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ORIGINAL ARTICLE

Genetic variation and relationships between Azerbaijani and Turkish olive genetic resources

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Abstract
Olive (*Olea europaea* L.) is one of the most economically important crop from east to the west around the world. The aim of this research was to investigate the genetic relationship among 41 olive genotypes, including 11 well-known Turkish cultivars and 30 Azerbaijani olive genotypes using simple sequence repeat (SSR) markers. In this study, 19 SSR markers were amplified 115 polymorphic SSR alleles. The number of polymorphic alleles ranged from 3 to 10 with an average of 6.05. The observed heterozygosity (Ho) varied from 0.05 to 0.93 with an average of 0.63 and expected heterozygosity (He) differed from 0.26 to 0.86 with an average of 0.72. The polymorphism information content (PIC) ranged from 0.23 to 0.85 with a mean of 0.68. A UPGMA cluster analysis grouped olive genotypes into two distinct clusters and both clusters were divided into two subgroups. Similarly, STRUCTURE analysis assigned olive genotypes into two different gene pools (K = 2) and four gene pools were identified representing the two subgroups by STRUCTURE analysis for K = 4. The genetic similarity of olive genotypes ranged from 0.36 to 0.95. These results revealed that there was a high genetic variation among 30 Azerbaijani olive genotypes. 'Ayvalık 1'and 'Ayvalık 2' from Azerbaijani olive genotypes were different from Turkish local olive cultivar, "Ayvalık" indicating homonymy. This research also highlighted that Azerbaijani olive genotypes were totally distinct from Turkish olive cultivars demonstrating that these olive genotypes might have been imported to Azerbaijan from different countries other than Turkey. The outcomes of this study indicated that these diverse olive genotypes could be useful for development of new olive varieties in Azerbaijan and future breeding programs between two countries could be enhanced by means of these results.

Keywords *Olea europea* L. · Genetic diversity · SSR marker · STRUCTURE analysis

Introduction

Olive (*Olea europaea* L.) is one of the oldest tree species which has been cultivated for approximately 6000 years in the Mediterranean basin. The area of olive tree cultivation has been expanded widely since ancient times and olive production has been spread from Mediterranean basin to many other new regions around the world due to its high economic value [1]. In recent years, the world olive production has been consistently increasing worldwide while it was nearly 9 million tonnes at the beginning of 1990 s. In 2019, it exceeded 19 million tonnes which were grown on approximately 10 million ha and more than 90 % of total production concentrated in Mediterranean countries [2].

Olives have been traditionally grown for olive oil and table olive production which are important dietary complements in the Mediterranean diet. Currently, olive consumption has been substantially increasing in the other parts of the world due to understanding of beneficial effects olive oil on human health [3, 4].

At present, olive has been known as one of the most diverse tree species with more than 1200 olive cultivars grown in 54 countries and this genetic material has been gathered in more than 100 collections worldwide [5].

Olive has a significant commercial importance for Turkey which is the fourth largest olive producer country with an annual production of 1.5 million tonnes after Spain, Italy and Morocco in the world [2]. Olive cultivation in

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Turkey has been spread in a wide area from the Aegean and Marmara Regions to the Mediterranean and Southeastern Anatolia regions since ancient times. In addition, olive production has been well carried on with almost 90 local olive varieties such as "Gemlik", "Ayvalik", "Memecik", "Domat", "Uslu" etc. for a long time [6].

