant phosphorus concentration and PUE characteristics of the genotypes on P fertilized and unfertilized greenhouse trial.*

Genotypes	With Phosphorus						Without Phosphorus					
	SP (g/kg)	GP (g/kg)	PHI (%)	PUtE (g/g)	PUpE (g/g)	GY (g/p)	SP (g/kg)	GP (g/kg)	PHI (%)	PUtE (g/g)	PUpE (g/g)	GY (g/p)
Obse	2.70ab	3.40ab	51.98a	152.78a-c	0.33ab	12.7c	2.02a-c	2.74a	53.61a-c	196.08a-c	1.00bc	9.8cd
Hachalu	2.67ab	3.38a-c	51.83a	153.29a-c	0.36a	13.9ab	2.03a-c	2.83a	55.90a-c	197.98a-c	1.16a	11.5ab
ILB4358	2.81ab	3.31a-c	48.04a	145.33bc	0.34ab	12.4cd	1.98bc	2.71a	53.00a-c	195.64a-c	1.07a-c	10.5bc
Selale	2.70ab	3.49a	47.59a	136.40c	0.34ab	11.4de	2.06a-c	2.77a	50.97bc	184.08c	1.04a-c	9.6de
Didea	2.77ab	3.47a	52.02a	150.20a-c	0.35ab	13.3bc	2.04ac	2.77a	53.45a-c	193.23a-c	1.12ab	10.8bc
Gora	2.66ab	3.27a-c	50.58a	154.77a-c	0.35ab	13.4b	1.92bc	2.76a	55.03a-c	199.81a-c	1.06a-c	10.6bc
Dosha	2.67ab	3.23a-c	52.73a	163.25a	0.35ab	14.4a	1.95bc	2.69a	56.62a-c	213.76ab	1.12ab	11.8a
Walki	2.82a	3.27a-c	49.96a	152.68a-c	0.32b	12.3c-e	2.10a-c	2.76a	50.92bc	184.59c	1.01bc	9.4de
Moti	2.86a	3.35a-c	53.43a	159.40ab	0.37a	14.6a	2.15ab	2.71a	57.97a	210.75ab	1.12ab	12.0a
Tumsa	2.79ab	3.37a-c	47.17a	140.09bc	0.32b	11.4e	2.23a	2.72a	50.44c	185.18c	0.99c	9.2e
Gebelcho	2.52b	3.10c	52.45a	168.79a	0.33b	13.8ab	1.88c	2.61a	56.76ab	217.52a	1.06a-c	11.6ab
Wayu	2.67ab	3.17bc	49.27a	155.58a-c	0.33b	12.6c	2.00ac	2.75a	51.95a-c	188.88bc	1.08a-c	10.2cd
Mean	2.72	3.32	50.59	152.71	0.34	13.01	2.03	2.73	53.89	197.29	1.07	10.55
CV	5.71	3.13	4.34	4.85	5.68	6.97	4.45	4.17	3.81	5.21	5.42	6.67

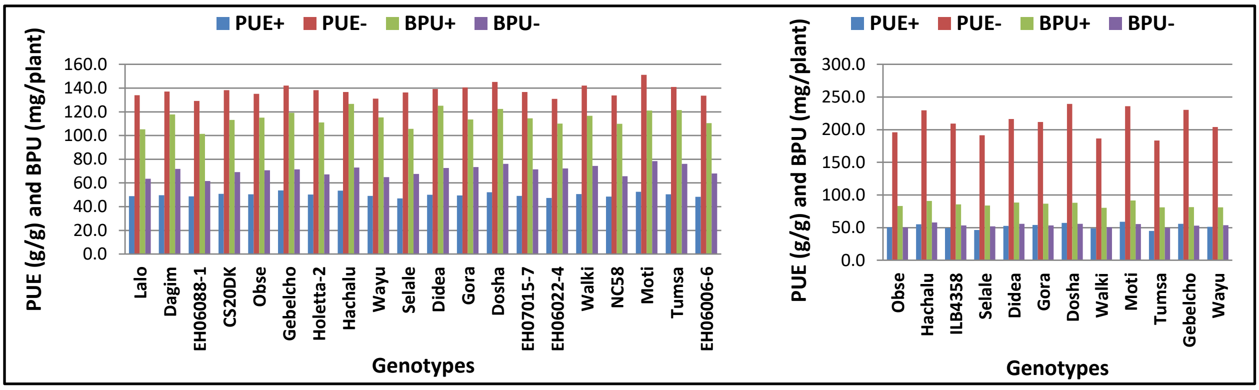

Figure 1. PUE and BPU of the genotypes under P fertilized (+) and unfertilized (-) field (left) and greenhouse (right) conditions.

