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RESEARCH ARTICLE

Genotypic variation in diverse bread wheat (*Triticum aestivum* L.) for photosynthesis related traits, biomass and yield in response to low phosphorus stress

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Abstract

Phosphorus (P) is an indispensable nutrient for plant growth and development. Deficiency of P adversely affects photosynthesis, biomass accumulation and yield potential in wheat. We evaluated 103 diverse bread wheat (*Triticum aestivum* L.) genotypes under low P (LP) and optimum P (OP) conditions in terms of photosynthetic traits, biomass, and yield. Results revealed that under LP, transpiration rate (E) significantly increased while net assimilation or photosynthetic rate (A), stomatal conductance (g_s), instantaneous-water use efficiency (IWUE), biomass, yield, and harvest index (HI) decreased. The LP stress tolerant and sensitive genotypes were identified using principal component analysis (PCA) ranking values of genotypes based on the relative values of six most contributing traits. Further, hierarchical cluster analysis also validated the variability among the genotypes and grouped P stress-tolerant and sensitive genotypes into distinct clusters. The P stress-tolerant genotypes exhibited a relatively lesser reduction in photosynthetic rate, g_s, yield, and HI as compared to P stress-sensitive genotypes in response to LP. Our results substantiate the genetic potential inherent in Indian bread wheat genotypes, which can be used as donors in breeding programs to develop P-efficient wheat varieties.

Keywords: Diversity index, cluster analysis, low phosphorus stress, net assimilation rate, correlation

Introduction

Bread wheat (*Triticum aestivum* L.) is a primary cereal globally, providing 20% of the world's population with calories (Maqbool et al. 2022). The wheat production and productivity under abiotic stresses such as abrupt climatic change, high temperature, drought and a lack of mineral nutrients is not increasing substantially. Wheat removes phosphorus (P) at a rate of 2.5 to 8.0 kg P per tonne of grain produced. The P is crucial for uniform tillering, heading, maturity, growth, and better yield in wheat. Plant growth and development are restricted by low P (LP) stress, which can be improved by using phosphatic fertilizers. However, the primary challenges related to P use efficiency (PUE) in wheat include an inadequate response and a low recovery rate after the application of phosphatic fertilizers (Manske et al. 2000). Excessive use of phosphatic fertilizers leads to environmental and ecological associated problems such as eutrophication and metal pollution. According to an estimate from the International Fertilizer Association (IFA), over 73% of soils worldwide are P deficient. Additionally, about 15% of the world's fertilizers are used to grow wheat [https://www.fertilizer.org, (IFA 2023)]. Moreover, only 20% of soil-applied P fertilizer is available for plants, and the remaining 80% of it is fixed with Ca in alkaline soils and with Fe and Al oxides and hydroxides in acidic soils. Efforts have been made to develop P use efficient cultivars that can

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utilize P more effectively. The adoption and development of novel P fertilizer management systems as well as breeding for increased PUE are, thus, essential for modern crop production.

P deficiency significantly affects the dry matter accumulation and yield potential of various crops, including wheat (Meena et al. 2020; Soumya et al. 2021). The P not only plays a significant role in phospholipids and nucleic acid metabolism, but it is also the main component of NADPH and ATP which is crucial for plant growth, photosynthesis and signal transduction (Lu et al. 2023). Due to P participation in cellular functions such as energy conservation, regulation of metabolism, and signal transduction, photosynthesis is affected by P deficiency (Carstensen et al. 2018). The deficiency of P preduces stomatal opening, resulting in less CO_2 capture, significant reduction in triose phosphate (ATP) and NADPH turnover, thereby impeding the photosynthetic capacity of plants (Neocleous and Savvas 2019). The feedback inhibition resulting from decreased leaf growth may also reduce photosynthesis under P stress (Kayoumu et al. 2023). Moreover, a reduction in the concentration of photosynthetic pigments (*i.e.,* chlorophyll and carotenoids) under low P conditions might be one of the reasons for the lower photosynthetic rate. Alipanah et al. (2018) reported that inadequate P levels in diatom (*Phaeodactylum tricornutum*) resulted in decreased action of Rubisco, a similar response observed in cotton (*Gossypium hirsutum* L.) (Liu et al. 2021). Further, P deficiency diminishes net CO_2 assimilation rate, causing a decline in stomatal conductance in cotton (Kayoumu et al. 2023). The ability to sustain optimal levels of photosynthetic activity under P limitations varies among plant species and genotypes (Pang et al. 2018; Meena et al. 2020). A deficiency in P might inhibit the regeneration of RuBP in the TCA cycle by decreasing the activity of enzymes related to this cycle, particularly the early action of Ru5P kinase. Moreover, P is essential for ATP production in the TCA cycle, crucial for the regeneration of RuBP (Verlinden et al. 2022). Given the limitations cited and the lack of information about the genetic variation in traits related to photosynthesis, biomass and yield across diverse wheat genotypes, the present study was aimed at the identification of genotypes with relatively better performance in terms of photosynthesis, biomass and yield in response to low P stress conditions and can be used as donors or genetic stocks.

