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Phenotypic diversity and agro-morphological characterization of a global durum wheat (Triticum durum Desf.) panel using standardized morphological descriptors

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Abstract

Durum wheat (*Triticum durum* Desf.) genetic improvement depends on the effective utilization of diverse germplasm conserved in international genebanks. Comprehensive phenotypic characterization of these resources is essential for identifying novel variation and broadening the genetic base of breeding programmes. In the present study, 708 globally diverse durum wheat accessions from the International Center for Agricultural Research in the Dry Areas (ICARDA) Global Durum Panel (GDP) were evaluated over two consecutive cropping seasons (2019–2020) under field conditions in central India using 15 standardized agro-morphological descriptors comprising 10 qualitative and 5 quantitative traits. Significant ($P < 0.01$) genotypic variation was observed for all quantitative traits, indicating substantial phenotypic diversity within the panel. Broad-sense heritability was high for days to heading (0.76), plant height (0.85), and grain yield (0.74), demonstrating strong genetic control of these traits. Grain yield showed a strong negative correlation with days to heading ($r = -0.80$) and moderate positive association with thousand-grain weight ($r = 0.46$), suggesting that earlier maturity combined with heavier grains contributed to improved productivity. Cluster analysis classified the accessions into six distinct phenotypic groups, revealing considerable divergence for maturity, plant architecture, and yield-related traits. Germplasm originating from Africa and Europe exhibited the greatest phenotypic diversity, whereas superior yielding accessions were identified across multiple geographical regions, emphasizing the value of accession-level rather than regional selection. Qualitative descriptors further revealed extensive variation in plant growth habit, flag leaf characteristics, grain morphology, and pigmentation, reflecting the broad evolutionary and breeding history represented within the GDP. The observed diversity demonstrates that the Global Durum Panel constitutes an invaluable resource for parent selection, pre-breeding, and climate-resilient durum wheat improvement. The comprehensive phenotypic dataset generated in this study provides an important foundation for integrating genomic information, genome-wide association studies, and marker-assisted breeding to accelerate the genetic improvement and conservation of global durum wheat genetic resources.

Introduction

Durum wheat (*Triticum durum* Desf.) is the second most widely cultivated wheat species after bread wheat, occupying approximately 13–17 million ha worldwide and producing over 35 million tonnes annually. It is the principal raw material for pasta, couscous, bulgur, semolina, and numerous traditional foods, particularly across the Mediterranean Basin, West Asia, North Africa, Europe, North and South America, and South Asia (Royo et al. 2021; Reynolds et al. 2022; FAO 2024). Besides its economic importance, durum wheat is valued for its high protein content, gluten quality, carotenoid pigments, dietary fibre, and essential micronutrients, making it an important contributor to food and nutritional security (Ficco et al. 2014; Royo et al. 2021).

The sustainability of durum wheat production increasingly depends on the effective conservation and utilization of plant genetic resources. Modern breeding programmes face major challenges from recurrent drought, terminal heat stress, emerging diseases, and increasing climatic variability, while

decades of intensive selection have narrowed the genetic base of elite cultivars (Maccaferri et al. 2019; Khoury et al. 2022). Consequently, broadening the genetic diversity available to breeding programmes has become a priority for improving adaptation, productivity, grain quality, and resilience under changing environments (Reynolds et al. 2022; CGIAR 2024).

Plant genetic resources conserved in national and international genebanks provide an invaluable reservoir of allelic diversity for crop improvement. These collections include landraces, obsolete cultivars, breeding lines, and wild relatives that represent the evolutionary history and geographical adaptation of a species. Their systematic characterization facilitates the identification of unique germplasm, supports the development of representative core collections, improves genebank management, and enhances the efficient utilization of genetic resources in breeding programmes (Khoury et al. 2022; FAO 2024; ICARDA 2025).

Phenotypic characterization remains a fundamental component of germplasm evaluation. Standardized agro-morphological descriptors enable the assessment of diversity, classification of accessions, identification of distinct phenotypes, and selection of genetically diverse parents for crop improvement. Although genomic tools have greatly accelerated diversity analyses, phenotypic evaluation continues to provide essential information on the expression of agronomically important traits under field conditions and complements molecular characterization for germplasm utilization (Maccaferri et al. 2019; Reynolds et al. 2022; ICARDA 2025).

Previous studies have demonstrated substantial phenotypic and genetic diversity in durum wheat using morphological and molecular approaches (Nazco et al. 2012; Soriano et al. 2018; Maccaferri et al. 2019; Royo et al. 2021). However, many investigations have been restricted to regional collections or relatively small germplasm panels, limiting the representation of the global diversity available for breeding. Comprehensive characterization of internationally diverse germplasm remains essential for identifying novel alleles, understanding patterns of phenotypic variation across geographical regions, and broadening the genetic base of breeding populations (Khoury et al. 2022; Reynolds et al. 2022).

To address this need, the International Center for Agricultural Research in the Dry Areas (ICARDA), together with the Wheat Initiative and international partners, developed the Global Durum Panel (GDP), which captures approximately 94–97% of the diversity present in more than 2,500 tetraploid wheat accessions (Maccaferri et al. 2019). The panel includes landraces, breeding lines, modern cultivars, and primitive tetraploid wheats originating from the Mediterranean Basin, West Asia, North Africa, Europe, North and South America, and South Asia. This globally representative resource has become an important platform for germplasm characterization, allele discovery, pre-breeding, and genomic research (Royo et al. 2021; ICARDA 2025).

The evaluation of globally diverse durum wheat germplasm is particularly relevant for India, where cultivation is largely confined to the Central and Peninsular Zones and breeding programmes have historically relied on a relatively narrow pool of adapted parents. Characterizing exotic germplasm according to geographical origin provides opportunities to identify novel adaptive variation, broaden the

breeding gene pool, and improve tolerance to drought, heat stress, and other production constraints while maintaining grain quality and productivity (Reynolds et al. 2022; ICARDA 2025). Moreover, geographical classification facilitates the assessment of phenotypic diversity among eco-geographical groups and supports the strategic conservation and utilization of genetic resources.

In the present study, a globally representative panel of 708 durum wheat accessions originating from diverse geographical regions was evaluated over two consecutive growing seasons using fifteen standardized agro-morphological descriptors. The objectives were to (i) quantify phenotypic diversity within the Global Durum Panel, (ii) characterize variation among geographical origin groups, (iii) examine relationships among key agronomic traits, (iv) classify accessions based on phenotypic similarity, and (v) identify diverse and breeding-relevant germplasm for parent selection, pre-breeding, and genetic resource management. The findings provide a comprehensive phenotypic framework for the effective conservation and utilization of global durum wheat genetic resources and support the development of climate-resilient breeding programmes.

Materials and Methods

Plant materials

The study was conducted using 708 durum wheat (*Triticum durum* Desf.) accessions selected from the Global Durum Panel (GDP), one of the most comprehensive international collections of durum wheat genetic resources developed by the International Center for Agricultural Research in the Dry Areas (ICARDA) in collaboration with the Wheat Initiative and global breeding partners. The GDP was assembled to maximize the representation of worldwide durum wheat diversity by capturing approximately 94–97% of the genetic variation present in more than 2,500 tetraploid wheat accessions and has been widely used as a reference panel for germplasm characterization, genome-wide association studies, allele discovery, and pre-breeding (Mazzucotelli et al. 2020; Maccaferri et al. 2019; Milner et al. 2021).

The panel comprised landraces, released cultivars, advanced breeding lines, and elite breeding materials originating from diverse agro-ecological regions, including the Mediterranean Basin, West Asia, North Africa, Europe, North America, South America, and South Asia. Passport information describing the country of origin, biological status, pedigree (where available), and geographical region was obtained from the ICARDA Germplasm Information System. For diversity analysis, accessions were grouped according to their geographical origin to investigate patterns of phenotypic variation associated with eco-geographical adaptation and breeding history. (**Supplementary table 1 (a)**. Such grouping also enabled the assessment of the potential value of exotic germplasm for broadening the genetic base of Indian durum wheat breeding programmes.

Experimental site

Field evaluations were conducted during two consecutive winter cropping seasons (2019–2020 and 2020–2021) at the ICARDA–Food Legume Research Platform (FLRP), Amlaha, Sehore District, Madhya Pradesh, India (23°07' N, 77°06' E; 485 m above sea level). The site represents the Central Indian durum wheat production environment and is characterized by a semi-arid subtropical climate with cool winters and hot summers. The soil is a deep black Vertisol with high clay content, good water-holding capacity, and moderate fertility, providing suitable conditions for reliable phenotypic evaluation. Daily weather data, including maximum and minimum temperature, rainfall, and relative humidity, were recorded throughout the crop season using an automated weather station located at the experimental site. **(Supplementary figure 1)**

Experimental design and crop management

The experiment was laid out in an alpha-lattice design with two replications to improve the precision of evaluating a large and diverse germplasm collection under field conditions. Each accession was planted in two rows, each 2.5 m long, with 20 cm spacing between rows and approximately 10 cm spacing between plants within rows. Standard agronomic practices recommended for irrigated durum wheat production in central India were followed uniformly across both seasons, including fertilizer application, irrigation, weed control, and plant protection measures. Uniform crop management ensured that observed phenotypic variation predominantly reflected genetic differences among accessions rather than management effects.

Phenotypic characterization

All accessions were characterized using fifteen standardized agro-morphological descriptors following the Test Guidelines for Durum Wheat (TG/120/3). The descriptors included ten qualitative and five quantitative traits representing plant architecture, phenology, spike characteristics, and grain morphology. Standardized descriptor definitions and scoring procedures ensured consistency of observations and enabled comparison with other durum wheat germplasm characterization studies (UPOV 2012; Bioversity International et al. 2017).

