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Decoding the Dynamics of Root System Architecture in Chickpea (*Cicer arietinum* L.) under Contrasting Phosphorus Regimes

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ABSTRACT

Background: Limiting phosphorus (P) availability severely reduces chickpea productivity by impairing P uptake, thereby stunting plant growth. Since root system architecture (RSA) drives P uptake efficiency yet remains insufficiently characterized in chickpea, decoding RSA plasticity under P limited conditions is crucial to uncover target traits. This understanding will accelerate breeding of chickpea lines optimized for P efficient nutrient uptake.

Methods: During 2025, 31 chickpea accessions were assessed for root-related traits under limiting and non-limiting P conditions to characterize trait variability, RSA plasticity and inter trait correlations. To integrate diverse root-related traits and rank accessions by cumulative performance under contrasting P regimes, the multi-trait genotype ideotype distance index (MGIDI) was applied to pinpoint accessions exhibiting superior overall root-trait performance.

Result: Root-traits showed highly significant differences due to genotype and P availability ($p<0.001$), with genotype × P level interaction non-significant except for primary root length (PRL), which was significant ($p<0.001$), reflecting adaptive variation under P stress. Under limiting P conditions, growth of root-related traits of tolerant genotypes increased, indicating adaptive responses for enhanced P foraging, while average root diameter (ARD) declined, suggesting finer root formation. MGIDI identified Pusa72, BG3022 and Pusa2085 under limiting P and BG3022, Pusa 5023 and PG0515 under non-limiting P as the top performing genotypes. Furthermore, it confirmed that a superior P foraging capacity under limiting P conditions is underpinned by a combination of traits including longer total root length (TRL) and PRL, greater total surface area (TSA) and total root volume (TRV), a reduced ARD and a higher number of total root tips (TRT). These findings enhance understanding of RSA dynamics and provide a physiological foundation for genotype specific responses to contrasting P regimes.

Key words: Chickpea, MGIDI, Phosphorus, RSA.

INTRODUCTION

Chickpea (*Cicer arietinum* L.) is increasingly vulnerable to climate change, which intensifies production constraints and yield uncertainty and this is further aggravated by edaphic stresses like low-fertility soils (Chen *et al.,* 2017). Among the key contributors to low soil fertility is limiting phosphorus (P) availability, which is recognized as one of the most critical constraints on agricultural production (Ahmed *et al.,* 2020). Globally, it is estimated that approximately 5.7 billion hectares of land suffer from insufficient P availability, severely affecting crop growth (Niu *et al.,* 2013). P, which makes up about 0.2% of a plant's dry matter, is crucial for key metabolic processes such as photosynthesis and respiration. It also serves as a structural element in vital biomolecules like ATP, nucleic acids, phospholipids and sugar phosphates and plays a role in cellular signalling by enabling signal transduction (Choudhary *et al.,* 2025; Ramchander *et al.,* 2021). Soluble inorganic phosphate (Pi) fertilizers are commonly used to combat P limitation, yet their effectiveness is restricted, as soil processes like adsorption, immobilization and precipitation rapidly reduce P availability, making it highly immobile and inaccessible (Santoro *et al.,* 2024). To overcome the challenges posed by limiting P conditions, plants have developed a range of tightly regulated adaptive mechanisms to maintain P homeostasis. One of the primary strategies is enhancing the root's capacity to absorb P from the soil. Modifying root system architecture (RSA) is considered an effective approach for improving P use

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efficiency (PUE) in crops. RSA refers to the three-dimensional spatial arrangement of the root system in the soil and plays a crucial role in P uptake (Lu *et al.,* 2024). It is highly responsive to limiting P conditions, showing plasticity in development depending on genetic and environmental factors and this variation can significantly influence a plant's ability to acquire P (Lynch and Brown, 2008). Identifying genotypes with superior performance across multiple root traits is challenging, as traditional muti trait selection indices are affected by multicollinearity and the arbitrary assignment of weights, potentially limiting genetic gains. The multi-trait genotype ideotype distance index (MGIDI) method offers a modern solution by selecting genotypes based on their distance from an ideotype, effectively addressing these limitations without relying on weighting coefficients or being influenced by multi collinearity, making the process more robust and interpretable (Olivoto and Nardino, 2021). This study characterizes how the RSA of chickpea cultivars responds to differential P availability, aiming to elucidate genetic variation in root traits and, using MGIDI, to identify cultivars and root traits that optimize P acquisition.

MATERIALS AND METHODS

Plant material and growth conditions

A total of 31 chickpea cultivars were used in the experiment conducted during 2025, with seeds provided by the Division of Genetics, ICAR-IARI (Supplementary Table 1). We opted for a hydroponic system because detecting root characteristics in the seedling stage is difficult in soil and it provides greater flexibility in managing nutrient levels. Furthermore, the controlled environment eliminates the confounding factors that are common in soil studies, making it easier to directly attribute plant responses to P availability. Seeds were treated with carbendazim 50 WP (Bavistin 50 WP) at 1 g/L and germinated in rolled germination paper. Uniform seven-day-old seedlings were then transplanted into nutrient media containing 15 L trays, with the experiment conducted under controlled conditions using two P regimes: non-limiting P (1000 μM) and limiting P (10 μM), supplied in the form of $NH_4H_2PO_4$. The nutrient solution was composed of Ca $(NO_3).4H_2O$ (4 mM), KNO_3 (6 mM), $MgSO_4.7H_2O$ (4 mM), H_3BO_3 (0.01 mM), $MnCl_2.4H_2O$ (0.00 2 mM), $ZnSO_4.7H_2O$ (0.0003 mM), $CuSO_4.5H_2O$ (0.0002 mM), $Na_2MoO_4.2H_2O$ (0.00008 mM), Co $(NO_3)2.\ 6H_2O$ (0.025 mM), NaOH (0.16 mM) and Fe- EDTA (0.1 mM). During the experiment, the growth parameters were set to a daytime temperature of 25±2°C, a nighttime temperature of 15±2°C, relative humidity of 45±5% and a light cycle of 10 hours of light followed by 14 hours of darkness. The nutrient solution was replaced every 48 hours and its pH was maintained at 6.5 through regular monitoring and adjustment.

