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# Genetic Relationships of Azerbaijani *Aegilops tauschii* Coss. Accessions Revealed by SNP Markers in Coding Regions

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## Abstract

*Aegilops tauschii* Coss., a wild wheat relative, likely originated in the Transcaucasus region, including Azerbaijan. Natural variation in *Ae. tauschii* populations, particularly ssp. *strangulata*, offers opportunities to improve modern bread wheat varieties. This study assessed genetic relationships among 64 *Ae. tauschii* genotypes from Azerbaijan using 56837 coding sequence (CDS)-derived single nucleotide polymorphism (SNP) markers from coding regions. The SNPs comprised 67.9% transitions and 32.1% transversions. The genetic diversity index (GDI) in local *Ae. tauschii* collection averaged 0.220, and the polymorphism information content (PIC) was 0.183. Pairwise genetic distances ranged from 0 to 0.392. A dendrogram revealed three distinct clusters, with clusters II and III being the closest (genetic distance 0.0749), while cluster I was similarly distant from both (0.224 and 0.23). No correlation was observed between clustering, geographic origin, or altitude. The lack of Lineage 1 (L1) accession co-clustering may result from limited genetic variation within coding regions, the small number of studied L1 accessions, and overall low genetic distances. However, distinct sublineages or populations of ssp. *strangulata* were identified in Azerbaijan, with close genetic distances. The principal coordinate analysis (PCoA) revealed three distinct groups (A, B, and C) without intermediate genotypes, with the first axis accounting for 68.3% of the total variation. Genetic distances between groups A and B, A and C, and B and C were low, measuring 0.14, 0.137, and 0.194, respectively. These findings highlight the importance of conserving Aegilops genetic resources, which could contribute to wheat breeding and crop resilience.

**Keywords:** *Aegilops tauschii; single nucleotide polymorphism; genetic relationship; ssp. strangulate*

## Introduction

*Ae. tauschii* Coss. (2n = 2× = 14), a wild wheat relative, belongs to the Triticeae tribe of the grass family, which includes important crops such as wheat and barley. The species is thought to have primarily originated in the Transcaucasus region, where diploid *Aegilops* species, including *Ae. tauschii*, diversified approximately 2.5 to 4.5 million years ago [1, 2].

*Ae. tauschii* is commonly divided into two primary lineages, referred to as lineage 1 (L1) and lineage 2 (L2) [3]. L1 is predominantly linked with *Ae. tauschii* Coss. ssp. *tauschii*, while L2 is mainly

associated with *Ae. tauschii* Coss. ssp. *strangulata* (Eig) Tzvel. The ssp. *tauschii* has a broad distribution across the species' range, whereas ssp. *strangulata* is more restricted, extending from Transcaucasia to eastern Caspian Iran [4, 5]. Recently, a third lineage (L3) was identified by Gaurav et al. (2022), localized to modern-day Georgia [6].

*Ae. tauschii* ssp. *strangulata* is a progenitor of the D genome in hexaploid wheat, responsible for the end-use quality of bread wheat [1]. However, the wheat D genome exhibits the lowest genetic diversity compared to its other two genomes (A and B) and to *Ae. tauschii* itself [7]. This is likely due to the fact that only a limited number of *Ae. tauschii* accessions from a small geographic area hybridized with wheat during its evolution, resulting in a restricted genetic base for the wheat D genome [8]. It is estimated that only about 25% of the genetic diversity within *Ae. tauschii* contributed to the early gene flow into hexaploid wheat [6]. Consequently, *Ae. tauschii*, characterized by significant genetic diversity and its compatibility for hybridization with wheat, presents a valuable genetic resource for enhancing the genetic background of wheat. The specie harbors numerous beneficial genes that are important for the bread-making performance of bread wheat [9]. Several *Ae. tauschii* genes have been identified for resistance to a range of diseases, including Ug99 [10], leaf rust, and stripe rust [11, 12]. Additionally, traits associated with improved grain yield [13], salt and drought tolerance, and frost resistance [14] have been incorporated into wheat. Moreover, the introgression of D genome chromosomes from *Ae. tauschii* into triticale has improved its end-use quality characteristics [15].

