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Genetic variability of spike and kernel traits in a collection of bread wheat landraces

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Abstract

Objective: Wheat landraces are a valuable source of allelic diversity for various traits that could be used to broaden the genetic basis of elite germplasms. Assessment of genetic variation of grain yield (GY) and correlated traits is essential for implications in wheat yield improvement.
Methods: In the present study, 140 spring wheat landrace accessions, collected from various geographical regions of Iran, were evaluated for GY and spike-related characters at two successive cropping seasons.
Results: Higher genetic variation was observed among the landraces for the studied traits as revealed by phenotypic (PCV) and genotypic (GCV) coefficient of variation. For all traits, PCV was higher than GCV indicating the influence of the growing season on the variation of the traits. Although the heritability estimate (h^2) for GY was low (0.35), the yield-related traits showed higher h^2 ranging from 0.63 to 0.93. The distribution patterns of landraces, as revealed by cluster analysis and principal component analysis, did not align closely with their geographical distribution. However, accessions with similar phenotypic characteristics were grouped together.
Conclusion: The population structure and genetic relationships of the Iranian bread wheat landraces presented here highlight their diverse genetic architecture. The results of this study provide valuable information for the utilization of landraces in the genetic improvement of bread wheat.

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Introduction

Wheat accounts for approximately 20% of global caloric consumption and protein. It is cultivated on more land area than any other commercial crop, thereby playing an indispensable role in ensuring food security (Curtis and Halford 2014). To meet the demands of the world's growing population, wheat production should increase by about 50% by 2050 (Kettlewell *et al.* 2023). Urbanization, development, and climate constraints limit the expansion of wheat cultivation areas globally. Therefore, utilizing the potential yield of wheat through genetic improvement is a possible way to increase wheat production. Significant genetic variability in a source population, which increases the chances of selecting superior genotypes, is essential for the success of breeding programs (Tehseen *et al.* 2022). However, continuous breeding practices, such as artificial selection for quality and yield traits, and the presence of few genotypes in the background of most wheat varieties, have narrowed the genetic diversity in bread wheat over the past decades. This has resulted in the vulnerability of elite wheat germplasms to biotic and abiotic stresses, as well as climate changes (Novoselović *et al.* 2016; Tehseen *et al.* 2022).

Wheat landraces are genetically heterogeneous populations that have evolved over many generations under local farming systems and in a multitude of environments. Landraces consist of abundant patterns of variation with novel alleles for the genes controlling useful traits for adaptation and tolerance to biotic and abiotic stresses, which are not utilized in elite wheat breeding programs (Harlan 1992; Cseh *et al.* 2021). Dissecting the genetic diversity and variability in a collection of landraces from different geographical regions would be the first step in broadening the genetic base of elite wheat germplasm. Iran is one of the primary gene centers for *Triticum* species, especially *T. aestivum*, and a large collection of bread wheat landraces from wheat-growing areas in the country has been gathered (Vikram *et al.* 2021). Characterizing the genetic diversity of Iranian wheat landraces for yield-related traits can provide valuable information that can be used to broaden the narrow genetic base in the Iranian wheat breeding program.

Grain yield, as the primary candidate in wheat breeding programs, is a complex trait influenced by morphological and physiological characteristics, grain-related traits, and environmental factors. These factors make yield enhancement increasingly challenging (Liu *et al.* 2018). However, dissecting GY into its components, such as spike length (SL), the number of spikes per unit area, the number of spikelets per spike (NSS), the number of kernels per spike (NKS), and 1,000-kernel weight (TKW), which exhibit higher heritability than that of GY and are less influenced by environmental factors, could enhance the efficiency of GY improvement in wheat. The NKS, TKW, and the number of spikes per unit area are major components that collectively determine the final yield of wheat (Hai *et al.* 2008). Other spike-related traits, such as NSS, SL, and the number of spikes per plant, also play a significant role in wheat yield improvement (Guo *et al.* 2017). This study aimed to characterize a collection of spring wheat landraces for spike and kernel traits and to identify superior landraces for utilization in breeding programs.

Materials and Methods

Plant materials and field trials

In the current study, we utilized 140 Iranian spring bread wheat landrace accessions collected from diverse geographical regions across the country. The accessions were evaluated at the East Azarbaijan Agricultural and Natural Resources Research Center in Iran during the 2019-2020 and 2020-2021 growing seasons, employing a randomized complete block design with two replications. Each accession was planted in a 1.50 m long two-row plot with an inter-row spacing of 20 cm and a 7 cm spacing between plants within the row. The trials were managed using recommended agronomic practices to ensure proper growth and development.

Nine spike and kernel traits, including GY, TKW, SL, NSS, NKS, spike weight (SW), grain weight per spike (GWS), and awn length (AL), were measured. Ten random spikes from each accession per replication in each year were used for trait measurements. TKW (gr) was determined by weighing 250 kernels from each accession and multiplying the result by four in two replicates for each year. SL (cm) was measured from the base of the rachis to the topmost spikelet, excluding the awns. NSS was counted from the basal sterile spikelet to the top fertile spikelet. Spikelet fertility (SF) was computed as the number of kernels per spike divided by the number of spikelets per spike. SL, NSS, GWS (gr), and AL (cm) were the means of 10 randomly selected spikes in each replication.

