

Article **Genetic Variation for Traits Related to Phosphorus Use Efficiency in** *Vigna* **Species**

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Abstract: Phosphorus (P) is a major limiting nutrient reducing crop yields especially in weathered soils of the subtropics and tropics. P exhibits poor mobility and availability to plants in soil. To overcome P deficiency in soil, phosphatic fertilizers are added. Global phosphate rock reserves are finite, and the addition of phosphatic fertilizers is not financially and ecologically sustainable. Mungbean (*Vigna radiata* (L.) Wilczek) is important grain legume for nutritional security. Attempts are being made to develop mungbean varieties with better P-use efficiency through enhanced P uptake and utilization. In the present study, 327 accessions of 18 *Vigna* species were examined for inter- and intra-specific variation for traits related to phosphorus uptake and utilization efficiency under hydroponic conditions at two levels of phosphorus. Significant species-specific variation was recorded for studied traits. Among the studied *Vigna* species, mungbean exhibited higher phosphorus use efficiency. Seven mungbean genotypes (IC 251950, IC 585931, V1002532AG, IC 371653, IC 331615, V1001400AG, and V1000532BG) were found to be promising for both PupE and PutiE. Using mean and standard deviation as criteria, mungbean genotypes identified with high phosphorus-use efficiency include IC 25950 and IC 583664. Mungbean genotypes KPS 1546, IC 277060, IC 697141, IC 343440, and Pusa 0831 were identified based on the stress tolerance index as genotypes that performed better under P stress. Cultivated species revealed higher PUE in comparison withwild forms. The most promising genotype identified from this study for PUE can be used as a parent for the development of a mapping population of mungbean for understanding genetics of PUE under a low-phosphorus environment.

Keywords: *Vigna*; phosphorus uptake efficiency; phosphorus utilization efficiency; phosphorus-use efficiency

1. Introduction

More than 100 species are included in the genus *Vigna*. These species are acclimatized to wetlands, sandy beaches, deserts, acid soils, and limestone rocks in subtropical and tropical regions of the world and are valuable reservoirs of genes for biotic and abiotic stresses [\[1](#page-17-0)[,2\]](#page-17-1). Only seven *Vigna* species are domesticated. Among *Vigna* species, mungbeans (*V. radiata* (L.) Wilczek], urdbeans (*V. mungo* (L.) Hepper) and cowpeas (*V. unguiculata* (L.) Walp.) are staple crops and ricebeans (*V. umbellate* (Thunb.) Ohwi& Ohashi), adzuki beans (*V. angularis* (Willd.) Ohwi& Ohashi), moth beans (*V. aconitifolia* (Jacq.) Marechal) and bambara groundnuts (*V. subterranean* (L.) Verdn.) are economically important in several regions of world. *Vigna* species are grown for seeds and are also used as cover, forage, and green manure. Mungbean is endemic to India and Central Asia. Globally, mungbean is

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grown in about 7 million hectares with a 5-million-tonproduction [\[3\]](#page-17-2). Mungbean seeds are rich in easily digestible proteins [\[4\]](#page-17-3), vitamins, minerals, dietary fibres, and bioactive compounds [\[5\]](#page-17-4). Mungbean incites low flatulence in comparison to other grain legumes [\[6\]](#page-17-5). In India, mungbean is grown on marginal soils. In marginal lands, nutrient management is important to realize the potential yield of crop variety. Nitrogen and phosphorus are the major macronutrients for mungbean. About 18 kg of nitrogen per hectare is applied through fertilizers as a basal dose and the rest is fixed by rhizobium. Around 50 kg of P_2O_5 is required to produce one ton of mungbean from one hectare of land. The required P is provided by fertilizer application. Improvement in phosphorus uptake and utilization efficiency is required to enhance productivity. Crop wild relatives (CWR) are the valuable reservoirs of genes for tolerance/resistance to biotic and abiotic stresses [\[7\]](#page-17-6).

Phosphorus (P) is essential for functioning, growth, and reproduction. Phospholipids, nucleic acids, phosphorylated proteins, and P esters are main pools of P in plants. P plays a role in phosphorylation/dephosphorylation, photosynthesis, energy production, and redox reactions. Crops absorb 15–30% of applied P in the year of its application [\[8\]](#page-17-7). There is scope for improving P-uptake efficiency. Increased P uptake will benefit yields; however, regular inputs are required to level the total P imported from the field. Phosphorus exists in an insoluble form in soil. P chelates with metal oxides in acidic soil and in alkaline soil with carbonate compounds, and also subsists as organic P [\[9\]](#page-17-8). Phosphorus deficiency is routine in agricultural lands. The global phosphate reserves attribute for 80–90% of P fertilizer production. The global phosphate reserves are based in Morocco, Russia, USA, and China [\[10\]](#page-17-9). These are finite, priceless, and non-replenishable. Increasing fertilizer cost and water pollution from the use of fertilizers is alarming [\[11\]](#page-17-10). The predicted food production/demand and consumption pattern requires efficacy of P use.

