

Evaluation of General and Specific Combining Ability and Genetic Parameters for Morphological Traits in Open-Field Tomato (*Solanum lycopersicum* L.)

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ABSTRACT

The tomato (*Solanum lycopersicum* L.), a globally recognized fruit, stands as a pivotal industrial crop, underpinning a vast processing industry. The genetics and inheritance knowledge about target traits are required for improving tomato hybrids. Therefore, the present study was conducted to evaluate gene actions and the combining ability of tomato parental lines. 20 hybrids derived from diallel crossing between 5 parents and 4 commercial hybrids were evaluated. Analysis of variance revealed the presence of a significant general combining ability (GCA) effect for all traits and a significant specific combining ability (SCA) effect for fruit dry weight and fruit average weight. Despite the nuclear genome effects, maternal effects, including maternal nuclear and cytoplasmic effects, played a significant role in controlling fruit dry weight, fruit volume, fruit average weight, fruit diameter, and fruit length-to-diameter ratio traits. The maternal effect was high and significant for fruit volume ($p < 0.001$), fruit diameter, and fruit average weight. The GCA/SCA ratio ranged from 0.65 to 1, indicating the greater effect of additive gene actions in controlling traits. P_1 and P_5 parents exhibited the highest GCA for fruit number average fruit weight, and fruit volume traits, respectively. Furthermore, the $R_{1 \times 3}$ hybrid was identified as the superior combiner for fruit number per plant and average fruit weight traits. Overall, additive gene action effects had a significant proportion in the inheritance of the traits, and maternal genetic effects showed a great impact on the regulation of tomato fruit size-related traits. Consequently, the female parent fruit shape and size should be considered in tomato breeding programs.

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1. Introduction

Beyond its culinary appeal, the tomato is a significant industrial crop, essential to various processing sectors worldwide. Tomato (*Solanum lycopersicum* L.) is one of the most important species in the Solanaceae family and a diploid plant with $2n=2x=24$ chromosomes. This family includes more than 3000 species (Mishra, 2022). Tomato varieties can be classified based on their unlimited or limited growth habit. Varieties for processing purposes have a limited growth habit, and their fruits simultaneously ripen for mechanical harvesting. In addition, processing fruits should have specific characteristics related to processing quality and quantity, such as high viscosity, dry matter content, pH level and high soluble solids. An

industrial application of this crop has led to the creation of a processing industry for tomato fruit. This industry depends on tomato seed cultivar type and crop management and production systems (Amr and Raie, 2022). Plant breeding to improve crops for adaptation to climate changes and increasing yield production is essential in the changing world with a growing population and facing severe environmental changes (Tester and Langridge, 2010). For improving traits in tomatoes, hybridization, and selection are used as the main interbreeding methods (Palmgren et al., 2015).

The selection to achieve a successful breeding program is very important and requires precise evaluation. This could lead to gaining progenies that were better than their parents. The tomato breeders

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focus on fruit yield, fruit size, fruit appearance (lack of defects and attractive color), disease resistance, and recently, fruit firmness and shelf life (Nie *et al.*, 2024). Fruit yield in tomatoes is mainly affected by assimilate allocation, number of fruits per cluster, and final fruit size. Generally, through domestication, tomato fruit performance has significantly increased due to genetic gain (Azzi *et al.*, 2015).

The first step in breeding programs is availability of the genetic diversity and then having knowledge about inheritance and genetic control of desired traits. Various genetic designs have been developed to examine the inheritance and genetic of traits, depending on the plants pollination behavior. Among them, the most important are crossing designs and generation mean analysis for self-pollinating plants (Laurentin Táriba, 2023). In the diallel cross design, parents are crossed together to produce hybrids (Griffing, 1956). The Diallel method is a suitable tool for obtaining genetic information including allele distribution, dominance level, gene action, heritability, and general and specific combining ability. In the diallel cross, parents are selected based on their genetic distance, especially their ability to combine and produce valuable hybrids (Blank *et al.*, 2012).

Based on the latest agricultural statistics, the area under cultivation of tomatoes in the country was over 80,000 hectares, with a production of over 7.3 million tons, placing Iran 6th in the world production ranking (Anonymous, 2022). However, the tomato seeds used for cultivation in Iran are mostly imported. Over 1170 tons of vegetables improved and hybrid seeds have been imported and made available for farmers, while domestic production had been reported to be very low in Iran. Most of the imported seeds have high prices and are sometimes not acclimated to the Iran climate. The production of agricultural and especially vegetable seeds will be effective in preventing foreign currency outflow and increasing entrepreneurship nationwide. Furthermore, considering the seed as one of the main agricultural inputs, breeding for yield improvement under the country's climatic conditions could lead to more adaptability and productivity.