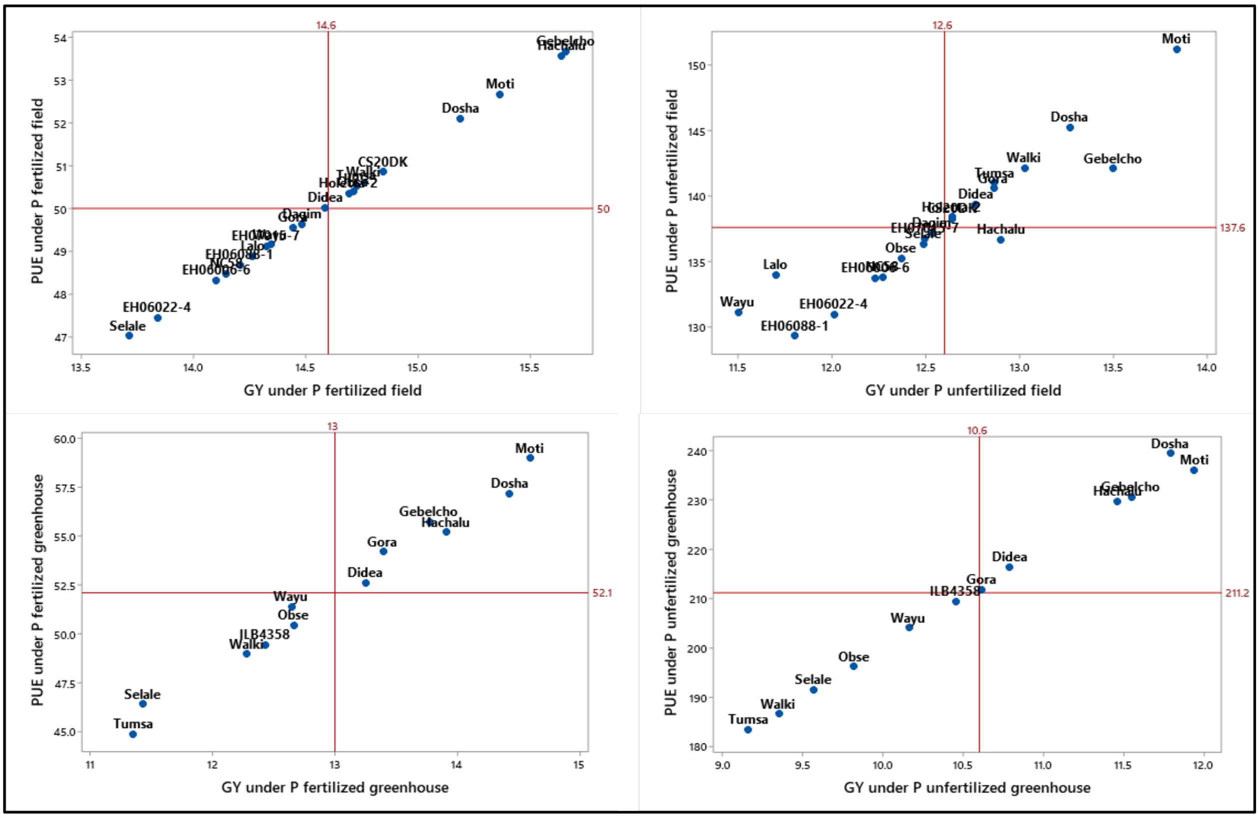

Figure 2. Performance of the genotypes for grain yield (GY) and phosphorus use efficiency (PUE) under P fertilized and unfertilized field and greenhouse conditions.

Table 6. Phosphorus efficiency characteristics of the genotypes in the field.