Statistical analysis

The mixed linear model based on restricted maximum likelihood (REML) was used to assess the effects of cropping seasons, accessions, and their interaction in explaining the phenotypic variance in the studied traits. This followed the Mixed Linear Model (MLM) variance component analysis procedure of SAS 9.2 (SAS Institute 2004), considering seasons as a fixed factor and genotypes as a random factor. META-R (Multi-Environment Trial Analysis with R) v6.04 (Alvarado *et al.* 2020) was used to estimate the best linear unbiased predictions (BLUPs) for all the traits. BLUPs over two cropping seasons (years) were obtained using the following model: $yijk = \mu + Yi + Rk(\mathrm{i}) + G\mathrm{j} + YGij + eijk$, where $yijk$ is the trait of interest, μ is the overall mean, Yi is the fixed effect of the i^{th} year, $Rk(j)$ is the random effect of the kth replicate nested within the i*th* year, Gj is the random effect of the jth genotype, YGij is the random effect of the year × genotype interaction, and $eijk$ is the random error term. To estimate the broad-sense heritability (h^2) across years, variance components were estimated and h^2 was calculated as follows: $h^2 = \frac{\sigma_g^2}{\sigma_g^2+\sigma_{gy}^2/y+\sigma_e^2/ry}$, where σ_g^2, σ_{gy}^2, and σ_e^2 are genetic, genetic by year interaction, and residual variance components, respectively. The r term represents the number of replications within each year and y term represents the number of years in the analysis. The phenotypic (PCV) and genotypic (GCV) coefficient of variations expressed as percentages were calculated as The phenotypic (PCV) and genotypic (GCV) coefficient of variations expressed as percentages were calculated as $PCV = \frac{\sqrt{\sigma_p^2}}{\bar{X}} x100$ and $GCV = \frac{\sqrt{\sigma_g^2}}{\bar{X}} x100$, respectively, where σ_p^2, σ_g^2, and $\bar{X}$ are phenotypic and genotypic variances, and grand mean, respectively. Phenotypic and genetic correlations were calculated as follows: $r_{p(xy)}=\frac{\sigma_{P(x,y)}}{\sqrt{\sigma_{Px}^2\sigma_{Py}^2}}$, and $r_{g(xy)}=\frac{\sigma_{G(x,y)}}{\sqrt{\sigma_{Gx}^2\sigma_{G\,y}^2}}$, where $r_{p(x)y}$ and $r_{g(x)y}$ are the phenotypic and genotypic correlation coefficients between traits x and y, $\sigma_{P\,(x,y)}$ and $\sigma_{G\,(x,y)}$ are phenotypic and genotypic covariances between traits x and y, σ_{Px}^2 and σ_{Py}^2 are phenotypic variances for traits x and y, σ_{Gx}^2 and $\sigma_{G\,y}^2$ are genotypic variances for traits x and y, respectively. The structural equation modeling (SEM) option implemented in JMP Pro 17.0.0 (SAS Institute Inc, Cary, NC, USA, 2021) was used to further partition the correlations between traits into direct and indirect effects.

Principal component analysis (PCA) using adjusted means of all the traits across years (BLUPs) was executed using JMP Pro 16.0.0 (SAS Institute Inc, Cary, NC, USA, 2021). The number of principal components (PCs) was determined by inspecting the eigenvalues of PCs, and the first two PCs were subjected to a biplot to display shifts occurring in the morphological traits measured on the landraces across two years. A heatmap of 352 wheat landraces and 16 morpho-agronomics traits was constructed based on the hierarchical cluster analysis (Ward's methods) and squared Euclidian distance using JMP Pro 17.0.0 (SAS Institute Inc, Cary, NC, USA, 2021). Mahalanobis' D^2 statistic was used to calculate the pairwise distance between inferred clusters.

Results

Genetic variability

Phenotypic variation of the traits among genotypes, assessed by using mean, standard error (SE), PCV, (GCV, and h^2 values are presented in Table 1. The SE for the studied traits ranged from 0.01(SF) to 2.60 (GY). The PCV and GCV ranged from 7.84% to 50.77% and 5.69% to 46.19%, respectively. The highest PCV (50.77%) was observed for AL, followed by GY (32.04%), while the lowest PCV

Table 1. Mean squares from the combined analysis of variance, mean, phenotypic (PCV), and genotypic (GCV) coefficients of variation, and broad sense heritability (h2) for eight spike and kernel traits of 140 spring bread wheat accession tested in two successive years.

Traits	Mean Squares					Mean ± SE	PCV	GCV	h^2
	Year (Y) df = 1	Rep df = 2	Genotype (G) df = 139	G x Y df = 139	Error df = 278				
GY (gr/plot)	119661.77^{ns}	326746.37	30218.64***	19512.50***	12067.34	424.18± 2.60	32.04	12.20	0.35
(TKW (gr)	47554.93***	49.41	65.86***	24.17***	6.05	37.32 ± 0.22	13.54	8.66	0.63
SL (cm)	30.63*	0.77	10.93***	0.75*	0.60	11.39 ± 0.13	15.75	13.99	0.93
SW (gr)	40.78*	2.40	0.71***	0.19**	0.14	3.06 ± 0.04	17.90	11.78	0.73
NSS	147.95*	2.20	5.078***	1.12***	0.66	17.48 ± 0.07	7.84	5.69	0.78
NKS	682.67^{ns}	448.01	198.11***	54.16*	41.16	53.61 ± 0.43	17.06	11.19	0.73
GWS (gr)	52.00*	1.88	0.48***	0.17**	0.11	2.25 ± 0.02	20.37	12.57	0.69
AL (cm)	3.03^{ns}	4.67	16.54***	0.98**	0.65	4.27 ± 0.16	50.77	46.19	0.94
SF					0.11	3.07± 0.01	14.20	6.51	0.50

ns, *, **, and *** are non-significant, and significant at 0.05, 0.01, and 0.001 probability levels, respectively; GY: Grain yield; TKW: Thousand kernel weight; SL: Spike length; SW: Spike weight; NSS: Number of spikelets per spike; NKS: Number of kernels per spike; GWS: Grain weight per spike; AL: Awn length (cm); SF: Spikelet fertility.