Globally, around 5.7 billion hectares of land is P-deficient [\[12\]](#page-17-11). A P concentration of $\lt 10 \mu m$ in soil solution is considered as below the critical level for optimal crop yield [\[13\]](#page-17-12). Root architecture is crucial for P acquisition by plants. Root architecture is flexible and responds to low P in soil for facilitating the P acquisition. At low P, primary root growth is reduced and lateral root growth and root hair development is enhanced [\[12](#page-17-11)[,14\]](#page-17-13). The root system alteration is influenced by variation in localized P concentration and sensitivity of growth regulators such as auxin, ethylene, sugar, reactive oxygen species, cytokinins, nitric oxide, and abscisic acid. The changes in phytohormone concentration and composition are controlled by the expression of several genes [\[12\]](#page-17-11). Cellular, molecular, and physiological processes are triggered due to the activation of genes. At low P, a plant responds by altering its root system for better exploration of soil P, secreting organic acids and protons that chelate Ca^{2+} , Al^{3+} , and Fe^{3+} and solubilise insoluble Pi forms [\[15\]](#page-17-14), evolving Pi and adenylate-independent glycolytic bypass enzymes that allow glycolytic flux [\[15\]](#page-17-14), remobilizing Pi in the plant to meet the requirements of growing sink tissue [\[16\]](#page-17-15), and increasing anthocyanin pigment [\[17\]](#page-17-16).

Genetic variation for root architectural traits within and between crossable species can be exploited to improve phosphorus-use efficiency. In mungbean, root traits such asbiomass, root carboxylate exudation capacity area, and volume were significantly higher in phosphorus-efficient genotypes [\[18\]](#page-17-17). In urdbean, important contributors to phosphorus uptake were the number of lateral roots, root surface area, root length, and root volume [\[19\]](#page-17-18). It was reported that lupin genotypes with deep lateral roots and a large root system were phosphorus-use efficient [\[20\]](#page-17-19). In response to phosphorus deficiency in lentils, total root length, primary root length, and the number of lateral roots increased [\[21\]](#page-17-20). In soybean and common beans, lateral and adventitious roots were associated with a higher P uptake [\[22](#page-17-21)[,23\]](#page-17-22). Root hair density and length increased in rice [\[24\]](#page-17-23) under phosphorus deficiency. Root biomass and root length were reported as important traits in wheat under phosphorus stress [\[25\]](#page-17-24). The study on phosphorus uptake and use efficiency in field crops revealed a high phosphorus concentration in grain legumes as compared withcereals. Higher phosphorus-use efficiency in cereals was reported in comparison withlegumes [\[26\]](#page-17-25). In legumes, limited efforts have been made to evaluate wild species for traits related to

PUE. In response to P deficiency, QTLs for PUE traits have been reported in several crops, such as chickpea [\[27\]](#page-17-26), mungbean [\[28\]](#page-18-0), groundnut [\[29\]](#page-18-1), common bean [\[30\]](#page-18-2), soybean [\[31\]](#page-18-3), wheat [\[32](#page-18-4)[,33\]](#page-18-5), rice [\[34](#page-18-6)[,35\]](#page-18-7), and maize [\[36,](#page-18-8)[37\]](#page-18-9).

In marginal lands, P deficiency is a limitation for crop productivity, and in high-input ecologies, intensive fertilization results in environmental pollution. Phosphorus uptakeand utilization-efficient crops are essential for improving food security and reducing environmental impacts. Improved phosphorus-use efficiency (PUE) implies a reduced P requirement for a higher yield under suboptimal P availability. The topsoil forging ideotype is efficient in P uptake. Breeding PUE mungbean cultivars with optimal root system architecture is essential for genetic improvement of the crop cultivated in marginal soil. Phosphorus-use efficiency can be defined as the amount of yield or biomass produced per unit of P uptake. Improving PUE means enhancing P acquisition from soil and enhancingthe use of P, resulting in higher growth and assignment of biomass to the economic part of plant. The present study was conducted to evaluate different *Vigna* species for phosphorus-use-efficiency-related traits and identify PUE-efficient genotype (s).

2. Materials and Methods

2.1. Plant Material and Growing Condition

Three hundred and twenty-seven *Vigna* genotypes, includingeighteen species/subspecies (*Vigna radiata* var. *bourneae* Gamble, *V. pilosa* (Willd.) Baker, *V. minima* (Roxb.) Ohwi & H.Ohashi, *V. dalzelliana* (Kuntze) Verdc., *V. hainiana* Babu, Gopin. & S.K.Sharma, *V. mungo* (L.) Hepper, *V. mungo* var. *silvestris* Lukoki, Marechal & Otoul *V. trilobata* (L.) Verdc., *V. trinervia* var. *bourneae* (Gamble) Tateishi & Maxted, *V. membranaceae* A. Rich., *V. umbelleta* (Thunb.) Ohwi & H.Ohashi, *V. unguiculata* (L.) Walp., *V. unguiculata* ssp. *sesquipedalis* (L.) Verdc., *V. racemosa* (G.Don) Hutch. & Dalziel ex Baker f., *V. radiata* var. *sublobata (Roxb.) Verdc.*, *V. radiata* var. *setulosa* (Dalzell) Ohwi & *H. Ohashi*, *V. radiata* (L.) *R. Wilczek* and unknown *V. species*) were characterized for PUE-related traits under optimum-phosphorus (OP) and low-phosphorus (LP) conditions. The characterization was carried out at the Indian Agricultural Research Institute, New Delhi, India in the National Initiative on Climate Resilient Agriculture (NICRA)-controlled environment facility from June to November 2021. New Delhi is in the North-West Plain Zone; $28°$ 400" N $77°$ 120" E, 218 m above sea level [masl]. The day and night temperatures were maintained as 30 and 18 ◦C, respectively, the photoperiod duration was 12 h, and relative humidity was 90% in the greenhouse. The mungbean seeds were surface-sterilized with 0.1% (w/v) HgCl₂. The seeds were immersed in $HgCl₂$ for 3 min and rinsed twice with double-distilled water. The seeds of the wild *Vigna* species were scarified using a blade, to ensure seed germination. The seeds were wrapped in distilled water-soaked germination paper, placed in a plastic tray containing 1/10 volume water, and kept in the dark for seed germination. Upon the emergence of cotyledonary leaves (8 days after sowing), uniform seedlings were identified and transferred to Hoagland solution. The Hoagland solution included macronutrients K_2SO_4 (0.92 mM) , Fe-EDTA (0.04 mM) , MgSO₄ (1 mM) , CaCl₂·2H₂O (0.75 mM) , Urea (5 mM)] and micronutrients $[ZnSO_4 (0.6 \mu M), H_3BO_3 (2.4 \mu M), CuSO_4 (0.62 \mu M), MnSO_4 (0.9 \mu M), and$ Na_2MoO_4 (0.6 µM)] [\[38\]](#page-18-10). The studied genotypes were screened at two levels of phosphorus optimum P (250 μM) and low P (3 μM) using KH_2PO_4 as reported by Reddy et al. [\[39\]](#page-18-11). The pH of the solution was maintained at 6.0 with 1 M HCL or 1 M KOH. The Hoagland solution was aerated using an aquarium pump and replaced after 48 h. The seedlings were raised in plastic trays of size 30 cm \times 45 cm \times 15 cm with a capacity of 10 liters. A thermocol sheet of 2 thickness was used to cover the trays and support the seedlings by maintaining spacing of $5 \text{ cm} \times 5 \text{ cm}$. Randomized complete block design was followed with 3 replications.

