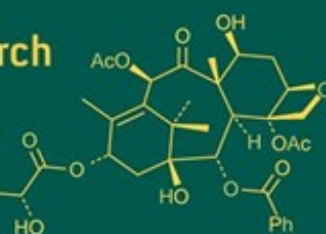
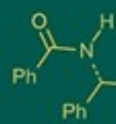


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Shaurya Singh

Department of Genetics and Plant Breeding, College of Agriculture, G.B. Pant University of Agriculture and Technology, Pantnagar, Uttarakhand, India

JP Jaiswal

Department of Genetics and Plant Breeding, College of Agriculture, G.B. Pant University of Agriculture and Technology, Pantnagar, Uttarakhand, India

Mitali Tiwari

Department of Genetics and Plant Breeding, College of Agriculture, G.B. Pant University of Agriculture and Technology, Pantnagar, Uttarakhand, India

Amit Kumar Singh

Division of Genomic Resources, ICAR-National Bureau of Plant Genetic Resources, New Delhi, Delhi, India

Genetic divergence and path coefficient analysis in indigenous wheat (*Triticum aestivum* L.) germplasm

Shaurya Singh¹, JP Jaiswal², Mitali Tiwari³, Amit Kumar Singh⁴

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ABSTRACT

Correlation analysis describes associations among traits but does not distinguish their direct and indirect relationships with grain yield or identify phenotypically divergent groups within a germplasm collection. The present study therefore evaluated two hundred indigenous bread wheat (*Triticum aestivum* L.) accessions using path coefficient analysis and Mahalanobis D^2 -based clustering of fifteen agro-morphological and phenological traits. Path coefficients were estimated from the correlation matrix, with grain yield per plot as the dependent variable. Biological yield (direct effect = 1.163) and harvest index (0.634) exhibited the largest estimated direct effects on grain yield, with a residual path coefficient of 0.223. Despite its positive direct effect, harvest index showed a weak negative correlation with grain yield ($r = -0.053$), largely due to its negative indirect association through biological yield. Similarly, thousand-grain weight and grains per spike showed positive correlations with grain yield ($r = 0.232$ and 0.200 , respectively), despite negligible direct effects, with substantial indirect effects through harvest index. Mahalanobis D^2 analysis followed by Ward's minimum-variance clustering grouped the accessions into eight phenotypically divergent clusters ranging from 5 to 61 accessions. The contribution of individual traits to divergence ranged from 4.7 to 9.0%, indicating that multivariate divergence was distributed across the trait set rather than being dominated by a few characters. The maximum inter-cluster distance was observed between clusters 1 and 6 ($D^2 = 53.85$). These clusters exhibited contrasting phenotypic profiles, with cluster 1 characterized by tall stature, high biological yield and grain yield, whereas cluster 6 exhibited shorter stature, lower biomass and grain yield, but higher harvest index. The contrasting accessions identified from these clusters may serve as candidate parents for subsequent crossing and evaluation for complementary variation in biomass production and partitioning efficiency.

Keywords: *Triticum aestivum*, Landrace, Path coefficient analysis, Genetic divergence, Mahalanobis D^2 , Ward's clustering

Introduction

Bread wheat (*Triticum aestivum* L.) is a major staple crop contributing substantially to global food and nutritional security, and further improvement in grain yield requires the effective exploitation of available genetic variability and a better understanding of the traits underlying yield formation (Shiferaw *et al.*, 2013) [1]. Intensive selection and repeated use of a relatively narrow set of elite parents during modern wheat breeding have contributed to a reduction in the genetic diversity available within cultivated germplasm (Cavanagh *et al.*, 2013) [2]. In contrast, indigenous landraces represent valuable reservoirs of adaptive and agronomically important variation accumulated through long-term selection under diverse environments and farmer-managed production systems (Lopes *et al.*, 2015) [3]. In a previous study, two hundred indigenous Indian bread wheat accessions were shown to possess substantial phenotypic variability for fifteen agro-morphological and phenological traits, along with significant associations between several traits and grain yield per plot (Singh *et al.*, 2026) [4]. However, correlation coefficients alone do not distinguish the direct association of a trait with grain yield from its indirect associations mediated through other interrelated traits, potentially leading to misleading interpretations of the relative importance of yield-associated characters. Path coefficient analysis provides a useful extension of correlation analysis by partitioning the observed correlation between each component trait and grain yield into direct and indirect effects through other traits (Dewey *et al.*, 1959) [5]. Thus, path analysis can provide a more informative basis for identifying traits that are closely associated with yield and may be considered in selection strategies for improving grain yield in diverse wheat germplasm.