Materials and methods

Plant material, experimental site and cultivation conditions

A total of 103 diverse wheat genotypes used in the study were acquired from ICAR-Indian Institute of Wheat and Barley Research (ICAR-IIWBR), Karnal, India, and Punjab Agricultural University, Ludhiana, India (Supplementary Table S1). The ICAR-Indian Agricultural Research Institute (ICAR-IARI), New Delhi, India is situated at 28.08°N and 77.12°E and 228.61 m above mean sea level. All the genotypes were sown in the earthen pots during the growing season 2019–20 at New Delhi. Plants were grown in the low P (LP) and OP conditions in the soil with P concentrations 2.58 and 41.60 mg P kg^{-1} soil, respectively (Olsen et al. 1954). The soil pH (soil:water:1:2) and electrical conductivity were 7.2 and 1.4 mS cm^{-1}, respectively. To the soil, nitrogen (@ 120 kg N ha^{-1}) and potassium (@40 kg K_2O ha^{-1}) were added at the recommended dose. Each pot (30 × 30 cm diameter and height) was initially sown with six seeds and after the emergence of three to four leaves, thinning was done to keep four healthy plants per pot, constituting one experimental unit. Data were recorded from three such experimental units for photosynthesis-related traits, ensuring three replicates for each accession and P treatment. Biomass and yield-related traits were recorded from four experimental units. Adhering to recommended agricultural practices, the plants were maintained free from weeds, diseases and pests. Weather-related information during the experimental period is presented in Supplementary Fig. 1.

Photosynthetic traits, biomass, yield and harvest index

Leaf photosynthetic traits, including stomatal conductance (g_s, mol m^{-2} s^{-1}), transpiration rate (E, mmol m^{-2} s^{-1}), and net assimilation rate (A, µmol m^{-2} s^{-1}) were measured using an infrared-gas-analyzer (IRGA) (Li-6800, Li-COR Inc., Lincoln, NE, USA). The leaf chamber was maintained at a temperature of 28°C, relative humidity at 64 to 67%, CO_2 concentration of 400 mol mol^{-1}, and the photosynthetic photon-flux density of 1200 mol m^2 s^{-1}. The observations were made between 09:00 and 12:30 h on the flag leaves two days after anthesis. The IWUE was computed by dividing the photosynthetic rate by the transpiration rate (Seibt et al. 2008). After harvest, total biomass accumulation was recorded by drying aboveground parts in a hot-air oven at 60°C to a constant weight. Harvest-Index (HI) [(Economic yield/Biological yield) ×100] was calculated from biomass and total grain yield per plant.

Identification of sensitive and low-P stress-tolerant genotypes was done according to Meena et al. (2021) and Rajamanickam et al. (2024), and the ranking value of the principal component analysis (PCA) was utilized to assess the stress tolerance of genotypes under various P treatments.