Azerbaijan, recognized as a key region within the Asiatic center of origin for cultivated plants, has a wide range of endemic wild and cultivated species from the genera *Aegilops, Triticum*, and *Secale*. Tsunewaki (1966) identified *Ae. tauschii* in the southwestern Caspian region of Iran and the adjacent mountainous areas of Azerbaijan as a probable source of the D genome in *T. aestivum*, largely due to the presence of the waxybloom allele [16]. Later, Hammer (1980) traced the origins of *Aegilops* to the Transcaucasian region, which includes Azerbaijan [17]. Northwestern Iran, bordering Azerbaijan, is noted for its significant diversity of *Aegilops* species. Kilian et al. (2011) reported that *Ae. tauschii* is predominantly distributed along the southern Caspian Sea shores and throughout Azerbaijan, emphasizing the region's potential as a reservoir for valuable alleles in *Ae. tauschii* [18]. The natural variation in *Ae. tauschii* populations, particularly subspecies *strangulata*, within Azerbaijan offers significant opportunities for enhancing modern bread wheat varieties.

The genetic diversity of *Ae. tauschii* has been extensively studied both globally and in Azerbaijan using various molecular techniques. These include RFLP [1], microsatellites [19, 20], IRAP [21], single nucleotide polymorphism (SNPs) [22], and DNA sequencing [23]. The draft genome of *Ae. tauschii* was first sequenced in 2013 [24], which has enabled the development of new DNA markers for further research. Gaurav et al. (2022) provided sequence data for 242 *Ae. tauschii* accessions and compared them to the wheat D subgenome, characterizing the genomic diversity within the species [6]. In Azerbaijan, numerous studies have also explored the genetic diversity of *Aegilops* species, including *Ae. tauschii*, using morpho-agronomic traits [25] and various molecular markers such as SSR [26], DArT-seq [27], and SNP [28]. These molecular studies have provided important insights into the genetic structure of *Ae. tauschii* germplasm. However, further research utilizing advanced molecular markers is essential to fully characterize the genetic diversity and identify valuable traits within this germplasm for effective breeding programs.

In recent decades, SNP markers have emerged as a powerful tool in molecular genetics, largely due to their abundance in genomes and compatibility with high-throughput detection methods. SNPs are found in nearly all genomic regions, including coding sequences (CDS). Although the number of SNPs in the coding regions is relatively low due to the higher conservation of these regions compared to other genomic regions, these SNPs offer a crucial tool for detecting causative mutations [29].

The primary objective of this study is to assess the genetic relationships among Azerbaijani *Ae. tauschii* genotypes using SNP markers in the CDS regions. This research aims to provide a targeted analysis of genetic relationships within these local genotypes, contributing to a more detailed understanding of genetic diversity and its potential applications in breeding.

## Materials and Methods

Sixty-four *Aegilops tauschii* accessions from various regions of Azerbaijan were selected from a broader set provided by Gaurav et al. (2022) for use in this study [6]. The accession numbers, and geographic coordinates are provided in Table 1. The regions were identified using Google Maps, based on these coordinates.

SNP data were obtained from the Open Wild Wheat Consortium Variant (SNP) dataset [6]. To manage the large dataset, Python was used to automate tasks such as extracting information from VCF files and selecting SNPs located in coding sequence (CDS) regions.

Genetic diversity index (GDI) and polymorphism information content (PIC) for the studied SNP loci were calculated according to Weir (1990) [30] and Botstein et al. (1980) [31], respectively. Cluster analysis, principal coordinate analysis (PCoA), and an Unweighted Neighbor-Joining (UNJ) tree with 1000 bootstraps were constructed using the DARwin 6.0 software package.