2.2. Trait Measurement

On twenty-one-day-old seedlings, the root and shoot properties of the genotypes under study were evaluated. The roots and shoots were separated, and the root system was placed out on an acrylic tray for scanning. The Epson Perfect V700 Pro scanner was used to scan the roots (Seiko Epson, Suwa, Japan). The gray scale images in TIFF format were studied with WinRHIZO Pro 2016a software. The observations on the roots were based on image analysis (primary root length (PRL, cm), total root length (TRL, cm), total surface area (TSA, cm²), average root diameter (ARD, cm), total root volume (TRV, cm³), total root tips (TRT, cm), and root fork (RF). The clean root and shoot were dried in an oven for 48 h at 65 ◦C for the calculation of shoot dry weight (SDW, g per plant), root dry weight (RDW, g per plant), total dry weight (TDW, g per plant), and root-to-shoot ratio (RSR, g per g). 4.3.

2.3. Estimation of Phosphorus Concentration

The phosphorus was estimated following the method from Murphy and Reley [\[40\]](#page-18-12). Grounded samples (0.1 gm) of each of the 327 *Vigna* genotypes were digested with a 10 mL di-acid mixture ($HNO₃:HClO₄$, 9:4) and a volume that was made up to 50 mL. The digested samples were filtered using Whatman No. 42 filter paper. The supernatant samples were run on an inductively coupled plasma optical emission spectrometer (ICP-OES; model 5110, Agilent Technologies (Santa Clara, CA, USA) calibrated using the standard for measuring the absorbance of the blue-colored phosphor-molybdate complex at 660 nm [\[40\]](#page-18-12). The results of the four replications were averaged, and the P concentration was expressed as mg g^{-1} dry weight. The phosphorus uptake and utilization efficiency were calculated as per Irfan et al. and Neto et al. [\[41](#page-18-13)[,42\]](#page-18-14).

PupE (mg per plant) = P concentration (mg per mg) \times dry matter (mg per plant)

PutiE (
$$
\degree
$$
) = TDW (LP)/TDW (SP) \times 100

2.4. Estimation of Phosphorus-Use Efficiency

The PUE of the studied *Vigna* genotypes was measured using two different methods. In the first method, suggested by Osborne and Rengal and Aziz et al. [\[43,](#page-18-15)[44\]](#page-18-16), the population mean and standard deviation were used to characterize the genotypes as efficient $(>\mu + SD)$, medium (μ + SD to μ – SD) and inefficient (< μ – SD). The second method computes the PUE stress tolerance score (STC) for each genotype [\[45,](#page-18-17)[46\]](#page-18-18) using the formula:

$$
(STC) = SSI + MPI + GMPI + HMI + STI + TI + SI
$$

Here, the stress susceptibility index (SSI) = $(1 - T/C)/(1 - xT/xC)$, mean productivity index (MPI) = $(C + T)/2$, geometric mean productivity index (GMPI) = $\sqrt{C \times T} \sqrt{C}$, harmonic mean index (HMI) = 2 (C × T)/(C + T), stress tolerance index (STI) = (C × T)/(xC) 2, tolerance index (TI) = $C - T$, and stress index (SI) = T/C

Here, C represents the total dry mass under control conditions and T represents the total dry mass under treatment conditions. xC and xT represent the average total dry mass (TDM) of all studied *Vigna* genotypes under OP (control) and LP (treatment) conditions, respectively.

2.5. Statistical Analysis

The data obtained was subjected to analysis for mean, standard deviation, coefficient of variation, analysis of variance, and Pearson correlation coefficient susing the STAR (Statistical Tool for Agricultural Research) 2.1.0 software under both the OP and LP condition [\[47\]](#page-18-19). The broad-sense heritability under the OP and LP condition and combined and variance due to genotype \times P level interaction were measured as the following [\[48\]](#page-18-20):

Broad-sense heritability H = $σ2G/(σ2 G+σ2 e/r)$

Combined heritability Hcom = σ 2G/(σ 2G+(σ 2GE)/e) + (σ 2e)/re))

where σ2G, σ2GE, and σ2 e are genotypic variance, variance due to genotype \times P level interaction, and error variance, respectively; 'r' is the replication.