Statistical analysis

The current experiment was designed using a completely randomized design (CRD) with two factors: P levels and genotypes. All statistical analyses, including analysis of variance (ANOVA) and descriptive statistics were carried out in R-studio software (version-4.3.0)(R Core Team 2019). Broad-sense heritability (H^2) was estimated using Equation (Hallauer et al. 2010). PCA was performed using package

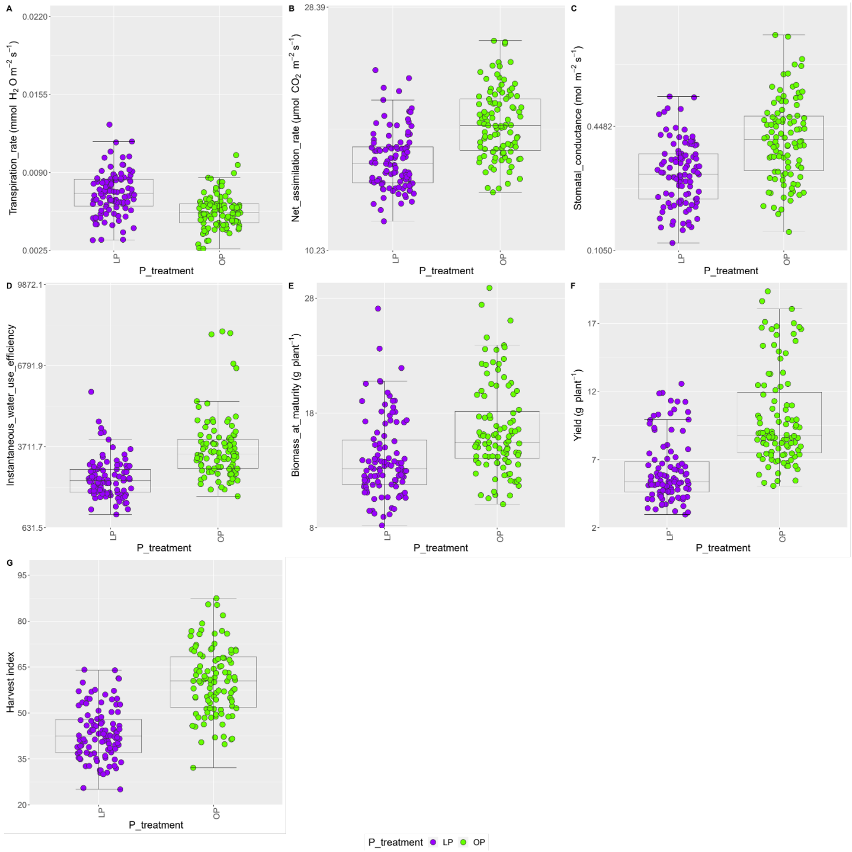

Fig. 1A-G. Jitter plot showing variation in (A) transpiration rate (E), (B) net assimilation rate (A), (C) stomatal conductance (g_s), (D) instantaneous-water use efficiency (IWUE), (E) biomass at maturity, (F) yield, (G) harvest index of 103 wheat accessions. Jitter plots display the median values as the horizontal lines in the centre, the upper and lower quartiles as the length of the box, the minimum and maximum values as the whiskers, and outliers as the filled circle outside of the whiskers. Filled circles represent individual plant and P condition

'factoextra' version-1.0.7. Data visualization for all the traits was performed using package *'ggplot2'* version-3.4.2.

A Shannon-Weaver diversity index (H'), was computed for each trait using the formula H′= (Shannon and Weaver 1950). Dendrogram of agglomerative hierarchical clustering (AHC) was derived using the ward. D method with squared Euclidean distance as the interval measurement on relative values of LP and OP condition of selected six traits with *'factoextra'* version-1.0.7.

Results

Genotypic variation in photosynthetic traits, biomass, yield, and harvest index

Genotypes showed a significant (*P*<0.05) and wide range of variation for all traits including transpiration (E), net assimilation rate (A), stomatal conductance (g_s), instantaneous water use efficiency (IWUE), biomass at maturity stage, and yield except for harvest index (HI) under different P conditions (Table 1). Significant variation among the genotypes under P treatments has been illustrated in Supplementary Table S2 and Figs. 1A-G. A significant decrease was recorded in A (16.4%), g_s (33.1%), IWUE (48.6%), biomass (18%), yield (65.6%), and HI (41%) but the transpiration rate (E) (19%) increased under LP over OP condition. Among genotypes, no significant reduction in net assimilation rate was observed in HP1209 and WH542, whereas highest reduction was observed in DWR162 and PBW746. Likewise, less than 10% reduction in IWUE was found in BWL 5202 and HD 2987 under LP as compared to OP condition. A few genotypes, Kharchia-65-R, UP 301, and HI 1500, showed <10% reduction in biomass, whereas the highest reduction (>38%) was observed in WH542 and DBW17 under LP in comparison to OP treatment. In terms of grain yield, HUW12 and KENPHAD-25 recorded < 35% reduction under LP over OP condition. The HI ranged from 32.1 to 87.5% under OP condition, while under LP condition, it ranged between 43 and 64%. The genotypes DPW 621-50, WH 542, DBW17 and HPW 251 recorded less than 10% reduction in HI under LP in comparison to OP condition.