Root scanning, image analysis and data collection on root related traits

Roots were carefully separated from shoots on 35th day, following previous research findings (Chen *et al.,* 2017), for root scanning, image analysis and data recording. The excised roots were immediately placed on transparent trays containing 600 ml of water and gently spread to minimize overlap. Roots were then scanned in grayscale at 400 dpi using an Epson Perfect V700 Pro scanner (Seiko Epson, Suwa, Japan). The resulting grayscale TIFF images were analysed with WinRHIZO Pro 2016a software (Regent instruments Inc., Canada) to extract data on total root length (TRL, cm/plant), total surface area (TSA, cm^2/plant), average root diameter (ARD, mm/plant), total root volume (TRV, cm^3/plant) and total root tips (TRT, number/plant). Primary root length (PRL, cm/plant) was measured manually using a meter scale.

Statistical analysis

The experiment was executed using completely randomized design with 5 replications of each genotype under both limiting P and non-limiting P conditions. The statistical analysis performed in R software (version 4.5.0) includes violin plots (with inset box plots), two-way analysis of variance (ANOVA), variability analysis and Pearson correlation. The precent change in the mean of the trait in response to P stress created due to limiting P supply was calculated using the following formula.

$$\text{Per cent change in mean of } n^{th} \text{ trait} = \frac{\overline{LP}_n - \overline{NP}_n}{\overline{NP}_n} \times 100$$

Where,

$\overline{LP}_n$ = Mean of the n^{th} trait of all the genotypes under limiting P conditions.

$\overline{NP}_n$ = Mean of the of the n^{th} trait of all the genotypes under non-limiting P conditions.

MGIDI based genotype selection and trait prioritization

We employed MGIDI based analysis to select genotypes and prioritize traits with the highest potential for genetic improvement. According to olivoto and Nardino (2021), the computation of the MGIDI index follows a structured four-step approach: (i) standardizing trait values by rescaling them to a uniform range between 0 and 100, (ii) conducting factor analysis on the correlation matrix to reduce data dimensionality, (iii) defining an ideotype by specifying the desired target values for each trait; and (iv) calculating the MGIDI index based on the distance of each genotype from the defined ideotype.

The MGIDI for the pth genotype (*MGIDIp*) is computed using the following expression:

$$MGIDI_p = \sqrt{\sum_{j=1}^{z} (Y_{pj} - Y_j)^2}$$

In this equation:

Y_{pj} = Score of the p^{th} genotype on the j^{th} factor, where, p = 1,2,…,u and j = 1,2,…,*z*.

Yj = Score of the ideotype on the j^{th} factor.

u and z correspond to the total number of genotypes and factors, respectively.

This formulation quantifies the Euclidean distance between each genotype and the ideotype within the reduced dimensionality trait space derived from factor analysis. A lower MGIDI value indicates a genotype's closer proximity to the ideotype, suggesting a more desirable multitrait profile.

The contribution of the jth factor to the MGIDI index for the *p*th genotype (ω_{pj}) is employed to characterize the strengths and weaknesses of genotypes. The calculation of (ω_{pj}) is given by:

$$\omega_{pj} = \frac{\sqrt{D_{pj}^2}}{\sum_{j=1}^{z} \sqrt{D_{pj}^2}}$$

Where,

D_{pj} = Distance between the p^{th} genotype and the ideotype for the j^{th} factor.

z = Corresponds to the total number of factors.

This formulation enables the assessment of each factor's relative contribution to the overall MGIDI, there by facilitating the identification of traits that most influence a genotypes de*via*tion from the ideotype. Low contributions of a factor indicate that the traits within such factor are close to the ideotype, suggesting that the genotype aligns well with the ideal values for that factor. Conversely, high contributions indicate that the genotype de*via*tes more from the ideotype for that factor.

The estimated genetic gain (SG, expressed as percentage) for each trait was determined by applying a selection intensity of α%, with the calculation performed as follows:

$$SG(\%) = \frac{(\bar{X}_s - \bar{X}_0) \times H}{\bar{X}_0} \times 100$$

Where,

X_s = Mean of the selected genotypes.

X_0 = Mean of the original population.

H = Heritability (Broad sense).

The statistical analysis of MGIDI was performed using mgidi function in the metan package (version 1.19.0) within R-Studio (version 4.5.0).

