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ORIGINAL ARTICLE

Effects of phosphorus availabilities on growth and yield of foxtail millet: insights from high-throughput phenotyping platforms

Tharanya Murugesan[1] · Sivasakthi Kaliamoorthy[1] · Sunita Choudhary[1] · Keerthi Vysyaraju[1,2] · Devan Sai Gudela[1,2] · Annepu Anusha[1,2] · Kommireddypally Sowmya Goud[3] · Sara Loftus[4] · Michaela A. Dippold[4] · Suresh Kanuri[1] · Rekha Baddam[1] · Alison Baker[5] · S. Antony Ceasar[6] · Jana Kholova[1,7]

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Abstract

Main conclusion **Foxtail millet performance under low phosphorus (P) is determined by growth potential, with tiller number as a key indicator. Yield is influenced by P dilution rather than total P concentration.**

Abstract Foxtail millet, renowned for its high nutrient content and drought resilience, faces limited breeding investment despite being cultivated in vulnerable agri-systems. Low phosphorus (P) levels affect approximately 50% of global agricultural soils, and particularly impact regions like Sub-Saharan Africa and Southeast Asia, the latter where foxtail millet is extensively grown. This study explores the effects of low P (< 5 ppm; Hedley Fractionation Method; Cross and Schlesinger 1995) on foxtail millet plant growth and yield-related traits, utilizing high-throughput platforms (HTP) with a selected subset of genotypes ($n = 10$) from the core collection of ICRISAT Genebank. Results uncover substantial variation in plant growth and agronomical traits at both treatment and genotype levels. Under low-P conditions, genotypic variation is noted, with a sixfold difference in tiller count, 2.4-fold in grain yield, 2.7-fold in 3D-leaf area, and 2.3-fold in root surface area. A significant relationship was found between grain yield under low-P and high-P conditions ($R^2 = 0.65$; $P < 0.01$). This suggests that genetic yield potential (vigor) under high-P conditions strongly influences grain yield and tiller numbers under low-P conditions. Residual grain yield under low-P conditions, not explained by high-P conditions, had a strong positive association with tiller numbers ($R^2 = 0.70$; $P < 0.01$) and showed a significant negative association with total P concentration ($R^2 = 0.54$; $P < 0.05$). Conversely, under high-P conditions, grain yield (GY_LF) from Lysi-Field exhibited significant positive correlations with P use efficiency (PUE) ($r = 0.94$; $P < 0.001$) and total biomass ($r = 0.84$; $P < 0.01$). These findings underscore the critical role of P availability in influencing grain yield and related traits. Under low-P conditions, performance is primarily driven by growth potential, with tiller number serving as a reliable marker of this potential. The significant genotypic variation observed highlights the importance of selecting for growth-related traits in P-limited environments. In addition, P dilution, rather than total P concentration, appears to play a key role in determining yield under low P. Optimizing P management strategies and breeding for improved growth potential may significantly enhance crop performance in regions facing P limitation.

Keywords Foxtail millet · Grain P content · High-throughput phenotyping platforms · Nutrient deficiency · Phosphorus stress · Phosphorus use efficiency · Resource poor soil

Abbreviations

DAS	Days after sowing
GY	Grain yield
PUE	Phosphorous use efficiency

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Murugesan Tharanya and Kaliamoorthy Sivasakthi were contributed equally.

Extended author information available on the last page of the article

Introduction

Phosphorus (P), essential alongside nitrogen (N) and potassium (K), is critical for plant growth (Roch et al. 2020). Despite being primarily sourced from inorganic phosphate (Pi), its limited soil availability often necessitates using P fertilizers (Roch et al. 2019). Concerns over depleting rock phosphate reserves and environmental impacts highlight the need for sustainable management (Baker et al. 2015; Ceasar et al. 2017). Globally, about 50% of agricultural soils, especially in Sub-Saharan Africa and Southeast Asia, face P limitations. In India, almost 98% of districts require P fertilizers due to varying deficiency levels (Hasan 1996), underscoring the need to address P deficiency for improved productivity.

P deficiency negatively impacts the growth and yield of various crop plants, including rice (*Oryza sativa*) (Wissuwa and Ae 2001), maize (*Zea mays*) (Plenet et al. 2000), wheat (*Triticum aestivum*) (Lazaro et al. 2010), sorghum (*Sorghum bicolor*) (Loftus et al. 2025), common bean (*Phaseolus vulgaris*) (Bonser et al. 1996), soybean (*Glycine max*) (Mahamood et al. 2009), foxtail millet (*Setaria italica*) (Ceasar et al. 2014, 2020) and other millets (Maharajan et al. 2019). P deficiency affects a significant portion of global agricultural land (Navea et al. 2023) raising concerns about potential food scarcity (Childers et al. 2011). Consequently, farmers resort to P fertilizer application to optimize soil fertility and enhance crop yield (Maharajan et al. 2018). However, prudent P management is essential to ensure a continuous supply of P to sustain soil fertility and prevent eutrophication and water pollution (Maharajan et al. 2021).

Low P levels in the soil profile have been observed to lead to poor seedling emergence (Valluru et al. 2010), representing a significant constraint for achieving higher millet yield (Rebafka et al. 1993). P use efficiency (PUE) is a ratio that quantifies the efficiency with which a plant utilizes P for growth and development and is calculated as the square of the total plant biomass divided by the total P content in the plant, which is derived from the weighted sum of P concentrations in the leaf, stem, and grain, each weighted by their respective dry weights (Gourley et al. 1993; Hayes et al. 2022). The inefficiency in P utilization, characterized by a low PUE in modern cultivars, poses a significant challenge in cropping systems heavily reliant on phosphate fertilizer inputs (Dixon et al. 2020). Despite external inputs, P deficiency persists, necessitating urgent efforts to improve PUE for sustainable agriculture (Vinod et al. 2015; Ceasar et al. 2020). In this context, breeding efforts for PUE focus on enhancing adaptation to P starvation.

Foxtail millet (*Setaria italica*), ranking as the second most cultivated millet crop globally, holds significance for both food and forage purposes (Jaiswal et al. 2019). This C4 self-pollinated cereal has a rich cultivation history dating back to 5000–6000 BC along the Yellow River in China. Foxtail millet is celebrated for its agronomic advantages, cost-effectiveness, stress resilience, efficient water utilization, and nutritional value. Its primary production hubs are situated in China and India (Lin et al. 2024). In Africa, foxtail millet is cultivated in upland regions across East Africa, Cameroon, and southern Africa (Brink 2006). With its relatively small diploid genome of 510 Mb, foxtail millet serves as an ideal C4 model for genetic studies. This includes investigating the molecular, genetic, and physiologic mechanisms underlying the C4 photosynthetic pathway, such as its efficiency in carbon fixation, adaptation to high temperature conditions, and water use efficiency. These traits make foxtail millet particularly valuable for research aimed at enhancing crop productivity and resilience (Ceasar et al. 2017, 2020; Jaiswal et al. 2019).

Among millets, foxtail millet stands out as an excellent source of protein (12.3 g/100 g), dietary fibers (14 g/100 g), minerals (3 g/100 g), and ß-carotene (126–191 µg/100 g), while containing a limited amount of bioavailable carbohydrates (60.9 g/100 g) (Ballolli et al. 2014). Despite these nutritional advantages, there is a noticeable gap in comprehensive studies exploring the responses of diverse foxtail millet cultivars to limited P conditions. A few studies have investigated aspects of plant growth, development, and the molecular expression of the PHT1 transporter family under P limitations (Ceasar et al. 2014, 2017, 2020; Ahmad et al. 2018; Roch et al. 2020). A systematic study aimed at characterizing foxtail millet genotypes for plant growth and development, water use efficiency, and agronomical trait values under a limited P regime, utilizing relevant phenotyping methodology, was notably absent. Our hypothesis is that under limited P conditions, overall plant growth and development are critical factors in determining the grain yield (GY) of foxtail millet. To examine this hypothesis, we undertook a comprehensive investigation involving ten foxtail millet genotypes from the core collection of the ICRISAT Genebank. This investigation explored responses to both P sufficiency (high P) and starvation (low P) using diverse phenotyping platforms, namely Lysi-Field, LeasyScan, and hydroponics. Our specific objectives were (i) to identify genotypic variations in plant canopy growth, root growth, phenology and agronomic traits under different P regimes (low P and high P) and (ii) to analyze functional trait associations under low-P and high-P conditions and propose potential driving factors or key component traits for foxtail millet breeding programs, with a specific emphasis on low-P adaptation.

Materials and methods

Plant materials

Ten foxtail millet genotypes were selected from the core collection based on the previous study (Krishnamoorthy et al. 2016). The primary objective was to investigate and comprehend the extent of plant growth and agronomical traits variation across diverse P regimes, employing various phenotyping platforms. Details on the experimental overview, including a list of traits assessed across different phenotyping platforms are available in Table 1. In the initial Lysimeter trial, ISe710 was utilized. However, in subsequent LeasyScan and Hydroponics experiments, the cultivar Maxima (cv Maxima) was chosen to replace ISe710 due to the scientific interest in evaluating the cultivar and space constraints in these setups.

