J. Agr. Sci. Tech. (2020) Vol. 22(3): 851-862

Genetic Structure Characteristic of *Aegilops tauschii* from Different Geographical Populations and the Origin of Chinese Population

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ABSTRACT

As the diploid progenitor of common wheat, *Aegilops tauschii* is used as a genetic resource for improving common wheat. In this study, the genetic differentiation index between Yellow River (Shaanxi and Henan) and Xinjiang groups (0.322, 0.377) were obviously higher than between the former and Central Asia groups (0.231, 0.289). Meanwhile, the genetic distances between Yellow River (Shaanxi and Henan) and Xinjiang groups (0.285, 0.329) exhibit larger values compared with those between the former and Central Asia groups (0.283, 0.321). These results reveal that the genetic constitution of Yellow River and Central Asia groups is of more similarity compared with Xinjiang group. The phylogenetic tree demonstrates that *Ae. tauschii* in Yellow River and part of that in Central Asia are firstly gathered to be a subset. Then the subset and Xinjiang group are classified into a clade, which could be assigned to Central Asia and Middle East populations, implying that *Ae. tauschii* in Yellow River has a closer relationship with part of that in Central Asia compared with Xinjiang. Our finding further clarifies that *Ae. tauschii* in Yellow River might be directly derived from one/several types from Central Asia such as Turkmenistan, Pakistan, and Afghanistan.

Keywords: Genetic differentiation, Genetic distance, Geographical population, Simple sequence repeat, Yellow River group.

INTRODUCTION

Aegilops tauschii Cosson (DD, 2n= 2x= 14) is an annual, self-pollinated plant with abundant valuable disease-resistance characters, productivity traits and abiotic stress resistances (Imtiaz *et al*., 2008; Sukhwinder *et al*., 2012; Goldasteh *et al*., 2019). As the diploid progenitor of common wheat, the superior genes of *Ae. tauschii* could be conveniently transferred into common wheat by recombination between homologous chromosomes, and most possibly, undesirable gene linkages could be easily broken simultaneously in repeated backcrossing with recurrent parent (Gill and Raupp, 1987). Up to now, lots of QTLs/genes from *Ae. tauschii* have been identified and located through advanced backcross population or introgression lines (Kunert *et al*., 2007; Naz *et al*., 2008; Yu *et al*., 2014; Dale *et al*., 2017; Zhang *et al*., 2018).

Ae. tauschii is a widely distributed species with high genetic diversity (Lubbers *et al*., 1991; Dvorak *et al*., 1998, 2011). It is mainly classified into *Ae. tauschii* ssp. *tauschii* and *Ae. tauschii* ssp. *strangulata* based on the morphological features of spike, in which the former is cylindrical, including var. *typical*, var. *meyeri* and var. *anathera*. As a monotype, the latter exhibits a prominent moniliform characteristic (Kihara and Tanaka, 1958). In addition, an intermediate type between the above two morphotypes is found in some *Ae. tauschii* (Matsuoka *et al*., 2013, 2015). Mainly

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[DOR: 20.1001.1.16807073.2020.22.3.8.8]

distributed in the Middle East, including Syria, South-east Turkey, Northern Iraq, and Western Iran, *etc*., *Ae. tauschii* is naturally spreading to Western China (Yili area of Xinjiang province) by way of Central Asia (Afghanistan, Tajikistan, Turkmenistan, Uzbekistan, *etc*.). Therefore, Yili area of Xinjiang is considered to be the easternmost of the natural distribution for wild *Ae. tauschii* population (Matsuoka *et al*., 2015; Gogniashvili *et al*., 2016).

Ae. tauschii was also found in the middle reaches of Yellow River in the eighties of the last century, including Shaanxi and Henan provinces (Yen *et al*., 1984), and is deemed as a kind of farmland weed accompanying common wheat. It could be noticed that large span in geographical isolation exists between the middle reaches of Yellow River and Yili area of Xinjiang. The detailed spreading route of *Ae. tauschii* in this case, which remains ambiguous scientifically, is very interesting and deserve intensive exploration. Interestingly, Yen *et al*. (1984) believed that the *Ae. tauschii* in the Yellow River could be directly spread from Xinjiang, which was accompanied with the original wheat cultivated varieties. Nevertheless, based on the established genetic similarity of 31 accessions from China and Iran by SSR markers, Wei *et al*. (2008) designated Iran as the origin of *Ae. tauschii* in the Yellow River. To clarify the dispute, the origin and evolution relationship of *Ae. tauschii* between Yellow River and Xinjiang areas were explored through SSR markers in this work, and the genetic structure characteristics of Yellow River, Xinjiang, Central Asia, and Middle East geographical population were analyzed, which may provide valuable germplasm resources for the improvement of common wheat.

MATERIALS AND METHODS

Plant Material

A total of 169 accessions of *Ae. tauschii* were used in this study (Table 1). Ninety-one *Ae. tauschii* accessions marked as 'XJ', 'T', and 'S' were originally derived from Xinjiang, Henan, and Shaanxi, respectively. They were preserved and cultivated in Plant Germplasm Resources and Genetic Engineering Laboratory, Henan University. The other 78 accessions named 'AY' were primarily distributed in Middle East and Central Asia, and were provided by the US National Plant Germplasm Center.

DNA Extraction and SSR Amplification

Genomic DNA was extracted from young leaves according to the approach reported by Han *et al*. (2015). The Simple Sequence Repeat (SSR) markers were referred from wheat D genome (http://wheat.pw.usda.gov/cgi-bin/GG3/). PCR reactions for SSR were performed using the method described by Li *et al*. (2018). PCR amplifications were performed in 50 µL reaction volume containing 2.5 U Taq polymerase (TaKaRa), 100 ng of template DNA, 5 µL of 10X buffer ($MgCl_2$ plus), 0.4 mM dNTP, 0.5 µM of each primer, and making up to 50 µL with ddH_2O. The reaction was carried out in a S1000 Thermal Cycler (Bio-Rad Corp., USA) using the following protocol: pre-denaturation at 94°C for 3 minUTES, cycled 30 times at 94°C for 45 seconds, primer specific annealing temperature for 45 seconds, and 72°C for 1 minute, and a final extension at 72°C for 10 minutes.