RESULTS AND DISCUSSION

ANOVA and root-trait variability parameters

Violin plots with boxplot insets illustrate per-genotype distributions and medians for TRL, TSA, ARD, TRV, TRT and PRL across 31 genotypes under limiting P and non-limiting P conditions (Fig 1). All assessed root traits varied significantly in response to both genotype and P availability ($p<0.001$), highlighting the independent effects of genetic and environmental factors. However, genotype × P level interactions were generally non-significant, with the exception of PRL, which showed a significant interaction ($p<0.001$), suggesting differential genotypic responsiveness to P conditions for this trait alone (Table 1). Under limiting P conditions, the BG3022 showed the highest TRL (1123.67), TSA (205.32) and TRV (2.99), while GNG1581, RSG888 and RSG888 recorded the lowest TRL (139.54), TSA (23.9) and TRV (0.31), respectively. PG0515 and BGD103 had the highest and lowest ARD (0.6596, 04011, respectively); BGM20211 and PUSA1103 had the highest and lowest TRT (3123, 87, respectively) and PRL ranged from 80.1 (PUSA72) to 22.3 (FG212). Under non limiting P conditions, BG3022 again had the highest TRL (767.16), TSA (140.31) and TRV (2.04), while, PUSA362 had the lowest TRL (76.88) and TSA (14.97) and JG315 exhibited the lowest TRV (0.23). ARD was highest in PG0515 (0.6641) and lowest in BGM20211 (0.4755); TRT ranged from 2333 (BGM10216) to 41 (PUSA362) and PRL from 63.1 (PUSA1103) to 18.9 (ICCV10). These results underscore the genotypic differences in root traits under contrasting P conditions (Table 2).

Supplementary Table 1: List of accessions used in the study.

Genotypes	Scientific name
BG1053	*Cicer arietinum* L.
BG3043	*Cicer arietinum* L.
BGD103	*Cicer arietinum* L.
BGD111-1	*Cicer arietinum* L.
C-235	*Cicer arietinum* L.
DCP92-3	*Cicer arietinum* L.
FG212	*Cicer arietinum* L.
GENESIS836	*Cicer arietinum* L.
GNG1581	*Cicer arietinum* L.
ICCV10	*Cicer arietinum* L.
IG5860	*Cicer arietinum* L.
ILC10456	*Cicer arietinum* L.
JG11	*Cicer arietinum* L.
JG14	*Cicer arietinum* L.
JG16	*Cicer arietinum* L.
JG315	*Cicer arietinum* L.
KWR108	*Cicer arietinum* L.
PG 0515	*Cicer arietinum* L.
Pusa1103	*Cicer arietinum* L.
Pusa2085	*Cicer arietinum* L.
Pusa3022(BG3022)	*Cicer arietinum* L.
Pusa362	*Cicer arietinum* L.
Pusa372	*Cicer arietinum* L.
Pusa5023	*Cicer arietinum* L.
Pusa72	*Cicer arietinum* L.
Pusa chickpea10216(BGM10216)	*Cicer arietinum* L.
Pusa chickpea manav(BGM20211)	*Cicer arietinum* L.
Pusa green112(BGD112)	*Cicer arietinum* L.
PusaJG16	*Cicer arietinum* L.
Pusa Vijay(BGM10217)	*Cicer arietinum* L.
RSG888	*Cicer arietinum* L.
RUPALI	*Cicer arietinum* L.
T-39-1	*Cicer arietinum* L.

High genotypic coefficient of variation (GCV) and phenotypic coefficient of variation (PCV) were observed for TRT (GCV: 48.39%, PCV: 60.8% in limiting P; GCV: 35.54%, PCV: 97.67% in non-limiting P) and TRV (GCV: 45.82%, PCV: 52.75% in limiting P; GCV: 42.42%, PCV: 52.46% in non-limiting P), indicating substantial genetic variability under both conditions. PRL showed high heritability in limiting P (0.87) and non-limiting P (0.80), suggesting stable genetic control. In contrast, ARD showed notably lower heritability in non-limiting P (0.36) than limiting P (0.74), reflecting stronger environmental influence under non stress conditions (Table 2).

Table 1: Summary of ANOVA results (F-value).

Traits	Genotype	Treatment	Genotype × Treatment
TRL	8.466***	70.853***	1.504^{ns}
TSA	9.136***	47.344***	1.284^{ns}
ARD	6.752***	91.075***	0.947^{ns}
TRV	10.126***	27.08***	1.155^{ns}
TRT	3.456***	37.163***	1.41^{ns}
PRL	16.14***	250.215***	7.196***

*** p<0.001, ** p<0.01, * p<0.05 and ns (non-significant) p≥0.05; TRL-Total root length (cm/plant), TSA-Total surface area (cm^2/plant), ARD-Average root diameter (mm/plant), TRV-Total root volume (cm^3/plant), TRT-Total root tips (number/plant) and PRL-Primary root length (cm/plant).

Per cent change in mean in response to limiting P stress and correlation under limiting P and non-limiting P conditions

Under limiting P conditions, marked increases were observed in key root traits, with TRT rising most sharply (89.05%), followed by TRL (54.73%), TSA (42.36%), PRL (35.65%) and TRV (31.17%). These enhancements reflect a coordinated morphological adaptation to optimize P foraging. Conversely, ARD declined modestly (-8.65),

Table 2: Estimates of ranges and means, genotypic coefficient of variation (GCV) and phenotypic coefficient of variation (PCV), heritability (broad sense) H(BS).

	LP	NP	LP	NP	LP	NP	LP	NP	LP	NP	LP	NP
	Maximum		Minimum		Mean		GCV		PCV		H (BS)	
TRL	1123.67	767.16	139.54	76.88	477.22	308.41	41.41	36.27	46.61	50.98	0.79	0.51
TSA	205.32	140.31	23.9	14.97	76.29	53.59	42.42	38.95	48.41	50.99	0.77	0.58
ARD	0.6596	0.6641	0.4011	0.4755	0.51	0.56	8.12	4.02	9.44	6.73	0.74	0.36
TRV	2.99	2.04	0.31	0.23	0.98	0.74	45.82	42.42	52.75	52.46	0.75	0.65
TRT	3123	2333	87	41	923.55	488.52	48.39	35.54	60.8	97.67	0.63	0.13
PRL	80.1	63.1	22.3	18.9	52.35	38.59	23.91	24.38	25.58	27.32	0.87	0.8

LP-(limiting P), NP-(non-limiting P), TRL-Total root length (cm/plant), TSA-Total surface area (cm^2/plant), ARD-Average root diameter (mm/plant), TRV-Total root volume (cm^3/plant), TRT-Total root tips (number/plant) and PRL-Primary root length (cm/plant).