In Azerbaijan, the olive is an important crop which has long been cultivated since seventh century and archaeological evidence have revealed that a number of precious olive trees have been preserved in some regions of Azerbaijan such as Nardaran, Mardakan and Absheron. Currently, olive has had major agricultural importance in Azerbaijan and olive production of 1163 tonnes [2], has been done with local olive cultivars such as "Azerbaycan", "Ağ Zeytun", "Ağbaba", "Abşeron", "Qaragöz" etc. and foreign varieties which were brought to Azerbaijan from different countries in the past. In recent years, the level of olive production has been considerably accelerated with the contributions of new olive orchards established particularly in the Absheron region. Besides, new investments have been done in order to establish new olive plantations due to increasing interest to transfer economically valuable cultivars to Azerbaijan and providing their adaptation to local ecological conditions. In addition, a collection orchard consisting of 60 olive varieties was established in Experimental Station of the Genetic Resources Institute of Azerbaijan National Academy of Sciences in order to conduct adaptation studies. Historically, olives have been brought to Azerbaijan from different countries such as Turkey, Syria, Georgia, Iran, Italy and Spain by vegetative propagation methods which can cause the existence of homonymy, synonymy and misnaming problems [7]. Reliable identification of these cultivars, ensuring the participation of these varieties in local production and setting up the new plantations with even these cultivars, has become important issues for development of olive and olive oil industry in Azerbaijan. Nevertheless, description of these genetically unidentified genotypes has not been properly investigated.

Previously, morphological and phenological traits were used to identify olive genotypes [8–10]. However, due to the fact that these characters can be easily affected by ecological factors and plant age; DNA based molecular markers such as RAPDS, AFLPs, ISSRs, SSRs (microsatellites) and more recently, SNPs have been preferred to analyse genetic diversity between olive genotypes. Initially, RAPD markers were the first molecular markers used for the assessment of genetic diversity between olive varieties [11, 12]. Later, AFLPs [13, 14] and ISSRs [15, 16] have been used effectively for cultivar identification of olives. Recently, there have been various studies reported that SSR markers are highly polymorphic, co-dominant and more accurate tools for genetic diversity analysis in olive [17–28].

The purpose of this research was to investigate the genetic relationship among 41 olive genotypes, and to compare 11 well-known Turkish cultivars and 30 Azerbaijani olive genotypes using SSR markers, and to determine potential synonyms and homonyms.

Materials and methods

Plant material

In the present study, the genetic relationship among 41 olive genotypes, including 11 well-known Turkish cultivars and 30 Azerbaijani olive genotypes, was analyzed (Table 1). These eleven Turkish olive cultivars with high economic importance in Turkey ("İzmir Sofralık", "Ayvalık", "Erkence", "Çilli", "Memeli", "Çekişte", "Memecik", "Domat", "Uslu", "Kiraz" and "Gemlik") were selected for this study and found together at the Experimental Plot of the Republic of Turkey Ministry of Agriculture and Forestry Olive Research Institute, İzmir. The olive genotypes from Azerbaijan included seven major autochthonous cultivars ("Abşeron", "Ağbaba", "Ağ Zeytun", "Azerbaycan", "Qaragöz", "EL-1", "EL-2") which dominate olive production in the country. The other twenty-three genotypes were genetically unidentified materials which were previously transferred from different countries (Georgia, Syria, Italy, Spain, and Turkey) to Azerbaijan for the purpose of olive production and named based on only their morphological characterization. Among Azerbaijani genotypes, the twenty-two genotypes were collected by visiting the Experimental Station of the Genetic Resources Institute of Azerbaijan National Academy of Sciences, Baku, Azerbaijan while the remaining genotypes were sampled from the old trees at the Institute of Dendrology of Azerbaijan National Academy of Sciences in Mardakan District and Nardaran Region, Baku, Azerbaijan.

DNA extraction

DNA samples were obtained from 25 mg lyophilized and fine powdered young leaves according to the modified CTAB method [29]. DNA concentrations carried out by using a Quibit fluorometer (Invitrogen, USA) and diluted to 50 ng/µL.