**Table 1.** The list and geographic coordinates of studied local *Aegilops tauschii* accessions.

| № | ID | Latitude | Longitude | Region | № | ID | Latitude | Longitude | Region |
|---|---|---|---|---|---|---|---|---|---|
| 6 | BW_01007 | 40.5691 | 48.4008 | Agsu | 58 | BW_01078 | 40.7042 | 48.4896 | Agsu |
| 7 | BW_01008 | 39.4731 | 46.4910 | Lachin | 66 | BW_01091 | 41.2160 | 48.9946 | Shabran |
| 8 | BW_01009 | 40.4093 | 49.8671 | Baku | 75 | BW_01102 | 40.3911 | 47.4426 | Agdash |
| 9 | BW_01010 | 41.4751 | 46.6228 | Zagatala | 76 | BW_01103 | NA | NA | NA |
| 10 | BW_01011 | 38.7529 | 48.8475 | Lankaran | 77 | BW_01104 | 40.0127 | 48.4788 | Sabirabad |
| 11 | BW_01012 | 41.2160 | 48.9946 | Shabran | 78 | BW_01105 | NA | NA | NA |
| 13 | BW_01015 | NA | NA | NA | 79 | BW_01106 | 40.3000 | 47.0100 | Tartar |
| 14 | BW_01016 | NA | NA | NA | 80 | BW_01107 | 39.0341 | 48.6589 | Masalli |
| 15 | BW_01019 | NA | NA | NA | 81 | BW_01108 | 40.5319 | 49.2400 | Khizi |
| 16 | BW_01020 | NA | NA | NA | 82 | BW_01109 | 40.3800 | 48.3700 | Agsu |
| 17 | BW_01021 | NA | NA | NA | 83 | BW_01110 | 40.3800 | 48.3700 | Agsu |
| 18 | BW_01022 | 39.0500 | 48.6667 | Masalli | 84 | BW_01111 | 40.3800 | 48.3700 | Agsu |
| 29 | BW_01039 | NA | NA | NA | 85 | BW_01112 | 40.5100 | 49.2400 | Qobustan |
| 30 | BW_01041 | 41.1975 | 47.1571 | Sheki | 86 | BW_01113 | 40.5900 | 47.5000 | Agdash |
| 31 | BW_01042 | 40.7430 | 48.2126 | Ismailli | 87 | BW_01114 | 38.9059 | 48.2496 | Yardimli |
| 32 | BW_01043 | 39.5379 | 47.3034 | Masalli | 89 | BW_01116 | 40.3900 | 48.3900 | Agsu |
| 33 | BW_01044 | 39.0857 | 46.6525 | Zangilan | 90 | BW_01117 | 40.4200 | 48.6500 | Shamakhi |
| 34 | BW_01045 | 39.0350 | 46.3627 | Zangilan | 91 | BW_01118 | 40.5100 | 49.2400 | Qobustan |
| 44 | BW_01060 | 39.9266 | 48.9206 | Shirvan | 92 | BW_01119 | 40.5700 | 48.3800 | Agsu |
| 45 | BW_01062 | 39.9266 | 48.9206 | Shirvan | 93 | BW_01120 | 41.1200 | 47.1000 | Sheki |
| 46 | BW_01063 | 39.9096 | 48.3595 | Saatli | 94 | BW_01121 | 40.5900 | 47.5000 | Agdash |
| 47 | BW_01065 | 40.6319 | 48.6364 | Shamakhi | 95 | BW_01122 | 41.1500 | 48.5400 | Quba |
| 48 | BW_01066 | 40.6319 | 48.6364 | Shamakhi | 96 | BW_01123 | 41.1200 | 49.2000 | NA |
| 49 | BW_01068 | 40.5742 | 48.3896 | Agsu | 97 | BW_01124 | 40.3800 | 48.3700 | Agsu |
| 50 | BW_01069 | 40.5742 | 48.3896 | Agsu | 138 | BW_01179 | 40.6300 | 48.6300 | Shamakhi |
| 51 | BW_01070 | 40.5742 | 48.3896 | Agsu | 139 | BW_01181 | 40.6300 | 48.6300 | Shamakhi |
| 52 | BW_01071 | 40.6042 | 48.4396 | Agsu | 140 | BW_01182 | NA | NA | NA |
| 53 | BW_01072 | 40.6042 | 48.4396 | Agsu | 153 | BW_23958 | 40.98369 | 47.122595 | Sheki |
| 54 | BW_01073 | 40.7042 | 48.4896 | Agsu | 193 | BW_23998 | 40.50005 | 48.980183 | Qobustan |
| 55 | BW_01074 | 40.7042 | 48.4896 | Agsu | 194 | BW_23999 | 39.45755 | 45.361033 | Babek |
| 56 | BW_01076 | 40.7042 | 48.4896 | Agsu | 198 | BW_23890 | 40.57015 | 48.747711 | Qobustan |
| 57 | BW_01077 | 40.7042 | 48.4896 | Agsu | 203 | BW_23895 | 40.39736 | 49.852447 | Baku |