Water use and agronomical traits assessment at lysi-field facility under different P regimes (low and high P)

The Lysimetric facility is located at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, India (17°30′N; 78°16′E; altitude 549 m). It provides an experimental setup to assess key crop agronomic features, track the crop's ability to convert water into biomass (grams of dry mass per unit of water transpired), and measure water use patterns throughout the cropping season (Vadez et al. 2016). Plants were grown in PVC plumbing pipe lysimeters with a diameter of 20 cm and a length of 1.2 m, positioned outdoors under a rain-out shelter. The procedures for preparing soil, filling, spacing arrangement, and plant cultivation followed the methods outlined by Vadez et al. (2008, 2016). The soil utilized in this study from the ICRISAT field exhibited a low-P level (2.11 ppm; available P) analyzed through Hedley Fractionation Method (Cross and Schlesinger 1995). The methodology for cultivating and testing plants in lysimeters adhered to the protocol established by Vadez et al. (2013). Seeds were sown in each PVC cylinder, and later, the plants were thinned to four per cylinder two weeks after sowing. Subsequently, the number was further reduced to two plants per cylinder at 3 weeks after sowing. Six replications were designated for the high-P treatment, and another six replications for the low-P treatment. Following the final thinning, high-P cylinders received 5 g of di-ammonium phosphate (DAP) per cylinder and 2 g of potash (K) per cylinder, while low-P cylinders received 2 g of K per cylinder and 2 g of urea per cylinder to compensate for the nitrogen provided by DAP in high-P cylinders (Kadirimangalam et al. 2022). At 28 days after sowing (DAS), polythene beads were applied to cover the surface of the soil in the cylinders, preventing direct evaporation (more details in Vadez et al. 2011). Starting from the 5th week, cylinder weighing was carried out on a weekly basis with flowering time visually recorded. Tiller numbers were manually scored at the time of harvest. At the end of the experiment, the plant samples of leaf, stem, and panicles were dried in a hot air oven at 72 °C for about 3 days. Individual biomass components, such as leaf dry weight, stem dry weight, and panicle dry weight, were measured using a KERN 3600-g precision balance (Kern & Sohn GmbH, Balingen, Germany). GY was obtained by threshing panicles. Thousand grain numbers were counted by the seed counter machine (Data Count S60 seed Counter, Data technologies, Israel (details in https://data-technologies.com/product/seed-counter-s60/)) and the thousand grain weights were recorded using a weighing scale (KERN 360-3N, Kern & Sohn GmbH). Plant transpiration was assessed based on consecutive cylinder weight differences and water additions. Total transpiration was determined as the sum of weekly plant transpiration. Transpiration efficiency (TE; grams of biomass per kilogram of water transpired; g kg^{-1}) was calculated as the ratio of total dry biomass to the unit of water transpired. Finally, Harvest Index (HI) was computed as the ratio of total GY to the total biomass. For additional details on the methodology and data collection, please refer to Vadez et al. (2011, 2013, 2015, 2022), Tharanya et al. (2018), and Sivasakthi et al. (2019). The dried samples of leaf, stem and grains were ground, weighed and subjected to total P estimation through nitric acid pressure digestion (Heinrichs et al. 1986), followed by measurement using an inductively coupled plasma optical emission spectrometer (ICP-OES) (Thermo Scientific iCap 6000 Series, Thermo Fisher Scientific, Bremen, Germany). This method allowed for the determination of leaf P (leaf P; mg g^{-1}), stem P (stem P; mg g^{-1}), and grain P (grain P; mg g^{-1}) concentration. Total P concentration (mg g^{-1}) was determined as the sum of P concentrations in leaves, stems, and grains, weighted by their relative contributions to the total plant biomass. The PUE (g^2 mg^{-1}) was calculated as the square of the total plant biomass divided by the total P content in the plant, which is derived from the weighted sum of P concentrations in the leaf, stem, and grain, each weighted by their respective dry weights (Gourley et al. 1992; Irfan et al. 2020). The percent reduction in traits under low-P conditions compared to high-P conditions was calculated using the formula

$$\text{Percent Reduction in Trait} = \left(\text{Trait}_{HP} - \text{Trait}_{LP}\right) / \left(\text{Trait}_{HP}\right) \times 100,$$

Table 1 Details on genotypes, treatments, and replications, along with a list of phenotyped traits obtained from various phenotyping platforms (Lysi-Field, HTP-LeasyScan, and Hydroponics)

Sl. no.	Phenotyping platform	Trait description	Unit	Trait code	Trait category	No. of genotypes	No. of treatments	Replication per treatment	Method employed for trait measurement
1	Lysi-Field (LF)	Tiller Numbers	count	TLR-LF	Growth	10	2 (Low and high P)	6	Manual counting
2	Lysi-Field (LF)	Leaf dry weight	g	LDW	Biomass	10	2 (Low and high P)	6	Weighing
3	Lysi-Field (LF)	Stem dry weight	g	StDW	Biomass	10	2 (Low and high P)	6	Weighing
4	Lysi-Field (LF)	Panicle dry weight	g	PnDW	Biomass	10	2 (Low and high P)	6	Weighing
5	Lysi-Field (LF)	Total biomass	g	TBM	Biomass	10	2 (Low and high P)	6	Weighing
6	Lysi-Field (LF)	Days to flowering	count	DFL	Phenology	10	2 (Low and high P)	6	Visual scoring based on days after sowing
7	Lysi-Field (LF)	Grain yield	g	GY	Agronomy	10	2 (Low and high P)	6	Weighing
8	Lysi-Field (LF)	Harvest Index	%	HI	Agronomy	10	2 (Low and high P)	6	Weighing
9	Lysi-Field (LF)	1000-Grain weight	g	ThGW	Agronomy	10	2 (Low and high P)	6	Mechanical counting
10	Lysi-Field (LF)	Total transpiration	kg	Tot-T	Water use	10	2 (Low and high P)	6	Weighing
11	Lysi-Field (LF)	Transpiration efficiency	gkg^{-1}	TE	Water use	10	2 (Low and high P)	6	Weighing
12	Lysi-Field (LF)	Phosphorus concentration in leaf	mg g^{-1}	Leaf P	Nutrient	10	2 (Low and high P)	6	Chemical
13	Lysi-Field (LF)	Phosphorus concentration in stem	mg g^{-1}	Stem P	Plant nutrient uptake	10	2 (Low and high P)	6	Chemical
14	Lysi-Field (LF)	Phosphorus concentration in grain	mg g^{-1}	Grain P	Plant nutrient uptake	10	2 (Low and high P)	6	Chemical
15	Lysi-Field (LF)	Total phosphorus concentration	mg g^{-1} dry	Tot-P conc	Plant nutrient uptake	10	2 (Low and high P)	6	Chemical
16	Lysi-Field (LF)	Phosphorus use efficiency	g^2mg^{-1}	PUE	Pla nt nutrient use efficiency	10	2 (Low and high P)	6	Chemical
17	LeasyScan (LS)	Digital biomass	mm^{-3}	DBM	Biomass	10	2 (Low and high P)	8	3D imaging
18	LeasyScan (LS)	Plant height	mm	PH	Growth	10	2 (Low and high P)	8	3D imaging
19	LeasyScan (LS)	3D-Leaf area	mm^{-2}	3DLA	Biomass	10	2 (Low and high P)	8	3D imaging
20	LeasyScan (LS)	Pojected leaf area	mm^{-2}	Proj.LA	Biomass	10	2 (Low and high P)	8	3D imaging
21	Hydroponics (Hydro)	Root length	cm	RL	Growth	10	2 (Low and high P)	8	Manual measurement with a ruler
22	Hydroponics (Hydro)	Crown root numbers	count	Crown root No	Growth	10	2 (Low and high P)	8	Manual counting

Table 1 (continued)

Sl. no.	Phenotyping platform	Trait description	Unit	Trait code	Trait category	No. of genotypes	No. of treatments	Replication per treatment	Method employed for trait measurement
23	Hydroponics (Hydro)	Shoot dry weight	g	ShDW	Biomass	10	2 (Low and high P)	8	Weighing
24	Hydroponics (Hydro)	Root dry weight	g	RDW	Biomass	10	2 (Low and high P)	8	Weighing
25	Hydroponics (Hydro)	Root: Shoot ratio		RDW/ShDW	Biomass	10	2 (Low and high P)	8	Weighing
26	Hydroponics (Hydro)	Root surface area	cm^2	RSA	Biomass	10	2 (Low and high P)	8	Digital imaging
27	Hydroponics (Hydro)	Leaf area	cm^2	LA	Biomass	10	2 (Low and high P)	8	Area quantification
28	Hydroponics (Hydro)	Tiller numbers	count	TLR-LS	Growth	10	2 (Low and high P)	8	Manual counting

where Trait $_{HP}$ = Value of the trait under high-P conditions.

Trait $_{LP}$ = Value of the trait under low-P conditions.

