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Assessment of genetic diversity and population structure of almond germplasm in Van Province, Türkiye, using iPBS-retrotransposon-based markers

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Abstract: The genetic characterisation of naturally occurring almond genotypes can guide the selection of genetic resources to be used in the breeding programme. Therefore, this study aims to assess the genetic diversity and population structure of almond germplasm comprising 50 accessions naturally occurring in Van, Türkiye, along with two commercial varieties (Pabuç and Dokuzoğuz). Thirteen inter-primer binding site (iPBS) retrotransposon markers generated a total of 102 bands, of which 95 were polymorphic. The average polymorphic band number per marker was 7.3, with a range of 5 to 13. A formula yielding a maximum of 0.5 resulted in polymorphic information content (PIC) values between 0.27 and 0.43, with a mean value of 0.36. Unweighted pair group method algorithm (UPGMA), principal coordinate analysis (PCoA), and STRUCTURE analysis, based on Bayesian clustering analysis, yielded consistent results, indicating that local populations (Akdamar and Çarpanak) were distinctly grouped, while commercial accessions were clustered with Çarpanak accessions. The diversity metrics and classification analysis utilising 13 iPBS-retrotransposon markers demonstrated that the iPBS-retrotransposon marker system possesses significant promise for evaluating the genetic variety and population structure of almonds.

Keywords: almond; genetic resources; genetic variation; iPBS-retrotransposon markers; molecular characterisation

Almond (*Prunus dulcis* (Mill.) D.A. Webb), marked by the commercial production of its kernels globally, is a member of the *Rosaceae* family. The USA, Australia, Spain and Türkiye are the most important countries for almond production in the world (Halász et al. 2019). In 2024, the global almond production value was approximately $13.8 billion, with a total production of 3.9 million tonnes; Türkiye contributed 200 thousand tonnes, achieving a yield of 2 589.4 kg/ha (FAOSTAT 2026).

The almond is native to the mountainous regions of Central Asia and is one of the oldest fruit trees, likely domesticated in the third millennium BC. It spread to the Mediterranean via the northern, southern, and maritime routes of the Phoenicians, Greeks, and Romans. Cultivated almonds reached the Mediterranean in the second millennium BC, and trade became widespread in the fourth century BC. This process led to the separation of two genetic groups: Mediterranean and Central Asian. Until the nineteenth century, it was mostly propagated by seed, creating high genetic diversity through local seedling populations; for this reason, the Mediterranean region is considered the second centre of the almond's domestication (Elhamzaoui et al. 2012).

The genetic diversity in plant germplasm provides an efficient tool to improve new varieties that have some desired traits, such as resistance to diseases and

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pests, yield increase, and large seeds. Determining the structure and level of genetic diversity between and within populations is crucial for breeding plants and benefiting from them (Erdinç et al. 2021). Molecular markers have been recognised as a crucial method for understanding the genetic background controlling genetic diversity and quantitatively inherited features in plants. DNA markers define the differences in sequences among individuals within a species, and due to their insensitivity to environmental, pleiotropic, and epistatic influences, they exhibit stability. Markers reveal the concept of genetic diversity among genotypes, populations, higher taxa, or species (Adhikari et al. 2017).

Superior kernel quality, late blooming, prolonged ripening season, resilience to winter and late spring frost, and environmental adaptability (Khadivi et al. 2019), self-compatibility, sweet kernel, and shell hardness (Perez de los Cobos et al. 2024) have been attractive traits for the breeding of almonds. Some of these traits have previously been investigated using molecular markers. Mougiou et al. (2023) investigated the self-compatibility of a genotype named 'Mars' in Greece, employing the *Sf* allele as a marker. Estaji et al. (2016) identified self-compatible genotypes derived from crosses between self-incompatible female parents and a self-compatible male parent. Ozkan et al. (2023) assessed self-incompatibility in certain naturally occurring almond genotypes in Erzincan, Turkey, based on RNase activity and the presence of S-alleles. Silva et al. (2005) examined the genes that control flowering time in almonds using the candidate gene method. Otaghvari and Ghaffarian (2011) determined the genetic diversity of 19 late-flowering almond accessions with ISSR primers. Perez de los Cobos et al. (2024) constructed a quantitative trait locus (QTL) mapping to offer more information about the genetic background of physical and chemical kernel quality traits. Ricciardi et al. (2018) identified cleaved amplified polymorphic sequences (CAPS) molecular markers suitable for marker-assisted breeding programs associated with a mutation in the *Sk* locus that inhibits amygdalin accumulation and promotes the formation of sweet, edible kernels. Catalano et al. (2025) conducted a genome-wide association study (GWAS) and identified nine SNP markers linked to tolerance against *Diaporthe amygdali* in almonds.