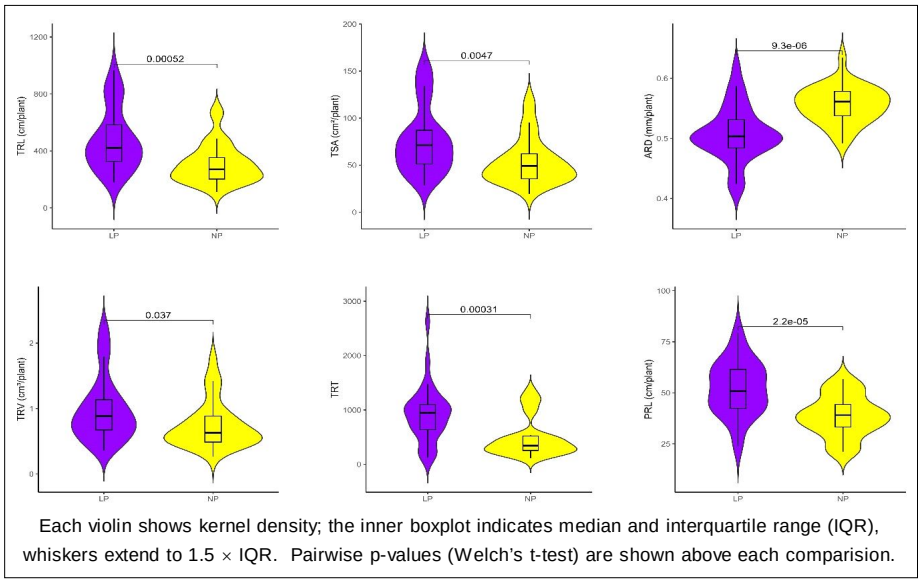
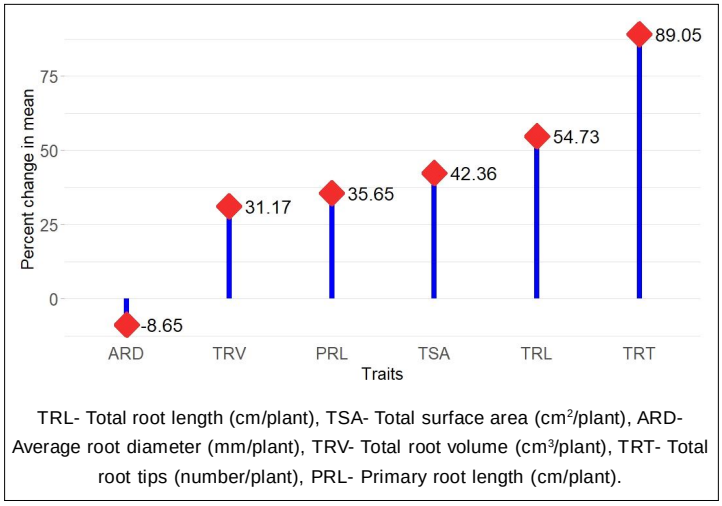


Fig 1: Violin plots (with boxplots) showing trait distributions of TRL- Total root length (cm/plant), TSA- Total surface area (cm^2/plant), ARD- Average root diameter (mm/plant), TRV- Total root volume (cm^3/plant), TRT- Total root tips (number/plant) and PRL- Primary root length (cm/plant) across 31 genotypes under limiting P (LP) and non-limiting P (NP) conditions.

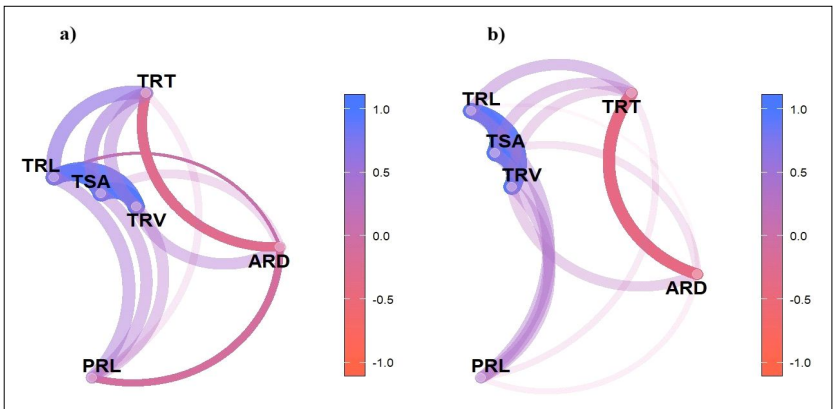
indicating a shift toward finer roots, likely facilitating greater absorptive surface per unit biomass under stress (Fig 2). Enhancement of primary root elongation was reported in several legume species, including soyabean (Zhou *et al.,* 2014; Guo *et al.,* 2011). Azevedo *et al.* (2015) also reported an overall increase in root traits and a decline in root diameter in the P efficient maize lines.