The qualitative descriptors included plant growth habit, Foliage colour, anthocyanin pigmentation of flag leaf auricles, flag leaf anthocyanin pubescence, flag leaf attitude, grain colour, grain shape, grain brush hair length, grain crease and grain germ width. These descriptors were recorded according to predefined descriptor states. **(Table 1).**

The quantitative traits comprised days to heading (DH), plant height (PH), spike length (SL), grain yield per plot (GY), and thousand-grain weight (TGW). Days to heading were recorded as the number of days from sowing until approximately 50% of the plants in a plot had completely emerged spikes. Plant height and spike length were measured from five representative competitive plants per plot. Grain yield was recorded on a plot basis after physiological maturity, and thousand-grain weight was determined by weighing 1,000 healthy grains adjusted to standard grain moisture content (**Supplementary table 2**). (UPOV 2012; Reynolds et al. 2022)

Statistical analysis

Quantitative trait data from the two growing seasons were analysed using mixed linear models implemented in META-R (version 6.0). Best Linear Unbiased prediction (BLUPs) were calculated for each accession across environments, while variance components were estimated using the Restricted Maximum Likelihood (REML) method. Broad-sense heritability (H^2) was estimated to quantify the proportion of phenotypic variation attributable to genetic effects.

Descriptive statistics, including minimum, maximum, mean, standard deviation, and coefficient of variation, were computed for each quantitative trait. Pearson's correlation coefficients were estimated to determine relationships among agronomic traits associated with productivity and adaptation.

Phenotypic diversity analysis

The frequency distribution of descriptor states was calculated for each qualitative trait to assess the extent of phenotypic variation within the collection. Phenotypic diversity was quantified using the Shannon–Weaver Diversity Index (H'), which measures both the richness and evenness of descriptor classes. Diversity indices were calculated for the entire panel and, where appropriate, for geographical origin groups to compare levels of variation among different eco-geographical regions.

Analysis of geographical variation

To investigate the influence of geographical origin on phenotypic diversity, accessions were classified according to their passport information into major geographical regions. Comparisons among regional groups were performed using descriptive statistics and diversity indices to identify region-specific phenotypic characteristics, unique adaptive traits, and potential sources of novel variation relevant to durum wheat improvement. This analysis facilitated the identification of exotic germplasm with complementary characteristics for broadening the genetic base of Indian breeding programmes.

Cluster analysis

Phenotypic relationships among accessions were examined using hierarchical cluster analysis based on standardized agro-morphological data. Euclidean distance matrices were calculated, and clustering was performed using Ward's minimum variance method. The resulting dendrogram was used to identify distinct phenotypic groups and to evaluate the correspondence between cluster membership and geographical origin, thereby providing insights into the distribution of diversity within the Global Durum Panel.

Data visualization

Frequency distributions, boxplots, principal component biplots, correlation heatmaps, and hierarchical dendrograms were generated using R software (version 4.3.0) to visualize phenotypic variation, trait relationships, and diversity patterns among accessions and geographical origin groups.

Identification of breeding-relevant germplasm

Accessions possessing desirable combinations of agronomic and phenotypic traits, including high grain yield, high thousand-grain weight, early heading, optimum plant height, and favourable spike characteristics, were identified through multi-trait evaluation. Particular emphasis was placed on identifying genetically diverse exotic accessions representing different geographical regions that could serve as donor parents for pre-breeding, broadening the genetic base of Indian durum wheat, and developing climate-resilient cultivars.

Results

3.1 Phenotypic variation of qualitative traits

A total of 708 durum wheat accessions were characterized for ten qualitative UPOV descriptors over two consecutive growing seasons (2019–2020 and 2020–2021). Considerable phenotypic variation was observed among the accessions, demonstrating the broad morphological diversity present within the Global Durum Panel.

Plant growth habit exhibited substantial variability and was classified into five descriptor states. The majority of accessions showed semi-erect growth habit (317 accessions; 44.8%), followed by intermediate (295; 41.7%), semi-prostrate (58; 8.2%), erect (32; 4.5%), and prostrate (6; 0.8%) growth habits. Foliage colour was represented by three classes, with green being the predominant class (405 accessions; 57.2%), followed by dark green (295; 41.7%) and pale green (8; 1.1%).

Variation was also observed for flag leaf characteristics. Semi-erect flag leaf attitude predominated (552 accessions; 78.0%), whereas erect and drooping attitudes were recorded in 116 (16.4%) and 40 (5.6%) accessions, respectively. Flag leaf pubescence exhibited very limited variation, with pubescence absent in 693 accessions (97.9%), medium in seven (1.0%), and strong in nine (1.3%) accessions. In contrast, anthocyanin pigmentation of the flag leaf auricles displayed greater polymorphism, with pigmentation absent in 390 accessions (55.1%), medium in 188 (26.6%), and very strong in 130 (18.4%).

Grain-related descriptors showed varying levels of diversity. Amber grain colour was predominant, occurring in 613 accessions (86.6%), followed by red (54; 7.6%) and white (41; 5.8%) grains. Grain shape was largely oblong (674 accessions; 95.2%), whereas ovate (24; 3.4%), elliptical (9; 1.3%), and round (1; 0.1%) grains were infrequent. Grain crease depth was predominantly deep (526 accessions; 74.3%), followed by medium (158; 22.3%) and shallow (24; 3.4%). Brush hair length at the distal end of the grain was mainly short or absent (556 accessions; 78.5%), while medium and long brush hairs were observed in 98 (13.8%) and 54 (7.6%) accessions, respectively. Grain germ width exhibited appreciable variation, with wide, medium, and narrow germ width recorded in 409 (57.8%), 226 (31.9%), and 73 (10.3%) accessions, respectively.

The Shannon–Weaver diversity index (H') revealed differences in phenotypic diversity among the qualitative descriptors **(Figure; 1)**. Traits such as plant growth habit, flag leaf attitude, anthocyanin pigmentation, grain colour, and grain germ width recorded comparatively higher H' values, indicating greater phenotypic diversity, whereas flag leaf pubescence, grain shape, and coleoptile colour exhibited lower H' values due to the predominance of a single descriptor class.

When grouped according to geographical origin, the germplasm was classified into seven regions: Africa, Asia, Australia, Europe, Middle East, North America, and Unknown **(Fig. 2; Supplementary Table S1 (b)**. Europe (268 accessions; 37.8%) and Africa (267 accessions; 37.7%) accounted for the largest proportion of the panel, whereas Australia (12 accessions; 1.7%) and the Unknown group (9 accessions; 1.3%) were least represented. Accessions originating from Africa and Europe exhibited the widest range of descriptor states for plant architecture and grain morphology, while Australian accessions showed comparatively limited phenotypic variation. Despite regional differences in descriptor frequencies, similar qualitative trait states were observed across all geographical groups, indicating extensive phenotypic diversity within the Global Durum Panel.

3.2 Geographic distribution of germplasm among clusters

The distribution of the 708 durum wheat genotypes across the six clusters varied according to their geographic origin **(Supplementary Table S1 (b); Figure 3).** European accessions constituted the largest proportion of the germplasm, accounting for 268 genotypes (37.9%), followed by Africa (267; 37.7%), North America (73; 10.3%), Asia (52; 7.3%), Middle East (27; 3.8%), Australia (12; 1.7%), and unknown origin (9; 1.3%).

Cluster III was the largest group, comprising 178 genotypes, predominantly from Africa (100), followed by Europe (31) and North America (30). Cluster IV included 140 genotypes and was dominated by European accessions (83), whereas Cluster VI contained 131 genotypes, with most entries originating from Europe (65) and Africa (35). Cluster II comprised 118 genotypes, with a relatively balanced representation of Europe (51) and Africa (45).

Clusters V and I contained 89 and 52 genotypes, respectively. Cluster V included accessions primarily from Europe (33) and Africa (31), while Cluster I consisted mainly of African (33) and North American (13) accessions, with only limited representation from other geographic regions.

3.3 Variation in quantitative traits

The analysis of variance revealed highly significant ($P < 0.01$) genotypic effects for all evaluated traits, namely days to heading (DH), plant height (PH), spike length (SL), thousand-grain weight (TGW), and grain yield (GY), in both 2019 and 2020 **(Supplementary table 2)**. These results indicate the presence of substantial phenotypic variation among the 708 wheat genotypes evaluated.

In 2019, genotype mean squares were highly significant for DH (166.4), PH (543.1), SL (3.2), TGW (171.5), and GY (81,567.1). Similar results were observed in 2020, with significant genotype mean

squares of 611.3, 591.9, 2.7, 100.3, and 59,051.7 for DH, PH, SL, TGW, and GY, respectively. Grain yield exhibited the largest genotypic variation in both years, whereas spike length showed comparatively lower variation **(Table 2).**

The combined ANOVA across years also detected highly significant ($P < 0.01$) effects of genotype and genotype × year (G × Y) interaction for all traits. The G × Y interaction mean squares were 148.9 for DH, 144.8 for PH, 1.8 for SL, 95.2 for TGW, and 28,812.3 for GY, indicating differential genotype responses across years. Nevertheless, the genotype mean squares remained substantially greater than the corresponding interaction mean squares for all traits, suggesting that genotypic variation was the major source of phenotypic variation.

Replication and block effects were significant for most traits in both years, while the residual mean squares were comparatively low, indicating good experimental precision. The significant genotypic variation observed across all agronomic traits demonstrates the diversity present within the germplasm collection and supports its suitability for identifying superior accessions for wheat improvement.

The estimates of variance components, broad-sense heritability, and descriptive statistics for the evaluated traits are presented in **Table 3**. Significant ($P < 0.01$) genotypic variance was detected for all traits in both years, indicating substantial phenotypic variability among the wheat genotypes.

In 2019, broad-sense heritability ranged from 0.45 for thousand-grain weight (TGW) to 0.99 for grain yield (GY). High heritability estimates were also observed for days to heading (DH, 0.97) and plant height (PH, 0.96), whereas spike length (SL) showed moderately high heritability (0.86). Genotypic variance was highest for grain yield (40,768.8) followed by plant height (256.3) and days to heading (82.8). Residual variances remained comparatively low for DH and SL, indicating high experimental precision.

In 2020, broad-sense heritability remained high for most traits, ranging from 0.73 (SL) to 0.99 (DH). Grain yield (0.98) and thousand-grain weight (0.98) also exhibited high heritability, while plant height showed moderately high heritability (0.89). Genotypic variance was greatest for grain yield (28,503.2) and days to heading (305.3), whereas residual variance was highest for grain yield (906.3) and plant height (60.6).

Across environments, broad-sense heritability ranged from 0.46 (TGW) to 0.85 (PH). Genotypic variance was significant ($P < 0.01$) for all traits, with the highest estimates observed for grain yield (20,484.4) and plant height (204.7). Genotype × environment variance was also significant for all traits, indicating differential genotype responses across environments. The largest genotype × environment variance was observed for grain yield (14,215.6), followed by days to heading (74.1) and plant height (51.5), whereas spike length exhibited the lowest interaction variance (0.6).