To find the common trends among the multidimensional data sets, principal component analysis was used. With the aid of the R software package "FactoMineR", the principal component analysis (PCA) was carried out for several root and shoot attributes utilizing relative values under LP to identify the traits that contributed the most [\[49\]](#page-18-21).

3. Results

3.1. Descriptive Statistics of Measured Traits

The descriptive statistics of 14measured traits related to PUE among the 327 studied *Vigna* genotypes grown in OP and LP conditions are presented in Table [1.](#page-4-0) The mean values of TRL, TSA, TRT, SDW, RF, TDW, PC, and PUpE were higher in the OP condition compared to the LP condition. PRL, ARD, TRV, RSR, and PUtiE were higher under LP conditions. The highest percentage reduction was noticed for PUpE (-78.62) followed by percentage P (−72.13) under the LP condition compared to OP condition. Whereas, the highest gain was noticed for PUtE (403.57) followed by RSR (50.00) under the LP condition. Among the studied genotypes, the PUpE ranged from 4.75 to 0.06 mg P/plant and 1.74–0.00 mg P/plant under OP and LP conditions, respectively, whereas PUtE ranged from 2.95 to 0.07 g dry mass/mg P and 31.25 to 0.20 g dry mass/mg P under OP and LP conditions, respectively, among the tested genotypes. The analysis of variance of the measured traits (except ARD under the OP condition) revealed significant variation among the genotypes studied in the experiment (Table [2\)](#page-5-0). Combined analysis indicated a significant interaction between the genotype and P treatment. High broad-sense heritability was recorded for all the studied traits under the OP and LP condition (Table [2\)](#page-5-0).

Table 1. Descriptive statistics of the measured traits in Vigna genotypes under optimum- and low-phosphorus conditions.

3.2. Variation of PUE Traits in Studied Vigna Species

A total of 327 accessions of 18 *Vigna* species were characterized for 14traits related to phosphorus-use efficiency (PUE). The trait-wise performance of different *Vigna* species is presented in Figure [1.](#page-7-0)

Table 2. Estimates of variance components and broad-sense heritability (H) for root and shoot traits under optimum- and low-phosphorus conditions.

** Significance at $p < 0.05$ and ns not significant.

Primary root length: Eleven species/subspecies of *Vigna* exhibited an increase in primary root length in theLP condition (Figure [1\)](#page-7-0). A high increase was recorded in *Vigna unguiculata*, *Vigna unguiculata* ssp. *Sesquipedalis*, *Vigna racemosa,* and wild *Vigna*. The maximum increase was recorded in *Vigna unguiculata*. The remaining seven species/subspecies exhibited a decline in primary root length in theLP condition. The maximum reduction in primary root length in theLP condition was recorded for *Vigna pilosa*.

Total root length: Twelve species/subspecies of *Vigna* exhibited an increase in total root length. The highest increase was recorded in *Vigna unguiculata*, followed by *Vigna unguiculata* ssp. *sesquipedalis*, *Vigna racemosa*, and wild *Vigna. Vigna pilosa* exhibited the maximum reduction in TRL in theLP conditions.

Total surface area: The maximum total surface area was recorded for *Vigna unguiculata*. This species exhibited an increase in TSA under the LP condition. Twelve species/subspecies exhibited an increase in TSA under the LP condition. *Vigna radiata* recorded a decrease in TSA in theLP condition and *Vigna mungo* revealed an increase in TSA in theLP condition.

Average root diameter: Only three studied species/subspecies, *Vigna pilosa, Vigna radiata* var. *setulosa,* and *Vigna radiata,* exhibited an increase in ARD under theLP condition. The remaining fifteen species/subspecies exhibited a reduction in ARD in theLP condition.

Total root volume: Three species/subspecies, *Vigna pilosa, Vigna racemosa* and unknown wild *Vigna*, exhibited a reduction in TRV under theLP condition. Fifteen species/subspecies revealed an increase in TRV in theLP condition. The maximum increase in TRV in theLP condition was recorded for *Vigna unguiculata* and *Vigna unguiculata* ssp. *sesquipedalis*.

Total root tips: The total root tips increased in 11 species/subspecies in response to low phosphorus. The maximum increase was recorded in *Vigna unguiculata* ssp. *sesquipedalis*, followed by *Vigna unguiculata* and *Vigna membranaceae*. Among the studied species, the highest TRT was recorded for *Vigna membranaceae* under both the LP and OP condition.

Figure 1. *Cont*.

Figure 1. Performance of *Vigna* spp. under optimum-phosphorus (OP) and low-phosphorus (LP) conditions. (**I**) Primary root length (cm), (**II**) total root length (cm), (**III**) total surface area (cm²), (**IV**) average root diameter (mm), (**V**) total root volume (cm³), (**VI**) total root tips, (**VII**) root forks, (**VIII**) shoot dry weight (g per plant), (**IX**) root dry wight (g per plant), (**X**) total dry weight (g per plant), (**XI**) P (%), (**XII**) P uptake efficiency (g per plant), (**XIII**) P utilization efficiency, (**XIV**) root-to-shoot ratio.(A) Vigna radiata var. bourneae, (B) Vigna pilosa, (C) Vigna minima, (D) Vigna dalzelliana, (E) V. hainiana, (F) Vigna mungo, (G) Vigna mungo var. silvestris, (H) Vigna trilobata, (I) Vigna trinervia var. bourneae, (J) Vigna membranaceae, (K) Vigna umbelleta, (L) Vigna unguiculata, (M) Vigna unguiculata ssp. sesquipedalis, (N) Vigna racemosa, (O) *Vigna radiata* var. *sublobata*, (P) *Vigna radiata* var. *setulosa*, (Q) *Vigna radiata*, (R) *Vigna* species (unknown).