The aims of this research were to evaluate the general and specific compatibility of 5 parental lines and to investigate the heritability and gene action mode in controlling morphological and fruit yield-related traits using diallel crossing design.

2. Materials and methods

2.1. Plant materials and experimental conditions

In this study, 5 parental lines of tomato were crossed together in diallel design and resulting in a total of 20 F₁ hybrids. The parents included P₁ (Cylindrical fruit, high flowering potential), P₂ (Cylindrical fruit, clustered and high yielding), P₃ (Cylindrical fruit, high shelf life), P₄ (Round fruit, high fruit firmness), and P₅ (Egg-shaped fruit, high yielding). The hybrids, along with 4 commercial hybrids as controls including hybrids 8320, 1585, 15-GS, and 6216-Sun were evaluated. The experiment was conducted at the agricultural research farm of the Agriculture College of Tarbiat Modares University, in 2022. Seedlings were grown in the greenhouse in March 2022. After 40 days, transplanting was done. An experimental design was alpha lattice 2×12 with 2 replications. Crop management such as irrigation, pest and weed control were carried out as usual.

2.2. Trait measurement

Morphological traits including tissue firmness, fruit shape, fruit length and diameter, fruit dry weight, fruit volume, fruit average weight, fruit density, fruit number per plant, and calyx presence were measured. Tissue firmness was measured using a Brookfield texture analyzer. The penetration test was performed using a cylindrical probe with a diameter of 4 millimeters perpendicular to the geometric center of the fruit. The probe speed was set to 3 millimeters per second and its penetration depth was 9 millimeters. Fruit shape was determined according to the IPGRI descriptor. The fruit density was obtained by dividing the weight by the volume of the fruit in grams per cubic centimeter. Fruit dry weight was determined by weighing 100 grams of each fruit, placing them in an oven at 70°C for 72 hours, and then weighing them again. Fruit volume in cubic centimeters was calculated by measuring the changes in water level in a graduated cylinder.

2.3. Statistical analysis

The analysis of variance assumptions including normality of experimental errors distribution and their uniformity were examined using the Shapiro-Wilk and Leven tests, respectively. Analysis of variance based on an alpha-lattice experimental design was performed. The blocking effect within the replications was not

significant for the studied traits. Therefore, the genetic variance analysis was analyzed on the basis of a randomized complete block design. General and specific combining ability, and maternal variance effects were estimated according to Griffing's III method and I model (Zhang et al., 2005). The Griffing's II model was used to estimate the values of σ_g^2 , σ_s^2 for estimating the additive variance (σ_A^2), and dominance variance (σ_D^2), and then after used to calculate the broad sense (h_B^2) and narrow sense (h_n^2) heritability (Zhang et al., 2005). The h_B^2 and h_n^2 were estimated using Equations 1 and 2.

$$(1) \quad h_b^2 = \frac{\sigma_g^2}{\sigma_g^2 + \sigma_s^2} = \frac{\sigma_g^2}{\sigma_A^2 + \sigma_D^2 + \sigma_E^2}$$

$$(2) \quad h_n^2 = \frac{\sigma_A^2}{\sigma_A^2 + \sigma_D^2 + \sigma_E^2} = \frac{\sigma_A^2}{\sigma_A^2 + \sigma_D^2 + \sigma_E^2}$$

where, σ_A^2 is the additive variance, σ_D^2 is the dominance variance and σ_E^2 is the error variance. The genetic variance components were calculated based on the method proposed by Griffing (1956) using the values of general (σ_g^2) and specific (σ_s^2) combining ability variances (Equations 3 and 4).

$$(3) \quad \sigma_g^2 = \left(\frac{1+F}{4} \right) \sigma_A^2$$

$$(4) \quad \sigma_s^2 = \left(\frac{1+F}{2} \right) \sigma_D^2$$

The parental lines were homozygous. Therefore, inbreeding coefficient (F) was considered to be 1. Accordingly, the values of additive and dominance variances were calculated using the Equations 5 and 6.

$$(5) \quad \sigma_A^2 = 2\sigma_g^2$$

$$(6) \quad \sigma_D^2 = \sigma_s^2$$

The GCA/SCA ratio was calculated using Equation 7 (Backer, 1978). The GCA/SCA ratio reflects the proportion of the additive and dominant genetic effects in controlling a trait. Values close to 1 indicate the additive nature of gene effect (Backer, 1978).

$$(7) \quad GCA/SCA = \frac{2\sigma_g^2}{2\sigma_g^2 + \sigma_s^2}$$

Data analysis was performed using SPSS v 26 and SAS v 9.3 software.

