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Association Analysis and Estimation of Breeding Values of Table Grapevine Germplasm by Integrating Pomological and Molecular Data

Mitra Razi[1], Reza Darvishzadeh[1]*, Hamed Doulati Baneh[2], Hadi Alipour[1]

1 Department of Plant Production and Genetics, Urmia University, Urmia, Iran
2 Horticultural Crops Research Department, Kurdistan Agricultural and Natural Resources Research and Education Center, Agricultural Research, Education and Extension Organization (AREEO), Sanandaj, Iran

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ABSTRACT

In any country, genetic resources are valuable assets for sustainable development. Having an accurate knowledge of genetic behavior and identification of genomic loci associated with important economic traits can help breeders run their breeding programs efficiently. Fourteen important pomological traits were measured in 45 table grape cultivars during three successive years (2016, 2017, and 2018). The molecular profile of the studied cultivars was prepared with 39 (simple sequence repeat) SSR primer pairs. Based on the SSR markers, genetic structure analysis revealed two subpopulations (K= 2) in the association panel. In association analysis, while using the mixed linear model, seven loci were found to be significantly associated with the studied traits ($p \leq 0.05$). Breeding values were also estimated for the pomological traits using the best linear unbiased prediction (BLUP). 'Saghal Solian', 'At Ouzum', 'Garmian', 'Rishbaba Qermez', 'Taifi', 'Shahroudi', 'Sahebi Qermez', 'Lal Qermez', 'Alhaghi', 'Sarghola', 'Chava Ga', 'Qzl Ouzum' and 'Agh Shani' table grape cultivars showed high and positive breeding values for cluster length, width, and weight. 'Garmian', 'Rishbaba Qermez', 'Fakhri', 'Agh Shani', 'Lal Sefid', and 'Shirazi' had positive and high breeding values for pollen germination, fruit set in open pollination, and fruit set under controlled pollination. Finally, 'Sarghola' and 'Qzl Ouzum' showed positive, highest breeding values for berry weight, flesh weight, cluster length, cluster width, and cluster weight. Cultivars with high and positive breeding values can be used as good parents for the breeding of traits in hybridization programs because they can better transfer the desirable characteristics to progeny in each case.

Introduction

Table grape (*Vitis vinifera* L.) is one of the most important horticultural crops and has been a historic part of human diets for many centuries (Commbe, 1992). Archaeological studies have shown that Iran is one of the centers of the domestication of grapes (McGovern, 2003). The size of the grape genome (38 chromosomes) is

* Corresponding author's email: r.darvishzadeh@urmia.ac.ir

about 4.75 × 108 bp. This genome is a combination of duplicate and non-duplicate sequences that duplicate DNA and makes up more than 95% of the genome (Grassi et al., 2002). Investigation of the genetic basis of quantitative traits has become possible through the development of molecular markers (Tuberosa et al., 2002 a; Semagn et al., 2010). Simple sequence repeat (SSR) markers are considered ideal molecular markers in fingerprinting, genetic diversity studies, population structure analysis, linkage, and association mapping due to their advantages of multi-allelic, co-dominant, stability, ease of detection, and extensive genome coverage (Jose et al., 2017). In many plants, the identification of genomic regions controlling quantitative traits could provide valuable genetic information about the genetic basis and structure of complex traits (Gomez et al., 2011). The development of molecular marker technology together with appropriate statistical genomic techniques has facilitated the achievement of this goal. Identification of the genomic regions associated with quantitative inheritance is usually accomplished by two main methods. These are, namely, linkage mapping and association analysis. So far, the use of linkage mapping has been limited due to numerous drawbacks. For instance, the production of artificial populations as a prerequisite is difficult, especially in fruit trees (Gupta et al., 2005).

To overcome linkage mapping limitations, association analysis has been widely used in mapping programs in recent years (Yu and Buckler, 2006). In this method, the relationship between the genotype and phenotype of individuals coming from natural populations is examined directly to identify the chromosomal regions involved in controlling trait variations (Roy et al., 2006). Unlike linkage analysis in which the linkage disequilibrium is only due to physical linkage, in association analysis where natural populations are used, the linkage disequilibrium is caused in addition to physical linkage by other factors such as small population size and migration. Recent factors, however, have led to the identification of false-positive markers that are not important from the viewpoint of plant breeding (Zhang et al., 2012). Accordingly, with a decrease in false-positive associations, it is necessary to consider population structure and kinship in association models (Yu and Buckler, 2006).

Furthermore, several studies were conducted on grapes via genome-wide association analysis to identify genomic regions involved in important traits such as berry skin (Fournier-Level et al., 2011; Lijavetzky et al., 2006), berry proanthocyanidin compound (Huang et al., 2012) and fleshless berry (Houel et al., 2010). Fanniza et al. (2005) recognized QTLs as effective on fruit yield in grapes using AFLP (Amplified Fragment Length Polymorphism) and SSR markers. Also, in grapevine, some association studies have been conducted via the candidate genes approach, including Myb (This et al., 2007; Fournier-Level et al., 2009), VvDXS (Emanuelli et al., 2010), VvPel (Vargas et al., 2013 b), VvGAI (Vargas et al., 2013a), VvTFL1A (Fernandez et al., 2014), and 183 candidate genes associated with cluster architecture (Tello et al., 2015). In a relevant study, the genetic basis of grapevine leaf shape was reported for the first time by genome-wide association analysis (GWAS), including 961 grapevine accessions genotyped with 6114 SNPs (Chitwood et al., 2014).

Selecting parents for hybridization programs is mostly a great challenge for plant breeders. Several methodologies have been utilized in helping the identification of genotypes with promising and appropriate agronomical characters for hybridization. Parent selection based on the predicted breeding values (Henderson, 1977, 1983; Hansche, 1983; White and Hodge, 1988) is a method used extensively in animal breeding (Falconer, 1989). Two common methods for predicting the breeding value of parents are the selection index and the best linear unbiased prediction (BLUP). In the selection index, it is not possible to estimate the effect of environmental factors, so the data used in this method must be corrected for environmental factors before use (Bernardo, 2010). In fact, by this method, the best prediction of breeding value is estimated in populations with similar environmental conditions. For this reason, in recent years this method has been less used for predicting breeding values. On the contrary, in the BLUP method, corrected data for environmental factors is not required for statistical analysis. Another advantage of this method is the use of all kinship relationships in predicting breeding value. The genetic change that occurs in populations with continuous genetic selection can be estimated by BLUP.

Another feature of BLUP is its applicability in multiple traits (Bernardo, 2010). The type of model in use depends on the specificity of the data and the purpose of breeding programs. When the phenotypic data come from different conditions, they should be tested using robust statistical procedures for correcting the data for disturbing factors to increase the heritability coefficient, which will increase the accuracy of selection. Traditionally, for estimating breeding values (BLUP), pedigree information of lines is

used in software packages such as Wombat (Meyer, 2007). It is possible to use the Kinship matrix instead of the genetic relationship matrix (pedigree information) for predicting breeding values in the model (Bauer et al., 2006). In the BLUP context, the main purpose of breeders is to increase the correlation of true genotypic values and predicted genotypic values, whereupon the correct method can maximize this correlation (Searle et al., 2009).

The objectives of the present study are to find SSR loci associated with pomological traits using association analysis and to evaluate breeding values for selecting the best cultivars from table grape germplasm by integrating the pomological and molecular data. This research is hypothesized to introduce appropriate cultivars as parents, based on breeding values. To do this, source populations and associated SSR markers are used for selecting desirable individuals from source populations. This has an advantage over progeny tests. The major disadvantage of progeny tests in fruit trees is the long juvenile stage of each generation and the need for large areas of plant evaluation.

Materials and Methods

Plant materials

Forty-five Iranian table grape (*V. vinifera subspecies vinifera*) cultivars (Table 1) were provided by the germplasm bank of Kahriz Horticultural Research Station in 2018 (Urmia, West Azarbaijan) 44° 58' E longitude and 37° 4' N latitude. The grapevines were 10 years old. Vine spacing was 2 to 3 m. All cultivars were managed in the same experimental vineyard according to standard vineyard management protocols. The grapevines were pruned to a bilateral cordon.

Table 1. Characteristic of grape cultivars utilized in evaluating genetic diversity using SSR markers

Entry	Cultivars	Use	Seed	Entry	Cultivars	Use	Seed
1	Rezghi	Table	Yes	24	Kalati	Table	Yes
2	Hosseini	Table	Yes	25	Mam Braima	Table, Raisin	Yes
3	Tabarze Sefid	Table	Yes	26	Bol Mazu	Juice	Yes
4	Saghal Solian	Table	Yes	27	Lal Qermez	Table	Yes
5	At Ouzum	Juice	Yes	28	Sefid Shakh Shakh	Juice	No
6	Lal Seyah	Table	Yes	29	Alhaghi	Table	Yes
7	Seyah Sardasht	Table, Raisin	Yes	30	Askari	Table	No
8	Garmian	Table	Yes	31	Bidane Sefid	Table, Raisin	No
9	Maiemo	Juice	Yes	32	Rejin	Juice	No
10	Rishbaba Qermez	Table	Yes	33	Sarghola	Table	Yes
11	Taifi	Table	Yes	34	Chava Ga	Juice	Yes
12	Bidane Qermez	Table	No	35	Yaghoti	Table	Yes
13	Fakhri	Table, Raisin	Yes	36	Qara Gandoma	Juice	Yes
14	Shahroudi	Table	Yes	37	Gazandaii	Table	Yes
15	Qara Shani	Juice	Yes	38	Qzl Ouzum	Table	Yes
16	Sahebi Qermez	Table	Yes	39	Agh Shani	Table	Yes
17	Inah Amjai	Table	Yes	40	Jig Jiga	Table	Yes
18	Tabarze Qermez	Table	Yes	41	Lal Sefid	Table	Yes
19	Dastarchin	Juice	Yes	42	Klkarevi	Juice	Yes
20	Rishbaba Sefid	Table	Yes	43	Sachakh	Juice	Yes
21	Agh Melhi	Juice	Yes	44	Shirazi	Table	Yes
22	Goi Melki	Table	Yes	45	Angotka	Juice	Yes
23	Sayani	Table	Yes				

Phenotyping protocols

Fourteen pomological traits were measured in 12 vines per cultivar. The pomological traits included total soluble solids (Brix), fruit juice pH, fruit juice titratable acidity (TA), berry weight (g), fresh weight (g), juice volume (ml), seed weight (g), seed number per berry, cluster width (cm), cluster length (cm), cluster weight (g), fruit set in open pollination (%), fruit set in controlled pollination (%), and pollen germination rate (%).