Root shoot ratio: *Vigna pilosa, Vigna mungo* var. *silvestris,* and *Vigna radiata* var. *sublobata* exhibited a decline in RSR under theLP condition. The otherfifteen species/subspecies showed enhanced RSR in theLP condition. *Vigna mungo* var. *silvestris* is a progenitor of cultivated urdbean, and *Vigna radiata* var. *sublobata* is a progenitor of cultivated mungbean.

Root forks: Root forks increased in theLP condition in *Vigna pilosa, Vigna hainiana, Vigna mungo* var. *silvestris*, *Vigna trilobata, Vigna trinervia* ssp. *bourneae, Vigna unguiculata*, *Vigna unguiculata* ssp. *sesquipedalis,* and *Vigna racemosa*. The maximum decline in RF was recorded for *Vigna radiata* var. *setulosa* in theLP condition.

Root dry weight: Ten *Vigna* species/subspecies exhibited a higher dry root weight in theLP condition. Avery high increase was found in *Vigna unguiculata*, *Vigna unguiculata* ssp. *sesquipedalis*, and wild *Vigna.*

Shoot dry weight: *Vigna hainiana* and *Vigna unguiculata* ssp. *sesquipedalis* exhibited a minor improvement in SDW under the LP condition. The remaining sixteen species revealed a decline in SDW in theLP condition.

Total dry weight: Sixteen species recorded a decrease in TDW under the LP condition. However, *Vigna hainiana* and *Vigna unguiculata* ssp. *sesquipedalis* exhibited an increase in TDW under the LP condition.

Phosphorus (%): Phosphorus (%) increased under LP conditions in *Vigna mungo* and *Vigna trinervia* ssp. *bourneae* and reduced significantly in the other sixteen studied species/subspecies.

Phosphorus uptake efficiency:Phosphorus uptake efficiency declined in fourteen species/subspecies in theLP condition. However, PUpE increased in the LP condition in *Vigna pilosa, Vigna hainiana, Vigna mungo,* and *Vigna trinervia* var. *bourneae.*

Phosphorus utilization efficiency: The maximum PUtE was recorded for *Vigna mungo* var. *silvestris* under both the conditions, followed by *Vigna radiata* var. *bourneae*. Nine species/subspecies revealed a decrease in PUtE in the OP/LP conditions.

3.3. Correlation Coefficients between Measured Traits

The correlation coefficients among the studied traits are presented in Table [3.](#page-10-0) Under low-P conditions, primary root length was correlated with total root length, total surface area, total root volume, total root tips, root forks, root dry weight, root-to-shoot ratio, P (%) and phosphorus uptake efficiency. Total root volume and total root tips were correlated with each other and correlated to root forks, shoot dry weight, root dry weight, total dry weight, root-to-shoot ratio, P (%) and phosphorus uptake efficiency. Total root length was correlated with total surface area, total root volume, total root tips, root forks, root dry weight, root-to-shoot ratio, P (%) and phosphorus uptake efficiency. Total surface area was positively correlated with total root volume, total root tips, root forks, root dry weight, root-to-shoot ratio, P (%) and phosphorus uptake efficiency. Average root diameter was correlated to total root volume, root forks, shoot dry weight, root dry weight, and phosphorus uptake efficiency. Root forks were correlated to shoot dry weight, root dry weight, total dry weight, and phosphorus uptake efficiency. Seed dry weight was correlated to root dry weight, total dry weight, and phosphorus uptake efficiency. Root dry weight was correlated to total dry weight, root-to-shoot ratio, phosphorus utilization efficiency, and phosphorus uptake efficiency. Total dry weight was correlated to phosphorus uptake efficiency and phosphorus utilization efficiency. Root-to-shoot ratio was correlated to P (%) and phosphorus uptake efficiency.

Under optimum-P conditions, phosphorus utilization efficiency was correlated to average root diameter, total root volume, root forks, shoot dry weight, root dry weight and root-to-shoot ratio. Similarly, phosphorus uptake efficiency was correlated to primary root length, total root length, total surface area, total root volume, total root tips, root forks, shoot dry weight, total dry weight, root dry weight, and P (%). P (%) was correlated to primary root length, total root length, total surface area and total root tips. Root-to-shoot ratio was correlated to primary root length, total root length, total surface area, and root dry weight. Total dry weight was correlated to total root length, total surface area, average

root diameter, total root volume, total root tips, root forks, seed dry weight, and root dry weight. Root dry weight was correlated to total root length, total surface area, average root diameter, total root volume, total root tips, root forks, and shoot dry weight. Shoot dry weight was correlated to total root length, total surface area, average root diameter, total root volume, total root tips and root forks. Root forks were correlated to primary root length, total root length, total surface area, total root volume, and total root tips. Total root tips were correlated to primary root length, total root length, total surface area, and total root volume. Total root volume was correlated to primary root length, total root length, total surface area, and average root diameter. Total surface area was correlated to primary root length and total root length.Total root length was correlated to primary root length.