## Results

The genetic diversity of *Aegilops tauschii* accessions collected from different regions of Azerbaijan was evaluated using 56,837 SNP markers located within coding DNA sequence (CDS) regions.

A total of 67.9% of the SNPs identified in the CDS regions were transitions (Ts), whereas 32.1% were transversions (Tv) (Table 2). Among the transition mutations, G→A was the most frequent (12,376 occurrences), followed by C→T (12,326 occurrences). In total, 18,231 transversions were detected. All

eight transversion classes were represented, with C→G being the most frequent (3193 occurrences) and T→A the least frequent (1396 occurrences). The overall Ts/Tv ratio was 2.1.

**Table 2.** The types of SNP substitutions in the coding regions of *Aegilops tauschii* genome.

| Substitutions | Number | Substitutions | Number |
|---|---|---|---|
| Transitions (Ts) | 38606 | Transversions (Tv) | 18231 |
| A/G | 7013 | C/G | 3193 |
| C/T | 12326 | A/T | 1481 |
| G/A | 12376 | G/T | 2800 |
| T/C | 6891 | A/C | 1612 |
| | | G/C | 3253 |
| | | C/A | 2897 |
| | | T/G | 1599 |
| | | T/A | 1396 |
| Ts% | 67.9 | Tv% | 32.1 |
| **Total** | **56837** | | |
| **Ts/Tv** | **2.1** | | |

The average genetic diversity index (GDI) across the 56,837 SNP loci was 0.220, while the polymorphism information content (PIC) was 0.183. For comparison, the GDI was also calculated for a broader panel of 254 *Ae. tauschii* accessions originating from different countries, including the 64 Azerbaijani accessions analyzed in this study, using the same SNP loci. The resulting GDI was 0.21.

Pairwise genetic distances among the studied accessions ranged from 0 to 0.392. The minimum genetic distance was observed between four pairs of accessions, whereas the maximum distance occurred between BW_01020 (No. 16) and BW_01044 (No. 33).

Cluster analysis based on SNP markers grouped the accessions into three major clusters (Figure 1). Most branches were supported by bootstrap values of 100%. Clusters II and III were the most closely related, with a genetic distance of 0.0749, whereas cluster I was similarly distant from clusters II and III, with genetic distances of 0.224 and 0.230, respectively. Cluster I contained the majority of the analyzed accessions and was further divided into two subclusters (Ia and Ib) separated by a genetic distance of 0.229. Subcluster Ia comprised 16 accessions and showed the closest relationship to cluster II, with a genetic distance of 0.106. Subcluster Ib formed two distinct groups connected by a relatively long branch in the dendrogram. Three accessions (BW_01044, BW_01070, and BW_01110) were clearly separated from the remaining members of subcluster Ib, with a genetic distance of 0.14. Two of these accessions originated from the Agsu region and one from the Zangilan district. No comparable subdivision was observed within clusters II or III.