SSR analysis

A total of nineteen SSR primer pairs which were previously developed were used for amplification of SSR analysis in this research (Table 2). Amplification reactions were carried out in a final volume of 20 µL in the presence of 50 ng of template DNA, 1X reaction buffer, 1.0 U Taq DNA

Table 1 List of genotypes and their collection locations

Number	Genotype name	Locations
1	KA19-13	Baku, Azerbaijan
2	EL-2	Baku, Azerbaijan
3	Nikita	Baku, Azerbaijan
4	Qaragöz	Baku, Azerbaijan
5	Qardal	Baku, Azerbaijan
6	İspan	Baku, Azerbaijan
7	EL-1	Baku, Azerbaijan
8	Della Madonna	Baku, Azerbaijan
9	Tibilisi	Baku, Azerbaijan
10	KA27-7	Baku, Azerbaijan
11	Abşeron	Baku, Azerbaijan
12	Kausi	Baku, Azerbaijan
13	Jiqirina	Baku, Azerbaijan
14	Saurani	Baku, Azerbaijan
15	Ayvalık-2	Baku, Azerbaijan
16	Ayvalık-1	Baku, Azerbaijan
17	Ascolano	Baku, Azerbaijan
18	Pikvalis	Baku, Azerbaijan
19	Azerbaycan	Baku, Azerbaijan
20	Tossiyskaya	Baku, Azerbaijan
21	St. Agostino	Baku, Azerbaijan
22	SS	Baku, Azerbaijan
23	Ağbaba	Nardaran, Baku, Azerbaijan
24	M-1	Mardakan, Baku, Azerbaijan
25	M-2	Mardakan, Baku, Azerbaijan
26	M-3	Mardakan, Baku, Azerbaijan
27	M-4	Mardakan, Baku, Azerbaijan
28	Muxtarov	Mardakan, Baku, Azerbaijan
29	Verrucosa	Mardakan, Baku, Azerbaijan
30	Ağ Zeytun	Mardakan, Baku, Azerbaijan
31	İzmir Sofralık	Edremit, Balıkesir, Turkey
32	Ayvalık	Edremit, Balıkesir, Turkey
33	Erkence	Edremit, Balıkesir, Turkey
34	Çilli	Edremit, Balıkesir, Turkey
35	Memeli	Edremit, Balıkesir, Turkey
36	Çekişte	Edremit, Balıkesir, Turkey
37	Memecik	Edremit, Balıkesir, Turkey
38	Domat	Edremit, Balıkesir, Turkey
39	Uslu	Edremit, Balıkesir, Turkey
40	Kiraz	Edremit, Balıkesir, Turkey
41	Gemlik	Edremit, Balıkesir, Turkey

polymerase (Thermo Scientific, USA), 0.10 µM M13 sequence tailed forward primer, 0.20 µM reverse primer, 0.20 µM M13 primer labelled with infrared dye either 700 nm or 800 nm (Licor, USA) and 0.25 mM dNTPs. PCR reactions were conducted by using a Veriti 96 well thermal cycler (Applied Biosystems, USA). PCR conditions were as follows: 2 min at 94 °C; 6 cycles of 45 s at 94 °C, 1 min at 61 °C (annealing temperature was reduced 1 °C after every cycle for touchdown PCR protocol), 1 min at 72 °C; 28 cycles of 45 s at 94 °C, 1 min at 55 °C and 1 min and 30 s at 72 °C; 7 cycles of 45 s at 94 °C, 1 min at 54 °C and 1 min and 30 s at 72 °C and final extension step of 10 min at 72 °C. The PCR products were separated on 6.0 % polyacrylamide gels at 30 W for 2 to 3 h using a Li-COR 4300 DNA analyzer (LI-COR) (Fig. 1).