The genetic diversity in almond species has been previously investigated with random amplified polymorphic DNA (RAPD) by MirAli and Nabulsi (2003), Shiran et al. (2007), Gouta et al. (2008), Sharma et al. (2012), Pinar et al. (2015), and Mahood and Hama-Salih (2020); with inter-simple sequence repeats (ISSR) by Pinar et al. (2015), Mahood and Hama-Salih (2020), and Rahimi-Dvin et al. (2020); and with simple sequence repeats (SSR) by Fathi et al. (2008), Tahan et al. (2009), Gouta et al. (2010), Kadkhodaei et al. (2011), Elhamzaoui et al. (2012), Zeinalabedini et al. (2012), Rahemi et al. (2012), Delplancke et al. (2013), Distefano et al. (2013), El Hamzaoui et al. (2014), Rigoldi et al. (2015), Halász et al. (2019), Hasanbegovic et al. (2021), Esgandaripirmorad et al. (2022), and Yangöz and Güney (2024). Despite the fact that these papers report genetic diversity in almonds using RAPD, ISSR, and SSR markers, to the best of our knowledge, no publication has ever reported genetic diversity in almonds using inter-primer binding site (iPBS) retrotransposon markers in the literature.

Retrotransposons, also called class-I transposons, have the ability to move by self-replicating in the genome via an RNA product. They are mobile genetic elements capable of relocating throughout the genome, resulting in an increase in genomic size. Retrotransposons can cause changes in the genome and the quantity of DNA, increase genetic diversity, and induce mutations. Kalendar et al. (2010) developed a novel and universal retrotransposon marker system known as iPBS, applicable in both plants and animals, that does not require sequence information from regions adjacent to retrotransposon regions of any species. The iPBS method relies on amplifying the DNA segment located between the reverse transcriptase primer binding sites of long-terminal repeat (LTR) retrotransposons that are close enough for PCR amplification. Retrotransposons have excellent potential as a source of molecular markers due to their ubiquitous distribution throughout the genome, their high copy number in the genome and their wide distribution in chromosomes (Kalendar et al. 2010).

iPBS-Retrotransposon markers have been previously used to investigate genetic diversity in various trees, including *Tetradium ruticarpum* (Jing-Yuan et al. 2018), hawthorn (Sagbas et al. 2023), chestnut (Orhan & Kara 2023), grapevine (Güler et al. 2024), *Zanthoxylum* species (Zhang et al. 2024), fig (Uçer et al. 2025). Additionally, these markers have been applied to other species such as *Fritillaria imperialis* (Koçak et al. 2020), oregano (Karagoz et al. 2020), common bean (Haliloğlu et al. 2022), *Aegilops* (Kizilgeci et al. 2022), parsley (Coşkun 2023), cotton (Baran et al. 2023), salep orchid (Palaz et al. 2023), bottle gourd (Coskun 2024) and sugar beet (Sadık et al. 2025).

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Almond accessions show distribution as two populations in two different ranges: Akdamar Island and Çarpanak Peninsula in Van, Türkiye. Therefore, the aim of this study was to investigate genetic diversity and population structure in almond germplasm from Akdamar Island and Çarpanak Peninsula in Van, Türkiye, as well as to evaluate the efficacy of the iPBS-retrotransposon marker system for assessing these aspects in almonds.

MATERIAL AND METHODS

In the present study, a total of 52 samples (Table S1 in Electronic Supplementary Material (ESM)), comprising 20 accessions from Akdamar Island, 30 accessions from Çarpanak Peninsula, and two commercial varieties, were utilised to assess genetic diversity and population structure.

DNA isolation. Fresh, healthy, and pest-free leaf samples were harvested from the trees in early spring and stored at –20 °C in the freezer. The leaves were dried in a lyophilizer over two days. The dry leaf samples were ground with beads in tubes using a tissue lyser. The resulting leaf powders were stored in dry and cool conditions until DNA extraction. DNA isolation was performed according to a minor modification of Boiteux et al. (1999) to the cetyltrimethylammonium bromide (CTAB) method of Doyle and Doyle (1990). The concentration and purity of extracted total DNA samples were assessed with a NanoDrop spectrophotometer (DeNovix DS-11 FX, USA), and a final concentration of each sample was diluted to 25 ng/μL for polymerase chain reaction (PCR), then stored at –20 °C.