The coefficient of variation (CV) varied among traits and environments. In the combined analysis, CV ranged from 0.97% for days to heading to 18.49% for thousand-grain weight, while grain yield showed a relatively low CV (6.53%), indicating good experimental precision. The grand means across environments

were 86.08 days for DH, 87.84 cm for PH, 6.83 cm for SL, 37.25 g for TGW, and 352.11 g plot^{-1} for grain yield.

3.4 Trait associations

Pearson's correlation analysis revealed significant associations among the evaluated agronomic traits **(Figure 4 and supplementary table 3).** Grain yield (GY) was strongly and negatively correlated with days to heading (DH) ($r = -0.80$, $P < 0.001$), indicating that earlier-heading genotypes generally produced higher grain yield. Grain yield also exhibited weak but significant negative correlations with plant height (PH) ($r = -0.12$, $P < 0.01$) and spike length (SL) ($r = -0.30$, $P < 0.001$), whereas it was moderately and positively correlated with thousand-grain weight (TGW) ($r = 0.46$, $P < 0.01$).

Days to heading showed a moderate positive correlation with spike length ($r = 0.33$, $P < 0.001$) but was negatively associated with thousand-grain weight ($r = -0.51$, $P < 0.001$). Plant height exhibited only weak correlations with the remaining traits, showing a slight negative association with TGW ($r = -0.12$, $P < 0.01$) and grain yield ($r = -0.12$, $P < 0.01$), while its correlation with spike length was not significant ($r = 0.06$). Similarly, spike length was negatively correlated with thousand-grain weight ($r = -0.19$, $P < 0.001$).

The correlation analysis identified days to heading and thousand-grain weight as the traits most strongly associated with grain yield, whereas plant height showed comparatively weaker relationships with the other agronomic traits.

3.5 Cluster characterization of durum wheat germplasm

The 708 durum wheat genotypes were classified into six distinct clusters based on quantitative traits **(supplementary table 4).** Considerable variation was observed among clusters for days to heading (DH), plant height (PH), spike length (SL), thousand-grain weight (TGW), and grain yield (GY), demonstrating substantial phenotypic diversity within the germplasm collection.

Cluster I was characterized by the earliest heading genotypes (73.3 days), relatively tall plants (87.2 cm), the highest thousand-grain weight (42.2 g), and the highest grain yield (638.7 g). Cluster III also comprised early heading genotypes (73.5 days) with high TGW (41.0 g) and the second-highest grain yield (527.2 g). Cluster II exhibited intermediate values for most traits, with moderate grain yield (409.3 g) and TGW (38.3 g).

In contrast, Clusters IV and V consisted of late-heading genotypes (97.6 and 96.2 days, respectively) with comparatively lower thousand-grain weight (33.0–33.4 g) and grain yield (135.6–203.9 g). Cluster V contained the tallest plants (101.4 cm), whereas Cluster IV recorded the longest spikes (7.2 cm). Cluster VI represented an intermediate group, characterized by relatively long spikes (7.1 cm), moderate plant height (87.9 cm), and intermediate grain yield (282.8 g).

The distinct differences among clusters for phenological, morphological, and yield-related traits indicate substantial phenotypic diversity within the durum wheat collection. The superior performance of

Clusters I and III for grain yield and thousand-grain weight highlights these groups as valuable sources of germplasm for durum wheat improvement.

3.Variation in grain yield among geographical origin groups

The distribution of grain yield among 708 durum wheat accessions grouped according to their continental origin. Considerable variation in grain yield was observed both within and among continental groups, indicating the broad phenotypic diversity represented in the Global Durum Panel **(Figure 5)**.

North American germplasm exhibited the highest mean grain yield (398.8 g plot^{-1}), followed closely by African accessions (382.3 g plot^{-1}). Both groups displayed wide boxplots and long whiskers, indicating substantial variability among accessions. Grain yield of North American accessions ranged from approximately 70 to 630 g plot^{-1}, while African germplasm showed the broadest overall range, extending from approximately 80 to 780 g plot^{-1}. The higher median values and upper quartiles observed in these two groups indicate that they contained a larger proportion of high-yielding accessions than the remaining continental groups.

Middle Eastern germplasm recorded an intermediate mean grain yield of 335.6 g plot^{-1}. Although the median was lower than that of North America and Africa, the group exhibited a wide distribution, with yields ranging from approximately 80 to 730 g plot^{-1}. The large interquartile range suggests considerable heterogeneity, reflecting the coexistence of both low- and high-yielding genotypes.

Australian accessions produced a mean grain yield of 321.0 g plot^{-1}. Grain yield varied from approximately 170 to 490 g plot^{-1}, with a relatively symmetrical distribution around the median. The moderate spread indicates the presence of useful genetic variability, although the overall productivity was lower than that of African and North American germplasm.

Asian germplasm exhibited a comparatively lower mean grain yield (247.6 g plot^{-1}) and a median of approximately 210 g plot^{-1}. Grain yield ranged from nearly 95 to 520 g plot^{-1}, with most accessions concentrated below 300 g plot^{-1}. Nevertheless, a few high-performing genotypes were observed, indicating that valuable alleles for grain yield are also present within Asian germplasm.

The Unknown-origin group showed the lowest mean grain yield (196.1 g plot^{-1}) and the narrowest distribution among all continental groups. Grain yield ranged from approximately 100 to 350 g plot^{-1}, with most accessions clustered below 250 g plot^{-1}, suggesting relatively limited phenotypic variation compared with the other continental groups.

The boxplot revealed substantial variation in grain yield across continental groups. Africa, North America, and the Middle East showed wider interquartile ranges and longer whiskers, indicating greater within-group diversity and the presence of both high- and low-yielding accessions. North American and African germplasm exhibited the greatest yield potential, while Australian and Middle Eastern groups were intermediate. Asian and Unknown-origin groups showed comparatively lower productivity but

retained exploitable variation. Inclusive, overlapping distributions highlight the importance of accession-level evaluation and targeted selection for grain yield improvement.

Discussion

4.1 Phenotypic diversity and characterization of qualitative traits

The extensive qualitative variation observed among the 708 durum wheat accessions demonstrates that the Global Durum Panel (GDP) successfully captures a wide spectrum of phenotypic diversity and confirms its importance as a global genetic resource for durum wheat improvement. Morphological characterization remains the foundation of germplasm evaluation because it provides readily observable descriptors for accession identification, diversity assessment, and the efficient management of genebank collections. Despite rapid advances in genomic technologies, standardized phenotypic characterization continues to play a critical role in linking genetic diversity with agronomically important traits and identifying germplasm suitable for breeding and pre-breeding programmes (Mazzucotelli et al. 2020; Sansaloni et al. 2020; Khoury et al. 2022). Recent studies have further emphasized that integrating comprehensive phenotypic datasets with genomic information substantially enhances the utilization of global genetic resources in modern crop improvement (Royo et al. 2021; Reynolds et al. 2023).

Among the qualitative descriptors, plant growth habit exhibited considerable diversity, with semi-erect and intermediate growth habits predominating, whereas erect and prostrate types occurred at lower frequencies. Such variation reflects both historical domestication and breeding under contrasting agro-ecological conditions. Semi-erect plant architecture has been widely favoured because it improves canopy structure, light interception, lodging resistance, and harvestability. Nevertheless, the presence of erect and prostrate growth habits indicates that the GDP has retained valuable allelic variation originating from landraces and exotic germplasm, thereby providing opportunities for breeding programmes targeting diverse production systems and climate adaptation (Maccaferri et al. 2019; Soriano et al. 2021; Khoury et al. 2022).

Flag leaf traits also displayed contrasting levels of variation. The predominance of semi-erect flag leaves is consistent with breeding objectives aimed at maximizing radiation interception and photosynthetic efficiency. Conversely, the limited variation observed for flag leaf pubescence suggests strong directional selection during domestication and cultivar improvement. In contrast, anthocyanin pigmentation exhibited appreciable polymorphism, indicating that adaptive variation has been retained despite intensive breeding. Anthocyanin accumulation has been associated with tolerance to drought, high irradiance, and temperature stress, making this descriptor valuable for identifying climate-resilient germplasm (Reynolds et al. 2023; FAO 2024; CGIAR 2024).

Grain-related descriptors revealed both conserved and variable characteristics within the GDP. The predominance of amber grain colour and oblong grain shape reflects long-term selection for superior semolina and pasta quality, which has guided durum wheat improvement worldwide. However, variation in grain colour, grain germ width, grain crease depth, and brush hair length demonstrates that

considerable morphological diversity remains available within the collection. Such diversity contributes not only to varietal identification but also to grain quality, processing characteristics, and market acceptability. The conservation of these alternative phenotypes broadens the pool of alleles available for improving nutritional quality and value-added durum products (Royo et al. 2021; Lafiandra et al. 2022; Reynolds et al. 2023).

The comparatively high diversity observed for plant growth habit, flag leaf attitude, anthocyanin pigmentation, grain colour, and grain germ width, together with the relatively low diversity for grain shape and flag leaf pubescence, indicates that different descriptors have experienced different intensities of artificial selection. Traits associated with commercial grain quality and varietal uniformity exhibited lower variability because favourable phenotypes have been consistently selected during cultivar development. In contrast, traits associated with environmental adaptation retained greater diversity, suggesting the continued presence of exploitable genetic variation. Similar conclusions have been reported for the Global Durum Panel and other international germplasm collections (Sansaloni et al. 2020; Mazzucotelli et al. 2020; Khoury et al. 2022).

Grouping the germplasm according to geographical origin further demonstrated that Europe and Africa contained the largest numbers of accessions and exhibited the widest range of qualitative descriptor states. These findings are consistent with the evolutionary history of durum wheat, where the Mediterranean Basin represents the primary centre of domestication, diversification, and modern breeding. However, all geographical groups contributed unique phenotypic variation, indicating that useful adaptive alleles are distributed throughout the collection rather than being confined to a single region. Similar observations have been reported from recent evaluations of the Global Durum Panel, where geographical origin explained a significant proportion of phenotypic and genetic variation (Sansaloni et al. 2020; Royo et al. 2021; Maccaferri et al. 2019).