The PCA for all 14 root traits recorded 59% of the variation in the first two PCA axes, with the first component capturing 33.9% of the variation under the LP treatment conditions (Figure [2\)](#page-9-0),while the treatment OP contributed 65.9% of the total variation through the first two components, and the first PCA contributed 37.5% of the total variation. The graph above also shows the relationships between all 14 variables at once. Variables that contribute similar information are grouped together or correlated. RDW and TRV are two variables that are positively correlated when subjected to the LP treatment. The same pattern can be seen with TRT, TRL, and TSA in the OP treatment. The trait P uptake was constant and did not change its position under both the treatments, while ARD and P utilization pattern differed in the LP and OP treatments.

Figure 2. (**A**) Biplot PupE and (**B**) Biplot PutiE using the relative values of tested root and shoot traits of *Vigna* species under LP conditions (PupE, phosphorus uptake efficiency; PutiE, phosphorus utilization efficiency; LP, low phosphorus).

In the case of the LP treatment, the scree plot indicated that 4major PCs explained about 83% of the total variation. Figure [3](#page-11-0) the remaining minor PCs explained about 17% of the variation. However, under the OP treatment, the first 3major PCs explained about 76.5% of the total variation. The remaining minor PCs explained about 23.5% of the variation.

Table 3. Pearson's correlation analysis for the studied root and shoot traits under optimum-phosphorus (upper diagonal) conditions and low-phosphorus (lower diagonal) conditions.

** Significance at $p < 0.05$ and ns not significant.

Figure 3. Scree plot under LP and OP conditions.

3.4. Identification of Superior Genotypes for Important PUE Traits in Vigna Species

A total of 10superior genotypes were identified for key traits contributing to PUE in *Vigna* species, based on the characterization of 327 *Vigna* accessions (Table [4\)](#page-11-1). A total of 9genotypes, IC 343440, V1002190BG, V1001162AG, V1003959BG, V1002872BG, V1001066BG, V1002672AG, V1001698BG, and V1000470AG, were in the top 10 genotypes for TDW and SDW. Among these genotypes, V1002190BG, IC 343440,and IC 273244 possessed a higher RDW. Seven genotypes (IC 251950, IC 585931, V1002532AG, IC 371653, IC 331615, V1001400AG, and V1000532BG) exhibited both high PupE and PutiE.

Table 4. Top 10 genotypes for traits contributing to PUE in 327 accessions of studied *Vigna* species.

TDW, total dry weight; SDW, shoot dry weight; RDW, root dry weight; PupE, phosphorus uptake efficiency; PutiE, phosphorus utilization efficiency.

3.5. Categorization of Vigna Genotypes for PUE

Based on the standard deviation and mean, the studied genotypes were characterized as efficient, medium, or inefficient [\[42,](#page-18-14)[43\]](#page-18-15). The 327 studied *Vigna* genotypes exhibited differences in the studied traits in both low-phosphorus and optimum-phosphorus conditions (Table [4\)](#page-11-1). Under the LP condition, genotype V1003948B-BR (*V. radiata*) recorded the highest score (13/15), and IC 25950 (*V. radiate bourneae*), IC 58367 (*V. dazelliana*), and V 1001066BG (*V. radiata*) recorded the highest score (13/15) in the OP condition. The lowest score of 8

was recorded by 27 genotypes in the LP condition and 9 by 40genotypes inthe OP condition. The overall performance of the studied *Vigna* genotypes identified IC 25950 and IC 583664 as the best genotypes with the highest score of 25/30 obtained by summing up the score at both P levels (Table [5\)](#page-13-0). A total of 23 genotypes (IC 251950, IC 277000, IC 305153, IC 202643, IC 259502, IC 371653, IC 248206, IC 585931, IC 251419, IC 583670, IC 583662, IC 331450, IC 331615, IC 331452, IC 583665, V1001339AG, V1000532BG, V1001400AG, V1004734AG, V1001806BG, andV1002532AG) exhibited an overall score of 24 (efficient) based on RDW, SDW, RSR, TPU, and PUtE. The poor genotypic performance of the genotypes is due to low P uptake resulting in low root and shoot biomass production.

In the second method [\[45](#page-18-17)[,46\]](#page-18-18), the stress tolerance score STS was calculated using seven P deficiency tolerance indices of 327 genotypes (Table [6\)](#page-13-1). Among the studied genotypes, the highest STS score was recorded by EESM 18-163 (18.85), followed by Pusa 1431 (17.703) and SM 18–21 (14.28).

Table 5. Efficient genotypes identified based on population mean and standard deviation under low-phosphorus and optimum-phosphorus conditions [\[43](#page-18-15)[,44\]](#page-18-16).

Table 5. *Cont*.

RDW, root dry weight; SDW, shoot dry weight; RSR, root-to-shoot ratio; TPU, total phosphorus uptake; PUtE, phosphorus utilization efficiency.

Table 6. Phosphorus deficiency tolerance indices of promising genotypes identified under optimumand low-phosphorus conditions [\[45,](#page-18-17)[46\]](#page-18-18).

SSI, stress susceptibility index; MPI, mean productivity index; GMPI, geometric mean productivity index; HI, harmonic men index; STI, stress tolerance index; TI, tolerance index; SI, stress index; STC, stress tolerance index.