We examined the interrelationships among key root traits under both limiting and non-limiting P conditions using Pearsons's correlation analysis (Fig 3). Under P limited conditions, strong positive correlations were observed among TRL, TSA, TRV and TRT, indicating coordinated root elongation, surface expansion and branching to enhance P acquisition. In contrast, ARD showed weak or negative associations, suggesting a trade-off toward finer and longer roots for efficient P foraging. Under non-limiting P, correlations weakened, particularly between TRT and other root traits and ARD showed a significant negative correlation with TRT, implying thicker roots with fewer tips. These shifts reflect adaptive plasticity in RSA depending on P availability, with finer, proliferative roots favoured under deficiency. The observed correlations are consistent with previous findings in mungbean (Kothari *et al.,* 2023). Similar trends have been reported in other legumes, where specific root traits confer advantages under P limitation. Thudi *et al.* 2021 reported that greater total root length, higher lateral root density and larger root biomass correlate with improved P uptake and P utilization efficiency. Dhanapal *et al.* 2021 showed that shallow root growth angle and greater crown-root number improve top soil exploration and nutrient capture. Likewise, Kohli *et al.* (2022) observed that increased root-hair length and density under low P expands absorptive surface area and directly enhances P uptake.



TRL- Total root length (cm/plant), TSA- Total surface area (cm²/plant), ARD- Average root diameter (mm/plant), TRV- Total root volume (cm³/plant), TRT- Total root tips (number/plant), PRL- Primary root length (cm/plant).

Fig 2: Lollipop plot depicting percentage change in mean values under limiting P conditions.



TRL- Total root length (cm/plant), TSA- Total surface area (cm²/plant), ARD- Average root diameter (mm/plant), TRV- Total root volume (cm³/plant), TRT- Total root tips (number/plant), PRL- Primary root length (cm/plant).

Fig 3: Pearson correlation network plot under (a) limiting P conditions and (b) non-limiting P conditions.

MGIDI

MGIDI-based analysis was conducted with a selection intensity of 10% to select genotypes and prioritize traits with the highest potential for genetic improvement. This method enabled the systematic evaluation of genotype performance relative to the ideotype, while also quantifying the contribution of individual traits to the overall genotype profile. By assessing the deviation of each genotype from the ideotype, we identified key traits influencing genotype selection, facilitating more precise, multitrait based breeding decisions.

Loadings, factor descriptions and genetic gains obtained through MGIDI

We identified two orthogonal factors, each with eigenvalues exceeding one (applying kaiser criterion), which together captured 80.0% of total variance under limiting P conditions and 78.4% under non-limiting P conditions. Communality refers to the proportion of each trait's variance explained by the retained factors. Under limiting P conditions, the mean communality was 0.8, with values ranging from 0.28 (PRL) to 0.98 (TSA,TRV). In contrast, under non-limiting P conditions, the mean communality was 0.78, with values ranging from 0.25 (PRL) to 0.97 (TRL, TSA, TRV). Uniquenesses indicates the proportion of variance attributed solely to each trait, with lower values reflecting stronger inter-trait relationships. In limiting P conditions, uniquenesses values ranged from 0.02 (TSA, TRV) to 0.72 (PRL), while in non-limiting P conditions, they ranged from 0.03 (TRL, TSA, TRV) to 0.75 (PRL) (Table 3).

In limiting P conditions, TRL, TSA, TRV, TRT and PRL loaded strongly onto FA1, while FA2 was defined by ARD (Table 4). In non-limiting P conditions, TRL, TSA, TRV and PRL contributed predominantly to FA1 whereas FA2 was associated with ARD and TRT (Table 5). Positive selection differentials were obtained for all the traits under both limiting P and non-limiting P conditions, except TRT (-20.6) under non-limiting P conditions. Mean selection differential (SD%) under limiting P conditions was 48.03%, ranging from 5.35% (ARD) to 89.1% (TRV). Under non-limiting P conditions mean SD% was 33.78%, spanning from -4.21% (TRT) to 83.7% (TRV). The mean selection gain (%) [SG (%)] was 41.86% under limiting P conditions, ranging from 4.54% for ARD to 77.3 for TRV, whereas, the mean SG (%)

Table 3: Eigenvalues, explained variance and factorial loadings after varimax rotation, communality and uniquenesses obtained in the factor analysis under limiting P conditions (LP) and non-limiting P conditions (NP).

Variable	FA1		FA2		Communality		Uniquenesses	
	LP	NP	LP	NP	LP	NP	LP	NP
TRL	-0.99	-0.96	0.03	0.2	0.97	0.97	0.03	0.03
TSA	-0.97	-0.99	-0.18	0.06	0.98	0.97	0.02	0.03
ARD	-0.07	-0.23	-0.96	-0.87	0.92	0.8	0.08	0.2
TRV	-0.92	-0.98	-0.37	-0.07	0.98	0.97	0.02	0.03
TRT	-0.67	-0.32	0.46	0.8	0.66	0.74	0.34	0.26
PRL	-0.5	-0.5	0.15	-0.02	0.28	0.25	0.72	0.75
Eigenvalues	3.49	3.3	1.31	1.41	-	-	-	-
Variance (%)	58.1	55	21.9	23.4	-	-	-	-
Cumulative variance (%)	58.1	55	80	78.4	-	-	-	-

TRL- Total root length (cm/plant), TSA- Total surface area (cm^2/plant), ARD- Average root diameter (mm/plant), TRV- Total root volume (cm^3/plant), TRT- Total root tips (number/plant) and PRL- Primary root length (cm/plant). Communality refers to proportion of variance in each trait explained by retained factors. Uniquenesses refers to extent of variance specific to each trait not explained by the retained factors.