(7.84%) was noted for NSS. Regarding GCV, AL exhibited the highest value (46.19%), followed by SL (13.99%), while NSS showed the lowest GCV (5.69%) value. The h^2 reached its highest value for AL (0.94), followed by SL (0.93), while GY (0.35) had the lowest h^2 value, followed by SF (0.50) (Table 1).

The analysis of variance for nine spike and kernel-related traits using the data combined over the two seasons (years) is presented in Table 1. Most of the traits (six out of the total nine) exhibited significant variation over the years. Mean square values for all the traits indicated highly significant variation among landrace accessions ($p < 0.0001$). The genotype x year interaction was very highly significant ($p < 0.0001$) for GY, TKW, and NSS, highly significant ($p < 0.01$) for SW, NSS, GWS, and AL, and significant ($p < 0.05$) for SL and NKS.

Correlation between traits

The phenotypic correlation coefficient between all pairs of traits was significant except those of Al with other traits and TKW with NSS and NKS (Table 2). A highly significant positive correlation ($p < 0.0001$) was observed between GY and TKW, SW, SL, NSS, and GWS. The correlation of GY with NKS and SF was also positive and significant ($p < 0.001$). A significant positive correlation was observed among SW, SL, NSS, NKS, GWS, and SF. GY showed a positive significant genetic correlation with all the traits studied except AL where the correlation was negative and non significant. A significant positive genetic correlation was observed between TKW and GY, SW, SL, as well as GWS, and its correlation with SF was significant and negative. Unlike phenotypic correlation, AL had a significant positive genetic correlation with SW, NKS, and SF. Genetic correlations among SW, SL, NSS, NKS, GWS, and SF were positive and significant.

Table 2. Genetic (below diagonal) and phenotypic (above diagonal) correlation coefficient among nine spike and kernel related traits in 140 Iranian spring bread wheat landrace accessions.

Traits	GY	TKW	AL	SW	SL	NSS	NKS	GWS	SF
GY		0.43^{****}	-0.01^{ns}	0.72^{****}	0.72^{****}	0.52^{****}	0.44^{****}	0.78^{****}	0.29^{***}
TKW	0.46^{****}		-0.01^{ns}	0.48^{****}	0.31^{***}	-0.13^{ns}	-0.16^{ns}	0.56^{****}	-0.17^{*}
AL	0.01^{ns}	-0.06^{ns}		0.18^{*}	0.01^{ns}	0.00^{ns}	0.17^{ns}	0.06^{ns}	0.28^{***}
SW	0.62^{****}	0.48^{****}	0.15^{ns}		0.56^{****}	0.65^{****}	0.78^{****}	0.98^{****}	0.72^{****}
SL	0.48^{****}	0.26^{**}	0.02^{ns}	0.55^{****}		0.45^{****}	0.43^{****}	0.57^{****}	0.33^{****}
NSS	0.31^{***}	-0.08^{ns}	0.00^{ns}	0.56^{****}	0.44^{****}		0.86^{****}	0.64^{****}	0.57^{****}
NKS	0.38^{****}	-0.13^{ns}	0.14^{ns}	0.74^{****}	0.40^{****}	0.70^{****}		0.72^{****}	0.91^{****}
GWS	0.64^{****}	0.54^{****}	0.05^{ns}	0.97^{****}	0.52^{****}	0.52^{****}	0.70^{****}		0.63^{****}
SF	0.31^{***}	-0.13^{ns}	0.19^{*}	0.62^{****}	0.25^{**}	0.28^{***}	0.88^{****}	0.59^{****}	

ns, *, **, ***, and **** are non-significant, and significant at 0.05, 0.01, 0.001, and 0.0001 probability levels, respectively; GY: Grain yield, TKW: Thousand kernel weight, ALL: Awn length, SW: Spike weight, SL: Spike length, NSS: Number of spikelets per spike, NKS: Number of kernels per spike, GWS: Grain weight per spike, SF: Spikelet fertility.

Structural equation modeling

The correlations between traits were further partitioned into direct and indirect effects using SEM. Best-fit SEM showing the direct standardized effects of spike and kernel traits on GY, had χ^2 = 855.75 (df = 14, p = < 0.0001), RMSEA = 0.66, CFI = 0.35, AIC = 3786.23, and -2 Log Likelihood = 3709.17. GY was considered as the dependent variable and TKW, SL, and GWS as the causal variables. Also, the NSS and SF were chosen as the casual variables for SL and GWS. AL and NKS were treated as casual variables for TKW (Figure 1). In the diagram, significant and non-significant effects were shown by solid and dashed lines, respectively. The highest significant direct effect on GY was shown by GWS (57.602) followed by SL (4.150). These two traits, however, exhibited a substantial indirect counter-balance effect via one another. TKW which had a strong positive correlation (r = - 0.46**) with GY showed a significant direct effect but smaller than the effects of GWS and SL. Its significant correlation with GY was largely due to the positive indirect effects *via* the GWS and SL. The direct effects of NSS on SL (0.689) and GWS (0.101) were positive and significant, while SF only showed a positive significant direct effect on GWS (0.811). The direct effect of NKS on TKW was negative but negligible and Al had a positive and non-significant direct effect on TKW.