Another limitation of correlation and variability data is that neither indicates which accessions in a collection are sufficiently distinct from one another to serve as useful crossing parents; two accessions can occupy opposite ends of a trait distribution and still be closely related overall, or vice versa. Mahalanobis' generalised distance, D^2 (Mahalanobis, 1936) [6], addresses this directly by quantifying multivariate genetic distance across the full trait set simultaneously, and grouping accessions by that distance is a standard tool for identifying

Corresponding Author:**JP Jaiswal**

Department of Genetics and Plant Breeding, College of Agriculture, G.B. Pant University of Agriculture and Technology, Pantnagar, Uttarakhand, India

fying divergent parental combinations in wheat breeding programmes (Singh *et al.*, 1985) [7]. The present study applies both methods to the same panel and trait set already characterised phenotypically, in order to identify which component traits are the true direct determinants of grain yield in this germplasm and to resolve the collection into genetically divergent groups from which crossing parents can be chosen.

Materials and Methods

Plant material and phenotypic data

The panel comprised two hundred indigenous bread wheat accessions obtained from the ICAR-National Bureau of Plant Genetic Resources, New Delhi, evaluated over two rabi seasons in an augmented block design (Singh *et al.*, 2026) [4]. Best linear unbiased predictions (BLUPs) for the same fifteen agro-morphological and phenological traits reported in that study were used for the analyses for following traits i.e days to heading, days to maturity, grain filling duration, days to flowering, plant height, peduncle length, spike length, spikelets per spike, leaf length, leaf breadth, grains per spike, thousand-grain weight, grain yield per plot, biological yield and harvest index.

Genetic divergence and clustering

Mahalanobis generalized distance (D^2) was calculated between all pairs of the 200 wheat accessions using the fifteen agro-morphological and phenological traits. The distance matrix was calculated using the inverse of the pooled covariance matrix of the standardized trait data, following Mahalanobis (1936) [6]. The accessions were subsequently grouped using Ward's minimum-variance hierarchical clustering method (Ward, 1963) [8]. To ensure consistency between the clustering criterion and Mahalanobis distance, the trait matrix was transformed using the Cholesky decomposition of the inverse covariance matrix before applying Ward's clustering procedure. The number of clusters was determined from the resulting dendrogram, with the dendrogram cut to obtain eight clusters. The mean intra-cluster D^2 was calculated from all pairwise distances among accessions within each cluster, whereas mean inter-cluster D^2 was calculated from all pairwise distances between accessions belonging to different clusters. The relative contribution of individual traits to multivariate divergence was estimated following Singh *et al.* (1985) [7]. For each pair of accessions, the trait associated with the largest standardized squared difference was identified, and the contribution of each trait was expressed as the percentage of the total number of accession pairs for which that trait had the largest contribution. With 200 accessions, a total of 19,900 unique accession pairs were considered. Because several traits were correlated, particularly days to heading with days to flowering and days to maturity with grain-filling duration, the correla-

tion and covariance matrices were examined for numerical conditioning before distance and clustering analyses. These interrelationships were considered when interpreting the resulting multivariate distances and cluster structure. Canonical discriminant analysis (CDA) was subsequently performed on the standardized trait data using the Ward-derived clusters as predefined grouping variables. The analysis was used to visualize the multivariate separation among the predefined clusters through canonical axes obtained from the between-cluster and within-cluster covariance structures. CDA was therefore used as a descriptive visualization of cluster separation rather than as an independent validation of the Ward clustering.

Path coefficient analysis

Path coefficient analysis was performed using the Pearson correlation matrix reported in the companion study, following the matrix approach described by Dewey *et al.* (1959) [5] and Singh *et al.* (1985) [7]. Grain yield per plot was considered the dependent variable, while the remaining fourteen agro-morphological and phenological traits were included as explanatory variables. The vector of direct path coefficients (b) was estimated by solving the simultaneous equations $b = R^{-1}r$, where R represents the 14×14 correlation matrix among the explanatory traits and r represents the vector of their correlations with grain yield per plot. Indirect effects of trait i via trait j were calculated as the product of the direct effect of j and the simple correlation between i and j . The residual (unexplained) path coefficient was calculated as the square root of one minus the sum of the products of each direct effect and its corresponding correlation with yield.