Table 2 Number of detected alleles, observed heterozygosity (Ho), expected heterozygosity (He) and polymorphism information content (PIC) of 19 SSR markers

SSR markers	Number of alleles	Ho	He	PIC
DCA10	5	0.90	0.74	0.71
DCA18	7	0.83	0.77	0.73
EMO2	7	0.60	0.79	0.76
EMO3	6	0.93	0.76	0.73
EMO13	3	0.05	0.26	0.23
EMO30	6	0.66	0.73	0.68
EMO88	8	0.41	0.80	0.78
EMO90	5	0.48	0.62	0.58
EMOL	3	0.45	0.48	0.38
GAPU89R	7	0.90	0.74	0.70
GAPU101R	7	0.69	0.80	0.77
GAPU103A	6	0.75	0.75	0.72
UDO99-26	6	0.60	0.75	0.71
UDO99-27	10	0.72	0.86	0.85
UDO99-28	5	0.40	0.73	0.68
UDO99-35	4	0.75	0.63	0.56
UDO99-36	8	0.82	0.84	0.83
UDO99-39	7	0.36	0.79	0.76
UDO99-42	5	0.63	0.78	0.74
Total	115			
Mean	6.05	0.63	0.72	0.68

DCA, EMO, GAPU and UDO99 primers were developed by [17], [39], [40] and [41] respectively

Data analysis

A genetic similarity matrix was prepared according to the coefficient of Dice [30]. Cluster analysis was performed by using the unweight pair group method with arithmetic averages (UPGMA) dendrogram based on the Dice similarity matrix with the NTSYSpc v2.21 program (Exeter Software, New York, NY, USA). The polymorphism information content (PIC) values for SSR markers were calculated according to the method of [31]. Expected heterozygosity (He) and observed heterozygosity (Ho) values were calculated using POPGEN32 software v.1.32 [32] according to the method of [33].

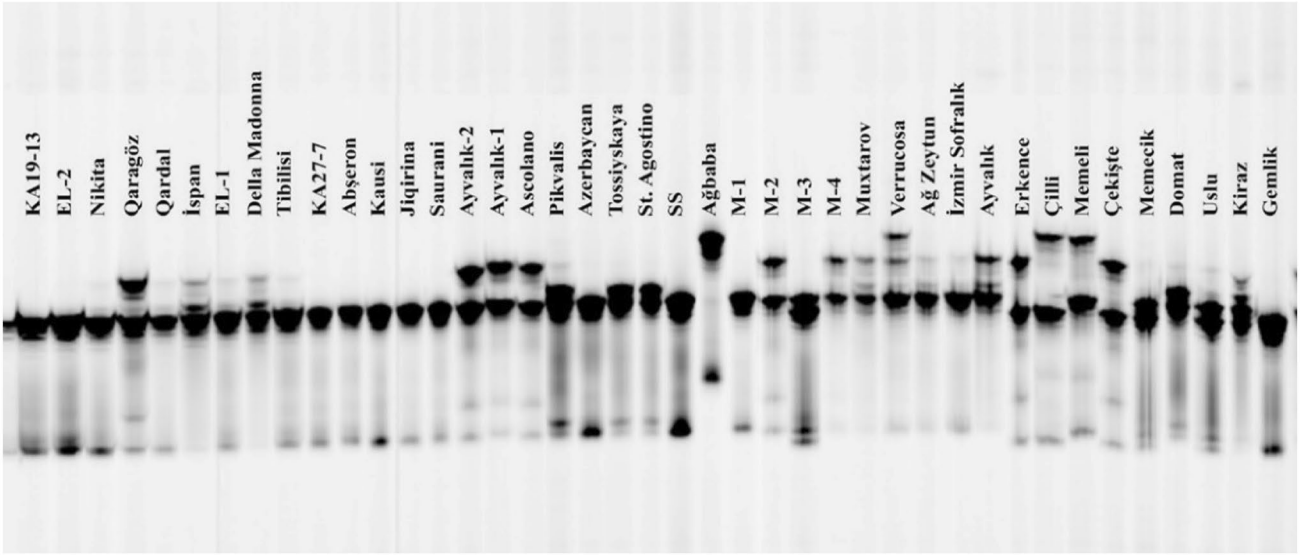

Fig. 1 Polyacrylamide gel picture showing the alleles of EMO90 SSR marker among 11 Turkish olive cultivars and 30 Azerbaijani olive genotypes

Identification of population structure was determined in the software STRUCTURE v.2.3.4 by using Bayesian clustering model. The range of possible numbers of clusters (K) varied from 1 to 12 with 5 replications for each K value. Each independent run was carried out with a burn-in period of 100.000 steps followed by 100.000 Monte Carlo Markov Chain (MCMC) replications. Furthermore, the method defined by [34] was used to detect the most likely number of subpopulations (K).