Canopy development-related traits assessed at LeasyScan under different P regimes (low and high P)

LeasyScan, a high-throughput phenotyping platform, was designed to effectively monitor crop canopy-related parameters during the vegetative phase with exceptional throughput and accuracy. For a detailed understanding of LeasyScan technology and its setup, please refer to the works of Vadez et al. (2015), Sivasakthi et al. (2018, 2019) and Tharanya et al. (2018). Ten seeds were sown in individual 10-inch pots during November 2022 post-rainy season. The soil used in this experiment displayed a low-P level (2.11 ppm), sourced from the ICRISAT field, which was also the origin of the soil used in the Lysi-field experiment. Each genotype and treatment combination involved eight replications, with each replication consisting of two pots, and after the final thinning, two plants were retained per pot. The treatments with low P (1 g of urea and 1 g of potash per pot) and high phosphorus (2.5 g of DAP and 1 g of potash per pot) were applied (Kadirimangalam et al. 2022). Throughout the experiment, plants were maintained under well-watered conditions. Continuous measurements of canopy size-related parameters, including 3D-leaf area, projected leaf area, plant height and digital biomass (estimate of biomass based on observed plant dimensions—height and volumes), were taken from 15 to 40 DAS, with the final harvest conducted at 40 DAS. The daily temperature and humidity fluctuated between 11/35.8 °C and 17.2/93.2% on average during the crop growth period, as recorded by the attached weather station (Model: WxPRO™; Campbell Scientific Ltd., Shepshed, UK).

Hydroponic facility for plant shoot and root morphologic traits under different P regimes (low and high P)

To evaluate plant growth, especially root-related traits under high and low-P conditions, plants were cultivated in a greenhouse under natural daylight fluctuations, with an average day/night temperature of around 28/22 °C and relative humidity ranging from 70 to 90%. Seeds were initially sown in sand, and when the plants reached the 3rd leaf stage, they were transferred to trays with nutrient solution (modified Hoagland solution; macronutrients: $MgSO_4$ (2.05 mM), K_2SO_4 (1.25 mM), $CaCl_{2*}2H_2O$ (3.3 mM), Fe-EDTA (0.04 mM), urea (5 mM) and micronutrients: H_3BO_3 (4 mM), $MnSO_4$ (6.6 mM), $ZnSO_4$ (1.55 mM), $CuSO_4$ (1.55 mM), $CoSO_4$ (0.12 mM), Na_2MoO_4 (0.12 mM)). Subsequently, the plants were grown in hydroponic solutions within trays measuring 40 cm x 20 cm (length and width), utilizing the modified Hoagland solution in accordance with the protocol outlined in Tharanya et al. (2018) and Sivasakthi et al. (2020). However, concerning KH_2PO_4, the high-P treatment involved a nutrient solution with 300 µM KH_2PO_4, while the low-P treatment received 10 µM KH_2PO_4 (Ceasar et al. 2020). The pH of the nutrient solution was maintained between 6.0 and 6.3, with continuous aeration to facilitate root nutrient absorption. The nutrient solution was replenished every 3 days. At 45 DAS, the plants cultivated through hydroponics underwent phenotypic assessment for morphologic characteristics, including root length, crown root numbers and leaf area. Leaf area was measured

utilizing a leaf area meter (LI-3100C area meter, LI-COR BioSciences, Lincoln, NE, USA). The root surface area was determined by scanning the roots with a Shimadzu scanner and analyzing the scans with Winrhizo software (Winrhizo, Regent Ltd). In addition, plant samples comprising leaves, stems, and roots were dried at 60 °C in an oven for a minimum of 72 h, and their dry weights were measured using a KERN 3600-g precision balance (Kern & Sohn GmbH).

Data analysis

The datasets collected from LeasyScan, hydroponics, and Lysimetric systems were statistically analyzed. One-way ANOVA was used to assess differences among genotypes, while two-way ANOVA evaluated the effects of genotypes, treatments, and their interactions. The Tukey–Kramer test was subsequently applied to identify significant variations between genotypes or treatments. All analyses were performed using the statistical software package CoStat version 6.204 (Cohort Software, Monterey, CA, USA). Residual yields can be effectively used to assess key adaptation traits under low-P conditions. In the absence of genotype-by-treatment interaction (GxTrt) for yield components, the performance of genotypes under low-P conditions reflects both their inherent GY potential and residual yield variation. This residual component includes the genotypes' adaptation to low P and an error factor, capturing the part of yield variation under low P that is not explained by GY potential (Bidinger et al. 1987; Vadez et al. 2007; Beggi 2014). Residual yields were calculated by taking the difference between the predicted yields (based on a linear regression model comparing low P to high-P yields) and the observed yields under low P.

Graphical representations such as box plots, bar graphs, and simple linear regressions were created using Microsoft Excel 2017 (Microsoft Office 365, Microsoft Corp., Redmond, WA, USA). To evaluate correlations among selected phenotypic traits, a simple Pearson correlation analysis was carried out with R software (version 2.11.1) using the 'metan' library. In addition, Principal Component Analysis (PCA) was conducted with R software (version 2.11.1) using the 'factoextra' library.

Results

Treatment and genotypic variation due to varying P conditions

Plant growth, water use and agronomical traits

The study focused on evaluating various traits of foxtail millet genotypes using multiple phenotyping platforms, including Lysi-field, LeasyScan, and hydroponics facilities under low P and high-P conditions. Using two-way analysis of variance, significant variations in genotype and treatment were identified for most traits under both low and high-P conditions (Table 2). In the one-way analysis, a range of plant traits, including growth, water use, and agronomical features, exhibited significant genotypic differences under both low- and high-P conditions (Table 3). Under high-P conditions, the majority of genotypes exhibited enhanced plant growth and agronomic parameters compared to low-P conditions (Table 2).

GY from the Lysi-Field experiment, ranged from 4.86 g to 50.41 g, with an average of 24.26 g under high-P condition. Under low-P conditions, it ranged from 1.17 g to 27.95 g, with an average of 14.12 g (Fig. 1), indicating a 42% decline compared to high-P conditions. This decline underscores the sensitivity of grain production to low-P availability. The genotypic differences in yield across both P conditions are illustrated in Fig. 1b and detailed in Table 3. Subsequently, biomass accumulation also varied across the treatments with high P having higher biomass than the low-P conditions (Table 2). TE exhibited a significant reduction under low-P conditions, with a mean of 2.01 g biomass per kg water under high-P conditions compared to 1.10 g biomass per kg water under low-P conditions, representing a 50% reduction. This substantial decline highlights the critical role of P availability in influencing water use (Table 2).

Tiller counts under high-P conditions ranged from 3.17 to 32.67, with a mean of 17.5. Conversely, under low-P conditions, tiller counts ranged from 2.17 to 11.50, with a mean of 6.37, representing a 64% reduction compared to the high-P treatment (Suppl. Fig. S1a). Furthermore, genotypic variability in tiller counts under both low and high-P conditions is illustrated in Suppl. Fig. S1b and detailed in Table 3.

In the LeasyScan facility, the 3D leaf area under high-P conditions ranged from 6000 mm^2 to 50,565 mm^2, with a mean of 23,356 mm^2. Conversely, under low-P conditions, the 3D leaf area ranged from 2500 mm^2 to 21,000 mm^2, with a mean of 10,595 mm^2, representing a 50% reduction compared to the high-P treatment (Fig. 2a, Suppl Fig. S2). In hydroponic experiments, root surface area under high-P conditions varied from 211 cm^2 to 726 cm^2, with a mean of 454 cm^2. In contrast, under low-P conditions, root surface area ranged from 94 cm^2 to 575 cm^2, with a mean of 291 cm^2, indicating an average of 34% reduction compared to the high-P treatment (Fig. 2a). Notably, the reduction in root surface area was considerably smaller than the reduction in 3D leaf area, which may be due to the plant's prioritization of root growth to enhance P acquisition under P-nutrient limitation. Genotypic variability in 3D leaf area and root

Table 2 Two-way ANOVA results for plant growth, water use, phenology, and agronomical traits across various phenotyping platforms