PCR conditions. A total of 40 iPBS-retrotransposon markers (Table S2 in ESM) were initially evaluated on eight randomly selected almond accessions. 13 iPBS-retrotransposon markers produced a higher number and denser bands than others, so they were selected for further polymerase chain reactions. Polymerase chain reactions were performed in a total volume of 25 μL, containing 25 ng genomic DNA, 1X Dream*Taq* PCR buffer (Fermentas), 1 μM primer (for 12–13 nucleotide primers) or 0.6 μM primer (for 17–18 nucleotide primers), 0.2 mM dNTPs, 2.5 mM $MgCl_2$, 1 unit *Taq* DNA polymerase (Fermentas), and distilled water for the rest of the volume. The thermal cycler was programmed according to Kalendar et al. (2010). The PCR products were separated by electrophoresis in 1.7% (w/v) agarose gel prepared using 1× tris-acetate-EDTA (TAE) buffer solution and stained with ethidium bromide and visualised under ultraviolet (UV) light using the Gel Doc XR + system (Bio-Rad, USA).

Statistical analyses. The visual data of iPBS fragments were converted to numerical values by coding as "1" in the presence of a band and "0" in the absence of a band. Only clear and distinct bands were scored to exclude artificial bands from the analysis. Polymorphic band percentages and polymorphic information content (PIC) values were calculated using an online tool (Abuzayed et al. 2016) for the calculation of dominant marker gene diversity. Past (Ver. 4.08, 2021) software was used to assess the genetic diversity of almond genotypes using unweighted pair group method algorithm (UPGMA) with arithmetic mean based on Jaccard's similarity coefficient (Jaccard 1908), to analyse population distribution with principal coordinate analysis (PCoA), and to create a heat map that presents pairwise genetic similarity of accessions. Analysis of molecular variance (AMOVA) was computed using GenAlEx (Ver. 6.5, 2012) to assess molecular variance between and within populations. The structure of the almond population was analysed with STRUCTURE (Ver. 2.3, 2010) software based on the Bayesian clustering technique.

RESULTS AND DISCUSSION

A total of 102 scorable and reproducible bands, 95 of them showing polymorphism, were produced with 13 iPBS-retrotransposon markers to identify genetic diversity in wild and commercial almond accessions. Nine of the primers showed 100% polymorphism, whereas four of them had monomorphic bands. While the highest band production per primer was obtained from primer-2233 with 13 bands, the lowest band yield was obtained from primer-2401 with 5 bands, and the average band number per primer was calculated as 8.84 bands. The mean polymorphic band number per primer was 7.3 (Table 1). Similar results were indicated by Gouta et al. (2008) with 7.6 polymorphic bands per marker from Tunisian almond cultivars using RAPD markers and Mahood and Hama-Salih (2020) with 8 polymorphic bands per marker from the almond population in Iraq with ISSR markers. Pinar et al. (2015) reported lower values, 4.41 polymorphic bands per primer, for the amplifications of RAPD and ISSR markers. Sharma et al. (2012) found an average of 5.4 polymorphic bands using RAPD markers to study the genetic diversity in a group of 32 almond genotypes. In contrast to our findings, other studies reported a greater average number of polymorphic bands than we obtained. Shiran et al. (2007) and Mahood and Hama-Salih (2020) reported average polymorphic band numbers of 15.8 and 9.5, respectively, for almond populations analysed with RAPD markers. The origins of the accessions in the assessed population can influence the number of polymorphic bands. A high mean polymorphic band of 15.8 can be explained because the population comprised different-origin accessions.

The PIC value ranged from 0.29 (from primer-2394 and primer-2237) to 0.42 (from primer-2251), and the mean PIC value was 0.35 (Table 1). The results of Naeem et al. (2021), with the PIC values ranging from 0.22 to 0.35 and the mean value of 0.32, are compatible with our findings. Nhat et al. (2022) reported a very low average PIC value of 0.06. Using a limited population of six accessions in their study probably resulted in a low PIC. In some other studies assessing genetic diversity in almonds, higher mean PIC values were reported. Shiran et al. (2007), Sharma et al. (2012), and Rahimi-Dvin et al. (2020) reported average PIC values of 0.77, 0.68, and 0.93, respectively. While these PIC values are higher than our findings, it is not reasonable to compare them with ours because of the use of a formula that yields PIC values between 0 and 1. Opposite to these studies, we used a formula defined for dominant markers that gives a PIC value between 0 and 0.5.