Genotypes	APFR (%)			PAE (%)			PPE (%)		
	Holetta	Adadi	Mean	Holetta	Adadi	Mean	Holetta	Adadi	Mean
Lalo	14.65i-k	21.30b-g	18.32b-d	8.92b-i	11.26a-f	10.09b-d	60.90a-f	51.09c-h	55.99a-c
Dagim	15.52f-k	23.15b-e	19.34a-d	8.23c-i	11.28a-f	9.75c-e	53.51b-g	49.06c-h	51.28a-c
EH06088-1	12.50k	21.70b-h	17.10d	9.61b-h	14.44ab	12.02a-c	77.60a-c	66.96a-e	72.28a
CS20DK	14.18i-k	23.79a-d	18.98a-d	8.76b-i	13.30a-c	11.03b-d	63.38a-e	56.22b-g	59.80a-c
Obse	14.03i-k	24.14a-c	19.08a-d	10.19a-g	13.23a-c	11.71bc	73.96a-c	54.38b-g	64.17ab

Genotypes	APFR (%)			PAE (%)			PPE (%)		
	Holetta	Adadi	Mean	Holetta	Adadi	Mean	Holetta	Adadi	Mean
Gebelcho	15.97f-k	24.70a-c	20.33a-d	11.52a-f	15.49a	13.51ab	71.93a-c	63.80a-e	67.86a
Holetta-2	15.30g-k	22.38b-f	18.84b-d	8.93b-i	11.59a-f	10.26b-d	58.65a-f	52.86c-h	55.75a-c
Hachalu	16.69e-k	30.13a	23.41a	15.47a	15.63a	15.55a	92.97a	51.76c-h	72.36a
Wayu	16.92d-k	27.22ab	22.07a-c	11.20a-g	12.37a-d	11.78bc	66.24a-e	45.80c-h	56.03a-c
Selale	13.95j-k	18.55c-k	16.25d	8.76b-i	3.49i	6.10e	62.71a-e	18.45h	40.58c
Didea	18.41c-k	26.59ab	22.50ab	12.03a-e	6.17f-i	9.10c-e	65.79a-e	23.16gh	44.47bc
Gora	14.80h-k	19.26c-k	17.03d	11.52a-f	4.30h-i	7.91de	79.63a-c	22.19gh	50.91a-c
Dosha	15.79f-k	23.97a-c	19.88a-d	11.01a-g	8.22c-i	9.61c-e	70.38a-d	34.28ef	52.33a-c
EH07015-7	14.57i-k	24.12a-c	19.35a-d	10.28a-g	8.01c-i	9.14c-e	70.53a-d	33.16e-h	51.81a-c
EH06022-4	14.00i-k	18.07c-k	16.04d	12.03a-e	6.24e-i	9.14c-e	88.05ab	33.83e-h	60.94a-c
Walki	15.48f-k	20.57b-j	18.03cd	11.96a-f	5.37g-i	8.66c-e	77.56a-c	26.35f-h	51.96a-c
NC58	14.39i-k	24.426ac	19.40a-d	10.64a-g	8.11c-i	9.38c-e	75.11a-c	33.34e-h	54.23a-c
Moti	14.84h-k	20.92bi	17.88cd	8.30c-i	6.98d-i	7.64de	55.42b-g	33.53e-h	44.48bc
Tumsa	16.63e-k	21.97bg	19.30a-d	10.62a-g	7.97c-i	9.30c-e	64.60a-e	36.63d-h	50.62a-c
EH06006-6	15.17g-k	22.02bg	18.60b-d	8.82b-i	9.88a-h	9.35c-e	58.80a-f	45.21c-h	52.00a-c

Means followed by different letters within a column are significantly different at $P < 0.05$.
APFR, Apparent phosphorus fertilizer recovery; PAE, Phosphorus agronomic efficiency; PPE, Phosphorus physiological efficiency.

