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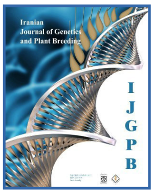

General and specific combining ability for fruit-related traits in watermelon (*Citrullus Lanatus*) using Griffing's method I

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ABSTRACT

One of the key goals of watermelon breeding is to develop superior hybrids with enhanced yield and quality. Hybrid efficiency depends on the general (GCA) and specific (SCA) combinatorial abilities of the inbred lines used in crosses. A complete diallel analysis was conducted to evaluate the breeding values of five watermelon ecotypes: Orzoeiyeh (P1), Hejrak (P2), Gerd (P3), Neyshabour (P4), and Yazd (P5). While most studied traits showed high GCA effects, all displayed significant SCA effects. A high Baker's ratio, coupled with GCA being greater than SCA for days to fruit formation, number of fruits per plant, days to fruit maturity, and fruit weight, suggests the involvement of both additive and non-additive gene effects. Conversely, Baker's ratios for fruit length (0.44), fruit rind thickness (0.42), and fruit sugar content (0.2) indicated the dominance of non-additive gene effects, whereas ratios for fruit weight (0.56), fruit rind weight (0.51), and fruit flesh weight (0.57) suggested an equal contribution of additive and non-additive gene effects in controlling these traits. Parents P4 and P2 demonstrated the best GCA for fruit number per plant and fruit quality, respectively. Based on SCA findings, the P2×P4 and P1×P2 crosses are recommended for producing high-yielding and high-quality hybrids, respectively.

Key words: Diallel, Gene effects, GCA, Hybrid.

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INTRODUCTION

Watermelon (*Citrullus lanatus*) belongs to the Cucurbitaceae family and is renowned worldwide for its high nutritional value, great taste, and pleasant aroma (Dou *et al.,* 2018). It thrives in tropical regions and is widely cultivated across the globe (Dan and Liu, 2007). In terms of vegetable production, watermelon ranks second after tomatoes (Zheng *et al.,* 2024).

Watermelon cultivars vary significantly in size and shape, with sweetness-related traits being crucial for product development and marketing. Modern breeding programs prioritize fruit quality characteristics such as sugar content, flesh color, and skin pattern (Dutta *et al.,* 2023). According to FAO statistics (2022), Iran ranks third in global watermelon production, with an average annual yield of 2,451,979 tonnes, following China (79,278,300 tonnes) and Turkey (4,011,313 tonnes). The next largest producers are the United States (1,725,236 tonnes), Brazil (1,675,146 tonnes), and Egypt (1,524,150 tonnes) (FAO, 2022). China leads in watermelon cultivation with 1,495,331 hectares harvested, while Iran ranks ninth in hybrid watermelon cultivation with 58,446 hectares (World Ranking, 2023).

Improving watermelon cultivars, particularly by developing new hybrids with superior fruit qualities compared to imported varieties, is essential. Selecting superior parental lines for hybridization is a critical step in this process. F1 hybrids outperform their parental lines in productivity, quality, and adaptability to varying climatic conditions, leading to higher yields, better-quality fruit, and increased farmer incomes, thereby supporting agricultural economic growth (Chakrabarty *et al.,* 2023).

Hybrid efficiency depends on the general (GCA) and specific (SCA) combining abilities of the inbred lines involved in the cross (Bahari *et al.,* 2012). GCA, defined as the average trait expression in a parent's half-sibling progeny, reflects additive gene effects and the parent's overall usefulness in breeding (Griffing, 1956a, b). SCA represents the interaction between parental pairs for specific traits and measures the non-additive gene effects contributing to trait expression in hybrid progeny (Baker, 1978).

Diallel crossing is a widely used breeding method that provides extensive information on GCA, SCA, heterosis, heritability, gene effects, and potential interactions (Muraya *et al.,* 2006; Hallauer, 2007; Feyzian *et al.,* 2009; Pagliosa *et al.,* 2017; Esmaeili *et al.,* 2022). The Griffing (1956) method, which evaluates parental potential for superior hybrid production by considering additive and non-additive gene action (Rainey and Griffiths, 2005), remains a valuable approach for estimating genetic parameters (Biabani *et al.,* 2012).

