



Genetic insights into phosphorus use efficiency and resilience in Indian mustard (*Brassica juncea* L. Czern & Coss)

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Abstract

Phosphorus (P) deficiency is a major constraint limiting productivity of Indian mustard (*Brassica juncea* L. Czern & Coss.). The present study was conducted to assess phenotypic variability and phosphorus use efficiency (PUE) in a Diversity Fixed Foundation Set (BjDFFS) comprising 280 genotypes under three phosphorus regimes, viz., control (0 kg P₂O₅ha⁻¹), low phosphorus (15 kg P₂O₅ha⁻¹) and normal phosphorus (30 kg P₂O₅ha⁻¹) at PAU, Ludhiana in an alpha lattice design with two replications. Analysis of variance revealed highly significant differences among genotypes, phosphorus levels and their interactions for most yield and yield-related traits. Mean seed yield per plant increased from 7.30g under control to 8.61g under normal phosphorus, while number of siliquae on main shoot increased from 28.84 to 39.47, indicating strong responsiveness to phosphorus supply. High variability was observed for seed yield and branching traits, suggesting scope for selection. Genotypes such as RGN-48, RB-50, CN-101846 and DINGAHINI exhibited superior performance under low phosphorus conditions. The study highlights substantial genetic variability and identifies promising genotypes for improving phosphorus use efficiency and developing nutrient-efficient mustard cultivars.

Keywords: BjDFFS, *Brassica juncea*, genetic variability, nutrient stress, yield traits

Introduction

Indian mustard (*Brassica juncea* L. Czern & Coss.) is a pivotal oilseed crops cultivated in South Asia and several other regions of the world. It plays a crucial role in the edible oil economy and contributes significantly to global vegetable oil and protein meal production. In India, Rapeseed-mustard crops occupy nearly 9 million hectares with an annual production exceeding 13 million tonnes, making the country the third-largest producer globally (DRMR 2023). Among the cultivated Brassica species, *B. juncea* (2n = 4x = 36; genome AABB) is the predominant species grown in India because of its wide adaptability to diverse agro-climatic conditions, particularly semi-arid and subtropical environments. However, despite its economic importance and expanding cultivation area, the productivity of Indian mustard remains considerably lower than its genetic potential due to multiple biotic and abiotic constraints, including nutrient deficiencies and poor soil fertility. Among essential plant nutrients, phosphorus (P) is one of the most critical macronutrients regulating plant growth and productivity. Phosphorus plays a fundamental role in several physiological and biochemical processes

such as energy transfer through ATP, nucleic acid synthesis, membrane integrity, photosynthesis, signal transduction, and root development (Marschner 2012). Adequate phosphorus nutrition is therefore essential for optimal vegetative growth, reproductive development, and seed formation. However, phosphorus availability in agricultural soils is often limited due to its strong fixation with calcium in alkaline soils and with iron and aluminum oxides in acidic soils, which significantly reduces its bioavailability to plants (Vance *et al.*, 2003). As a result, phosphorus deficiency has emerged as one of the major constraints affecting crop productivity worldwide.

Plants have evolved a range of morphological, physiological and molecular adaptations to cope with phosphorus deficiency. These adaptive responses include modifications in root system architecture, enhanced secretion of organic acids and phosphatases, increased expression of phosphate transporter genes, and efficient internal recycling of phosphorus within plant tissues (Hammond *et al.*, 2009; Lopez-Arredondo *et al.*, 2014). Collectively, these mechanisms contribute to phosphorus use efficiency (PUE), which refers to the ability of plants

to produce greater biomass or grain yield per unit of phosphorus absorbed or available in the soil. Improving PUE has become an important objective in crop improvement programs because phosphate fertilizers are derived from finite phosphate rock reserves and their excessive use can lead to environmental degradation (Cordell *et al.*, 2009). Genetic improvement of crops for enhanced phosphorus use efficiency largely depends on the availability of genetic variability within the germplasm. Diverse germplasm collections provide valuable genetic resources for identifying traits associated with nutrient uptake efficiency and utilization. Estimation of genetic parameters such as phenotypic and genotypic coefficients of variation, heritability, and genetic advance provides important insights into the inheritance pattern of agronomic traits and their potential response to selection. Traits exhibiting high heritability coupled with substantial genetic advance are generally governed by additive gene action and can be effectively improved through phenotypic selection (Falconer and Mackay, 1996). In Brassica crops, considerable genetic variation has been reported for yield and its associated traits, suggesting significant opportunities for improving productivity through targeted breeding strategies. Nevertheless, information regarding phenotypic variability and genotype $\times$ phosphorus interactions in diverse Indian mustard germplasm remains limited.

