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Genome-wide association links candidate genes to fruit firmness, fruit flesh color, flowering time, and soluble solid content in apricot (*Prunus armeniaca*)

Filiz Ferik: Ege University, Engineering Faculty, Department of Bioengineering, 35040 Bornova Izmir Turkey

Duygu Ates: Ege University, Engineering Faculty, Department of Bioengineering, 35040 Bornova Izmir Turkey,

Sezai Ercisli: Ataturk University, Agriculture Faculty, Department of Horticulture, 25030 Yakutiye/ErzurumTurkey,

Abdullah Erdogan: Institute for Apricot Research of Malatya, 44090 Malatya, Turkey

Emine Orhan: Ataturk University, Agriculture Faculty, Department of Horticulture, 25030 Yakutiye/ErzurumTurkey

Corresponding author: Muhammed Bahattin Tanyolac: Ege University, Engineering Faculty, Department of Bioengineering, 35040 Bornova Izmir Turkey. ORCID: 0000-0002-4368-0988

E-mail address: bahattin.tanyolac@ege.edu.tr

Phone: +90 232 3115815

This work is a part of Master of Science Thesis of Filiz Ferik who is the first author of the manuscript.

Genome-wide association links candidate genes to fruit firmness, fruit flesh color, flowering time, and soluble solid content in apricot (*Prunus armeniaca*)

Filiz Ferik, Duygu Ates, Sezai Ercisli, Abdullah Erdogan, Emine Orhan, Muhammed Bahattin Tanyolac*

Abstract:

Apricots originated from China, Central Asia and the Near East and arrived in Anatolia, and particularly in their second homeland of Malatya province in Turkey. Apricots are outstanding summer fruits, with their beautiful attractive colour, delicious sweet taste, aroma and high vitamin and mineral content. In the current study, a total of 259 apricot genotypes from different geographical origins in Turkey were used. Significant variations were detected in fruit firmness (FF), fruit flesh color (FFC), flowering time (FT), and soluble solid content (SSC). A total of 11,532 SNPs based on DArT were developed and used in the analyses of population structure and association mapping (AM). According to the STRUCTURE (v.2.2) analysis, the apricot genotypes were divided into three groups. The mixed linear model with Q and K matrixes were used to detect the associations between the SNPs and four traits. A total of 131 SNPs were associated with FF, FFC, and SSC. The results demonstrated that AM had high potential of revealing the markers associated with economically important traits in apricot.

Keywords: association mapping, apricot, fruit firmness, fruit flesh color, flowering time, soluble solid content

Introduction

Rosaceae is one of the most important fruit tree family from temperate regions, including apple, peach, strawberry, plum, almond, pear, European plum, and sweet cherry which are economically important fruit species (1)(2)(3). Apricot, *Prunus armeniaca* (Lam.), is also a member of this family and an important stone fruit with a total world production of about 3.8 million tons (4). The major apricot producing countries are Turkey (730.000 tons), Uzbekistan (662.123 tons), and Iran (306.115 tons) in the world (4).

Various parameters affect fruit quality in apricot (5)(6)(7). Consumer preferences are based on fruit quality which refers to sensorial properties, such as appearance, texture, taste and

aroma, high nutritional components, chemical components, functional properties, and mechanical characteristics (8). The appearance of fruit is the main criterion for consumers, while a low level of sweetness and hard texture are undesired (9). Thus, fruit firmness and fruit flesh color are important for consumer satisfaction (10).

Another important parameter affecting fruit quality is soluble solid content (SSC), which includes sugars, organic acids, proteins, minerals, lipids, amino acids, and vitamins, and it is the main criteria that determines the taste, flavor and nutritional value of the fruit (11). In addition to being a delicious edible product, the fruit of apricot is also considered as functional due to its chemical ingredients (12)(13)(14)(15). The apricot fruit makes a significant contribution to human health through its phenolic compounds content with immune-stimulating, anti-inflammatory and antioxidants properties (16)(15).