Results

Genetic divergence and clustering

Ward's clustering of the two hundred accessions on Mahalanobis distance resolved the panel into eight groups ranging from five to sixty-one accessions (Fig. 1, Table 1). Intra-cluster D^2 values (19.58 to 28.96) were lower than every inter-cluster value for the corresponding cluster in all eight cases, confirming that the grouping captured genuine multivariate structure rather than an arbitrary partition. The maximum inter-cluster distance was between clusters 1 and 6 ($D^2 = 53.85$), and the minimum between clusters 2 and 5 ($D^2 = 26.80$). Canonical discriminant analysis of the same clusters (Fig. 3) supported this grouping: the first two canonical axes, accounting for 27.3 and 19.5 per cent of total discriminant power respectively, cleanly separated clusters 1, 4 and 6 from the remainder of the panel, while clusters 2, 3, 5, 7 and 8 continued to overlap substantially, consistent with a full separation that depends on more than two of the seven possible discriminant dimensions.

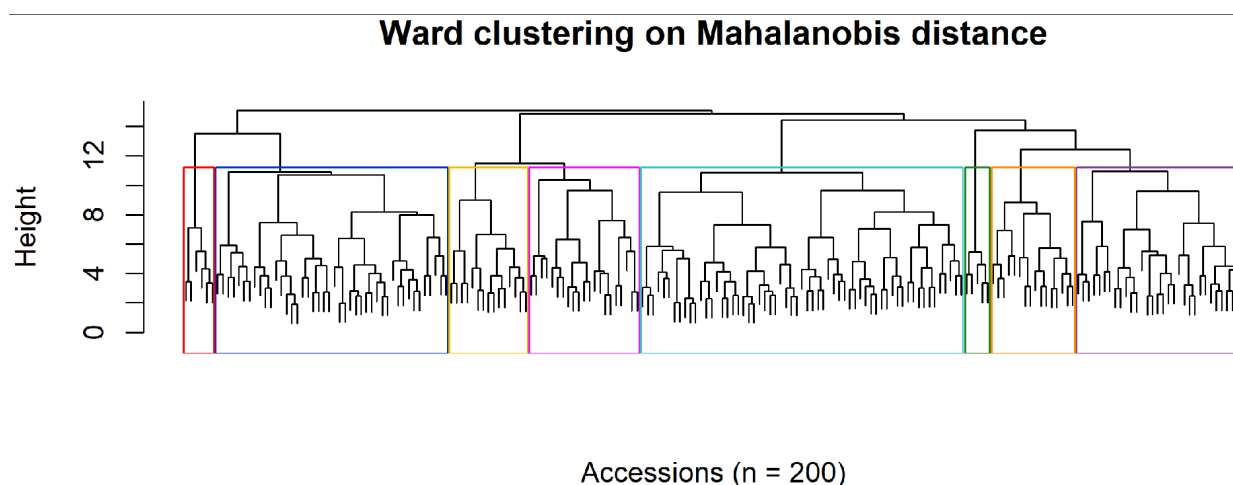


Figure 1. Dendrogram of 200 accessions from Ward's minimum-variance clustering of Mahalanobis distance across fifteen agro-morphological traits, cut at eight clusters (coloured boxes)