Sl. No.	Phenotyping platform	Trait code	Treatment (T)	*P* value	Genotype (G)	*P* value	T x G Int	*P* value	Error	High P mean	Low P mean	LSD (0.05)
1	Lysi-Field (LF)	TLR-LF	3646.52	***	536.06	***	145.37	***	32.68	17.5a	6.37b	2.088
2		LDW	387.735	***	26.463	***	4.51	ns	3.631	8.91a	5.32b	0.696
3		StDW	852.929	***	216.746	***	33.86	*	13.504	15.0a	9.74b	1.342
4		DFL	542.417	***	125.715	***	6.22	ns	5.784	47.0a	42.7b	0.878
4		PnDW	4949.259	***	304.701	***	57.14	ns	60.117	29.0a	16.2b	2.832
6		TBM	13,749.789	***	1201.165	***	140.46	ns	144.963	52.6a	31.3b	4.398
7		GY	3063.63	***	203.64	***	74.84	ns	53.45	24.2a	14.1b	2.671
8		HI	14.416	ns	316.766	***	138.79	**	52.713	45.6a	44.7a	2.652
9		ThGW	0.815	***	0.508	***	0.01	ns	0.0348	2.78a	2.63b	0.07
10		Tot-T	6.312	ns	47.554	***	5.51	ns	11.9	23.2a	22.7b	1.26
11		TE	24.707	***	1.311	***	0.16	ns	0.181	2.01a	1.10b	0.155
12		Leaf P	18.82	***	0.73	***	0.283	***	0.089	2.27a	1.46b	0.114
13		Stem P	24.41	***	0.247	***	0.209	***	0.058	1.41a	0.47b	0.093
14		Grain P	10.77	***	0.503	***	0.403	***	0.089	3.17a	2.55b	0.114
15		Tot-P	17.15	***	0.322	***	0.302	***	0.063	2.45a	1.66b	0.096
16		PUE	20.26	ns	359.54	***	161.59	***	32.91	19.38a	18.88a	2.19
17	HTP-LeasyScan	DBM	9.815	***	2.597	*	2.09	ns	1.09	7,158,113 a	2,600,247 b	1,018,793
18		PH	175,664	***	11,828	***	3562	ns	2711	302 a	239 b	16.059
19		3DLA	7.693	***	2.635	**	1.673	*	84,406,052	23,356 a	10,595 b	2834
20		Proj.LA	2.159	***	90,734,768	**	56,400,038	ns	30,118,890	13,233 a	6512 b	1693
21	Hydroponics	RL	9402	***	890	***	155	*	63.961	38.502 a	23.51 b	2.58
22		Crown Root No	900	***	96.9	***	7.714	ns	5.662	-	-	0.795
23		ShDW	2.014	***	0.336	***	0.044	**	0.014	0.563 a	0.333 b	0.039
24		RDW	0.196	***	0.024	***	7.916	ns	9.97	0.403 a	0.337 b	0.009
25		RDW/ShDW	6.235	***	2.937	***	0.092	ns	0.266	1.319a	0.873b	0.188
26		RSA	629,404	***	90,144	***	9860	ns	7078	454a	291b	30.5
27		LA	8453	***	4970	***	754	***	128	50.464 a	35.582 b	4.404

The table includes Mean Sum of squares for treatment (T), genotypes (G), and T x G interactions, along with corresponding *P* values and significance levels. The use of different alphabets in the Tukey–Kramer test with trait mean values denote significant differences between low and high-P treatments. At least significant difference at $*P<0.05$; $**P<0.01$; $***P<0.001$. "ns" denote non-significant differences. Abbreviations of trait code see Table 1

Table 3 One-way ANOVA results for plant growth, water use, phenology, and agronomical traits of foxtail millet across various phenotyping platforms

S. no.	Phenotyping platform	Trait code	Trt	G_MS	*P* value	Error	ISE 710 (LF) & CV Maxima (LS &Hydro)	ISE 480	ISE 1134	ISE 160	ISE 1593	ISE 90	ISE 1736	ISE 1888	ISE 1859	ISE 758	LSD (0.05)
1	Lysi-Field (LF)	Leaf P	High P	0.79	***	0.13	2.22 abc	2.38 abc	1.88 c	2.65 ab	2.18 abc	1.88 cd	2.35 abc	2.85 a	2.66 a	1.73 c	0.47
			Low P	0.22	***	0.05	1.12 c	1.55 ab	1.42 abc	1.46 abc	1.71 a	1.28 bc	1.40 abc	1.75 a	1.57 ab	1.38 abc	0.28
2		Stem P	High P	0.39	***	0.09	1.43 abc	1.33 abc	1.24 bc	1.54 abc	0.96 c	1.09 bc	1.66 ab	1.90 a	1.44 abc	1.44 abc	0.39
			Low P	0.04	ns	0.03	0.34 a	0.43 a	0.41 a	0.43 a	0.53 a	0.56 a	0.50 a	0.60 a	0.42 a	0.56 a	0.21
3		Grain P	High P	0.54	***	0.12	3.22 abc	2.98 abc	3.09 abc	3.47 a	2.61 c	3.35 ab	3.25 abc	3.52 a	3.50 a	2.75 bc	0.44
			Low P	0.34	***	0.06	2.09 c	2.45 abc	2.71 ab	2.33 bc	2.40 bc	2.72 ab	2.65 ab	2.91 a	2.55 abc	2.74 ab	0.32
4		Tot-P	High P	3.41	***	0.08	2.43 abc	2.18 bc	2.22 bc	2.56 abc	2.16 c	2.51 abc	2.58 abc	2.85 a	2.76 ab	2.21 bc	0.35
			Low P	0.28	***	0.05	1.26 c	1.54 abc	1.94 a	1.43 bc	1.86 a	1.78 ab	1.72 ab	1.91 a	1.64 abc	1.61 abc	0.28
5		PUE	High P	79.02	ns	40.18	19.95 a	26.10 a	16.08 a	17.81 a	17.27 a	21.55 a	19.49 a	14.23 a	25.45 a	17.70 a	8.08
			Low P	442.15	***	26.38	37.67 a	24.50 b	9.05 e	23.92 bc	11.74 e	18.17 bcde	14.22 cde	11.47 e	22.87 bcd	13.54 de	6.52
6		DFL	High P	73.2	***	5.96	44.0 abc	48.5 a	37.0 d	47.3 ab	39.8 cd	41.2 cd	42.7 bc	39.8 cd	44.0 abc	42.5 c	2.83
			Low P	59.72	***	5.6	50.3 ab	50.7 ab	42.6 d	51.8 a	44.0 d	45.3 cd	44.3 cd	45.2 cd	48.8 abc	46.5 bcd	3.01
7		StDW	High P	162.97	***	23.58	16.0 abcd	24.9 a	11.2 cd	17.9 abc	7.49 d	13.3 bcd	15.5 bcd	13.0 bcd	20.7 ab	10.0 cd	5.63
			Low P	87.21	***	3.22	15.8 a	13.2 ab	4.58 d	13.1 ab	4.79 d	9.80 bc	7.74 cd	7.22 cd	12.7 ab	7.60 cd	2.28
8		LDW	High P	14.72	*	5.95	10.2 ab	11.6 a	7.65 ab	8.72 ab	6.40 b	9.69 ab	9.07 ab	8.10 ab	10.3 ab	7.45 ab	2.83
			Low P	15.89	***	1.27	8.39 a	6.44 ab	2.32 d	5.42 bc	3.94 cd	5.79 bc	4.57 bcd	4.10 cd	6.54 ab	5.55 bc	1.43
9		PnDW	High P	268.35	*	100.88	29.9 ab	35.1 ab	20.1 b	29.5 ab	25.4 ab	33.9 ab	27.2 ab	23.9 ab	42.5 a	23.0 b	11.65
			Low P	97.66	***	18.53	22.2 a	20.0 ab	12.4 bc	18.6 ab	14.2 abc	18.4 abc	13.4 bc	12.4 bc	19.6 ab	10.3 c	5.47
10		GY	High P	195.53	*	82.86	22.4 ab	26.2 ab	17.5 b	23.2 ab	22.2 ab	28.94 ab	23.5 ab	19.8 b	37.8 a	21.2 ab	10.55
			Low P	85.73	**	23.44	21.1 a	16.3 ab	13.4 ab	13.5 ab	12.6 ab	16.23 ab	11.8 ab	9.44 b	17.7 ab	8.88 b	6.15
11		TBM	High P	854.17	**	248.17	56.2 abc	69.7 ab	38.9 c	56.2 abc	39.3 c	56.9 abc	51.7 abc	45.0 abc	72.0 a	40.5 bc	18.27
			Low P	491.69	***	39.65	46.4 a	39.7 ab	19.3 e	37.2 abc	22.8 de	34.0 bcd	25.7 cde	23.7 de	38.8 ab	23.4 de	8
12		ThGW	High P	0.27	***	0.03	3.02 abc	2.70 bcd	2.48 d	2.70 bcd	2.81 abcd	2.83 abcd	2.55 d	3.10 a	3.05 ab	2.68 cd	0.21
			Low P	0.26	***	0.04	2.95 a	2.48 bc	2.29 c	2.54 abc	2.66 abc	2.69 abc	2.44 c	2.83 ab	2.89 a	2.44 c	0.27
13		TLR-LF	High P	612.07	***	56.72	32.7 a	30.8 ab	23.2 abc	22.0 abc	3.17 e	18.2 bcd	13.5 cde	17.3 bcde	10.2 cde	4.00 de	8.73
			Low P	70.92	***	8.15	11.5 a	11.3 a	9.20 ab	6.84 abc	2.17 c	7.00 abc	5.84 bc	3.34 c	5.00 bc	2.00 c	3.62
14		Tot-T	High P	24.31	ns	17.93	24.9 a	24.9 a	21.4 a	22.8 a	21.5 a	22.8 a	22.0 a	21.3 a	27.4 a	22.2 a	4.91
			Low P	28.66	***	5.75	27.2 a	23.7 abc	20.4 c	21.0 bc	22.3 bc	23.0 abc	21.3 bc	21.8 bc	25.5 ab	20.7 c	3.05
15		TE	High P	0.91	**	0.3	2.01 ab	2.59 a	1.55 ab	2.20 ab	1.54 b	2.29 ab	2.05 ab	1.8 ab	2.53 ab	1.62 ab	0.64
			Low P	0.57	***	0.06	1.48 a	1.42 a	0.72 d	1.49 a	0.78 d	1.25 abc	0.94 bcd	0.82 cd	1.29 ab	0.85 bcd	0.31
16		HI	High P	239.86	***	55	39.8 bc	36.7 c	43.0 abc	39.3 bc	55.7 a	50.3 abc	45.5 abc	42.7 abc	50.8 abc	52.0 ab	8.6
			Low P	210.59	***	50.38	39.7 b	41.3 ab	55.2 a	39.3 b	54.0 a	47.7 ab	46.0 ab	43.3 ab	45.3 ab	37.0 b	9.02
17	LeasyScan (LS)	DBM	High P	3.893	ns	2.21	6,401,059 ab	5,875,710 ab	4,406,207 b	8,166,179 ab	5,727,012 ab	12,385,575 a	8,156,354 ab	9,001,382 ab	5,507,217 ab	8,414,657 ab	5,410,949
			Low P	4.636	**	1.537	1,529,939 b	2,735,205 ab	2,870,798 ab	2,895,631 ab	1,979,291 ab	2,976,411 ab	1,661,432 b	3,707,089 a	3,297,371 ab	2,645,904 ab	1,232,316