3.4. Grouping of the Genotypes into Phosphorus Efficiency Classes

Based on the grain yield and phosphorus utilization efficiency classification methods, the genotypes were categorized under four phosphorus efficiency classes; namely ER (efficient, responder), INR (inefficient, non-responder), ENR (efficient, non-responder) and IR (inefficient, responder) (Figure 3). Efficient and responsive (ER) are plants that produce above average biomass at lower nutrient concentrations and respond to nutrient addition. Inefficient and non-responsive (INR) are plants that produce less than average biomass at lower nutrient concentrations, and which do not respond to nutrient addition. Efficient and non-responsive (ENR) are plants that produce above average biomass at lower nutrient concentrations, but do not respond to the addition of nutrients. Inefficient and responsive (IR) are plants that produce less than average biomass at lower nutrient concentrations but still respond to nutrient addition.

As shown in Figure 3, under both field and greenhouse conditions, most genotypes fall under either ER (efficient, responder) or INR (inefficient, non-responder); while there were very few to no genotypes grouped under both ENR (efficient, non-responder) and IR (inefficient, responder) efficient classes. Nine genotypes each were categorized under INR and ER classes for both grain yield and phosphorus utilization efficiency; at field trial. At greenhouse, six INR and five ER genotypes were grouped for grain yield; while five INR and six ER categories of genotypes were identified for phosphorus utilization efficiency. This indicated that majority of the genotypes exhibited similar responses to different levels of phosphorus fertilizer application.

Under field condition, Moti, Gebelcho, Hachalu, Dosha and Walki were the genotypes grouped under ER efficiency class based on the grain yield categorization scheme; while EH06088-1, Lalo, Holetta-2, Gebelcho and CS20DK are grouped under ER based on the phosphorus utilization efficiency categorization scheme. In the greenhouse, Moti, Dosha, Hachalu, Gebelcho and Didea under the grain yield categorization scheme and Gebelcho, Gora, Dosha, Wayu and Didea under the phosphorus utilization efficiency categorization scheme, were categorized under ER efficiency class. Only one genotype (Selale) have fallen under INR class for the grain yield categorization scheme; while six genotypes, including Selale, Tumsa, ILB4358, Wayu, Walki and Obse, were categorized under INR for the phosphorus utilization efficiency categorization scheme in the greenhouse condition.