The effective number of alleles ranged from 1.30 to 1.53, and the mean value for 13 iPBS markers was calculated as 1.37. While the lowest effective number of alleles was obtained from primer-2237, the highest value was calculated for primer-2251 (Table 1). Gouta et al. (2010), Kadkhodaei et al. (2011), Rahemi et al. (2012), Zeinalabedini et al. (2012), El Hamzaoui et al. (2014), Rahimi-Dvin et al. (2020), Hasanbegovic et al. (2021), Esgandaripirmorad et al. (2022), Hasanbegović et al. (2024), and Yangöz and Güney (2024) documented a greater effective number of alleles in their investigations utilising SSR markers. SSR markers can yield a greater effective number of alleles compared to dominant marker systems, as they are capable of distinguishing between homozygous and heterozygous alleles.

Shannon's information index is an important parameter that presents genetic diversity in a population. In our study, primer-2237 and primer-2251 presented the lowest (0.27) and the highest (0.41) Shannon's information index value, respectively. The mean

Table 1. Total number of bands, number of polymorphic bands, percentage of polymorphism, polymorphic information content (PIC), number of active alleles, and Shannon information index values for each iPBS marker

iPBS marker	Number of bands		P%	PIC	N_e	I
	total number of bands	number of polymorphic bands				
2228	9	9	100	0.38	1.38	0.33
2230	7	7	100	0.34	1.36	0.32
2232	13	13	100	0.37	1.43	0.38
2237	7	7	100	0.27	1.30	0.27
2239	10	9	90	0.40	1.38	0.34
2251	7	6	85.71	0.43	1.53	0.41
2272	7	5	71.42	0.34	1.34	0.31
2273	6	6	100	0.39	1.33	0.30
2374	8	6	75	0.34	1.32	0.30
2383	8	8	100	0.31	1.45	0.37
2390	7	7	100	0.42	1.38	0.33
2394	8	7	87.50	0.32	1.32	0.29
2401	5	5	100	0.32	1.34	0.31
Total	102	95				
Mean	7.84	7.30	93.05	0,36	1.37	0.33

iPBS – inter-primer binding site; P% – percent polymorphism, PIC – polymorphic information content; N_e – effective number of alleles, I – Shannon's information index

Shannon's information index value was calculated as 0.33 (Table 1). While Rahimi-Dvin et al. (2020) found a lower Shannon's information index value, Fathi et al. (2008), Kadkhodaei et al. (2011), Rahemi et al. (2012), Hasanbegovic et al. (2021, 2024) reported higher values than us. These results indicated that codominant markers can give a higher Shannon's information index value than dominant markers.

It has previously been reported that the iPBS-retrotransposon markers are a universal, practical, powerful, fast, reliable, effective, and inexpensive method (Aydın et al. 2020; Krasòevska et al. 2022; Haliloğlu et al. 2022; Yildiz and Arbizu 2022; Sadık et al. 2025). Our findings from the present study also support these results. When comparing our diversity metrics, such as the number of polymorphic bands, the percentage of polymorphism, polymorphic information content (PIC), the number of active alleles, and findings from the Shannon information index, to other studies on genetic diversity in almonds using different markers, we conclude that the efficiency of ISSR and RAPD markers in assessing genetic diversity in almonds is generally comparable to that of iPBS-retrotransposon markers. Consequently, iPBS-retrotransposon markers may serve as an alternative to ISSR and RAPD methods. While iPBS-retrotransposon markers offer certain advantages over SSR markers, such as being universal, cost-effective, and not requiring sequence information, SSR markers provide greater informational value.