One of the important traits for apricot producers is flowering time, which is a substantial agronomic trait with an impact on fruit and seed growth in temperate fruit tree species. In cold regions, early flowering individuals are damaged by late frost, while in warm regions, late flowering individuals could lead to some problems concerning leaf and flower bud break, resulting in a decrease in the amount of harvest (17). In addition, early flowering species have economic value in terms of early market prices.

Complex traits including most of the fruit quality properties are controlled by interacting genes called quantitative traits (18)(1). Therefore, the clarification of transmission of complex traits is one of the main topic for agricultural sciences (19). Quantitative trait locus (QTL) mapping is a prevalent method for the mapping of these kinds of traits and bases on biparental mapping populations (20). Constructing a new cross population is a tedious, time consuming and expensive process (21). Considering the long generation and juvenile period of fruit trees, it is more difficult to apply QTL mapping (19)(1). To date, a certain number of QTL maps have been constructed for apricot, such as flowering time (22)(23), resistance to sharka disease (24)(10)(25)(26), fruit quality traits (27)(28), chilling requirements (29), and tree architectural traits (28).

AM is an alternative method to pedigree-based QTL mapping (30) and uses natural populations, contrary to QTL mapping, to determine the correlations between phenotypes and genotypes (31). AM also utilizes historical recombination and natural variation as a basis and provides high map resolution in shorter time due to no requirement of developing a new cross population (30). This method has been previously employed for different fruit trees, such as peach (32)(33)(34)(35)(30), apple (36), almond (30), and apricot (29)(37).

The objective of this study was to investigate the associations between SNPs based on the diversity arrays technology (DArT) and the pomological traits of apricot, namely fruit firmness (FF), fruit flesh color (FFC), flowering time (FT), and SSC using 259 apricot genotypes.

Materials and Methods

Plant Material and DNA Isolation

A total of 259 apricot (*Prunus armeniaca* L.) genotypes, which were grown together at Malatya Apricot Research Institute in Turkey, were used in this study (S1Table). All genotypes had been planted (with 3 replications for each genotype) with eight-meter spacing between and within the rows in the experimental station of Malatya Apricot Research Institute, and all trees were 20 years old. Standard management practices concerning chemical fertilization, pruning, and disease control were being applied to the trees.

Young leaves were collected from each apricot genotype, cooled in liquid nitrogen, and stored at -80 °C for future analyses. The leaf samples were ground into small pieces with a tissue lyser (Technogen Co., Turkey). DNA extraction was carried out with 0.1 g samples of each individual following the protocol described by Deshmukh et al. (2007) with minor modifications. Tris-EDTA (TE) buffer (100 µl) was used to dissolve the extracted DNA. For the purification and quantification assessment of the isolated DNA, 1% agarose gel and a spectrophotometer (NanoDrop ND 1000) were used, respectively. After confirmation, the DNA samples were stored at -80 °C until they were used for SNP analyses.

Pomological Evaluation

Forty fruits from each replication of genotype were randomly selected and harvested separately for each tree. FFC was measured with a Minolta Chroma Meter CR-400 (Minolta-Konica, Japan). For FT, observations were made by experts, and the first day of flowering was noted as FT. The juice of the 40 apricots was measured with a digital refractometer (Model RA-250HE Kyoto Electronics, Kyoto, Japan), and the SSC values were recorded in °Brix. FF was measured with an acoustic firmness sensor (Aweta BV, the Netherlands). These fruit traits were measured for two consecutive years (2016 and 2017).

Variance Analysis

To define the variations in FF, FFC, FT and SSC among the 259 genotypes over two years (2016 and 2017), an analysis of variance (ANOVA) was performed using TOTEMSTAT

software (39) according to the significance level of $P \leq 0.01$. The variations were determined according to year (Y), genotype (G), and Y x G interactions.