From the perspective of Indian durum wheat improvement, the observed qualitative diversity has considerable practical significance. Modern Indian cultivars have been developed from a relatively narrow genetic base, increasing the need to introduce novel alleles from globally diverse germplasm. The broad morphological diversity identified in the present study provides an important resource for selecting genetically divergent parents with complementary adaptive traits for pre-breeding and cultivar development. Furthermore, systematic characterization enhances genebank documentation, facilitates the identification of unique accessions, and supports the strategic deployment of global genetic resources to improve resilience against drought, terminal heat stress, and emerging production constraints. The establishment of representative core subsets from the Global Durum Panel further reinforces the value of comprehensive phenotypic characterization as the foundation for efficient germplasm conservation and utilization in future breeding programmes (Sansaloni et al. 2020; Khoury et al. 2022; ICARDA 2024).

4.2 Geographical variation and origin-wise diversity

The geographical distribution of the Global Durum Panel (GDP) demonstrated that the evaluated germplasm represents a broad range of eco-geographical regions, thereby capturing extensive phenotypic diversity shaped by domestication, environmental adaptation, and breeding history. Although accessions originating from Europe and Africa constituted nearly three-quarters of the collection and were represented across all phenotypic clusters, each geographical region contributed unique morphological variation, indicating that useful diversity is distributed throughout the global germplasm rather than being confined to a single centre of origin. These observations are consistent with the development strategy of the Global Durum Panel, which was specifically assembled to maximize worldwide allelic and phenotypic diversity for genetic studies and pre-breeding (Mazzucotelli et al. 2020; Milner et al. 2021).

The predominance of European and African accessions reflects the evolutionary history and domestication of durum wheat in the Fertile Crescent and Mediterranean Basin, followed by centuries of farmer selection and modern breeding (Mazzucotelli et al. 2020). Southern Europe and North Africa remain major centres of durum wheat cultivation and improvement, where breeding programmes have continuously incorporated local landraces, elite cultivars, and internationally exchanged germplasm to enhance adaptation, grain quality, and productivity (Peters Haugrud et al. 2025). Consequently, the broader range of descriptor states observed in European and African germplasm likely reflects both historical diversification and intensive breeding efforts. Similar conclusions were reached by Mazzucotelli et al. (2020), who demonstrated that Mediterranean germplasm contains substantial allelic richness and represents one of the major reservoirs of diversity within the Global Durum Panel.

Despite regional differences in the frequency of qualitative descriptors, similar phenotypic classes were identified across all geographical groups, indicating considerable overlap among breeding materials. This pattern reflects the extensive international exchange of germplasm through collaborative breeding programmes coordinated by ICARDA, CIMMYT, and national agricultural research systems over recent decades (Milner et al. 2021; Khoury et al. 2022). Continuous introgression of elite germplasm among breeding programmes has facilitated the dissemination of favourable alleles across continents, reducing geographical isolation while maintaining region-specific adaptive characteristics. Consequently, geographical origin alone explains only part of the observed phenotypic diversity, whereas historical germplasm exchange, selection, and adaptation collectively contribute to the present diversity structure.

The occurrence of European and African accessions across all six phenotypic clusters further demonstrates that considerable diversity exists within individual geographical regions. Conversely, accessions originating from Asia, Australia, North America, and the Middle East, although fewer in number, also contributed to multiple clusters, indicating that these regions harbour unique and complementary sources of phenotypic variation. Similar observations have recently been reported for internationally representative wheat diversity panels, where phenotypic clustering frequently reflects both adaptation to local environments and breeding history rather than geographical origin alone (Peters Haugrud et al. 2025; Puglisi et al. 2026). The distribution of accessions from different regions within the

same clusters also suggests convergent selection for desirable agronomic traits under comparable production environments.

From a plant genetic resources perspective, geographical origin represents an important component of passport information that enhances the value of germplasm characterization. Grouping accessions according to their origin facilitates the identification of region-specific adaptive traits, enables the establishment of representative core collections, and supports the strategic conservation of genetic diversity within genebanks (Khoury et al. 2022). Furthermore, integrating passport information with standardized phenotypic descriptors and genomic data substantially improves the efficiency of germplasm utilization by enabling breeders to identify genetically diverse parental lines possessing complementary adaptive traits (Milner et al. 2021; Mazzucotelli et al. 2020). Such integrated characterization approaches have become increasingly important for optimizing the utilization of large international germplasm collections.

The geographical diversity observed in the present study has particular significance for Indian durum wheat improvement. Modern Indian durum cultivars have been developed primarily from a relatively limited pool of adapted breeding materials, resulting in a comparatively narrow genetic base. Under projected climate change scenarios, expanding this genetic base through the introduction of exotic germplasm is essential for enhancing tolerance to terminal heat stress, drought, emerging diseases, and other production constraints (Khoury et al. 2022; Reynolds et al. 2022). The substantial morphological diversity identified among accessions originating from Europe, Africa, North America, Asia, Australia, and the Middle East therefore represents an important opportunity for broadening Indian breeding populations through pre-breeding and strategic introgression of novel alleles.

The identification of geographically diverse accessions possessing distinct phenotypic characteristics also provides opportunities to develop representative core subsets that maximize diversity while minimizing redundancy. Recent efforts to establish core collections from the Global Durum Panel have demonstrated that carefully selected subsets can efficiently capture the majority of available phenotypic and genetic variation, thereby facilitating germplasm evaluation and utilization in breeding programmes (Mazzucotelli et al. 2020; Kumar et al. 2026). Such approaches are particularly valuable for large international collections, where comprehensive evaluation of every accession is often impractical.

The origin-wise characterization confirms that the Global Durum Panel represents an exceptionally diverse international germplasm resource for conservation, pre-breeding, and genetic improvement. The broad geographical representation, together with the extensive phenotypic variation observed both within and among regions, provides valuable opportunities to identify genetically divergent parents, discover novel adaptive variation, and broaden the genetic base of modern durum wheat breeding. These findings reinforce recent recommendations that integrating geographical origin, standardized phenotypic characterization, and genomic information should be considered a central strategy for maximizing the utilization of global durum wheat genetic resources under changing climatic conditions (Milner et al. 2021; Peters Haugrud et al. 2025; Puglisi et al. 2026).

4.3 Variation in quantitative traits, heritability, and genotype × environment interaction

The highly significant genotypic differences observed for all quantitative traits demonstrate the extensive phenotypic variation retained within the Global Durum Panel (GDP), highlighting its value as a representative genetic resource for durum wheat improvement. Significant variation for days to heading, plant height, spike length, thousand-grain weight, and grain yield indicates the presence of substantial exploitable genetic diversity that can be utilized for parent selection, pre-breeding, and cultivar development. Similar levels of variation have been reported in recent evaluations of globally diverse durum wheat germplasm, where broad phenotypic diversity was attributed to the inclusion of landraces, elite cultivars, breeding lines, and primitive tetraploid wheats originating from contrasting agro-ecological regions (Mazzucotelli et al. 2020; Milner et al. 2021). The significant differences among genotypes therefore confirm that the GDP effectively captures worldwide variation for economically important agronomic traits.

The considerable variability observed for grain yield and thousand-grain weight is particularly important because these traits directly influence breeding progress and cultivar productivity. Grain yield exhibited the largest genotypic variance among all evaluated traits, reflecting its complex polygenic inheritance and the broad adaptation represented within the panel. Similarly, the substantial variation for thousand-grain weight indicates the availability of diverse alleles controlling grain development and sink capacity. Previous studies have demonstrated that the incorporation of exotic germplasm into breeding populations increases allelic diversity for yield-related traits and contributes to long-term genetic gain under changing climatic conditions (Reynolds et al. 2022; Peters Haugrud et al. 2025). Therefore, the wide range of quantitative variation identified in the present study provides an important opportunity for selecting complementary parental combinations to improve productivity while maintaining broad genetic diversity.

Broad-sense heritability estimates ranged from moderate to high for all evaluated traits, indicating that a large proportion of the observed phenotypic variation was genetically controlled rather than environmentally determined. High heritability estimates for days to heading and plant height across both years suggest that these traits are relatively stable and can be efficiently improved through phenotypic selection. Likewise, the consistently high heritability observed for grain yield and thousand-grain weight within individual years indicates that these traits possess substantial genetic variation under relatively uniform environmental conditions. Similar findings have been reported in recent durum wheat diversity studies, where phenological traits generally exhibit higher heritability than complex adaptive traits because they are controlled by fewer major loci and are less influenced by environmental fluctuations (Puglisi et al. 2026; Reynolds et al. 2022).

In the combined analysis across years, heritability estimates declined for several traits, particularly thousand-grain weight, reflecting the influence of environmental variation and genotype × environment interactions. Such reductions are expected because quantitative traits are strongly affected by seasonal climatic conditions, including temperature, rainfall distribution, and water availability during critical

developmental stages. Nevertheless, the moderate to high heritability estimates observed across environments indicate that reliable genetic improvement remains feasible through multi-environment evaluation and appropriate selection strategies. Recent studies have emphasized that estimating heritability across contrasting environments provides more realistic predictions of breeding progress than single-environment evaluations and is therefore essential for identifying stable donor parents (Reynolds et al. 2022; Peters Haugrud et al. 2025).

The significant genotype × year interaction detected for all quantitative traits demonstrates that genotype performance varied between cropping seasons, reflecting differential responses to environmental conditions. Such interactions are commonly observed in durum wheat because traits related to phenology, biomass accumulation, grain filling, and yield are highly sensitive to seasonal fluctuations in temperature and moisture availability. Although genotype × environment interactions were significant, the genotypic variance remained substantially greater than the interaction variance for all traits, indicating that genetic effects were the principal source of phenotypic variation. This finding suggests that the evaluated accessions possess relatively stable genetic differences despite environmental fluctuations and therefore constitute valuable material for breeding programmes targeting broad adaptation. Comparable results have been reported in recent multi-environment evaluations of durum wheat, where genetic variance exceeded genotype × environment variance for most agronomic traits, supporting the effectiveness of selection across representative target environments (Puglisi et al. 2026; Reynolds et al. 2022).