The measurements were made in 2016, 2017, and 2018. TSS was determined by a refractometer in Brix°. TA was measured by the amount of 0.10 N NaOH used for adjusting the fruit juice pH to 8.1. Fruit juice pH values were measured by a pH meter. Berry and flesh weight, cluster weight, and also single seed weight were determined by a digital scale. Fruit juice (100 g) of each cultivar was evaluated with a graded cylinder. To measure the length and width of the cluster, three clusters from each vine were selected from the same positions and the traits were measured. To determine pollen germination, clusters were harvested up to the points of 50% and 70% of the flowering stage. Pollen were cultured on a medium with 1% agar and 5% sucrose for 24h at 26 °C. The number of germinated pollen was counted in seven microscopic areas. The fruit set percentage was calculated through the following formula: Fruit set = number of berries/number of flowers × 100.

The phenotypic coefficient of variation (PCV), genotypic coefficient of variation (GCV), and broad sense heritability (h^2_{bs}) were calculated by the following formulae, respectively.

$$\% PCV = \frac{\sqrt{V_p}}{\bar{X}_{oo}} \times 100$$

$$\% GCV = \frac{\sqrt{V_G}}{\bar{X}_{oo}} \times 100$$

$$\% h_b^2 = \frac{V_G}{V_G + \frac{\sigma_e^2}{r}} \times 100$$

Where VP is the phenotypic variance, VG is the genotypic variance, σ_e^2 is the experimental error variance and r is replication.

Marker identification and analysis

Genomic DNA was extracted according to a method used by Doyle and Doyle (1990). Thirty-nine SSR primer pairs were used for preparing the molecular profile of the studied cultivars (Table 2). PCR was carried out in a final volume of 20 µl, including 20 ng of genomic DNA, 1.75 mM magnesium chloride, 2 µl 10 × polymerase chain reaction buffer (500 mM KCl, 500 mM Tris–Hydrogen chloride; pH 8.4), 0.25 mM of each dNTP (Cinagene Co., Tehran, Iran), 10 µM of each primer, 1.1 Unit of Taq DNA polymerase (Cinagene Co., Tehran, Iran), and distilled water in a 96-well Mastercycler Gradient thermal cycler (Type 5331; Eppendorf AG, Hamburg, Germany). The PCR reaction program consisted of an initial denaturation at 94 °C for 4 minutes, followed by 35 cycles of 94 °C for 1 minute, annealing temperatures (50 to 59 ºC) for 1 minute, and 72 °C for 2 minutes, with a final extension of 7 minutes at 72 °C. The amplification was checked with 3% ultra-pure agarose gel. All PCR amplifications were scored in codominant manners.

Descriptive statistics and correlation coefficients among pomological features were calculated in SAS 9.4 software. Genetic parameters included the number of alleles per SSR loci, gene diversity ($\widehat{D}_l = \left(1 - \sum_{u=1}^{k} \tilde{p}_{lu}^2\right) / \left(1 - \frac{1+f}{n}\right)$, $\tilde{p}_{lu}$ and f which indicate allele frequency for the lth locus and inbreeding coefficient, respectively), heterozygosity ($\widehat{H}_l = 1 - \sum_{u=1}^{k} \tilde{p}_{luu}^2$), and PIC ($\widehat{PIC}_l = 1 - \sum_{u=1}^{k} \tilde{p}_{lu}^2 - \sum_{u=1}^{k-1} \sum_{v=u+1}^{k} 2\tilde{p}_{lu}^2 \tilde{p}_{lv}^2$) were calculated by GenAlEx 6 software (Peakall and Smouse, 2006).

Cluster and discriminant ways of principal component analyses (DAPC) for testing genetic relationships between groups were performed by the Adegenet package in the R environment (Jombart et al., 2010). The cluster function was carried out to identify the number of subpopulations. It uses a K-mean clustering algorithm which decomposes the total variance of a variable into within- and between-group components. The best number of subpopulations shows the lowest Bayesian Information Criterion (BIC) value. An accurate classification of table grape cultivars was done into appropriate sub-populations and the detection of cultivars with mixed structure was performed using the Bayesian method in Structure 2.3.4 software (Pritchard et al., 2000). The initial K value was considered in the range of 1 to 10. For each subpopulation, 10 replicates were assigned. The burn-in period length was adjusted to 100,000, followed by 100,000 Markov Chain Monte Carlo (MCMC) replications. Marker-trait association was tested by the Q + K mixed model in TASSEL 2.1 software (Yu et al., 2006). The linkage disequilibrium (LD) was calculated with TASSEL (Bradbury et al., 2007).

Predicting the breeding values was carried out using BLUP in SAS software (Bernardo, 2010). The structure of the mixed model for estimating breeding values followed accordingly:

$Y = Xb + Zu + e$

Where Y is the vector of phenotypic values, b is the vector of fixed effects, u is the vector of random effects, X and Z are the design matrices, and e is the vector of random residual (Piepho et al., 2008). The breeding value estimates can be realized by solving the mixed model equations (MME) according to Henderson (1990).

$$\begin{bmatrix} x'R^{-1}x & x'R^{-1}z \\ z'R^{-1}x & z'R^{-1}z + G^{-1} \end{bmatrix} \begin{bmatrix} \hat{\beta} \\ \hat{u} \end{bmatrix} = \begin{bmatrix} x'R^{-1}y \\ z'R^{-1}y \end{bmatrix}$$

$$BLUP(U) = [z'x \quad z'z + I\alpha]^{-1} \begin{bmatrix} x'y \\ z'y \end{bmatrix} = \begin{bmatrix} u_1 \\ u_2 \\ \vdots \\ u_n \end{bmatrix}$$

Table 2. Genetic parameters of SSR loci assayed in the characterization of table grape cultivars

Markers	Type	Primer sequence (5′→3′)	Annealing temperature (°C)	Genotype No.	Allele No.	Gene Diversity	Heterozygosity	PIC
ZAG 62	Forward Reverse	ggtgaaatgggcaccgaacacacgc ccatgtctctcctcagcttctcagc	53	14	8	0.71	0.73	0.68
VVS2	Forward Reverse	cagcccgtaaatgtatccatc aaattcaaaattctaattcaactgg	53	22	10	0.86	0.95	0.85
VVMD5	Forward Reverse	ctagagctacgccaatccaa tataccaaaaatcatattcctaaa	56	21	10	0.83	0.78	0.81
VVMD7	Forward Reverse	agagttgcggagaacaggat cgaaccttcacacgcttgat	54	15	6	0.80	0.78	0.77
G7	Forward Reverse	caacagaattcaaatgaaatgga caaacagcataaatacacaagca	50	26	14	0.90	0.93	0.89
G10	Forward Reverse	catcattcatccaaattatgtag tttagtaggttagggataccagt	51	7	5	0.58	0.40	0.50
D12	Forward Reverse	ctctcttttccgaaattggggt attttccctggaaacaaagtgg	54	18	10	0.75	0.91	0.71
UCH29	Forward Reverse	aaacatgatctgatgcaggtga caacctgttgatgaaagggaaa	62.5	16	9	0.74	0.71	0.71
ISV2	Forward Reverse	cactggcctgttgggagataat ccttcaactggaaaagcctgtc	58	17	10	0.77	0.69	0.75
ISV3	Forward Reverse	aaggaggagttgagatgtagta gagtaagagagaagcaagaaaa	58	8	4	0.64	0.82	0.57
ISV4	Forward Reverse	tgcatagtgctgtaggccattg tctgtcattgctgtccctttca	59	12	6	0.73	0.62	0.69
VVS3	Forward Reverse	tgccctatcaattagttcaccta tcgactttgatatattgatgatt	52	3	2	0.48	0.69	0.37
VVS4	Forward Reverse	ccatcagtgataaaacctaatgcc cccaccttgcccttagatgtta	58	6	4	0.46	0.44	0.42
ZAG 47	Forward Reverse	ggtctcaatacatccgtaagtatat acggtgtgctctcattgtcattgac	54	11	6	0.75	0.84	0.72
ZAG64	Forward Reverse	tatgaaagaaacccaacgcggcacg tgcaatgtggtcagcctttgatggg	58	17	10	0.83	0.98	0.81
ZAG83	Forward Reverse	ggcggaggcggtagatgagagggcg acgcaacggctagtaaatacaacgg	52	3	2	0.41	0.22	0.33
VVMD8	Forward Reverse	taacaaacaagaagaggaat agcacatccacaacataatg	56	20	12	0.84	0.89	0.82
VVMD17	Forward Reverse	tgactcgccaaaatctgacg cacacatatcatcaccacacgg	56	6	4	0.51	0.51	0.44
VVMD21	Forward Reverse	ggttgtctatggagttgatgttgc gcttcagtaaaaagggattgcg	56	7	5	0.66	0.82	0.59
VVMD25	Forward Reverse	ttccgttaaagcaaaagaaaaagg ttggatttgaaatttattgagggg	56	14	7	0.78	0.76	0.75
VVMD26	Forward Reverse	gagacgactggtgacattgagc ccatcaccaccatttctactgc	56	5	4	0.52	0.60	0.41
VVMD27	Forward Reverse	gtaccagatctgaatacatccgtaagt acgggtatagagcaaacggtgt	56	10	5	0.72	0.78	0.67
VVMD32	Forward Reverse	tatgatttttttaggggggtgagg ggaaagatgggatgactcgc	59	14	8	0.71	0.71	0.67
Scu8vv	Forward Reverse	cgagacccagcatcgtttcaag gcaaaatcctccccgtacaagtc	56	2	2	0.12	0.13	0.12
Scu10vv	Forward Reverse	taccccacaaccctttt ttctccgccacctccttttcac	56	2	2	0.37	0.49	0.30

Table 2. Continued.