3. Results and discussion

3.1. Descriptive statistics and variance analysis

The maximum and minimum number of fruits per plant were recorded for $H_{1 \times 3}$ (79 No.) and $R_{2 \times 5}$ (10 No.) hybrids, respectively. $R_{2 \times 4}$ hybrid had the highest value for fruit dry weight (9.72%), flesh firmness (19.91 kg cm⁻²) and density (1.29 g cm⁻³). $R_{2 \times 5}$ hybrid had the highest value for fruit volume (166.6 cm³), diameter (67.1 mm) and average fruit weight (152.83 g) and $H_{1 \times 2}$ hybrid showed the highest fruit length (74.97 mm) (Table 1).

The fruit diameter average ranged from 44.51 mm to 67.1 mm and the fruit length average ranged from 50.8 mm to 74.97 mm. Considering the length/diameter ratio, the hybrids' fruit shape was frequently elongated. The frequency of fruit shapes from highest to lowest included: High rounded shape in $H_{3 \times 5}$, $R_{1 \times 4}$, $R_{2 \times 4}$, $R_{3 \times 4}$, $H_{4 \times 5}$, $R_{1 \times 5}$ and $R_{2 \times 5}$ hybrids; cylindrical shape in $H_{3 \times 5}$, $R_{3 \times 4}$ and $R_{1 \times 5}$ hybrids; rounded shape in $R_{2 \times 4}$, $H_{4 \times 5}$ and $R_{2 \times 5}$ hybrids; Slightly flattened shape in $H_{2 \times 3}$, $R_{1 \times 3}$ and $R_{2 \times 3}$ hybrids; pyriform shape in $H_{1 \times 2}$ and $R_{3 \times 5}$ hybrids; Ellipsoid shape in $R_{1 \times 2}$ hybrid; and Flattened shape in $H_{2 \times 5}$ hybrid (Table 1).

Table 1. Descriptive statistics of the studied traits in tomato hybrids resulting from a diallel crossing design

Statistics	Fruit number per plant (No.)	Fruit firmness (kg cm ⁻²)	Fruit average weight (g)	Fruit dry weight (%)	Fruit volume (cm ³)	Fruit density (g cm ⁻³)	Fruit length (mm)	Fruit diameter (g cm ⁻³)
Mean	34.67	10.71	87.39	4.61	100.11	0.87	60.38	53.54
Minimum	10	5.28	52.89	2.18	66.6	0.54	50.8	44.51
Maximum	78.75	19.91	152.83	9.72	166.6	1.29	74.97	67.1
Standard deviation	13.11	2.89	21.26	1.70	20.84	0.15	5.46	4.94

The analysis of variance showed that there was a significant difference between hybrids for all traits except for number of fruits per plant and fruit length. Partitioning genotypic variance revealed the significant general combining ability effect for all traits, while the

specific combining ability effect was only significant for fruit dry weight and average fruit weight (Table 2). The GCA and SCA effects reflect the contribution of genes with additive and dominance effects in controlling traits, respectively (Khodadadi et al., 2017).

These results indicate that the selected parents were different for the frequency and nature (dominance or recessive) of alleles involved in controlling these traits and exhibited desirable performance when combined with other parents for the studied traits. Also, significant GCA and SCA effects for fruit dry weight and average fruit weight indicate the presence of both additive and non-additive gene actions in controlling these traits.

Kumar et al. (2013) showed that both GCA and SCA effects were significant for all studied traits, including plant height, days to 50% flowering, number of primary branches, average fruit weight, number of fruits per cluster, total yield per plant, soluble solids, ascorbic acid, titratable acidity, and lycopene, except for number of fruits per plant. Pavan and Gangaprasad (2022) showed that both additive and non-additive gene effects

contributed to controlling fruit weight, but the impact of the additive gene effect was greater. Biswas et al. (2011) evaluated tomato genotypes in two climatic conditions and observed significant additive gene action in controlling fruit weight.

In addition to the nuclear genetic effects of the parental genotypes, the results showed that maternal effects including nuclear and cytoplasmic maternal effects also played a significant role in controlling fruit dry weight, fruit volume, average fruit weight, fruit diameter and fruit length/diameter ratio (Table 2). Specifically, the cytoplasmic genome effect was significant at 1% level of probability and had high impact on controlling fruit volume, fruit diameter and average fruit weight. Therefore, in tomato breeding programs more attention should be paid to the fruit shape and size of the maternal parent.