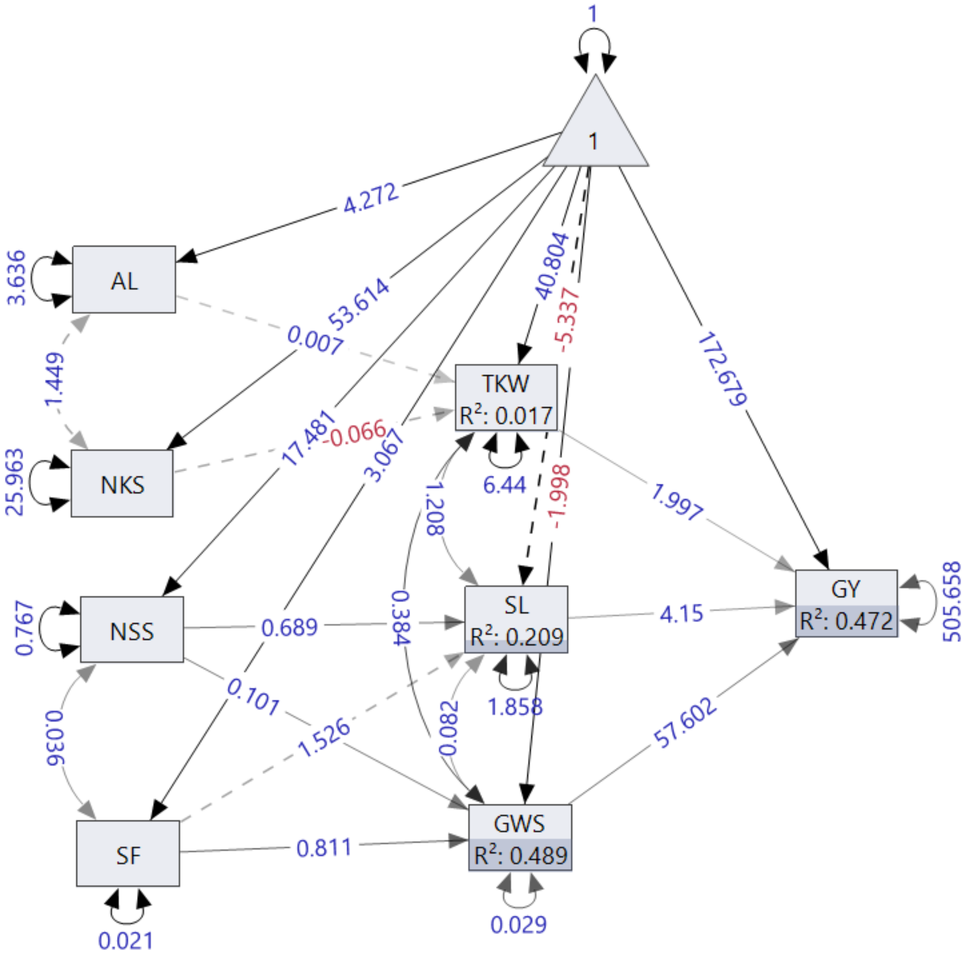

Figure 1. Best-fit structural equation model showing the direct standardized effects of spike and kernel traits on grain yield. The model-fitting parameters are: chi-square = 855.75 (df = 14, p = <0.0001), RMSEA = 0.66 and CFI = 0.35, AIC = 3786.23, and -2 Log Likelihood = 3709.17. GY: Grain yield, TKW: Thousand kernel weight, AL: Awn length, SW: Spike weight, SL: Spike length, NSS: Number of spikelets per spike, NKS: Number of kernels per spike, GWS: Grain weight per spike, SF: Spikelet fertility.

Genetic relationships and population structure

Principal component analysis using the BLUP values of nine spike and kernel-related traits in 140 spring wheat landraces across two seasons revealed that three components with eigenvalue > 1 explained 49.71, 18.38, and 11.35% of the total phenotypic variation of the traits studied. GY, SW, NKS, GWS, and SF showed a positive association with PC1, while TKW had a positive and NKS and SF negative association with PC2. AL showed a positive association with PC3, while NSS showed a negative association. A two-dimensional graphical representation (loading plot) of landraces and projection of nine spike and kernel traits on PCs are presented based on the first two components (Figure 2). There was low correspondence between the distribution of landraces based on two PCs and their geographical origins.

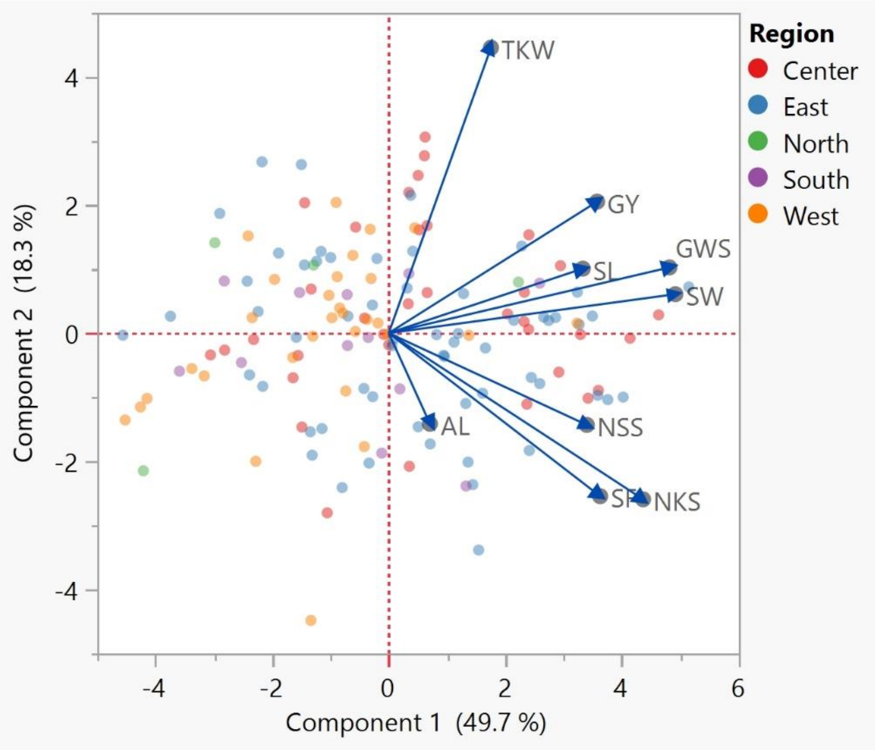

Figure 2. A biplot of principal component analysis of 140 Iranian bread wheat landraces with their contribution value based on nine spike and kernel traits. The genotypes are colored based on their geographical regions. Arrows indicate the loadings for each trait along the first two components, which comprised 68% of the total genetic variation for nine traits. GY: Grain yield, TKW: Thousand kernel weight, AL: Awn length, SW: Spike weight, SL: Spike length, NSS: Number of spikelets per spike, NKS: Number of kernels per spike, GWS: Grain weight per spike, SF: Spikelet fertility.