UDV047	Forward Reverse	tgtatgataatccataatgtgc taggcatgcttgacttattc	50	3	2	0.50	0.33	0.38
VMC6E10	Forward Reverse	ctaggtgtgccaagagatcaga catttgtgggtagttgtgagga	53	5	3	0.61	0.38	0.53
VMC7a4	Forward Reverse	taaggtggattagttttgggtc aaactccaaacgatctgattct	51	6	4	0.73	0.13	0.68
Vmc7b1	Forward Reverse	cacgcaatctctcatttcacaaa tggtttaggtgacccaaccttta	55	3	2	0.50	0.33	0.37
Vmc7c3	Forward Reverse	ctttggagagtttccagaggta actgctctaacagtcctttgct	51	2	2	0.08	0.08	0.08
Vmc7f2	Forward Reverse	aagaaagtttgcagtttatggtg aagatgacaatagcgagagagaa	51	2	2	0.29	0.36	0.25
Vmc7f6	Forward Reverse	attgcttccaaaaagaga acccaaacccaaatagat	50	3	2	0.19	0.17	0.17
Vmcng2b7.2	Forward Reverse	ttttggagtgaatagagacccct cagaatttggctccatatttgaa	54	4	3	0.40	0.38	0.33
Vmcng2h7	Forward Reverse	acgttaaatagaacatggtccc caacctctttttttgaggtagc	51	6	3	0.63	0.68	0.56
VVIV67	Forward Reverse	aacttgattgaacaaaggccta tattatgcctatccagtttcga	50	3	2	0.37	0.39	0.30
VVIV67.2	Forward Reverse	attctcatttgggttctcac ttcagtagtcactctcaac	50	3	2	0.45	0.60	0.35
VVs16	Forward Reverse	tcaaactattattcaaaccaaagtac tcgatttcaacaaatttagaaata	51	3	3	0.11	0.12	0.11
VVs29	Forward Reverse	ccccaaggctctgaaaacaat tgcaaagcaaataaagcttcca	56	2	2	0.45	0.68	0.35
UDV015	Forward Reverse	tgcacatttccctccttag cgggttactgggaagggtat	53	3	2	0.27	0.15	0.23
Mean				8.82	5.10	0.57	0.56	0.51

Genotype No: number of different genotypes, allele No: number of alleles, PIC: Polymorphism information content.

Results

Descriptive phenotypic analysis

The highest and lowest levels of phenotypic and genotypic coefficients of variation were observed for pollen germination (PCV= 59.53, GCV= 59.07) and juice volume (PCV= 9.60, GCV= 9.41) among the studied table grape cultivars, respectively. The highest mean value based on the data of three years was observed in cluster weight (544.95 gr). The highest broad sense heritability (98.46%) was observed in the pollen germination rate (Table 3). Correlation coefficients among pomological traits of grape cultivars in the first and second cropping seasons, and the third and mean values of the three cropping seasons are shown in Tables 4 and 5. In cluster analysis, based on agro-morphological characteristics, the studied genotypes were subdivided into four main groups (Fig. 1).

Marker-trait analyses

A total of 199 alleles were amplified with 39 SSR primer pairs with an average of 5.10 alleles per locus. To identify the level of polymorphism, the amount of PIC was calculated for each of the 39 SSR loci which ranged from 0.08 for locus Vmc7c3 to 0.89 for locus VVMD8 with an average value of 0.51. The observed heterozygosity ranged from 0.083 for locus Vmc7c3 to 0.98 for locus ZAG64 with an average of 0.56 across the SSR markers (Table 2). The studied genotypes were grouped into four main groups based on SSR data (Fig. 1). Hierarchical groupings of cultivars by phenotypic and genotypic data were compared, revealing that 67% of the cultivars were grouped into similar positions across the two hierarchical clusters (Fig. 1). The genetic structure of the studied grape population was also analyzed with the Bayesian clustering method. The results revealed two possible subpopulations (K= 2) in the studied germplasm (Fig. 2). Based on the Barplot (Fig. 2), from 45 studied cultivars, 34 cultivars (75.56%) belonged to sub-population 1, and 8 cultivars (17.78%) to sub-population 2. Three cultivars (6.67%) with Q<0.70 were assigned as admixed (Fig. 2).

The r^2 values among SSR markers showed an average value of 20.37 ($r^2 \geq 0.1$, P-value < 0.01) (Fig. 2). Using a mixed linear model, seven loci were found to be significantly associated with the studied traits ($p \leq 0.05$) (Table 6). One locus (Scu8vv) was identified to be associated with total soluble solids, one locus (Vmc7f2) with pollen germination, one locus (VVMD17) with seed weight, one locus (Vmc7f2) with cluster

weight, one locus (Scu8vv) with fruit set in open pollination, one locus (ISV3) with seed number and one locus (Udv015) with titratable acidity. The results showed that Scu8vv was common for total soluble solids and fruit set in open pollination and also Vmc7f2 was common for pollen germination and cluster weight (Table 6).

Table 3. Descriptive statistics for pomological traits of grape cultivars during three successive years

Trait	Year 1			Year 2			Year 3		
	Range	Mean	Std. Deviation	Range	Mean	Deviation	Range	Mean	Std. Deviation
TSS	14.8-24.6	18.95	2.64	14.5-26	19.86	3.06	15-26.5	18.86	2.49
pH	2.22-5.4	3.04	0.68	3.1-5.4	3.56	0.34	2.56-4.76	3.38	0.34
TA	0.09-2.6	0.8	0.51	0.09-1.51	0.59	0.23	0.09-1.12	0.65	0.22
BW	1.31-5.15	3.02	1.08	1.36-5.15	3.01	1.05	1.44-6.5	3.44	1.28
FW	1.23-4.93	2.88	1.05	1.36-5.05	2.91	1.02	1.43-6.4	3.36	1.26
SSW	0-0.15	0.06	0.03	0-0.15	0.05	0.03	0-0.15	0.03	0.02
SN	0.95-3.5	2.13	0.64	1.1-3.4	2.09	0.62	1-3.5	2.2	0.61
JV	31-49	41.32	3.63	30-50	42.13	4.22	32-51.8	43.77	4.73
FSOP	10.6-63.3	32.6	11.57	10-76	31.07	13.42	5.6-64	32.42	11.46
PG	0.5-65.5	28.3	17.03	1.2-65	28.95	17.15	0.4-62.3	26.07	16.16
CL	9-26	18.83	4.48	9-32.7	19.68	4.65	13-26	19.91	3.27
CWid	5-17.5	10.1	2.82	4-20	10.01	3.18	5.5-15.5	10.13	2.25
CW	67.1-874.9	402.37	185.5	300-950	636	132.21	223.3-1387	597.61	268.52
FSCP	0-58.5	24.65	13.14	0-70.9	27.32	16.18	1.8-51	24.34	11.99

Trait	Average of three years			PCV	GCV	h^2_{bs}	GA5%	GA5% mean
	Range	Mean	Std. Deviation					
TSS	15.33-23.56	19.22	2.17	11.35	9.58	71.23	3.20	16.66
pH	2.84-5.03	3.32	0.38	11.41	9.47	68.83	0.54	16.18
TA	0.09-1.38	0.68	0.24	35.46	24.22	46.65	0.23	34.08
BW	1.4-5.06	3.14	1.05	33.31	31.82	91.25	1.98	62.62
FW	1.39-4.92	3.04	1.03	33.65	32.05	90.75	1.92	62.90
SSW	0-0.15	0.05	0.02	50.14	44.12	77.43	0.04	79.98
SN	1.03-3.2	2.13	0.55	25.70	23.87	86.25	0.98	45.67
JV	20.7-50.26	41.96	5.19	9.60	9.41	96.25	8.07	19.03
FSOP	8.7-67.7	31.98	11.02	34.43	32.48	88.95	20.21	63.09
PG	1-64.2	27.27	16.97	59.53	59.07	98.46	33.53	120.74
CL	12.2-24.7	19.44	3.24	16.59	13.51	66.32	4.41	22.66
CWid	5-15.5	10.24	2.38	22.01	18.65	71.77	3.28	32.55
CW	326-905	544.95	145.92	26.75	19.46	52.90	158.96	29.15
FSCP	3.8-52	25.4	10.79	42.54	35.00	67.69	15.09	59.32

PCV: Phenotypic coefficient of variation, GCV: Genotypic coefficient of variation, h^2_{bs}: Narrow sense heritability, GA 5%: Genetic advance ($p \leq 0.05$). TSS: Total soluble solids, TA: Titratable acidity, BW: Berry weight, FW: Flesh weight, SSW: Single seed weight, SN: Seed number, JV: Juice volume, FSOP: Fruit set in open pollination, PG: Pollen germination, CL: Cluster length, Cwi: Cluster width, CW: Cluster weight, FSCP: Fruit set under controlled pollination.

Table 4. Correlation coefficients among agronomic traits of grape cultivars in the first (upper diagonal) and second (low diagonal) cropping season.