Genetic Diversity and Phylogenetic Analysis

The polymorphic bands amplified for each pair of SSR markers were assigned the number of alleles at the site. The Polymorphic Information Content (PIC) of SSR marker, *Nei's* Genetic Diversity (GD) between *Ae. tauschii* populations, and phylogenetic tree constructed based on the Unweighted Pair-Group Method with Arithmetic means (UPGMA) algorithm were analyzed by PowerMarker V3.25 software

[DOR: 20.1001.1.16807073.2020.22.3.8.8]

Table 1. *Aegilops tauschii* accessions used in this work.

No	Source	No	Source	No	Source
XJ001	Huocheng, Xinjiang	T011	Yima, Henan	AY26	Afghanistan, Central Asia
XJ002	Huocheng, Xinjiang	T014	Lushi, Henan	AY27	Afghanistan, Central Asia
XJ006	Huocheng, Xinjiang	T015	Lushi, Henan	AY28	Azerbaijan, Middle East
XJ014	Huocheng, Xinjiang	T016	Lushi, Henan	AY29	Azerbaijan, Middle East
XJ015	Huocheng, Xinjiang	T017	Luanchuan, Henan	AY30	Afghanistan, Central Asia
XJ023	Yining, Xinjiang	T019	Luoning, Henan	AY31	Afghanistan, Central Asia
XJ028	Nilka, Xinjiang	T024	Jiyuan, Henan	AY32	Turkey, Middle East
XJ029	Gongliu, Xinjiang	T025	Jiyuan, Henan	AY33	Dagestan, Middle East
XJ030	Gongliu, Xinjiang	T026	Jiyuan, Henan	AY34	Tajikistan, Central Asia
XJ038	Gongliu, Xinjiang	T027	Qinyang, Henan	AY35	Turkmenistan, Central Asia
XJ039	Gongliu, Xinjiang	T035	Wuzhi, Henan	AY37	Turkmenistan, Central Asia
XJ040	Gongliu, Xinjiang	T038	Mengzhou, Henan	AY38	West Asia, Middle East
XJ041	Gongliu, Xinjiang	T045	Mengzhou, Henan	AY39	Azerbaijan, Middle East
XJ042	Gongliu, Xinjiang	T050	Wenxian, Henan	AY40	Azerbaijan, Middle East
XJ043	Gongliu, Xinjiang	T052	Wenxian, Henan	AY41	Iran, Middle East
XJ065	Xinyuan, Xinjiang	T054	Wenxian, Henan	AY42	Afghanistan, Central Asia
XJ066	Xinyuan, Xinjiang	T057	Wenxian, Henan	AY43	Turkmenistan, Central Asia
XJ069	Xinyuan, Xinjiang	T058	Wenxian, Henan	AY44	Turkey, Middle East
XJ070	Xinyuan, Xinjiang	T061	Wenxian, Henan	AY45	Afghanistan, Central Asia
XJ071	Xinyuan, Xinjiang	T062	Wenxian, Henan	AY46	Iran, Middle East
XJ073	Xinyuan, Xinjiang	T065	Wenxian, Henan	AY47	Afghanistan, Central Asia
XJ074	Xinyuan, Xinjiang	T066	Wenxian, Henan	AY48	Turkmenistan, Central Asia
SX01	Lantian, Shaanxi	T068	Wenxian, Henan	AY49	Iran, Middle East
SX03	Lantian, Shaanxi	T072	Wenxian, Henan	AY50	Turkey, Middle East
SX06	Weinan, Shaanxi	T074	Yuanyang,Henan	AY51	Turkey, Middle East
SX07	Weinan, Shaanxi	T077	Yanjin, Henan	AY52	Turkmenistan, Central Asia
SX08	Weinan, Shaanxi	T079	Yanjin, Henan	AY53	Azerbaijan, Middle East
SX09	Weinan, Shaanxi	T081	Fengqiu, Henan	AY54	Afghanistan, Central Asia
SX10	Weinan, Shaanxi	T082	Fengqiu, Henan	AY55	West Asia, Middle East
SX12	Xianyang, Shaanxi	T094	Puyang, Henan	AY56	Afghanistan, Central Asia
SX14	Lantian, Shaanxi	T102	Fanxian, Henan	AY57	Turkmenistan, Central Asia
SX17	Pucheng, Shaanxi	T108	Taiqian,Henan	AY58	Turkey, Middle East
SX18	Yanliang, Shaanxi	T109	Taiqian,Henan	AY60	Iran, Middle East
SX19	Pucheng, Shaanxi	T111	Dongming,Henan	AY61	Iran, Middle East
SX21	Yanliang, Shaanxi	AY01	Azerbaijan, Middle East	AY62	Turkmenistan, Central Asia
SX25	Yanliang, Shaanxi	AY02	Qinghai	AY63	Pakistan, Central Asia
SX26	Jingyang, Shaanxi	AY03	Iran, Middle East	AY64	Turkey, Middle East
SX28	Sanyuan, Shaanxi	AY04	Azerbaijan, Middle East	AY65	Iran, Middle East
SX29	Jingyang, Shaanxi	AY05	Turkmenistan, Central Asia	AY66	Iran, Middle East
SX30	Sanyuan, Shaanxi	AY06	Iran, Middle East	AY67	Azerbaijan, Middle East
SX31	Sanyuan, Shaanxi	AY07	Tajikistan, Central Asia	AY68	West Asia, Middle East
SX35	Chengxian, Shaanxi	AY08	Iran, Middle East	AY69	Turkmenistan, Central Asia
SX40	Chayang, Shaanxi	AY10	Afghanistan, Central Asia	AY70	Turkey, Middle East
SX62	Zhouzhi, Shaanxi	AY11	Turkmenistan, Central Asia	AY72	Georgia, Middle East
SX65	Qishan, Shaanxi	AY12	Pakistan, Central Asia	AY73	Azerbaijan, Middle East
SX66	Qishan, Shaanxi	AY13	Georgia, Middle East	AY74	Turkey, Middle East
SC1	Xi'an, Shaanxi	AY14	Armenia, Middle East	AY75	Dagestan, Middle East
SC5	Xi'an, Shaanxi	AY15	Turkmenistan, Central Asia	AY76	Kazakhstan, Central Asia
SC6	Xi'an, Shaanxi	AY16	Iran, Middle East	AY77	Iran, Middle East
SL2	Xi'an, Shaanxi	AY17	Turkey, Middle East	AY78	Afghanistan, Central Asia
T001	Lingbao, Henan	AY18	Tajikistan, Central Asia	AY79	Turkmenistan, Central Asia
T002	Lingbao, Henan	AY19	Afghanistan, Central Asia	AY80	Iran, Middle East
T003	Lingbao, Henan	AY20	India, Central Asia	AY81	Turkey, Middle East
T004	Shanxian, Henan	AY21	Tajikistan, Central Asia	AY172	Pakistan, Central Asia
T005	Sanmenxia, Henan	AY22	Pakistan, Central Asia	AY173	Iran, Middle East
T006	Mianchi, Henan	AY23	Iran, Middle East		
T009	Yimian, Henan	AY25	Afghanistan, Central Asia		