The *Brassica juncea* Diversity Fixed Foundation Set (BjDFFS) represents a valuable genetic resource comprising historical cultivars, exotic accessions, resynthesized lines, and introgression materials with a broad genetic base. Evaluation of such diversity panels provides an excellent opportunity to explore genetic variability for nutrient use efficiency and yield-related traits. Understanding the extent of phenotypic variation and genetic parameters under different phosphorus regimes is essential for identifying phosphorus-efficient genotypes and designing effective breeding strategies. Therefore, the present investigation was undertaken to evaluate phenotypic variability and genetic responses associated with phosphorus use efficiency in a diversity fixed foundation set (BjDFFS) of Indian mustard. The findings of this study will provide insights into the genetic architecture of phosphorus efficiency and facilitate the identification of promising genotypes for developing nutrient-efficient and climate-resilient mustard cultivars.

Materials and Methods

Experimental site

The field experiment was conducted during the *Rabi* season at the research farm of the Department of Plant

Breeding and Genetics, Punjab Agricultural University (PAU), Ludhiana, Punjab, India (30°54'2" N latitude, 75°48'2" E longitude; 247 m above mean sea level). The region falls in the Trans-Gangetic agro-climatic zone of north-western India and is characterized by a semi-arid subtropical climate with hot summers and cool winters. The soil of the experimental field was alluvial in origin with loam to sandy loam texture, well drained and moderately fertile with neutral to slightly alkaline reaction.

Experimental material and growth conditions

The experimental material used in the present study comprised an association panel representing a Diversity Fixed Foundation Set of *Brassica juncea* (BjDFFS) with a broad genetic base of approximately 280 genotypes (Supplementary Table 1). The panel represents extensive genetic diversity and includes historical varieties, exotic *B. juncea* accessions, resynthesized *B. juncea* lines, alloplasmic lines, and alien introgression lines. These diverse genetic resources were assembled to capture substantial phenotypic variability for agronomic and yield-related traits and to facilitate the evaluation of genotype performance under varying phosphorus environments. The genotypes were evaluated under three phosphorus regimes, namely control phosphorus (CP; 0 kg P₂O₅ ha⁻¹), low phosphorus (LP; 15 kg P₂O₅ ha⁻¹), and normal phosphorus (NP; 30 kg P₂O₅ ha⁻¹). The selected phosphorus levels represent deficient and recommended fertilizer doses commonly used in mustard cultivation. Phosphorus was applied through single superphosphate (SSP) according to the respective treatment levels. The experiment was laid out in an alpha lattice design with two replications, and each genotype was grown in paired rows of two meters length following the recommended agronomic package of practices for mustard cultivation.

Observations recorded

Observations were recorded on five randomly selected plants from each genotype in each replication at maturity. Data were recorded for plant height, main shoot length, number of primary and secondary branches per plant, and number of siliquae on the main shoot. Silique length and number of seeds per silique were determined from representative siliquae samples. Seed yield per plant and thousand seed weight were recorded after harvest, and oil content (%) was estimated using Nuclear Magnetic Resonance (NMR) spectroscopy (Oxford Instruments, MQC).

Statistical analysis

Descriptive statistical parameters including mean, range, variance, and coefficient of variation were computed to

assess the extent of phenotypic variability among genotypes under different phosphorus regimes. Analysis of variance (ANOVA) was performed to determine the significance of genotype, phosphorus levels, and genotype $\times$ phosphorus interaction effects on the studied traits. ANOVA was performed using Minitab statistical software (Version 19.0) to determine the significance of genotypic differences and phosphorus treatments for the studied traits (Upadhyay *et al.*, 2022; 2025). The best linear unbiased estimates (BLUES) and best linear unbiased predictions (BLUPs) were estimated using META-R (Multi Environment Trial Analysis with R for Windows), Version 6.0 developed by CIMMYT (Alvarado *et al.*, 2015). The BLUP values were further utilized for calculating descriptive statistics of the evaluated traits.