	TSS	pH	TA	BW	FW	SSW	SN	JV	FSOP	PG	CL	CWid	CW	FSCP
TSS	1	0.196^{ns}	-0.105^{ns}	-0.296*	-0.293^{ns}	-0.210^{ns}	-0.011^{ns}	-0.051^{ns}	0.188^{ns}	0.328*	0.069^{ns}	0.110^{ns}	0.192^{ns}	0.03^{ns}
pH	0.209^{ns}	1	-0.494**	0.194^{ns}	0.206^{ns}	-0.049^{ns}	0.10493^{ns}	-0.252^{ns}	0.003^{ns}	0.112^{ns}	-0.105^{ns}	-0.258^{ns}	0.166^{ns}	0.08^{ns}
TA	-0.175^{ns}	-0.621**	1	-0.271^{ns}	-0.275^{ns}	-0.012^{ns}	-0.096^{ns}	0.123^{ns}	0.264^{ns}	-0.000^{ns}	0.201^{ns}	0.205^{ns}	-0.015^{ns}	-0.023^{ns}
BW	-0.242^{ns}	0.105^{ns}	-0.170^{ns}	1	0.997**	0.388**	0.315*	0.119^{ns}	-0.071^{ns}	-0.274^{ns}	-0.047^{ns}	0.193^{ns}	0.330*	0.069^{ns}
FW	-0.248^{ns}	0.111^{ns}	-0.164^{ns}	0.998**	1	0.327*	0.283^{ns}	0.108^{ns}	-0.077^{ns}	-0.264^{ns}	-0.061^{ns}	0.175^{ns}	0.324*	0.052^{ns}
SSW	-0.181^{ns}	-0.128^{ns}	0.001^{ns}	0.375*	0.332*	1	0.063^{ns}	0.133^{ns}	-0.141^{ns}	-0.296*	0.074^{ns}	0.091^{ns}	0.075^{ns}	0.010^{ns}
SN	0.227^{ns}	0.038^{ns}	-0.177^{ns}	0.185^{ns}	0.171^{ns}	-0.235^{ns}	1	0.241^{ns}	0.307*	0.112^{ns}	0.056^{ns}	0.369*	0.308*	0.442**
JV	-0.144^{ns}	-0.092^{ns}	-0.073^{ns}	0.185^{ns}	0.185^{ns}	-0.035^{ns}	0.228^{ns}	1	0.136^{ns}	0.048^{ns}	0.203^{ns}	0.313*	0.440**	0.072^{ns}
FSOP	0.294*	0.325*	-0.296^{ns}	-0.072^{ns}	-0.072^{ns}	-0.175^{ns}	0.216^{ns}	0.012^{ns}	1	0.2917^{ns}	-0.129^{ns}	0.259^{ns}	0.142^{ns}	0.547**
PG	0.129^{ns}	0.102^{ns}	-0.148^{ns}	-0.338*	-0.323*	-0.503**	0.274^{ns}	0.008^{ns}	0.148^{ns}	1	-0.235^{ns}	0.255^{ns}	0.076^{ns}	0.347*
CL	0.045^{ns}	0.244^{ns}	-0.066^{ns}	0.157^{ns}	0.164^{ns}	-0.141^{ns}	0.106^{ns}	0.176^{ns}	0.053^{ns}	-0.090^{ns}	1	0.206^{ns}	0.177^{ns}	-0.202^{ns}
CWid	0.018^{ns}	0.115^{ns}	-0.235^{ns}	0.157^{ns}	0.164^{ns}	-0.234^{ns}	0.292^{ns}	0.447**	0.390**	0.030^{ns}	0.372*	1	0.563**	0.192^{ns}
CW	-0.207^{ns}	-0.198^{ns}	0.002^{ns}	0.499**	0.497**	0.172^{ns}	0.203^{ns}	0.417**	0.139^{ns}	-0.173^{ns}	0.141^{ns}	0.364*	1	0.046^{ns}
FSCP	0.071^{ns}	0.225^{ns}	-0.276^{ns}	0.073^{ns}	0.077^{ns}	-0.190^{ns}	0.290^{ns}	-0.182^{ns}	0.473**	0.168^{ns}	-0.034^{ns}	0.193^{ns}	0.061^{ns}	1

TSS: Total soluble solids, TA: Titratable acidity, BW: Berry weight, FW: Flesh weight, SSW: Single seed weight, SN: Seed number, JV: Juice volume, FSOP: Fruit set in open pollination, PG: Po llen germination, CL: Cluster length, Cwi: Cluster width, CW: Cluster weight, FSCP: Fruit set under controlled pollination.

Table 5. Correlation coefficients among agronomic traits of grape cultivars in the third (upper diagonal) and mean values of three (low diagonal) cropping seasons

	TSS	pH	TA	BW	FW	SSW	SN	JV	FSOP	PG	CL	CWid	CW	FSCP
TSS	1	0.041^{ns}	0.157^{ns}	-0.176^{ns}	-0.165^{ns}	-0.275^{ns}	0.026^{ns}	0.077^{ns}	0.138^{ns}	0.350*	0.003^{ns}	-0.011^{ns}	0.014^{ns}	0.253^{ns}
pH	0.149^{ns}	1	-0.519**	-0.205^{ns}	-0.210^{ns}	0.159^{ns}	-0.146^{ns}	-0.176^{ns}	0.014^{ns}	0.210^{ns}	-0.082^{ns}	0.056^{ns}	0.013^{ns}	0.055^{ns}
TA	0.085^{ns}	-0.664**	1	-0.047^{ns}	-0.047^{ns}	-0.062^{ns}	-0.152^{ns}	-0.014^{ns}	-0.068^{ns}	-0.235^{ns}	-0.016^{ns}	-0.242^{ns}	-0.039^{ns}	-0.137^{ns}
BW	-0.339*	-0.004^{ns}	-0.259^{ns}	1	0.999**	0.147^{ns}	0.239^{ns}	0.083^{ns}	-0.095^{ns}	-0.453**	0.085^{ns}	-0.156^{ns}	0.071^{ns}	-0.023^{ns}
FW	-0.336*	-0.006^{ns}	-0.258^{ns}	0.999**	1	0.109^{ns}	0.224^{ns}	0.081^{ns}	-0.107^{ns}	-0.454**	0.095^{ns}	-0.169^{ns}	0.071^{ns}	-0.029^{ns}
SSW	-0.300*	0.006^{ns}	-0.046^{ns}	0.420**	0.383**	1	-0.047^{ns}	0.052^{ns}	0.165^{ns}	-0.001^{ns}	-0.209^{ns}	0.143^{ns}	-0.090^{ns}	0.099^{ns}
SN	0.115^{ns}	0.033^{ns}	-0.238^{ns}	0.234^{ns}	0.218^{ns}	-0.113^{ns}	1	0.149^{ns}	0.455^{ns}	0.071^{ns}	-0.073^{ns}	0.255^{ns}	0.187^{ns}	0.250^{ns}
JV	-0.148^{ns}	-0.589**	0.269^{ns}	0.144^{ns}	0.143^{ns}	0.139^{ns}	0.100^{ns}	1	0.229^{ns}	-0.036^{ns}	0.148^{ns}	0.073^{ns}	0.232^{ns}	0.125^{ns}
FSOP	0.287^{ns}	0.099^{ns}	0.060^{ns}	-0.116^{ns}	-0.123^{ns}	-0.096^{ns}	0.385**	-0.002^{ns}	1	0.186^{ns}	-0.172^{ns}	0.242^{ns}	0.284^{ns}	0.332*
PG	0.366*	0.176^{ns}	-0.121^{ns}	-0.369*	-0.365*	-0.299*	0.176^{ns}	-0.095^{ns}	0.212^{ns}	1	-0.206^{ns}	0.304*	-0.130^{ns}	0.378**
CL	0.072^{ns}	0.007^{ns}	0.137^{ns}	0.089^{ns}	0.091^{ns}	-0.146^{ns}	0.030^{ns}	0.084^{ns}	-0.088^{ns}	-0.217^{ns}	1	-0.015^{ns}	0.428**	-0.192^{ns}
CWid	-0.069^{ns}	-0.007^{ns}	0.01^{ns}	0.076^{ns}	0.074^{ns}	-0.136^{ns}	0.318*	0.218^{ns}	0.452**	0.097^{ns}	0.321*	1	-0.112^{ns}	0.053^{ns}
CW	-0.036^{ns}	0.094^{ns}	-0.175^{ns}	0.339*	0.342*	-0.053^{ns}	0.303*	0.279^{ns}	0.249^{ns}	-0.179^{ns}	0.454**	0.585**	1	-0.016^{ns}
FSCP	0.242^{ns}	0.137^{ns}	-0.141^{ns}	0.011^{ns}	0.008^{ns}	-0.106^{ns}	0.489**	-0.083^{ns}	0.582**	0.380**	-0.202^{ns}	0.221^{ns}	0.166^{ns}	1

TSS: Total soluble solids, TA: Titratable acidity, BW: Berry weight, FW: Flesh weight, SSW: Single seed weight, SN: Seed number, JV: Juice volume, FSOP: Fruit set in open pollination, PG: Pollen germination, CL: Cluster length, Cwi: Cluster width, CW: Cluster weight, FSCP: Fruit set under controlled pollination.