4. Discussion

The present study characterized a panel of 327 *Vigna* genotypes from 18 *Vigna* species for different root and shoot traits at contrasting P levels under controlled conditions. The purpose of this study was to identify superior *Vigna* species/genotypes with a significant P-use efficiency. Phosphorus-use efficiency (PUE) can be enhanced by improving both uptake and utilization efficiencies of crop plants [\[50\]](#page-18-22). Root architectural traits are critical for nutrient and water uptake from the soil. In mungbean, limited studies have been conductedon root traits [\[28\]](#page-18-0). Studies on root traits of other *Vigna* species are lacking. Variation inroot traits is essential for enhancing PUE. Under LP conditions, the genotypes with a higher root length and density exhibit enhanced P uptake [\[51\]](#page-18-23). In the present study, 327 genotypes from 18 *Vigna* species were screened for 14 traits related to phosphorus-use efficiency in *Vigna* species. Significant variationsinstudied traits with high heritability and significant correlations were recorded at different P levels. These variations can be attributed to the genetic variations among the studied *Vigna* species for PUE traits. Similar results have been reported in mungbean [\[39\]](#page-18-11), lentil [\[52\]](#page-18-24), common beans [\[52\]](#page-18-24), maize [\[53\]](#page-19-0), and *Brassica* [\[54\]](#page-19-1).

For the variables under study, a substantial interaction between genotypes and P treatment was noted. The study also showed substantial differences between the several *Vigna* species under LP conditions for traits with strong heritability, suggesting potential genetic gain through selection. In comparison to the OP condition, the mean values of PRL, ARD, TRV, RSR, and PUtiE were greater under LP conditions. According to earlier reports by [\[55\]](#page-19-2) for rice and [\[33\]](#page-18-5) for wheat, PUtE was greater under the LP condition.

The higher biomass produced per unit of P uptake and P harvest index contribute to the higher PUtE [\[56\]](#page-19-3). Shoot dry mass drops while RSR increases under LP conditions. Under LP conditions, plants' adaptive strategy is to increase RSR. The results were in agreement with earlier research by [\[57\]](#page-19-4).

Higher TRV, RSA, and carbon exudation efficiency were found in mungbean P-efficient genotypes in a prior study [\[58\]](#page-19-5). In the case of rice, a rise in RSR and RDW was correlated with a reduction in SDW [\[59\]](#page-19-6).Between PRL and TRL, TSA, TRV, TRT, RF, RDW, RSR, P, and PUpE, there is a strong positive association. Under LP conditions, TRL was favourably connected with TRV and TSA in maize [\[60\]](#page-19-7), and with TRT and RF in mungbean [\[19\]](#page-17-18). RF, SDW, RDW, TWD, and PUpE were all linked with ARD in this study. Nevertheless, a prior study on chickpea [\[61\]](#page-19-8) found no significant association between ARD and the majority of characteristics. Under both the LP and OP conditions, SDW was associated with RDW and TDW.

Under the OP condition, RDW was positively correlated to TDW, and in the LP condition, RDW was correlated to TDW and SDW. PCA revealed that TSA, TRL, and TRT contributed the most for total variation. In a previous study on mungbean, it was reported that the LP condition alters TSA, TRT, TRL, and SDW [\[39\]](#page-18-11), and TSA and TRL in common beans [\[52\]](#page-18-24).

Positive correlations between PUpE and biomass attributes and TPU and root traits, PRL, TRL, TSA, TRV, and RSR were seen under LP circumstances. RDW and TDW had a favourable correlation with PUtE. The study found a substantial and favourable association between biomass attributes and TPU. This characteristic may result from increased cytokinin production, which would increase biomass partitioning [\[62\]](#page-19-9). Total P uptake in cotton showed a favourable and substantial connection with plant roots and shoots dry mass [\[63\]](#page-19-10). Additionally, P uptake is benefiting leaf photosynthetic and transpiration rates [\[64\]](#page-19-11). In cotton, Singh et al. (2013) [\[65\]](#page-19-12) observed that P deficiency drastically impairs photosynthetic characteristics and reduces plant development. To understand how leaf photosynthetic features affect P transport to the root surface and, ultimately, P uptake, it is possible to study their effects under low-P conditions. The success of plant breeding programmes mostly depends on the selection of genotypes that perform well under both stressful and non-stressful conditions.

The enhancement of PUE in upcoming breeding projects requires further genotype categorization. For the classification and selection of effective genotypes for PUE in wheat [\[66](#page-19-13)[–68\]](#page-19-14), a variety of techniques and attributes were applied. Two procedures were used in this investigation to choose P-efficient genotype(s). In the first procedure, the genotypes were divided into efficient, medium, and inefficient kinds based on the attributes RDM, SDM, RSR, TPU, and PUtE. In order to find the efficient genotypes in wheat [\[69\]](#page-19-15) and *brassica* [\[70\]](#page-19-16), a similar classification method was applied. However, under sufficient P conditions, the efficient genotype under LP conditions was unable to achieve the same

type of performance [\[71,](#page-19-17)[72\]](#page-19-18). The genotypes that perform better at various P levels are able to thrive in soils with a range of P conditions $[51]$. Therefore, it is necessary to classify genotypes under both LP and OP situations. Both LP and OP conditions were used to categorize genotypes, and the scores for each genotype were added up to obtain the overall genotype score. The genotype IC 25950 and IC 583664 showed a higher root, shoot biomass, and P uptake with a cumulative score of 25 out of 30, combining both control and stress conditions. Whereas, the genotypes IC 282094 and M1443 recorded the lowest score of 15 out of 30, combining both P conditions. The low root, shoot biomass output, and total P uptake of genotypes under normal and low P circumstances are the key causes of the genotypes' poor performance. The performance of genotypes supported the claim that biomass and P absorption efficiency features have a linear relationship.

