Paradigm

Mitteilungen Klosterneuburg 76 (2026): 46-68; DOI: 10.2478/mittklbg-2026-0004
ISSN: 3061-063X (Online); 3061-0621 (Print)

Genetic Transmission, Heterosis, and Reciprocal Effects on Total Phenolic Content and Antioxidant Activity in F_1 Apricot Populations

Cemil Ernim[1], Ibrahim Bolat[2]*, Ozkan Kaya[3]*

[1]Graduate School of Natural and Applied Sciences, Department of Horticulture
Harran University
63050 Sanliurfa, Turkey

[2]Faculty of Agriculture, Department of Horticulture,
Harran University
63050 Sanliurfa, Turkey

[3]Erzincan Horticultural Research Institute
Republic of Türkiye Ministry of Agriculture and Forestry
24060 Erzincan, Türkiye

*Corresponding authors: ibolat@harran.edu.tr; kayaozkan25@hotmail.com

Summary

Elucidating the genetic control of total phenolic content and antioxidant activity in apricot is essential for breeding programs aimed at developing cultivars with enhanced nutritional quality and health-promoting properties. However, knowledge about inheritance patterns, heterosis effects, and reciprocal cross influences on these biochemical traits in apricot remains limited. We investigated the genetic transmission, heterosis, and phenotypic variation of total phenolic content and antioxidant activity in F_1 populations derived from reciprocal crosses between 'İmrahor' and 'Hasanbey' apricot cultivars. Both cross combinations and parental genotypes significantly influenced all measured parameters ($p \leq 0.001$). Both F_1 populations exhibited negative mid-parent heterosis for total phenolic content (−20.05% to −24.31%) and antioxidant activity (−13.69% to −32.62%), with the majority of F_1 individuals (80.77% to 100%) falling below the lower parent value. Reciprocal cross effects were particularly pronounced for antioxidant activity, with İmrahor (♀) × Hasanbey (♂) producing F_1 individuals with significantly higher antioxidant capacity (203.33 µmol TE·100g^{-1} FW difference, $p < 0.001$) compared to the reciprocal cross, demonstrating strong maternal effects. Principal component analysis revealed that PC1 explained 92.8-94.3% of total variance, indicating a strong positive correlation between phenolic content and antioxidant activity. Despite overall negative heterosis, substantial phenotypic variation among F_1 individuals (CV: 11.76-18.12%) enabled identification of superior genotypes, with A13, A15, and A25 ranking highest in the İmrahor × Hasanbey population. We conclude that while both traits show predominantly additive genetic control with negative heterosis in these cross combinations, significant transgressive segregation and maternal effects provide valuable opportunities for selection of elite individuals with enhanced antioxidant properties. The quantitative genetic parameters and phenotypic distributions identified offer valuable insights for marker-assisted selection and breeding strategies targeting improved nutritional quality in apricot.

Keywords: additive genetic effects, genotype selection, maternal inheritance, nutraceutical traits, quantitative variation

Zusammenfassung

Vererbung, Heterosis und reziproke Effekte auf den Gesamtphenolgehalt und die antioxidative Aktivität in F_1-Marillenpopulationen. Die Aufklärung der genetischen Steuerung des Gesamtphenolgehalts und der antioxidativen Aktivität bei Marille (*Prunus armeniaca* L.) ist für Züchtungsprogramme die darauf abzielen, Sorten mit verbesserter ernährungsphysiologischer Qualität und gesundheitsfördernden Eigenschaften zu entwickeln, von essenzieller Bedeutung. Die Erkenntnisse zu Vererbungsmustern, Heterosiseffekten sowie zu den Einflüssen reziproker Kreuzungen auf diese biochemischen Merkmale sind jedoch noch begrenzt. Wir untersuchten Vererbung, Heterosis und phänotypische Variation des Gesamtphenolgehalts sowie der antioxidativen Aktivität in F_1-Populationen, die aus reziproken Kreuzungen der Marillensorten ‚İmrahor' und ‚Hasanbey' hervorgingen. Beide Kreuzungskombinationen sowie die Elterngenotypen beeinflussten sämtliche untersuchten Parameter hochsignifikant ($p \leq 0{,}001$). Beide F_1-Populationen zeigten eine negative Heterosis gegenüber dem Elternmittel für den Gesamtphenolgehalt (−20,05 % bis −24,31 %) sowie für die antioxidative Aktivität (−13,69 % bis −32,62 %). Die Mehrheit der F_1-Individuen (80,77 % bis 100 %) lag unterhalb des Wertes des jeweils schwächeren Elternteils. Reziproke Effekte waren bei der antioxidativen Aktivität besonders ausgeprägt: Die Kreuzung İmrahor (♀) × Hasanbey (♂) erzeugte F_1-Individuen mit signifikant höherer antioxidativer Kapazität (Differenz: 203,33 µmol TE·100 g^{-1} Frischmasse; $p < 0{,}001$) im Vergleich zur reziproken Kreuzung, was auf starke maternale Effekte hinweist. Die Hauptkomponentenanalyse ergab, dass PC1 92,8–94,3 % der Gesamtvarianz erklärte, was auf eine starke positive Korrelation zwischen Gesamtphenolgehalt und antioxidativer Aktivität hindeutet. Trotz der insgesamt negativen Heterosis ermöglichte die beträchtliche phänotypische Variation innerhalb der F_1-Populationen (Variationskoeffizient: 11,76–18,12 %) die Identifizierung überlegener Genotypen. In der Population İmrahor × Hasanbey wiesen die Genotypen A13, A15 und A25 die höchsten Werte auf. Zusammenfassend kommen wir zu dem Schluss, dass beide Merkmale in diesen Kreuzungskombinationen unter einer vorwiegend additiven genetischen Steuerung mit negativer Heterosis stehenGleichzeitig bietet eine signifikante transgressive Aufspaltung sowie maternale Effekte wertvolle Selektionsmöglichkeiten für die Identifizierung herausragenden Pflanzenmaterials mit erhöhten antioxidativen Eigenschaften. Die ermittelten quantitativen genetischen Parameter und phänotypischen Verteilungen liefern wichtige Einblicke für die markergestützte Selektion und für Züchtungsstrategien zur Verbesserung der ernährungsphysiologischen Qualität der Marille.

Schlagwörter: additive genetische Effekte, Genotypenselektion, maternale Vererbung, nutrazeutische Eigenschaften, quantitative Variation

Introduction

Apricot (*Prunus armeniaca* L.) is a stone fruit belonging to the Rosaceae family, cultivated extensively in temperate regions worldwide for both fresh consumption and processing industries. The fruit is recognized as a valuable source of bioactive compounds, including phenolic acids, flavonoids, carotenoids, and organic acids, which contribute significantly to human health through their antioxidant, anti-inflammatory, and anticarcinogenic properties (Leccese et al., 2007, Dragovic-Uzelac et al., 2007). Turkey, as one of the world's leading apricot producers, possesses rich genetic diversity with numerous local cultivars adapted to different ecological conditions (Korkmaz et al., 2023). Phenolic compounds, in particular, serve as the primary contributors to the antioxidant capacity of apricot tissues, functioning through hydrogen donation and free radical scavenging mechanisms (Sochor et al., 2010). Studies have demonstrated that total phenolic content in apricot fruits ranges significantly among cultivars, with values varying between 150 and 800 mg GAE/100g fresh weight,

while antioxidant activity measured by DPPH and FRAP assays shows parallel variation (Korekar et al., 2011, Ruiz et al., 2005). These compounds exhibit diverse biological effects including protection against oxidative stress, cardiovascular diseases, and certain types of cancer, making them crucial components for functional food development (Madrau et al., 2009). The accumulation of phenolic substances varies considerably among cultivars, developmental stages, ripening periods, and environmental conditions, with genetic background serving as the most critical determinant of fruit biochemical quality (Drogoudi et al., 2008, Fratianni et al., 2018). Recent metabolomic studies have revealed that apricot phenolic profiles are complex, consisting of hydroxycinnamic acids (chlorogenic acid, neochlorogenic acid), flavonols (quercetin derivatives, kaempferol glycosides), and flavan-3-ols (catechin, epicatechin), each contributing differently to overall antioxidant capacity (Erdogan-Orhan and Kartal, 2011, Campbell et al., 2013).

Hybrid breeding represents one of the most effective strategies for improving genetic traits in fruit trees, enabling the exploitation of heterosis to develop superior cultivars with enhanced nutritional, pomological, and functional properties (Janick and Moore, 1996). Understanding heritability patterns, heterosis expression, and gene action is fundamental for systematic crop improvement programs and efficient parent selection (Wünsch and Hormaza, 2002). In stone fruits, F_1 hybrid populations frequently exhibit substantial phenotypic variation in secondary metabolite content, reflecting the complex polygenic inheritance of these quantitative traits (Faust and Nyujtó, 1998, Badenes and Byrne, 2012). Previous research on apricot has shown that pomological traits such as fruit weight, total soluble solids, and titratable acidity display moderate to high heritability, while biochemical traits including total phenolic content and antioxidant capacity exhibit more variable inheritance patterns depending on the specific parental combination (Asma et al., 2007, Zargar et al., 2023). Karaat and Serce (Karaat and Serce, 2020) investigated heritability estimates in two apricot progenies and reported moderate heritability for total phenolic compounds (h^2 = 0.45-0.62) and TEAC antioxidant activity (h^2 = 0.38-0.54), indicating that both genetic and environmental factors significantly influence these traits. Studies on various fruit species have demonstrated that the chemical composition of fruits from different genotypes is significantly influenced by specific parental combinations, with certain crosses exhibiting positive, negative, or no heterosis in phytochemical accumulation depending on the trait examined (Mihaylova et al., 2024, Kaczmarska and Radzki, 2017). The expression of fruit quality characteristics within offspring populations is substantially affected by genotypic factors, with mid-parent heterosis rates varying widely from -40% to +60% for different biochemical compounds (Kumar et al., 2020, Butcher et al., 2013). Additionally, reciprocal cross effects, where the direction of hybridization (which parent serves as the female versus male) influences offspring phenotype, have been documented in several crops but remain poorly characterized in apricot breeding programs (Kr, 2018, Luo et al., 2024).