DArT analysis

The DArT analysis was performed as described by NEMLI et al. (2017). The polymorphism information content (PIC) values represent the discrimination power of the markers. The PIC values were calculated for each marker according to Lynch and Ritland (1999) with the following equation: $PIC = 1 - \sum p_i^2$, where p_i demonstrates the proportion of the population with the i^{th} allele.

Genetic Variation Analysis

STRUCTURE software (v.2.3.4), which is based on Bayesian modelling, was used to determine the population structure of 259 apricot genotypes (42). The software was run with a burn-in period of 10,000 and 10,000 Markov Chain Monte Carlo (MCMC) replications. Ten runs were performed for each number of populations (K), ranging from 1 to 10. The best number of subpopulations was determined with the Delta K (ΔK) value using STRUCTURE HARVESTER (43). For cross checking, the principle component analysis (PCA) was carried out with R Software [R statistical functions (R stats) and Gaussian mixture modelling for model-based clustering, classification, and density Estimation (mclust)], and a dendrogram tree was drawn with the same software with reference to Nei's genetic distance (44).

Association Mapping Analysis

TASSEL (v.5.2.3) software with a mixed linear model (MLM (K+Q) model) was used for the detection of the associations between DNA markers and pomological traits (FF, FFC, FT, and SSC) (45). The relative kinship matrix, which shows the genetic relationships between the individuals, was calculated by TASSEL (v.5.0) based on the centered IBS method (45). The Q matrix was obtained from STRUCr software at the $\Delta K = 3$ value. The associations between the SNP markers and pomological traits were visualized as Manhattan plots in R software with the "qqman" package. The designation of significant markers was performed in the same software with the false discovery rate (FDR) (46) and Bonferroni correction (47) being calculated separately for each pomological trait (FF, FFC, FT and SSC). Furthermore, the quantile-quantile (Q-Q) plots were visualized with the same software.

Identification of candidate genes

The sequences of the SNP markers associated with FF, FFC, and SSC were analyzed to determine the functions of the candidate genes using the Phytome (v12.1) database.

Results

Phenotypic Variation

In the present study, FF, FFC, FT, and SSC were measured for two years (2016-2017), and showed normal distribution (S1-4 Fig). These findings indicated the importance of the genetic background of each genotype for the *Prunus* phenotyping profile. The minimum, maximum and mean values of each year showed high consistency, and no significant differences were observed between the years (2016 and 2017) for the mean values. The minimum, maximum and mean values of all phenotypic traits are presented in S2 Table.

The mean values of four traits (FF, FFC, FT and SSC) only slightly differed between the two years (2016 and 2017). However, there were fourfold differences between the SSC and FFC values obtained from 2016 and 2017 (Table 1). FT ranged from 95 to 125 days with a mean value of 114.2 days in 2016, and it ranged from 95 to 126 days with a mean value of 112 days in 2017 (Table 1). FF varied between 0.1 N and 9.60 N in 2016 and 0.03 N and 6.62 N in 2017 (Table 1). There was a nearly 90-fold difference in the ranges obtained for FF from the two years. The individuals showing the highest and lowest average values are listed in S2 Table.

Table 1 Minimum, maximum and mean values of all phenotypic traits

Trait	2016			2017		
	Min	Max	Mean	Min	Max	Mean
FF	0.1 N	9.60 N	1.86 N	0.03 N	6.62 N	1.71 N
FFC	11.6°	46.72°	34.04°	13.99°	46.77°	34.12°
FT	95 days	125 days	114.24 days	95 days	126 days	112 days
SSC	8.22°Brix	29.92°Brix	15.28°Brix	8.23°Brix	32.37°Brix	16.27°Brix

The results of the correlation analysis showed no significant correlation between the four traits (FF, FFC, FT and SSC) (S3 Table). The results of ANOVA are presented in S4 Table. ANOVA demonstrated significant variations according to year, genotype, and year x genotype interactions for all apricot traits at the $P \leq 0.01$ significance level (S4 Table).