Results and discussion

In this research, a total of 19 SSR markers were used to investigate the genetic relationship among 30 olive genotypes from Azerbaijan and 11 well-known olive cultivars from Turkey (Table 2). Many SSR markers have been effectively used to identify genetic relationship among olive cultivars so far. The number of SSR markers used in this study was enough to explain genetic variation among olive genotypes and varieties compare to the previous studies [22, 25, 35–38].

Among 41 olive genotypes, 19 SSR markers amplified 115 polymorphic SSR alleles and the number of polymorphic alleles per SSR marker varied from 3 (EMO13 and EMOL) to 10 (UDO99-27) with an average of 6.05 (Table 2). In a genetic diversity study with 128 Mediterranean olive accessions from four different Mediterranean countries, a total of 179 number of alleles were scored ranging from 9 (EMO90) and 25 (DCA16) (Di Rienzo et al., 2018). In another research with 19 olive cultivars revealed that a total of 110 fragments per locus were amplified and the number of SSR markers ranged from 5 (DCA15, EMO13 and EMO90) to 16 alleles (UDO43) [36]. Thus, similar results obtained from present study and [36] demonstrated that EMO13 produced the lowest number of polymorphic alleles per locus. Of course, number of polymorphic alleles per SSR marker also depends on genetic variation present among the olive genotypes studied. In this study, the number of average polymorphic alleles per locus was higher than obtained by [19]; [22]; [42]; [27] and comparable to [20]; [43]and lower than those reported by [44]; [25]; [36].

In order to assess discrimination performance of 19 SSR primer pairs used in this study, the observed (Ho) and expected (He) heterozygosity values were calculated. Ho values of each SSR marker ranged from 0.05 (EMO13) to 0.93 (EMO3) with an average of 0.63 whereas He values differed from 0.26 (EMO13) to 0.86 (UDO99-27) with an average of 0.72. These results demonstrated that both Ho and He values were the lowest at EMO13 locus. Besides, considering all SSR loci used in this work, the mean of He was higher than that of Ho in accordance with that reported in the previous researches [14, 22, 23, 37, 38, 43–45]. When comparing both Ho and He values of the primer pairs together, there was a heterozygote excess (Ho > He) for DCA10, DCA18, EMO3, GAPU89R and UDO99-35 while a significant heterozygote deficiency (Ho < He) was observed for the remaining SSR markers except GAPU103A which had a Ho value was equal to the expected. According to [22] and [43], most of He values of SSR loci were higher than Ho values including DCA18 locus.

The polymorphism information content (PIC) value ranged from 0.23 (EMO13) to 0.85 (UDO99-27) with a mean of 0.68 in this study indicating that all loci except EMO13 were highly informative (PIC > 0.50). [27], found that the highest, the lowest and the average PIC values were 0.76 (GAPU103A), 0.48 (GAPU71A) and 0.63, respectively. In a recent research conducted with newly developed SSR markers for olive genotypes, it was reported that PIC values varied from 0.44 (BFU1309) to 0.79 (BFU0803) with an average of 0.61 [46].

All 19 SSR markers used in this research were polymorphic and demonstrated the genetic variation between 30 Azerbaijani olive genotypes and 11 Turkish olive cultivars was very high. In addition, both He, Ho and PIC values indicated that UDO99-27 was the most powerful locus for discriminating olive genotypes whereas EMO13 was found to be the least informative SSR marker.