The relatively low coefficients of variation observed for most quantitative traits further demonstrate the reliability and precision of the phenotypic data. Low experimental error is particularly important when evaluating large germplasm collections because accurate phenotyping is essential for distinguishing true genetic differences from environmental noise. The use of an alpha-lattice design together with standardized crop management and replicated field trials likely contributed to the high experimental precision observed in the present study. Accurate phenotypic characterization remains fundamental for maximizing the value of plant genetic resources because reliable phenotypic data provide the basis for genomic analyses, association mapping, and donor parent identification (Milner et al. 2021; Mazzucotelli et al. 2020).

From a plant genetic resources perspective, the combination of significant genetic variability, moderate-to-high heritability, and manageable genotype × environment interaction demonstrates that the Global Durum Panel represents a robust resource for both conservation and utilization. The extensive quantitative variation observed among accessions provides opportunities to identify superior donor genotypes possessing favourable combinations of early maturity, optimum plant height, improved grain weight, and high productivity. Furthermore, integrating these phenotypic data with genomic information available for the Global Durum Panel will facilitate the identification of favourable alleles controlling complex quantitative traits and accelerate marker-assisted and genomic selection approaches (Mazzucotelli et al. 2020; Milner et al. 2021).

These findings have particular significance for Indian durum wheat improvement, where breeding programmes increasingly require novel sources of variation to address climate change, terminal heat stress, and declining genetic diversity. The substantial quantitative variation identified in the present study indicates that exotic germplasm from the Global Durum Panel constitutes a valuable reservoir of adaptive alleles that can be exploited through pre-breeding to broaden the genetic base of Indian cultivars. Multi-environment phenotypic evaluation, together with high heritability estimates for key agronomic traits, provides confidence that genetically superior accessions identified in this study will contribute effectively to the development of climate-resilient and high-yielding durum wheat cultivars adapted to the diverse wheat-growing environments of India and other durum-producing regions.

4.4 Trait associations and implications for selection

Understanding the relationships among agronomic traits is fundamental for the efficient utilization of plant genetic resources because the improvement of complex traits such as grain yield depends on the simultaneous selection of multiple interacting characteristics. Correlation analysis provides valuable insights into the genetic and physiological relationships among traits, enabling breeders to identify indirect selection criteria and optimize parent selection for breeding programmes. In the present study, the observed trait associations indicate that several yield-related traits are genetically interconnected and can therefore be exploited simultaneously to accelerate genetic improvement. Similar observations have been reported in recent studies of globally diverse durum wheat germplasm, where phenotypic correlations have been used to identify complementary traits for selection and genomic prediction (Mazzucotelli et al. 2020; Reynolds et al. 2022).

Grain yield exhibited significant positive associations with thousand-grain weight and spike length, indicating that accessions producing heavier grains and longer spikes generally achieved higher productivity. These relationships are biologically meaningful because longer spikes often support a greater number of fertile spikelets and grains, whereas higher thousand-grain weight reflects improved assimilate partitioning during grain filling. The simultaneous improvement of these traits therefore represents an effective strategy for increasing grain yield without compromising adaptation. Similar positive relationships among grain yield, grain weight, and spike characteristics have recently been reported in multi-environment evaluations of durum wheat, confirming their importance as major components contributing to final grain productivity (Puglisi et al. 2026; Reynolds et al. 2022).

The association between days to heading and grain yield provides valuable information for breeding programmes targeting different production environments. In environments where terminal heat stress frequently limits grain filling, earlier heading genotypes may escape high temperatures and maintain stable grain yield, whereas in favourable environments slightly later heading may permit greater biomass accumulation and yield potential. Consequently, the direction and magnitude of this relationship should be interpreted within the context of the target production environment. For the Central and Peninsular Zones of India, where terminal heat stress is a major production constraint, optimum phenology rather than extremely early or late maturity is expected to maximize productivity. Recent studies have similarly

emphasized that flowering time remains one of the principal adaptive traits controlling yield stability under climate change and should therefore be considered a primary selection criterion in durum wheat breeding (Reynolds et al. 2022; Peters Haugrud et al. 2025).

Plant height also exhibited significant associations with several agronomic traits, reflecting its central role in determining crop architecture and biomass production. Moderate plant height is generally preferred because it combines adequate biomass production with improved lodging resistance and harvest index. The continued predominance of semi-dwarf germplasm within modern breeding programmes demonstrates the long-term success of optimizing plant height for enhanced productivity. However, the presence of considerable variation within the Global Durum Panel suggests that additional opportunities exist to optimize plant architecture for specific production systems, including conservation agriculture and stress-prone environments. Similar conclusions have been reached in recent studies, where plant height has remained an important component of selection indices despite advances in genomic breeding approaches (Puglisi et al. 2026).

The significant correlations observed among the evaluated quantitative traits also indicate that simultaneous improvement of multiple agronomic characteristics is feasible through multi-trait selection. Rather than selecting exclusively for grain yield, breeders can improve selection efficiency by combining complementary traits such as thousand-grain weight, spike length, optimum plant height, and appropriate phenology into integrated selection indices. Recent advances in genomic prediction and multi-trait breeding have further demonstrated that exploiting correlated traits substantially improves prediction accuracy and accelerates genetic gain in durum wheat (Puglisi et al. 2026; Peters Haugrud et al. 2025).

From a genetic resources perspective, the observed trait associations provide valuable information for identifying complementary parental combinations within the Global Durum Panel. Accessions combining favourable expressions of multiple correlated traits are particularly valuable because they increase the likelihood of recovering superior segregants in subsequent breeding generations. Conversely, genetically divergent accessions possessing contrasting trait combinations may serve as useful parents for broadening the genetic base and generating novel recombination events. Integrating phenotypic correlations with passport information and genomic data therefore enhances the strategic utilization of germplasm conserved in international genebanks and supports the efficient identification of donor parents for pre-breeding (Mazzucotelli et al. 2020; Milner et al. 2021).

By exploiting correlated traits through multi-trait selection, breeders can accelerate the development of climate-resilient cultivars while maintaining sufficient genetic diversity to sustain long-term breeding progress. These results therefore reinforce the importance of integrating comprehensive phenotypic characterization with genomic information to maximize the utilization of globally diverse durum wheat genetic resources for future crop improvement.

4.5 Cluster analysis and identification of breeding-relevant germplasm

Hierarchical cluster analysis revealed substantial phenotypic diversity within the Global Durum Panel (GDP), separating the 708 accessions into six distinct clusters based on their agro-morphological characteristics. The formation of multiple clusters confirms the existence of considerable genetic divergence among accessions and demonstrates that the GDP effectively captures the broad phenotypic variation present in globally diverse durum wheat germplasm. Similar clustering patterns have been reported for international durum wheat collections, where agro-morphological characterization successfully differentiated accessions according to their breeding history, adaptation, and evolutionary origin (Mazzucotelli et al. 2020; Milner et al. 2021). The identification of distinct phenotypic groups provides an important framework for the conservation, characterization, and strategic utilization of genetic resources.

The distribution of accessions among clusters indicated that genetic diversity was not restricted to a single geographical region. Accessions originating from Europe, Africa, Asia, the Middle East, North America, South America, and Australia were represented across multiple clusters, demonstrating that geographical origin alone does not determine phenotypic similarity. This pattern reflects the extensive international exchange of germplasm among breeding programmes coordinated by ICARDA, CIMMYT, and national agricultural research systems, where repeated hybridization and selection have generated genetically admixed breeding populations (Mazzucotelli et al. 2020; Khoury et al. 2022). Nevertheless, some clusters contained a higher proportion of accessions from particular regions, suggesting that local adaptation, historical selection, and breeding objectives have contributed to regional differentiation for important agronomic traits.

The occurrence of genetically divergent accessions within different clusters has important implications for parent selection. Crosses involving parents selected from distinct phenotypic clusters are generally expected to maximize genetic recombination, increase segregation, and improve the probability of recovering transgressive segregants with superior combinations of desirable traits (Milner et al. 2021; Reynolds et al. 2022). In contrast, crosses among closely related accessions within the same cluster are likely to contribute relatively limited additional genetic variation. Therefore, cluster analysis provides a practical approach for identifying complementary parental combinations capable of broadening the genetic base of breeding populations while maintaining desirable agronomic performance.

The considerable within-cluster variation observed in the present study further indicates that individual clusters contain valuable diversity for multiple agronomic traits rather than representing genetically uniform groups. This finding reflects the complex evolutionary history of durum wheat, where repeated domestication, farmer selection, international germplasm exchange, and modern breeding have generated extensive phenotypic variation within geographical regions (Peters Haugrud et al. 2025). Such within-cluster diversity provides opportunities to identify elite donor accessions possessing unique combinations of favourable traits while maintaining sufficient diversity for long-term breeding progress.

The identification of superior accessions combining high grain yield, greater thousand-grain weight, desirable plant height, appropriate maturity, and favourable spike characteristics is one of the most

important outcomes of comprehensive germplasm characterization. These accessions represent valuable parental resources for pre-breeding because they combine adaptation with favourable agronomic performance while simultaneously expanding the genetic diversity available to breeding programmes. Recent studies have highlighted that systematic evaluation of global germplasm collections substantially increases the probability of identifying novel alleles controlling complex quantitative traits and accelerates the development of climate-resilient cultivars through genomic-assisted breeding (Puglisi et al. 2026; Peters Haugrud et al. 2025).

From a plant genetic resources perspective, cluster analysis also provides valuable information for improving the management of international genebank collections. The identification of distinct phenotypic groups facilitates the development of representative core collections, reduces redundancy among conserved accessions, and enables more efficient allocation of resources for regeneration and evaluation. Integrating cluster analysis with passport information, geographical origin, and genomic data further strengthens the characterization of germplasm collections and enhances their accessibility for crop improvement programmes (Khoury et al. 2022; Milner et al. 2021). Such integrated approaches are increasingly recommended for maximizing the utilization of large international collections while ensuring the long-term conservation of genetic diversity.

The clustering pattern observed in the present study also provides valuable insights for the utilization of exotic germplasm in India. Although Indian durum wheat breeding programmes have successfully developed cultivars adapted to the Central and Peninsular Zones, the repeated use of a relatively small number of elite parental lines has narrowed the breeding gene pool. Accessions belonging to genetically distinct clusters, particularly those originating from Europe, North Africa, West Asia, North America, and South America, represent valuable sources of novel alleles for improving drought tolerance, terminal heat tolerance, grain quality, and yield potential. Strategic introgression of these exotic genetic resources into locally adapted backgrounds will contribute to broadening the genetic base of Indian durum wheat while enhancing resilience to future climatic challenges (Reynolds et al. 2022; Khoury et al. 2022).