Principal components analysis (PCA)

In the present study, seven traits were incorporated into the PCA to comprehend the percentage of the overall variation exhibited by these traits. All the principal components (PCs) in OP and LP conditions showed Eigenvalues >1. A total of 63.4% genotypic variations were explained by PC1 (34.9%) and PC2 (28.5%) under OP conditions, while

Table 1. Summary of ANOVA results (*p-value*) and heritability (H^2) for all traits measured under two P conditions and for all 103 accessions.

Trait	Accession	P conditions	Accession x P conditions	Heritability (H^2)
Transpiration rate (E)	$<2e^{-16}$ 0.0001	$<2e^{-16}$ 0.0001	$<2e^{-16}$ 0.0001	0.66
Net assimilation rate (A)	$<2e^{-16}$ 0.0001	$<2e^{-16}$ 0.0001	$3.33e^{-09}$ 0.0001	0.94
Stomatal conductance (g_s)	$<2e^{-16}$ 0.0001	$<2e^{-16}$ 0.0001	$<2e^{-16}$ 0.0001	0.93
Instantaneous-water use efficiency	$<2e^{-16}$ 0.0001	$<2e^{-16}$ 0.0001	$<2e^{-16}$ 0.0001	0.93
Biomass at maturity	$<2e^{-16}$ 0.0001	$5.1e^{-16}$ 0.0001	0.00656 0.001	0.98
Yield	$<2e^{-16}$ 0.0001	$<2e^{-16}$ 0.0001	$3.3e^{-15}$ 0.0001	0.97
Harvest index	$<2e^{-16}$ 0.0001	$<2e^{-16}$ 0.0001	ns 0.249	0.96

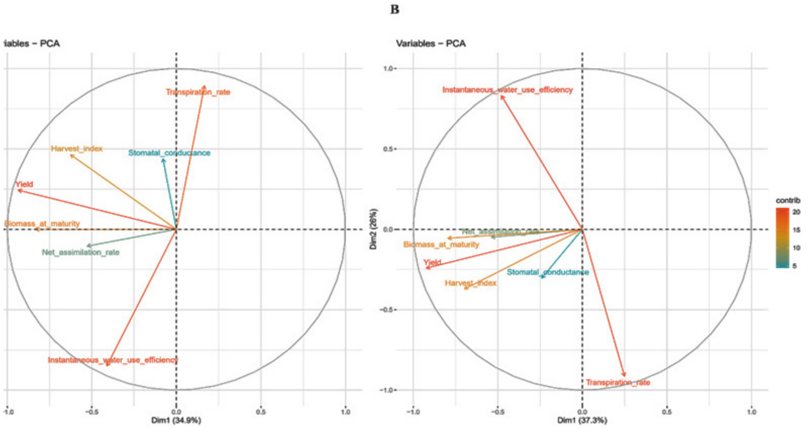

Fig. 2A-B. Two Principal components (PC) analysis displaying contribution among seven traits studied (A) under OP condition, (B) under LP condition. Arrows represent the direction of loadings for each trait and are color-coded based on their contribution to the percentage (%) variation of the component

Table 2. Principal components analysis of seven traits under two P conditions and the proportion of variation of each principal component

Traits	Optimum P		Low P	
	PC1	PC2	PC1	PC2
Transpiration rate	**0.61***	0.12	**0.62**	0.26
Net assimilation rate	-0.19	-0.18	-0.10	-0.22
Stomatal conductance	0.28	-0.19	0.16	-0.23
Instantaneous-water use efficiency	**-0.63**	-0.22	**-0.63**	-0.31
Biomass at maturity	-0.28	**0.46**	-0.32	**0.4**3
Yield	-0.17	**0.62**	-0.27	**0.5**6
Harvest index	0.07	**0.53**	-0.10	**0.4**8
Variation proportion				
Eigen value	2.44	2.00	2.61	1.82
Variance percent	34.85	28.52	37.25	37.25
Cumulative variant percent	34.85	63.37	25.98	63.23
Most contributing traits	Transpiration rate, Instantaneous-water use efficiency, Biomass at maturity, Yield	Biomass at maturity, Yield, Harvest index	Transpiration rate, Instantaneous-water use efficiency, biomass at maturity, yield	Instantaneous-water use efficiency, biomass at maturity, Yield, Harvest index

*For each trait, the large variable loading score appears in bold.