With the use of the UPGMA-based dendrogram, the population, which consisted of 50 wild almond accessions and two commercial almond accessions, was divided into four distinct groups. Out of the nine Çarpanak accessions, there were two commercial accessions that were included in Group 1. Group 2 included only the genotype C11, which is one of the genotypes of the Çarpanak population. Two genotypes from the Akdamar population and 20 genotypes from the Çarpanak population came together to form the biggest cluster, group 3. Group 4, comprising only 11 Akdamar genotypes, represented the most homogeneous cluster regarding population origin (Figure 1). This result indicated that the genetic variation observed in the Çarpanak population was higher than that observed in the Akdamar

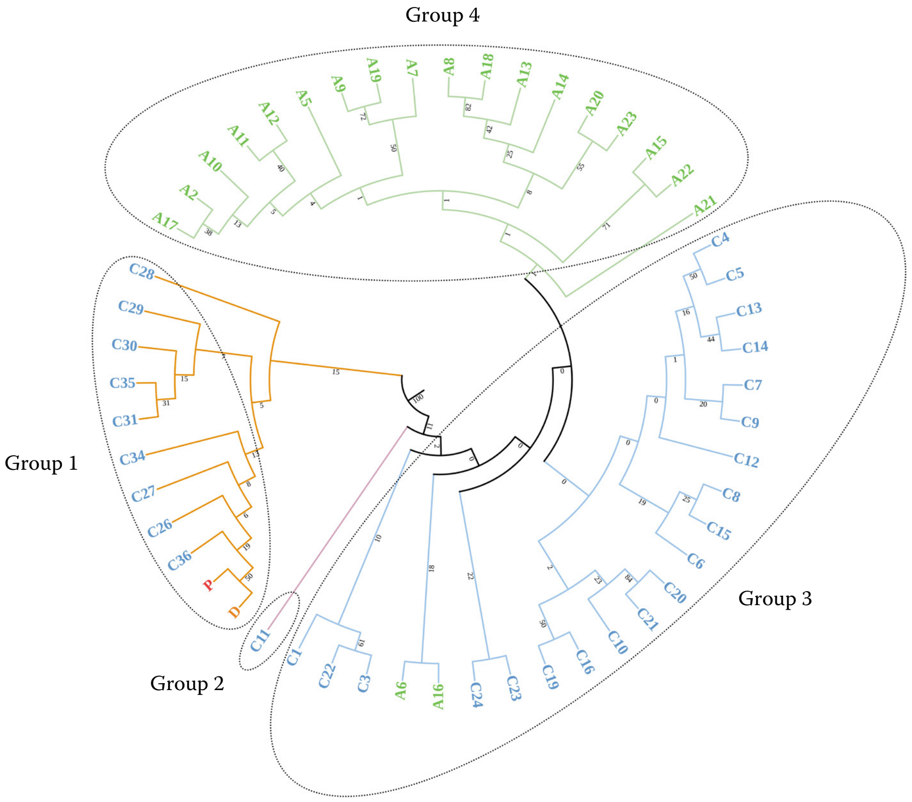

Figure 1. Genetic clustering of 52 almond accessions based on the unweighted pair group method algorithm (UPGMA) method

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population. The clustering of commercial accessions (Pabuç and Dokuzoğuz) with Çarpanak accessions indicates a greater genetic variety in the Çarpanak population compared to the Akdamar population. This can be elucidated by the characteristics of the location. Akdamar Island is a small and isolated island relative to Çarpanak Peninsula, which may facilitate increased gene flow among Akdamar accessions. The clustering of almond accessions based on their geographical origin using iPBS primers illustrates the efficacy of the iPBS-retrotransposon marker system in evaluating the genetic diversity of almonds. Pinar et al. (2015) demonstrated that almond samples exhibited no geographic patterns in the dendrograms constructed using RAPD and ISSR markers.

Principal coordinate analysis (PCoA) was employed to gain greater insight of the genetic relationships among 52 almond germplasms. PCoA substantially corroborated the UPGMA-derived dendrogram, classifying the germplasm into four distinct classes. The commercial genotypes Pabuç and Dokuzoğuz were classified together with Çarpanak germplasms in Group A, as indicated by the UPGMA-based dendrogram. Groups B and C exclusively comprised Çarpanak accessions, while Group D solely consisted of Akdamar accessions (Figure 2). These results were entirely consistent with those derived from the UPGMA-based dendrogram.