The hierarchical clustering confirms that the Global Durum Panel possesses extensive phenotypic diversity suitable for germplasm conservation, genetic enhancement, and pre-breeding. The identification of genetically divergent clusters together with breeding-relevant accessions provides a scientific basis for selecting complementary parental combinations, developing representative core subsets, and integrating phenotypic diversity with genomic information. Such approaches will accelerate the discovery and deployment of favourable alleles while improving the efficiency of durum wheat breeding programmes in India and other durum-growing regions. These findings further demonstrate that comprehensive phenotypic characterization remains an indispensable component of modern plant genetic resource management and complements emerging genomic approaches for sustainable crop improvement (Mazzucotelli et al. 2020; Puglisi et al. 2026).

4.6 Geographic variation in grain yield

Substantial variation in grain yield among the continental origin groups of the Global Durum Panel, demonstrating the broad phenotypic diversity available within global durum wheat germplasm. The differences observed among African, North American, Australian, Asian, Middle Eastern, and unknown-origin accessions reflect the influence of geographical adaptation, breeding history, and genetic background. These findings emphasize the value of globally diverse germplasm collections as reservoirs of novel alleles for enhancing productivity and broadening the genetic base of durum wheat breeding.

African germplasm exhibited high grain yield together with the greatest phenotypic variation. This is consistent with the Mediterranean Basin and North Africa being major centres of durum wheat domestication and diversification, where prolonged natural and artificial selection has generated extensive genetic variability. The wide yield distribution suggests the coexistence of elite breeding lines and traditional landraces, providing valuable opportunities for identifying complementary parents with superior productivity and adaptation. Similar patterns of diversity have been reported in Mediterranean durum germplasm (Maccaferri et al., 2020; Royo et al., 2021).

North American accessions recorded the highest average grain yield, reflecting the success of breeding programmes that have prioritized yield potential, agronomic performance, and adaptation to intensive production systems. Nevertheless, the broad interquartile range indicates considerable genetic variability within this group, suggesting further opportunities for genetic improvement. Previous genomic and phenotypic studies have similarly identified North American germplasm as an important source of elite, high-yielding breeding material (Soriano et al., 2021; Reynolds et al., 2023).

Australian germplasm displayed intermediate yield performance, likely reflecting breeding efforts focused on drought tolerance, terminal heat adaptation, and grain quality under water-limited environments. Likewise, Asian and Middle Eastern accessions generally exhibited lower average grain yields but maintained substantial phenotypic variation. Many of these accessions originated from drought-prone and low-input production systems, where selection has favoured stress adaptation rather than maximum productivity. Consequently, they represent valuable sources of alleles for drought and heat tolerance, resource-use efficiency, and climate resilience (Khoury et al., 2022; FAO, 2024).

Although continental groups differed in average grain yield, considerable overlap among their yield distributions indicated that superior accessions occurred across multiple geographical regions. This finding highlights that accession-level evaluation is more informative than geographical origin alone for identifying promising breeding materials. Similar observations have been reported in global diversity studies, where within-population variation often exceeded differences among geographical groups (Sansaloni et al., 2020; Mazzucotelli et al., 2020).

Hence, the extensive phenotypic diversity observed confirms that the Global Durum Panel is a valuable resource for parent selection, pre-breeding, and allele discovery. For Indian durum wheat improvement, where the cultivated gene pool remains relatively narrow, the superior African and North American accessions represent promising donor parents for increasing yield potential, while Asian and Middle Eastern germplasm offer complementary adaptive traits for improving resilience under future climate

scenarios. Integrating these diverse genetic resources with genomic-assisted breeding will accelerate the development of high-yielding, climate-resilient durum wheat cultivars.

4.7 The implications for germplasm management and Indian durum wheat improvement

The comprehensive phenotypic characterization of 708 accessions from the Global Durum Panel (GDP) revealed substantial diversity for qualitative and quantitative traits, supported by moderate to high heritability and distinct phenotypic clustering. These findings confirm the GDP as a valuable reservoir of genetic variation for durum wheat improvement and highlight the importance of systematic phenotypic characterization alongside genomic information for effective germplasm conservation and utilization (Mazzucotelli et al. 2020; Milner et al. 2021).

The broad geographical representation of the GDP, encompassing Europe, North Africa, West Asia, the Americas, Australia, and South Asia, provides complementary adaptive variation shaped by diverse environments and breeding histories. Such diversity offers opportunities to identify novel alleles for phenology, plant architecture, grain characteristics, productivity, and adaptation to abiotic stresses, thereby supporting climate-resilient breeding (Khoury et al. 2022; Peters Haugrud et al. 2025).

The identified variation has particular relevance to Indian durum wheat breeding, where the repeated use of elite parents may constrain further genetic gain. Genetically diverse and agronomically superior accessions identified in this study can therefore serve as valuable donors for broadening the breeding gene pool through targeted pre-breeding and introgression. Accessions exhibiting superior grain yield, thousand-grain weight, desirable plant height, phenology, and spike traits provide promising parental resources for developing high-yielding and stress-resilient cultivars (Reynolds et al. 2022; Puglisi et al. 2026).

Furthermore, the phenotypic dataset provides a strong foundation for integrating GWAS, genomic prediction, marker-assisted selection, and haplotype-based breeding. Overall, strategic utilization of the GDP will strengthen genetic diversity, accelerate breeding progress, and support sustainable, climate-resilient durum wheat production.

Conclusion

The present study provides a comprehensive phenotypic characterization of 708 globally diverse durum wheat (*Triticum durum* Desf.) accessions of the Global Durum Panel (GDP) evaluated under Indian conditions across two cropping seasons. Substantial variation in qualitative and quantitative traits, moderate to high heritability, significant genotype × environment interactions, and distinct phenotypic clustering confirmed the broad exploitable diversity conserved within the GDP. Geographical variation further reflected the influence of adaptation, domestication, and breeding history on durum wheat diversity.

The identification of genetically divergent and agronomically superior accessions with desirable phenology, plant architecture, thousand-grain weight, grain yield, and grain characteristics provides valuable donors for parent selection and pre-breeding. Exotic germplasm from diverse regions offers opportunities to broaden the genetic base of Indian durum wheat and enhance adaptation to terminal heat, drought, productivity, and grain quality.

Overall, the study establishes a robust phenotypic resource for integrating germplasm characterization with genomic approaches, supporting GWAS, genomic prediction, allele discovery, and development of climate-resilient durum wheat cultivars. The phenotypic dataset generated in this study therefore provides a valuable resource for future genome-wide association studies, genomic prediction, pre-breeding, and the development of climate-resilient durum wheat cultivars in India and other durum-growing regions.

Declarations

Authers contribution

The experiments were conceived by RK & AG. designed the experiments. SS and SKS helped in data recording. NBD and SY analyzed the data of the paper. SKA, RK and AG reviewed and edited the paper.

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Conflict of interest

The authors declare that they have no competing interests.

Data availability statement

The details data will be provided on request

References

1. Bioversity International, ICARDA, CIMMYT (2017) *Key access and utilization descriptors for wheat genetic resources*. Bioversity International, Rome, Italy.
2. CGIAR System Organization (2024) *CGIAR Annual Report 2024: Transforming food, land, and water systems in a climate crisis*. CGIAR System Organization, Montpellier, France.
3. FAO (2024) *World Food and Agriculture – Statistical Yearbook 2024*. Food and Agriculture Organization of the United Nations, Rome. https://doi.org/10.4060/cd2971en
4. Ficco DBM, Mastrangelo AM, Trono D, Borrelli GM, De Vita P, Fares C, Beleggia R, Platani C, Papa R (2014) The colours of durum wheat: a review. Crop Pasture Sci 65:1–15. https://doi.org/10.1071/CP13293

5. ICARDA (2024) *ICARDA Annual Report 2024: A New Era of Dryland Resilience*. International Center for Agricultural Research in the Dry Areas (ICARDA), Beirut, Lebanon.
6. ICARDA (2025) ICARDA Annual Report 2024. International Center for Agricultural Research in the Dry Areas (ICARDA), Beirut, Lebanon.
7. Khoury CK, Brush S, Costich DE, Curry HA, de Haan S, Engels JMM, Guarino L, Hoban S, Mercer KL, Miller AJ, Nabhan GP, Perales HR, Richards C, Riggins C, Thormann I (2022) Crop genetic erosion: understanding and responding to loss of crop diversity. New Phytol 233:84–118. https://doi.org/10.1111/nph.17733
8. Kumar V, Kumar P, Gupta A, Kumari J, Singh C, Bairwa RK, Tyagi BS, Singh GP, Singh G, Tiwari R (2026) Creation of a core set of durum wheat accessions based on agro-morphological traits with maximum diversity and lower redundancy. Plant Genet Resour 24:17–26. https://doi.org/10.1017/S1479262125100208
9. Lafiandra D, Sestili F, Sissons M, Kiszonas A, Morris CF (2022) Increasing the versatility of durum wheat through modifications of protein and starch composition and grain hardness. Foods 11:1532. https://doi.org/10.3390/foods11111532
10. Maccaferri M, Harris NS, Twardziok SO, Pasam RK, Gundlach H, Spannagl M, Ormanbekova D, Lux T, Prade VM, Milner SG, Himmelbach A, Mascher M, Bagnaresi P, Faccioli P, Cozzi P, Lauria M, Lazzari B, Stella A, Manconi A, Gnocchi M, Moscatelli M, Avni R, Deek J, Biyiklioglu S, Frascaroli E, Corneti S, Salvi S, Sonnante G, Desiderio F, Marè C, Crosatti C, Mica E, Özkan H, Kilian B, De Vita P, Marone D, Joukhadar R, Mazzucotelli E, Nigro D, Gadaleta A, Chao S, Faris JD, Melo ATO, Pumphrey M, Pecchioni N, Milanesi L, Wiebe K, Ens J, MacLachlan RP, Clarke JM, Sharpe AG, Koh CS, Liang KYH, Taylor GJ, Knox R, Budak H, Mastrangelo AM, Xu SS, Stein N, Hale I, Distelfeld A, Hayden MJ, Tuberosa R, Walkowiak S, Mayer KFX, Ceriotti A, Pozniak CJ, Cattivelli L (2019) Durum wheat genome highlights past domestication signatures and future improvement targets. Nat Genet 51:885–895. https://doi.org/10.1038/s41588-019-0381-3
11. Mazzucotelli E, Sciara G, Mastrangelo AM, Desiderio F, Xu SS, Faris J, Hayden MJ, Tricker PJ, Özkan H, Echenique V, Steffenson BJ, Knox R, Niane AA, Udupa SM, Longin FCH, Marone D, Petruzzino G, Corneti S, Ormanbekova D, Pozniak C, Roncallo PF, Mather D, Able JA, Amri A, Braun H, Ammar K, Baum M, Cattivelli L, Maccaferri M, Tuberosa R, Bassi FM (2020) The Global Durum Wheat Panel (GDP): an international platform to identify and exchange beneficial alleles. Front Plant Sci 11:569905. https://doi.org/10.3389/fpls.2020.569905
12. Milner SG, Jost M, Taketa S, Mazon ER, Himmelbach A, Oppermann M, Weise S, Knüpffer H, Basterrechea M, König P, Schüler D, Sharma R, Pasam RK, Rutten T, Guo G, Xu D, Zhang XQ, Herren G, Müller T, Krattinger SG, Keller B, Wicker T, Stein N (2021) Genebank genomics highlights the diversity of a global barley collection. Nat Genet 53:319–326. https://doi.org/10.1038/s41588-021-00790-4
13. Nazco R, Villegas D, Ammar K, Peña RJ, Moragues M, Royo C (2012) Can Mediterranean durum wheat landraces contribute to improved grain quality attributes in modern cultivars? Euphytica 185:1–17. https://doi.org/10.1007/s10681-011-0586-8