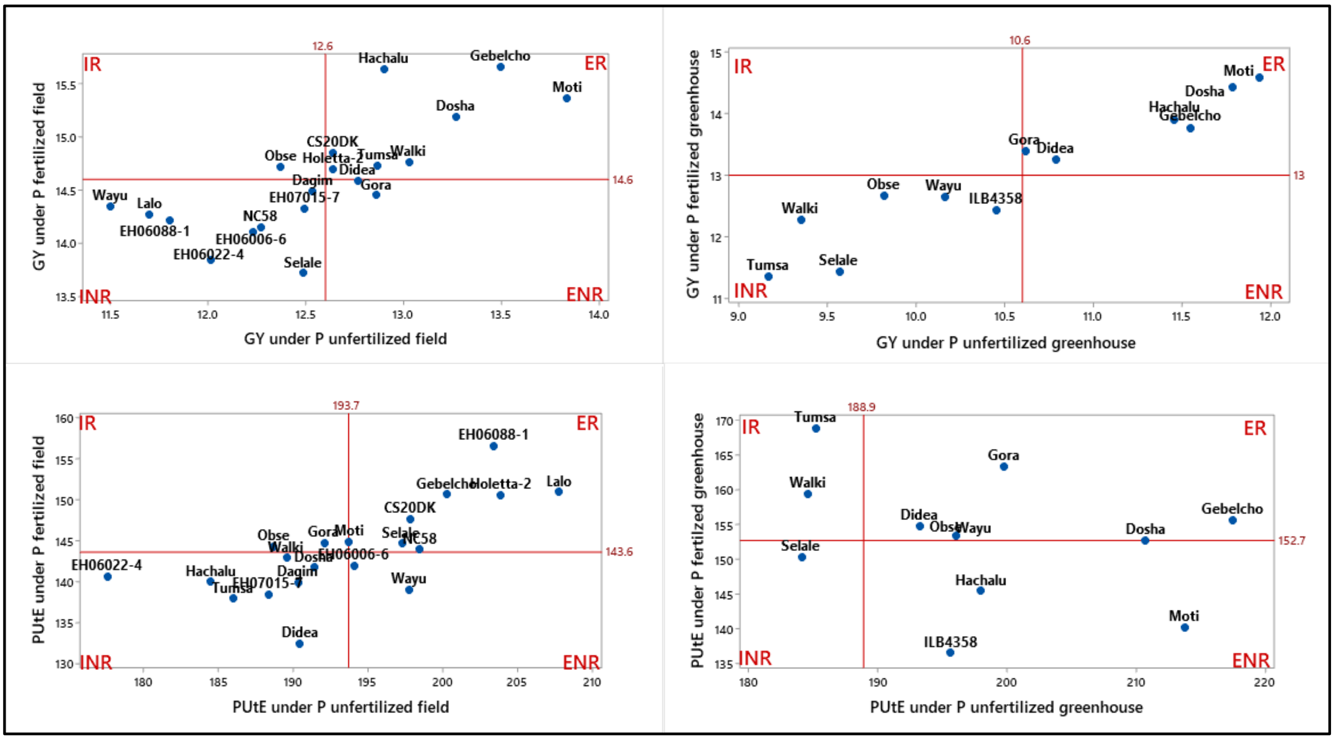

Figure 3. Phosphorus efficiency classes of the genotypes based on grain yield (GY) and phosphorus utilization efficiency (PUtE) at field and greenhouse. Note: IR, inefficient inefficient; ER, efficient responder; INR, inefficient non-responder; ENR, efficient responder.

3.5. Biplot Analysis and Trait Relationships

Genotype by trait (GT) biplot analysis showed that the first two principal components accounted for 71.1 and 84.0% variation under P-fertilized and P-unfertilized trials, respectively (Figure 4). The result displayed in the GT biplot is interpreted based on the principles described in [39]. Accordingly, under both P levels, shoot phosphorus concentration (ShootP), total phosphorus uptake (TotPU), phosphorus uptake efficiency (PUpE), apparent phosphorus fertilizer recovery (APFR), phosphorus use efficiency (PUE) and grain yield (GY) had high positive loading and longer vectors and are thus responsible for large genetic divergence in the PC1. Phosphorus utilization efficiency (PUtE), phosphorus physiological efficiency (PPE), phosphorus agronomic efficiency (PAE) and PUE had high positive loading and longer vectors and are thus responsible for large genetic divergence in the PC2. These traits have much influence (most discriminating power) during selection and can be selected together and thus are more useful as they provide better discriminating information about the genotypes. Grain phosphorus concentration (GrainP), phosphorus harvest index (PHI) and phosphorus efficiency ratio (PER) were the least contributors for the genetic variation (short vectors) and provide little information on the genotypes and, therefore, should not be used as a trait of interest in selecting a genotype.

In the biplot, the cosine of the angle between two traits approximates the correlation between the traits; and hence associations among traits could easily be visualized from the biplot [40]. According to the authors, two traits are positively correlated if the angle between the vectors is acute (90°); negatively correlated if the angle between the vectors is obtuse (>90°) and not correlated if the angle is right angle. Based on this assumption, PUE was positively and significantly correlated to most traits except for its negative correlation with PHI, PER and PUtE. These relationships suggest that it is possible to combine higher yield, higher PUE, higher PUpE, and higher TotPU in a single genotype. The trait relationship observed in the biplot could be witnessed in the correlation results presented in Table 7.

The GT biplot also showed the trait profiles of the genotypes. Genotypes excelling in a particular trait were plotted closer to the vector line and further in the direction of that particular vector, often on the vertices of the convex hull. Accordingly, Hachalu had the highest PUE, GY, TotPU, and PUpE under P-fertilized condition; while Moti had the highest mean performance for the traits under P-fertilized condition. Gebelcho had the second highest PUE, GY, TotPU, and PUpE performance under both P-fertilizer regimes. As shown in Figure 4, the genotypes were found at acute angle to the traits. On the other hand, vectors of genotypes such as EH06022-4, EH06006-6 and Lalo formed obtuse angle with the traits and had below-average performance for the traits.

Based on the traits profile of the genotypes, breeding objectives can easily be determined. For example, higher GY or PUE of the above genotypes can be transferred to the genotypes with lower performance for the two traits but having higher performance for other traits. For instance, the cross between Moti x Lalo will combine higher PUtE of Moti and higher PHI of Lalo.