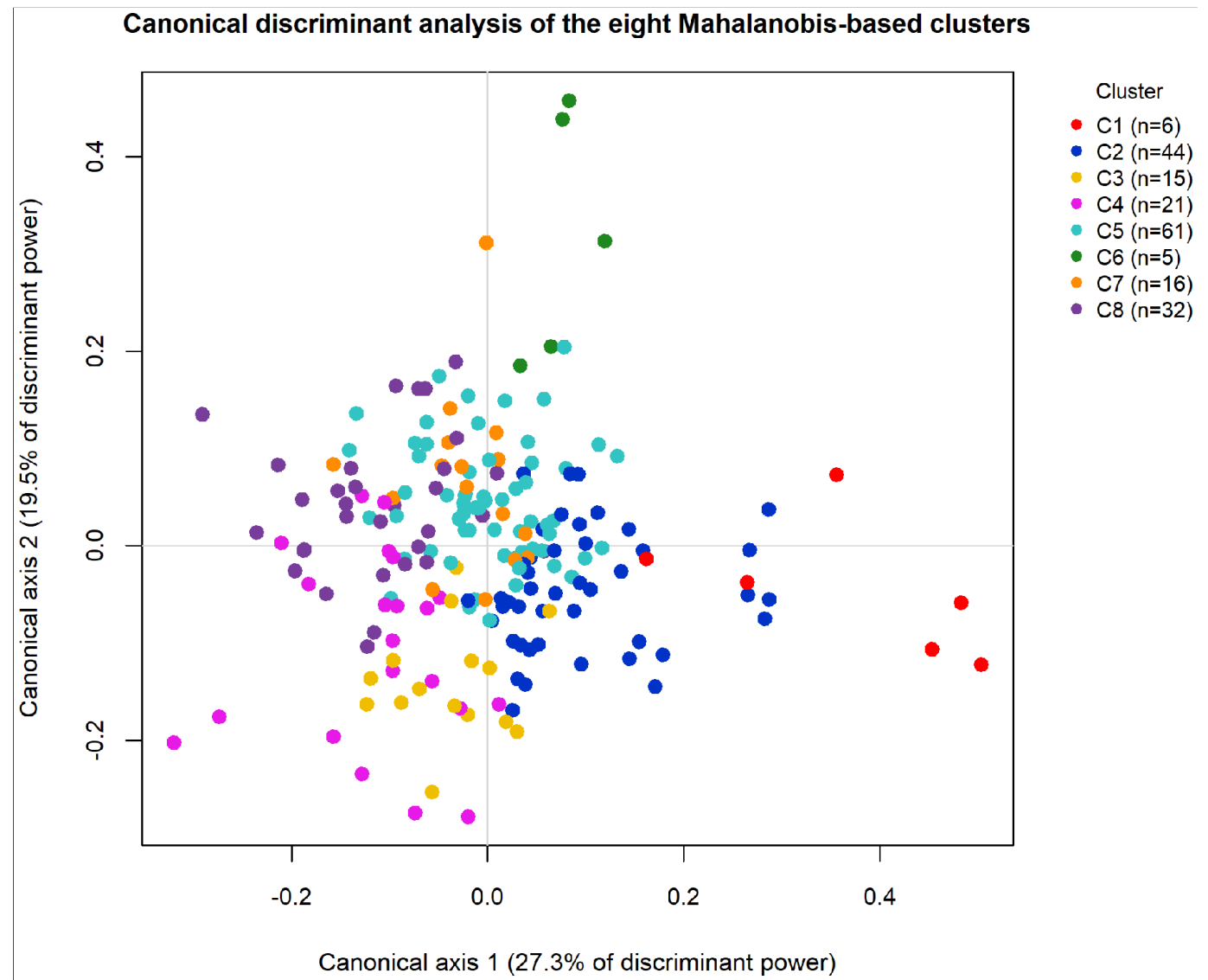


Figure 2. Canonical discriminant analysis of the eight Ward/Mahalanobis clusters across the fifteen standardised traits, showing the two axes that best separate the clusters. Unlike an unsupervised PCA, this projection is constructed using the cluster assignments themselves

Table 1. Intra-cluster (diagonal) and inter-cluster (off-diagonal) mean Mahalanobis D^2 values among eight clusters resolved by Ward's method

	C1 (n = 6)	C2 (n = 44)	C3 (n = 15)	C4 (n = 21)	C5 (n = 61)	C6 (n = 5)	C7 (n = 16)	C8 (n = 32)
C1	24.52	39.60	45.18	46.11	40.05	53.85	45.16	45.22
C2	39.60	24.85	29.09	33.44	26.80	42.53	32.00	29.73
C3	45.18	29.09	22.09	31.61	28.42	44.48	32.67	31.78
C4	46.11	33.44	31.61	28.96	30.79	47.43	35.61	32.95
C5	40.05	26.80	28.42	30.79	21.84	39.93	30.20	27.71
C6	53.85	42.53	44.48	47.43	39.93	19.58	41.39	43.31
C7	45.16	32.00	32.67	35.61	30.20	41.39	27.23	32.21
C8	45.22	29.73	31.78	32.95	27.71	43.31	32.21	25.18

Contribution to total divergence was distributed relatively evenly across the fifteen traits, ranging from 4.74 per cent (days to maturity) to 8.97 per cent (leaf breadth), with no single trait accounting for a disproportionate share (Table 2). This even spread is consistent with the six largely independent, none-dominant principal components already reported for morphological variation in this panel (Singh *et al.*, 2026) [4], and indicates that genetic divergence in the collection is multidimensional rather than driven by variation in one or two characters.