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(Liu and Muse, 2005). The Analysis of Molecular Variance (AMOVA) was carried out by GenAlEx 6.1 software (Peakall and Smouse, 2006), and the value of *F*-Statistics (F_{ST}) was used to evaluate the level of genetic differentiation among populations.

RESULTS

Genetic Diversity Revealed by SSR Markers

To evaluate the genetic diversity of *Ae. tauschii* population, altogether 72 SSR markers were selected from GrainGene 2.0 database, 51 of which (70.8%) were established to be polymorphic. They were found distributed on seven chromosomes with relative uniformity based on the Wheat-Composite-2004 reference mapping from GrainGene 2.0 website, which exhibited desirable detection efficiency in *Ae. tauschii* population (Figure S1). In 169 *Ae. tauschii* accessions, a total of 369 alleles ranging from 2 (Xcfd27) to 16 (Xgwm314) were obtained, with an average of 7.2 alleles per locus (Table 2). The major allele frequencies varied from 0.142 (Xgwm44) to 0.947 (Xcfd27), with the overall mean of 0.506. In detail, 148 rare alleles (40.11%) were detected with the frequency lower than 5%, while only one was found over 90% (Figure 1). According to the Polymorphic Information Content (PIC), 34 SSR loci (66.7%), 13 SSR loci (25.5%) and only 4 SSR loci (7.8%) were determined to be highly (PIC> 0.5), moderately (0.5> PIC> 0.25), and lowly (PIC< 0.25) informative, respectively. The values of *Nei's* Gene Diversity (GD) for 51 loci were found to be

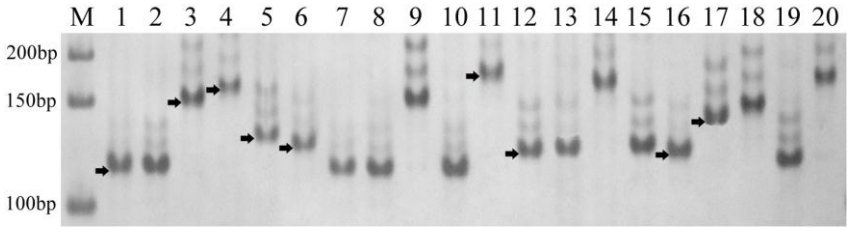

Figure S1. PCR amplification of Xgwm456 site in partial strains (M: 50 bp DNA Ladder marker; 1-20: Partial strains of *Ae. tauschii* population). Black arrows: Polymorphic sites.

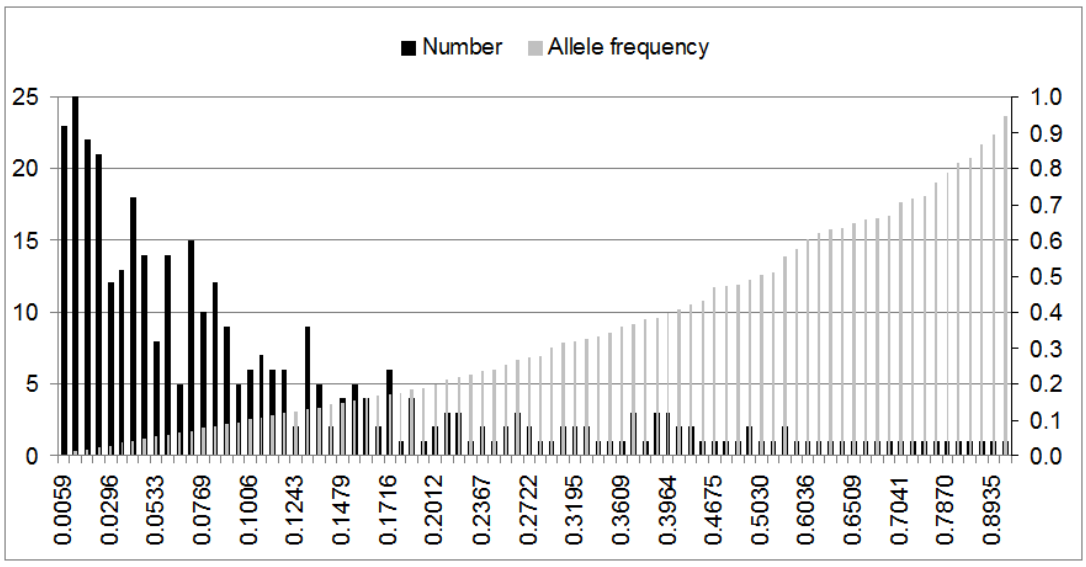

Figure 1. Frequency distribution of the total 369 alleles in *Ae. tauschii* population.