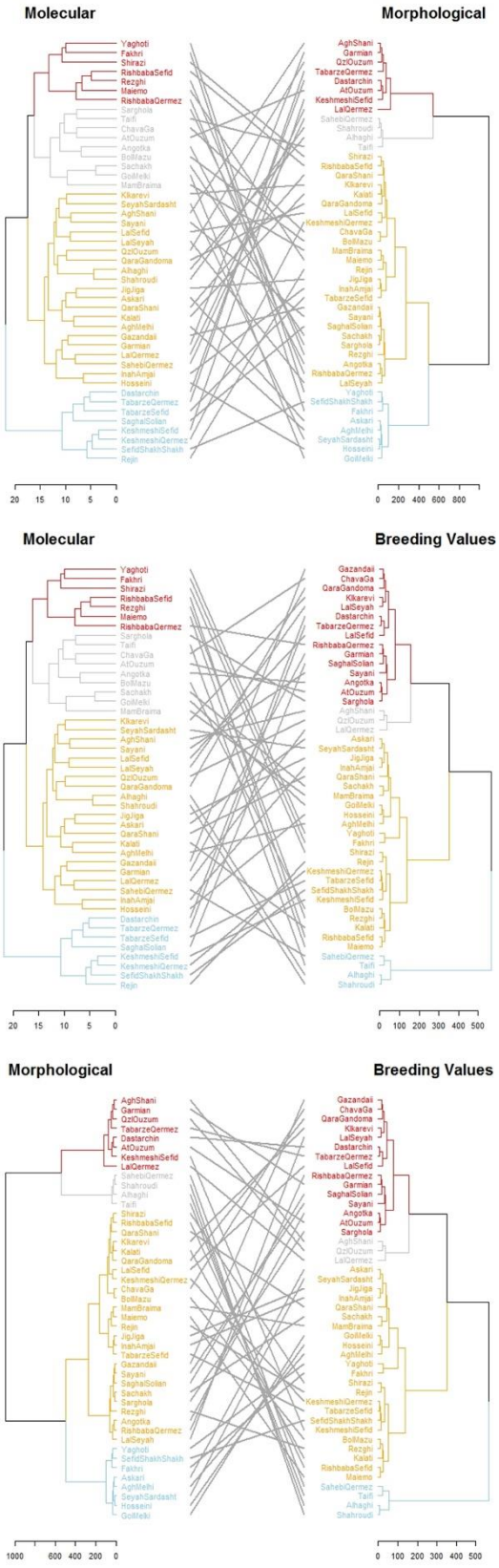

Fig. 1. Synteny analysis of the distribution of genotypes across dendrograms including the comparison of morphological and molecular data hierarchical cluster dendrograms, comparison of morphological and breeding value hierarchical cluster dendrograms, and comparison of molecular data and breeding value hierarchical cluster dendrograms.

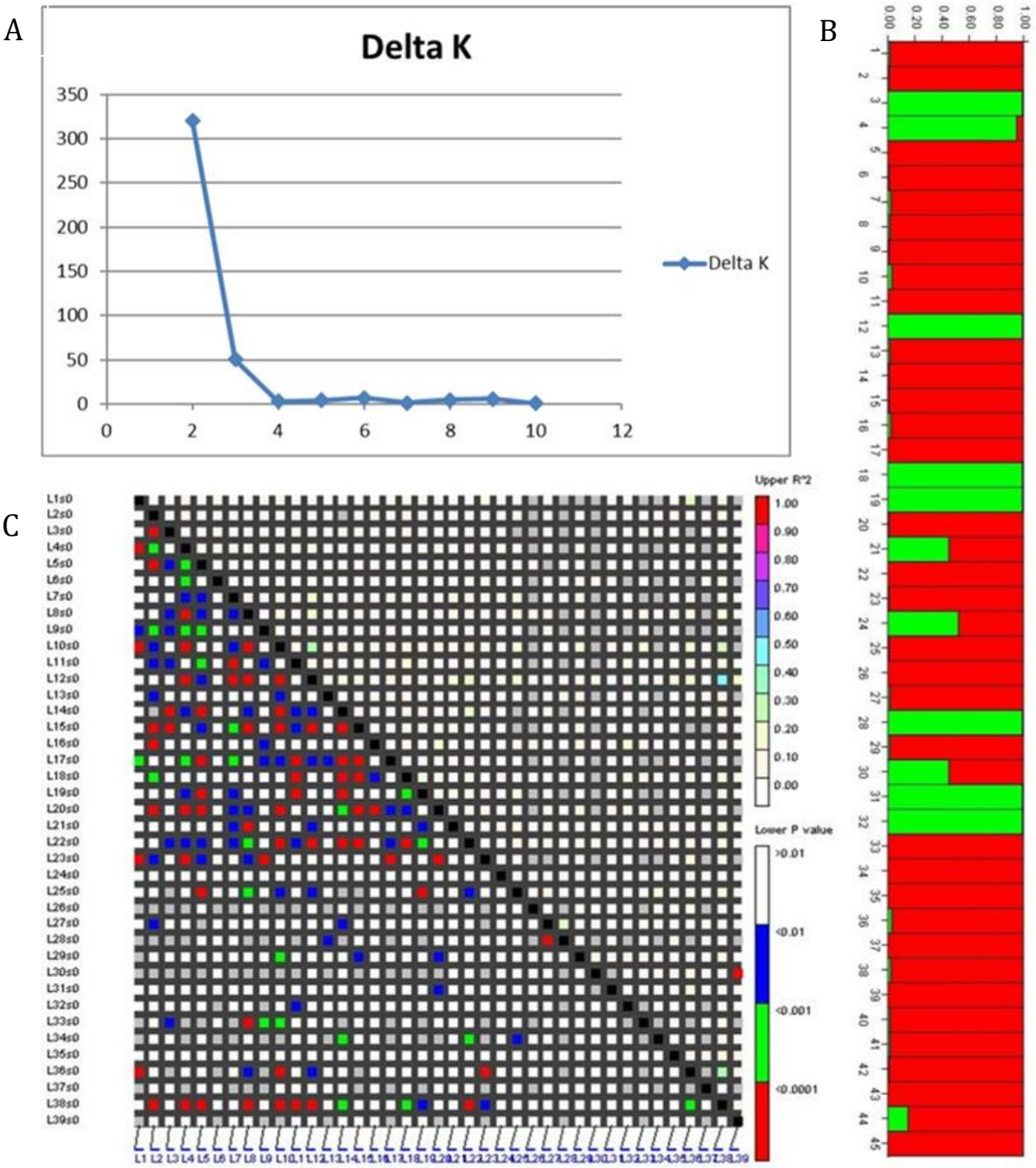

Fig. 2. (A) Bilateral charts to determine the optimal number of K identified by the Structure program. (B) Population structure indicates the two groups identified with different color bars. (C) LD plot generated by retrotransposon marker pairs in 45 Iranian grapevine cultivars (*V.vinifera* subspecies *vinifera*). The upper diagonal shows r^2 among each pair of markers. The lower diagonal shows the levels of significance between each pair of markers.

Table 6. SSR loci linked to the studied morphological traits in the analyzed grapevine germplasm using a mixed linear model (MLM) procedure

Trait	SSR locus	F-marker	P-marker	Trait	SSR locus	F-marker	P-marker
Total Soluble Solids	Scu8vv	5.69	0.022	Cluster weight (g)	Vmc7f2	4.86	0.033
Pollen germination (%)	Vmc7f2	5.08	0.029	Fruit set in open pollination (%)	Scu8vv	4.66	0.037
Seed weight (g)	VVMD17	2.76	0.032	Seed number	ISV3	2.44	0.038
				Titratable acidity	Udv015	3.47	0.044

F-marker: F test value marker, P-marker: p-value marker.

Predicting breeding values

The highest (2.4342) and lowest (-2.976) breeding values for total soluble solids (TSS) were observed in 'Klkarevi' and 'At Ouzum' cultivars, respectively. The highest (0.2052) and lowest (-0.0773) breeding value for pH was observed in 'Tabarze Qermez' and 'Garmian', respectively. The highest (0.0942) and lowest (-0.0645) breeding value for TA was seen in 'Klkarevi' and 'Shirazi' cultivars, respectively. For berry weight, the highest breeding value (1.4583) was observed in 'Qzl Ouzum' and the lowest one (-2.9236) was observed in 'Rejin'. The highest breeding value (1.4914) for flesh weight was observed in 'Qzl Ouzum' and the lowest one (-2.4007) was seen in 'Rejin'. Regarding single seed weight, the highest breeding value (0.0521) was seen in 'Shirazi' and the lowest one (-0.309) was observed in 'Askari'. The highest (0.6241) and lowest (-0.5183) breeding value for seed number was observed in 'Chava Ga' and 'Mam Braima' cultivars. For juice volume, the highest breeding value (4.6295) was seen in 'Sahebi Qermez' and the lowest one (-4.5384) was observed in 'Agh Shani' cultivar. The highest (17.8417) and lowest (-19.7354) breeding value for fruit set in open pollination was observed in 'Qara Shani' and 'Mam Braima' cultivars. Concerning pollen germination, the highest (24.9031) and lowest (-20.3949) breeding values were observed in 'Fakhri' and 'Mam Braima' cultivars, respectively. The highest breeding value (2.8615) for cluster length was observed in 'Qzl Ouzum' and the lowest one (-3.3038) was seen in 'Lal Sefid' cultivar. The highest breeding value (2.2685) for cluster width was observed in 'Lal Qermez' and the lowest one (-1.3292) was seen in 'Mam Braima' cultivar. Regarding cluster weight, the highest (211.783) and lowest (-121.986) breeding values were observed in 'Shahroudi' and 'Yaghoti' cultivars, respectively. For fruit set under controlled pollination, the highest (9.1738) and lowest (-9.7768) breeding values were observed in 'Qara Shani' and 'Bol Mazu' cultivars, respectively (Table 7).

Considering the breeding values of all studied traits, top ranks were attributed to 'Taifi', 'Qzl Ouzum', 'Rishbaba Qermez', 'Garmian', 'Agh Shani', 'Lal Qermez', 'Sahebi Qermez', 'Saghal Solian' cultivars, whereas the worst ranks were given to 'Askari', 'Hosseini', 'Inah Amjai', 'Goi Melki', 'Mam Braima', 'Sachakh' and 'Agh Melhi' cultivars (Table 7).

Narrow sense heritability was calculated for all studied traits based on predicted breeding values. Narrow sense heritabilities were 46.21%, 3.83%, and 1.97% for total soluble solids (TSS), pH, and titratable acidity (TA), respectively. For berry and flesh weights, it was estimated around 88.51% and 83.51%, respectively. For seed weight and seed number, narrow sense heritabilities were 32.13% and 32.33%. For juice volume, the value was estimated at 17.46%. Concerning fruit set in open pollination and fruit set under controlled pollination, narrow sense heritabilities were estimated at 38.25% and 15.37%, respectively. However, the value was 46.19% for pollen germination. For cluster length, cluster width, and cluster weight, narrow sense heritabilities were estimated at 25.37%, 9.32%, and 27.34%, respectively (Table 7). The highest heritability was observed in berry and flesh weights and the lowest was seen in TA, pH, and cluster width (Table 7).