The resulting dendrogram from Ward's clustering algorithm, based on the squared Euclidean distance coefficient, was presented as a heatmap and constellation plot (Figures 3 and 4). The 140 spring wheat landraces were categorized into five clusters as revealed by the heatmap and constellation trees. Although these clusters did not necessarily consist of accessions from identical origins, naturally, the accessions with greater phenotypic similarity tended to group together. Clusters I, II, III, IV, and V consisted of 29 (20.71%), 30 (21.43%), 19 (13.57%), 21 (15.00%), and 41 (29.29%) accessions, respectively. Cluster I comprised accessions with a higher mean value than the grand mean for GY, TKW, SW, NSS, and GWS. In contrast, accessions in Cluster II showed a higher mean value for TKW, AL, and SL compared to the grand mean. The mean of accessions in Cluster III was higher than the grand mean for AL, NSS, NKS, and SF, while in Cluster IV, the accession mean for all traits was less than the grand mean. Cluster V comprised accessions with the highest mean values for all the traits studied except TKW and AL (Table 3). Pairwise Mahalanobis' distances (D^2 statistics) between the clusters are presented in Table 4. The maximum divergence was observed between Clusters III and V (43.21), followed by Clusters III and IV (23.86), while Clusters I and II (8.16) showed the minimum between-cluster distance, followed by Clusters II and III (14.71). The intra-cluster variation of Clusters I to V was estimated as 3.15, 3.08, 3.99, 3.79, and 2.46, respectively.

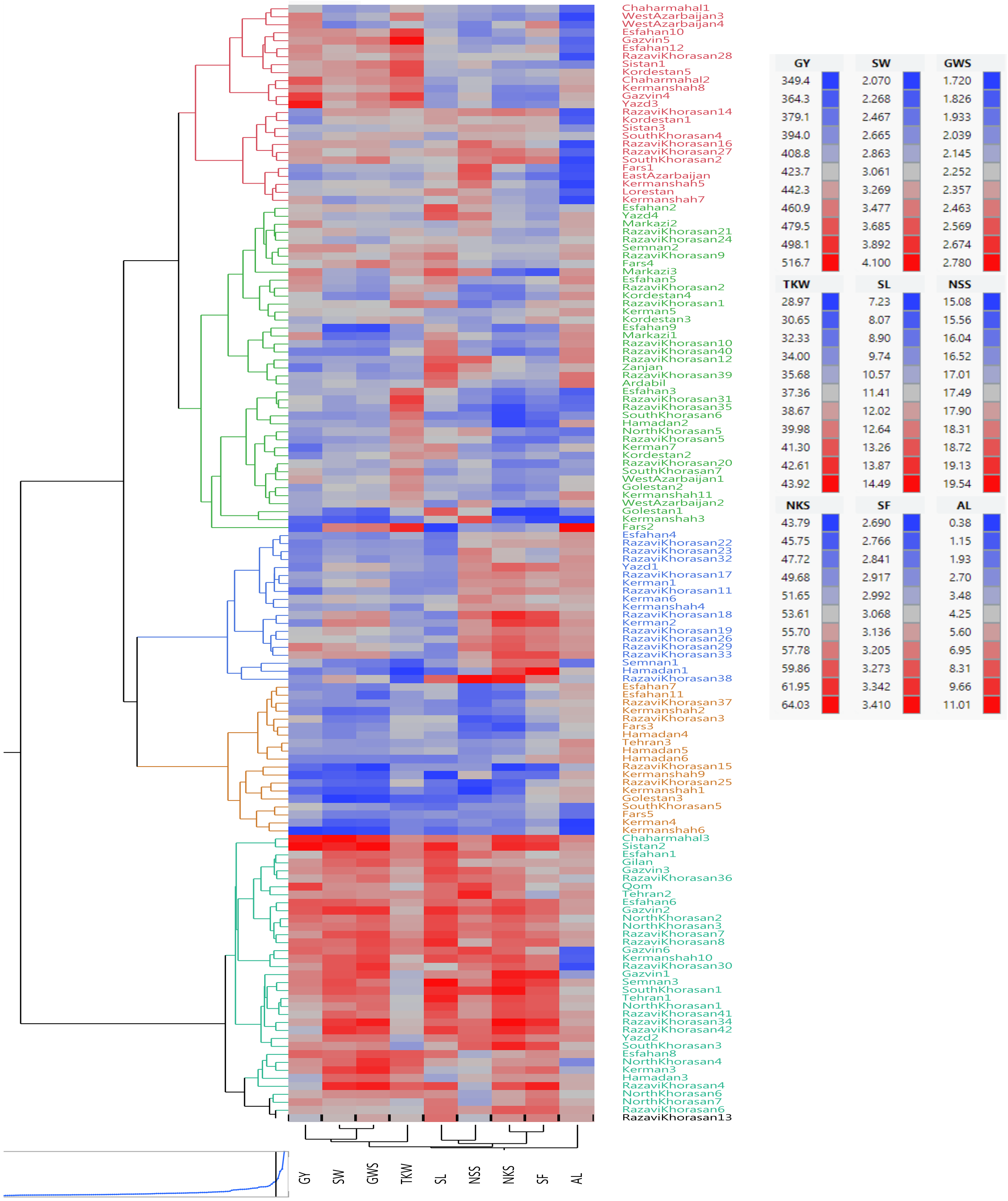

Figure 3. Heatmap of the spike and kernel traits measured on 140 Iranian spring bread wheat landraces; GY: Grain yield, TKW: Thousand kernel weight, AL: Awn length, SW: Spike weight, SL: Spike length, NSS: Number of spikelets per spike, NKS: Number of kernels per spike, GWS: Grain weight per spike, SF: Spikelet fertility.