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Table 2. Genetic diversity revealed by 51 SSR markers in 169 *Aegilops tauschii* accessions.[a]

Markers	Chromosomes	Na	MAF	GD	PIC
Xcfd27	1D	2	0.947	0.111	0.105
Xcfd63	1D	4	0.669	0.509	0.465
Xgdm126	1D	8	0.432	0.759	0.735
Xgpw315	1D	9	0.408	0.719	0.676
Xgpw2224	1D	3	0.704	0.454	0.399
Xgwm106	1D	6	0.479	0.681	0.636
Xgwm232	1D	6	0.385	0.730	0.686
Xwmc216	1D	9	0.396	0.770	0.743
Xbarc145	2D	3	0.604	0.489	0.380
Xcfd50	2D	6	0.657	0.533	0.497
Xgdm19	2D	2	0.787	0.334	0.278
Xgpw338	2D	12	0.320	0.824	0.805
Xgpw1184	2D	5	0.651	0.546	0.516
Xgwm102	2D	7	0.408	0.733	0.696
Xgwm157	2D	8	0.343	0.787	0.759
Xgwm382	2D	12	0.266	0.842	0.824
Xcfd34	3D	3	0.556	0.574	0.498
Xgpw322	3D	9	0.278	0.808	0.783
Xgpw1149	3D	12	0.396	0.734	0.697
Xgwm314	3D	16	0.154	0.906	0.898
Xgwm456	3D	12	0.379	0.793	0.771
Xwmc375	3D	6	0.509	0.676	0.638
Xcfd193	4D	2	0.864	0.242	0.213
Xgpw311	4D	9	0.213	0.846	0.828
Xgwm165	4D	2	0.894	0.189	0.171
Xgwm538	4D	7	0.325	0.762	0.723
Xwmc48	4D	6	0.396	0.759	0.727
Xwmc206	4D	8	0.574	0.628	0.596
Xwmc331	4D	8	0.370	0.776	0.748
Xcfd8	5D	7	0.420	0.682	0.628
Xcfd57	5D	7	0.633	0.572	0.553
Xgwm16	5D	9	0.385	0.741	0.703
Xgwm182	5D	12	0.254	0.849	0.833
Xgwm192	5D	10	0.370	0.774	0.745
Xgwm205	5D	6	0.370	0.724	0.677
Xgwm565	5D	6	0.663	0.530	0.498
Xwmc96	5D	4	0.491	0.539	0.432
Xwmc357	5D	6	0.556	0.618	0.570
Xcfd13	6D	9	0.420	0.752	0.723
Xcfd38	6D	8	0.491	0.705	0.675
Xcfd80	6D	6	0.817	0.331	0.319
Xcfd213	6D	3	0.621	0.510	0.427
Xgwm55	6D	2	0.828	0.283	0.243
Xbarc70	7D	9	0.627	0.587	0.568
Xbarc154	7D	6	0.757	0.416	0.397
Xbarc305	7D	10	0.716	0.479	0.464
Xcfd14	7D	8	0.503	0.682	0.645
Xgpw351	7D	11	0.468	0.737	0.715
Xgwm44	7D	12	0.142	0.901	0.892
Xgwm295	7D	10	0.201	0.865	0.850
Xwmc273	7D	6	0.722	0.459	0.433
Mean		7.235	0.506	0.632	0.598

[a] Na: Number of alleles, MAF: Major allele Frequency, GD: *Nei's* Gene Diversity, PIC: Polymorphism Information Content.

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ranging from 0.906 (Xgwm314) to 0.111 (Xcfd27), with an average of 0.632. These results indicate that high genetic variations of alleles are present in *Ae. tauschii* population.

Genetic Differentiation among Populations

Ae. tauschii population was geographically divided into five sample groups: Middle East, Central Asia, Xinjiang, Shaanxi and Henan (Table 1). To investigate genetic differentiation, the variability parameters were compared among five sample groups (Table 3). The values of Na, GD, and PIC in the Middle East group were highest among the five groups, exhibiting 346, 0.746, and 0.708, respectively. This indicates much higher genetic diversity in the Middle East group, further confirming the assumption that this area could be the diversity center of *Ae. tauschii*. In China, the number of alleles found in Shaanxi and Henan groups was similar, and was fewer than that in Xinjiang group, resulting in a general increase in GD from 0.283, 0.272 to 0.455. Likewise, PIC of Xinjiang group was calculated to be 0.409, higher than the other two groups in China. Relatively, the variability parameters of the Central Asia group fall in between those of Middle East and China groups. In addition, AMOVA (analysis of molecular variance) indicated significant genetic differentiation (P= 0.010) among the five sample groups. As shown in Table 4, the lowest genetic differentiation index was observed between Middle East and Central Asia groups (F_{ST}= 0.074), implying similar genetic constitution of the two groups. Secondly, the F_{ST} value between Central Asia and Xinjiang groups was determined to be 0.158. Surprisingly, the F_{ST} between Yellow River (Shaanxi and Henan) and Xinjiang groups (0.322, 0.377) were obviously higher than between Yellow River and Central Asia groups (0.231, 0.289). Meanwhile, the genetic distance among the five sample groups was calculated by PowerMarker V3.25 software. As presented in Table 5, the genetic distance between Yellow River (Shaanxi and Henan) and Xinjiang groups (0.285, 0.329) were also higher than between Yellow River and Central Asia groups (0.283, 0.321). In addition, the genetic distance between Xinjiang and Central Asia groups was 0.225. The results indicate that the genetic constitution of Yellow River and Central Asia groups is relatively more similar in comparison with that of the former and

Table 3. The difference of genetic diversity among five sample groups. [a]

Populations	Sample Sizes	Na	GD	PIC
Middle East	43	346	0.746	0.708
Central Asia	35	283	0.633	0.591
Xinjiang	22	182	0.455	0.409
Shaanxi	28	125	0.283	0.244
Henan	41	112	0.272	0.235

[a] Na: Number of alleles, GD: *Nei's* Gene Diversity, PIC: Polymorphism Information Content.