Table 7. Breeding values of *V. vinifera* cultivars among the traits

Number	Cultivar	TSS	Rank	pH	Rank	TA	Rank	BW	Rank	FW	Rank	SSW	Rank	SN	Rank
1	Rezghi	-0.6385	21	-0.0075	14	0.0168	39	-1.0902	12	-1.0133	12	-0.0041	25	-0.2511	12
2	Hosseini	-2.4015	5	-0.0085	13	-0.0373	15	0.2769	30	0.4187	31	-0.0116	10	-0.2902	9
3	Tabarze Sefid	1.5597	40	0.1891	44	-0.0549	5	-0.8497	15	-0.8001	15	-0.0095	16	-0.1594	21
4	Saghal Solian	1.0926	34	0.1799	42	-0.0463	8	0.0462	28	0.1245	28	-0.0031	26	0.0325	29
5	At Ouzum	-2.9760*	1	-0.0643	3	0.0023	33	0.6809	39	0.7630	38	-0.0098	15	0.4067	39
6	Lal Seyah	0.5610	32	-0.0219	10	-0.0113	28	-0.6362	19	-0.6202	18	0.0028	34	0.3193	38
7	Seyah Sardasht	1.2420	36	0.0183	19	-0.0045	30	-1.7427**	2	-1.6217**	2	-0.0110	13	0.4132	40
8	Garmian	-0.2857	23	-0.0773	1	0.0219	41	0.7280	40	0.7869	41	-0.0049	23	0.2872	36
9	Maiemo	-0.9128	16	-0.0143	11	0.0044	35	-1.1177	11	-0.9748	13	-0.0094	17	-0.1049	24
10	Rishbaba Qermez	0.2513	30	0.0415	26	-0.0293	19	-0.8159	16	-0.6876	17	-0.0075	21	0.3178	37
11	Taifi	-0.0364	25	-0.0122	12	-0.0402	12	0.6112	36	0.6477	36	0.0029	35	0.6065*	44
12	Keshmeshi Qermez	1.3684	38	0.1285	39	-0.0159	26	-1.1752*	10	-1.1400*	10	-0.0224*	3	-0.1837	19
13	Fakhri	2.0662	44	0.0929	35	-0.0639	2	-0.5695	20	-0.4567	21	0.0014	32	-0.3179	5
14	Shahroudi	-2.4115	4	0.0781	32	-0.0308	18	-0.4257	24	-0.3069	25	-0.0101	14	-0.2643	11
15	Qara Shani	1.2783	37	-0.0431	5	0.0592	44	-0.3569	25	-0.3220	24	-0.0087	19	0.5828*	43
16	Sahebi Qermez	-1.0808	13	0.0186	20	-0.0225	23	0.9778	42	1.0421	42	-0.0024	27	0.1786	32
17	Inah Amjai	-2.1367	8	0.0395	25	-0.0559	4	0.3703	33	0.4735	34	-0.0067	22	-0.2860	10
18	Tabarze Qermez	1.3766	39	0.2052	45	-0.0382	14	-0.5135	21	-0.5489	20	-0.0128	9	-0.2468	13
19	Dastarchin	1.0645	33	0.1732	41	-0.0209	24	-0.7601	17	-0.7148	16	-0.0116	10	-0.3113	6
20	Rishbaba Sefid	-1.5506	11	0.0068	17	0.0027	34	-1.7275**	4	-1.5865**	3	-0.0081	20	-0.2170	16
21	Agh Melhi	0.0413	28	-0.0352	6	-0.0003	32	-1.3364*	8	-1.1931	9	-0.0139	8	-0.1902	18
22	Goi Melki	-1.6139	10	0.0370	24	-0.0429	10	0.3337	32	0.4207	32	0.0091	41	-0.2937	8
23	Sayani	-0.7039	19	0.0208	21	-0.0466	7	-1.0822	13	-0.9724	14	0.0008	31	-0.1426	22
24	Kalati	-1.5012	12	0.0476	28	-0.0261	21	-0.1787	26	-0.0832	27	-0.0048	24	-0.0261	28
25	Mam Braima	-2.4737	3	0.0736	31	-0.0156	27	0.7358	41	0.7742	40	0.0279*	44	-0.5183	1
26	Bol Mazu	-0.4542	22	-0.0282	9	0.0113	37	0.6793	38	0.7728	39	0.0024	33	-0.2109	17
27	Lal Qermez	-1.0505	14	0.0512	30	-0.0489	6	0.1149	29	0.1475	29	-0.0015	28	0.5315	42
28	Sefid Shakh Shakh	1.6054	41	0.1485	40	-0.0240	22	-1.4358*	6	-1.2961*	6	-0.0222*	4	-0.1006	25
29	Alhaghi	-2.4973	2	0.1064	38	-0.0420	11	-0.7402	18	-0.6033	19	-0.0140	7	-0.4194	2
30	Askari	-2.1175	9	0.0436	27	0.0217	40	-1.7321**	3	-1.5386*	4	-0.0309*	1	-0.2336	15
31	Keshmeshi Sefid	1.8917	43	0.0995	36	-0.0181	25	-1.4123*	7	-1.2717*	7	-0.0229	2	-0.1229	23
32	Rejin	1.8828	42	0.1890	43	-0.0278	20	-2.9236**	1	-2.4007**	1	-0.0187	5	-0.0825	26
33	Sarghola	0.0062	27	-0.0310	7	-0.0600	3	1.2493*	43	1.3487*	44	-0.0008	30	0.4917	41
34	Chava Ga	0.3101	31	-0.0731	2	0.0082	36	0.5232	35	0.4403	33	0.0128	42	0.6241*	45
35	Yaghoti	-0.1852	24	-0.0029	16	0.0499	43	-1.3076*	9	-1.2099*	8	0.0089	40	-0.3102	7

Number	Cultivar	TSS	Rank	pH	Rank	TA	Rank	BW	Rank	FW	Rank	SSW	Rank	SN	Rank
36	Qara Gandoma	-0.9326	15	0.0221	22	-0.0028	31	-0.4893	23	-0.4284	22	0.00881	39	-0.1675	20
37	Gazandaii	-2.2117	7	-0.0045	15	-0.0326	17	1.2770*	44	1.3305*	43	-0.0093	18	0.2204	33
38	Qzl Ouzum	0.1568	29	0.1033	37	-0.0456	9	1.4583*	45	1.4914*	45	0.0080	37	0.1409	31
39	Agh Shani	1.1959	35	0.0171	18	0.0148	38	0.3055	31	0.4025	30	-0.0112	12	0.0642	30
40	Jig Jiga	-0.7944	17	-0.0461	4	0.0308	42	-1.0584	14	-1.0549	11	0.0080	37	0.2285	34
41	Lal Sefid	-0.6458	20	0.0282	23	-0.0051	29	-0.5030	22	-0.3747	23	-0.0162	6	-0.0306	27
42	Klkarevi	2.4342	45	-0.0287	8	0.0942	45	-1.6757**	5	-1.5302*	5	-0.0012	29	-0.4108	3
43	Sachakh	-0.7598	18	0.0499	29	-0.0341	16	0.4987	34	0.5552	35	0.0139	43	-0.3665	4
44	Shirazi	-2.3412	6	0.0906	34	-0.0645	1	-0.0194	27	-0.0927	26	0.0521**	45	-0.2433	14
45	Angotka	-0.0311	26	0.0818	33	-0.0400	13	0.6746	37	0.7053	37	0.0071	36	0.2513	35
	Narrow sense heritability (%)	46.21		3.83		1.97		88.51		83.51		32.13		32.33	

TSS: Total soluble solids, TA: Titratable acidity, BW: Berry weight, FW: Flesh weight, SSW: Single seed weight, SN: Seed number
*and**: Significant at 5% and 1% probability levels, respectively.

Table 7. Continued.

Number	Cultivar	JV	Rank	FSOP	Rank	PG	Rank	CL	Rank	CWi	Rank	CW	Rank	FSCP	Rank	Sum of ranks
1	Rezghi	2.8965	42	-12.5984*	3	-8.1994	8	2.3681	41	0.0536	22	-31.423	16	-4.7609	7	274
2	Hosseini	-0.8817	20	-9.5757	6	3.9173	22	-3.1628	3	-0.9271	3	-78.435	4	1.3099	29	200
3	Tabarze Sefid	-3.8019*	3	-8.5253	9	12.5161	37	0.0463	15	-0.2859	13	-37.536	15	1.5955	34	282
4	Saghal Solian	-0.6768	22	-6.4190	18	16.0167	40	0.8406	27	0.4573	35	23.029	34	2.3219	36	407
5	At Ouzum	0.7094	36	-5.4238	22	-0.1167	17	0.9101	30	0.0831	26	16.473	32	-0.9321	18	349
6	Lal Seyah	-2.0783	12	8.0225	43	-4.9109	14	-2.1832	6	-0.8408	5	4.068	28	7.8283	43	330
7	Seyah Sardasht	-0.1224	29	-6.2370	19	8.1469	28	-1.6229	7	-0.4276	11	-65.036	6	1.3020	28	270
8	Garmian	-1.2243	17	0.3276	34	8.8130	31	0.7535	25	0.6913	39	37.042	37	8.7279	44	432
9	Maiemo	1.7818	38	-9.3284	7	2.4785	19	1.6377	35	0.7302	40	-31.235	17	-4.2791	9	292
10	Rishbaba Qermez	0.3599	33	2.4234	37	22.5191*	43	2.2945	38	1.3263	43	35.210	36	3.2429	38	434
11	Taifi	3.3511	44	-1.7388	30	4.9552	24	0.0794	16	0.7582	41	171.652*	42	3.4740	40	437
12	Keshmeshi Qermez	-3.4054*	5	-8.2283	10	8.2316	30	0.3833	21	-0.0931	18	-40.898	14	1.5136	32	275
13	Fakhri	-2.2115	11	2.8535	40	24.9031**	45	-2.3826	4	0.0556	23	-108.296	2	1.2595	27	311
14	Shahroudi	-0.2711	25	1.7806	36	-8.0582	9	2.5863	43	0.0758	25	211.783*	45	-3.9068	11	322
15	Qara Shani	-0.1970	28	17.8417**	45	-5.4311	12	-0.4402	10	0.1703	28	-47.266	12	9.1738	45	377
16	Sahebi Qermez	4.6295*	45	-0.3362	32	-13.8949	4	0.8705	28	2.0291*	44	174.977*	43	-1.2320	17	412
17	Inah Amjai	-1.0278	18	-8.1471	11	4.9079	23	-3.2069	2	-0.6583	8	-49.957	10	0.6135	26	234
18	Tabarze Qermez	-3.3934	6	-6.0394	20	11.5504	33	1.1631	34	0.3336	32	-2.446	26	1.3201	30	342
19	Dastarchin	-2.5875	9	-7.6361	14	10.1940	32	1.1442	31	0.3937	34	-9.197	24	0.5005	25	316