Table 7. *Correlation among PUE traits of faba bean under P fertilized and unfertilized field.*

	P-										
		SP	GP	BPU	PHI	PUtE	PUpE	PUE	PAE	PPE	PER
	SP	1	0.189	0.722	-0.794	-0.788	0.786	0.388	--	--	--
	GP	0.116	1	0.487	-0.107	-0.55	0.473	0.165	--	--	--
	BPU	0.76	0.397	1	-0.821	-0.687	0.992	0.797	--	--	--
	PHI	-0.796	0.124	-0.721	1	0.75	-0.836	-0.502	--	--	--
	PUtE	-0.719	-0.592	-0.65	0.614	1	-0.743	-0.118	--	--	--
P+	PUpE	0.803	0.386	0.988	-0.711	-0.686	1	0.752	--	--	--
	PUE	0.407	-0.07	0.742	-0.449	0.017	0.708	1	--	--	--
	PAE	0.111	-0.016	0.242	0.154	0.202	0.283	0.53	1	--	--
	PPE	-0.196	-0.181	-0.091	0.376	0.467	-0.064	0.309	0.882	1	--
	PER	0.015	0.194	0.049	-0.033	-0.093	-0.005	-0.088	-0.37	-0.199	1
	APFR	0.61	0.374	0.691	-0.292	-0.468	0.752	0.531	0.619	0.208	-0.365

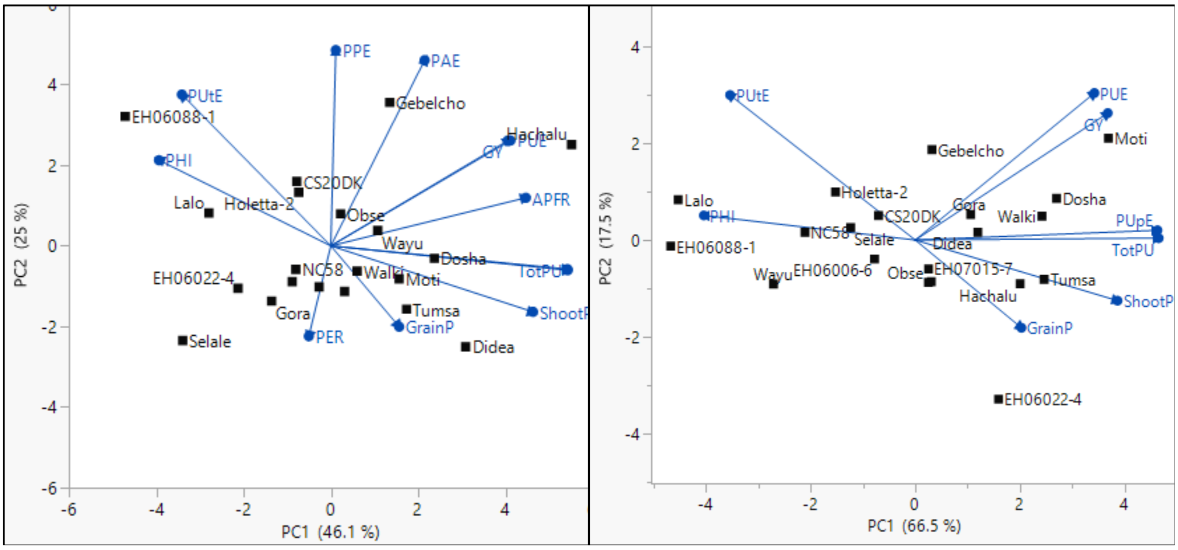

Figure 4. *Genotype by trait biplot for the PUE traits of the faba bean genotypes grown with phosphorus fertilizer (left) & without phosphorus fertilizer (right).*

4. Discussions

The development of phosphorus (P) efficient crops capable of accessing P reserves in P deficient soils of Sub-Saharan Africa is very important in order to maximize yield and ensure sustainability of crop production. P efficiency can be enhanced by improving P scavenging and uptake (P uptake efficiency) and, more economically, by improving internal P-use efficiency (P utilization efficiency) [17, 41]. In the current study, we assessed genetic variability of faba bean genotypes for P-use efficiency traits at field and greenhouse. The study has found a wide variation of different components of PUE and growth traits in response to contrasting soil P availability (Table 3).