Table 4. The genetic differentiation index of *Ae. tauschii* among five sample groups. [a]

Populations	Middle East	Central Asia	Xinjiang	Shaanxi	Henan
Middle East	-	0.010	0.010	0.010	0.010
Central Asia	0.074	-	0.010	0.010	0.010
Xinjiang	0.192	0.158	-	0.010	0.010
Shaanxi	0.280	0.231	0.322	-	0.010
Henan	0.315	0.289	0.377	0.266	-

[a] The upper and lower parts of the diagonal present the P values of the paired test and the F_{ST} values between two populations, respectively.

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Table 5. The genetic distance among five sample groups.

Populations	Middle East	Central Asia	Xinjiang	Shaanxi	Henan
Middle East	-	0.158	0.305	0.404	0.421
Central Asia	0.158	-	0.225	0.283	0.321
Xinjiang	0.305	0.225	-	0.285	0.329
Shaanxi	0.404	0.283	0.285	-	0.138
Henan	0.421	0.321	0.329	0.138	-

Xinjiang groups.

Phylogenetic Tree

The phylogenetic tree was constructed based on the genetic distance among 169 *Ae. tauschii* through UPGMA method (Figure 2). Six subgroups could be classified from the phylogenetic tree. The outermost subgroup I was the one containing 27 and three *Ae. tauschii* from Middle East and Central Asia, respectively. The subgroup II contained 27 and 15 *Ae. tauschii* from Central Asia and Middle

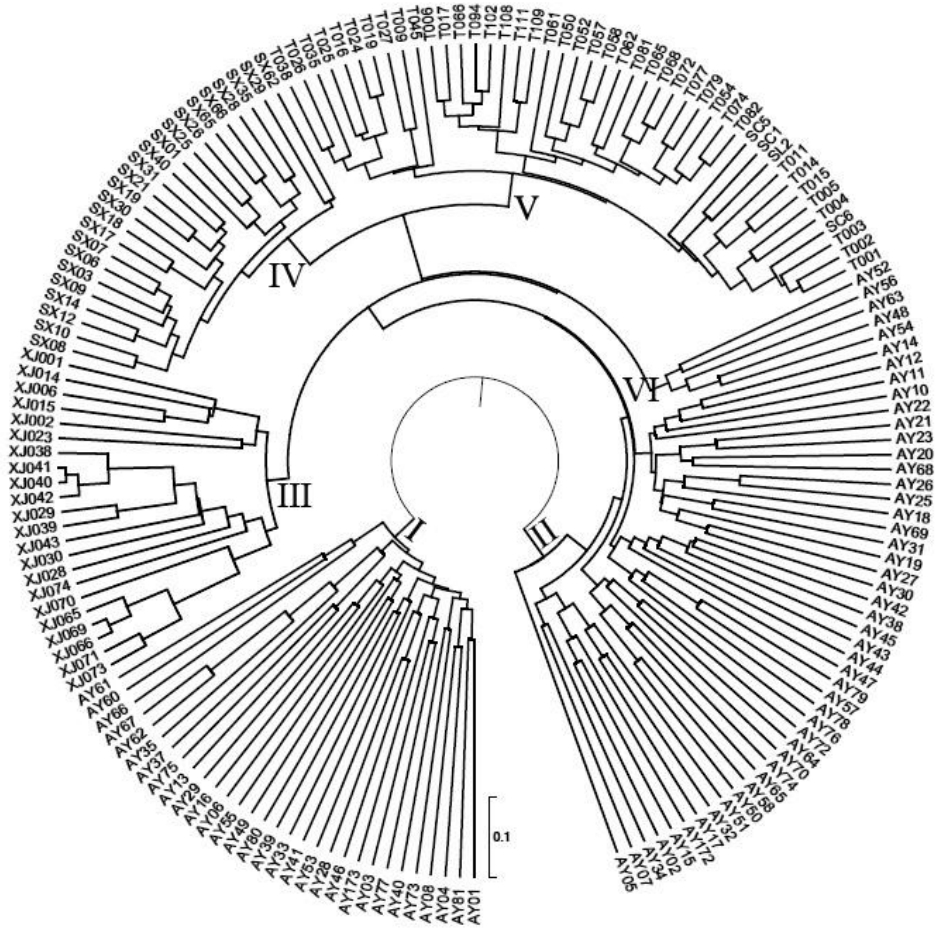

Figure 2. The cluster tree of 169 *Ae. tauschii* accessions acquired through the method of Unweighted Pair Group Method with Arithmetic means (UPGMA) according to genetic distances. Subgroup I: *Ae. tauschii* from Middle East and few from Central Asia; Subgroup II: *Ae. tauschii* from Central Asia and partial from Middle East; Subgroup III: *Ae. tauschii* from Xinjiang; Subgroup IV: *Ae. tauschii* from Shaanxi; Subgroup V: *Ae. tauschii* from Henan; Subgroup VI: *Ae. tauschii* from Central Asia.

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East. The subgroups III and IV were individually formed by *Ae. tauschii* from Xinjiang and Shaanxi, respectively. The subgroup V presented all Henan population and four *Ae. tauschii* from Shaanxi, while the subgroup VI presented *Ae. tauschii* from Central Asia, including three accessions from Turkmenistan, one from Pakistan, and one from Afghanistan. As shown in Figure 2, subgroups IV, V and VI were firstly gathered into a subset. Then, the subset could be classified into a clade with subgroup III, which was afterwards attributed to subgroup II. This reveals that *Ae. tauschii* in Xinjiang (subgroup III) and Yellow River (subgroups IV and V) are derived from Central Asia and Middle East (subgroup II). Moreover, *Ae. tauschii* in Yellow River has a closer relationship with part of those in Central Asia (subgroup VI) compared with Xinjiang.