Genetic studies on both intraspecific and interspecific hybrids have shown that F_1 generations can exhibit superior total phenolic, flavonoid, and antioxidant activities compared to their parental varieties, although the frequency and magnitude of such heterosis varies considerably (Fridman, 2015, Zhu et al., 2025). In apricot, limited information exists regarding the inheritance patterns of antioxidant compounds and the genetic tendency of functional traits in segregating populations. Dragovic-Uzelac et al. (2005) analyzed phenolic compounds and antioxidant capacity in several apricot cultivars and emphasized the importance of genotypic variation in breeding programs targeting enhanced nutritional quality. Recent investigations on other fruit crops have documented both additive and non-additive modes of inheritance for primary and secondary metabolites in F_1 hybrids, with different traits showing positive heterosis (over-high parent performance) for certain compounds while displaying negative heterosis (below mid-parent performance) for others (Ortuño-Hernández et al., 2025, Ning et al., 2022). For instance, studies on pepper, tomato, and eggplant

have revealed that phenolic compounds can exhibit transgressive segregation, producing offspring that exceed both parents in either direction (Chowdhury et al., 2023, Hochholdinger and Yu, 2025). The genetic transmission ability (Ta), defined as the ratio of F_1 mean to mid-parent value, provides insight into the overall tendency of trait inheritance, with values below 80% indicating small inheritance tendency and values above 100% suggesting high inheritance tendency (Ning et al., 2022). Comprehensive evaluation approaches combining principal component analysis (PCA) and cluster analysis have proven effective for assessing complex trait relationships, reducing multidimensional data into interpretable components, and selecting superior hybrid individuals based on multiple biochemical parameters simultaneously (Iezzoni and Pritts, 1991, Liu et al., 2020). Such multivariate statistical methods enable breeders to develop composite scores that integrate multiple quality attributes, facilitating more objective and efficient selection of elite genotypes (Mahmoud et al., 2023).

Despite extensive utilization of apricot fruits in food, beverage, and pharmaceutical industries due to their rich antioxidant content and health-promoting properties, research on the genetic predisposition analysis of antioxidant activity and systematic breeding strategies for developing high-antioxidant varieties remains very limited. This study aimed to investigate the genetic tendency, mid-parent heterosis, reciprocal effects, and phenotypic variation of total phenolic content and antioxidant activity in F_1 apricot populations derived from reciprocal crosses between 'İmrahor' and 'Hasanbey' cultivars. These two cultivars were selected because they are widely cultivated in Türkiye and exhibit contrasting phenolic content and antioxidant capacity, making them suitable parents for genetic and heterosis analysis. The specific objectives of our study were to: (1) determine the inheritance patterns and heritability trends of functional traits in hybrid offspring, (2) evaluate the extent and direction of heterosis expression for antioxidant components, (3) assess whether maternal effects and reciprocal differences significantly influence biochemical composition, and (4) identify superior hybrid individuals through comprehensive multivariate evaluation for potential cultivar development with enhanced antioxidant properties.

Materials and Methods

Plant Materials

The experimental materials consisted of F_1 hybrid apricot genotypes at full bearing age and their parental cultivars, located at the Malatya Apricot Research Institute, Battalgazi campus, Turkey. The hybrid population was derived from reciprocal crosses between two table apricot cultivars, 'İmrahor' and 'Hasanbey', conducted in 2009 (Fig. 1).

Fig. 1: Fruit morphology of apricot cultivars 'İmrahor' and 'Hasanbey' showing whole fruits and longitudinal sections with pit characteristics.

Initially, 26 F_1 plants were established for each cross combination. The healthy F_1 individuals currently present in each combination constituted the plant material for this study. Two reciprocal cross combinations were evaluated: (1) İmrahor (♀) × Hasanbey (♂) with 26 F_1 individuals, and (2) Hasanbey (♀) × İmrahor (♂) with 26 F_1 individuals, resulting in a total of 52 F_1 genotypes plus two parental cultivars. All experimental trees were maintained under uniform orchard management conditions. Standard cultural practices included open-center training system with dormant season pruning for canopy management. Drip irrigation was applied based on evapotranspiration rates and phenological stages. Fertilization programs followed soil analysis results, with nitrogen applied in split applications and micronutrients corrected through foliar sprays when necessary. Integrated pest and disease management strategies targeted key pests and diseases using chemical control only when economic thresholds were exceeded. Weed control included both, mechanical cultivation and herbicide applications**.** Fruit samples were collected from each tree in early July 2022 at the commercial maturity stage. Fruits were immediately treated with liquid nitrogen and stored at −80 °C until analysis. A comprehensive genetic tendency analysis and evaluation of antioxidant components and activities were conducted on the collected fruit samples.

Chemicals and Reagents

Methanol, gallic acid, Folin-Ciocalteu reagent, sodium carbonate, Trolox (6-hydroxy-2,5,7,8-tetramethylchroman-2-carboxylic acid), DPPH (1,1-diphenyl-2-picrylhydrazyl radical), and all other reagents were purchased from Sigma-Aldrich (St. Louis, MO, USA) or Merck (Darmstadt, Germany). All reagents were of analytical grade unless indicated otherwise. Standard solutions were freshly prepared for each analysis batch.

Sample Preparation and Extract Preparation

Frozen apricot fruit samples were ground into fine powder using a high-throughput tissue grinder under liquid nitrogen. For each sample, 0.5 g of powdered material was accurately weighed and extracted with 25 mL of anhydrous methanol. The mixture was stirred thoroughly and kept at 4 °C for 12 h in darkness. After incubation, the samples were centrifuged at 10,000× *g* for 20 min at 4 °C. The supernatant was collected and stored at −20 °C until analysis. Each sample was extracted in triplicate. The methanolic extracts were used for determination of total phenolic content and antioxidant capacity.

Total Phenolic Content Analysis

Total phenolic content (TPC) was determined using the Folin-Ciocalteu colorimetric method as described by Tareen et al. (2021) with minor modifications. Gallic acid standard solutions were prepared at concentrations of 0, 0.1, 0.2, 0.4, 0.6, and 0.8 $mg \cdot mL^{-1}$. For the assay, 0.1 mL of appropriately diluted extract or standard solution was pipetted and diluted to 1 mL with distilled water. Subsequently, 5 mL of 0.2 $mol \cdot L^{-1}$ Folin-Ciocalteu reagent was added, mixed well, and allowed to stand for 5 min at room temperature. Then, 4 mL of 150 $g \cdot L^{-1}$ Na_2CO_3 solution was added and mixed thoroughly. The reaction mixture was incubated in darkness at room temperature for 60 min. Subsequently, 200 µL of the reaction solution was transferred to a 96-well microplate. Anhydrous methanol served as the blank. The absorbance was measured at 765 nm using a microplate reader (BioTek Instruments, Winooski, VT, USA). The experiment was performed in triplicate for each sample. The total phenolic content was calculated using the gallic acid calibration curve and expressed as mg gallic acid equivalent (GAE)$\cdot 100 g^{-1}$ fresh weight (FW).

Antioxidant Capacity Determination

DPPH Free Radical Scavenging Activity

The DPPH free radical scavenging activity was determined according to the method described by Tareen et al. (2021) with slight modifications. A fresh DPPH solution (0.1 mmol·L^{-1}) was prepared by dissolving DPPH in methanol. For the assay, 0.1 mL of appropriately diluted extract was pipetted, and 3 mL of DPPH solution was added. The mixture was vortexed and allowed to react in darkness at room temperature for 30 min. Then, 200 µL of the reaction mixture was transferred to a 96-well microplate. Anhydrous methanol was used as the blank. The absorbance was measured at 517 nm using a microplate reader. Trolox standard solutions (0, 0.1, 0.2, 0.4, 0.6, and 0.8 mmol·L^{-1}) were prepared and treated similarly to construct a calibration curve. The experiment was performed in triplicate for each sample. The DPPH radical scavenging activity was calculated using the Trolox calibration curve and expressed as µmol Trolox equivalent (TE)·100g^{-1} FW.

Statistical Analysis

All data were processed using Microsoft Excel 2016 and analyzed using IBM SPSS Statistics 26.0 and Python 3.10 (scikit-learn library). Descriptive statistics including mean, standard deviation, range, coefficient of variation, kurtosis, and skewness were calculated for each trait. The genetic parameters were calculated using the following formulae according to Ning et al. (2022):

Mid-parent value (MP) = $(P_1 + P_2)/2$, where P_1 and P_2 represent the values of the two parents

Coefficient of variation (CV, %) = $(S/\bar{F}) \times 100$, where S is the standard deviation and $\bar{F}$ (mean value of the F_1 population) represents the average of all F_1 individuals.

Genetic transmission ability (Ta, %) = $(\bar{F}/MP) \times 100$, where $\bar{F}$ (mean performance of the F_1 generation) indicates the average trait value of the hybrid population

Genetic transmission ability (Ta, %) = $(\bar{F}/MP) \times 100$

Mid-parent heterosis rate (MPH, %) = $[(\bar{F} - MP)/MP] \times 100$

Over-high parent heterosis rate (HH, %) = $(hp/n) \times 100$, where hp is the number of F_1 plants with values higher than the high parent and n is the total number of F_1 individuals

Inferior-low parent heterosis rate (LH, %) = $(lp/n) \times 100$, where lp is the number of F_1 plants with values lower than the low parent

In order to evaluate reciprocal effects, the difference between the means of the two reciprocal crosses was calculated as $\Delta = \bar{F}(A\times B) - \bar{F}(B\times A)$. Independent samples *t*-tests were performed to determine whether reciprocal differences were statistically significant ($p < 0.001$). Cohen's *d* was calculated to assess the effect size of reciprocal differences, where values of 0.2, 0.5, and 0.8 indicate small, medium, and large effects, respectively (Ning et al., 2022).