Results and Discussion

Effect of phosphorus regimes on growth and yield traits

Phosphorus application significantly influenced growth and yield-related traits in the BjDFFS population (Table 1). Analysis of variance revealed highly significant ($P \leq 0.001$) effects of phosphorus levels for most traits, including plant height (PH), main shoot length (MSL), number of siliquae on main shoot (NSMS), number of seeds per siliqua (NSPS), primary branches (PB), siliqua length (SL), seed yield per plant (YIELD) and thousand seed weight (TSW). The high mean squares observed for PH (11555.8), MSL (11340.7) and NSMS (16123.2) indicate strong responsiveness of both vegetative and reproductive traits to phosphorus supply. Similar responses have been reported in Indian mustard under varying phosphorus regimes (Chouksey *et al.*, 2016; Nandan *et al.*, 2022). A consistent increase in growth traits was observed with increasing phosphorus levels (Table 2). Mean plant height increased from 131.89 cm (CP) to 140.23 cm (NP), while main shoot length increased from 48.62 cm to 57.61 cm, indicating enhanced vegetative growth under adequate phosphorus supply. This is consistent with the established role of phosphorus in regulating energy transfer, cell division and plant development (Marschner, 2012; Vance *et al.*, 2003). Reproductive traits exhibited a stronger response to phosphorus availability. The number of siliquae on the main shoot increased from 28.84 under CP to 39.47 under NP, representing an increase of approximately 37%. Seed yield per plant also increased from 7.30 g to 8.61 g, reflecting an approximate 18% improvement under normal phosphorus conditions. Thousand seed weight showed a slight increase, indicating improved seed filling. These findings corroborate earlier reports highlighting the importance of phosphorus in enhancing reproductive

Table 1: Analysis of variance for yield and yield related traits across three Pi levels

Source	DF	Mean square								
		PH	MSL	NSMS	NSPS	PB	SB	SL	YIELD	TSW
Pi doses	2	11555.8***	11340.7***	16123.2***	68.52***	57.51***	2.79	27.30***	260.73***	14.124***
Blocks	13	298.4	28	46.1	5.1979	0.17	3.0923	0.1389	5.79	0.4389
Genotype	279	765.4***	131.9***	70.4***	10.40***	0.83***	9.80***	0.34***	28.78***	1.88***
Replications	1	56.8	19.6	0.5	1.3	0.03	4.3666	0.89*	5.548	1.5754
Pi doses*Blocks	26	283.6*	103.4*	40	7.049	0.46	2.3075	0.1875	5.664*	0.8281
Pi doses*Genotype	558	255.4***	75.6	55.7*8	11.83***	0.55***	7.14***	0.1667	9.32***	1.13***
Pi doses*Reps	2	197.5	129.2	6.5	0.9	0.27	2.9191	1.58***	4.819	0.4922
Blocks*Reps	13	273.7	37.1	62.9	4.99	0.15	0.7898	0.089	3.068	0.4447
Genotype*Reps	279	167.6	57	46.8	5.26	0.38	2.353	0.1648	3.265	0.96
Error	506	185.2	67.4	45	6.3457	0.43	2.1486	0.1478	3.428	0.7426
Total	1679									

*, ** and *** Significant at 5, 1 and 0.1% probability level respectively.

Table 2: Descriptive statistics for yield and yield related traits across three Pi levels

Traits	Mean $\pm$ SE			Range			CV (%)			Variance		
	CP	LP	NP	CP	LP	NP	CP	LP	NP	CP	LP	NP
PH	131.89 $\pm$ 0.89	139.11 $\pm$ 0.92	140.23 $\pm$ 0.85	90.8-177.9	97.2-174.6	101.2-178.1	11.29	11.11	10.18	221.74	238.89	203.84
MSL	48.62 $\pm$ 0.40	52.89 $\pm$ 0.43	57.61 $\pm$ 0.43	29.2-66.2	35.1-73	35.8-81.1	13.59	13.51	12.51	43.655	51.077	51.92
PB	4.04 $\pm$ 0.03	4.66 $\pm$ 0.04	4.21 $\pm$ 0.03	2.3-5.9	2.7-6.6	2.8-6	14.33	13	13.1	0.336	0.367	0.305
SB	5.62 $\pm$ 0.13	5.7 $\pm$ 0.12	5.77 $\pm$ 0.13	1.4-10.4	2.1-11.1	1.7-11.2	37.88	34.93	36.16	4.531	3.96	4.346
NSMS	28.84 $\pm$ 0.29	35.42 $\pm$ 0.32	39.47 $\pm$ 0.37	17.9-46.8	21.6-51.3	23.5-55.3	16.72	15.17	15.7	23.262	28.873	38.407
SL	3.83 $\pm$ 0.02	4.27 $\pm$ 0.02	4.03 $\pm$ 0.02	2.9-4.8	3.4-5.3	3.2-5.4	8.34	7.69	9.01	0.102	0.108	0.132
NSPS	14.57 $\pm$ 0.12	14.73 $\pm$ 0.15	15.23 $\pm$ 0.15	9.4-19	9.6-21.6	8.8-21.4	14.29	17.52	16.19	4.333	6.658	6.08
YIELD	7.3 $\pm$ 0.19	7.75 $\pm$ 0.16	8.61 $\pm$ 0.17	0.8-17.7	2.2-16.8	2.6-18	43.67	34.22	32.4	10.153	7.027	7.786
TSW	3.91 $\pm$ 0.05	4.2 $\pm$ 0.05	4.22 $\pm$ 0.05	2.1-6.4	1.8-6.6	2-6.7	20.83	19.57	21.5	0.664	0.676	0.825
OC	37.67 $\pm$ 0.08	38.15 $\pm$ 0.09	38.37 $\pm$ 0.09	34-41.8	34-41.2	34.9-41.7	3.63	3.87	3.89	1.874	2.182	2.229