Table 4: Selection differential and selection gains based on the MGIDI under limiting P conditions.

Variable	Factor	Xo	Xs	SD	SD (%)	h^2	SG	SG (%)
TRL	FA1	477	825	347	72.8	0.888	308	64.6
TSA	FA1	76.3	138	61.6	80.8	0.875	53.9	70.7
TRV	FA1	0.977	1.85	0.87	89.1	0.868	0.755	77.3
TRT	FA1	924	1141	217	23.5	0.789	171	18.5
PRL	FA1	52.4	61	8.67	16.6	0.936	8.12	15.5
ARD	FA2	0.508	0.535	0.0272	5.35	0.848	0.023	4.54
Mean		255.2	361.23	105.86	48.03	0.87	90.3	41.86

TRL- Total root length (cm/plant), TSA- Total surface area (cm^2/plant), ARD- Average root diameter (mm/plant), TRV- Total root volume (cm^3/plant), TRT- Total root tips (number/plant), PRL- Primary root length (cm/plant), Xo- Original population mean, Xs- Selected population mean, SD- Selection differential, SD (%)- Selection differential (%), h^2- Heritability, SG- Selection gain and SG (%)- Selection gain (%).

Table 5: Selection differential and selection gains based on the MGIDI under non-limiting P conditions.

Variable	Factor	Xo	Xs	SD	SD (%)	h^2	SG	SG (%)
TRL	FA1	308	464	156	50.6	0.672	105	34
TSA	FA1	53.6	89.2	35.7	66.5	0.737	26.3	49
TRV	FA1	0.745	1.37	0.624	83.7	0.791	0.493	66.2
PRL	FA1	38.6	39.3	0.715	1.85	0.886	0.634	1.64
ARD	FA2	0.556	0.58	0.0237	4.26	0.503	0.0119	2.14
TRT	FA2	489	468	-20.6	-4.21	0.234	-4.81	-0.986
Mean		148.42	177.08	28.74	33.78	0.64	21.27	25.33

TRL- Total root length (cm/plant), TSA- Total surface area (cm^2/plant), ARD- Average root diameter (mm/plant), TRV- Total root volume (cm^3/plant), TRT- Total root tips (number/plant), PRL- Primary root length (cm/plant), Xo- Original population mean, Xs- Selected population mean, SD- Selection differential, SD (%)- Selection differential (%), h^2- Heritability, SG- Selection gain and SG (%)- Selection gain (%).

Table 6: MGIDI scores of the genotypes under limiting P conditions (LP) and non-limiting P conditions (NP).

LP		NP	
Genotype	MGIDI	Genotype	MGIDI
PUSA72	1.3	BG3022	0.626
BG3022	1.45	PUSA5023	1.94
PUSA2085	1.47	PG 0515	2.07
PUSA5023	1.79	PUSA2085	2.1
KWR108	2.32	PUSA1103	2.48
GENESIS836	2.69	PUSA72	2.57
BGM10216	2.7	BG1053	2.88
PUSA1103	2.94	GENESIS836	3.03
PUSA362	3.01	JG11	3.08
JG16	3.02	BGD111-1	3.19
JG14	3.09	BGM10216	3.23
PG 0515	3.1	RUPALI	3.41
BG1053	3.18	JG14	3.47
BGD111-1	3.24	BGM20211	3.68
RUPALI	3.44	PUSA112	3.7
JG11	3.46	DCP92-3	3.76
T-39-1	3.46	RSG888	3.77
BGM20211	3.47	T-39-1	3.83
BG3043	3.59	FG212	3.84
JG315	3.6	C-235	3.85
BGD103	3.66	JG16	3.86
PUSA JG 16	3.76	GNG1581	3.89
ICCV10	3.85	KWR108	3.91
PUSA112	3.86	BG3043	3.99
DCP92-3	3.9	PUSA362	4
C-235	3.92	PUSA JG 16	4.05
PUSA372	4.1	PUSA372	4.14
RSG888	4.13	ICCV10	4.15
GNG1581	4.14	BGD103	4.42
FG212	4.53	BGM10217	4.48
BGM10217	4.65	JG315	4.78

was 25.33%, ranging from -0.986% for TRT to 66.2 for TRV under non-limiting P conditions.

Selection of genotypes

Genotype ranking was performed using the MGIDI index scores, where lower scores indicate greater proximity to the ideotype (Table 6). Based on a predefined selection intensity of 10%, three genotypes were identified in each P regime. Under limiting P conditions, Pusa72 (1.3), BG3022 (1.45) and Pusa2085 (1.47) exhibited the closest alignment with the ideotype. In non-limiting P conditions, BG3022 (0.626), Pusa5023 (1.94) and PG0515 (2.07) were identified as the most desirable performers. Under both P conditions, BG3022 emerged as high performing genotype, exhibiting traits closely aligned with the ideal phenotypic profile. The scanned root images of the selected genotypes were presented in the Fig 4. Olivoto *et al.* (2022) demonstrated that MGIDI effectively ranked strawberry cultivars across treatments using multiple traits.

Strength and weakness view of selected genotypes

The strengths and weakness view, which depicts the proportion of the MGIDI index attributable to each factor (Fig 5 and Fig 6), offers a powerful and intuitive tool for dissecting genotypic performance. A smaller proportion explained by a given factor, shown by segments positioned closer to the outer edge of the plot, indicates that the traits within that factor are more aligned with the ideotype.