Principal Component Analysis (PCA)

Principal component analysis was conducted to evaluate the comprehensive antioxidant performance of F_1 individuals and their parents. The analysis was performed using the scikit-learn library in Python 3.10. Prior to PCA, all variables were standardized using Z-score transformation to ensure equal contribution regardless of measurement units: $Z = (X - \mu)/\sigma$, where X is the original value, µ is the mean, and σ is the standard deviation. Following standardization, the covariance matrix was constructed, and eigenvalue-eigenvector decomposition was performed. Two principal components (with PC1 explaining 94.3%

of the total variance and PC2 explaining 5.7% of the total variance) were extracted. The proportion of variance explained by each component was calculated, and component loadings were examined to interpret the biological meaning of each component. A composite score representing the overall biochemical performance of each genotype was calculated by weighting each principal component by its proportion of variance explained, according to Zhu et al. (2025):

Composite Score =
(PC1 × Variance Proportion_{PC1}) +
(PC2 × Variance Proportion_{PC2})

This formula, known as the *component-weighted sum* in PCA literature, is implemented in XLSTAT (Addinsoft, Paris, France) for the calculation of principal component scores. Higher composite scores indicate superior combined performance for phenolic content and antioxidant activity. Based on the composite scores, all genotypes including parents and F_1 individuals were ranked. Biplots were constructed to visualize the relationships between variables and genotypes in the PC1-PC2 space using the matplotlib library in Python.

Results

Genetic Analysis of Total Phenolic Content in F_1 Apricot Populations

The total phenolic content and antioxidant activity of F_1 individuals derived from reciprocal crosses between 'İmrahor' and 'Hasanbey' cultivars, along with their parental values, are presented in Tab. 1. The mid-parent value (MP) for total phenolic content was calculated as 1007.09 mg GAE·100g^{-1} FW. In the İmrahor (♀) × Hasanbey (♂) cross combination, the mean total phenolic content of F_1 individuals was 805.13 mg GAE·100g^{-1} FW with a standard deviation of 95.23, resulting in a coefficient of variation of 11.83%. The genetic transmission ability (Ta) was 80.0%, and the mid-parent heterosis rate (MPH) was −20.05%, indicating that the F_1 mean was lower than the mid-parent value. None of the F_1 individuals (0.0%) exceeded the higher parent, while all individuals (100.0%) fell below the lower parent value. In the reciprocal cross Hasanbey (♀) × İmrahor (♂), the mean total phenolic content of F_1 individuals was 762.22 mg GAE·100g^{-1} FW with a standard deviation of 138.12, yielding a coefficient of variation of 18.12%. The genetic transmission ability was 75.7%, and the mid-parent heterosis rate was −24.31%. Only 3.85% of F_1 individuals exceeded the higher parent, while 96.15% fell below the lower parent value. The total phenolic content in both F_1 populations showed continuous distribution with considerable phenotypic variation among individuals (Tab. 1).

Tab. 1: Genetic parameters and heterosis analysis of total phenolic content and antioxidant activity in F_1 apricot populations derived from reciprocal crosses between 'İmrahor' and 'Hasanbey'.

Combination	Trait	F1	S	MP %	CV%	MPH %	HH%	LH%	n
İmrahor × Hasanbey	Phenolics	805.13	95.23	1007.09	11.83	-20.05	0.0	100.0	26
Hasanbey × İmrahor	Phenolics	762.22	138.12	1007.09	18.12	-24.31	3.85	96.15	26
İmrahor × Hasanbey	Antioxidant	927.27	109.05	1074.38	11.76	-13.69	3.85	80.77	26
Hasanbey × İmrahor	Antioxidant	723.94	105.28	1074.38	14.54	-32.62	0.0	96.15	26

F_1 Mean: mean value of F_1 generation; S: standard deviation; MP: mid-parent value; CV: coefficient of variation; Ta: genetic transmission ability; MPH: mid-parent heterosis rate; HH: over-high parent heterosis rate; LH: inferior-low parent heterosis rate; n: number of F_1 individuals. Phenolics expressed as mg GAE·100g^{-1} FW; Antioxidant activity expressed as µmol TE·100g^{-1} FW.

Genetic Analysis of Antioxidant Activity in F_1 Apricot Populations

The mid-parent value for antioxidant activity was 1074.38 µmol TE·100g^{-1} FW. In the İmrahor (♀) × Hasanbey (♂) cross, the mean antioxidant activity of F_1 individuals was 927.27 µmol TE·100g^{-1} FW with a standard deviation of 109.05, giving a coefficient of variation of 11.76%. The genetic transmission ability was 86.3%, and the mid-parent heterosis rate was −13.69%. Only 3.85% of F_1 individuals exceeded the higher parent, while 80.77% fell below the lower parent value. In the reciprocal cross Hasanbey (♀) × İmrahor (♂), the mean antioxidant activity of F_1 individuals was 723.94 µmol TE·100g^{-1} FW with a standard deviation of 105.28, resulting in a coefficient of variation of 14.54%. The genetic transmission ability was 67.4%, and the mid-parent heterosis rate was −32.62%. None of the F_1 individuals (0.0%) exceeded the higher parent, while 96.15% fell below the lower parent value. The antioxidant activity in both F_1 populations exhibited wide separation ranges, indicating substantial genetic variability for this trait (Tab. 1).

Reciprocal Cross Effects on Total Phenolic Content and Antioxidant Activity

The reciprocal cross effects were evaluated by comparing the means of F_1 populations from the two reciprocal crosses (Tab.2). For total phenolic content, the mean difference (Δ) between İmrahor × Hasanbey and Hasanbey × İmrahor was 42.91 mg GAE·100g^{-1} FW. This difference was not statistically significant ($p = 0.1989$), with a Cohen's d value of 0.3617, indicating a small to medium effect size. The İmrahor (♀) × Hasanbey (♂) cross produced F_1 individuals with slightly higher phenolic content compared to the reciprocal cross, but this maternal effect was not significant. For antioxidant activity, the mean difference (Δ) between the two reciprocal crosses was 203.33 µmol TE·100g^{-1} FW. This difference was highly statistically significant ($p < 0.001$), with a Cohen's d value of 1.8971, indicating a large effect size. The İmrahor (♀) × Hasanbey (♂) cross produced F_1 individuals with significantly higher antioxidant activity compared to the Hasanbey (♀) × İmrahor (♂) cross, demonstrating a strong maternal effect for this trait (Tab. 2).

Tab. 2: Reciprocal cross effects on total phenolic content and antioxidant activity in F_1 apricot populations.

Pair	Trait	Mean (A×B)	Mean (B×A)	Δ(A×B−B×A)	*p*-value	cohen d	n(A×B)	n(B×A)
İmrahor↔Hasanbey	Phenolics	805.1296	762.2215	42.9081	0.1989	0.3617	26	26
İmrahor↔Hasanbey	Antioxidant	927.2735	723.9404	203.3331	0.0	1.8971	26	26

A×B: İmrahor (♀) × Hasanbey (♂); B×A: Hasanbey (♀) × İmrahor (♂); Δ: difference between reciprocal crosses; Cohen's d: effect size (0.2 = small, 0.5 = medium, 0.8 = large). ***Significant at $p < 0.001$.

Principal Component Analysis of İmrahor × Hasanbey F_1 Population

Principal component analysis was performed on the İmrahor (♀) × Hasanbey (♂) F_1 population including both parents to evaluate the comprehensive antioxidant performance based on total phenolic content and antioxidant activity (Tab. 3).

Tab. 3: Principal component analysis results for İmrahor × Hasanbey F_1 population including parental cultivars.

Component	Eigenvalue	Variance (%)	Cumulative Variance (%)	Variable	PC1 Loading	PC2 Loading
PC1	1.886	94.3	94.3	Total Phenolic Content	0.707	0.707
PC2	0.114	5.7	100.0	Antioxidant Activity	0.707	−0.707

Two principal components were extracted, with PC1 explaining 94.3% of the total variance and PC2 explaining 5.7% of the total variance. Together, the two components accounted for 100% of the cumulative variance.

The high variance explained by PC1 indicated a strong positive correlation between total phenolic content and antioxidant activity, meaning that as phenolic content increased, antioxidant activity increased proportionally.

Tab. 4: Ranking of F_1 individuals and parental cultivars based on composite scores from principal component analysis for İmrahor × Hasanbey cross combination.

Germplasm No.	PC1 Score	PC2 Score	Composite Score	General Rank
A13	2.9557	0.4456	2.8127	1
A15	2.1519	0.0377	2.0315	2
A25	2.0432	-0.0206	1.9256	3
A19	1.9555	0.4006	1.8670	4
A16	1.8089	0.0110	1.7065	5
A12	1.3097	-0.1847	1.2246	6
A1	0.8789	-0.1507	0.8202	7
A2	0.6598	-0.0444	0.6197	8
A14	0.5781	-0.0830	0.5404	9
A23	0.5418	-0.1714	0.5012	10
A3	0.3787	-0.0844	0.3523	11
A5	0.3502	0.1175	0.3370	12
A10	0.2125	-0.2878	0.1840	13
A7	0.0440	-0.0062	0.0411	14
A22	-0.0567	-0.3890	-0.0756	15
A21	-0.2805	-0.3733	-0.2858	16
A4	-0.5104	-0.2283	-0.4943	17
A26	-0.5307	-0.2630	-0.5154	18
A6	-0.5546	-0.2792	-0.5389	19
A24	-1.1177	0.4253	-1.0298	20
A18	-1.1401	0.6061	-1.0406	21
A9	-1.1258	-0.3510	-1.0817	22
A8	-1.1864	-0.0606	-1.1223	23
A17	-1.4691	0.5805	-1.3523	24
A20	-1.5967	0.4701	-1.4790	25
İmrahor	-1.8358	-0.6429	-1.7678	26
A11	-1.9991	0.6848	-1.8462	27
Hasanbey	-2.4655	-0.1587	-2.3341	28

Bold text indicates parental cultivars and top five F_1 individuals.

Based on the composite scores calculated from the weighted combination of PC1 and PC2, all 28 genotypes (26 F_1 individuals plus two parents) were ranked (Tab. 4). The top-ranked genotype was A13 with a composite score of 2.8127, followed by A15 (2.0315), A25 (1.9256), A19 (1.8670), and A16 (1.7065). These five genotypes exhibited the highest combined performance for total phenolic content and antioxidant activity. In contrast, the parental cultivars ranked poorly, with 'Hasanbey' ranked 28th (composite score: −2.3341) and 'İmrahor' ranked 26th (composite score: −1.7678). The F_1 individual A11 ranked 27th (composite score: −1.8462), positioned between the two parents.