PH: Plant height (cm); MSL: Main shoot length (cm); PB: Number of primary branches per plant; SB: Number of secondary branches per plant; NSMS: Number of siliques on main shoot; SL: Siliqua length (cm); NSPS: Number of seeds per siliqua; YIELD: Yield per plant (g); TSW: Weight of 1000 seeds (g); OC: Oil content (%).

efficiency and yield in Brassica crops (Shen *et al.*, 2011; Veneklaas *et al.*, 2012).

Phenotypic variability and distribution of traits

Substantial phenotypic variability was observed for all traits across phosphorus regimes (Table 2). High coefficients of variation were recorded for seed yield (43.67% under CP) and secondary branches (37.88% under CP), indicating greater environmental influence and selection potential. In contrast, oil content exhibited low variability (3.63–3.89%), suggesting relative stability across phosphorus conditions. The frequency distribution curves further illustrated the extent of variability among genotypes (Fig 1 & 2). Most traits exhibited near-normal distribution, indicating quantitative inheritance and polygenic control. Traits such as seed yield, secondary branches and NSMS showed wider spread and slight skewness, particularly under low phosphorus conditions, suggesting differential genotypic responses to phosphorus stress. Under NP conditions, the distribution curves were relatively more uniform and

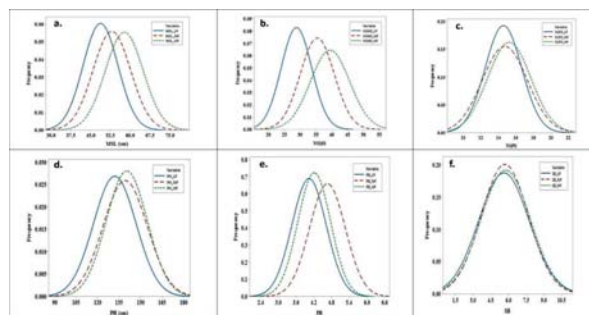


Fig. 1: Frequency distribution for yield and yield related traits across three Pi levels (a) MSL: main shoot length (cm); (b) NSMS: number of siliques on main shoot; (c) NSPS: number of seeds per siliqua; (d) PH: plant height (cm); (e) PB: number of primary branches per plant; and (f) SB: number of secondary branches per plant.

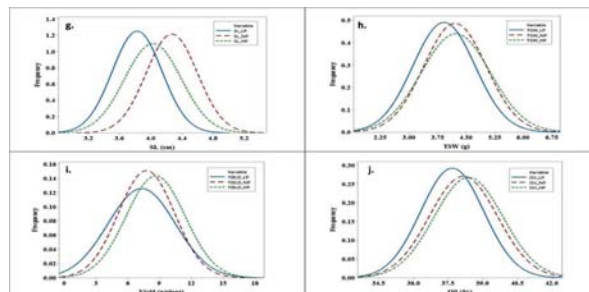


Fig. 2: Frequency distribution for yield and yield related traits across three Pi levels SL: siliqua length (cm); TSW: weight of 1000 seeds (g); YIELD: yield per plant (g); and OIL: Oil content (%).

centered, indicating stabilization of trait expression under adequate nutrient supply. Similar distribution patterns for yield and its components have been reported in Brassica germplasm, indicating the quantitative nature of these traits (George *et al.*, 2014; Upadhyay *et al.*, 2022).