Table 2. Percentage contribution of each trait to total genetic divergence among 200 accessions

Trait	Contribution (%)
Leaf breadth	8.97
Leaf length	8.30
Thousand grain weight	8.19
Spike length	7.09
Peduncle length	7.04
Harvest index	6.92
Days to heading	6.82
Biological yield	6.73
Grain filling duration	6.33
Plant height	6.22
Grains per spike	6.11
Days to flowering	5.93
Spikelets per spike	5.64
Grain yield per plot	4.95
Days to maturity	4.74

The eight clusters differed appreciably in mean performance (Table 3). Cluster 1, the smallest at six accessions, combined the tallest plants among the higher-yielding groups with by far the highest mean biological yield (2.86 kg/plot) and the highest mean grain yield (0.88 kg/plot) in the panel, despite carrying the lowest mean harvest index (32.89 per cent). It included three of the five highest-yielding individual accessions in the whole panel (IC 1802, IC 1895 and IC 1048). Cluster 6, the cluster most distant from cluster 1, comprised

five short-statured accessions (mean plant height 75.5 cm, some 44 cm shorter than cluster 1) with the lowest mean biological yield (0.44 kg/plot) and grain yield (0.23 kg/plot) in the panel, but the highest mean harvest index (49.95 per cent) and among the highest thousand-grain weights. The contrast between these two clusters reproduces, at the level of genetically distinct groups, the same biomass-partitioning trade-off identified independently by the path coefficient analysis above.

Table 3. Mean values for key traits across the eight clusters resolved by Ward's method

Cluster	n	Grain yield(kg/plot)	Biological yield (kg/plot)	Harvest index (%)	Plant height (cm)	1000-grain wt (g)	Days to maturity
C1	6	0.88	2.86	32.89	119.25	36.53	124.91
C ₂	44	0.63	1.62	40.88	105.20	41.64	124.33
C3	15	0.54	1.21	44.82	117.13	43.14	123.33
C ₄	21	0.46	1.26	37.45	130.44	39.58	124.91
C ₅	61	0.54	1.28	42.61	106.34	36.59	129.03
C ₆	5	0.23	0.44	49.95	75.49	44.73	128.47
C7	16	0.50	1.13	45.03	98.90	39.29	120.49
C8	32	0.45	1.20	38.59	110.26	33.98	123.26

Path coefficient analysis

Biological yield and harvest index exhibited the largest estimated direct path coefficients for grain yield per plot, with values of 1.163 and 0.634, respectively (Fig. 2; Table 4). The residual path coefficient was 0.223, indicating that the traits included in the path model collectively accounted for a substantial proportion of the variation associated with grain yield. Biological yield showed a strong positive correlation with grain yield ($r = 0.824$) and a large positive direct path coefficient

(1.163), indicating that its association with grain yield was predominantly represented by its direct component in the fitted path model. In contrast, harvest index exhibited a small negative correlation with grain yield ($r = -0.053$) despite its positive direct path coefficient (0.634). This discrepancy was primarily associated with a substantial negative indirect effect through biological yield (-0.668), consistent with the negative correlation observed between biological yield and harvest index ($r = -0.574$) in the companion study.