DISCUSSION

The investigation in the genetic diversity of *Ae. tauschii* can provide a great chance in quality and adaptability improvement of common wheat. Zhukovsky (1928) found that the origin of *Ae. tauschii* was in the Eastern Mediterranean at the end of Tertiary period. Hammer (1980) regarded Caucasia as the origin area of *Ae. tauschii*. Based on SSR analysis, the genetic diversity of *D*-genome species of *Aegilops* and *Triticum* (Triticeae, Poaceae) from Iran was systematically surveyed, revealing a wide range of alleles in *Ae. tauschii*. Moreover, the maximum PIC value of this species indicated higher genetic differentiation than in any of the studied D-genome polyploids (Bordbar *et al*., 2011). Similarly, high levels of genetic diversity in *Ae. tauschii* in the same region were reported by Saeidi *et al*. (2006) and Naghavi *et al*. (2009) using SSR and AFLP markers, respectively. These results suggested the possibility of Iran as the center of origin of *Ae. tauschii*. Nevertheless, based on the variation analysis in chloroplast SSR loci in *Ae. tauschii*, Matsuoka *et al*. (2005) deemed the Caspian region, northern of Iran, to be the area with highest haplotype diversity. In this work, the values of Na, GD, and PIC in the Middle East group (mainly from Iran and its surrounding areas) were found the highest among the five groups, indicating much higher genetic diversity in the Middle East group compared with other groups. This result further confirms the origin of *Ae. tauschii* in this area. The variability parameters of the Central Asia group fall in between those of Middle East and China groups. This clearly reveals the degradation of genetic diversity of *Ae*. *tauschii* accompanied with its expansion, thus generally reflecting the broadcast route (towards east) of this species. In China, the Yellow River group is actually deemed as a kind of farmland weed. Yili area of Xinjiang is considered to be the easternmost of the natural distribution for wild *Ae. tauschii* population. Unexpectedly, the values of F_{ST} and genetic distance between Yellow River (Shaanxi and Henan) and Central Asia groups are found obviously lower than those between Yellow River and Xinjiang groups, indicating that the genetic constitution of Yellow River and Central Asia groups is more similar compared with that of the former and Xinjiang groups.

It has been widely reported that the western *Ae*. *tauschii* groups (Turkey and Western Iran) are more closely related to the eastern groups (Afghanistan, Turkmenistan, and China) than to those from the geographically closer Southwestern Caspian Iran and North-central Iran (Lubbers *et al*., 1991; Dvorak *et al*., 1998). Therefore, *Ae. tauschii* is preferable to be subdivided into two phylogenetic lineages (L1 and L2) based on its nuclear genome sequences, broadly affiliating with *Ae. tauschii* ssp. *tauschii* and *Ae. tauschii* ssp. *strangulata*, respectively (Lubbers *et al*., 1991; Dvorak *et al*., 1998, 2012; Mizuno *et al*., 2010; Sohail *et al*., 2012; Wang *et al*., 2013; Zhao *et al*., 2018). In this study, a phylogenetic tree was constructed based on the genetic distances among 169 *Ae. tauschii*, in which subgroup I displayed a distant genetic relationship with

[DOR: 20.1001.1.16807073.2020.22.3.8.8]

the other five subgroups as the outermost subgroup (Figure 2). Based on these results and the previous literatures as mentioned above, subgroup I and the other five subgroups could be generally assigned to L2 and L1, respectively. Additionally, the Yellow River group (Henan and Shannxi) prefers to cluster with part of those in Central Asia in the phylogenetic tree, implying a closer relationship between them compared with Xinjiang. Based on the analysis in genetic structure among 402 *Ae. tauschii*, Wang *et al*. (2013) believed that this species in Yellow River could be easily separated from L1 lineage when the genetic structure parameter *k* reached 6, exhibiting peculiar genetic variation due to geographical isolation for a long time. Moreover, *Ae. tauschii* from Yellow River exhibits very special FISH hybridization pattern (Zhao *et al*., 2018). Wei *et al*. (2008) speculated that *Ae. tauschii* in Yellow River could be directly originated from Iran or adjacent areas through the silk road in way of accompanying weeds of crops. From the perspective of genetic differentiation and evolution relationship, our results further reveal that obvious genetic variation between the Yellow River and Xinjiang groups was generated in the spreading process of *Ae. tauschii* from Central Asia to China, while *Ae. tauschii* in Yellow River might be directly derived from one/several types of the species from Central Asia regions such as Turkmenistan, Pakistan, and Afghanistan.

CONCLUSIONS

Abundant genetic diversities of *Ae. tauschii* were observed among five geographical populations of Middle East, Central Asia, Xinjiang, Shaanxi and Henan. Based on the investigation of genetic differentiation and genetic distances among the populations, genetic constitution of the Yellow River (Shaanxi and Henan) and Central Asia groups is relatively of more similarity compared with that between the former and Xinjiang groups. The phylogenetic tree was constructed based on the genetic distance of 169 *Ae. tauschii*, confirming that *Ae. tauschii* in Yellow River has a closer relationship with part of those from Central Asia than with Xinjiang.

ACKNOWLEDGEMENTS

This work was supported by National Natural Science Foundation of China (Grant No. 31601297 and 31871615) and Key Scientific Research Projects of Higher Education Institutions in Henan Province (Grant No. 20A210007).