Population Structure Analysis

A total of 24,864 SNP markers were generated from the DArT analysis, and after filtering the missing data (max 5% missing data, Marker Allele Frequency (MAF)>0.5), 11,532 high-quality SNP markers were obtained. The PIC value was 0.77, ranging between 0.05 and 0.99. These markers were assigned to the related scaffolds and were used in the STRUCTURE (v.2.2) analysis. This analysis was performed for K from 1 to 10, and the peak was observed at K = 3 according to the ΔK computation data. The STRUCTURE results showed that the 259 genotypes were divided into three main populations: namely POPI (red), POPII (green) and POPIII (blue) (S5 Fig). All these genotypes were also further divided into three groups according to Nei's genetic distance analysis: The first group consisted of Geno 185 (Nigde - Turkey) and Geno 186 (Malatya-Turkey), the second comprised Geno 38 (Siverek/Urfa – Turkey), Geno 230 (USA) and Geno 255 (Russia), and the third contained the remaining 254 genotypes. These results indicate that the genotypes used in this study were not clustered according to their geographical origin. In addition, PCA revealed three groups for the population used in this study (S6 Fig), confirming the results obtained from STRUCTURE (S7 Fig) and Nei's genetic distance analyses (S4 Fig).

The expected heterozygosity and fixation index (F_{st}) are parameters that explain the heterozygosity level of a population. In this study, the expected heterozygosity was determined as 0.20 for Cluster 1, 0.06 for Cluster 2, and 0.11 for Cluster 3, with a mean value of 0.12. On the other hand, the F_{st} value varied between 0.14 and 0.81 with a mean value of 0.55, representing a high genetic variation level for the population.

AM Analysis

AM analyses were carried out for four pomological traits (FF, FFC, FT and SSC) using TASSEL (v.5.2.3) software and the MLM (Q+K) model in two consecutive years (2016 and 2017). These analyses detected a large number of associations related to the pomological traits. FDR and Bonferroni corrections were applied to eliminate the false positives among the associations. Eventually, 131 SNP markers were found to be associated with three traits (FF, FFC, and SSC). Among these associations, three, 57 and 71 SNPs were associated with FFC, FF and SSC respectively.

A total of 88 and 228 SNPs were associated with FF in 2016 and 2017, respectively (FDR correction applied, $-\log_{10}P \geq 2.90$ for 2016 and ≥ 2.78 for 2017), and 57 of these markers

were common for both 2016 and 2017 (S5 and S6 Tables and Fig 1). Most of the significant SNPs for FF were detected in 2017 but not in 2016 (S5 and S6 Tables and Fig 1).

For FFC, three SNPs ($-\log_{10} P$ value is ≥ 3.27 , FDR correction applied) and 13 SNPs ($-\log_{10} P \geq 3.10$, FDR correction applied) were associated with FFC in 2016 and 2017, respectively, and three of these SNPs (SNP 4257, SNP 17194 and SNP 22875) was common for both years (S5 Table and Fig 2).

The marker-trait association analysis for FT revealed that it was associated with 10 SNPs (FDR correction applied, $-\log_{10} P \geq 3.28$) in 2016 and 22 SNPs (FDR correction applied, $-\log_{10} P \geq 3.06$) in 2017. However, none of these SNPs was commonly seen in both years (S5 Table and Fig 3).

For SSC, 167 SNPs ($-\log_{10} P \geq 2.82$, FDR correction applied) and 352 SNPs ($-\log_{10} P \geq 2.72$, FDR correction applied) were found related in 2016 and 2017, respectively. Of these SNPs, 71 were detected in both years (Fig 4 and S5 and S7 Tables). The P values presenting the significance level of the associations between the markers and pomological traits are given in Q-Q plots in S8 Fig.