Principal Component Analysis of Hasanbey × İmrahor F_1 Population

Principal component analysis was conducted on the Hasanbey (♀) × İmrahor (♂) F_1 population including both parents (Tab. 5). Two principal components were extracted, with PC1 explaining 92.8% of the total variance and PC2 explaining 7.2% of the total variance, together accounting for 100% of the cumulative variance. Similar to the reciprocal cross, PC1 represented the strong positive relationship between total phenolic content and antioxidant activity.

Tab. 5: Principal component analysis results for Hasanbey × İmrahor F_1 population including parental cultivars.

Component	Eigenvalue	Variance (%)	Cumulative Variance (%)	Variable	PC1 Loading	PC2 Loading
PC1	1.856	92.8	92.8	Total Phenolic Content	0.707	0.707
PC2	0.144	7.2	100.0	Antioxidant Activity	0.707	−0.707

Based on composite scores, all 28 genotypes were ranked (Tab. 6). Notably, in this cross combination, the parental cultivar 'Hasanbey' had the highest composite score among the parental cultivars (2.91), followed by 'İmrahor' (composite score: 2.41) and the F_1 individual C21 ranking third (composite score: 2.32). The top five F_1 individuals were C21, C19 (1.44), C25 (1.06), C15 (0.98), and C26 (0.86). The lowest-ranked genotype was C4 with a composite score of −1.98. This contrasted sharply with the İmrahor × Hasanbey cross, where both parents ranked at the bottom. The difference indicated strong reciprocal effects and maternal influences on the expression of antioxidant traits.

Phenolic Composition and Phenotypic Variation in the İmrahor × Hasanbey F_1 Population

The PCA biplot (Fig. 2A) illustrated the spatial distribution of 26 F_1 individuals and two parental cultivars in the two-dimensional PC1-PC2 space. PC1 (Dim1) explains 94.3% of the total variance, while PC2 (Dim2) explains 5.7%. F_1 individuals were distributed across the entire PC1 axis, demonstrating substantial phenotypic variation. High-performing genotypes such as A13, A19, A11, A17, A18, and A20 were positioned in the upper portion of the plot with positive PC2 values, while genotypes A16, A25, A15, and A1 clustered in the central region with PC2 values near zero.

Tab. 6: Ranking of F_1 individuals and parental cultivars based on composite scores from principal component analysis for Hasanbey × İmrahor cross combination.

Germplasm No.	PC1 Score	PC2 Score	Composite Score	General Rank
Hasanbey	3.0700	0.7995	**2.91**	1
Imrahor	2.5618	0.3956	2.41	2
C21	2.4383	0.7978	2.32	3
C19	1.6011	-0.6838	1.44	4
C25	1.1850	-0.5548	1.06	5
C15	1.0859	-0.4054	0.98	6
C26	0.9769	-0.6281	0.86	7
C12	0.9094	-0.1008	0.84	8
C18	0.7983	-0.0175	0.74	9
C24	0.5781	-0.2296	0.52	10
C10	0.3541	-0.4773	0.29	11
C13	0.1572	-0.2589	0.13	12
C16	0.1198	-0.1498	0.10	13
C6	-0.0194	0.5163	0.02	14
C14	-0.2259	-0.1204	-0.22	15
C22	-0.5156	0.0026	-0.48	16
C3	-0.6550	0.0167	-0.61	17
C2	-0.6391	-0.2524	-0.61	18
C17	-0.7036	-0.0701	-0.66	19
C23	-0.8227	-0.0886	-0.77	20
C8	-1.1476	0.0981	-1.06	21
C20	-1.1716	0.2047	-1.07	22
C11	-1.3477	0.2690	-1.23	23
C1	-1.4223	0.4341	-1.29	24
C5	-1.5268	-0.1465	-1.43	25
C7	-1.5756	0.0775	-1.46	26
C9	-1.8990	0.1497	-1.75	27
C4	-2.1637	0.4225	**-1.98**	28

Bold text indicates parental cultivars and top-ranked F_1 individual.

Both parental cultivars 'İmrahor' and 'Hasanbey' were located on the right side of the biplot in the negative PC2 region, indicating relatively lower antioxidant performance compared to several F_1 individuals when considering the PC2 dimension.

The majority of F_1 genotypes (A2, A3, A5, A7, A10, A12, A14, A23) were distributed in the central-left region, representing intermediate performance levels. Low-performing genotypes (A4, A6, A8, A21, A22, A26) occupied the left side of the biplot with negative PC1 scores.

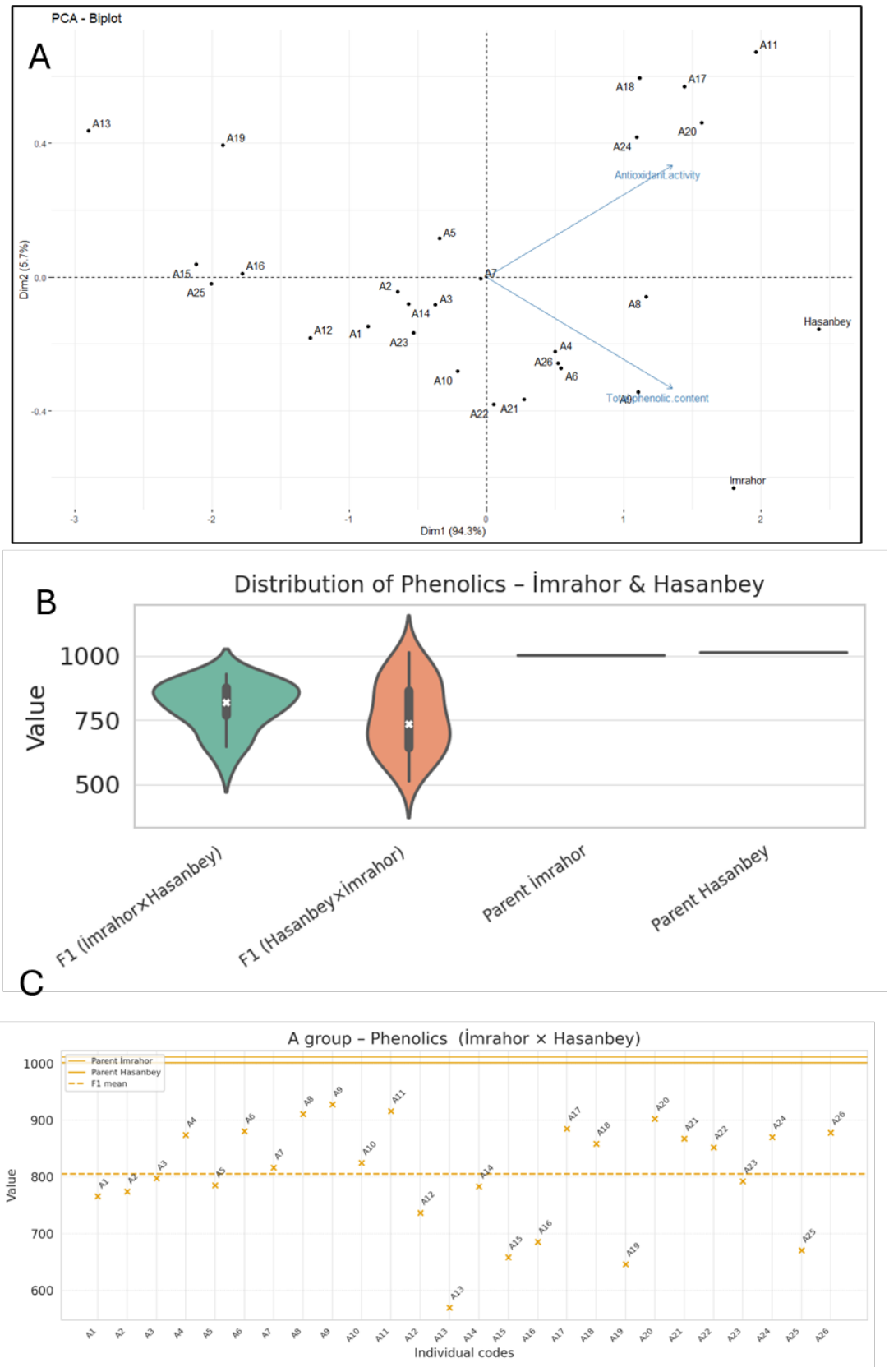

Fig. 2: Distribution and comparative analysis of F_1 individuals and parental cultivars for İmrahor × Hasanbey cross combination. (A) PCA biplot showing the distribution of genotypes in PC1-PC2 space. The parental cultivars 'İmrahor' and 'Hasanbey' are positioned in the lower right quadrant with negative composite scores. (B) Violin plots showing the distribution of total phenolic content in F_1 (İmrahor×Hasanbey) and F_1 (Hasanbey×İmrahor) populations compared to the two parental cultivars. (C) Individual ranking of all F_1 genotypes and parents based on total phenolic content.

The violin plot analysis (Fig. 2B) revealed distinct distributional characteristics of total phenolic content across the two reciprocal F_1 populations and their parents. The F_1 population from İmrahor (♀) × Hasanbey (♂) displayed a relatively compact distribution with a median centered around 805 mg GAE·100g^{-1} FW. The distribution was slightly skewed, with the bulk of the population concentrated between 700 and 900 mg GAE·100g^{-1} FW, and a narrower tail extending toward lower values around 600 mg GAE·100g^{-1} FW. The reciprocal cross Hasanbey (♀) × İmrahor (♂) exhibited a broader distribution with a median around 762 mg GAE·100g^{-1} FW. A large cluster of F_1 genotypes (A1, A2, A3, A5, A7, A10, A12, A14, A23) exhibited intermediate performance levels between 750 and 850 mg GAE·100g^{-1} FW, clustered around the population mean. The lower-performing individuals (A4, A6, A8, A9, A17, A18, A20, A21, A22, A24, A26) ranged from 650 to 750 mg GAE·100g^{-1} FW. The ranking pattern revealed that none of the F_1 individuals exceeded the higher parent value (100% inferior-low parent rate). However, the wide phenotypic range spanning 300 mg GAE·100g^{-1} FW among F_1 individuals indicated substantial genetic variation and the presence of transgressive segregation.