Table 3 (continued)

S. no.	Phenotyping platform	Trait code	Trt	G_MS	*P* value	Error	ISE 710 (LF) & CV Maxima (LS &Hydro)	ISE 480	ISE 1134	ISE 160	ISE 1593	ISE 90	ISE 1736	ISE 1888	ISE 1859	ISE 758	LSD (0.05)
18		PH	High P	5676	ns	3559	340 a	269 a	292 a	301 a	301 a	352 a	283 a	302 a	275 a	322 a	68.662
			Low P	9635	***	2000	272 ab	208 bcd	279 a	242 abcd	206 cd	271 abc	191 d	268 abc	235 abcd	226 abcd	44.453
19		3DLA	High P	3.433	*	1.631	17,395 a	21,539 a	14,801 a	26,347 a	19,414 a	36,228 a	29,057 a	29,921 a	19,628 a	26,052 a	14,702
			Low P	68,697,120	***	18,466,113	5180 b	12,622 a	9964 ab	11,712 a	9246 ab	11,243 ab	8188 ab	13,794 a	13,836 a	10,930 ab	4271
20		Proj.LA	High P	1.147	*	56,487,665	9766 a	12,276 a	8682 a	14,855 a	10,171 a	20,152 a	16,325 a	17,660 a	10,940 a	15,455 a	8650
			Low P	26,746,652	**	8,042,707	3082 b	7843 a	6131 ab	7332 a	5625 ab	7171 ab	4961 ab	7581 a	8759 a	6978 ab	2819
21		TLR-LS	High P	16.858	ns	11.481	9.67 a	10.5 a	8.38 a	11.43 a	11:00 AM	13.15 a	9.17 a	9.63 a	12.5 a	11.88 a	3.913
			Low P	1.631	ns	2.817	5.2 a	5.1 a	5.4 a	5.5 a	4.7 a	5.125 a	4.6 a	5.75 a	5.6 a	5.8 a	1.668
22	Hydroponics (Hydro)	RL	High P	667	***	73.633	23.09 d	40.84 b	39.32 bc	56.48 a	46.94 ab	34.69 bcd	44.06 ab	35.56 bcd	38.12 bcd	27.03 cd	9.894
			Low P	334	***	56.476	12.3 c	27.77 ab	19.63 bc	26.42 ab	33.35 a	23.76 ab	28.18 ab	21.72 abc	23.32 ab	18.56 bc	7.47
23		Crown Root No	High P	63.38	***	5.169	8.43 e	17.84 a	10.34 de	13 bcd	15.84 ab	14.5 abc	14.43 abcd	17.72 a	13.72 abcd	11.13 cde	2.625
			Low P	38.867	***	6.023	5.8 c	10.23 ab	5.5 c	8.8 abc	11.63 a	9.75 ab	9.5 ab	11 ab	9.4 ab	7.4 bc	2.609
24		ShDW	High P	0.263	***	0.013	0.35 cd	0.55 b	0.52 bc	0.84 a	0.83 a	0.61 b	0.59 b	0.59 b	0.61 b	0.17 d	0.144
			Low P	0.096	***	0.016	0.2 bc	0.32 abc	0.38 ab	0.4 a	0.48 a	0.38 ab	0.33 abc	0.36 ab	0.39 a	0.12 c	0.134
25		RDW	High P	0.014	***	0.001	0.36 cd	0.43 ab	0.4 bcd	0.44 ab	0.48 a	0.4 bc	0.42 bc	0.43 ab	0.39 bcd	0.34 d	0.039
			Low P	0.011	***	8.448	0.29 e	0.36 bc	0.32 cde	0.37 ab	0.41 a	0.34 bcde	0.34 bcd	0.36 b	0.33 bcde	0.31 de	0.027
26		RDW/ ShDW	High P	1.142	***	0.036	1.14b	0.8bc	0.81bc	0.57c	0.64c	0.66c	0.73c	0.74bc	0.66c	2.13a	0.315
			Low P	2.055	***	0.415	1.63 ab	1.51 b	1.05 b	1.19 b	0.88 b	0.93 b	1.09 b	1.3 b	1.08 b	2.57 a	0.685
27		RSA	High P	55,996	***	8165	248 c	546 ab	406 bc	553 ab	556 a	378 bc	466 ab	470 ab	466 ab	318 bc	181.5
			Low P	41,491	***	5990	177 b	291 ab	255 ab	348 a	421 a	185 b	390 a	292 ab	271 ab	219 ab	155.45
28		LA	High P	5860	***	150	4.04 d	55.96 bc	18.06 d	101 a	70.08 b	65.23 bc	43.97 c	54.8 bc	61.16 bc	19.04 d	14.165
			Low P	1321	***	98.223	2.52 e	38.38 bc	11.13 de	44 ab	60.77 a	32.19 bcd	30.71 bcd	36.72 bc	44.92 ab	15.29 cde	16.33
29		TLR-Hydro	High P	2.468	**	0.704	2.45 a	1.71 a	2.78 a	1.28 a	–	–	2.24 a	1a	–	1a	2.41
			Low P	1.464	**	0.324	1.62 ab	1.25 ab	2.56 a	1.34 ab	1.34 ab	–	1.62 ab	1b	–	1 ab	1.64

The table includes mean sum of squares for genotypes (G) along with corresponding *P* values and significance levels. The use of different alphabets in the Tukey–Kramer test with trait mean values indicates differences between genotypes at least significant difference at $*P<0.05$; $**P<0.01$; $***P<0.001$; while "ns" denotes non-significant differences. Abbreviations of trait code, see Table 1

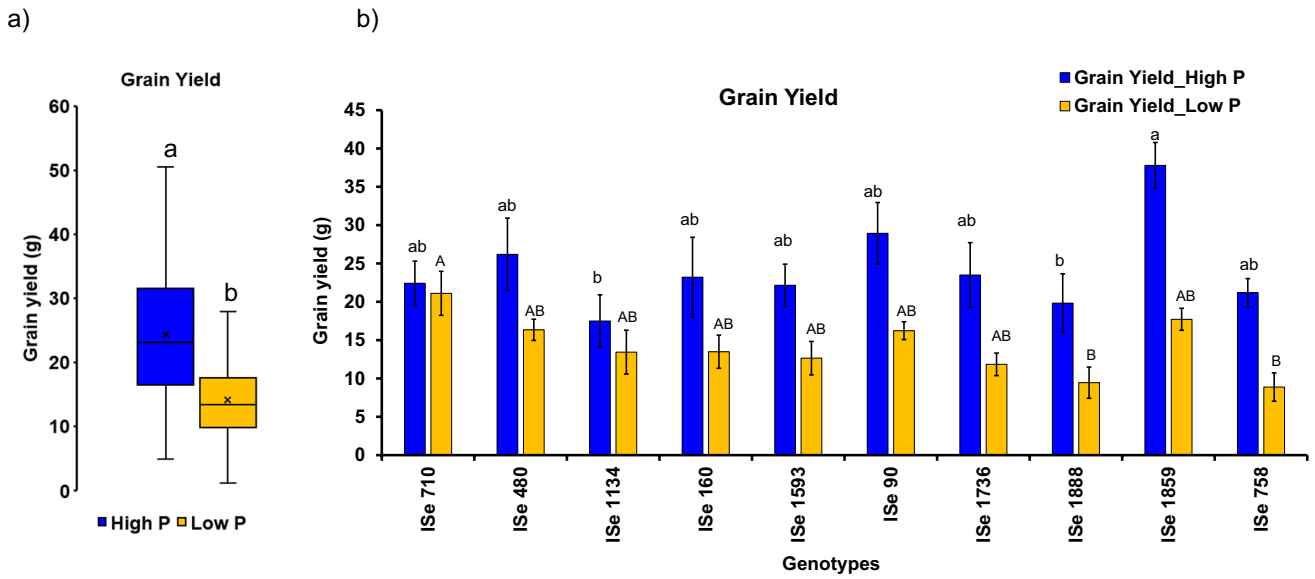

Fig. 1 **a** Boxplot depicting the variation in grain yield of foxtail millet under low and high phosphorus (P) treatments, measured using a Lysimeter. The blue boxplot represents the high-P treatment, and the orange boxplot represents the low-P treatment. The boxplot is based on replicated data ($n=6$), displaying the median, interquartile range (IQR), and whiskers extending to 1.5 × IQR. Statistically significant differences between treatments at $P<0.05$ are indicated by different letters on the boxplots. **b** Bar graph (mean values ± SE; $n=6$) showing genotypic variation in grain yield under low and high-P treatments, assessed using a Lysimeter. Blue bars represent the high-P treatment, and orange bars represent the low-P treatment. Statistically significant differences among genotypes ($P<0.05$) are indicated by distinct upper-case letters for low-P treatment and lower-case letters for high-P treatment, while bars with the same letters denote no significant differences

surface area under both low and high-P conditions is provided in Table 3 and Suppl. Fig S2, S3.