REFERENCES

1. Bordbar, F., Rahiminejad, M. R., Saeidi, H. and Blattner, F. R. 2011. Phylogeny and Genetic Diversity of *D*-Genome Species of *Aegilops* and *Triticum* (Triticeae, Poaceae) from Iran Based on Microsatellites, ITS, and *trnL*-F. *Plant. Syst. Evol*., **291:** 117-131.
2. Dale, Z., Jie, H., Luyu, H., Cancan, Z., Yun, Z., Yarui, S. and Suoping, L. 2017. An Advanced Backcross Population through Synthetic Octaploid Wheat as a "Bridge": Development and QTL Detection for Seed Dormancy. *Front. Plant. Sci*., **8:** 2123.
3. Dvorak, J., Luo, M. C., Yang, Z. L. and Zhang, H. B. 1998. The Structure of the *Aegilops tauschii* Genepool and the Evolution of Hexaploid Wheat. *Theor. Appl. Genet*., **97:** 657-670.
4. Dvorak, J., Luo, M. C. and Akhunov, E. D. 2011. N.I Vavilov's Theory of Centres of Diversity in the Light of Current Understanding of Wheat Diversity, Domestication and Evolution. *Czech. J. Genet. Plant. Breed*., **47:** 20-27.
5. Dvorak, J., Deal, K. R., Luo, M. C., You, F. M., von Borstel, K. and Dehghani, H. 2012. The Origin of Spelt and Free-Threshing Hexaploid Wheat. *J. Hered*., **103:** 426-441.
6. Gill, B. S. and Raupp, W. J. 1987. Direct Genetic Transfers from *Aegilops squarrosa* L. to Hexaploid Wheat. *Crop. Sci*., **27(3):** 445-450.
7. Gogniashvili, M., Jinjikhadze, T., Maisaia, I., Akhalkatsi, M., Kotorashvili, A., Kotaria,

[DOR: 20.1001.1.16807073.2020.22.3.8.8]

N., Beridze, T. and Dudnikov, A. J. 2016. Complete Chloroplast Genomes of *Aegilops tauschii* Coss. and *Ae. cylindrica* Host Sheds Light on Plasm on D Evolution. *Curr. Genet.*, **62(4):** 1-8.
8. Goldasteh, M., Mehregan, I., Naghavi, M. R. and Nejadsattari, T. 2019. Molecular Characterization of *Low Molecular Weight Glutenin* (*LMW*) Genes in *Triticeae* Species with *D* Genome. *J. Agr. Sci. Tech.*, **21(5)**: 1287-1299.
9. Hammer, K. 1980. Vorarbeiten Zur Monographischen Darstellung von Wildpflanzensortimenten: *Aegilops* L. *Kulturpflanze*., **28:** 33-180.
10. Han, Y. J., Chen, W. C., Yang, F. B., Wang, X. H., Dong, M. F., Zhou, P. and Shang, F. D. 2015. cDNA-AFLP Analysis on 2 *Osmanthus fragrans* Cultivars with Different Flower Color and Molecular Characteristics of MYB1 Gene. *Trees-Struct. Funct.*, **29(3):** 931-940.
11. Imtiaz, M., Ogbonnaya, F. C., Oman, J. and Van Ginkel, M. 2008. Characterization of Quantitative Trait Loci Controlling Genetic Variation for Preharvest Sprouting in Synthetic Backcross-Derived Wheat Lines. *Genetics*, **178:** 1725-1736.
12. Kihara, H. and Tanaka, M. 1958. Morphological and Physiological Variation among *Aegilops squarossa* Strains Collected in Pakistan, Afghanistan and Iran. *Preslia*, **30:** 241-251.
13. Kunert, A., Naz, A. A., Dedeck, O., Pillen, K. and Léon, J. 2007. AB-QTL Analysis in Winter Wheat: I. Synthetic Hexaploid Wheat (*T. turgidum* ssp. *dicoccoides*×*T. tauschii*) as a Source of Favourable Alleles for Milling and Baking Quality Traits. *Theor. Appl. Genet.*, **115:** 683-695.
14. Li, P., Kirungu, J. N., Lu, H., Magwanga, R. O., Lu, P., Cai, X., Zhou, Z., Wang, X., Hou, Y., Wang, Y., Xu, Y., Peng, R., Cai, Y., Zhou, Y., Wang, K. and Liu, F. 2018. SSR-Linkage Map of Interspecific Populations Derived from *Gossypium trilobum* and *Gossypium thurberi* and Determination of Genes Harbored within the Segregating Distortion Regions. *PLoS ONE*, **13(11):** e0207271.
15. Liu, K. and Muse, S. V. 2005. PowerMarker: An Integrated Analysis Environment for Genetic Marker Analysis. *Bioinformatics*, **21(9):** 2128-2129.
16. Lubbers, E. L., Gill, K. S., Cox, T. S. and Gill, B. S. 1991. Variation of Molecular Markers among Geographically Diverse Accessions of *Triticum tauschii*. *Genome*, **34:** 354-361.
17. Matsuoka, Y., Mori, N. and Kawahara, T. 2005. Genealogical Use of Chloroplast DNA Variation for Intraspecific Studies of *Aegilops tauschii* Coss. *Theor. Appl. Genet.*, **111:** 265-271.
18. Matsuoka, Y., Nasuda, S., Ashida, Y., Nitta, M., Tsujimoto, H., Takumi, S. and Kawahara, T. 2013. Genetic Basis for Spontaneous Hybrid Genome Doubling during Allopolyploid Speciation of Common Wheat Shown by Natural Variation Analyses of the Paternal Species. *PLoS ONE*, **8(8):** e68310.
19. Matsuoka, Y., Takumi, S. and Kawahara, T. 2015. Intraspecific Lineage Divergence and Its Association with Reproductive Trait Change during Species Range Expansion in Central Eurasian Wild Wheat *Aegilops tauschii* Coss. (Poaceae). *BMC Evol. Biol.*, **15:** 213.
20. Mizuno, N., Yamasaki, M., Matsuoka, Y., Kawahara, T. and Takumi, S. 2010. Population Structure of Wild Wheat *D*-Genome Progenitor *Aegilops tauschii* Coss.: Implications for Intraspecific Lineage Diversification and Evolution of Common Wheat. *Mol. Ecol.*, **19:** 999-1013.
21. Naghavi, M. R., Aghaei, M. J., Taleei, A. R., Omidi, M., Mozafari, J. and Hassani, M. E. 2009. Genetic Diversity of the *D*-Genome in *T. aestivum* and *Aegilops* Species Using SSR Markers. *Genet. Resour. Crop. Evol.*, **56:** 499-506.
22. Naz, A. A., Kunert, A., Lind, V., Pillen, K. and Léon, J. 2008. AB-QTL Analysis in Winter Wheat: II. Genetic Analysis of Seedling and Field Resistance against Leaf Rust in a Wheat Advanced Backcross Population. *Theor. Appl. Genet.*, **116:** 1095-1104.
23. Peakall, R. and Smouse, P. E. 2006. GENALEX 6: Genetic Analysis in Excel. Population Genetic Software for Teaching and Research. *Mol. Ecol. Notes.*, **6(1):** 288-295.
24. Saeidi, H., Rahiminejad, M. R., Vallian, S. and Heslop-Harrison, J. S. 2006. Biodiversity of Diploid *D*-Genome *Aegilops tauschii* Coss. in Iran Measured Using