14. Peters Haugrud AR, Achilli AL, Martínez-Peña R, Klymiuk V (2025) Future of durum wheat research and breeding: Insights from early career researchers. Plant Genome 18:e20453. https://doi.org/10.1002/tpg2.20453
15. Puglisi D, Crossa J, Cuevas J, Fania F, Afshari-Behbahanizadeh S, Vitale P, De Vita P (2026) Multi-trait and multi-environment genomic prediction enhances yield components improvement in durum wheat. Front Plant Sci 17:1759897. https://doi.org/10.3389/fpls.2026.1759897
16. Reynolds MP, Molero G, Chapman SC, Stöckle C, Sukumaran S, Slafer GA, et al. (2023) Variations in phenological, physiological, plant architectural and yield-related traits, their associations with grain yield and genetic basis. Ann Bot 131:503–519. https://doi.org/10.1093/aob/mcad003
17. Reynolds MP, Slafer GA, Foulkes JM, Griffiths S, Murchie EH, Carmo-Silva E, Asseng S, Chapman SC, Sawkins M, Gwyn J, Flavell RB, et al. (2022) A wiring diagram to integrate physiological traits of wheat yield potential. Nat Food 3:318–324. https://doi.org/10.1038/s43016-022-00512-z
18. Royo C, Ammar K, Villegas D, Soriano JM (2021) Agronomic, physiological and genetic changes associated with evolution, migration and modern breeding in durum wheat. Front Plant Sci 12:674470. https://doi.org/10.3389/fpls.2021.674470
19. Sansaloni C, Franco J, Santos B, Percival-Alwyn L, Singh S, Petroli C, Campos J, Dreher K, Payne T, Marshall D, Kilian B, Milne I, Raubach S, Shaw P, Stephen G, Carling J, Saint Pierre C, Burgueño J, Li H, Kehel Z, Amri A, Kilian A, Wenzl P, Uauy C, Bänziger M, Caccamo M, Pixley K (2020) Diversity analysis of 80,000 wheat accessions reveals consequences and opportunities of selection footprints. Nat Commun 11:4572. https://doi.org/10.1038/s41467-020-18404-w
20. Soriano JM, Colasuonno P, Marcotuli I, Gadaleta A (2021) Meta-QTL analysis and identification of candidate genes for quality, abiotic and biotic stress in durum wheat. Sci Rep 11:11877. https://doi.org/10.1038/s41598-021-91446-2
21. UPOV (2012) *Durum wheat (Triticum turgidum L. subsp. durum (Desf.) Husn.): Guidelines for the conduct of tests for distinctness, uniformity and stability*. TG/120/4. International Union for the Protection of New Varieties of Plants (UPOV), Geneva, Switzerland.

Tables

Tables 1 to 3 are available in the supplementary files section

Figures



Figure 1

Graphical representation of agro-morphological traits of durum wheat evaluated according to the guidelines for the conduct of tests for Distinctness, Uniformity and Stability (UPOV TG/3/12), presenting levels of expression for each trait along with their percentage distribution.

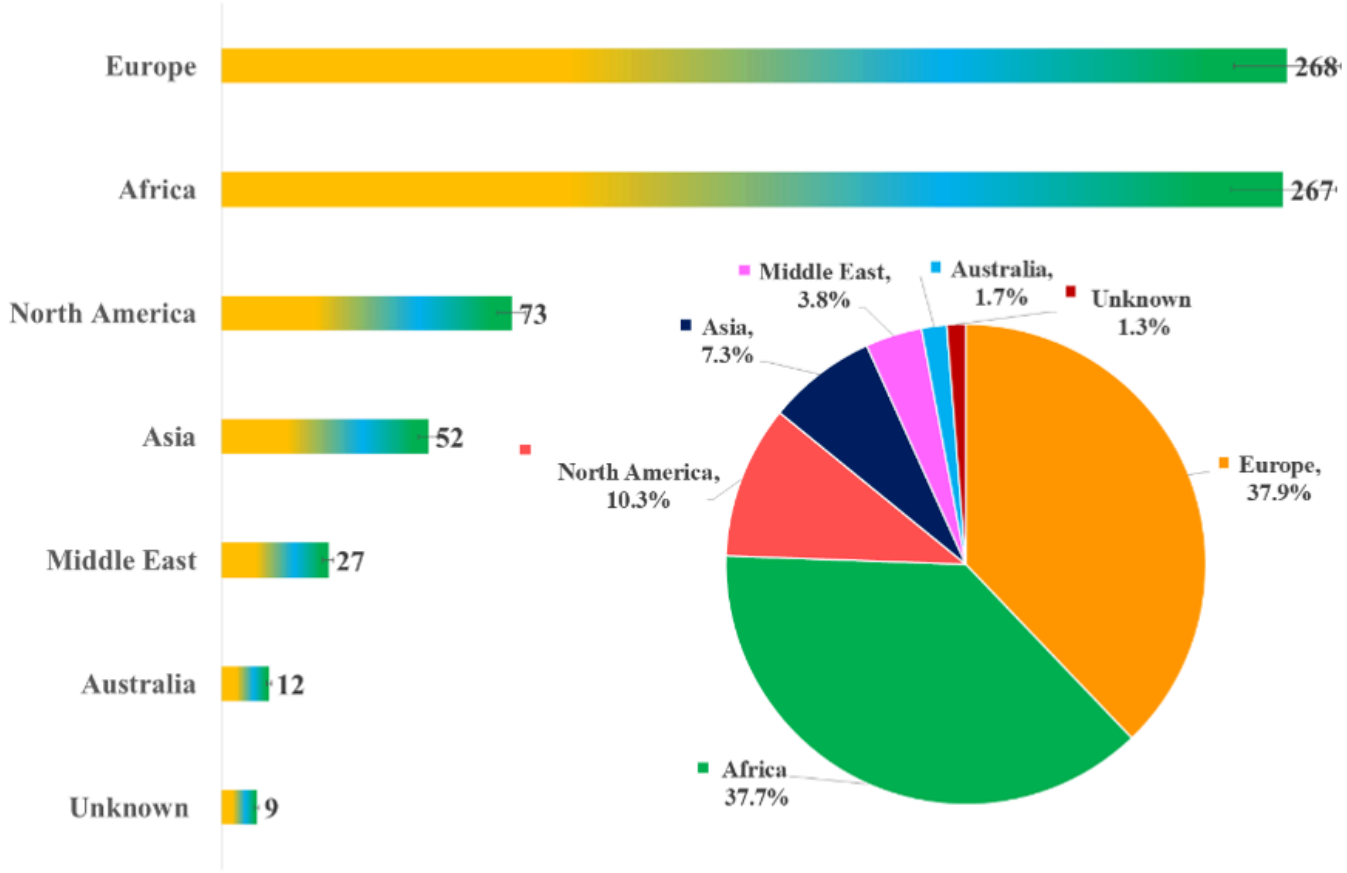


Figure 2

Geographic distribution of the global durum wheat panel, illustrating the grouping of genotypes based on their origin and country of germplasm collection.