Under limiting P conditions, FA1 had the smallest contribution to the Pusa72 suggesting that the traits retained in the FA1 namely, TRL, TSA, TRV, TRT and PRL have higher values. This indicates strong performance for these root related traits, placing Pusa72 closer to the ideotype for this factor. But a higher contribution of FA2 to the Pusa72 indicates the lower values of the trait ARD retained in FA2. In contrast, Pusa2085 showed a high contribution from the FA1, indicating lower performance for the traits grouped within this dimension. BG3022 exhibited a balanced performance with low contributions from both factors, indicating close alignment with the ideotype across all evaluated traits. Under non-limiting P conditions, BG3022 exhibited smaller contributions from both FA1 and FA2, reflecting superior trait performance and a close proximity to the ideotype. The traits grouped in FA1 including, TRL, TSA, TRV and PRL, along with those in FA2, namely ARD and TRT, showed favourable values in BG3022. In case of Pusa5023, the minimal contribution from FA2 suggests optimal expression for ARD and TRT, whereas the higher contribution from FA1 implies relative limitations

in traits retained in FA1. PG0515 exhibited relatively higher contributions from both FA1 and FA2, indicating greater deviation from the ideotype. Similarly, Wang *et al.* (2024) applied MGIDI to *Populus* hybrids across two planting densities, identifying genotypes with enhanced growth and leaf morphology while revealing spacing specific trait limitations. MGIDI has also proven effective in selecting high-performing genotypes with desirable trait profiles in lentil (Amin *et al.,* 2023), black bean (Klein *et al.,* 2023) and oats (Ambrósio *et al.,* 2024). Thus, this trait level dissection clearly highlights the physiological strengths and limitations of the selected genotypes under contrasting P regimes. It helps to unravel the dynamics of RSA by pinpointing genotypes with desirable combinations of root-

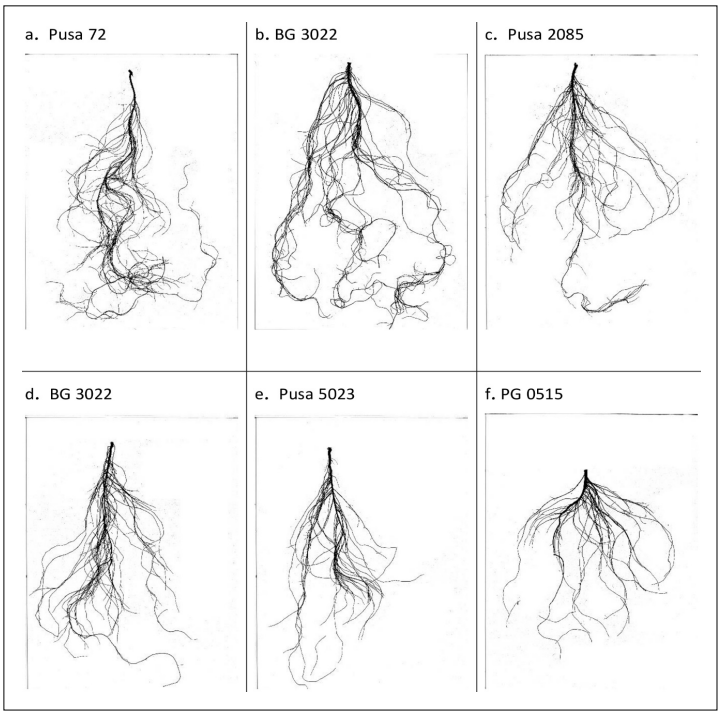


Fig 4: The scanned root images of the selected genotypes based on MGIDI under limiting P conditions (a, b and c) and the scanned root images of the selected genotypes based on MGIDI under non-limiting P conditions (d, e and f).

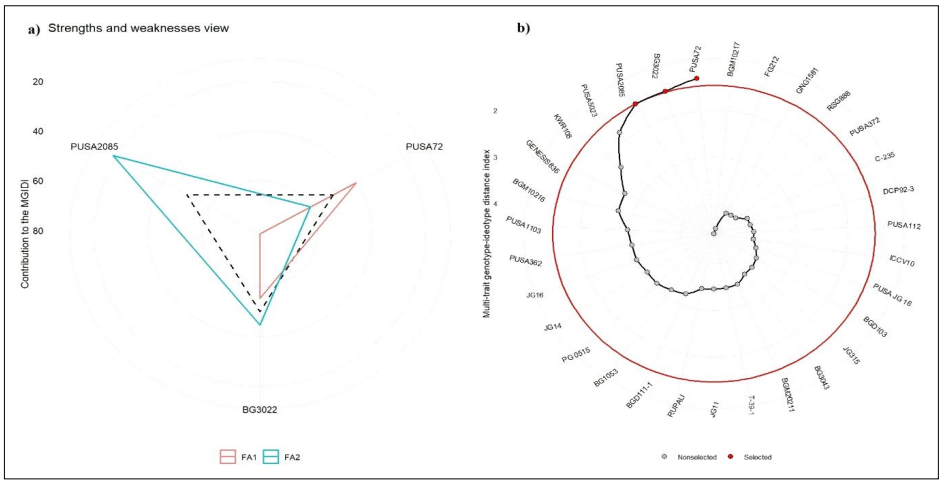


Fig 5: Under limiting P conditions, plot a) indicates the strength and weakness view of the selected genotypes, shown as the proportion of each factor on the computed MGIDI. The dashed line indicates the expected contribution if all factors contributed equally to the MGIDI index. Plot b) depicting genotype ranking in ascending order for the MGIDI index. The selected genotypes are shown in red dots and the red circle represents the cutpoint according to the selection pressure.