Antioxidant Activity and Phenotypic Variation in the İmrahor × Hasanbey F_1 Population

The PCA biplot for the Hasanbey × İmrahor cross (Fig. 3A) showed a markedly different pattern compared to the reciprocal cross. Both parental cultivars were positioned in the upper right quadrant with strongly positive PC1 scores, indicating high antioxidant performance. PC1 (Dim1) explains 92.8% of the total variance, while PC2 (Dim2) explains 7.2%. The F_1 genotype C21 was located near the parents with a high composite score (2.32), while genotypes C19, C25, C26, and C15 occupied the lower right region with moderate positive PC1 values. The majority of F_1 individuals (C2, C3, C6, C8, C10, C12, C13, C14, C16, C18, C22, C23, C24) clustered around the origin. Low-performing genotypes (C1, C4, C5, C7, C9, C11, C17, C20) were distributed in the left side with negative PC1 scores. The violin plot analysis (Fig. 3B) revealed that the İmrahor × Hasanbey F_1 population exhibited a relatively broad distribution centered around 927 µmol TE·100g^{-1} FW, with individuals ranging from approximately 750 to 1250 µmol TE·100g^{-1} FW.

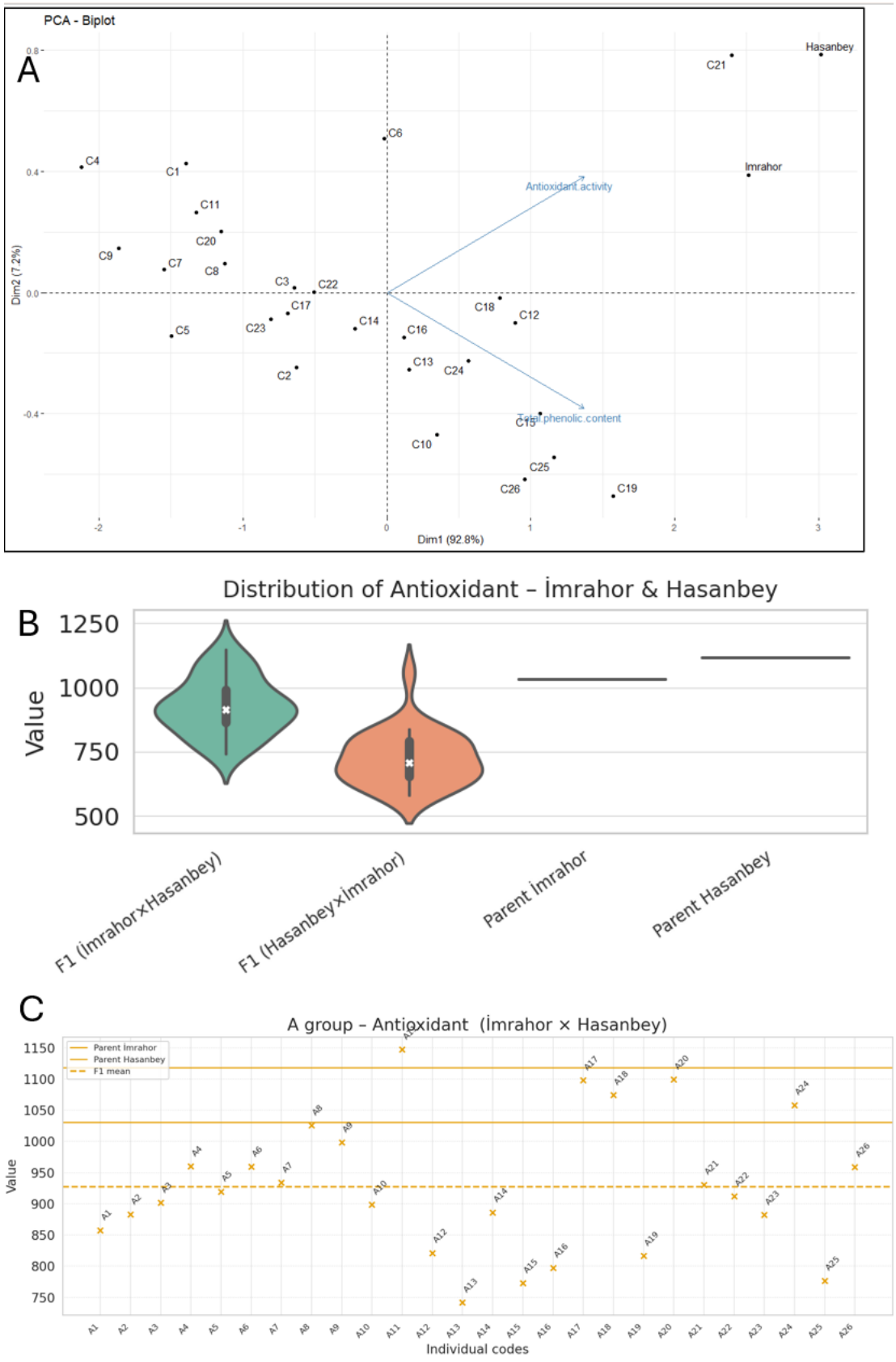

Fig. 3: Distribution and comparative analysis of antioxidant activity in F_1 individuals and parental cultivars for İmrahor × Hasanbey and Hasanbey × İmrahor reciprocal crosses. (A) PCA biplot showing the distribution of genotypes in PC1-PC2 space for Hasanbey × İmrahor cross. (B) Violin plots showing the distribution of antioxidant activity in both reciprocal F_1 populations compared to the two parental cultivars. (C) Individual ranking of all F_1 genotypes and parents based on antioxidant activity for İmrahor × Hasanbey cross.

In contrast, the Hasanbey × İmrahor F_1 population displayed a narrower, more compact distribution centered around 724 µmol TE·100g^{-1} FW, ranging from approximately 500 to 1000 µmol TE·100g^{-1} FW. Both parental cultivars showed values around 1050-1150 µmol TE·100g^{-1} FW, substantially higher than both F_1 population means. The individual ranking plot (Fig. 3C) demonstrated that F_1 individuals from the İmrahor × Hasanbey cross ranged from approximately 750 to 1150 µmol TE·100g^{-1} FW. Top-performing genotypes (A11, A17, A20, A19, A13, A18) showed antioxidant activities between 1070 and 1150 µmol TE·100g^{-1} FW, with only A11 exceeding the lower parent 'İmrahor' but not surpassing 'Hasanbey'. The F_1 mean (927 µmol TE·100g^{-1} FW) was positioned well below both parental values, confirming negative mid-parent heterosis. The wide phenotypic range of approximately 400 µmol TE·100g^{-1} FW among F_1 individuals indicated substantial genetic variation and potential for selection of superior genotypes despite overall negative heterosis.

Hierarchical Cluster Analysis of Biochemical Traits

The hierarchical cluster analysis grouped F_1 individuals and parental cultivars based on their standardized phenolic content and antioxidant activity values (Fig. 4). In the İmrahor × Hasanbey cross (left panel), three distinct clusters were identified. The first cluster included high-performing genotypes (A11, A17, A20, A18, A24, A8, A9) along with both parental cultivars 'Hasanbey' and 'İmrahor', characterized by red-colored cells indicating high standardized values for both traits. The second cluster comprised intermediate-performing genotypes (A13, A19, A16, A15, A25, A12, A1, A23, A2, A14, A3, A5, A7, A10), displaying yellow to light blue colors representing near-average to slightly below-average values. The third cluster contained low-performing genotypes (A4, A6, A26, A21, A22), characterized by predominantly yellow cells indicating below-average standardized values. In the Hasanbey × İmrahor cross (right panel), the clustering pattern differed substantially. The highest-performing cluster included 'Hasanbey', C21, 'İmrahor', C19, and C26, showing intense red-orange coloration. A large intermediate cluster contained genotypes C15, C25, C12, C18, C13, C16, C10, and C24 with yellow coloration. The lowest-performing cluster comprised C4, C9, C5, C7, C8, C20, C1, and C11, displaying blue colors indicating low standardized values. Notably, the parental cultivars clustered with high-performing F_1 individuals in this cross direction, contrasting with the İmrahor × Hasanbey cross where parents formed a distinct high-value group separate from most F_1 individuals.