The Jaccard pairwise genetic similarity coefficient was computed for all almond accessions, yielding a mean pairwise genetic similarity coefficient of 0.44. This mean pairwise genetic similarity coefficient is greater than the values reported by Gouta et al. (2010) and Halász et al. (2019), but lower than the values reported by MirAli and Nabulsi (2003) and Mahood and Hama-Salih (2020). Gouta et al. (2010) obtained genetic similarities ranging from 0 to 0.9, with an average of 0.22 among Tunisian almond germplasm using SSR markers. Halász et al. (2019) evaluated the genetic diversity of an almond population from several geographical regions using SSR markers, revealing that genetic similarity varied from 0.03 to 1.00, with a mean of 0.29. MirAli and Nabulsi (2003) produced minimum, maximum, and average similarity coefficients of 0.70, 0.96, and 0.78, respectively, utilising RAPD primers. Mahood and Hama-Salih (2020) determined the genetic similarity indices for 38 almond accessions, which ranged from 0.32 to 0.75, with a mean value of 0.54, using RAPD and ISSR markers. Yangöz and Güney (2024) reported the lowest and highest

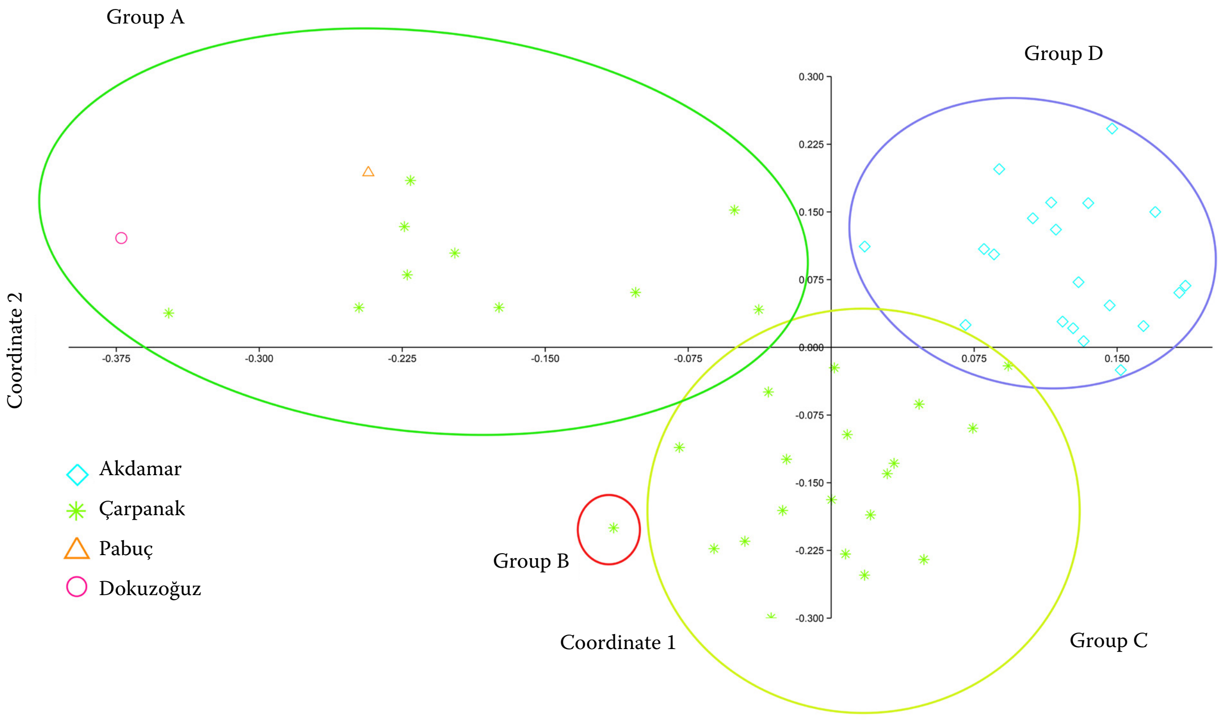

Figure 2. Genetic clustering of 52 almond accessions with principal coordinate analysis (PCoA)