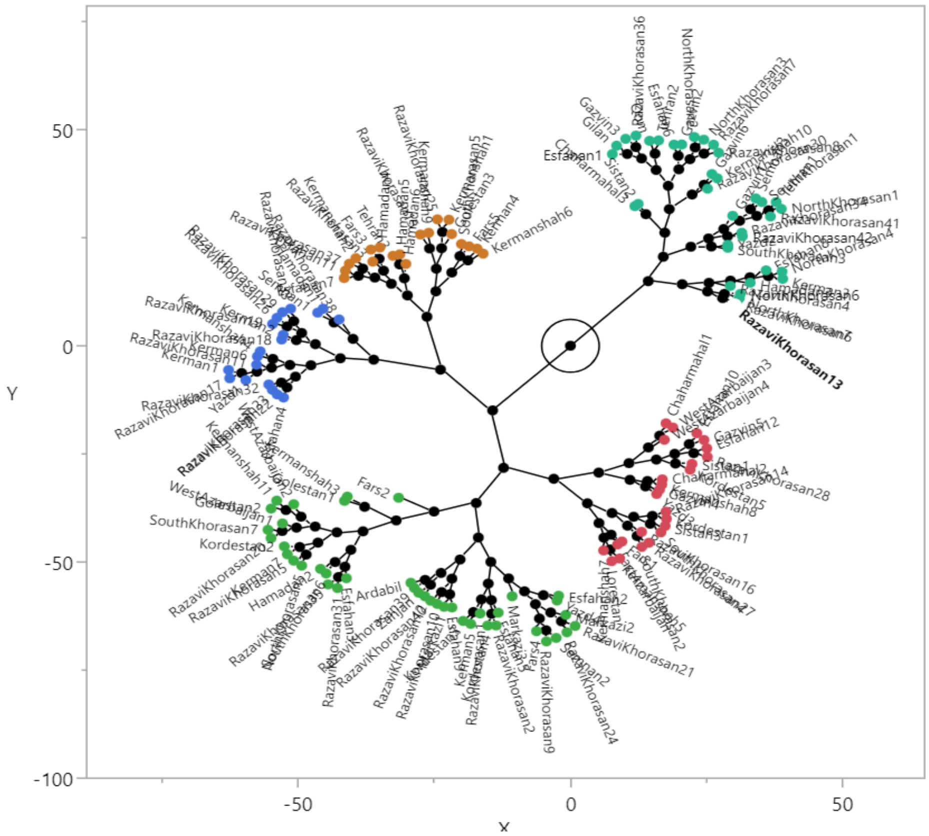

Figure 4. Constellation plot from hierarchical cluster analysis showing grouping of 140 Iranian bread wheat landraces in five clusters.

Table 3. Mean values of different spike and kernel traits of Iranian spring wheat landraces in cluster analysis.

Cluster	Count	GY	TKW	AL	SW	SL	NSS	NKS	GWS	SF
I	29	428.63	40.11	3.45	3.01	10.66	17.02	49.41	2.26	2.95
II	30	420.45	36.82	4.51	2.87	12.08	17.52	50.80	2.13	2.96
II	19	393.97	34.88	4.16	2.49	9.73	16.17	48.34	1.93	3.01
IV	21	405.47	34.64	5.14	3.01	10.08	18.02	57.77	2.19	3.17
V	41	447.34	38.21	4.28	3.53	12.84	18.11	58.96	2.52	3.20

GY: Grain yield, TKW: Thousand kernel weight, ALL awn length, SW: Spike weight, SL: Spike length, NSS: Number of spikelets per spike, NKS: Number of kernels per spike, GWS, Grain weight per spike, SF: Spikelet fertility.

Table 4. Inter- and intra-cluster distance for five clusters as revealed by Mahalanobis' D2 statistics in Iranian spring wheat landraces based on spike and kernel traits.

Cluster	I	II	III	IV	V
I	3.15				
II	8.16	3.08			
III	17.12	14.71	3.99		
IV	21.86	16.95	23.86	3.79	
V	19.90	14.88	43.21	15.88	2.46

Discussion

Bread wheat is the most widely grown staple crop which plays a crucial role in feeding 35% of the world's population by providing approximately 20% of proteins and calories (Tadesse *et al.* 2019). The current average annual increase in wheat production is 1%. However, to meet the demand of the world's growing population by 2050, the required increase rate of wheat production has been estimated to be 1.7% (Tadesse *et al.* 2019; Pal *et al.* 2022). Therefore, considering global climate changes and a gradual decrease in arable lands, yield improvement is the most important goal for global wheat breeding programs.