Several studies have emphasized the importance of evaluating GCA and SCA effects on fruit traits to develop high-yielding watermelon hybrids (El-Meghawry *et al.,* 2002; Gusmini *et al.,* 2004; Gvozdanovic *et al.,* 2011; Rakesh, 2011; Ghorbanian *et al.,* 2023). Since these estimates vary depending on experimental conditions and varieties, they must be assessed for each hybrid. This study aimed to evaluate GCA and SCA effects on fruit quality traits in five watermelon inbred lines using a full diallel cross design (Griffing, 1956b) to develop new hybrid genotypes.

MATERIALS AND METHODS

Experimental site

This study was conducted at the Graduate University of Advanced Technology in Kerman, Iran. The farm is located at latitude 30° 60′ N, longitude 57° 17′ W, at an altitude of 2020 m above sea level.

Plant material

Five ecotypes of *Citrullus lanatus* (P1, P2, P3, P4, P5) were collected from different regions of Iran (Table 1). These genotypes were selected based on their diverse morphological traits in fruit and seed characteristics. The single-plant (pure-line) selection method, commonly used for open-pollinated plants, was applied (Singh *et al.,* 2021). Purity was ensured

Table 1. Geographical coordinates of collection sites for watermelon ecotypes.

Ecotype code	Collection region	Longitude	Latitude
P1	Kerman - Orzoeiyeh	56° 21' 54.46''	28° 27' 21.56''
P2	South Khorasan- Hejarak	34° 13' 32''	58° 6' 19''
P3	Alborz-Sharif Abad	50° 9' 0.45''	36° 12' 41.8''
P4	Razavi Khorasan- Neyshabour	58° 47' 24''	36° 12' 36''
P5	Yazd	54° 22' 3''	31° 53' 49.92''

through eight generations of self-pollination.

Experimental design & hybrid development

A full diallel crossing among the five inbred lines produced 20 F1 hybrids between April and May 2017. Field evaluations of parents and hybrids took place from May to October 2018 using a randomized complete block design with three replications. Ten seeds per ecotype were planted, with an intra-row spacing of 0.5 m and a plant-to-plant distance of 2 m. Two weeks after sowing, the most vigorous seedlings were selected per hole. Cultivation followed standard practices, and regular weeding was performed during vegetative growth.

Fruit trait measurements

Ten ripe fruits and six plants per genotype were sampled to assess fruit and agronomic traits. Mean values were used for analysis. The evaluated traits included days to fruit formation (NDF), days to maturity (NDM), fruit number per plant (NFP), fruit weight (FWE), fruit length (FL), fruit width (FW), rind thickness (FRT), rind weight (FRW), flesh weight (FFW), sugar content (FSC), and pH (Table 2).

Statistical analysis & genetic parameters

Minimum, maximum, mean values, and coefficient of variation were calculated for the studied traits. The breeding value of the material was assessed via heterosis and combining ability analysis in the F1 generation. Data were analyzed using a general linear model (GLM), and least-square means were used to compute combining ability via Griffing's Method I (Griffing, 1956).

The model used:

$$X_{ij} = \mu + gca_i + gca_j + sca_{ij} + r_{ij} + e_{ij} \quad (1)$$

Table 2. Mean performance of parents and hybrids for watermelon fruit traits in a 5×5 diallel cross.