Identification of Candidate Genes

A total number of 30 putative candidate genes were found to be related to the SNPs associated with FF and SSC (S8 Table). SNPs which were associated with the FFC trait did not show similarity to any of the putative candidate genes. For the SSC of the apricots, the following proteins and enzymes related to putative candidate genes showed homology with SNPs (given in parentheses): putative 3,4-dihydroxy-2-butanone kinase (SNP526), putative leucine-rich repeat receptor-like protein kinase (SNP1023), pentatricopeptide repeat-containing protein (SNP1482), probable LRR receptor-like serine/threonine-protein kinase (SNP1494), vignain-like (SNP2823), transcription termination factor MTERF6 (SNP3309), LRR receptor-like serine/threonine-protein kinase GSO2 (SNP3842), WAT1-related protein At5g64700 (SNP4443 and SNP20435), cell division cycle 20.2, cofactor of APC complex-like (SNP4948), long-chain acyl-CoA synthetase8 (SNP5158), calcium-transporting ATPase 12 plasma membrane-type-like (SNP5444), probable LRR receptor-like serine/threonine-protein kinase At4g36180 (SNP13398), peroxidase 5 (SNP14227), UDP-glycosyltransferase TURAN (SNP15803), tRNA (guanine(37)-N1)-methyltransferase 1 (SNP16184), transcription factor TFIIIB component B" homolog (SNP16422), receptor like protein 30-like (SNP17431), putative disease resistance protein (SNP19126), putative pre-16S rRNA nuclease (SNP19568), DNA-directed RNA polymerase III subunit (SNP 20753), DEAD-box ATP-dependent RNA

helicase 3 (SNP22678), putative pentatricopeptide repeat-containing protein (SNP23251), S locus F-box protein f (SLFf) gene, partial cds; and Sf-RNase and S haplotype-specific F-box protein f (SFBf) genes, complete cds (SNP23325), putative disease resistance RPP13-like protein 1 (SNP23732), TMV resistance protein N-like (SNP23833), putative disease resistance protein (SNP23953), LRR receptor-like serine/threonine-protein kinase GSO2 (SNP24483), and receptor-like protein 12 (SNP24611) (S8 Table).

Discussion

Phenotypic Variation

Fruit quality parameters are of prime importance for both consumers and growers. Among these parameters, FT is the most widely studied physical attribute in apricot due to its economic importance related to early market prices (28)). In the present study, FT was detected between 95 and 126 days (Table 1). Among the genotypes studied, Geno115 was the earliest cultivar with 95 days. In previous studies, FT was reported to range from 59 to 84 days (23) and 55 to 78 days (28). The variation that was detected in the present study for FT was greater compared to the literature and can be attributed to the different genetic origins of the cultivars.

SSC is one of the main criteria affecting fruit taste, and SSC value greater than 12°Brix indicates good gustative quality (10). In the present study, SSC was measured between 8.22 and 32.36 °Brix, most genotypes (243 genotypes) had a value over 12°Brix, there was nearly a fourfold difference in the range (Table 1). In different studies, SSC was detected as 8.73 to 17.80 °Brix (27), 10.6 to 16.2 °Brix (10) and 6.2 to 19.5 °Brix (28). In our study, a larger variation was found in SSC compared to previous studies. This wide range of phenotypic discrepancy indicates the genotypic variation level of the apricot genotypes used in the study.

FFC and FF are two most important sensorial properties that affect consumer preferences at the purchase step. In the present study, FFC was measured between 11.6° and 46.77°, and there was nearly a fourfold difference in the range (Table1). In previous studies, FFC was measured from 67° to 100° (27) and 70° to 94.7° (10). In the current study, the range of FF was obtained as 0.03 to 9.60 N. In the literature, FF was reported to vary between 24.9 and 62.2 N (10) and 15 and 50 N (27). Both FFC and FF ranges measured in the current study were quite different from those of previous studies.

Population Structure

In genetic mapping studies, associations between DNA markers and traits are affected by the type and number of markers (48). The use of a high number of markers leads to high

genome coverage, and therefore high-throughput systems gain importance. In the current study, DArT, a high-throughput system, was used and a total of 20,264 SNP markers were developed. These markers were used in population diversity. This high number of markers provided high genome coverage.