To further examine the factors underlying the observed genetic clustering, the relationships between cluster membership and geographical origin, altitude, and subtaxonomic classification were evaluated. No clear association was observed between genetic clustering and the geographical origin of the accessions. Accessions collected from the same regions, including Masalli, Gobustan, and Shamakhi, were distributed among different clusters. Of the 17 accessions from Agsu, nine were assigned to clusters II and III, five to subcluster Ia, and three to subcluster Ib.

Similarly, clustering did not correspond to collection altitude. Accessions collected across a broad altitudinal range were distributed throughout all clusters and subclusters. For example, accession BW_01045 from Zangilan (2,175 m) clustered in subcluster Ia with BW_01008 from Lachin (1,125 m), whereas accession BW_01122 collected at 1,675 m was assigned to subcluster Ib, and the Babek accession collected at 1,350 m was grouped in cluster II. Nevertheless, 11 of the 26 genotypes (42.3%) in clusters II and III originated from elevations above 600 m, compared with 8 of the 38 accessions (21.0%) in cluster I.

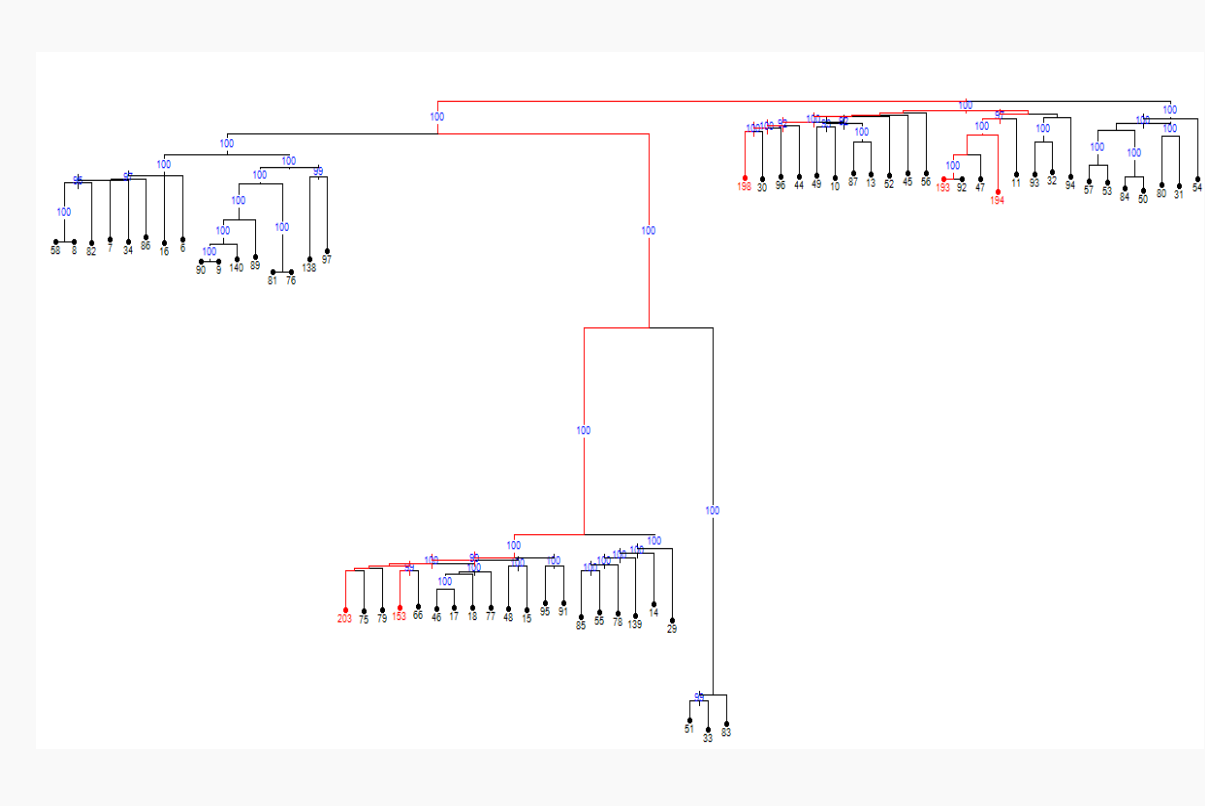

**Fig 1.** Dendrogram illustrating the genetic relationships among 64 Azerbaijani accessions based on 56837 SNP markers derived from coding regions. Accessions highlighted in red are classified as belonging to Lineage 1 (L1) and the subspecies *Ae*. *tauschii* ssp. *tauschii.*