Table 2. Estimation of variance components for studied traits in tomato diallel crosses

S.O.V	df	Fruit number per Plant	Fruit firmness	Fruit average weight	Fruit dry weight	Fruit volume	Fruit density	Fruit length	Fruit diameter	Length/diameter
Replication	1	38.08 ^{ns}	2.80*	955.21**	18.67**	1521.52*	0.0006 ^{ns}	28.99 ^{ns}	58.80**	0.003 ^{ns}
Genotype	19	226.46 ^{ns}	11.92*	793.83**	4.28**	696.30**	0.03*	38.95 ^{ns}	40.22**	0.05**
GCA	4	553.23**	42.85**	1477.59**	10.75**	1220.17**	0.07**	145.82**	103.58**	0.75**
SCA	5	116.48 ^{ns}	5.65 ^{ns}	480.15**	4.89**	486.97 ^{ns}	0.01 ^{ns}	12.69 ^{ns}	13.32 ^{ns}	0.11*
Rec	10	150.74 ^{ns}	2.68 ^{ns}	677.18**	1.39 ^{ns}	591.43*	0.02 ^{ns}	9.33 ^{ns}	28.32**	0.18*
MAT	4	128.24 ^{ns}	3.96 ^{ns}	1146.03**	0.67 ^{ns}	912.33**	0.01 ^{ns}	12.56 ^{ns}	38.49**	0.11*
NMAT	6	165.74 ^{ns}	1.83 ^{ns}	364.62**	1.87*	377.49 ^{ns}	0.03 ^{ns}	7.18 ^{ns}	21.55*	0.07 ^{ns}
Error	19	124.41	5.09	83.47	0.70	217.48	0.01	20.78	6.88	0.006

ns, *, ** indicate non-significant, and significant at 5% and 1% probability levels, respectively. GCA: General Combining Ability, SCA: Specific Combining Ability, Rec: Reciprocal, MAT: Maternal, NMAT: Nuclear Maternal.

3.2. Gene action

The Baker ratio (GCA/SCA) is a criterion for comparing the variance of general and specific combining ability. 0.5-1 values for GCA/SCA indicate a greater role of genes with additive effects, and values

less than 0.5 indicate the influence of genes with non-additive effects in controlling traits. Consistent with the analysis of variance results, the GCA/SCA ratio values were between 0.65 and 1, indicating the additive role of genes in controlling the studied traits (Table 3).

Table 3. Estimation of GCA/SCA ratio, broad sense heritability (h_B^2) and narrow sense heritability (h_N^2) for the studied traits in tomato

Estimate	Fruit number per plant	Fruit firmness	Fruit average weight	Fruit dry weight	Fruit volume	Fruit density	Fruit length	Fruit diameter	Length/diameter
GCA/SCA	1	0.98	0.77	0.65	0.78	1	1	0.94	0.92
h_B^2	0.53	0.71	0.86	0.85	0.63	0.58	0.68	0.82	0.90
h_N^2	0.53	0.69	0.54	0.41	0.40	0.58	0.68	0.74	0.78

In Javed et al. (2022) research, the GCA/SCA ratio for number of fruits per plant and average fruit weight traits was less than 0.5. While this ratio for fruit firmness was more than 0.5. These results are similar to the findings of the present study and indicate that control of fruit firmness is influenced by additive genes. Although, Shankar et al. (2013) and Garg et al. (2008) reported that both additive and non-additive

gene actions were involved in controlling fruit firmness. Compared to narrow sense heritability, the broad sense heritability does not provide enough information about the heritable component to the next generation, however, values higher than 0.5 indicate that trait expression is related to genetic variations and relative transfer of traits from the parents to progeny, and values less than 0.5 indicate the influence of

environment on the variations. If the proportion of additive genetic variance in controlling a trait is high, the narrow sense heritability will be between 0.5-1.

The broad sense heritability of traits ranged from 0.53 for number of fruits per plant to 0.90 for fruit length/diameter ratio, and the narrow sense heritability ranged from 0.40 for fruit volume to 0.78 for fruit diameter/length ratio (Table 3). Consistent with the GCA to SCA ratio, when the broad sense and narrow sense heritability are close together, indicates a greater role of genes with additive effects. Therefore, when both broad sense and narrow sense heritability are close to 1, it indicates that the traits can be transferred to the next generation. In Nezami et al. (2020) study, both additive and dominance genes actions involved in controlling number of fruits per plant and average fruit weight. Rasheed et al. (2023) observed 99.0% broad sense heritability for average fruit weight and yield per

plant, which shows these traits are strongly influenced by genetic factors. Also, Prajapati et al. (2015) reported the highest broad sense heritability (92.99%) for average fruit weight. Therefore, a large portion of the phenotypic variation in this trait can be attributed to genetic differences between individuals and could be utilized to improve performance through phenotypic selection.