P concentration and PUE in different plant organs

The distribution of P content exhibited significant variability among plant organs, with the highest concentration found in the grain, followed by the leaf and stem (Table 3). Grain P concentration ranged from 2.1 mg g^{-1} to 4.2 mg g^{-1} (mean 3.17 mg g^{-1}) under high-P conditions, and from 1.9 mg g^{-1} to 3.4 mg g^{-1} (mean 2.55 mg g^{-1}) under low-P conditions, indicating a 24% reduction compared to high-P conditions (Table 3). Similarly, leaf P concentration exhibited substantial variation, ranging from 1.27 mg g^{-1} to 3.2 mg g^{-1} (mean 2.26 mg g^{-1}) under high P, and from 0.86 mg g^{-1} to 2.35 mg g^{-1} (mean 1.46 mg g^{-1}) under low P, resulting in a 35% reduction (Table 3). Stem P concentration demonstrated significant variation, ranging from 0.65 mg g^{-1} to 2.13 mg g^{-1} (mean 1.41 mg g^{-1}) under high P, and from 0.23 mg g^{-1} to 1.25 mg g^{-1} (mean 0.47 mg g^{-1}) under low P, resulting in a 66% reduction (Table 3). Genotypic variability in grain, leaf, and stem P content under low and high-P conditions is shown in Suppl. Fig. S3, Fig. S4.

Total P concentration ranged from 1.72 mg g^{-1} to 3.6 mg g^{-1} (mean 2.45 mg g^{-1}) under high-P conditions and from 1.14 mg g^{-1} to 2.39 mg g^{-1} (mean 1.66 mg g^{-1}) under low-P conditions, reflecting a 35% reduction compared to high-P conditions (Suppl. Fig. S5A and Table 2). Genotypic variability in total P concentration under both low and P conditions is provided in Table 3 and Suppl. Fig. S5B.

Similarly, PUE ranged from 6.08 g^2 mg^{-1} to 53.55 g^2 mg^{-1} (mean 18.88 g^2 mg^{-1}) under low-P conditions and from 9.04 g^2 mg^{-1} to 35.14 g^2 mg^{-1} (mean 19.38 g^2 mg^{-1}) under high-P conditions, representing a 2.58% reduction in low P compared to high-P conditions (Table 2). Genotypic variability in PUE under both low and high-P conditions is shown in Table 3 and Suppl. Fig. S6.

Functional trait associations

GY under both low and high-P conditions demonstrated a significant association ($R^2=0.65$; Fig. 3), suggesting a certain level of consistency in performance across different P levels. This indicates that GY under low P was, in large part, influenced by the yield potential under high-P conditions, although other factors may also contribute to yield variations. To explore the factors contributing to yield variation under low-P conditions, the residuals of GY under low P, which were not explained by GY under high P, were calculated. These residuals revealed a strong relationship with

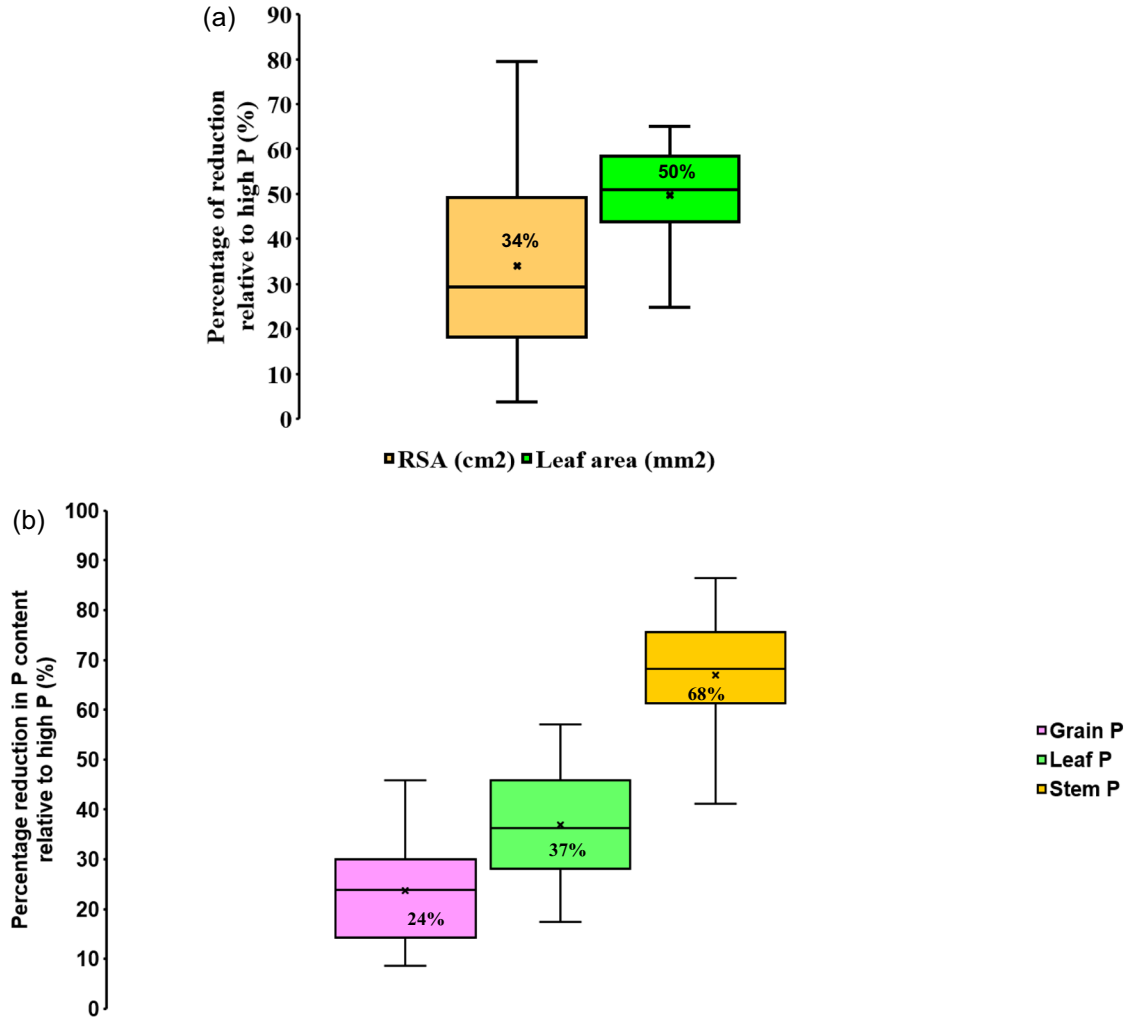

Fig. 2 **a** Boxplot illustrating the percentage reduction under low-P treatment relative to the high-P treatment [(high P – low P)/high P) * 100] in foxtail millet. Data are based on replicated measurements, showing the median, interquartile range (IQR), and whiskers extending to 1.5 × IQR. The orange boxplot represents root surface area (cm^2), measured in a hydroponics facility ($n = 10$), while the green boxplot represents leaf area (mm^2), measured using the HTP-Leasy-Scan facility ($n = 8$). The cross symbol within each boxplot denotes the mean percentage reduction. RSA, root surface area. **b** Boxplot showing the variation in percentage reduction of P content under low-P treatment relative to high-P treatment [(high P – low P)/high P) * 100]. The boxplot is based on replicated data ($n = 6$) and represents the median, interquartile range (IQR), and whiskers extending to 1.5 × IQR. Pink, green, and orange boxplots correspond to grain, leaf, and stem P content, respectively. The cross symbol inside each boxplot represents the mean percentage reduction

tiller numbers under both low P ($R^2 = 0.70$; Fig. 4) and high P ($R^2 = 0.66$; Fig. 4), indicating that tiller production plays a key role in determining yield, especially in P-limited environments. This suggests that increasing tiller numbers could help improve yield in conditions where P is limited.

A regression analysis was performed to examine the relationship between biomass and total P concentration. Under low-P conditions, a significant negative relationship was observed ($R^2 = 0.71$, $P < 0.05$; Fig. 5), indicating that genotypes maintaining growth under P-limited conditions are those that effectively dilute P. In contrast, genotypes unable to dilute P are more likely to experience biomass limitations. No significant relationship was found under high-P conditions (Fig. 5), suggesting that, when P is sufficient, biomass accumulation is less dependent on total P concentration.