Most of the analyzed material belonged to *Ae. tauschii* subsp. *strangulata*, whereas only five accessions were classified as subsp. *tauschii*. The subsp. *tauschii* accessions were distributed among different clusters rather than forming a distinct group. Two accessions (BW_23895 and BW_23958) were assigned to subcluster Ib with a genetic distance of 0.047, whereas the remaining three accessions (BW_23998, BW_23999, and BW_23890) were grouped within cluster II, with pairwise genetic distances ranging from 0.050 to 0.097. Consequently, no distinct clustering of the L1 lineage was observed in the dendrogram. Notably, accession BW_23998 (ssp. *tauschii*) from Gobustan showed an identical SNP profile to accession BW_01119 (ssp. *strangulata*) from Agsu.

Principal coordinate analysis (PCoA) further resolved the genetic relationships among the accessions (Figure 2). The first principal coordinate explained 68.3% of the total genetic variation, while the first three coordinates together accounted for 90.5%. Three distinct groups were identified, although their organization differed from that obtained by hierarchical cluster analysis. Group A comprised three accessions corresponding to subcluster Ib and exhibited within-group genetic distances ranging from 0.027 to 0.034 (mean = 0.030). Group B included the remaining accessions of subcluster Ib, with pairwise genetic distances ranging from 0.020 to 0.098 (mean = 0.066). Group C contained accessions from clusters II and III together with subcluster Ia and showed genetic distances ranging from 0 to 0.150 (mean = 0.100). Among the 17 accessions collected from Agsu, two belonged to Group A, one to Group B, and fourteen to Group C. The genetic distances between Groups A and B, A and C, and B and C were 0.140, 0.137, and 0.194, respectively.