Based on P efficiency and responsiveness, the mungbean genotypes were divided into four categories, namely efficient responsive(ER),efficient non-responsive (ENR), inefficient responsive (IR), and inefficient non-responsive (INR), in accordance with the categorization approach suggested by [\[69](#page-19-15)[,73\]](#page-19-19). Under both P circumstances, the most productive genotypes, PUSA 1333 and Pusa Ratna, fell into the ENR group. The genotypes ML 1666 and V6183, which were put in the ER category under the LP condition, were moved to the INR condition. This supports the idea that classification is important both at normal and low P levels [\[39\]](#page-18-11). The genotypes categorized under the ER category had good soil P-level adaptation. However, cultivars belonging to the ENR group could thrive in soils with low levels of P. The crossing programme may use the genotypes of the IR category to incorporate P-responsive characteristics. However, the PUE improvement programme does not significantly depend on the genotypes of the INR group [\[74\]](#page-19-20). This categorization method makes it possible to choose genotypes that are suitable for a variety of cultivation at different P levels [\[41\]](#page-18-13). However, the basic foundation of this strategy is the population mean. It therefore has a fairly limited range between types that are responsive or nonresponsive as well as efficient or wasteful [\[75\]](#page-19-21). For instance, the genotypes M 512, ML 818, Muskan, and RMG 1028 under the NP condition, and M 1316, M 961, MH 810, Muskan, and PUSA 1132 under the LP condition, were located along the boundary between the efficient and inefficient groups [\[39\]](#page-18-11). As a result, it is challenging to categorize genotypes as efficient or inefficient and responsive or nonresponsive given their low divergence from the population mean. Therefore, this method is not appropriate for investigating and classifying genotypes on a broad scale [\[41](#page-18-13)[,69\]](#page-19-15).

In order to categorize genotypes [\[46,](#page-18-18)[76\]](#page-19-22), stress tolerance indices were calculated for the dry mass of genotypes under control and stress circumstances. The P deficiency tolerance indices of all genotypes were determined in the current investigation using TDM under both OP and LP circumstances. The susceptibility indices SSI, TI, and SI tend to distinguish between genotypes that are stress-tolerant and susceptible to stress, and have a negative connection with yield and biomass [\[77\]](#page-19-23). While the indices MPI, GMPI, and STI can be used to identify genotypes with a high average yield/biomass and stress tolerance and demonstrate a positive connection with yield/biomass [\[78\]](#page-19-24). Based on PCA analysis, it is evident from the current study that two indices, MPI and SSI, were able to account for the majority of the variation among the analyzed indices. According to [\[79\]](#page-20-0), the most effective indices for locating stress-tolerant genotypes under both control and stressful circumstances are the GMPI, MPI, and STI. The stress-tolerant genotypes with high yields/biomass under both control and stress conditions, however, were not detectable by any of these tolerance and susceptible indices [\[80\]](#page-20-1). In order to find the genotypes that are more tolerant to stress, [\[76\]](#page-19-22) propose combining the susceptibility and tolerance indices as a relevant criterion. In the prior investigations, the genotype PUSA 1333 had the highest STS score, demonstrating its strong efficacy under various P circumstances. In the present study, genotype EESM 18-163 had the highest STC score.

Drought-tolerant genotypes of wheat [\[46\]](#page-18-18), pearl millet [\[45\]](#page-18-17), and sorghum were chosen using the classification of genotypes based on stress tolerance indices. A robust criterion for classifying genotypes with high productivity, resilience, and a clear visualization of contrast in genotypes for biomass under stress conditions is provided by this new selection technique. This research offers fresh perspectives on genotype selection and a deeper comprehension of genotype behaviour under phosphorus stress.

5. Conclusions

The identification and creation of more P-efficient genotypes in the mungbean breeding programme would depend on the categorization of the existing germplasm. Under optimum- and low-P conditions, the study found a significant variation in genotypes for the attributes RDM, SDM, TDM, PC, TPU, and PUtE. To create P-efficient genotypes, it is possible to take advantage of the strong interactions that exist between genotypes and P treatments. The characteristics and techniques used for classifying genotypes under optimum- and low-phosphorus conditions influence the P efficiency of the genotypes in different ways. The classification of 327 *Vigna* genotypes using the study's methodology showed that the optimum technique for analyzing the slight variation in genotype P efficiency is to first divide them based on efficiency, then distribute them into different groups. The best way to depict the contrast in genotypes in terms of biomass output and resistance under low-P conditions is to categorise them based on their score for stress tolerance. Under optimum and low-P conditions, seven genotypes (IC 251950, IC 585931, V1002532AG, IC 371653, IC 331615, V1001400AG, and V1000532BG) of *Vigna radiata* (L.) Wilczek were found promising for both PupE and PutiE. Using the mean and standard deviation as criteria, *Vigna radiata* (L.) Wilczek genotypes with high phosphorus utilization efficiency were found as IC 25950 and IC 583664. KPS 1546, IC 277060, IC 697141, IC 343440, and Pusa 0831 were selected by characterization based on the stress tolerance index as genotypes that performed better under P stress. The effective genotype IC 343440 performed better in terms of dry mass production and P absorption efficiency. Additionally, the characteristics RDM, SDM, TDM, TPU, and PUtE played a significant role in classifying the genotypes for PUE in mungbean. The tested genotypes should, nonetheless, undergo additional field testing for adult-stage features. The study's overall findings could be applied to the enhancement of genotypes with P efficiency, which will increase P uptake and utilization.

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