P fertilization level has significantly affected (positively and negatively) the performance of PUE traits; with positive relative reduction (RR) ranging from 13.8% for GY to 38.6%

BPU and negative RR ranging from -5.9% for PHI to -305.6% for PUE. A positive RR value shows better performance of the trait under P-fertilized soil (more sensitivity to reduced P); while negative RR value shows better performance under P-unfertilized soil (less sensitivity to reduced P). Comparable RR percentages of the traits to reduced P were reported by [7, 25, 42, 43]. Our study showed that plant P concentrations of the genotypes were higher for P fertilized than unfertilized trial, indicating that P uptake under P fertilized trial is higher than that for P unfertilized trial. Similar studies also reported that higher P fertilization level led to a higher SP and GP values [7, 43, 44]. Yang et al., [43] reported that higher shoot P resulting from increased root P uptake under +P led to a lower PUtE. This finding indicates that using cultivars with lower shoot P% in P-deficient soil is the most efficient approach for increasing PUtE and grain yield, in agreement with findings in potato [21], faba bean [42], wheat [43] and sorghum [45]. In accordance with our results, it was also reported that PHI, PUpE, PUtE and PUE were higher under low P than P high soils [21, 25, 28, 42, 43]. Similar to our results, reports indicated that PUtE was significantly lower in high P soil compared to low P soil [7, 43].

Genotypic variation for P use efficiency has been reported for faba bean and other crop species [20, 25, 26, 36, 46]. This is closely linked to genotypes with efficient and extensive root systems or those with effective associations with mycorrhizal fungi, in order to access a greater soil volume (as P is diffusion limited in most soils) [6]. Our study revealed the availability of genetic variability among the faba bean genotypes for PUE characteristics. In corroboration with our result, Nebiyu *et al.* [25] reported that faba bean genotypes varied for their shoot and grain P%, BPU and PUE. They also reported similar values of shoot and grain P%, for faba bean, as reported by this study; adding that grain P% of the genotypes was greater than their shoot P%; which is consistent with our findings. The reason for the difference may be supported by the finding of Raboy [47] who indicated that P levels in grains are well above the P levels required for normal cellular function. The author argued that most of the increase in seed P% is synchronous with a decrease in the shoot phosphorus concentration of the senescing leaves and stems. Phosphorus fertilizer management is also mainly driven by the export of P in harvested products [27]. Thus, P concentration is typically much higher in grain than in vegetative material. Our result is also supported by the notion that modern crop varieties use P more efficiently than older varieties (higher PUEy) [41]. Calderini *et al.* [48] found that PUtE was higher in modern wheat cultivars when compared to older cultivars, owing to the higher harvest indexes of modern wheat cultivars. It has been widely believed that traditional varieties tend to outperform modern varieties for nutrient acquisition under deficient conditions [45], which would indicate that they were selected under similarly deficient conditions in the pre-Green Revolution era, and that high yielding modern varieties may have lost adaptive traits and genes during the selection under high-input conditions that has been practiced over the past 50 years [49]. Plants tend to have high PUE on soils with low amount of phosphorus, as a means of adaptation mechanism [50].

It's also worth mentioning that genotypes with better PUE had higher grain yield. It was also reported by other researchers that Phosphorus use efficient genotype would ideally have higher grain yield [16, 25]. The result of APFR in this study fell within the commonly known range of 10-25% of efficiency of P fertilizer use by plants [51], which is low due to the strong fixation of phosphate ions by reactive soil components [52]. The study also found out that most phosphorus use efficiency traits were better at field than at greenhouse. It was also reported that binding and curling of roots at the bottom of the pots affected microbial activity and consequently the mobilization and uptake of P in pot experiments. In addition, the effects resulted in differences in performance of the same genotypes under greenhouse and field conditions [36].