Genotype	X1	X2	X3	X4	X5	X6	X7	X8	X9	X10	X11
P1	58.33	2.66	107.3	2.39	18.20	16.90	0.91	0.95	1.44	5.12	6.13
P2	56.33	1.33	103.0	1.60	15.13	14.76	0.76	0.50	1.09	4.99	4.73
P3	53.00	2.66	95.3	1.93	17.75	14.85	0.90	0.60	1.33	5.13	5.93
P4	56.66	2.00	97.0	1.73	15.95	16.05	0.95	0.59	0.94	4.99	6.93
P5	56.67	2.00	97.0	2.40	20.16	18.70	1.25	1.31	1.09	5.00	5.63
P1×P2	57.33	2.00	93.6	5.67	33.05	27.56	1.56	2.52	3.09	4.91	5.16
P1×P3	56.33	1.00	97.0	5.24	29.36	27.38	1.08	1.91	3.00	4.95	5.30
P1×P4	61.33	1.00	100	5.05	29.73	26.16	1.03	2.12	2.93	4.86	4.00
P1×P5	62.66	1.33	94.0	4.24	23.66	19.00	1.16	1.95	2.62	5.16	6.10
P2×P1	53.33	2.33	93.33	5.19	29.52	27.40	1.20	2.12	2.74	4.88	5.13
P2×P3	56.00	2.33	93.00	5.39	26.46	24.91	1.07	1.87	3.51	5.10	6.00
P2×P4	72.00	1.50	121.6	5.50	30.66	28.23	1.15	1.69	3.81	4.99	5.50
P2×P5	60.33	1.66	105.6	5.29	28.85	25.45	0.97	1.62	3.66	5.11	5.63
P3×P1	52.33	3.00	93.00	7.49	36.92	25.29	1.72	2.64	4.85	5.06	6.40
P3×P2	58.33	2.66	101.6	4.41	23.94	22.83	0.88	1.52	2.88	5.04	6.03
P3×P4	62.33	1.66	103.3	4.76	28.41	26.73	1.00	1.83	2.93	5.02	6.66
P3×P5	53.33	2.33	97.33	3.60	28.60	15.60	0.98	1.51	2.09	5.15	5.33
P4×P1	54.67	2.00	96.33	5.59	26.47	24.88	1.35	2.24	3.01	4.97	5.26
P4×P2	72.00	1.50	121.6	5.50	29.33	27.90	1.15	1.54	3.81	4.99	5.50
P4×P3	51.00	2.66	102.6	2.73	21.05	18.08	1.15	0.65	1.91	5.05	5.60
P4×P5	53.67	2.33	94.00	4.34	23.76	21.42	1.12	2.10	2.23	4.96	5.60
P5×P1	55.00	3.00	93.66	4.47	26.21	20.17	0.97	1.64	2.83	5.21	6.50
P5×P2	80.00	1.66	110.3	4.77	27.08	24.81	1.00	1.66	3.10	5.10	6.25
P5×P3	55.67	2.66	96.33	4.67	27.06	25.26	1.23	2.06	2.70	4.98	6.86
P5×P4	66.66	1.33	102.6	6.46	33.22	30.3	1.36	2.40	4.06	4.92	5.36
Min	51.00	1.00	93.00	1.60	15.13	14.76	0.76	0.50	0.94	4.86	4.00
Max	80.00	2.66	121.6	7.49	36.92	30.3	1.72	2.64	4.85	5.21	6.93
Average	59.0	2.0	100.4	4.41	26.0	22.82	1.11	1.66	2.70	5.03	5.74
Coefficient of variation (%)	4.33	29.3	1.44	28.2	9.65	6.73	16.0	23.9	25.1	1.78	11.3

X1: Days to fruit formation (NDF), X2: Fruit number per plant (NFP), X3: Days to fruit maturity (NDM), X4: Fruit weight (FWE), X5: Fruit length (FL), X6: Fruit width (FW), X7: Fruit rind thickness (FRT), X8: Fruit rind weight (FRW), X9: Fruit flesh weight (FFW), X10: pH, X11: Fruit sugar content (FSC).

where *Xij* is the observed measurement of parents i and j; μ is the population mean; gca_i and $gcaj$ are the GCA effects of parent i and j respectively; sca_{ij} is the SCA effect of the cross between parents i and j; r_{ij} is reciprocal effect and *eij* is the random environmental effects associated with ijth individual.