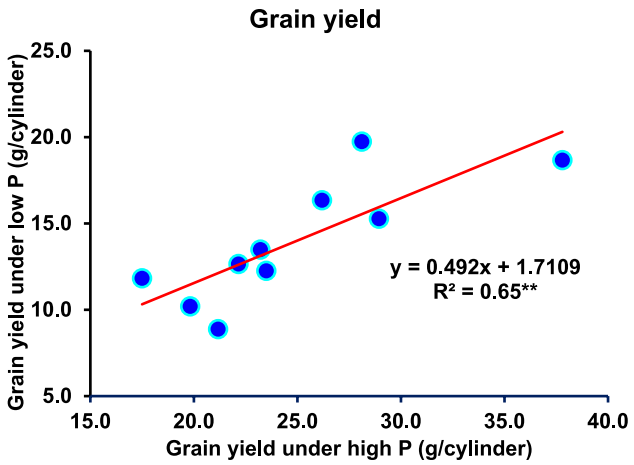

Fig. 3 Regression analysis showing the relationship between grain yield under low-P treatment and grain yield in foxtail millet under high-P treatment, measured at the Lysi-field facility. Data area based on mean values ($n=6$) and the figure includes the slopes, R^2, and r values of the regressions. R^2 and r values marked with an asterisk (**) indicate significant differences at $P<0.01$

Discussion

Growth potential as the key driver of performance under low-P conditions

The imposition of low-P deficiency significantly affected various plant traits, including tillers, leaf area, root surface area, agronomic characteristics (notably GY), and P concentration in different plant tissues. This deficiency led to an overall decrease in plant growth and GY, with reductions in plant growth and development traits ranging from 30 to 50% compared to high-P conditions (Fig. 1). These findings align with prior studies, showing similar trends observed in various crops like sorghum (Leiser et al. 2012), maize (Parentoni et al. 2010), common bean (Beebe et al. 2008), and foxtail millet (Ceasar et al. 2020) under low-P conditions.

The current study highlights a notable variability in the number of tillers and grain yields among tested foxtail millet genotypes under low-P conditions. Zhao et al. (2023) reported similar reductions in P accumulation, photosynthetic function, and biomass in wheat under low-P conditions. Rajamanickam et al. (2024) also observed significant genotypic variability in root traits and their association with P utilization efficiency in wheat seedlings under low-P conditions. These findings emphasize the critical role of growth potential in plant performance under low-P conditions.

Our findings align with previous studies by Beggi et al. (2015) and Gemenet et al. (2015), who investigated low-P adaptation in pearl millet. Beggi et al. (2015) reported a significant positive correlation (r = 0.69; $P<0.01$) between GY under low and high-P conditions and used residual yields as a proxy for assessing low-P adaptation in pearl millet genotypes. Consistent with Beggi et al. (2015), we observed a significant reduction in transpiration efficiency (TE) under low-P conditions, similar to their findings in pearl millet. However, while their study indicated that this decrease was less pronounced in genotypes adapted to low P (as shown by higher grain yields), our results suggest a stronger physiologic response to P deficiency, with a more pronounced reduction in TE.

Genetic variability in plant growth and agronomic traits under low-P conditions is essential for the success of breeding programs, as it enables the identification and selection

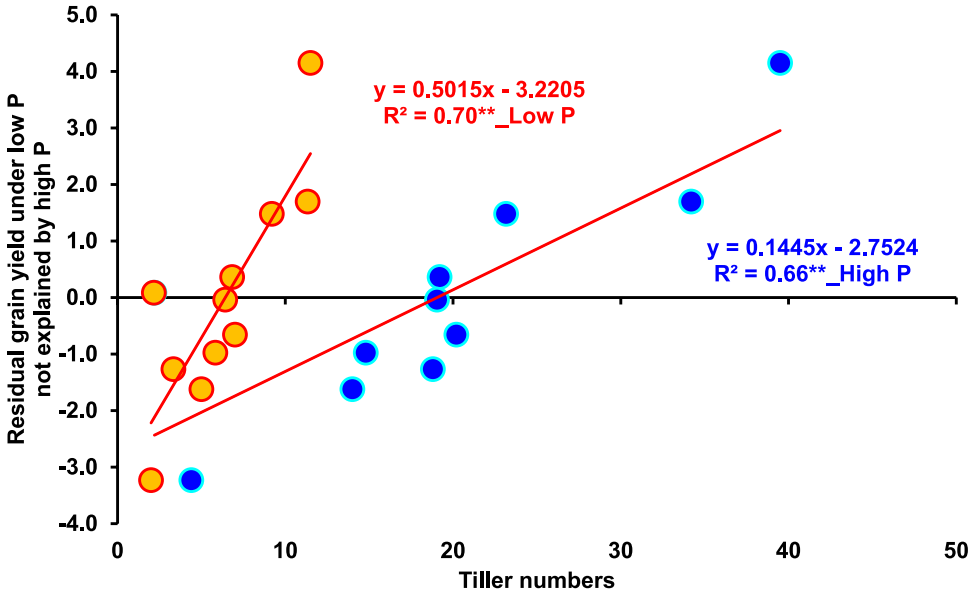

Fig. 4 Regression analysis showing the relationship between residual grain yield under low-P conditions (unexplained by high-P treatment) and tiller numbers from the Lysi-field, under both low and high-P treatment conditions. In the scatterplots, blue dots and a red trend line represent the high-P treatment, while orange dots and a red trend line represent the low-P treatment. Data are based on mean values ($n=6$) and the figure includes the slopes and R^2 values of the regressions. R^2 values marked with an asterisk (**) indicate significant differences at $P<0.01$

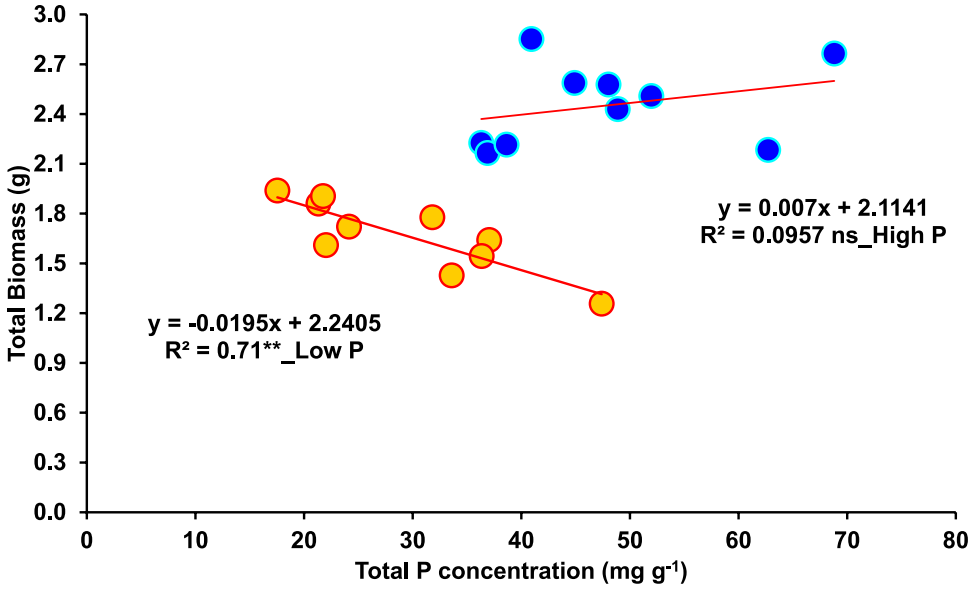

Fig. 5 Regression analysis showing the relationship between total biomass under low and high-P treatment conditions and total P concentration from the Lysi-field facility. In the scatterplots, blue dots and a red trend line represent the high-P treatment, while orange dots and a red trend line represent the low-P treatment. Data are based on mean values ($n=6$) and the figure includes the slopes and R^2 values of the regressions. R^2 values marked with an asterisk (**) indicate significant differences at $P<0.01$, while R^2 values labeled as "ns" indicate no significant difference

of traits that improve crop performance in nutrient-limited environments. The effectiveness of a breeding program depends on the availability of significant genetic variability for the targeted traits and the use of efficient selection methods to increase the frequency of desirable genes or gene combinations (Gemenet et al. 2016). In the present study, significant genotypic variation was observed in plant growth and agronomic traits among the foxtail millet genotypes, with more than a twofold difference under low-P treatments. These findings are consistent with previous research indicating greater genotypic variation in P uptake compared to PUE traits in crops such as wheat, maize, rice, sorghum, and foxtail millet (Jones et al. 1989; Wissuwa et al. 1998; Parentoni et al. 2010; Leiser et al. 2014; Ceasar et al. 2020). The considerable variation observed underscores the importance of breeding programs focusing on key traits like tiller development and PUE, which are crucial for improving crop performance under P-deficient conditions. Specifically, genotypes ISe 480 and ISe 710 exhibited enhanced tiller counts, PUE, and GY under low-P stress, highlighting the value of selecting for these traits to boost crop resilience and productivity in P-limited soils.

In the present study, a 24% reduction in grain P concentration under low-P conditions indicates that this variable is relatively less impacted by P deficiency. This suggests that the observed increase in GY under low-P conditions is likely due to the plant's enhanced ability to extract P from the soil. In contrast, more substantial changes were observed in P concentrations across other plant organs. Specifically, stem P concentration showed a significant decline, reflecting the limited role of stems in biomass accumulation under P-deficient conditions. Conversely, leaf P concentration experienced a relatively smaller reduction, likely due to the essential role of leaves in photosynthesis and biomass production. These results highlight a strategic redistribution of P within the plant, prioritizing critical organs like leaves to sustain growth and yield under low-P availability. This observation aligns with findings by Veneklaas et al. (2012), which emphasize that P allocation among plant organs is closely linked to crop growth and suggest that optimizing this distribution can improve overall PUE.