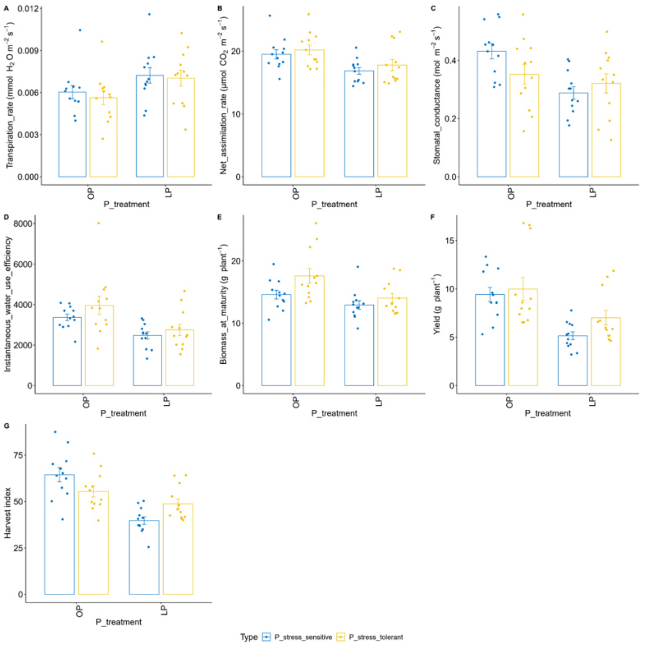

Fig. 3A-G. Bar plot showing phenotypic variation of P stress tolerant and sensitive genotypes under low and optimum P in (A) transpiration rate (E), (B) net assimilation rate (A), (C) stomatal conductance (g_s), (D) instantaneous-water use efficiency (IWUE), (E) biomass at maturity, (F) yield, and (G) harvest index. Bar plot show the mean and error bars indicate standard errors

under LP conditions, it was 37.4 and 26.0% at PC1 and PC2, respectively (Figs. 2A-B). The multivariate PCA analysis revealed that E, IWUE, biomass, yield, and HI were the most contributing traits with higher loading matrix values under LP than OP condition (Table 2). Furthermore, PCA under both conditions demonstrated a high correlation between net assimilation rate, biomass, yield, and HI with a significant negative association between transpiration rate and other traits.

Performance of low P tolerant and low P sensitive genotypes based on PCA rankings

Based on PCA ranking, the genotypes were classified as P stress-tolerant or sensitive. The PCA ranking values for P stress-tolerant genotypes were in the range of 66.7 to 77.5, while P stresses sensitive genotypes had ranking values in the range of 43.7 to 51.0 (Supplementary Table S3). The identified 12 each low P tolerant and low P sensitive genotypes are listed in Table 3. The low P stress tolerant genotypes showed a lesser reduction in the net assimilation rate, g_s, yield, and HI compared to low P stress sensitive genotypes. The low P stress tolerant genotypes showed an average reduction in A (14.6%), g_s(12%), IWUE (43.6%), biomass (24.7%), yield (40%), and HI (13.9%) while an increased E (19.2%). Likewise, the low P stress-sensitive genotypes showed an average reduction in A (15.9%), g_s (54%), IWUE (40%), biomass (13.2%), yield (83.1%), and HI (61.9%), whereas E increased by 16% (Figs. 3A-G).

Table 3. P stress tolerant and P stress sensitive wheat accessions (12 each) based on their response to optimum P and low P treatment conditions

S. No.	P stress tolerant accessions	P stress sensitive accessions
1	PBW621	NARBADA4
2	HUW12	HYB633
3	DPW62150	PBW502
4	WH542	NI917
5	DBW17	GW366
6	HPW251	LOK62
7	IWP72	Kharchia65R
8	KENPHAD25	HI1500
9	NP825	PBW343
10	DBW107	HI1544
11	K8027	K68
12	VL907	RAJ4102

These accessions were identified based on the principal component analysis ranking using loading scores from relative values under-treated conditions. The ranking values are presented in Supplementary Table S2.