Compared to most other species, wheat has restricted genetic variability due to its allohexaploid nature, which is contributed by three interrelated diploid species and a few plants of ancestral species involved in the formation of wheat (Cox 1997; Charmet 2011). Although wheat is a young species, it was one of the first species to be domesticated. Therefore, domestication, centuries of cultivation, and modern breeding have further restricted the genetic variability of wheat (Dubcovsky and Dvorak 2007, El Baidouri *et al.* 2017). These processes resulted in the loss of genetic diversity in elite wheat breeding materials, and commercial wheat cultivars are prone to various biotic and abiotic stresses. It has been found that the current genetic diversity cannot meet the requirements of future wheat breeding. To combat climate change and to provide a sufficient quantity of food with better quality, there is a need to harness wheat landraces (Nadeem *et al.* 2021).

In the present study, a set of 140 Iranian spring bread wheat landraces from diverse geographical regions of the country were characterized using nine spike and kernel-related traits. PCV and GCV are two genetic parameters commonly used to detect the amount of variability present in the germplasm. PCV and GCV estimates were categorized as low (< 10%), moderate (10–20%), and high (> 20%) (Burton and DeVane 1953). In our study, high PCV was observed for AL, GY, and GWS, while other traits, except NKS, showed moderate PCV. The GCV was high for AL, moderate for SP, GWS, GY, SW, and KNS, and low for TKW, SF, and NSS (Table 1).

Deciphering the phenotypic and genetic relationships among the traits could provide insight into identifying the selection criteria for improving traits with low heritability. The correlation between examined traits ranged from non-significant to highly significant. Among the studied traits, the associations of AL with other traits were not significant, as revealed by the phenotypic correlation coefficient. However, at the genetic level, it showed a positive and significant correlation with SW, NKS, and SF. Jung *et al.* (2021) reported a positive correlation between AL and TKW. They related this to the awn contribution to total ear net photosynthesis which can reach 50% or more.

Ntakirutimana and Xie (2020) mentioned that higher grain yield in grasses could be achieved by optimizing awn length to provide a surface for cooling through transpiration efficiency.

Knowledge of genetic variation, heritability, and correlations across distinct traits is essential for the development of breeding strategies and will benefit multi-trait selection gains. In the present study, the estimates of h^2 ranged from 0.35 for GY to 0.94 for AL. All the yield components and related traits showed a higher level of heritability (> 60%), ranging from 63% for TKW to 93% for SL. The degree of heritability and genetic advancement generally determine the effectiveness of selection, while genetic variability is important for continuous genetic improvement (Ehdaie and Waines 1989). Wheat GY is a complex trait with low heritability, collectively determined by spike number, NKS, and TKW. SL, as well as the NSS, play an important role in improving wheat GY by affecting the NKS and the number of spikes per plant (Li *et al.* 2019). Therefore, direct selection for superior yield may not be adequately effective for yield improvement in wheat (Moghaddam *et al.* 1997). In our study, yield-contributing traits such as TKW, SL, NSS, and NKS showed high heritability and strong correlations with GY, therefore selection based on these components can be effective for GY improvement of wheat.

PCA and cluster analysis, two common multivariate methods, were used to analyze the genetic relationships and population structure of 140 Iranian spring bread wheat landraces from diverse geographical regions of the country. Grouping of landraces using PCA and cluster analysis did not correspond well with their geographical regions. Vikram *et al.* (2022), in an assessment of Iranian bread wheat landrace accessions' potential for genetic improvement using morphological and molecular data, also reported no concordance between genetic and geographical groupings. This could be explained by the frequent exchange of landraces between farmers and the long-term transportation of seeds between various regions of the country. We grouped the 140 wheat landraces into five clusters based on spike and kernel-related traits using agglomerative clustering. According to Mahalanobis distances (D^2 statistics), cluster V accessions with high mean values for most of the studied traits depicted the utmost divergence against cluster III. The estimation of inter-group distance, which reflects the relative divergence of accessions in the clusters, facilitates the selection of highly diverse parental lines with contrasting traits and provides better exploitation of landrace germplasm resources (Kant and Mani 1999). Therefore, crossing between accessions from clusters III and V may help develop heterotic combinations to derive desirable recombination and select new genotypes.

Conclusion

It has been claimed that plant breeding activities reduce the genetic base of elite wheat germplasm, which could seriously restrict further wheat improvement to cope with climate change. Therefore, broadening the genetic base of the cultivated wheat germplasm pool is essential for the development of high-yielding, input-responsive, and next-generation climate-smart varieties. Iranian bread wheat landraces with a wide genetic background for the most valuable traits have been utilized in breeding programs in countries such as Mexico, India, and Pakistan. In the present study, we characterized a set of 140 spring bread wheat landraces collected from diverse regions based on spike and kernel-related traits. Various statistical analyses revealed high genetic variation among the landraces for the traits studied, which can be utilized in breeding programs as well as a panel for association analysis to map new allelic diversity.

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Ethical considerations

The authors avoided data fabrication and falsification.

Conflict of interest

The authors declare that they have no conflict of interest with any organization concerning the subject of the manuscript.

References

Burton GW, DeVane EH. 1953. Estimating heritability in tall fescue (*Festuca arundinacea* L.) from replicated clonal material. Agron J. 45: 478-481. https://doi.org/10.2134/agronj1953.00021962004500100005x

Charmet G. 2011. Wheat domestication: lessons for the future. C R Biol. 334: 212-120. https://doi.org/10.1016/j.crvi.2010.12.013

Cox TS. 1997. Deepening the wheat gene pool. J Crop Prod. 1: 1-25. https://doi.org/10.1300/J144v01n01_01

Cseh A, Poczai P, Kiss T, Balla K, Berki Z, Horváth Á, Kuti C, Karsai I. 2021. Exploring the legacy of Central European historical winter wheat landraces. Sci Rep. 11: 23915. https://doi.org/10.1038/s41598-021-03261-4

Curtis T, Halford NG. 2014. Food security: The challenge of increasing wheat yield and the importance of not compromising food safety. Ann Appl Biol. 164(3): 354-372. https://doi.org/10.1111/aab.12108