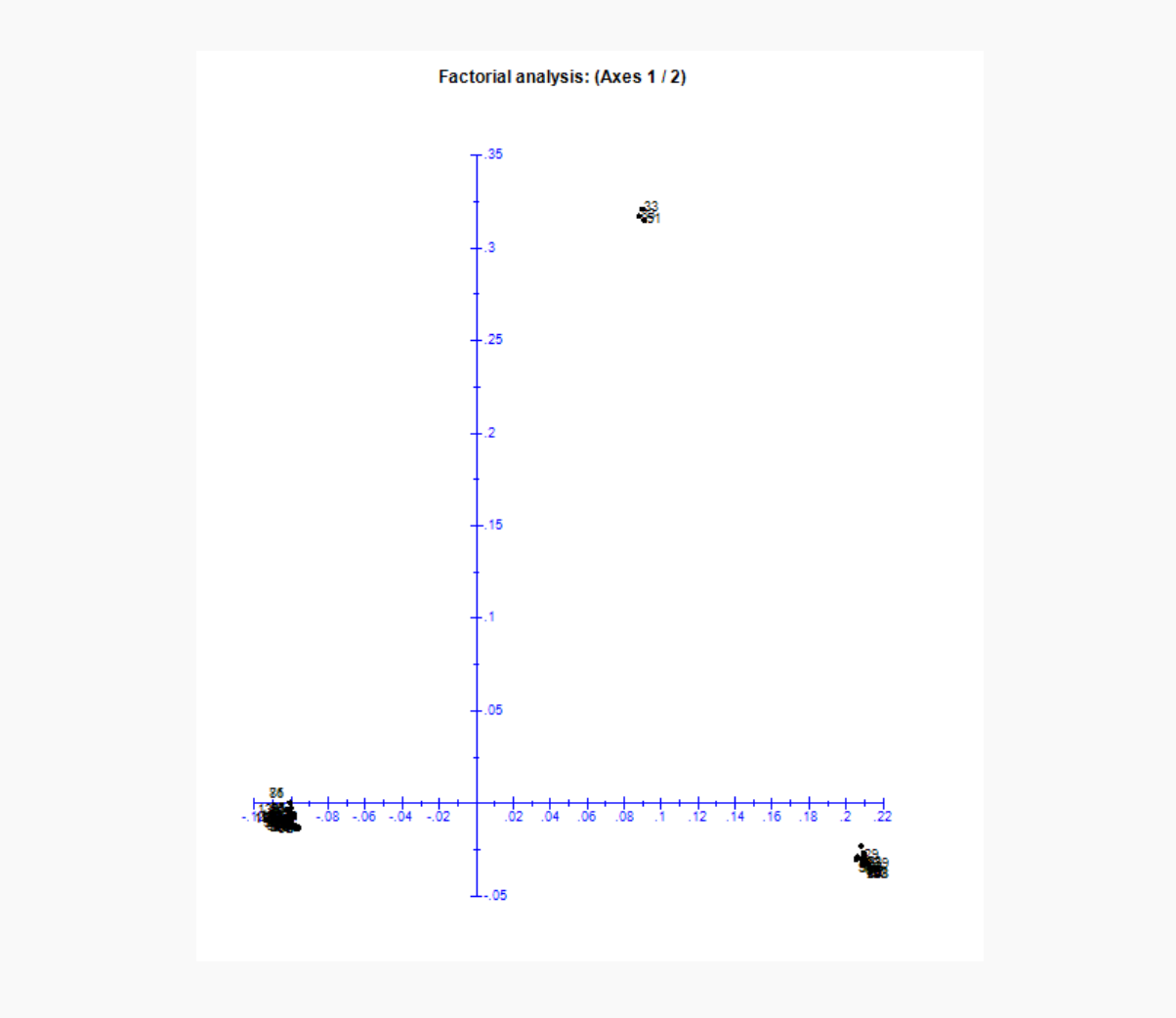


**Fig 2.** Scatter plot showing the distribution of 64 *Ae. tauschii* accessions based on SNP data from coding regions.

## Discussion

Uncovering the genetic diversity and relationships within *Aegilops tauschii* accessions is crucial for understanding their evolutionary potential and for utilizing their valuable traits in breeding programs. Careful selection of parental accessions is essential for enhancing genetic diversity in future cultivars.

In the current study a total of 56837 SNP markers in the CDS regions were used to study the genetic diversity of *A. tauschii* accessions.

The predominance of transition mutations over transversions is consistent with the mutational patterns commonly observed in coding regions of plant genomes. Transitions generally produce synonymous substitutions more frequently than transversions and are therefore less likely to alter protein function. In particular, the high frequency of C→T transitions is consistent with the spontaneous deamination of methylated cytosine, a well-recognized source of mutations in CpG-rich genomic regions. Likewise, the Ts/Tv ratio of 2.1 agrees with the expected transition bias reported in many plant genomes and reflects the evolutionary constraints acting on protein-coding sequences [32].

The moderate GDI and PIC values observed in this study are consistent with the conserved nature of coding regions and the biallelic characteristics of SNP markers, both of which generally reduce estimates of genetic diversity compared with multiallelic marker systems. The diversity estimates are comparable to those previously reported for *Ae. tauschii* and related wheat germplasm using SNP markers, although somewhat lower than values obtained with highly polymorphic marker systems such

as SCoT [3, 33]. Furthermore, the similar GDI values obtained for the Azerbaijani subset (0.22) and the broader global collection (0.21) suggest that the Azerbaijani germplasm captures a substantial proportion of the genetic diversity represented in the larger dataset. This finding highlights the potential value of Azerbaijani *Ae. tauschii* accessions as a genetic resource for wheat improvement.

The cluster analysis revealed clear genetic structuring within the Azerbaijani collection, with three principal clusters and further subdivision within cluster I. The distinct separation of three accessions within subcluster Ib suggests the presence of genetically differentiated germplasm that may represent unique breeding resources. The high bootstrap support across the dendrogram further indicates that the inferred genetic relationships are robust.