20	Rishbaba Sefid	2.7125	40	-7.2191	16	8.2271	29	2.3439	40	0.6698	38	-26.010	20	-4.7777	6	294
21	Agh Melhi	0.4595	34	-4.0021	27	16.0685	41	-1.5739	8	-0.5244	9	-85.569	3	-0.8058	19	250
22	Goi Melki	-0.3369	24	-12.5808*	4	6.0848	26	-0.3074	11	-0.8063	6	-75.823	5	-5.5572	3	236
23	Sayani	1.7232	37	-5.3235	23	-4.9499	13	1.1554	33	-0.2325	14	44.736	38	-3.9324	10	295
24	Kalati	0.0249	30	2.4369	38	-9.3695	7	0.7634	26	0.6215	37	-29.348	19	2.1190	35	358
25	Mam Braima	-0.3735	23	-19.7354**	1	-20.3949*	1	-0.1071	13	-1.3292	1	-57.176	9	-9.6850	2	237
26	Bol Mazu	2.0746	39	-10.3485	5	-13.6343	5	0.3451	20	-1.0033	2	-25.115	21	-9.7768	1	288
27	Lal Qermez	2.7605	41	-1.3236	31	11.7650	34	0.8706	29	2.2685*	45	101.809	41	-1.3095	16	415
28	Sefid Shakh Shakh	-3.1198	7	-7.4481	15	15.2255*	39	0.5322	24	0.0574	24	-31.013	18	2.5868	37	308
29	Alhaghi	-0.2127	27	2.6229	39	-12.5528	6	2.7001	44	0.2441	30	208.685*	44	-2.5854	15	302
30	Askari	-3.9114	2	-9.1625	8	14.0619	38	0.0066	14	-0.3783	12	-59.188	8	-3.6176	12	193
31	Keshmeshi Sefid	-1.5355	16	-7.6692	12	18.4415*	42	0.0946	17	-0.4602	10	-44.847	13	1.5324	33	286
32	Rejin	-2.5737	10	-4.4204	26	23.9810**	44	0.4288	22	-0.0803	19	-23.599	22	3.2739	39	320
33	Sarghola	-0.8607	21	-5.1890	24	3.5831	20	0.1044	18	0.3848	33	23.464	35	-0.3444	22	368
34	Chava Ga	-1.7135	14	-5.6535	21	-18.3529*	2	0.4452	23	0.2779	31	13.879	31	-3.1575	14	360
35	Yaghoti	-2.9675	8	0.0457	33	7.2376	27	-0.2837	12	0.0392	21	-121.986	1	-4.8387	5	254
36	Qara Gandoma	3.0149	43	-6.9581	17	-16.8250	3	1.7657	36	0.1327	27	-4.943	25	-0.3776	21	344
37	Gazandaii	0.2445	32	-7.6455	13	-4.6550	15	2.3883	42	-0.7836	7	6.706	30	-0.7871	20	336
38	Qzl Ouzum	0.1929	31	-5.0105	25	-6.9770	10	2.8615	45	0.1785	29	82.887	40	0.4623	24	437
39	Agh Shani	-4.5384*	1	3.1126	41	5.0923	25	2.2979	39	1.0296	42	68.073	39	5.6051	41	422
40	Jig Jiga	-1.8475	13	-2.5927	29	1.3384	18	1.1496	32	0.4889	36	-47.595	11	0.2801	23	321
41	Lal Sefid	-3.4780	4	5.7738	42	11.8121	35	-3.3038	1	0.0114	20	4.649	29	1.4563	31	312
42	Klkarevi	-0.2225	26	10.4248	44	-5.5205	11	2.0237	37	-0.2150	15	0.944	27	-4.6985	8	308
43	Sachakh	-1.6872	15	-14.0367*	2	-4.2272	16	0.1425	19	-0.9138	4	-64.211	7	-5.4802	4	246
44	Shirazi	0.4941	35	1.2941	35	12.2134	36	-2.2940	5	-0.1390	17	-20.502	23	5.7899	42	346
45	Angotka	-0.9521	19	-2.9218	28	3.7512	21	-0.6779	9	-0.2081	16	16.540	33	-3.5794	13	356
	Narrow sense heritability (%)	17.46		38.25		46.19		25.37		9.32		27.34		15.37		

JV: Juice volume, FSOP: Fruit set in open pollination, PG: Pollen germination, CL: Cluster length, Cwi: Cluster width, CW: Cluster weight, FSCP: Fruit set under controlled pollination.
*and**: Significant at 5% and 1% probability levels, respectively.

Synteny analysis of the distribution of genotypes across dendrograms

Comparing the phenotypic clustering with that produced by estimated breeding values, it was revealed that 26.67% of cultivars were grouped into the same groups across the two hierarchical clusters (Fig. 1). Cluster analysis by breeding values as well as that based on SSR genotypic data revealed the presence of four genetic groups in the studied germplasm (Fig. 1).

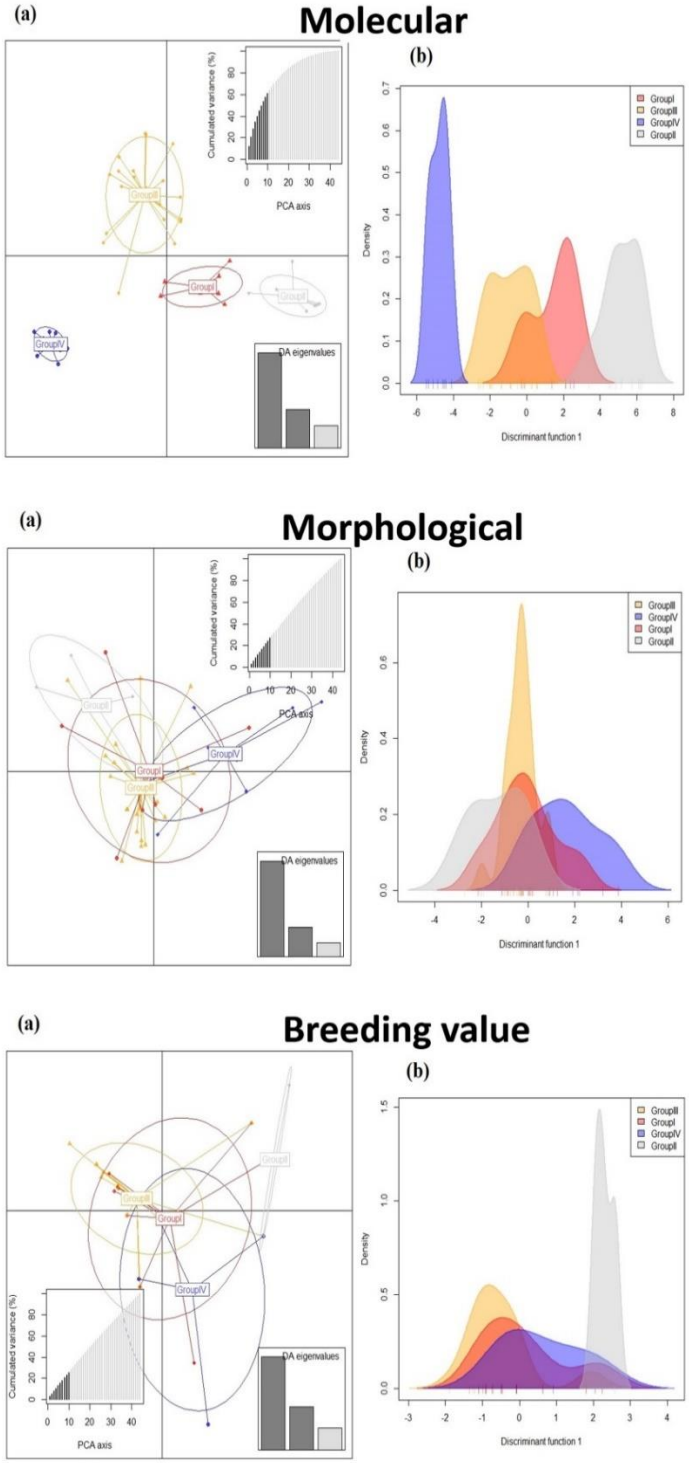

Fig. 3. Discriminant analysis of principal components (DAPC) between groups resulting from molecular, morphological, and breeding value cluster analysis. (A) Dots represent individuals with colors denoting cluster allocation. Percentages of cumulated variance explained by principal component 1 (PC1) to PC10 are shown in the top right corner. (B) Density plot of individuals along with the first discriminant function from the discriminant analysis of principal components (DAPC) for groups 1, 2, 3, and 4.