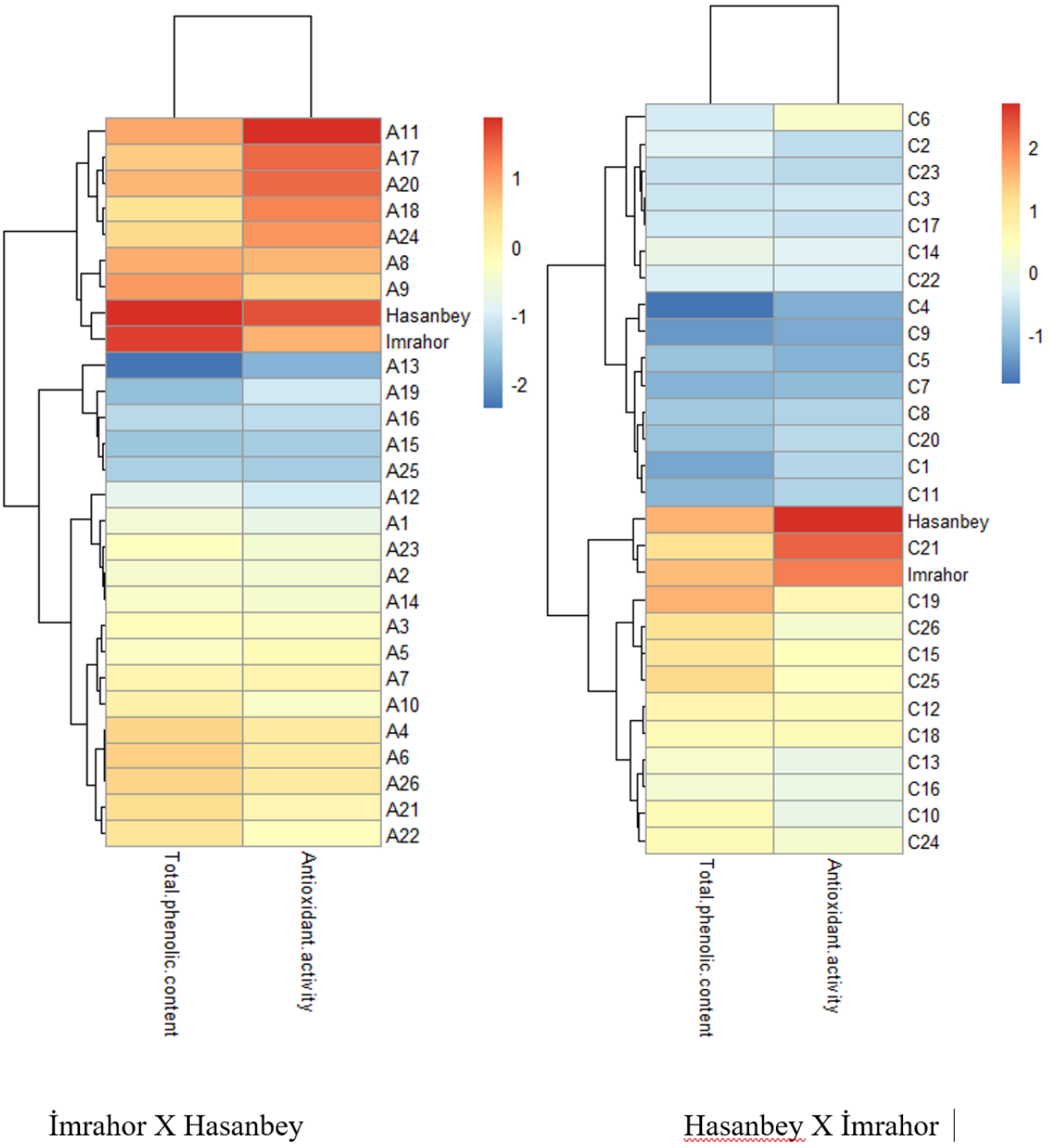

Fig. 4: Hierarchical cluster heatmaps showing the standardized values of total phenolic content and antioxidant activity for F_1 individuals and parental cultivars in both reciprocal crosses. Left panel: İmrahor × Hasanbey cross combination. Right panel: Hasanbey × İmrahor cross combination. Color intensity represents standardized Z-scores, with red indicating high values (positive Z-scores), yellow indicating intermediate values (near-zero Z-scores), and blue indicating low values (negative Z-scores).

Discussion

Genetic Tendency and Inheritance Patterns of Antioxidant Traits in Apricot F_1 Populations

The present study revealed that both total phenolic content and antioxidant activity in F_1 apricot populations derived from reciprocal crosses between 'İmrahor' and 'Hasanbey' exhibited negative mid-parent heterosis, with MPH values ranging from −13.69% to −32.62% (Tab. 1). The genetic transmission ability (Ta) for these traits was relatively low, ranging from 67.4% to 86.3%, indicating a trend toward small to medium inheritance. These findings align with previous research on stone fruits, where biochemical traits often display lower heritability compared to pomological characteristics (Ismaili et al., 2016). Also, Karaat and Serce, (2020) reported moderate heritability estimates for total phenolic content (h^2 = 0.45-0.62) and antioxidant capacity (h^2 = 0.38-0.54) in two apricot progenies, suggesting that these traits are significantly influenced by both genetic and environmental factors. The negative heterosis observed in our study is consistent with the phenomenon of inbreeding depression or the disintegration of favorable non-additive gene effects during hybridization, as documented by Fridman, (2015) and Sánchez-Pérez et al. (2006) in various crop species. The coefficient of variation (CV) for phenolic content ranged from 11.83% to 18.12%, while for antioxidant activity it ranged from 11.76% to 14.54% (Tab. 1), indicating moderate phenotypic variation within F_1 populations. This level of variation is comparable to that reported by Drogoudi et al. (2008), who found CV values of 15-25% for total phenolic content across 29 apricot cultivars and hybrids. The continuous distribution and substantial range of trait values observed in our F_1 populations (Fig. 2B and 3B) suggest polygenic inheritance, where multiple genes with small to moderate effects control the expression of antioxidant compounds (Sánchez-Pérez et al., 2006, Tohge et al., 2020). This genetic architecture provides opportunities for selection and improvement despite the overall negative heterosis trend.

Extent and Direction of Heterosis for Antioxidant Traits

The extent and direction of heterosis were further evaluated by examining mid-parent heterosis (MPH) values and the distribution of F_1 individuals relative to parental performance. Notably, the inferior-low parent heterosis rates (LH) were extremely high, with 80.77–100% of F_1 individuals falling below the lower parent value for both traits across both cross directions (Tab. 1). This phenomenon indicates that the parental cultivars 'İmrahor' and 'Hasanbey' possess relatively high antioxidant capacity compared to their hybrid offspring, likely due to the breakdown of epistatic interactions or complementary gene action that were optimally combined in the adapted parental genotypes (Geuna et al., 2024, Lippman and Zamir, 2007). Similar observations have been reported in other fruit crops; for instance, Butcher et al. (2013) found that certain flavonoid compounds in pepper F_1 hybrids showed negative heterosis, with many individuals performing below the mid-parent value. However, despite the predominance of negative heterosis, the presence of transgressive segregants, F_1 individuals approaching or occasionally exceeding mid-parent values, demonstrates that favorable allelic combinations can still arise through recombination. These individuals represent valuable genetic resources for selection and further breeding, particularly in later generations.

Reciprocal Effects and Maternal Influences on Biochemical Composition

One of the most striking findings of this study was the highly significant reciprocal effect observed for antioxidant activity (p < 0.001, Cohen's d = 1.90), but not for total phenolic content (p = 0.199) (Tab. 2). The İmrahor (♀) × Hasanbey (♂) cross produced F_1 individuals with mean antioxidant activity of 927.27 µmol TE·100g^{-1} FW, significantly higher than the reciprocal cross Hasanbey (♀) × İmrahor (♂) with 723.94 µmol TE·100g^{-1} FW,

a difference of 203.33 µmol TE·100g^{-1} FW representing approximately 28% variation. This large effect size indicates strong maternal inheritance or cytoplasmic effects influencing antioxidant metabolism in apricot fruits. Maternal effects in fruit crops can arise from several mechanisms, including cytoplasmic inheritance of organellar genomes (mitochondria and chloroplasts), maternal provisioning of mRNA and proteins to developing embryos, and epigenetic modifications transmitted through the female gamete (Greiner et al., 2015). In stone fruits, chloroplast-encoded genes play crucial roles in secondary metabolism, particularly in the phenylpropanoid pathway responsible for synthesizing phenolic compounds and related antioxidants (Jaakola, 2013). The differential antioxidant activity between reciprocal crosses, despite similar phenolic content, suggests that the enzymatic machinery involved in antioxidant defense may be maternally influenced. This could involve differential expression of key enzymes such as polyphenol oxidase, peroxidase, or superoxide dismutase, which are known to be encoded by both nuclear and organellar genomes (Gill and Tuteja, 2010). The contrasting patterns observed in the PCA biplots and cluster analyses between the two reciprocal crosses (Fig. 2A, 3A, and Fig. 4) further support the importance of cross direction. In the Hasanbey × İmrahor cross, both parental cultivars clustered with the highest-performing F_1 individuals and exhibited positive composite scores, whereas in the İmrahor × Hasanbey cross, parents were positioned separately with negative composite scores relative to several F_1 genotypes. This pattern suggests that 'Hasanbey' as a maternal parent contributes favorable genetic or cytoplasmic factors that maintain higher baseline antioxidant capacity in offspring, while 'İmrahor' as a maternal parent results in greater phenotypic variation and lower mean performance. Reciprocal effects have been documented in other fruit breeding programs. Rapisarda et al. (2009) reported significant differences in total phenolic and flavonoid content between reciprocal citrus hybrids, attributing these differences to maternal inheritance of plastid-encoded enzymes involved in secondary metabolism. Similarly, Kaczmarska et al. (2017) found that strawberry F_1 hybrids showed reciprocal differences in phytochemical properties depending on which parent served as the female. Our findings emphasize the critical importance of considering cross direction in apricot breeding programs targeting enhanced antioxidant traits, as the choice of maternal parent can substantially influence offspring biochemical composition.

Identification of Superior Genotypes Through Multivariate Analysis and Breeding Implications

The principal component analysis successfully reduced the dimensionality of the dataset, with PC1 explaining 92.8-94.3% of total variance across both reciprocal crosses (Tab. 3 and 5). The high variance explained by PC1 reflects the strong positive correlation between total phenolic content and antioxidant activity, confirming that phenolic compounds are the primary contributors to antioxidant capacity in apricot fruits, as previously reported by Su et al. (2022) and Sochor et al. (2010). This strong relationship validates the use of total phenolic content as a rapid screening tool for predicting antioxidant potential in breeding programs, reducing the need for multiple antioxidant assays. Based on composite scores integrating both traits, several superior F_1 genotypes were identified across both cross directions (Tab. 4 and 6). In the İmrahor × Hasanbey cross, genotypes A13 (composite score: 2.81), A15 (2.03), A25 (1.93), A19 (1.87), and A16 (1.71) exhibited the highest combined antioxidant performance, with phenolic contents ranging from 850-950 mg GAE·100g^{-1} FW and antioxidant activities of 1070-1150 µmol TE·100g^{-1} FW. Although these values did not exceed both parents, they approached the mid-parent value and demonstrated superior performance compared to the majority of F_1 individuals. In the Hasanbey × İmrahor cross, genotype C21 (composite score: 2.32) emerged as the top-performing F_1 individual, followed by C19 (1.44) and C25 (1.06). The hierarchical cluster analysis (Fig. 4) provided additional insights into the relationships among genotypes. In the İmrahor × Hasanbey cross, high-performing F_1 genotypes (A11, A17, A20, A18, A24) clustered closely with both parental cultivars, suggesting that these

individuals inherited favorable allelic combinations from both parents for antioxidant-related genes.