Genotypic variability and genotype $\times$ phosphorus interaction

Highly significant genotypic differences were observed for all studied traits (Table 1), indicating substantial genetic variability within the BjDFFS panel. The significant genotype $\times$ phosphorus interaction for traits such as PH, NSPS, PB, SB, YIELD and TSW suggests that genotypes responded differentially under varying phosphorus environments. Such interactions indicate the presence of genotypes with superior phosphorus use efficiency, capable of maintaining performance under nutrient stress. Similar genotype-dependent responses have been reported in Brassica species and are attributed to differences in nutrient acquisition and utilization efficiency (Hammond *et al.*, 2009; Lopez-Arredondo *et al.*, 2014). The identification of genotypes such as RGN-48, RB-50, CN-101846, DINGAHINI and RRN-443-2 with relatively better performance under low phosphorus conditions highlights their potential for use in breeding programmes targeting phosphorus-deficient environments.

Multivariate analysis and trait associations

Principal component analysis (PCA) revealed that the first two principal components explained a substantial proportion of total phenotypic variation across phosphorus regimes (Fig 3). Under control conditions, PC1 explained approximately 41% of variation, with major contributions from plant height, main shoot length, NSMS

and seed yield, indicating their importance in determining overall variability. Under low phosphorus conditions, branching traits and siliqua number were strongly associated with yield, suggesting that plant architecture plays a crucial role in maintaining productivity under nutrient stress. In contrast, under normal phosphorus conditions, seed yield showed stronger association with siliqua length and thousand seed weight, reflecting the importance of assimilate partitioning and seed development under adequate nutrient availability. These results are in agreement with previous findings that yield components such as siliqua number and seed weight are major contributors to yield variability in Brassica (Veneklaas *et al.*, 2012; Lynch 2019).

The combined analysis of ANOVA, descriptive statistics, frequency distribution and PCA clearly demonstrates substantial genetic variability and differential genotype response under contrasting phosphorus regimes. Traits such as NSMS, seed yield and branching pattern showed high responsiveness to phosphorus levels and can serve as reliable selection criteria for improving phosphorus use efficiency. The superior performance of selected genotypes under low phosphorus conditions suggests the presence of adaptive mechanisms such as efficient nutrient uptake, improved root architecture and better assimilate partitioning. These traits are critical for enhancing phosphorus acquisition and utilization efficiency (Lynch, 2019; Urlic *et al.*, 2023). Overall, the BjDFFS population represents a valuable genetic resource for identifying phosphorus-efficient genotypes. The findings of the present study provide important insights for developing nutrient-efficient and climate-resilient mustard cultivars suitable for sustainable agricultural systems.

Conclusion

The study revealed substantial genetic variability and significant genotype $\times$ phosphorus interaction for yield and related traits in Indian mustard under contrasting phosphorus regimes. Reproductive traits, particularly number of siliquae on main shoot and seed yield, exhibited high responsiveness to phosphorus and can serve as key selection criteria. Genotypes such as RGN-48, RB-50, CN-101846 and DINGAHINI exhibited superior performance under low phosphorus conditions, indicating their potential for phosphorus use efficiency. These findings provide a strong basis for developing nutrient-efficient and climate-resilient mustard cultivars for sustainable production systems.

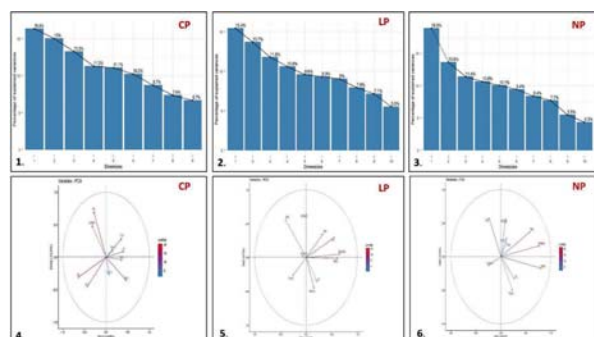


Fig. 3: Principal component analysis (PCA) for yield and yield related traits across three Pi levels. Scree plots of eigenvalues under (1) CP, (2) LP, and (3) NP respectively. PCA biplots showing variable contributions under (4) CP and (5) LP and (6) NP respectively.