It was observed that the genotypes distribution pattern in clustering with breeding values was different from that clustered by SSR genotypic data (Fig. 1). By comparing the two dendrograms, it was found that all the cultivars except 'Rishbaba Qermez' in group 1 of the molecular cluster were grouped into similar positions across hierarchical clustering with breeding values (Fig. 1).

Discriminant analysis of principal components (DAPC)

To further clarify the genetic relationship between groups resulting from each one of molecular, morphological, and breeding value cluster analyses, discriminant analysis of principal components (DAPC) was performed. DAPC results classified the collections into four groups (Fig. 3). The results of molecular DAPC showed high dissimilarity between groups. However, some similarity was observed between groups 1 and 2 and also between groups 1 and 3. The density plot of individuals along with the first discriminant function also indicated the presence of four groups based on the Bayesian information criterion (BIC). High genetic diversity was observed in group 3. Red- and orange-colored peaks corresponding to groups 1 and 3 largely overlapped. The blue-colored peak corresponding to group 4 is completely distinct. DAPC analysis of morphological and breeding values showed high similarity between groups. Groups 1, 2, 3, and 4 largely overlapped (Fig. 3).

Discussion

Two subpopulations (K=2) were identified in the studied grape germplasm. Based on a membership probability of greater than or equal to 70%, 75.56% of cultivars belonged to population 1 and 17.78% of cultivars belonged to population 2. Spataro et al. (2011) stated that when the membership probability of a genotype to a cluster is greater than or equal to 0.70, the genotype is assigned to one of the subpopulations, but if the membership probability is less, it is defined as an admixed genotype. The presence of structure in the studied population is a deterrent factor to achieving reliable results. As a result, when population structure and kinship relations exist in the association panel and are not to be considered in the association analysis, they produce false-positive results (Breseghello and Sorrells, 2006). Based on r^2 statistics, some SSR locus pairs showed a significant level of linkage disequilibrium. The extent of LD depended on different factors. For example, some factors such as small population size, inbreeding, population admixture, genetic draft, autogamy, and epistasis increased LD levels. On the other hand, allogamy, high recombination rate, and high mutation rate decreased LD levels (Al-Maskri et al., 2012). The description of LD was reported in French wild grapes for the first time by Barnaud et al. (2010). It was reported that the LD level was twelve times higher in native grapes than in wild grapes (Barnaud et al., 2010).

In this study, seven SSR loci were found to be significantly associated with genomic regions controlling studied traits. Several QTLs were reported for berry weight, seed number, and seed fresh weight in grapes, and among these, the one reported for seedlessness was a major effect QTL and was closely linked to VMC7F2 locus (Cabezas et al., 2006). In another study, close association of two SSR markers (VVIB23 and VVMD34) with flower sex was reported (Battilana et al., 2013; Lowe and Walker, 2006; Riaz et al., 2006). Several QTLs for sugar content on LGs 1, 2, 3, 4, 7, 9, and 11, as well as some others for total acid on LGs were reportedly 06, 13, and 18 (Chen et al., 2015). Sugar and total acid are important factors in the taste of grapes. Hexoses (fructose and glucose) are predominant sugars in grapes at the maturity stage (Shiraishi, 1993; Liu et al., 2006). Some QTLs were common among different traits. Identification of common markers for the studied traits may be due to linkage or pleiotropic effects (Jun et al., 2008). Identification of common markers is important in plant breeding programs because it enables a simultaneous selection for several traits (Hittalmani et al., 2003; Tuberosa et al., 2002 b).

Breeding values were estimated for 14 pomological traits in grape cultivars using the best linear unbiased prediction (BLUP). Developing and introducing new cultivars requires parental selection within large germplasm populations, so estimating the value of genotype is an important step in breeding programs. Falconer (1981) reported that the breeding value is an important criterion in plant and animal breeding. Breeding value was defined as the mean value of its offspring. Application of BLUP for estimating individual breeding value has been reported in forest trees (White and Hodge, 1989). de Souza and Byrne (2000) used BLUP for estimating breeding values in peach genotypes. Tancred and Zeppa (1995) applied BLUP to predict the general combining ability (GCA) and specific combining ability (SCA) for the ripening date of apples.

The organoleptic quality of table grapes depends on the sugar content, organic acid content, and the balance between them. Organic acids are present in a small amount compared to sugars,

but it generally plays an important role in the taste (Nelson, 1985). A few cultivars with high-sucrose concentrations were reported in *Vitis rotundifolia* and hybrids between *V. labrusca* and V. vinifera (Liu et al., 2006). In this study, the 'Klkarevi' cultivar had the highest breeding value of TSS and TA. Seedlessness is another important and desirable factor for consumers. The development of seeds in grapes is controlled by a1, a2, a3, and i genes. The i gene is a regulator gene. The expression of seedlessness, as a trait, occurs when a1, a2, and a3 are homozygous as recessive, and the regulator gene is homozygous as 'II' or heterozygous 'Ii' (Bouquet and Danglot, 1996). In the stenospermocarpy grape, fertilization occurs but the embryo is aborted in earlier stages and a seed trace remains (Winkler et al., 1997). Among seedless cultivars, the 'Rejin' and 'Askari' cultivars had the highest and lowest breeding values in terms of single seed weight and seed number. Among seeded cultivars, the 'Shirazi' and 'Lal Sefid' cultivars had the highest and lowest breeding value for single seed weight, respectively. For seed count, the 'Chava Ga' and 'Mam Braima' cultivars had the highest and lowest breeding values, respectively.

Pollination is an important factor that affects the percentage of fruit set. Tangolar et al. (1999) examined the variability of pollen germination and reported a wide percentage of pollen germination from 11.4% in 'Thompson Seedless' to 39.1% in 'King's Ruby' grapevine cultivars. Among the cultivars examined in the present study, 'Rishbaba Qermez', 'Fakhri', 'Sefid Shakh Shakh', 'Keshmeshi Sefid' and 'Rejin' cultivars had high, positive breeding values for pollen germination. Pereira et al. (2018) considered pollen germination in 14 grape cultivars and reported that Touriga Nacional, Cabernet Franc, and Cabernet Sauvignon cultivars had low pollen germination, whereas Castelao, Loureiro, Malbec, and Petit Verdot cultivars showed a high percentage of pollen germination.

The ultimate purpose of most breeders is to combine the appropriate situation of more than one trait in common background. From the view of estimated breeding values, 'Saghal Solian', 'At Ouzum', 'Garmian', 'Rishbaba Qermez', 'Taifi', 'Shahroudi', 'Sahebi Qermez', 'Lal Qermez', 'Alhaghi', 'Sarghola', 'Chava Ga', 'Qzl Ouzum' and 'Agh Shani' cultivars are suitable parents for cluster length, cluster width, and cluster weight improvement. They can be used in hybridization programs because they can better transfer their characteristics to the progeny. The best parents for high berry weight, flesh weight, cluster length, cluster width, and cluster weight were 'Sarghola' and 'Qzl Ouzum' cultivars. 'Garmian', 'Rishbaba Qermez', 'Fakhri', 'Agh Shani', 'Lal Sefid', and 'Shirazi' cultivars were the best parents for breeding pollen germination, fruit set in open pollination, and fruit set under controlled pollination. 'Yaghoti', 'Fakhri', 'Shirazi', 'Rishbaba Sefid', 'Rezghi', and 'Maiemo' cultivars were clustered into the same group in both breeding value and molecular clustering dendrograms. These cultivars had negative breeding values for berry weight, flesh weight, and cluster weight. The wide range of breeding values for most of the evaluated traits, and the possibility to select a genotype in good situations of more traits, can suggest that breeders evaluate the germplasm according to their purpose before selecting the best individuals. BLUP is an effective option for achieving this goal (Falconer, 1989). No cultivar has a high-grade breeding value for all traits. The solution is to intercross individuals with positive traits and then select progenies over several generations.

In the selection process, based on phenotypic value, success in changing population characteristics is predictable if the degree of conformity between phenotypic and genotypic values is high. Measuring the degree of conformity is made by calculating heritability (Falconer, 1989). Heritability is influenced by the type of trait, studied population, environmental conditions, and the method of phenotype measurement (Fehr, 1991). Berry weight and flesh weight showed high heritability and, compared to other traits, were more under control of the additive effects of genes (Eibach, 1989). Research has shown that the accuracy of estimating breeding values for traits with high heritability is higher than that with low heritability (Villumsen et al., 2009). In traits with high heritability, the phenotype of an individual is closer to the genetic value and, therefore, the breeding value of each individual is more accurately estimated (Piepho et al., 2008). Heritability for berry weight reportedly ranged from 0.49 to 0.92 (Eibach, 1990; Firoozabady and Olmo, 1987; Singh and Jalikop, 1986). In a study by Wei et al. (2002), narrow-sense heritability was estimated at 0.63 for berry weight, 0.69 for berry width, 0.68 for berry length, 0.58 for seediness, 0.48 for Brix index, and 0.36 for acidity.

Conclusions

The results of the present study revealed the importance of considering population structure and relatedness factors in the association analysis of table grapes. Seven DNA markers were found to be significantly associated with regions controlling the studied pomological traits that can

be useful in marker-assisted breeding programs. In addition, breeding values were estimated for table grapevine germplasm by integrating DNA maker data and pomological traits. Considering the sum of the breeding values of all the studied traits, 'Taifi', 'Qzl Ouzum', 'Rishbaba Qermez', 'Garmian', 'Agh Shani', 'Lal Qermez', 'Sahebi Qermez', 'Saghal Solian' cultivars had the highest rank. Cultivars with high, positive breeding values can be used as promising parents in hybridization programs because they can better transfer their suitable characteristics to the progeny.

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Conflict of interest
The authors indicate no conflict of interest for this work.

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