Cluster analysis and Shannon-Weaver diversity index (H')

Hierarchical clustering revealed four distinct groups of genotypes based on the relative values of all traits except E. Out of 103 genotypes, four were grouped under cluster I, 26 in cluster II, 33 belonged to cluster III, and 40 genotypes were grouped in cluster IV (Fig. 4). The clusters I and II comprised of LP stress tolerant genotypes. In contrast, all the LP stress-sensitive genotypes fall under cluster III and IV (Fig. 4). Cluster I showed a significant reduction in net assimilation rate, gs, IWUE, biomass, yield, HI but an increase in E. In contrast, all these traits were increased in cluster II, including E. Genotypes belonging to cluster III exhibited a higher percent reduction in the net assimilation rate (21%), g_s (26%), IWUE (58%), biomass (21%), yield (75%), and HI (44%) but an increased E (22%). Likewise, Cluster IV genotypes showed a reduction in net assimilation rate, g_s, IWUE, biomass, yield, HI by 10.7, 42, 35.57, 14.18, 72.8, and 50.64%, respectively. The H-values for the traits under study were found distinct and ranged from 0.61 to 0.86 under OP, whereas 0.62 to 0.86 under LP conditions. Under OP condition, the rate of transpiration and net assimilation showed higher H'-values, whereas under LP condition, HI, and g_s showed higher H'-values (Table 4).

Discussion

The diverse bread wheat genotypes exhibited a varied response to P levels. A drastic reduction in A (16.4%), g_s (33%), IWUE (48.6%), biomass (18%), yield (66%) and HI (41%) was noted, while transpiration rate increased under LP condition. Previous studies have demonstrated that P deficiency

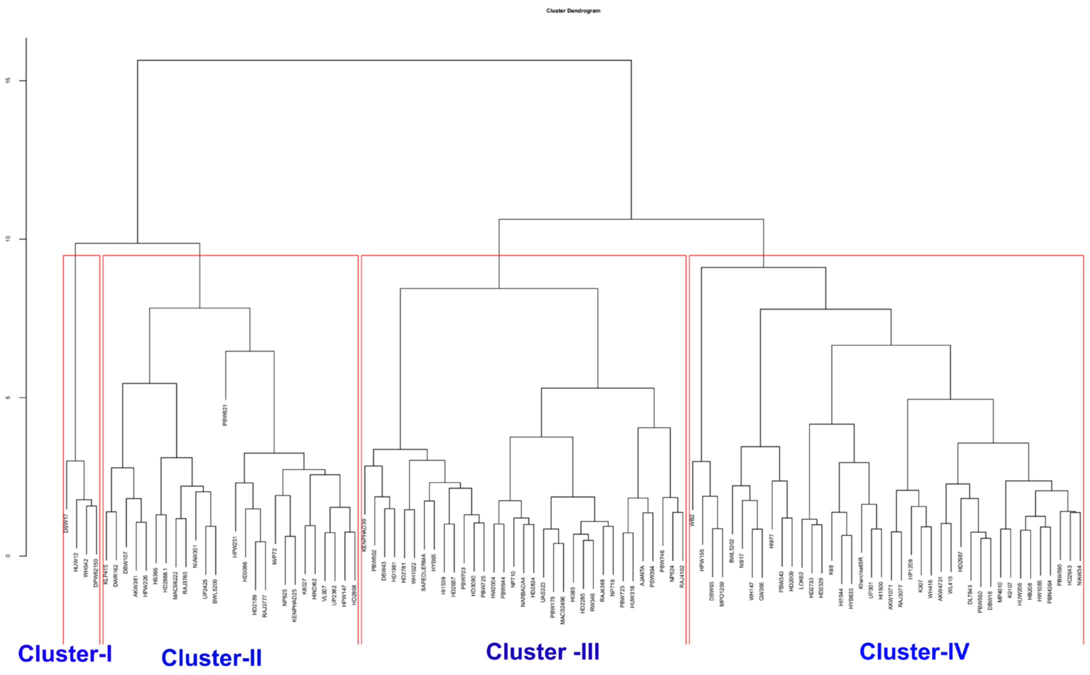

Fig. 4. Clustering of 103 Indian bread wheat accessions/genotypes by Ward's method using squared Euclidean distance matrix of relative values of net assimilation rate, stomatal conductance, instantaneous-water use efficiency, biomass, yield, and harvest index. Plants were grown in low and optimum soil P conditions