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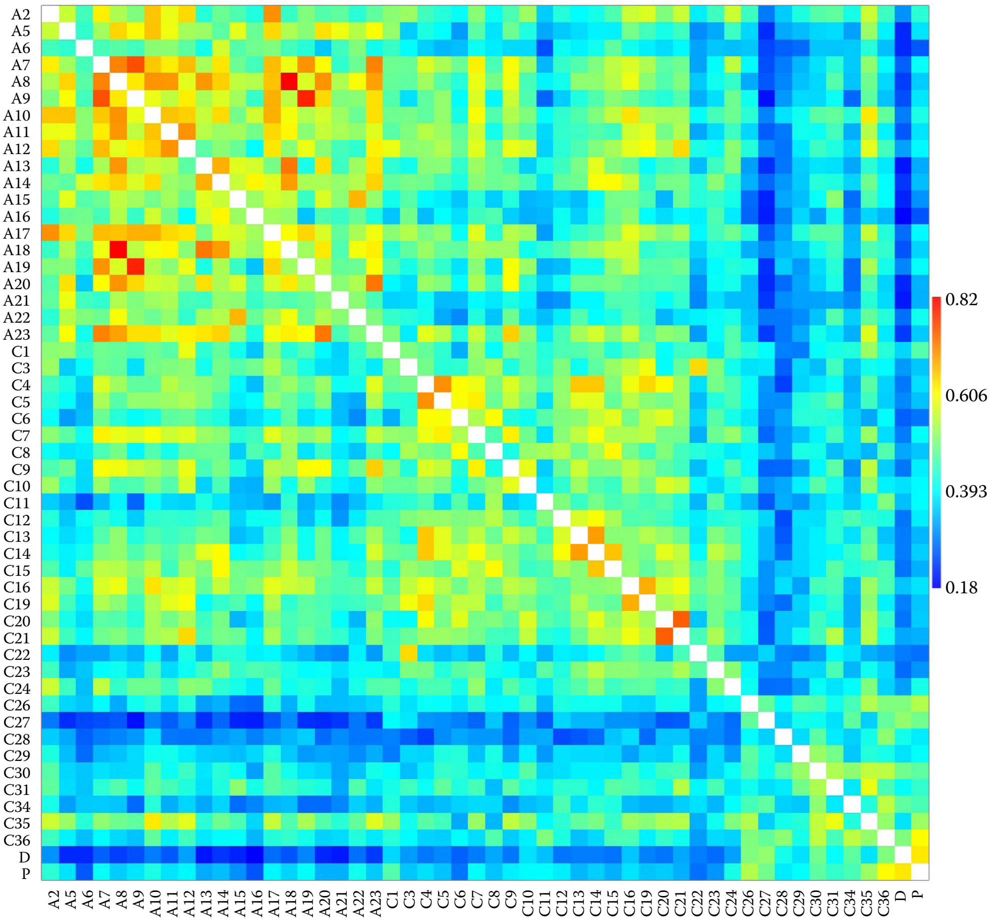

Figure 3. Heat map illustrating pairwise genetic similarity among 52 almond accessions

similarity indices as 0.24 and 0.88, respectively, in an almond population with SSR markers. In the study of Shiran et al. (2007), the genetic similarities varied from 0.32 to 0.92 for RAPD and from 0.14 to 1 for SSR between cultivar and wild almond species. In our study, the genetically closest accessions were A8 and A18, with a genetic similarity coefficient of 0.82, followed by A9-A19 and A7-A9 with coefficients of 0.79 and 0.75, respectively. The lowest genetic similarity coefficient was 0.18, indicating that Dokuzoğuz and A16 were the most distant accessions. A9-Ç27 and Dokuzoğuz-A13 were the subsequent most distant accessions, with coefficients of 0.19 and 0.20, respectively.

A heat map based on the Jaccard pairwise genetic similarity coefficient was generated to examine the genetic similarity among all almond accessions (Figure 3). The heat map revealed that Ç27 and Dokuzoğuz were the most distant accessions relative to all other accessions. It is observed that the Akdamar population exhibits a high level of pairwise genetic similarity within the population, whereas the Çarpanak population exhibits a low level of pairwise genetic similarity. The closest accessions, A8 and A18, have a similarity index of 0.82 and are part of the Akdamar population. Halász et al. (2019) also revealed that three genotypes from Akdamar Island demonstrated the highest genetic closeness in their study, which examined the genetic diversity of almond germplasm from different regions utilising SSR markers. C11, C22, C26, C27, C28, C29, and C34 are the most distinct genotypes from all of the other accessions, as seen from the heat map. These genotypes may serve as parental lines for a future almond breeding program.

Using Nei's genetic similarity coefficient, it was determined that the populations that were closest to each other were the Akdamar and Çarpanak populations. These populations had a value of 0.92, while the populations that were the most distant were Akdamar and the population of commercial almond accessions, which had a value of 0.73 (Table 2).