Based on the method suggested by [35], genotypes were grouped into four efficiency categories: inefficient, non-responder (INR); inefficient, responder (IR); efficient, non-responder (ENR); and efficient, responder (ER). As defined by [33], INR genotypes give low yield irrespective of nutrient availability; while IR genotypes give low yield when nutrient availability is less, but increases their yield as the nutrient availability increases. ENR genotypes are capable of giving high yield even when nutrient availability is less, but do not respond with increased yield under high input conditions. ER genotypes show high yield at low level of nutrient supply and their yield level increases as nutrient supply increases. Genotypes Moti, Gebelcho, Dosha, Hachalu, Didea, and Holetta-2 fall under ER efficiency class. This is a remarkable result because these genotypes were also better in performance with respect to other traits including grain yield. On the other hand, genotypes such as Selale, Dagim, EH06022-4, EH7015-7 and EH06022-4 are grouped under INR which also corresponded with lower performance of the genotypes for other traits. Furthermore, identification of the genotypes with different efficiency group may implicate the growers to choose genotypes depending on the capacity to use P fertilizer. It's unquestionable that efficient and responder genotypes are the best candidate for production. However, whenever yield is compromised with ER combination, farmers who can apply adequate amount of phosphorus may be recommended to use genotypes that are responsive to soil fertility and those who can't afford may choose efficient genotypes. Besides, breeding phosphorus efficient genotypes under phosphorus deficient conditions could be considered as an alternative strategy [37].

Genotype by trait (GT) biplot can help us understand the relationships among traits (breeding objectives) and help identify traits that are positively or negatively associated, traits that are redundantly measured, and traits that can be used in indirect selection for another trait. It also helps to visualize the trait profiles (strength and weakness) of genotypes, which is important for parent as well as variety selection [39, 40].

. Our studies showed that Shoot P%, BPU, PUpE, APFR, PUE and GY had high positive loading and longer vectors and are thus responsible for large genetic divergence in the PC1. PUtE, PPE, PAE and PUE had high positive loading and longer vectors and are responsible for large genetic divergence in the PC2. These traits have much influence (most discriminating power) during selection and can be selected together and thus are more useful as they provide better discriminating information about the genotypes. Grain P%, PHI and PER were the least contributors for the genetic variation (short vectors). Hachalu had the highest PUE, GY, BPU, and PUpE under P-fertilized condition; while Moti had the highest mean performance for the traits under P-fertilized condition. Gebelcho had the second highest PUE, GY, BPU, and PUpE performance under both P-fertilizer regimes.

As shown in the biplot figure and correlation analysis, PUE and GY were highly related to PUpE than they were to PUtE. This suggested that PUpE was more critical for GY and PUE variation than PUtE. Similar results were reported in maize [32], common bean [53], and wheat [54]. In contrary to our study, PUtE was more critical for GY and PUE variation in wheat [43], maize [55] and potato [56]. These contrasting conclusions indicate that the contribution of PUpE and PUtE to PUE improvement varies among crops, environments, and soil P availabilities. In corroboration with the present study, previous reports by [21] in potato and [25] in faba bean and indicated significant positive correlation of PUE with total biomass and grain yield. Similar to our results, other studies also reported that PUpE was well correlated to yield [21, 57, 58].

5. Conclusion

The study found out that the faba bean genotypes were significantly different for most of the measured PUE traits and there was no consistent superiority of a genotype across all study conditions. However, Gebelcho, Moti, Hachalu and Dosha were found to be phosphorus use efficient genotypes. Furthermore, it was found that the difference in P use efficiency was largely due to differences in P uptake efficiency and grain yield performance. Generally, the study revealed that most of the genotypes with good phosphorus efficiency classes were also the best performing ones for other traits; which is an added selection criterion to include these genotypes in breeding programmes. Hence, in order to incorporate these genotypes in further improvement programmes of the crop; they should undergo additional field and greenhouse trials. The study's overall findings could be applied to the enhancement of genotypes with P efficiency, which will increase P uptake and utilization particularly on phosphorus deficient soils of faba bean growing regions of Ethiopia.

Abbreviations

FAO	Food and Agriculture Organization of the United Nations
PC	Principal Component
PUE	Phosphorus Use Efficiency
SAS	Statistical Analysis Software

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Conflict of Interests

The authors declare no conflicts of interest.

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