Previously, [44] reported high discrimination power of DCA11 for cultivar identification. However, several studies reported that DCA09 was the most suitable marker for assessment genetic variation between olive genotypes [22, 45]. In other studies, a high polymorphism was found with UDO-43 primer [36, 47] while [22] that this marker showed the lowest polymorphism. The different results obtained from these studies suggested that the level of polymorphism detected by SSR markers were associated with the genetic relationship among the olive genotypes analysed, the number of genotypes analysed and the number of primer pairs tested [48].

Our present research confirmed the results of previous studies that there was a high level of SSR polymorphism among olive genotypes grown in different countries [22, 25, 36, 37, 45]. This genetic diversity between olive genotypes from different parts of the world might be helpful for developing new breeding programs.

The number of gene pools indicated by the STRUCTURE analysis was estimated to be K = 2 with the highest ΔK value (19.67), followed by K = 4 with ΔK of 5.30 (Fig. 2). As shown in Fig. 2, all Turkish olive cultivars were in gene pool 1 except "Gemlik" whereas the olive genotypes from Azerbaijan mostly placed in gene pool 2 for K = 2. For K = 4, 41 olive genotypes were more distinctly divided into four gene pools representing that there was a high genetic diversity between Turkish olive cultivars and olive genotypes from Azerbaijan according to their geographical region. For instance, all Turkish cultivars were placed in gene pool 4 along with two Azerbaijani olive genotypes. Remaining 28 Azerbaijani olive genotypes were present in the remaining three gene pools.

The results of structure analysis were accompanied with the results of prior studies supporting that geographical locations could be important for structuring the olive populations from different countries [49, 50]. Similarly, [51] showed the most probable grouping at K = 2; [36] found two separated groups between 19 olive cultivars (K = 2) and [37] found three main populations between olive accessions (K = 3) according to their geographical region confirming the results found by [52]. On the other hand, [14] clustered 22 Turkish olive genotypes in two basic gene pools (K = 2) and was not based on the geographical regions.

According to the UPGMA dendrogram, 41 olive genotypes mainly divided into two distinct clusters (A and B)