3.3. General and specific combining ability

According to the general combining ability estimates, parent P₁ with cylindrical fruit shape showed the highest nuclear general combining ability and high maternal general combining ability for fruit number per plant. The highest general combining ability for fruit firmness, fruit dry weight and fruit density belonged to parent P₄ and for average fruit weight, fruit volume and fruit diameter belonged to parent P₅ (Table 4).

Table 4. General and cytoplasmic combining ability estimates for parents.

	Fruit number per plant	Fruit firmness	Fruit average weight	Fruit dry weight	Fruit volume	Fruit density	Fruit length	Fruit diameter
Intercept	34.67**	10.71**	87.38**	4.61**	100.19**	0.87**	60.38**	53.54**
G ₁	8.85**	-2.30**	-6.98*	-1.11**	4.56 ^{ns}	-0.11**	2.80*	-0.73 ^{ns}
G ₂	-9.50**	1.78**	-7.65*	0.31 ^{ns}	-8.95*	-0.002 ^{ns}	2.43*	-2.58**
G ₃	2.43 ^{ns}	-0.77 ^{ns}	-8.45**	-0.74*	-8.67 ^{ns}	-0.002 ^{ns}	1.88 ^{ns}	-2.85**
G ₄	-2.91 ^{ns}	2.12**	6.69*	1.26**	-1.98 ^{ns}	0.10**	-5.28**	2.93**
G ₅	1.12 ^{ns}	-0.82 ^{ns}	16.39**	0.28 ^{ns}	15.05**	0.01 ^{ns}	-1.82 ^{ns}	3.24**
M ₁	3.09 ^{ns}	-0.04 ^{ns}	0.43 ^{ns}	-0.17 ^{ns}	0.25 ^{ns}	0.003 ^{ns}	0.63 ^{ns}	-0.41 ^{ns}
M ₂	0.06 ^{ns}	-0.59 ^{ns}	-8.06**	-0.22 ^{ns}	-8.69*	-0.01 ^{ns}	0.70 ^{ns}	-1.78**
M ₃	-3.64 ^{ns}	0.20 ^{ns}	-4.47 ^{ns}	0.12 ^{ns}	-4.48 ^{ns}	-0.008 ^{ns}	-1.03 ^{ns}	-0.43 ^{ns}
M ₄	1.39 ^{ns}	0.60 ^{ns}	0.11 ^{ns}	0.11 ^{ns}	5.16 ^{ns}	-0.02 ^{ns}	0.33 ^{ns}	0.71 ^{ns}
M ₅	-0.91 ^{ns}	-0.15 ^{ns}	11.99**	0.15 ^{ns}	7.75*	0.04 ^{ns}	-0.65 ^{ns}	1.91**

ns, *, ** indicate non-significant, and significant at 5% and 1% probability levels, respectively. G₁, ..., G₅: general combining ability parent 1, ..., 5; M₁, ..., M₅: maternal general combining parent 1, ..., 5.

Despite the highest combining ability for fruit number, P₁ had the lowest general combining ability for fruit firmness, density and dry weight. Also, the lowest combining ability for fruit number per plant, fruit volume and diameter belonged to parent P₂, average fruit weight belonged to parent P₃ and fruit length belonged to parent P₄. This information could help select parents containing increasing alleles for desirable traits and decreasing alleles for undesirable traits. So, in positive general combining ability, increasing alleles and in negative combining ability, decreasing alleles are usually present.

Similar to the general combining ability of parents for nuclear gene effects, P₅ had the highest maternal general combining ability for average fruit weight, volume and diameter. Also, P₂ which showed negative maternal general combining ability for fruit average

weight, fruit volume and diameter traits, similarly, showed negative nuclear general combining ability (Table 4). consideration of the general combining ability regarding the nuclear genome and the contribution of the genome with maternal effects (maternal nuclear and cytoplasmic genes), discovered the role of maternal effects in controlling fruit size traits viz. weight and volume, and fruit shape traits viz. fruit length and diameter.