Conversely, low-performing genotypes (A4, A6, A26, A21, A22) formed a distinct cluster characterized by consistently low standardized values for both traits, indicating homozygosity for unfavorable alleles or disruption of complementary gene interactions. The identification of transgressive segregants with antioxidant profiles approaching or exceeding mid-parent values demonstrates the potential for developing improved cultivars through recurrent selection and backcrossing strategies. Despite the overall negative heterosis observed at the population level, the presence of superior individuals indicates that favorable allelic combinations can be recovered and fixed in subsequent generations. This aligns with findings by Manzoor et al. (2012) and Gupta et al. (2012), who documented wide variation in phytochemical content among Turkish apricot germplasm, emphasizing the rich genetic diversity available for improvement programs. From a breeding perspective, our results suggest several practical strategies for developing apricot cultivars with enhanced antioxidant properties. First, the significant reciprocal effects for antioxidant activity (Tab. 2) indicate that breeders should carefully consider maternal parent selection, with 'İmrahor' as the female parent producing offspring with higher mean antioxidant activity than the reciprocal cross. Second, the high coefficient of variation and continuous distribution of traits within F_1 populations (Fig. 2 and 3) suggest that large segregating populations should be evaluated to identify rare transgressive segregants with exceptional antioxidant profiles. Third, the strong correlation between phenolic content and antioxidant activity (PC1 loadings in Tab. 3 and 5) allows for efficient indirect selection based on total phenolic assays, which are simpler and less expensive than multiple antioxidant activity measurements. The superior F_1 genotypes identified in this study, particularly A13, A15, A25, A19, A16, and C21, warrant further evaluation across multiple environments and growing seasons to assess stability and G×E interactions. Campbell et al. (Campbell et al., 2013) demonstrated that phenolic and carotenoid content in northeastern USA apricot varieties varied significantly with harvest maturity and environmental conditions, highlighting the importance of multi-location trials. Additionally, these elite genotypes should be subjected to detailed metabolomic profiling using HPLC-MS or LC-MS/MS to identify specific phenolic compounds (chlorogenic acid, quercetin derivatives, catechins) contributing to their superior antioxidant capacity, as suggested by Ali et al. (2011) and Erdogan-Orhan and Kartal (2011).

The negative heterosis observed in this study, while initially disappointing, does not preclude successful cultivar development. Comparable patterns have been reported in other crops where biochemical traits showed negative F_1 heterosis but subsequent generations (F_2, F_3, or backcross populations) yielded superior recombinants through transgressive segregation (Mahmoud et al., 2023, Ali et al., 2011, El-Gammaal and Yahya, 2018). Bajpai et al. (2019) documented heterotic patterns in *Brassica juncea* where different secondary metabolites exhibited contrasting modes of inheritance, with some showing positive and others negative heterosis. This genetic complexity necessitates multi-generational breeding approaches rather than relying solely on F_1 hybrid vigor. Future research should focus on molecular characterization of the identified elite genotypes to understand the genetic basis of superior antioxidant capacity. Quantitative trait locus (QTL) mapping in larger F_2 or backcross populations could identify genomic regions controlling phenolic biosynthesis and antioxidant activity, facilitating marker-assisted selection (Salazar et al., 2013). Additionally, transcriptomic and proteomic analyses comparing high- and low-performing genotypes could elucidate regulatory mechanisms governing the phenylpropanoid pathway and related antioxidant systems in apricot. Given the increasing consumer demand for functional foods with health-promoting properties, the development of apricot cultivars with enhanced antioxidant capacity represents both a commercial opportunity and a public health contribution (Fratianni et al., 2018).

Conclusions

Our study revealed that the inheritance of total phenolic content and antioxidant activity in apricot exhibits predominantly additive genetic control with significant negative heterosis effects. Comparing reciprocal crosses between 'İmrahor' and 'Hasanbey', we found that maternal genotype significantly influenced trait expression, particularly for antioxidant activity where reciprocal differences were highly significant and demonstrated strong maternal effects. Both F_1 populations demonstrated moderate to high genetic transmission abilities, with mid-parent heterosis values consistently negative, indicating that hybrid offspring generally exhibited lower biochemical trait values than the average of their parents. The divergent patterns between reciprocal crosses were particularly evident in principal component analysis results. While İmrahor × Hasanbey produced F_1 individuals that predominantly underperformed both parents (with parents ranking near the bottom), the reciprocal Hasanbey × İmrahor cross showed parental cultivars ranking at the top positions, demonstrating pronounced cytoplasmic or maternal effects. These differences translated to significant variations in phenotypic distributions, with moderate coefficients of variation indicating substantial genetic variability suitable for selection despite overall negative heterosis. These findings have immediate practical applications for apricot breeding programs targeting enhanced antioxidant properties and nutritional quality. Although negative heterosis limits the utility of F_1 hybrids for direct commercial use, the wide phenotypic variation and transgressive segregation observed among F_1 individuals provide valuable genetic resources for selection. Superior genotypes identified from both cross combinations represent promising candidates for further evaluation and potential cultivar development. The strong positive correlation between total phenolic content and antioxidant activity suggests that selection for either trait would simultaneously improve the other, simplifying breeding strategies. Future research should explore the molecular mechanisms underlying these maternal effects and negative heterosis patterns, particularly focusing on cytoplasmic inheritance and epistatic interactions controlling biochemical trait expression. Additionally, advancing these F_1 populations to subsequent generations would reveal segregation patterns and enable identification of quantitative trait loci associated with antioxidant properties, facilitating marker-assisted selection in apricot breeding programs.

Acknowledgements: The authors gratefully acknowledge the technical support provided by the research staff at the apricot breeding program. Special appreciation is expressed to the orchard management team for their assistance in maintaining the experimental plant materials and ensuring optimal growing conditions throughout the study period. The authors extend their sincere gratitude to Dr. Meral Doğan for her valuable contributions to the statistical analyses and to Dr. Rukiye Zengin for her expert assistance in conducting the chemical analyses.

Author Contributions: C.E., I.B., and O.K. contributed to the conceptualization, methodology, and investigation of the study. C.E. and I.B. were involved in data curation, formal analysis, software, visualization, and original draft preparation. Original draft and writing, review and editing were carried out by I.B. and O.K. All authors have read and approved the final version of the manuscript.

Data Availability Statement: The data that support the findings of this study are available from the corresponding author upon reasonable request.

Conflict of Interest Statement: The authors declare that they have no known competing financial interests or personal relationships that could have influenced the work reported in this article.

References

Ali, S., Masud, T., Abbasi, K. S. 2011: Physico-chemical characteristics of apricot (*Prunus armeniaca* L.) grown in Northern Areas of Pakistan. Scientia Horticulturae 130 (2): 386-392.

Asma, B. M., Kan, T., Birhanlı, O. 2007: Characterization of promising apricot (*Prunus armeniaca* L.) genetic resources in Malatya, Turkey. Genetic Resources and Crop Evolution 54 (1): 205-212.

Badenes, M. L., Byrne, D. H. (Eds.). 2012: Fruit breeding (Vol. 8). Springer Science & Business Media.

Bajpai, P. K., Reichelt, M., Augustine, R., Gershenzon, J., Bisht, N. C. 2019: Heterotic patterns of primary and secondary metabolites in the oilseed crop Brassica juncea. Heredity 123 (3): 318-336.

Butcher, J. D., Crosby, K. M., Yoo, K. S., Patil, B., Jifon, J. L., Rooney, W. L. 2013: Heterosis in different F1 Capsicum annuum genotypes for fruit traits, ascorbic acid, capsaicin, and flavonoids. Scientia Horticulturae 159: 72-79.

Campbell, O. E., Merwin, I. A., & Padilla-Zakour, O. I. 2013: Characterization and the effect of maturity at harvest on the phenolic and carotenoid content of Northeast USA apricot (*Prunus armeniaca*) varieties. Journal of Agricultural and Food Chemistry 61 (51): 12700-12710.

Campbell, O. E., Merwin, I. A., Padilla-Zakour, O. I. 2013: Characterization and the effect of maturity at harvest on the phenolic and carotenoid content of Northeast USA apricot (*Prunus armeniaca*) varieties. Journal of Agricultural and Food Chemistry 61 (51): 12700-12710.

Chowdhury, M. F. N., Rafii, M. Y., Ismail, S. I., Ramlee, S. I., Hosen, M., Karim, K. R., Sahmat, S. S. 2023: Growth and yield performances, pathogenicity, heat tolerance, antioxidant activity, and pungency level of anthracnose resistant and heat tolerant inbreed lines and their F1 hybrids of chili (*Capsicum annuum* L.). Scientia Horticulturae 309: 111606.

Dragovic-Uzelac, V., Levaj, B., Mrkic, V., Bursac, D., Boras, M. 2007: The content of polyphenols and carotenoids in three apricot cultivars depending on stage of maturity and geographical region. Food Chemistry 102 (3): 966-975.

Dragovic-Uzelac, V., Pospišil, J., Levaj, B., Delonga, K. 2005: The study of phenolic profiles of raw apricots and apples and their purees by HPLC for the evaluation of apricot nectars and jams authenticity. Food chemistry 91 (2): 373-383.

Drogoudi, P. D., Vemmos, S., Pantelidis, G., Petri, E., Tzoutzoukou, C., Karayiannis, I. 2008: Physical characters and antioxidant, sugar, and mineral nutrient contents in fruit from 29 apricot (*Prunus armeniaca* L.) cultivars and hybrids. Journal of agricultural and food chemistry 56 (22): 10754-10760.

El-Gammaal, A. A., Yahya, A. I. 2018: Genetic variability and heterosis in F1 and F2 generations of diallel crosses among seven wheat genotypes. Journal of Plant Production 9 (12): 1075-1086.