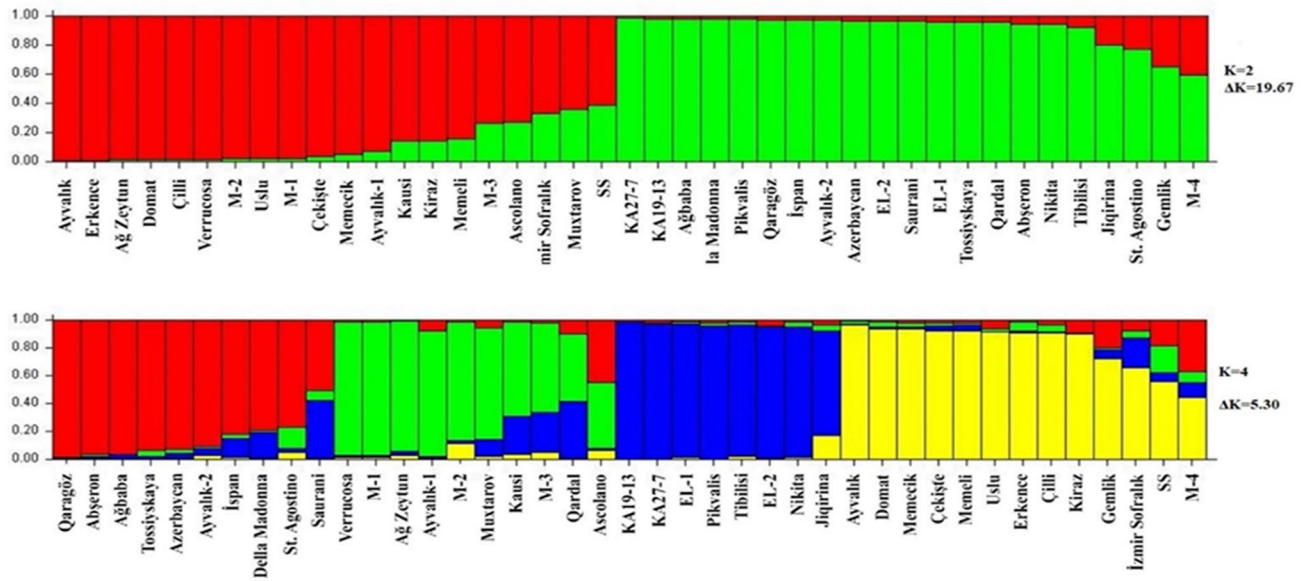

Fig. 2 The STRUCTURE bar graph based on 19 SSR markers. Different colours represent different gene pools. (Color figure online)

representing the two gene pools identified by STRUCTURE analysis for K = 2 (Fig. 3). Both Cluster A and Cluster B consisted of two subgroups Group I and Group II; Group III and Group IV, respectively. The subgroups were assigned similarly with the four gene pools identified by STRUCTURE analysis for K = 4.

The genetic similarity of olive genotypes ranged from 0.36 to 0.95 demonstrating high genetic variation in this study. Among olive genotypes, the highest similarity was observed between the genotypes 'EL-1 and Tibilisi' (0.95) placed in Group (I) Olive genotypes from Azerbaijan were clustered to three groups (Group I, II and III). However, group IV included only eight Turkish olive cultivars except 'Gemlik, Kiraz and İzmir Sofralık' which were placed in Group (II) Besides, the dendrogram demonstrated that there was a homonymous naming based on a high genetic variation between genotypes 'Ayvalık-1 from Group III, 'Ayvalık-2' from Group II and the well- known Turkish cultivar 'Ayvalık' from Group IV. The name "Ayvalık" was possibly given to these individuals according to their morphological traits because they are not genetically the same.

Our results showed that all olive genotypes from Azerbaijan are genetically different from well-known Turkish olive cultivars in this present study. Besides, this research indicated that all Azerbaijani 0 are unique and there were no mislabeling or synonymous problems in this study although there were two homonym genotypes (Ayvalık 1 and Ayvalık 2). Since olive cultivars or genotypes could be transferred from one area to another area by vegetative propagation without any passport information, it has been reported that there have been similar synonymy, homonymy or miscalling problems in olive genotypes worldwide [20, 35, 37]. Therefore, it is vital for these countries to identify unknown olive genotypes and discover their local olive germplasm for intensive olive cultivation.