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Table 2. Genetic similarity and distance indexes among the almond populations

	Akdamar	Çarpanak	Commercial
Akdamar	–	0.081	0.312
Çarpanak	0.92	–	0.174
Commercial	0.73	0.84	–

Nei's genetic identity (Nei 1972) (above diagonal) and genetic distance (below diagonal)

Table 3. Analysis of molecular variance (AMOVA) between and within populations of variation for studied almond populations

Source of variation	*df*	SS	MS	Est. Var.	%
Between populations	2	123.128	61.564	3.342	17
Within populations	49	812.333	16.578	16.578	83
Total	51	935.462		19.920	100

df – degree of freedom; SS – sum of squares; MS – mean square; Est. Var. – estimated variance

According to the findings of the analysis of molecular variance (AMOVA), the majority of the variance, which accounts for 83% of the total, originates from within populations, while just 17% originates from across populations (Table 3). The results of the study assessing the genetic diversity of almonds using RAPD and ISSR markers by Mahood and Hama-Salih (2020) are in agreement with our findings. Fathi et al. (2008) and Rahemi et al. (2012) reported lower variation among almond populations based on SSR markers, however Halász et al. (2019) indicated a higher value than our findings. The size of the populations studied, the origin of the almond species in those populations, and the composition of different species within them could cause differences in the level of variation between populations.

The optimal *k* value was found to be 2 in the study performed using the Evanno technique (Evanno et al. 2005) on the data acquired from 13 iPBS markers to assess the population structure of 52 almond accessions (Figure 4). According to the structure analysis, the almond population is divided into two sub-populations: cluster I, comprising Çarpanak and commercial accessions, and cluster II, comprising all the Akdamar and five Çarpanak accessions.

CONCLUSION

This study evaluated the genetic relationship and population structure among 50 local and two commercial almond accessions, utilising the iPBS marker system in almonds for the first time. The results

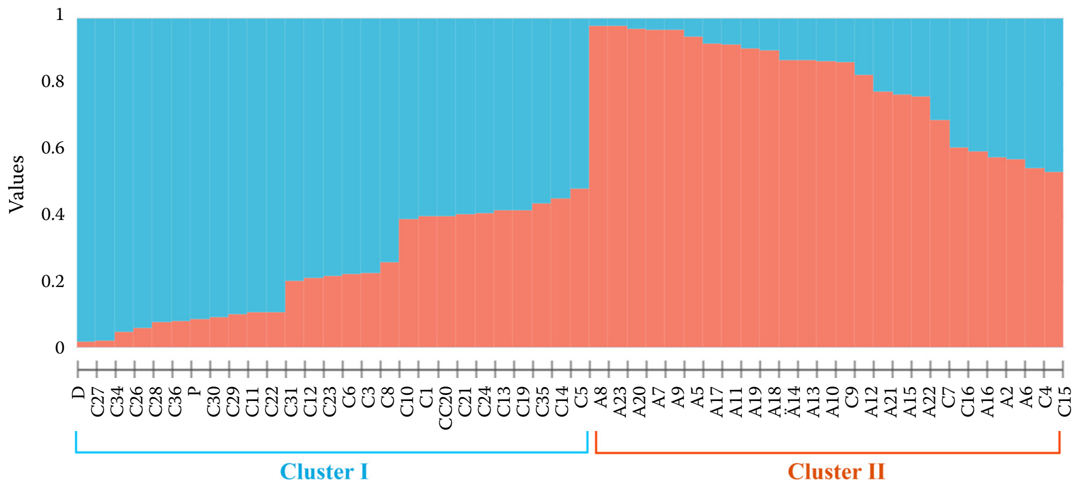

Figure 4. Population structure analysis of 52 almond accessions with 13 inter-primer binding site (iPBS) markers

showed that, as with some other species, the iPBS marker system was highly polymorphic and cost-effective in determining genetic diversity in almonds. While iPBS markers are comparable to ISSR and RAPD markers for assessing genetic diversity in almond, SSR markers provide greater informativeness. The clustering analyses (UPGMA, PCoA, and STRUCTURE) performed in this study produced largely consistent findings, indicating a clear separation between the Akdamar and Çarpanak populations and grouping the commercial accessions (Pabuç and Dokuzoğuz) with the Çarpanak population. The genetic variation in the Çarpanak population was wider than that of the Akdamar population. These results will assist breeders aiming to investigate the local accessions utilized in this research in the future.

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