Erdogan-Orhan, I., Kartal, M. 2011: Insights into research on phytochemistry and biological activities of *Prunus armeniaca* L. (apricot). Food research international 44 (5): 1238-1243.

Faust, M., Surányi, D., Nyujtó, F. 1998: Origin and dissemination of apricot. HORTICULTURAL REVIEWS-WESTPORT THEN NEW YORK 22: 225-260.

Fratianni, F., Ombra, M. N., d'Acierno, A., Cipriano, L., Nazzaro, F. 2018: Apricots: biochemistry and functional properties. Current Opinion in Food Science 19: 23-29.

Fridman, E. 2015: Consequences of hybridization and heterozygosity on plant vigor and phenotypic stability. Plant Science 232: 35-40.

Geuna, F., Salazar, J. A., Martinez-Gomez, P. 2024: Allele Mining in Apricot (*Prunus armeniaca* L.) Breeding: Current State and Future Prospect. Allele Mining for Genomic Designing of Fruit Crops: 292-308.

Gill, S. S., Tuteja, N. 2010: Reactive oxygen species and antioxidant machinery in abiotic stress tolerance in crop plants. Plant physiology and biochemistry 48 (12): 909-930.

Greiner, S., Sobanski, J., Bock, R. 2015: Why are most organelle genomes transmitted maternally?. Bioessays 37(1): 80-94.

Gupta, A., Sharma, P. C., Tilakratne, B. M. K. S., Verma, A. K. 2012: Studies on physico-chemical characteristics and fatty acid composition of wild apricot (*Prunus armeniaca* Linn.) kernel oil. Indian Journal of Natural Products and Resources 3 (3): 366-370.

Hochholdinger, F., Yu, P. 2025: Molecular concepts to explain heterosis in crops. Trends in Plant Science 30 (1): 95-104.

Iezzoni, A. F., Pritts, M. P. 1991: Applications of principal component analysis to horticultural research. HortScience 26 (4): 334-338.

Ismaili, A., Karami, F., Akbarpour, O., Rezaei Nejad, A. 2016: Estimation of genotypic correlation and heritability of apricot traits, using restricted maximum likelihood in repeated measures data. Canadian Journal of Plant Science 96 (3): 439-447.

Jaakola, L. 2013: New insights into the regulation of anthocyanin biosynthesis in fruits. Trends in plant science 18 (9): 477-483.

Janick, J., Moore, J. N. (Eds.). 1996: Fruit breeding, tree and tropical fruits (Vol. 1). John Wiley & Sons.

Kaczmarska, E., Gawroński, J., Jabłońska-Ryś, E., Zalewska-Korona, M., Radzki, W., Sławińska, A. 2017: General combining ability and heterosis regarding the phytochemical properties in strawberry (Fragaria× ananassa) hybrids. Plant Breeding 136 (1): 111-118.

Karaat, F. E., Serce, S. 2020: Heritability estimates and the variation of pomological traits, total phenolic compounds, and antioxidant capacity in two apricot progenies. Turkish Journal of Agriculture and Forestry 44 (1): 54-61.

Korekar, G., Stobdan, T., Arora, R., Yadav, A., Singh, S. B. 2011: Antioxidant capacity and phenolics content of apricot (*Prunus armeniaca* L.) kernel as a function of genotype. Plant Foods for Human Nutrition 66 (4): 376-383.

Korkmaz, K., Bolat, I., Uzun, A., Sahin, M., Kaya, O. 2023: Selection and molecular characterization of promising plum rootstocks (*Prunus cerasifera* L.) among seedling-origin trees. Life 13 (7): 1476.

Krška, B. 2018: Genetic apricot resources and their utilisation in breeding. Breeding and health benefits of fruit and nut crops: 63-82.

Kumar, A., Sharma, V., Jain, B. T., Kaushik, P. 2020: Heterosis breeding in eggplant (*Solanum melongena* L.): gains and provocations. Plants 9 (3): 403.

Leccese, A., Bartolini, S., Viti, R. 2007: Total antioxidant capacity and phenolics content in apricot fruits. International Journal of Fruit Science 7 (2): 3-16.

Leccese, A., Bartolini, S., Viti, R. 2008: Total antioxidant capacity and phenolics content in fresh apricots. Acta Alimentaria 37 (1): 65-76.

Lippman, Z. B., Zamir, D. 2007: Heterosis: revisiting the magic. Trends in genetics 23 (2): 60-66.

Liu, B., Zhao, D., Zhang, P., Liu, F., Jia, M., Liang, J. 2020: Seedling evaluation of six walnut rootstock species originated in China based on principal component analysis and cluster analysis. Scientia Horticulturae 265: 109212.

Luo, Y., Chen, W., Pan, Y., Ge, L., Wu, C., Wang, J., Yan, F. 2024: Comparison and genetic variation analysis of important fruit traits in jujube F1 hybrids by different male parents. Agronomy 14 (3): 459.

Madrau, M. A., Piscopo, A., Sanguinetti, A. M., Del Caro, A., Poiana, M., Romeo, F. V., Piga, A. 2009: Effect of drying temperature on polyphenolic content and antioxidant activity of apricots. European food research and technology 228 (3): 441-448.

Mahmoud, A. M., Osman, N. H., Mohamed, H. A. 2023: Characterization of tomato yellow leaf curl virus resistance genes and genetic variability in commercial tomato F1 hybrids. Scientia Horticulturae 318: 112088.

Manzoor, M., Anwar, F., Ashraf, M., Alkharfy, K. M. 2012: Physico-chemical characteristics of seed oils extracted from different apricot (*Prunus armeniaca* L.) varieties from Pakistan. Grasas y aceites 63 (2): 193-201.

Mihaylova, D., Desseva, I., Tumbarski, Y., Popova, A., Pandova, S., Lante, A. 2024: Evaluation of the enzyme inhibition, antioxidant, and antimicrobial activities of apricots, plums, and their hybrid fruits. Plants 13 (20): 2936.

Ning, X., Wang, Q., Zhang, X., Zhang, M., Su, J., Wang, H., Zhang, F. 2022: Heredity of active compounds and selection of elite hybrids in a segregating F1 population of tea chrysanthemum. Scientia Horticulturae 305: 111366.

Ortuño-Hernández, G., Silva, M., Toledo, R., Ramos, H., Reis-Mendes, A., Ruiz, D., Salazar, J. A. 2025: Nutraceutical Profile Characterization in Apricot (*Prunus armeniaca* L.) Fruits. Plants 14 (7): 1000.

Rapisarda, P., Fabroni, S., Peterek, S., Russo, G., Mock, H. P. 2009: Juice of new citrus hybrids (Citrus clementina Hort. ex Tan.× C. sinensis L. Osbeck) as a source of natural antioxidants. Food Chemistry 117 (2): 212-218.

Ruiz, D., Egea, J., Tomás-Barberán, F. A., Gil, M. I. 2005: Carotenoids from new apricot (*Prunus armeniaca* L.) varieties and their relationship with flesh and skin color. Journal of agricultural and food chemistry 53 (16): 6368-6374.

Salazar, J. A., Ruiz, D., Egea, J., Martínez-Gómez, P. 2013: Transmission of fruit quality traits in apricot (*Prunus armeniaca* L.) and analysis of linked quantitative trait loci (QTLs) using simple sequence repeat (SSR) markers. Plant molecular biology reporter 31 (6): 1506-1517.

Sánchez-Pérez, R., Martínez-Gómez, P., Dicenta, F., Egea, J., Ruiz, D. 2006: Level and transmission of genetic heterozygosity in apricot (*Prunus armeniaca* L.) explored using simple sequence repeat markers. Genetic Resources and Crop Evolution 53 (4): 763-770.

Sochor, J., Zitka, O., Skutkova, H., Pavlik, D., Babula, P., Krska, B., Kizek, R. 2010: Content of phenolic compounds and antioxidant capacity in fruits of apricot genotypes. Molecules 15 (9): 6285-6305.

Su, C., Li, T., Wang, Y., Ge, Z., Xiao, J., Shi, X., Wang, B. 2022: Comparison of phenolic composition, vitamin C, antioxidant activity, and aromatic components in apricots from Xinjiang. Journal of Food Science 87 (1): 231-250.

Tareen, A. K., Panezai, M. A., Sajjad, A., Achakzai, J. K., Kakar, A. M., Khan, N. Y. 2021: Comparative analysis of antioxidant activity, toxicity, and mineral composition of kernel and pomace of apricot (*Prunus armeniaca* L.) grown in Balochistan, Pakistan. Saudi Journal of Biological Sciences 28 (5): 2830-2839.

Tohge, T., Scossa, F., Wendenburg, R., Frasse, P., Balbo, I., Watanabe, M., Fernie, A. R. 2020: Exploiting natural variation in tomato to define pathway structure and metabolic regulation of fruit polyphenolics in the lycopersicum complex. Molecular Plant 13 (7): 1027-1046.

Wünsch, A., Hormaza, J. I. 2002: Molecular characterisation of sweet cherry (*Prunus avium* L.) genotypes using peach [*Prunus persica* (L.) Batsch] SSR sequences. Heredity 89 (1): 56-63.

Zargar, S. A., Wani, A. A., Saggoo, M. I. S., Kumar, N., Mir, J. I., Jan, S., Dabbou, S. 2023: Chemical quality attributes, phenolic compounds, and antioxidant properties of wild and cultivated apricot (*Prunus armeniaca* L.) accessions of North-Western Himalayas. Erwerbs-Obstbau 65 (6): 2325-2336.

Zhu, Q., Li, X., Ge, H., Wang, Z., Wang, B., Chen, J., Xu, H. 2025: Genetic Tendency Analysis and Comprehensive Antioxidant Activity Evaluation of Leaves and Flowers of Loquat F1 Generation. Current Issues in Molecular Biology 47 (1): 58.

Zhu, Q., Li, X., Ge, H., Wang, Z., Wang, B., Chen, J., Xu, H. 2025: Genetic Tendency Analysis and Comprehensive Antioxidant Activity Evaluation of Leaves and Flowers of Loquat F1 Generation. Current Issues in Molecular Biology 47 (1): 58.

Received November 19th, 2025