The absence of a clear relationship between genetic clustering and either geographical origin or altitude suggests that these factors have had only a limited influence on the current genetic structure of the Azerbaijani *Ae. tauschii* collection. Similar findings have been reported for Turkish and Syrian *Triticum durum* accessions, where SNP-based clustering showed no significant association with geographical origin [34]. In contrast, Abbasov et al. (2020) reported a partial correspondence between SNP-based clustering and geographical distribution in *Ae. tauschii* [27]. These differences may reflect variation in sampling strategies, marker systems, or the genetic composition of the analyzed populations.

Although *Ae. tauschii* has traditionally been divided into two subspecies based on spike morphology (ssp. *tauschii* and ssp. *strangulata*) [17], molecular studies have shown that the genetic lineages L1 and L2 provide a more informative framework for describing population structure. In the present study, the L1 accessions did not form a separate cluster, contrasting with previous studies in which STRUCTURE analysis consistently distinguished the L1 and L2 lineages [28]. The lack of differentiation observed here is likely attributable to the use of SNPs located exclusively within coding sequences, which represent the most evolutionarily conserved regions of the genome [35]. The limited number of L1 accessions and the relatively low overall genetic distances among the analyzed genotypes may have further reduced the ability to resolve lineage-specific clustering.

The identical SNP profile observed between one ssp. *tauschii* accession and one ssp. *strangulata* accession is noteworthy. Gene flow between these subspecies remains debated. Evidence from Iran has suggested historical hybridization and introgression between the two taxa [4], whereas studies from Transcaucasia have proposed that they are largely genetically isolated [5]. Nevertheless, occasional hybridization and the occurrence of intermediate forms have also been documented [1]. Consequently, the observed similarity between these two accessions may reflect historical introgression or shared ancestry, although additional analyses using more variable genomic regions would be required to clarify this relationship.

The overall topology of the dendrogram suggests that the genetic structure of the Azerbaijani collection is driven primarily by differentiation within *Ae. tauschii* subsp. *strangulata*. This observation is consistent with previous studies reporting multiple sublineages within the L2 lineage, including distinct groups identified in Azerbaijan and around the southwestern Caspian Sea [27, 28]. The presence of these sublineages supports the view that the southwestern Caspian region represents an important center of diversity for the D-genome progenitor of bread wheat.

The PCoA supported the existence of three genetically distinct groups, although their composition differed from that inferred by hierarchical clustering. Such differences are expected because hierarchical clustering and PCoA summarize genetic relationships using different mathematical approaches. While dendrograms impose a hierarchical structure on the data, PCoA preserves the overall variance and spatial relationships among genotypes without hierarchical constraints [36]. Therefore, the complementary use of both methods provides a more comprehensive assessment of population structure [37].

The low genetic distances observed among the PCoA groups, despite their clear separation in the ordination plot, suggest that differentiation among groups is driven by variation at a limited number of informative loci rather than by extensive genome-wide divergence. This pattern is consistent with the generally high genetic similarity expected when analyses are based on conserved coding regions.

## Conclusions

In conclusion, the results indicate moderate genetic diversity and the presence of distinct genetic groups within the Aegilops collection of Azerbaijani origin, as revealed by SNPs in the CDS regions. The analysis demonstrates that the coding regions are highly conserved between the two subspecies. The findings underscore the importance of conserving Aegilops genetic resources in Azerbaijan, as they may significantly contribute to advancements in wheat breeding and crop resilience in the region.

## Author Contributions

Conceptualization: M.A.; Methodology and bioinformatic analysis: U.H.-M., O.M.; Data interpretation: S.B., F.A., E.H.; Writing – original draft: S.B.; Review & editing: M.A., F.A., U.H.-M., O.M., E.H., S.B.; All authors have read and agreed to the published version of the manuscript.

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## Competing Interests

The authors have declared that no competing interests exist.

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