Variance analyses and combining ability (GCA, SCA, reciprocal) were estimated using the Diallel-SAS05 program (Zhang and Kang, 2005). GCA:SCA variance ratios were computed, with values above unity indicating additive gene action and values below unity indicating dominance genetic effects (i.e., non-additive gene action).

Baker's ratio (1978) was calculated as:

$$(2) \qquad \text{Baker's ratio} = \frac{2\delta 2\text{gca}}{(2\delta 2\text{gca} + \delta 2\text{sca})}$$

Broad-sense and narrow-sense heritabilities were calculated per Teklewold *et al.* (2005):

$$(3) \qquad h^2b = \frac{2\delta 2\text{gca} + \delta 2\text{sca}}{2\delta 2\text{gca} + \delta 2\text{sca} + \delta 2\text{e}}$$

$$(4) \qquad h^2\text{n} = \frac{2\delta 2\text{sca}}{2\delta 2\text{gca} + \delta 2\text{sca} + \delta 2\text{e}}$$

Maternal and non-maternal reciprocal effects were assessed per Zhang *et al.* (1996).

RESULTS

ANOVA analysis

The values and means of parents and their F1 hybrids for studied traits are presented in Table 2. The analysis of variance for the diallel cross of watermelon genotypes (Table 3) revealed highly significant differences among genotypes. The combining ability analysis showed significant general combining ability (GCA) effects for most traits except fruit number per plant (NFP), fruit length (FL), and rind thickness (FRT), indicating no parental superiority for these traits in the next generation. Specific combining ability (SCA) effects were significant for all traits measured.

The Baker ratio for NDF, NFP, NDM, and FW was near 1, with GCA higher than SCA, highlighting the contribution of both additive and non-additive gene effects, with additive effects playing a greater role in trait control. In contrast, FL (0.44), FRT (0.42), and FSC (0.2) showed a predominance of non-additive effects, while FW (0.56), FRW (0.51), and FFW (0.57) exhibited equal contributions of additive and non-additive effects.

Days to fruit formation and maturity

Days to fruit formation (NDF) ranged from 51 to 80 (Table 2). The P5×P2 combination exhibited the maximum value, while P4×P3 had the minimum. Significant maternal and non-maternal effects suggest interactions between nuclear and extra-nuclear factors in NDF inheritance. P3 (53 days) showed the highest positive GCA effect (13.33), while P1×P3 (56 days) had the highest positive SCA effect. P1 (58.33 days) exhibited the highest negative GCA effect (-16.83) (Tables 4 and 5).

Days to fruit maturity (NDM) ranged from 93 to 121 (Table 2). The late-maturing P5×P2 combination exhibited the maximum value (121 days), while

Table 3. Analysis of variances for general and specific combining abilities (GCA and SCA), reciprocal, maternal, and non-maternal effects, and variance components.

Source	df	X1	X2	X3	X4	X5	X6	X7	X8	X9	X10	X11
Rep	2	11.57	1.013	3.64	0.65	10.94	5.826	0.031	0.193	0.143	0.006	0.696
Genotype	24	145.7**	1.101**	192.6**	2.12**	14.60**	7.439**	0.14**	0.27**	0.84**	0.025**	1.36**
GCA	4	204.6**	0.615^{ns}	1172**	1.88*	6.33^{ns}	12.17**	0.06^{ns}	0.23**	0.85**	0.05**	0.61^{ns}
SCA	10	131.0**	0.49^{ns}	288.11	2.81**	15.80**	12.52**	0.17**	0.44**	1.26**	0.03**	1.694**
REC	10	285.7	2.182	57.06	2.85	15.46	9.1	0.254	0.31	0.98	0.019	2.132
MAT	4	227.6**	1.458**	36.75**	0.53^{ns}	1.546^{ns}	5.03*	0.06^{ns}	0.06^{ns}	0.2^{ns}	0.012^{ns}	1.104*
NMAT	6	58.11**	0.727^{ns}	20.31**	2.32**	13.92**	4.07*	0.12**	0.25**	0.74**	0.007^{ns}	1.028*
Error	48	6.545	0.353	2.112	0.519	3.433	1.352	0.032	0.058	0.174	0.008	0.4217
MS_{GCA}/MS_{SCA}		1.56	1.2	4.06	0.65	0.40	0.97	0.36	0.52	0.67	1.45	0.36
Baker ratio		0.75	0.711	0.89	0.56	0.44	0.66	0.42	0.512	0.57	0.74	0.42