The results showed that the specific combining ability of hybrids was only significant for average fruit weight, fruit dry weight and fruit diameter traits (Table 5). H₂×₅ hybrid was superior for fruit diameter and average fruit weight and H₂×₄ hybrid for fruit dry weight than the other hybrids. Also, H₃×₅ hybrid had the highest negative specific combining ability value for average fruit weight. Considering the maternal effect on general

combining ability of average fruit weight, fruit diameter and fruit number traits as mentioned above, in the specific combining ability in reciprocal hybrids, when P₁ contributed as the maternal parent in R_{1×3} hybrid, the fruit number increased (Table 5), but in combination with other parents, no significant difference was observed. Therefore, it can be concluded that the maternal effect of parent P₁ for fruits number was due to the interaction of maternal nuclear genes in combination with genes from parent 3. In H_{2×5},

when P₅ contributed as female, the highest SCA was observed for average fruit weight, while when contributed as male parent (R_{2×5}) a significant negative SCA value was observed for this trait. Therefore, P₅ contains maternal genes effective in controlling average fruit weight. Overall, the basic genetic information from crossing designs in under-breeding populations for successful tomato breeding programs is necessary to identify selection methods and management of segregating generations.

Table 5. Specific combining ability estimates for hybrids and reciprocal hybrids (cytoplasm and maternal nuclear) in tomato hybrids resulting from a diallel mating design

Hybrid	Fruit number per plant	Fruit firmness	Average weight	Dry weight	Volume	Density	Length	Diameter
H _{1×2}	2.67 ^{ns}	0.43 ^{ns}	-8.30*	-0.11 ^{ns}	-6.67 ^{ns}	-0.03 ^{ns}	0.60 ^{ns}	0.25 ^{ns}
H _{1×3}	0.45 ^{ns}	-0.07 ^{ns}	7.70 ^{ns}	0.35 ^{ns}	7.22 ^{ns}	0.02 ^{ns}	-1.57 ^{ns}	1.61 ^{ns}
H _{1×4}	0.86 ^{ns}	-1.04 ^{ns}	1.56 ^{ns}	-0.31 ^{ns}	5.10 ^{ns}	-0.03 ^{ns}	0.31 ^{ns}	0.10 ^{ns}
H _{1×5}	-3.99 ^{ns}	0.67 ^{ns}	-0.96 ^{ns}	0.08 ^{ns}	-5.65 ^{ns}	0.04 ^{ns}	0.66 ^{ns}	-1.97 ^{ns}
H _{2×3}	2.63 ^{ns}	-1.11 ^{ns}	4.60 ^{ns}	-0.90 ^{ns}	7.38 ^{ns}	-0.03 ^{ns}	2.33 ^{ns}	-2.17 ^{ns}
H _{2×4}	-0.12 ^{ns}	1.44 ^{ns}	-8.09*	1.59**	-10.12 ^{ns}	0.03 ^{ns}	-1.75 ^{ns}	-0.30 ^{ns}
H _{2×5}	-5.19 ^{ns}	-0.77 ^{ns}	11.79**	-0.57 ^{ns}	9.41 ^{ns}	0.03 ^{ns}	-1.18 ^{ns}	2.22*
H _{3×4}	-6.51 ^{ns}	0.33 ^{ns}	2.53 ^{ns}	-0.61 ^{ns}	-2.91 ^{ns}	0.04 ^{ns}	0.07 ^{ns}	0.50 ^{ns}
H _{3×5}	3.42 ^{ns}	0.84 ^{ns}	-14.83**	1.16*	-11.69 ^{ns}	-0.03 ^{ns}	-0.83 ^{ns}	0.05 ^{ns}
H _{4×5}	5.77 ^{ns}	-0.74 ^{ns}	4.00 ^{ns}	-0.66 ^{ns}	7.93 ^{ns}	-0.04 ^{ns}	1.35 ^{ns}	-0.30 ^{ns}
R _{1×2}	-6.83 ^{ns}	0.45 ^{ns}	5.94 ^{ns}	0.47 ^{ns}	10.82 ^{ns}	-0.02 ^{ns}	1.93 ^{ns}	0.33 ^{ns}
R _{1×3}	14.88**	-0.03 ^{ns}	11.81*	-0.10 ^{ns}	12.50 ^{ns}	0.02 ^{ns}	1.56 ^{ns}	2.43 ^{ns}
R _{1×4}	6.32 ^{ns}	-0.36 ^{ns}	7.24 ^{ns}	-1.30*	-7.07 ^{ns}	0.12 ^{ns}	-0.17 ^{ns}	-0.79 ^{ns}
R _{1×5}	1.08 ^{ns}	-0.29 ^{ns}	-22.84**	0.06 ^{ns}	-15.00 ^{ns}	-0.10 ^{ns}	-0.12 ^{ns}	-4.03*
R _{2×3}	-2.58 ^{ns}	-0.53 ^{ns}	4.17 ^{ns}	-0.14 ^{ns}	2.50 ^{ns}	0.01 ^{ns}	1.42 ^{ns}	-0.11 ^{ns}
R _{2×4}	-4.02 ^{ns}	-1.84 ^{ns}	-14.39*	-0.28 ^{ns}	-10.02 ^{ns}	-0.08 ^{ns}	0.80 ^{ns}	-2.10 ^{ns}
R _{2×5}	0.10 ^{ns}	-0.17 ^{ns}	-24.17**	-0.22 ^{ns}	-25.10**	-0.01 ^{ns}	3.23 ^{ns}	-6.34**
R _{3×4}	-4.93 ^{ns}	-0.88 ^{ns}	-4.05 ^{ns}	1.00 ^{ns}	1.67 ^{ns}	-0.06 ^{ns}	-1.06 ^{ns}	0.77 ^{ns}
R _{3×5}	-0.98 ^{ns}	1.33 ^{ns}	-2.33 ^{ns}	-0.62 ^{ns}	-9.07 ^{ns}	0.06 ^{ns}	-1.11 ^{ns}	-0.62 ^{ns}
R _{4×5}	4.36 ^{ns}	-0.07 ^{ns}	-10.62 ^{ns}	0.005 ^{ns}	10.40 ^{ns}	-0.16**	1.26 ^{ns}	1.45 ^{ns}