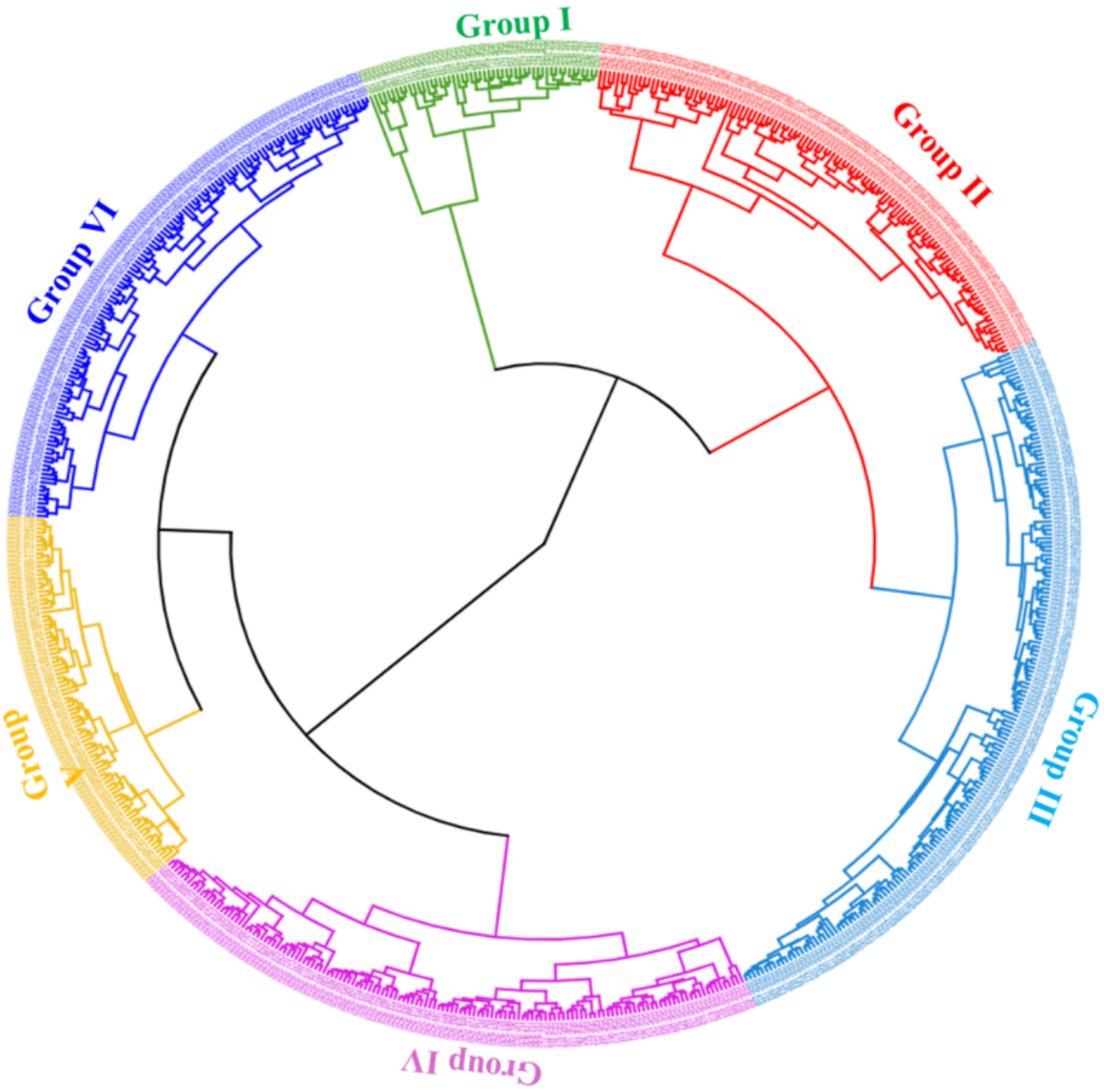


Figure 3

Cluster dendrogram of 708 durum wheat genotypes based on DUS (Distinctness, Uniformity, and Stability) traits, showing classification into six groups according to trait expression, geographical origin, and genotype distribution.

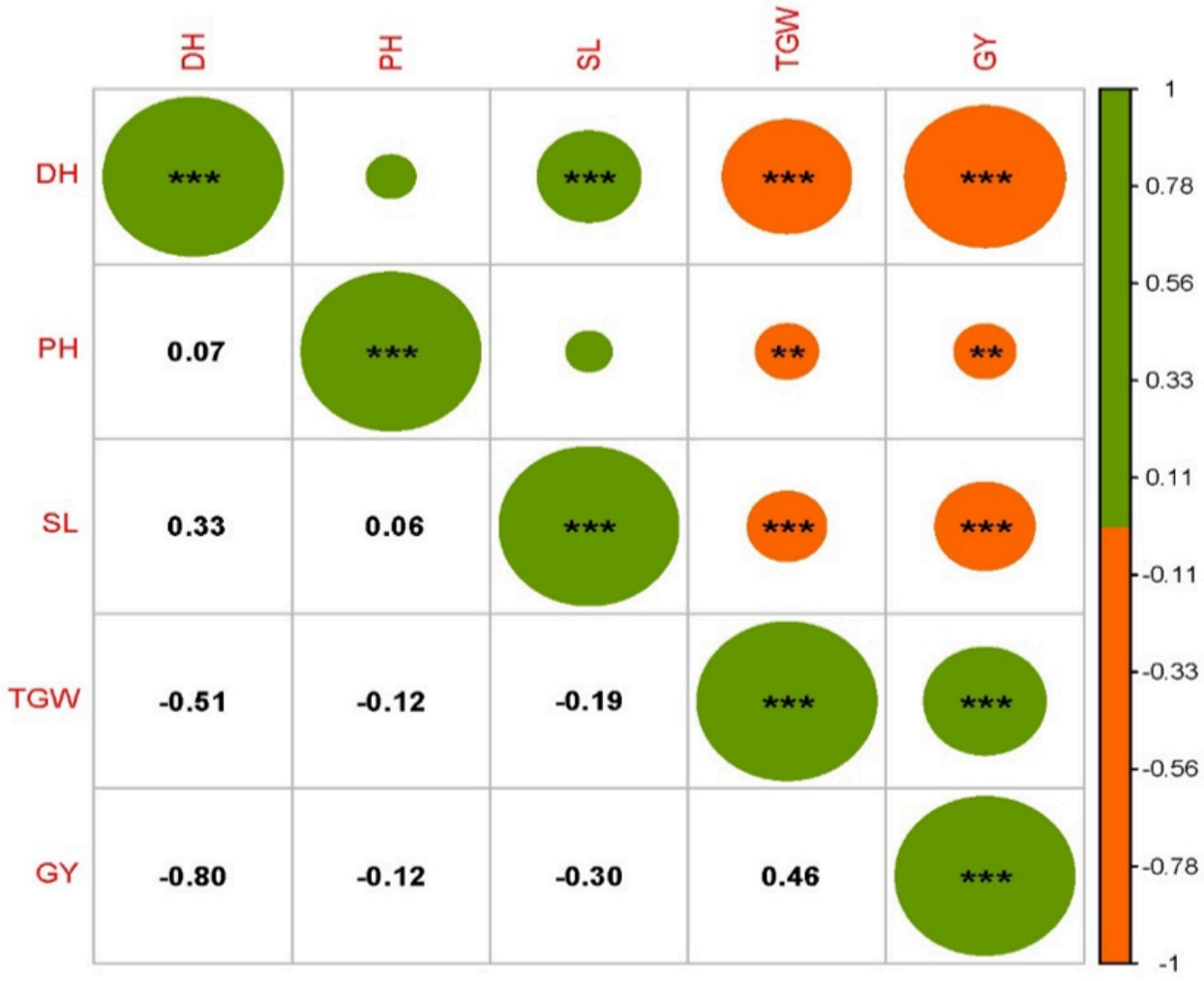


Figure 4

Phenotypic associations among grain yield and yield-contributing traits in durum wheat germplasm.

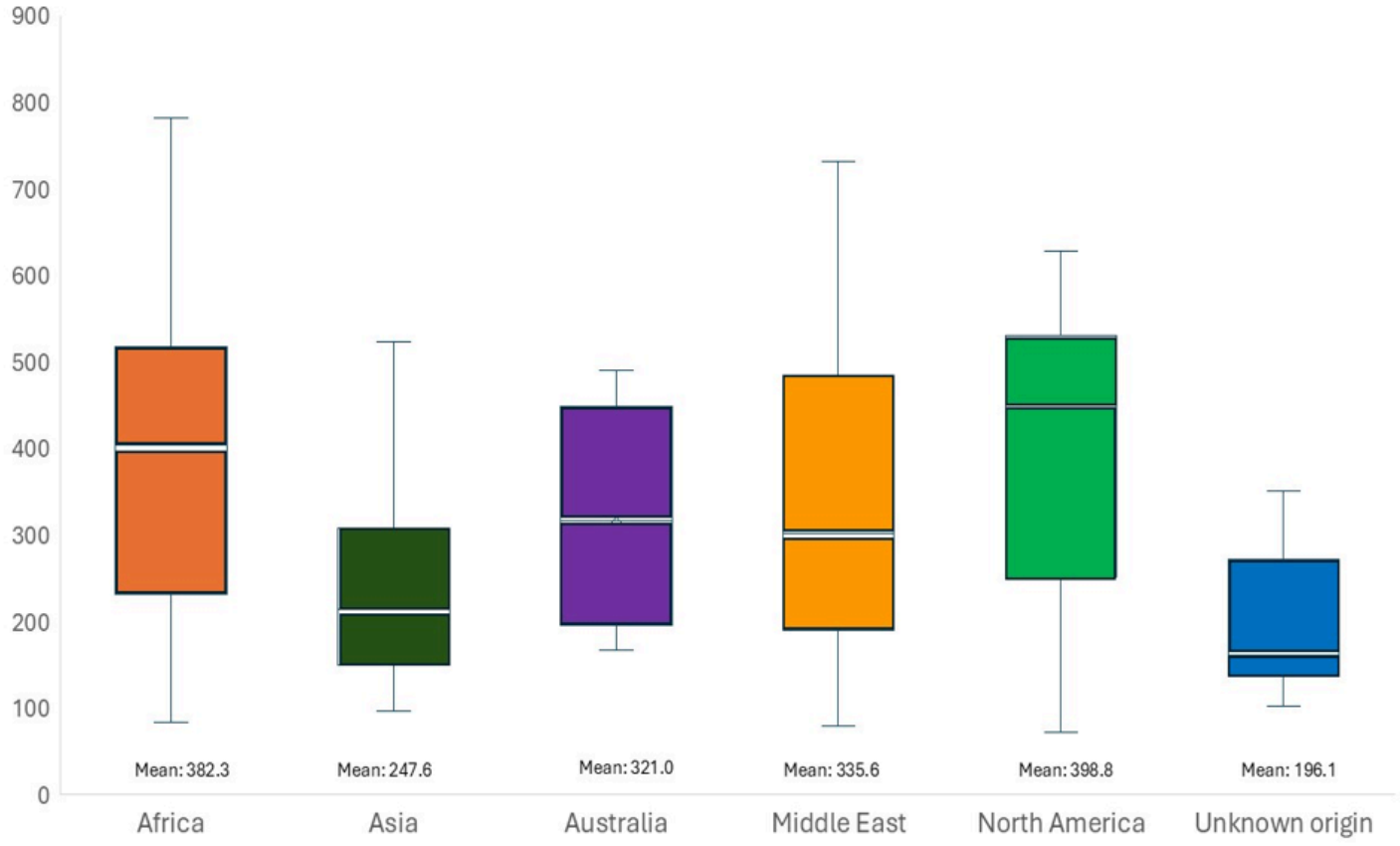


Figure 5

Distribution of grain yield (g plot⁻¹) among continental origin groups of the Global Durum Panel (708 *Triticum durum* Desf. accessions).

Supplementary Files

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