*, **, and ns indicate significance at P≤0.05, P≤0.01, and non-significance, respectively.

X1: Days to fruit formation (NDF), X2: Fruit number per plant (NFP), X3: Days to fruit maturity (NDM), X4: Fruit weight (FWE), X5: Fruit length (FL), X6: Fruit width (FW), X7: Fruit rind thickness (FRT), X8: Fruit rind weight (FRW), X9: Fruit flesh weight (FFW), X10: pH, X11: Fruit sugar content (FSC).

Table 4. Estimation of general combining ability (GCA) of parental lines for characters measured in the F1watermelon hybrids.

GCA	X1	X2	X2	X4	X5	X6	X7	X8	X9	X10	X11
P1	-16.83*	-0.16^{ns}	-9.0*	1.52^{ns}	-0.23^{ns}	6.43*	0.59^{ns}	1.15^{ns}	0.39^{ns}	-0.29^{ns}	-1.29^{ns}
P2	2.16^{ns}	0.16^{ns}	-3.16**	-0.71^{ns}	0.27^{ns}	-2.94**	-0.18^{ns}	-0.37*	-0.34^{ns}	0.18**	0.66*
P3	-13.33	-0.33^{ns}	-11.0**	-0.37^{ns}	0.635^{ns}	-1.56^{ns}	-0.26*	-0.34^{ns}	-0.05^{ns}	0.11^{ns}	0.31^{ns}
P4	-2.16^{ns}	0.50^{ns}	-0.16^{ns}	-0.93^{ns}	-1.66^{ns}	-2.43**	-0.14^{ns}	-0.44*	-0.48^{ns}	0.06^{ns}	0.46^{ns}
P5	3.50^{ns}	-0.16^{ns}	1.33^{ns}	0.49*	0.99^{ns}	0.51**	-0.01^{ns}	0.005^{ns}	0.49^{ns}	-0.06*	-0.15^{ns}

*, **, and ns indicate significance at P≤0.05, P≤0.01, and non-significance, respectively.

X1: Days to fruit formation (NDF), X2: Fruit number per plant (NFP), X3: Days to fruit maturity (NDM), X4: Fruit weight (FWE), X5: Fruit length (FL), X6: Fruit width (FW), X7: Fruit rind thickness (FRT), X8: Fruit rind weight (FRW), X9: Fruit flesh weight (FFW), X10: pH, X11: Fruit sugar content (FSC).

Table 5. Assessment of SCA, reciprocal, maternal and non-maternal effects for the studied traits.