[DOR: 20.1001.1.16807073.2020.22.3.8.8]

Microsatellites. *Genet. Resour. Crop. Evol.*, **53:** 1477-1484.
25. Sohail, Q., Shehzad, T., Kilian, A., Eltayeb, A. E., Tanaka, H. and Tsujimoto, H. 2012. Development of Diversity Array Technology (DArT) Markers for Assessment of Population Structure and Diversity in *Aegilops tauschii*. *Breed. Sci.*, **62:** 38-45.
26. Sukhwinder, S., Chahal, G. S., Singh, P. K. and Gill, B. S. 2012. Discovery of Desirable Genes in the Germplasm Pool of *Aegilops tauschii* Coss. *Indian. J. Genet.*, **72(3)**: 271-277.
27. Wang, J., Luo, M. C., Chen, Z., You, F. M., Wei, Y., Zheng, Y. and Dorak, J. 2013. *Aegilops tauschii* Single Nucleotide Polymorphisms Shed Light on the Origins of Wheat *D*-Genome Genetic Diversity and Pinpoint the Geographic Origin of Hexaploid Wheat. *New. Phytol.*, **198:** 925-937.
28. Wei, H., Li, J., Peng, Z., Lu, B., Zhao, Z. and Yan, W. 2008. Relationships of *Aegilops tauschii* Revealed by DNA Fingerprints: The Evidence for Agriculture Exchange between China and the West. *Prog. Nat. Sci.*, **18:** 1525-1531.
29. Yen, C., Yang, J. L., Cui, N. R., Zhong, J. P., Dong, Y. S., Sun, Y. Z. and Zhong, G. Y. 1984. The *Aegilops tauschii* Cosson from Yi-li, Xinjiang, China. *Acta. Agronomica. Sinica.*, **10(1):** 1-8.
30. Yu, M., Chen, G., Zhang, L., Liu, Y., Liu, D., Wang, J., Pu, Z., Zhang, L., Lan, X., Wei, Y., Liu, C. and Zheng, Y. 2014. QTL Mapping for Important Agronomic Traits in Synthetic Hexaploid Wheat Derived from *Aegiliops tauschii* ssp. *tauschii*. *J. Integr. Agric.*, **13:** 1835-1844.
31. Zhang, D. L., Zhou, Y., Zhao, X. P., Lv, L. L., Zhang, C. C., Li, J. H., Sun, G. L., Li, S. P. and Song, C. P. 2018. Development and Utilization of Introgression Lines Using Synthetic Octaploid Wheat (*Aegilops tauschii*×Hexaploid Wheat) as Donor. *Front. Plant. Sci.*, **9:** 1113.
32. Zhao, L., Ning, S., Yi, Y., Zhang, L., Yuan, Z., Wang, J., Zheng, Y., Hao, M. and Liu, D. 2018. Fluorescence *in Situ* Hybridization Karyotyping Reveals the Presence of Two Distinct Genomes in the Taxon *Aegilops tauschii*. *BMC Genom.*, **19:** 3.
33. Zhukovsky, P. M. 1928. A Critical-Systematical Survey of the Species of the Genus *Aegilops* L. *Bull. Appl. Bot. Genet. Plant. Breed.*, **18:** 417-609.

ویژگی ساختار ژنتیکی *Aegilops tauschii* از جوامع جغرافیایی مختلف و خاستگاه جمعیت چینی آن

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چکیده

اجداد دیپلوئیدی گندم معمولی *Aegilops tauschii* به عنوان منبعی ژنتیکی برای بهبود ژنتیکی گندم استفاده می شود. در این پژوهش، نمایه (شاخص) تمایز های ژنتیکی بین گروه های Yellow River(شامل Shaanxiو Henan) و Xinjiang در حد ۰/۳۲۲ و ۰/۳۷۷ بود و به روشنی بیشتر از تفاوت بین گروه اولی و گروه های آسیا مرکزی در حد ۲۳۱۰/ و۰/۲۸۹ بود. در عین حال، فواصل ژنتیکی بین Yellow River(شامل Shaanxiو Henan) و Xinjiang (برابر۰/۲۸۵ و ۰/۳۲۹) در مقایسه با فواصل بین گروه اول با گروه های آسیای مرکزی (برابر ۰/۲۸۳ و ۰/۳۲۱) فواصل بیشتری

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را نشان میدهد. این نتایج آشکار می سازد که ساختار ژنتیکی Yellow River و گروه های آسیای مرکزی در مقایسه با گروه Xinjiang شباهت بیشتری به هم داشتند. شجره تبارزایی (phylogenetic tree) نشان می دهد که *Ae. tauschii* در گروه Yellow River و بخشی از آن در گروه آسیای مرکزی در وحله نخست تجمع یافته تا زیرگروه(subset) باشند. سپس، این زیرگروه و گروه Xinjiang در یک هم نیا (clade) طبقه بندی می شود که می توان آن را به جوامع آسیای مرکزی و خاورمیانه منصوب کرد. این امر چنین اشارت دارد که *Ae. tauschii* در گروه Yellow River با بخشی از آن در آسیای مرکزی رابطه نزدیکتری در مقایسه با Xinjiang دارد. یافته های ما روشن می سازد که *Ae. tauschii* در گروه Yellow River احتمالا به طور مستقیم ازیک/یا چند تیپ از آسیای مرکزی مانند تیپ های ترکمنستان، پاکستان و افغانستان نشات گرفته است.

[DOR: 20.1001.1.16807073.2020.22.3.8.8]