Plants adapt to low-P conditions by allocating biomass to roots, increasing the root-to-shoot ratio, and adjusting root morphologic and physiologic traits to enhance P uptake efficiency (Lambers et al. 2015; Iqbal et al. 2020). Insights into the physiologic and molecular mechanisms of plant adaptation to P deficiency, including changes in root architecture and P acquisition strategies, have been provided by Vance et al. (2003). In addition, genetic variability in common bean for P uptake and use efficiency, highlighting the importance of root traits and P allocation under low-P conditions, was explored by Ramaekers et al. (2010).

Tiller number: a key trait for low-P adaptation

The current study observed substantial genotypic variation in tiller numbers among foxtail millet genotypes under low-P conditions. Specifically, there was a sixfold difference in tiller count among the tested genotypes. This variation underscores the importance of tiller number as a key trait for assessing growth potential under low-P conditions.

A strong correlation was observed between GY under low-P and high-P conditions ($R^2=0.65$; $P<0.01$), indicating that genetic yield potential (vigor) in high-P environments significantly influences GY and tiller numbers under low-P conditions. This suggests that genotypes with higher tiller numbers tend to perform well in both high and low-P conditions, making tiller number a reliable indicator of growth

potential. These results are consistent with Bhatta et al. (2021), who highlighted tiller number as a critical trait for improving crop performance in P-deficient environments. Their study emphasizes the importance of evaluating genotypes based on tiller number, along with shoot and root biomass, to enhance yield stability and optimize productivity under P-limited conditions.

Residual GY under low-P conditions, not explained by high-P conditions, had a strong positive association with tiller numbers ($R^2 = 0.70$; $P < 0.01$). This suggests that tiller number contributes significantly to yield under P-limited conditions, even after accounting for the overall vigor observed under high-P conditions. These results align with previous studies that indicate alterations in growth, biomass, and yield as key indicators of adaptation to P deficiency, as reported in various cereals, including oat (Żebrowska et al. 2017), rice (He et al. 2005; Wissuwa et al. 2020), maize (Mollier et al. 1999), sorghum (Yoneyama et al. 2007), and foxtail millet (Ceasar et al. 2020).

The observed genotypic differences in tiller development highlight its role in enabling plants to cope with low-P stress while maintaining yield. For example, genotypes ISe 480 and ISe 710 exhibited higher tiller counts, improved PUE, and increased GY in the Lysi-Field under low-P conditions compared to high-P conditions. These findings highlight the value of selecting for traits like tiller number to enhance crop resilience in limited environments.

Supporting evidence from other studies further underscores the significance of tiller number in crop performance. A genome-wide association study (GWAS) by Ren et al. (2021) identified multiple quantitative trait loci (QTLs) associated with effective tiller number (ETN) in rice, revealing the genetic basis of this trait and its influence on GY. Similarly, Cui et al. (2004) mapped QTLs for tiller number in rice and demonstrated strong correlations between tiller number, plant height, and heading date, underscoring its critical role in determining final GY. In addition, Chen et al. (2012) showed that overexpression of specific genes in rice resulted in increased tiller numbers, further highlighting the role of genetic regulation in this trait.

P dilution and its impact on yield in low-P environments

The current study reveals a strategic reallocation of P in foxtail millet under low-P conditions, highlighting significant differences in P uptake and utilization efficiency among genotypes. Grain P concentration exhibited the least reduction (24%) compared to high-P conditions, while leaf and stem P concentrations decreased by 37% and 68%, respectively. These results are consistent with those of Ceasar et al. (2020), who observed a reduction in total shoot P concentration under P-deficient conditions.

The relatively small reduction in grain P concentration suggests that foxtail millet maintains P allocation to reproductive structures, likely prioritizing reproductive success under nutrient stress. This trait is particularly important for ensuring yield stability in P-deficient soils. By contrast, the substantial reduction in stem P concentration suggests that stems, being less critical for immediate growth and productivity, serve as a lower priority reservoir for P under stress. Leaves, which are crucial for photosynthesis and biomass accumulation, experienced a lower reduction than observed in stems, reflecting their higher priority in P allocation under low-P conditions.

These findings highlight the physiologic adaptations of foxtail millet to low-P conditions. The observed changes in P allocation suggest that under P deficiency, plants employ mechanisms to optimize P use by prioritizing allocation to organs essential for photosynthesis and reproduction while reducing allocation to non-essential biomass components. This strategic redistribution of P within the plant underscores the importance of P dilution in determining yield under low P conditions.

The study also found that residual GY under low P conditions, not explained by high-P conditions, had a significant negative association with total P concentration ($R^2 = 0.54$; $P < 0.05$). This indicates that lower total P concentration, or P dilution, is associated with higher GY under low-P conditions. Conversely, under high-P conditions, grain yield (GY_LF) from Lysi-Field exhibited significant positive correlations with PUE ($r = 0.94$; $P < 0.001$) and total biomass ($r = 0.84$; $P < 0.01$).

Additional studies support the role of P dilution in crop performance. For instance, Zamuner et al. (2016) established a critical P dilution curve for potato, demonstrating that P dilution is a robust diagnostic tool for assessing crop P status and improving P fertilizer management. Similarly, Kong et al. (2024) validated the use of the P-nutrition index in potato, showing a significant relationship between P-nutrition index and relative tuber yield. Rose et al. (2013) highlighted the importance of P remobilization efficiency in maintaining grain P concentration under low-P supply.

Conclusion

This study underscores the critical role of P availability in shaping plant growth and yield-related traits in foxtail millet, particularly under low-P conditions. Plant performance in these environments is primarily influenced by growth potential, with tiller number serving as a reliable marker of this potential. The significant genotypic variation observed highlights the importance of selecting growth-related traits

to improve crop resilience and productivity in P-limited environments. The findings reveal substantial variation in plant growth and agronomic traits, such as tiller count, GY, leaf area, and root surface area, among foxtail millet genotypes under low-P conditions. This variation emphasizes the necessity for breeding programs to prioritize traits that enhance growth potential, including tiller development and PUE, to optimize crop performance in nutrient-deficient soils.

Moreover, the study highlights the strategic redistribution of P within the plant under low-P conditions, where critical organs like leaves maintain higher P concentrations to support growth and yield. This strategic P allocation suggests that P dilution, rather than total P concentration, plays a key role in determining yield under low-P conditions. The observed negative association between total P concentration and residual GY under low-P conditions further supports this finding. Optimizing P management strategies and breeding for improved growth potential are essential for enhancing crop performance in regions facing P limitation. By selecting for traits that enhance growth potential and understanding the mechanisms of P allocation and dilution, breeding programs can develop foxtail millet varieties that are better adapted to low-P environments, ensuring yield stability and food security in vulnerable agri-systems.

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Author contributions The experiment was conceptualized by JK, AB, and MT. The phenotyping experiments were conducted by MT, KS, SC, KV, DSG, AA, and SK, with the experimental design overseen by RB. Nutrient analysis was carried out by SL and MAD. Data analysis and summarization were undertaken by MT, KS, and KSG. Support in data interpretation was provided by AB, SAC, SC, and JK. The manuscript was drafted by MT and KS, and it underwent review by JK, SC, MAD, SL, AB, and SAC. The manuscript was read and approved by all authors, and their consent was given for the final version.

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Data availability The data supporting the conclusions of this study can be obtained from the corresponding author, upon request.

Declarations

Conflict of interest The authors declare that they have no competing interests.

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Authors and Affiliations

Tharanya Murugesan[1] · Sivasakthi Kaliamoorthy[1] · Sunita Choudhary[1] · Keerthi Vysyaraju[1,2] · Devan Sai Gudela[1,2] · Annepu Anusha[1,2] · Kommireddypally Sowmya Goud[3] · Sara Loftus[4] · Michaela A. Dippold[4] · Suresh Kanuri[1] · Rekha Baddam[1] · Alison Baker[5] · S. Antony Ceasar[6] · Jana Kholova[1,7]

✉ Jana Kholova
kholova@pef.czu.cz

[1] International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Crops Physiology Laboratory, Patancheru 502324, Telangana, India

[2] Centurion University of Technology and Management (CUTM), Bhubaneswar, Odisha, India

[3] Professor Jayashankar Telangana State Agricultural University, Rajendranagar, Hyderabad, India

[4] Geo-Biosphere Interactions, Department of Geosciences and Department of Biology, University of Tuebingen, Tuebingen, Germany

[5] Centre for Plant Sciences and School of Molecular and Cellular Biology, University of Leeds, Leeds LS2 9JT, UK

[6] Department of Biosciences, Rajagiri College of Social Sciences, Cochin 683 104, Kerala, India

[7] Department of Information Technologies, Faculty of Economics and Management, Czech University of Life Sciences, Prague, Kamýcká 129, 165 00 Prague, Czech Republic