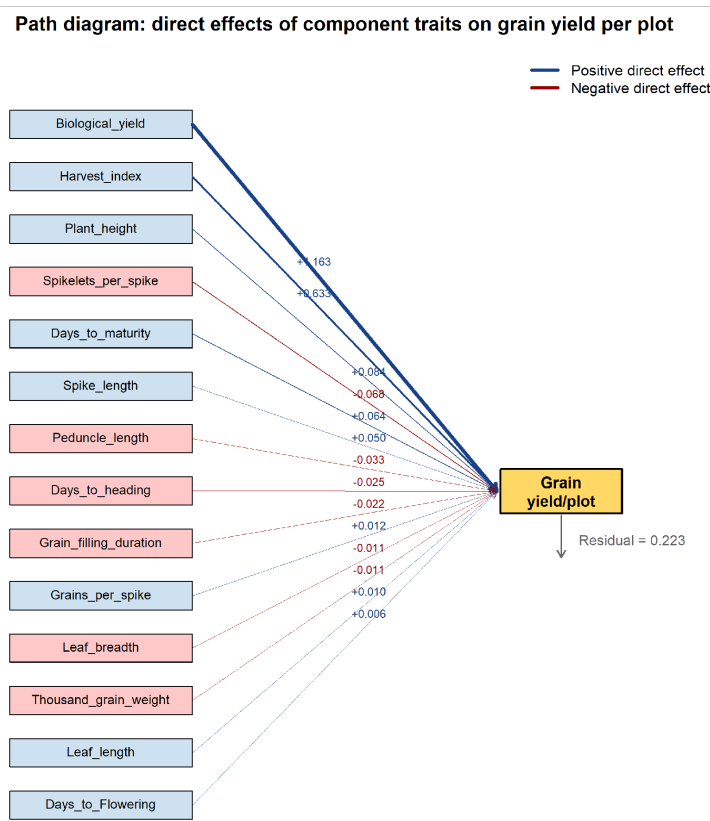


Figure 2. Path diagram showing the direct effect of each of the fourteen component traits on grain yield per plot. Arrow width is proportional to the magnitude of the direct effect; blue arrows are positive while, red arrows are negative

Table 4. Direct effects (path coefficients) of fourteen component traits on grain yield per plot, ranked by magnitude, with their simple phenotypic correlation with yield. Residual effect = 0.223. ** significant at $p < 0.01$ (from the companion correlation study)

Trait	Direct effect	r with yield
Biological yield	1.163	0.824**
Harvest index	0.634	-0.053
Plant height	0.084	0.196**
Spikelets per spike	-0.068	0.065
Days to maturity	0.064	0.133
Spike length	0.050	0.124
Peduncle length	-0.033	-0.035
Days to heading	-0.025	-0.008
Grain filling duration	-0.022	0.127
Grains per spike	0.012	0.200**
Leaf breadth	-0.011	-0.013
Thousand grain weight	-0.011	0.232**
Leaf length	0.011	-0.016
Days to flowering	0.007	0.042

A comparable pattern of correlation masking a genuine underlying effect was evident for thousand-grain weight and grains per spike. Both showed appreciable positive correlations with yield ($r = 0.232$ and 0.200) but negligible direct effects of their own (-0.011 and 0.012); in each case, the correlation with yield was carried almost entirely by an indirect pathway through harvest index (0.245 and 0.122 respectively), rather than by any direct contribution to yield formation. Plant height and spike length showed the converse relationship to biological yield, their moderate positive correlations with yield ($r = 0.196$ and 0.124) arising mainly through indirect effects transmitted via biological yield (0.330 and 0.106) rather than through direct effects, which were small in both cases (0.084 and 0.050).

Discussion

The relatively even contribution of the fifteen traits to multivariate phenotypic divergence, with individual traits accounting for approximately 4.7-9.0% of the pairwise divergence assignments, indicates that differentiation among the evaluated accessions was distributed across multiple agro-morphological and phenological attributes rather than being dominated by a single trait. This pattern differs from some wheat divergence studies in which phenology- or grain-related traits contributed more prominently to overall differentiation (Reddy *et al.*, 2022) [9]. Similarly, studies based on more uniform or selected wheat materials have reported substantial variation captured by a relatively small number of major multivariate axes (Khalid *et al.*, 2023; Siddique *et al.*, 2023) [10, 11]. The identification of eight clusters in the present study is also broadly comparable with previous reports of multiple divergent groups in Indian wheat germplasm based on agro-

morphological traits (Kumar *et al.*, 2013; Pandey *et al.*, 2017) [12, 13]. However, because the present clusters were derived from the same phenotypic trait set and the number of clusters was selected from the dendrogram, the eight-cluster structure should be interpreted as a useful representation of the multivariate phenotypic structure rather than definitive evidence of genetically distinct groups. The earlier observation that variation in this panel was distributed across several principal components (Singh *et al.*, 2026) [4] further supports the multidimensional nature of phenotypic variation. Collectively, these findings indicate that consideration of multiple traits may provide a more informative basis for identifying contrasting accessions than reliance on any single morphological or phenological character.