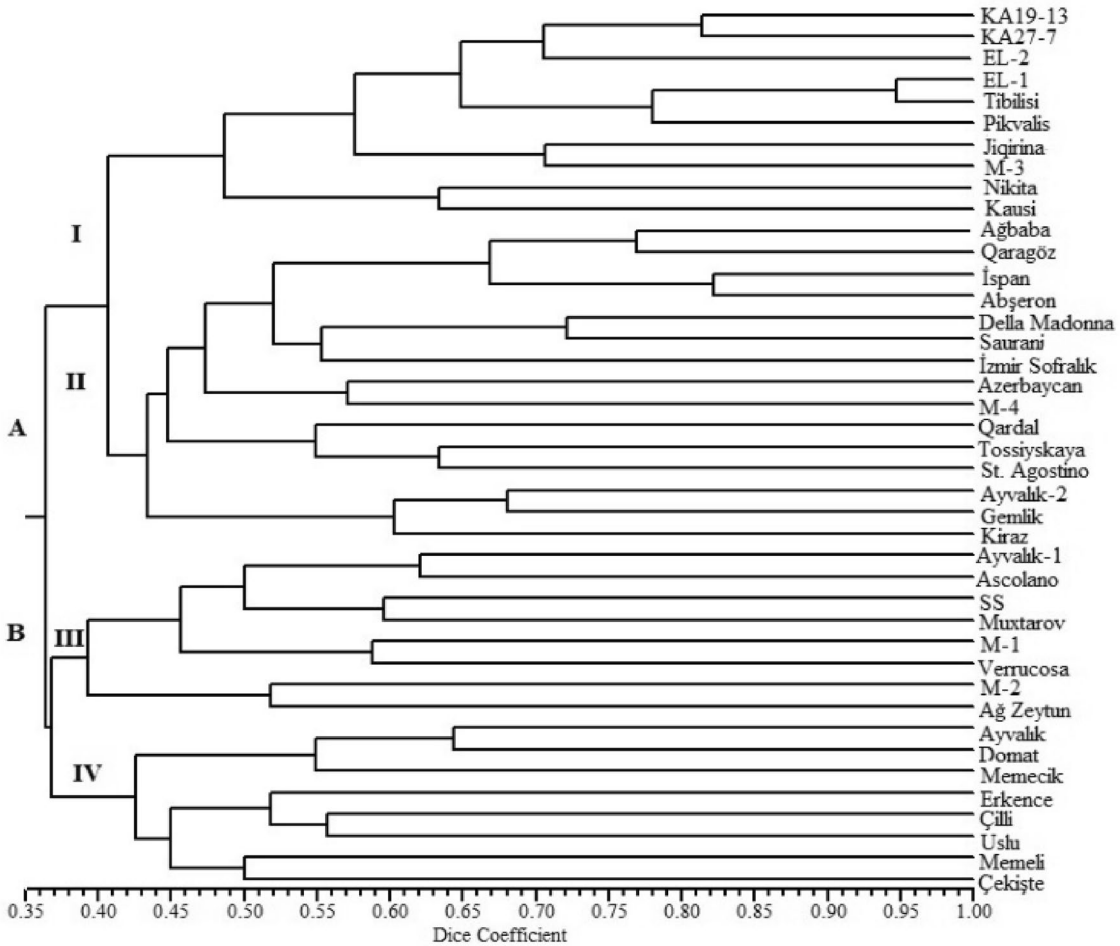

Fig. 3 UPGMA dendrogram based on the genetic relationships among 11 Turkish olive cultivars and 30 Azerbaijani olive genotypes

Conclusions

The present research demonstrated that SSR analysis was useful for identifying genetic differences between olive genotypes from Azerbaijan and well-known Turkish olive cultivars. Our results also illustrated that there was a high genetic variation among 30 olive genotypes from Azerbaijan and these Azerbaijani olive genotypes are distinct from common Turkish olive cultivars. This result indicates that olive genotypes or cultivars were brought to Azerbaijan from different countries other than Turkey. This work also detected the homonym problems and highlighted that olive genotypes investigated in this study were unique. In addition, olive growing and production in Azerbaijan could be enhanced by using these genetically diverse olive genotypes. Furthermore, the outcomes of this study could also help olive breeders in Azerbaijan for selection of the most suitable genotypes for variety development in breeding programs. In this respect, olive-cross breeding programs may be constructed and developed between Azerbaijan and Turkey using these diverse olive genotypes.

Author contributions Conceptualization, STD and AA; data curation, ZA; SE; EB; AI; UTD; OK; AM; RA and YU; formal analysis, STD; AI; EB; and YU; methodology, OK; AM; ZA; SA and AI; project administration, MI; AI; EB; SA and STD; visualization, AI; STD; SE; DB and ZA; writing-original draft, ZA; SE; EB; AI; UTD; OK; AM; RA and YU; writing-review and editing, ZA; SE; EB; AI; UTD; OK; AM; RA; DB and YU All authors have read and agreed to the published version of the manuscript.

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Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval None.

Research involving human and/or animal participants This article does not contain any studies with human or animal subjects.

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