Dhungana P, Eskridge KM, Baenziger PS, Campbell BT, Gill KS, Dweikat I. 2007. Analysis of genotype-by-environment interaction in wheat using a structural equation model and chromosome substitution lines. Crop Sci. 47: 477-484. https://doi.org/10.2135/cropsci2006.06.0425

Dubcovsky JA, Dvorak J. 2007. Genome plasticity a key factor in the success of polyploid wheat under domestication. Science 316: 1862-1866. https://doi.org/10.1126/science.1143986

Ehdaie B, Waines JG. 1989. Genetic variation, heritability, and path analysis in landraces of bread wheat from South Western Iran. Euphytica 41: 183-190. https://doi.org/10.1007/BF00021584

El Baidouri M, Murat F, Veyssiere M, Molinier M, Flores R, Burlot L, Alaux M, Quesneville H, Pont C, Salse J. 2017. Reconciling the evolutionary origin of bread wheat (*Triticum aestivum*). New Phytol. 213: 1477-1486. https://doi.org/10.1111/nph.14113

Evenson RE, Gollin D. 2003. Assessing the impact of the green revolution, 1960 to 2000. Science 300: 758-562. https://doi.org/10.1126/science.1078710

Guo Z, Chen D, Alqudah AM, Röder MS, Ganal MW, Schnurbusch T. 2017. Genome-wide association analyses of 54 traits identified multiple loci for the determination of floret fertility in wheat. New Phytol. 214: 257-270. https://doi.org/10.1111/nph.14342

Hai L, Guo H, Wagner C, Xiao S, Friedt W. 2008. Genomic regions for yield and yield parameters in Chinese winter wheat (*Triticum aestivum* L.) genotypes tested under varying environments correspond to QTL in widely different wheat materials. Plant Sci. 175: 226-232. https://doi.org/10.1016/j.plantsci.2008.03.006

Harlan JR (Ed). 1992. Crops and Man. 2nd ed. ASA, CSSA, Maison, WI, USA. 284pp.

Jung WJ, Lee YJ, Kang CS, Seo Y. 2021. Identification of genetic loci associated with major agronomic traits of wheat (*Triticum aestivum* L.) based on genome-wide association analysis. BMC Plant Biol. 21: 418. https://doi.org/10.1186/s12870-021-03180-6

Kant L, Mani VP. 1999. Evaluation and classification of facultative and winter wheat germplasm. IJPGR. 12: 348-351.

Kettlewell P, Byrne Ra, Jeffery S. 2023. Wheat area expansion into northern higher latitudes and global food security. Agric Ecosyst Environ. 351: 108499. https://doi.org/10.1016/j.agee.2023.108499

Li F, Wen W, Liu J, Zhang Y, Cao S, He Z, Rasheed A, Jin H, Zhang C, Yan J, *et al.* 2019. Genetic architecture in bread wheat based on genome-wide association studies. BMC Plant Biol. 19: 168. https://doi.org/10.1186/s12870-019-1781-3

Liu K, Sun X, Ning T, Duan X, Wang Q, Liu, T, An Y, Guan X, Tian J, Chen J. 2018. Genetic dissection of wheat panicle traits using linkage analysis and a genome-wide association study. Theor Appl Genet. 131: 1073-1090. https://doi.org/10.1007/s00122-018-3059-9

Moghaddam M, Ehdaie B, Waines JG. 1997. Genetic variation and interrelationships of agronomic characters in landraces of bread wheat from southeastern Iran. Euphytica 95: 361-369. https://doi.org/10.1023/A:1003045616631

Nadeem MA, Yeken MZ, Tekin M, Mustafa Z, Hatipoğlu R, Aktaş H, Alsaleh A, Cabi E, Habyarimana E, Zencirci N, *et al.* 2021. Contribution of landraces in wheat breeding. In: Zencirci N, Baloch FS, Habyarimana E, Chung G (eds.) Wheat landraces. Cham.: Springer, 215-258. https://doi.org/10.1007/978-3-030-77388-5_11

Novoselović D, Bentley AR, Šimek R, Dvojković K, Sorrells ME, Gosman N, Horsnell R, Drezner G, Šatović Z. 2016. Characterizing Croatian wheat germplasm diversity and structure in a European context by DArT markers. Front Plant Sci. 7: 184. https://doi.org/10.3389/fpls.2016.00184

Ntakirutimana F, Xie W. 2020. Unveiling the actual functions of awns in grasses: from yield potential to quality traits. Int J Mol Sci. 21(20): 7593. https://doi.org/10.3390/ijms21207593

Tehseen MM, Tonk FA, Tosun M, Amri A, Sansaloni CP, Kurtulus E, Yazbek M, Khaled A, Ozseven I, Bin Safdar L, *et al.* 2021. Genome-wide association study of resistance to *PstS2* and warrior races of *Puccinia striiformis* F. Sp. *Tritici* (stripe rust) in bread wheat landraces. Plant Genome 14: e20066. https://doi.org/10.1002/tpg2.20066

Tehseen MM, Tonk FA, Tosun M, Istipliler D, Amri A, Sansaloni CP, Kurtulus E, Mubarik MS, Nazari K. 2022. Exploring the genetic diversity and population structure of wheat landrace population conserved at ICARDA gene bank. Front Genet. 13: 900572. https://doi.org/10.3389/fgene.2022.900572

Vikram P, Franco J, Burgueño J, Li H, Sehgal D, Saint-Pierre C. 2021. Strategic use of Iranian bread wheat landrace accessions for genetic improvement: Core set formulation and validation. Plant Breed. 140: 87-99. https://doi.org/10.1111/pbr.12885