Table 4. The Shannon-Weaver diversity index (H') and performance categories under two P conditions

Traits	P treatment	103 wheat accessions			
		Low	Medium	High	H'
Transpiration rate (E)	Optimum P	18	70	15	0.85
	Low P	17	73	13	0.79
Net assimilation rate (A)	Optimum P	17	69	17	0.86
	Low P	13	74	16	0.80
Stomatal conductance (g_s)	Optimum P	17	71	15	0.83
	Low P	18	68	17	0.88
Instantaneous-water use efficiency (IWUE)	Optimum P	10	84	9	0.61
	Low P	8	83	12	0.62
Biomass at maturity	Optimum P	13	72	18	0.82
	Low P	9	77	17	0.73
Yield	Optimum P	10	75	18	0.76
	Low P	9	76	18	0.74
Harvest Index	Optimum P	17	71	15	0.83
	Low P	14	69	20	0.86

limits leaf photosynthetic capacity (Vengavasi and Pandey 2018; Meena et al. 2020, 2021), which is primarily due to the closure of stomata induced by abscisic acid (ABA) (Malini et al. 2023). The P-starvation lowers the Pi-concentration in the chloroplast stroma, which impairs the action of ATP-synthase and causes lumen acidification. This process inevitably hampers linear electron (e^-) transport (Carstensen et al. 2018). Low P-induced gas exchange traits were reported in chickpeas, mungbeans, and soybeans (Pang et al. 2018, Vengavasi and Pandey 2018; Meena et al. 2020). Higher P content in plants improves IWUE by maintaining g_s and regulating the reduction in photosynthetic rate per unit of transpired water (Singh et al. 2000; Jones et al. 2005; Meena et al. 2020, 2021). In the present study, LP conditions significantly impaired the accumulation of biomass and yield. A similar decline in shoot dry matter production was noted in mungbean (Pandey et al. 2014; Reddy et al. 2020; Meena et al. 2021), soybean (Krishnapriya and Pandey 2016), wheat and triticale (*Triticosecale*) (Soumya et al. 2021) under low P.

The H′ indicated phenotypic diversity whereas lower H′ value indicates an imbalanced frequency distribution and a lack of trait diversity (Reddy et al. 2020), while higher H′ values signify greater genetic diversity in traits (Aski et al. 2021). The transpiration and net assimilation rates showed higher H′ values under OP condition, whereas HI and g_s recorded higher H′-value under LP condition, indicating that P levels highly influence these traits. Multivariate PCA analysis revealed net assimilation rate, biomass, yield, and HI as highly contributing traits to genotypic variation under both P conditions. The genotypes grouped under Cluster I and II were better performing as it showed lesser reduction under low P in all the measured traits as compared to cluster III and IV. Low P stress tolerant genotypes showed relatively less reduction in net assimilation rate, g_s, yield, HI. Besides this, hierarchical cluster analysis also revealed genotypes PBW 621, HUW12, DPW 621-50, WH 542, DBW 17, HPW 251, IWP 72, KENPHAD 25, NP 825, DBW107, K 8027, and VL 907 as P-stress tolerant. The findings will be valuable for comprehending photosynthesis-related characteristics, yield, and biomass under various P conditions. Net assimilation rate, biomass, IWUE, yield, and HI are significant contributing traits that can be employed as physiological markers for assessing the germplasm under low P stress conditions. The low P stress-tolerant wheat genotypes identified in this study may be suitable for cultivation in low-fertility soils or used as genetic stocks for developing P-efficient cultivars.

Author's contribution

Conceptualization of research (RP); Designing of the experiments (RP, VR); Contribution of experimental materials (RP); Execution of field/lab experiments and data collection (VR); Analysis of data and interpretation (VR); Preparation of the manuscript (VR, KV, RP, AT).

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