ns*, ** indicate non-significant, and significant at 5% and 1% probability levels, respectively.

4. Conclusion

In this study, ten morphological and yield-related fruit traits were measured and analyzed in 20 tomato hybrids derived from complete 5×5 diallel crosses, along with 4 commercial hybrid checks. Based on genetic information such as heritability and gene action, necessary recommendations for further breeding in this tomato population were provided. Also, superior parents for hybrid production and promising hybrids for commercial cultivation were suggested based on general and specific combining abilities. According to the general combining ability analysis, parent P₁ was proposed for use as a maternal parent to increase the number of fruits per plant and fruit length. Parent P₅ showed the highest maternal combining ability for traits related to fruit size including weight, volume and dimensions. Therefore, the role of maternal genetic effects in controlling

tomato fruit size was very prominent. Based on the results of specific combining ability and progeny performance, the R_{1×3} hybrid was identified as the superior combination for traits of number of fruits per plant and average fruit weight. According to the GCA/SCA results, the role of genes with additive effects was effective in controlling most of the studied traits. The high values of general and specific heritability for most traits indicate the importance of genetic effects in controlling these traits. The results can be utilized in selecting suitable parents. This study provided a theoretical basis and scientific guidance for the tomato breeding program and development of new hybrids.

Conflict of interests

All authors declare no conflict of interest.

Ethics approval and consent to participate

No humans or animals were used in the present research. The authors have adhered to ethical standards, including avoiding plagiarism, data fabrication, and double publication.

Consent for publications

All authors read and approved the final manuscript for publication.

Availability of data and material

All the data are embedded in the manuscript.

Authors' contributions

All authors had an equal role in study design, work, statistical analysis and manuscript writing.

Informed consent

The authors declare not to use any patients in this research.