The phenotypic contrast between clusters 1 and 6, which showed the maximum inter-cluster Mahalanobis distance, provides a useful basis for interpreting the multivariate structure of the evaluated germplasm. Cluster 1 was characterized by tall stature, high biological yield and high grain yield, whereas cluster 6 comprised shorter accessions with lower biomass and grain yield but higher harvest index. This contrast corresponds to the tall, high-biomass versus short, high-partitioning phenotypic pattern previously described for this panel (Singh *et al.*, 2026) [4]. The contrasting profiles also illustrate the opposing relationships among biomass production, grain yield and harvest index observed in the present analyses. However, the path coefficients should be interpreted as statistical direct and indirect effects rather than as evidence of a causal mechanism, particularly because biological yield, harvest index and grain yield are mathematically interrelated.

Accessions from clusters 1 and 6, including the high-yielding cluster 1 accessions IC 1802, IC 1895 and IC 1048 and the high-harvest-index cluster 6 accessions such as IC 1765 and IC 2118, may therefore provide contrasting parental material for subsequent crossing and evaluation. Their phenotypic divergence suggests the possibility of generating progeny with complementary variation for biomass production and biomass partitioning; however, the occurrence of transgressive segregation cannot be inferred from Mahalanobis distance alone and would require evaluation of segregating progeny. The use of maximum inter-cluster distance as one criterion for identifying contrasting parents is consistent with previous divergence studies in indigenous Indian wheat germplasm (Yadav, 2014) [14], but parental selection should also consider agronomic adaptation, target traits, disease resistance, flowering and maturity, and combining ability where appropriate.

The large estimated direct path coefficients for biological yield and harvest index are broadly consistent with previous path coefficient studies in bread wheat, in which biomass production and biomass partitioning have frequently shown strong associations with grain yield (Ayer *et al.*, 2017 [15]; Dutamo *et al.*, 2015 [16]; Devesh *et al.*, 2021 [17]; Singh *et al.*, 2022 [18]; Abdurazek *et al.*, 2024) [19]. Similar relationships have also been reported under semi-arid conditions (Fellahi *et al.*, 2013) [20] and in wheat germplasm evaluated under north-western Himalayan environments (Sharma *et al.*, 2025) [21]. From a physiological perspective, grain yield is closely related to both biomass production and the proportion of assimilated biomass allocated to grain, and these processes are therefore important components of yield formation in wheat (Reynolds *et al.*, 2009; Foulkes *et al.*, 2011) [22, 23]. In the present study, the contrast between the correlation and path coefficient of harvest index illustrates the influence of indirect associations among yield-related traits. Although harvest index showed a weak negative correlation with grain yield ($r = -0.053$), it had a positive estimated direct path coefficient (0.634), while its indirect effect through biological yield was strongly negative (-0.668). Thus, the near-zero correlation between harvest index and grain yield resulted from opposing direct and indirect components in the fitted path model. This finding demonstrates that correlation coefficients alone may not fully describe the relationships among interrelated yield-associated traits. However, because harvest index is mathematically derived from grain yield and biological yield, its direct path coefficient should be interpreted cautiously and should not be consid-

ered independent evidence of a causal effect on grain yield. Consequently, the present results support the consideration of biomass production and partitioning traits in wheat yield studies, but further validation using independent selection experiments or appropriate multivariate models would be required before assigning selection weights to individual traits.

Several methodological considerations should be taken into account when interpreting these findings. First, several traits included in the analyses were moderately to strongly correlated, particularly the phenological traits, while the mathematical relationship among biological yield, harvest index and grain yield introduces an additional source of dependence. Such relationships can affect the stability and interpretation of individual path coefficients and should therefore be considered when assigning biological importance to specific traits. Second, the divergence analysis was based on accession-level BLUPs rather than raw plot-level observations and did not explicitly propagate the estimation uncertainty associated with the BLUPs into the distance estimates. Consequently, the resulting Mahalanobis distances represent divergence among the estimated phenotypic performance of accessions rather than direct estimates of molecular or genetic distance.

Taken together, the path coefficient and multivariate divergence analyses provide complementary information on yield-associated traits and phenotypic differentiation among the evaluated accessions. The results highlight contrasting groups with differences in biomass production and partitioning efficiency and identify accessions that could be considered for subsequent crossing experiments. Nevertheless, confirmation of the breeding value of these parental combinations will require evaluation of their progeny and, ideally, integration with molecular genetic information and combining-ability analysis.

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Conflict of interest

The authors declare that they have no conflict of interest.

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