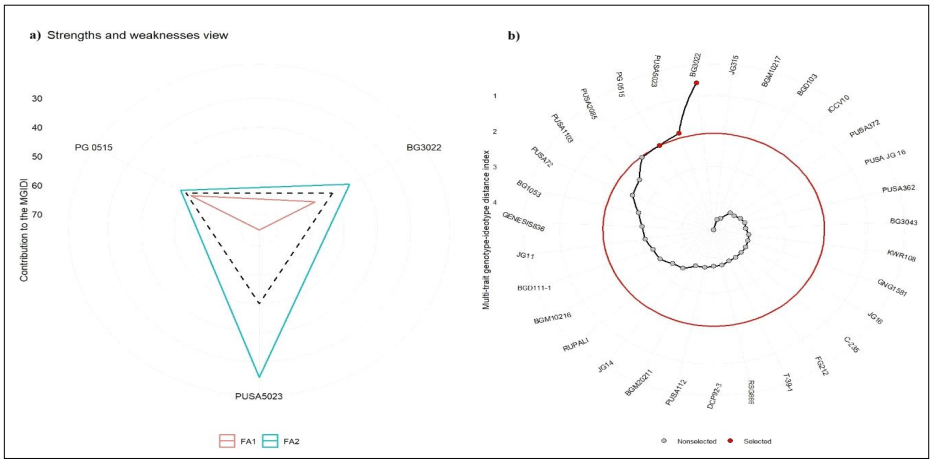


Fig 6: Under non-limiting P conditions, plot a) indicates the strength and weakness view of the selected genotypes, shown as the proportion of each factor on the computed MGIDI. The dashed line indicates the expected contribution if all factors contributed equally to the MGIDI index. Plot b) depicting genotype ranking in ascending order for the MGIDI index. The selected genotypes are shown in red dots and the red circle represents the cutpoint according to the selection pressure.

traits under varying P conditions which guides breeders in assembling trait combinations that optimize root development and enhance PUE.

Further, limiting P and moisture stress conditions create contrasting challenges when they co-occur as P is concentrated in the top soil while water is typically available at depth in rainfed systems. Because of this, the required root systems differ sharply. Under limiting P conditions, plants benefit from topsoil-foraging traits such as shallow growth angles, many short and dense lateral roots and abundant long root hairs (Postma *et al.,* 2014). In contrast, moisture stress requires steep, deep roots and fewer long laterals (Zhan *et al.,* 2015). Therefore, breeding should aim for integrated or dimorphic ideotypes that balance both functions (Rangarajan *et al.,* 2018; Lynch, 2022). At the functional level, longer TRL and larger TSA and TRV, combined with reduced ARD expand root growth medium (or soil) contact and the volume of medium (or soil) explored, so more P is intercepted by diffusion or mass flow to root surfaces. A higher number of TRT creates many active uptake sites and longer PRL increases access to localized P patches beyond the seedling rhizosphere while also aiding subsoil water exploration under moisture stress. Root hairs further enlarge absorptive surface per unit root. These processes together raise P flux to the plant (Hinsinger, 2001; Niu *et al.,* 2013; Lynch, 2019). Thus, all the measured traits are practical selection indices, as supported by our MGIDI results and using them as selection criteria (alone or as part of a selection index) will allow breeders to identify genotypes that explore more soil volume and acquire available P more efficiently. Cultivars with such optimized RSA can contribute to sustainable P management by reducing reliance on external P inputs and improving long term PUE. Advancing this research requires integrating RSA traits with genomic tools such as genome wide association studies (GWAS), QTL mapping and transcriptome profiling to identify candidate genes. Validated loci can then be used to design SNP markers and applied through marker-assisted or genomic selection to develop lines with enhanced PUE.

CONCLUSION

This study reveals the dynamic modulation of RSA in chickpea under contrasting P regimes. ANOVA results demonstrated significant effects of both genotype and P availability on root traits, with a notable genotype × treatment interaction for PRL, underscoring genotype specific responses to P supply and the complexity of PUE. Under P stress, tolerant genotypes exhibited coordinated root morphological adaptations, marked by increased total root traits and reduced diameter, enhancing foraging efficiency under limiting conditions. Correlation analysis further revealed P dependent plasticity in root architecture, with finer, more proliferative root systems favoured under limiting P conditions, reflecting integrated trait shifts to optimize P acquisition. MGIDI analysis identified Pusa72, BG3022 and Pusa2085 as the genotypes that best approximated the ideotype under limiting P conditions, while BG3022, Pusa5023 and PG0515 were the best fit under non-limiting P conditions. MGIDI results also revealed longer TRL and PRL combined with higher TSA and TRV and reduced ARD, act synergistically to enlarge root growth medium interface and the volume explored, identifying these traits as key drivers of improved P uptake. Thus, it provided a robust framework for multi trait genotype evaluation by quantifying deviations from the ideotype and disentangling trait contributions to overall performance, thereby enhancing selection precision. Selection of RSA traits enables breeding of P efficient cultivars and supports targeted nutrient management, thereby reducing reliance on P fertilizers and improving the sustainability of cropping systems. These insights deepen our understanding of RSA plasticity, providing

a physiological basis for genotype specific responses to contrasting P regimes and advancing our comprehension of RSA dynamics. However, hydroponic assays demonstrate physiological plasticity and field trials across multiple seasons and diverse locations should be conducted to confirm genotype performance under agronomic conditions.

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Disclaimers

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Informed consent

Not applicable.

Conflict of interest

The authors declare no conflicts of interest.

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