The STRUCTURE analysis was used for the identification of the population structure of the 259 apricots investigated in the current study. These genotypes were divided into three main populations (S2 Fig). PCA (S3 Fig) and dendrogram (S4 Fig) analyses confirmed the number of populations. These genotypes were not divided into populations according to their geographical origin. For example, the genotypes that originated from Turkey, Spain, Italy, Poland, Armenia, France, USA, and Hungary were included in the same (third) group (S4 Fig). The reason for this result could be the complex breeding history of these genotypes. In particular, the use of cultivars with different histories in introgression and intercrossing processes may have led to this situation (48). In addition, humans move plants from one geographic realm to another, which results in confusion concerning the origin of the plants (49). In a previous AM study on apricot, 72 genotypes were used, and the genotypes were divided into two main groups (37). The reason for the lower number of subpopulations in the current study could be the use of a population with a narrow genetic basis. Although the previous authors also selected the genotypes from different countries, they may have used those of the same origin.

In the present study, the mean *Fst* value was detected as 0.55 and the mean expected heterozygosity was 0.12, indicating the presence of a high genetic variation in the population structure. These findings also support the idea that DArT systems develop a large number of SNP markers distributed along the apricot genome. In previous studies, the *Fst* value was reported to be 0.51 (50) and 0.16 (51), and the expected heterozygosity value was 0.82 (50) and 0.29 (51). These differences between previous studies in terms of diversity may be due to the number and type of markers utilized, and genotyping being undertaken in distinct locations (52).

Association Mapping Analysis

AM is a powerful technique which is based on the accumulation of genetic variability through evolution in natural populations to identify DNA markers based on the association between genetic markers and phenotypes (53). AM analyses are used as a rapid and efficient alternative to linkage mapping analyses (30) for detecting the associations between traits and markers; therefore, these analyses are widely employed in the mapping of economically

important traits in many crop species (54)(55). In the present study, K and Q matrixes were used to correct the population structure in the MLM (Q+K) model included in AM analyses. This model effectively eliminates possible false positives with random and fixed effects according to Henderson's notation (56). In addition, FDR and Bonferroni corrections were applied to eliminate spurious associations (56). To date, no AM study has been undertaken to reveal the associations between SNP markers and pomological traits (FF, FFC, FT and SSC). However, an association map was constructed by MARIETTE et al. (2016) to identify the SNP markers that controlled resistance to plum pox virus in apricot. Furthermore, Olukolu (2010) constructed an AM on the chilling requirements of apricot. Apart from these studies, there are only a limited number of association studies on the economically important traits of the other members of the *Rosaceae* family (57)(33)(58)(30)(59)(55).

In the present study, a total of 131 SNPs were found significantly associated with three pomological traits (FF, FFC and SSC) of the apricot genotypes via AM analyses (S5-7 Tables and Fig 1-4). Three SNPs (SNP 4257, SNP17194 and SNP 22875) were found associated with FFC and 57 SNPs were found associated with FF (S5-7 Tables and Fig1-4). A total of 71 SNPs were associated with SSC in two consecutive years (2016 and 2017) (S5 and S7 Tables). In previous studies, (27) and (28) used control cross populations of apricot and found one QTL each that was related to SSC. The number of significant markers identified in the present study was higher than previously reported (27)(28) which may be related to the type of population investigated. In mapping studies, natural populations provide higher genome coverage and mapping resolution with regard to wide genotypical variations (56). Another reason for our high number of SNPs may be the use of DArT to produce the markers. This technology is known to produce a high number of SNP markers, and thus provide high genome coverage.