References

- Alvarado G, Lopez-Cruz MA, Vargas M, Pacheco Á, Rodríguez F, Burgueno J and Crossa J. 2015. META-R (Multi Environment Trial Analysis with R for Windows) Version 6.0. CIMMYT, Mexico.
- Bhari NR. 2000. Response of Indian mustard (*Brassica juncea*) to nitrogen and phosphorus fertilization. *Ind J Agron* **45**: 393–397.
- Chouksey H, Sardana V and Sharma P. 2016. Influence of phosphorus application on growth, yield and nutrient uptake in Indian mustard (*Brassica juncea*). *J Oilseeds Res* **33**: 245–249.
- Cordell D, Drangert JO and White S. 2009. The story of phosphorus: Global food security and food for thought. *Global Environ Change* **19**: 292–305. <https://doi.org/10.1016/j.gloenvcha.2008.10.009>.
- Falconer DS and Mackay TFC. 1996. *Introduction to Quantitative Genetics* (4th ed.). Longman, London.
- George TS, Brown LK, Ramsay L, White PJ, Newton AC, Bengough AG, Russell J, Thomas WTB and Broadley MR. 2014. Understanding the genetic control and physiological traits associated with phosphorus uptake and use efficiency in crops. *J Exp Botany* **65**: 3777–3790. <https://doi.org/10.1093/jxb/eru210>.
- Hammond JP, Broadley MR and White PJ. 2009. Shoot yield drives phosphorus use efficiency in *Brassica* species. *J Exp Botany* **60**: 1963–1973. <https://doi.org/10.1093/jxb/erp088>.
- Liu TY, Huang TK, Yang SY, Hong YT, Huang SM, Wang FN, Chiang SF, Tsai SY, Lu WC and Chiou TJ. 2024. Identification and regulation of phosphate transporters in plants. *Plant Physiol.* <https://doi.org/10.1093/plphys/kiad012>.
- Lopez-Arredondo DL, Leyva-González MA, González-Morales SI, Lopez-Bucio J and Herrera-Estrella L. 2014. Phosphate nutrition: Improving low-phosphate tolerance in crops. *Annual Rev Plant Biol* **65**: 95–123. <https://doi.org/10.1146/annurev-arplant-050213-035949>.
- Lynch JP. 2019. Root phenotypes for improved nutrient capture: An underexploited opportunity for global agriculture. *New Phytologist* **223**: 548–564. <https://doi.org/10.1111/nph.15738>.
- Marschner P. 2012. *Marschner's Mineral Nutrition of Higher Plants* (3rd ed.). Academic Press, London. <https://doi.org/10.1016/C2009-0-63043-9>.
- Nandan R, Singh V, Kumar R and Yadav S. 2022. Effect of phosphorus fertilization on seed yield and quality in Indian mustard (*Brassica juncea*). *Ind J Agric Sci* **92**: 512–516.
- Shen J, Yuan L, Zhang J, Li H, Bai Z, Chen X, Zhang W and Zhang F. 2011. Phosphorus dynamics: From soil to plant. *Plant Physiol* **156**: 997–1005. <https://doi.org/10.1104/pp.111.175232>.
- Ulic B, Ban SG, Spoljarevic M and Dikic M. 2023. Phosphorus use efficiency and adaptive responses in crop plants. *Agron* **13**: 1025. <https://doi.org/10.3390/agronomy13041025>.
- Upadhyay P, Gupta M, Sra SK, Sharda R, Sharma S, Sardana VK and Kaur G. 2022. Genome wide association studies for acid phosphatase activity at varying phosphorous levels in *Brassica juncea* L. *Front in Plant Sci* **13**: 1056028. <http://dx.doi.org/10.3389/fpls.2022.1056028>.
- Upadhyay P, Gupta M, Sra SK, Cheema G, Sardana VK, Sharda R and Kaur G. 2025. Association mapping for root system architecture under varying levels of phosphorus application in *Brassica juncea* L. Czern & Coss. *BMC genomics* **26**: 740. <https://doi.org/10.1186/s12864-025-11840-2>.
- Vance CP, Uhde-Stone C and Allan DL. 2003. Phosphorus acquisition and use: Critical adaptations by plants. *New Phytologist* **157**: 423–447. <https://doi.org/10.1046/j.1469-8137.2003.00695.x>.
- Veneklaas EJ, Lambers H, Bragg J, Finnegan PM, Lovelock CE, Plaxton WC, Price CA, Scheible WR, Shane MW, White PJ and Raven JA. 2012. Opportunities for improving phosphorus-use efficiency in crop plants. *New Phytologist* **195**: 306–320. <https://doi.org/10.1111/j.1469-8137.2012.04190.x>.
- Zhang Z, Liao H and Lucas WJ. 2014. Molecular mechanisms of phosphate sensing and transport in plants. *J Integrative Plant Biol* **56**: 192–220. <https://doi.org/10.1111/jipb.12163>.