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References

- Amr A., Raie W. 2022. Tomato components and quality parameters, A review. *Jordan Journal of Agricultural Sciences* 18(3): 199-220. <https://doi.org/10.35516/jjas.v18i3.444>
- Anonymous. 2022. Agricultural statistics of 2021. Ministry of Agriculture Jihad, Iran. (In Farsi). <https://www.maj.ir/>
- Azzi L., Deluche C., Gévaudant F., Frangne N., Delmas F., Hernould M., Chevalier C. 2015. Fruit growth-related genes in tomato. *Journal of Experimental Botany* 66(4): 1075-1086. <https://doi.org/10.1093/jxb/eru527>
- Backer J. 1978. Issues in diallel analysis. *Crop Science* 18(4): 533-536. <https://doi.org/10.2135/cropsci1978.0011183X001800040001x>
- Biswas V.R., Bhatt R.P., Kumar N. 2011. Gene action in tomato (*Lycopersicon esculentum* Mill) under open and protected environments. *Vegetable Science* 38(02): 206-208. <https://isvsvegsci.in/index.php/vegetable/article/view/704>
- Blank A.F., Santa Rosa Y.R., de Carvalho Filho J.L.S., dos Santos C.A., Arrigoni-Blank M.F., Niculau E.S., Alves P.B. 2012. A diallel study of yield components and essential oil constituents in basil (*Ocimum basilicum* L.). *Industrial Crops and Products* 38: 93-98. <https://doi.org/10.1016/j.indcrop.2012.01.015>
- Garg N., Cheema D.S., Dhatt A.S. 2008. Genetics of yield, quality and shelf life characteristics in tomato under normal and late planting conditions. *Euphytica* 159: 275-288. <https://doi.org/10.1007/s10681-007-9486-3>
- Griffing B. 1956. A generalised treatment of the use of diallel crosses in quantitative inheritance. *Heredity* 10(1): 31-50. <https://doi.org/10.1038/hdy.1956.2>
- Javed A., Nawab N.N., Gohar S., Akram A., Javed K., Sarwar M., Tabassum M.I., Ahmad N., Mallhi A.R. 2022. Genetic analysis and heterotic studies in tomato (*Solanum lycopersicum* L.) hybrids for fruit yield and its related traits. *SABRAO Journal of Breeding and Genetics* 54(3): 492-501. <https://doi.org/10.54910/sabao2022.54.3.3>
- Khodadadi M., Dehghani H., Jalali Javaran M. 2017. Quantitative genetic analysis reveals potential to genetically improve fruit yield and drought resistance simultaneously in coriander. *Frontiers in Plant Science* 8: 568. <https://doi.org/10.3389/fpls.2017.00568>
- Kumar R., Srivastava K., Singh N.P., Vasistha N.K., Singh R.K., Singh M.K. 2013. Combining ability analysis for yield and quality traits in tomato (*Solanum lycopersicum* L.). *Journal of Agricultural Science* 5(2): 213. <https://doi.org/10.5539/jas.v5n2p213>
- Laurentin Tária H.E. 2023. Population management and genetic improvement. *Agricultural Genetics*. Springer, Cham. https://doi.org/10.1007/978-3-031-37192-9_14
- Mishra A. 2022. Recent developments in breeding approaches of tomato (*Solanum lycopersicum* L.), A review. *International Journal of Farm Sciences* 12(1): 1-6. <https://doi.org/10.5958/2250-0499.2022.00002.7>
- Nezami S., Nemati S.H., Arouiee H., Kafi M. 2020. Half diallel analysis of related traits to yield and fruit quality in tomato lines. *Iranian Journal of Horticultural Science* 52(4): 1011-1025. (In Farsi). <https://doi.org/10.22059/ijhs.2020.296125.1759>
- Nie H., Yang X., Zheng S., Hou L. 2024. Gene-based developments in improving quality of tomato: Focus on firmness, shelf life, and pre-and post-harvest stress adaptations. *Horticulturae* 10(6): 641. <https://doi.org/10.3390/horticulturae10060641>
- Palmgren M.G., Edenbrandt A.K., Vedel S.E., Andersen M.M., Landes X., Østerberg J.T., Falhof J., Olsen L.I., Christensen S.B., Sandøe P., Gamborg C., Kappel K., Thorsen B.J., Pagh P. 2015. Are we ready for back-to-nature crop breeding? *Trends in Plant Science* 20(3): 155-164. <https://doi.org/10.1016/j.tplants.2014.11.003>
- Pavan M.P., Gangaprasad S. 2022. Studies on mode of gene action for fruit quality characteristics governing shelf life in tomato (*Solanum lycopersicum* L.). *Scientia Horticulturae* 293: 110687. <https://doi.org/10.1016/j.scienta.2021.110687>
- Prajapati S., Tiwari A., Kadwey S., Jamkar T. 2015. Genetic variability, heritability and genetic advance in tomato (*Solanum lycopersicon* Mill.). *International Journal of Agriculture, Environment and Biotechnology* 8(2): 245-251. <https://doi.org/10.5958/2230-732X.2015.00031.5>
- Rasheed A., Ilyas M., Khan T.N., Mahmood A., Riaz U., Chattha M.B., Al Kashgry N.A., Binothman N., Hassan M.U., Wu Z., Qari S.H. 2023. Study of genetic variability, heritability, and

- genetic advance for yield-related traits in tomato (*Solanum lycopersicon* MILL.). *Frontiers in Genetics* 13: 1030309. <https://doi.org/10.3389/fgene.2022.1030309>
- Shankar A., Reddy R.V., Sujatha M., Pratap M. 2013. Combining ability analysis to identify superior F1 hybrids for yield and quality improvement in tomato (*Solanum lycopersicum* L.). *Agrotechnology* 2(3): 1000114. <https://doi.org/10.4172/2168-9881.1000114>
- Tester M., Langridge P. 2010. Breeding technologies to increase crop production in a changing world. *Science* 327(5967): 818-822. <https://doi.org/10.1126/science.1183700>
- Zhang Y., Kang M.S., Lamkey K.R. 2005. DIALLEL-SAS05: A comprehensive program for Griffing's and Gardner–Eberhart analyses. *Agronomy Journal* 97(4): 1097-1106. <https://doi.org/10.2134/agronj2004.0260>

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