Identification of Candidate Genes

In the present study, 30 putative candidate genes showed homology with the sequences of SNPs associated with FF and SSC (S8 Table). Among these, transcription termination factor MTERF6 plays an important role in plastid development on *Arabidopsis thaliana* (60). WAT1-related protein is located on cell wall and responsible for transmembrane transporter activity (61). Long-chain acyl-CoA synthetase 8 is very important for lipid metabolism (62). UDP-glycosyltransferase TURAN is one of the responsible enzyme for development of pollen tube. LRR receptor-like serine/threonine-protein kinase (GSO2) and probable LRR receptor-like serine/threonine-protein kinase (GSO1) together play a role in root growth and the growth of epidermal surface in embryos and cotyledons in *Arabidopsis* (63). Putative pentatricopeptide

repeat-containing protein is a member of the pentatricopeptide repeat (PPR) protein family and is involved in the organellar RNA metabolism (64). Calcium-transporting ATPase 12, plasma membrane-type-like has a function in calcium-transporting ATPase activity and calmodulin binding (65). tRNA (guanine(37)-N1)-methyltransferase 1 is responsible for the methylation of cytoplasmic and mitochondrial tRNAs in the N1 position of guanosine-37 *Arabidopsis thaliana* (66). TMV resistance protein N-like provides resistance to tobacco mosaic virus in plants (67). Putative 3,4-dihydroxy-2-butanone kinase plays a role in ATP binding (68). Pentatricopeptide repeat-containing protein is a required protein for the intergenic processing between chloroplast *rsp7* and *ndhB* transcripts (69).

Conclusions

This is the first AM study that presents the associations between SNPs based on the DArT technology and economically important traits (FF, FFC, FT and SSC) in apricot. Large variations were determined for these four traits. The results of this study highlight the importance of using populations with wide variations in AM studies. AM revealed significant associations for FF, FFC and SSC. The SNPs identified in the study can be used in future breeding programs for marker-assisted selection in apricot. On the other hand, the genotypes with the shortest FT can be used as parents in developing earlier cultivars combined with other desirable traits.

Author Contribution Statement

FF: Association map analysis, writing manuscript; DA: writing manuscript, data obtaining; SE: PI of the projects; AE: obtained phenotyping data, EO: statistical analysis, data obtaining; MBT: corresponding author, conceived and designed research.

Acknowledgements: The study was financially supported by the Scientific and Technological Research Council of Turkey (TUBITAK) with the project number TUBITAK-215O445.

Conflict of interest: The authors declare no competing interests.

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599

600 **Figure Legends**

601

602 **Fig 1** Manhattan plots of fruit firmness for the two years

603 **Fig 2** Manhattan plots of fruit flesh color for the two years

604 **Fig 3** Manhattan plots of flowering time for the two years

605 **Fig 4** Manhattan plots of solid soluble content for the two years

606

Supporting Information

- S1 Fig** Histogram showing the distribution of fruit firmness in 2016 and 2017
- S2 Fig** Histogram showing the distribution of fruit flesh color in 2016 and 2017
- S3 Fig** Histogram showing the distribution of flowering time in 2016 and 2017
- S4 Fig** Histogram showing the distribution of solid soluble content in 2016 and 2017
- S5 Fig** STRUCTURE plot of 259 individuals by 20,264 SNPs at $\Delta K = 3$
- S6 Fig** PCA analysis of 259 individuals
- S7 Fig** Dendrogram tree analysis based on Nei's genetic distance
- S8 Fig** Q-Q plots of fruit firmness, fruit flesh color, flowering time, and solid soluble content
- S1 Table** List of 259 apricot genotypes
- S2 Table** Individuals with the highest and lowest average values of investigated traits
- S3 Table** Correlation analysis results
- S4 Table** Summary of ANOVA for fruit firmness, fruit flesh color, flowering time, and solid soluble content
- S5 Table** Number of SNP markers associated with the investigated traits according to the FDR correction threshold
- S6 Table** List of SNP markers identified as significantly associated with fruit firmness
- S7 Table** List of SNP markers identified as significantly associated with SSC
- S8 Table** Details of identification of putative candidate gene associations

a)

Fruit Firmness - 2016

b)

Fruit Firmness - 2017

Figure 1

a)

Fruit Flesh Color - 2016

b)

Fruit Flesh Color - 2017

Figure 2

a)

Flowering Time - 2016

b)

Flowering Time - 2017

Figure 3

a)

b)

Figure 4