SCA	X1	X2	X3	X4	X5	X6	X7	X8	X9	X10	X11
S12	26.1**	0.5^{ns}	-9.6*	-2.3^{ns}	4.74^{ns}	-13.9**	-1.22*	-1.73*	-1.7^{ns}	1.096**	4.72*
S13	56.0**	-0.66^{ns}	25.5**	-1.14^{ns}	11.14^{ns}	-7.92^{ns}	-0.92^{ns}	-1.2^{ns}	-0.53^{ns}	0.79**	3.65^{ns}
S14	13.3^{ns}	0.83^{ns}	5.66^{ns}	-2.96^{ns}	-2.59^{ns}	-8.27*	-0.52^{ns}	-1.51^{ns}	-1.47^{ns}	0.3^{ns}	1.75^{ns}
S15	123.1^{ns}	1.33^{ns}	-13.5^{ns}	1.99^{ns}	40.4^{ns}	-27.3^{ns}	-2.66^{ns}	-3.32^{ns}	0.59^{ns}	2.4^{ns}	10.1^{ns}
S23	-16.83**	0.33^{ns}	-11.3**	1.25^{ns}	-0.78^{ns}	4.79**	0.57**	0.71**	0.56^{ns}	-0.39*	-1.45*
S24	-2.33^{ns}	-0.66^{ns}	1.33^{ns}	1.94**	2.87^{ns}	4.022**	0.47**	0.77**	1.16**	-0.24**	-0.91^{ns}
S25	-1.66^{ns}	-0.83^{ns}	-13.6**	-0.97^{ns}	1.51^{ns}	-0.33^{ns}	0.10^{ns}	0.22^{ns}	-0.17^{ns}	0.03^{ns}	-0.7^{ns}
S34	-10.66**	0.33^{ns}	-10.5**	1.13^{ns}	-0.26^{ns}	3.67**	0.13^{ns}	0.62*	0.53^{ns}	-0.1^{ns}	-0.39^{ns}
S35	25.5**	-0.0^{ns}	28.3**	0.52^{ns}	2.5^{ns}	1.05^{ns}	0.13^{ns}	0.13^{ns}	0.87^{ns}	0.17*	1.22^{ns}
S45	-1.66^{ns}	0.16^{ns}	6.1*	0.83^{ns}	-1.84^{ns}	-1.47^{ns}	0.04^{ns}	-0.24^{ns}	-0.59^{ns}	0.03^{ns}	0.81^{ns}
R12	0.00^{ns}	0.00^{ns}	0.00^{ns}	0.00^{ns}	0.00^{ns}	0.00^{ns}	0.00^{ns}	0.00^{ns}	0.00^{ns}	0.03^{ns}	0.03^{ns}
R13	0.00^{ns}	0.00^{ns}	0.00^{ns}	0.00^{ns}	0.00^{ns}	0.00^{ns}	0.00^{ns}	0.00^{ns}	0.00^{ns}	0.00^{ns}	0.0^{ns}
R14	0.00^{ns}	0.00^{ns}	0.00^{ns}	0.00^{ns}	0.00^{ns}	0.00^{ns}	0.00^{ns}	0.00^{ns}	0.00^{ns}	0.00^{ns}	0.00^{ns}
R15	0.00^{ns}	0.00^{ns}	0.00^{ns}	0.00^{ns}	0.00^{ns}	0.00^{ns}	0.00^{ns}	0.00^{ns}	0.00^{ns}	0.00^{ns}	0.00^{ns}
R23	2.00^{ns}	-0.16^{ns}	0.16^{ns}	-2.18^{ns}	2.09**	0.58^{ns}	0.18*	0.2^{ns}	0.17^{ns}	0.01^{ns}	0.02^{ns}
R24	2.00^{ns}	-1.00*	2.00*	-0.53^{ns}	-3.27**	-0.95^{ns}	-0.31**	-0.36**	-0.75**	-0.057^{ns}	-0.5^{ns}
R25	3.33^{ns}	-0.50^{ns}	1.83*	2.4*	-1.03^{ns}	0.47^{ns}	0.16*	-0.06^{ns}	0.126^{ns}	-0.055^{ns}	-0.63*
R34	-1.16^{ns}	-0.16**	-4.33**	0.42^{ns}	0.26^{ns}	0.54^{ns}	0.09^{ns}	0.193^{ns}	0.29^{ns}	0.032^{ns}	-0.02^{ns}
R35	0.00^{ns}	0.00**	0.00^{ns}	-1.53**	0.00^{ns}	0.00^{ns}	0.00^{ns}	0.00^{ns}	-0.00^{ns}	0.00^{ns}	0.00^{ns}
R45	5.33**	-0.5*	0.33^{ns}	0.035^{ns}	2.18**	0.9^{ns}	-0.075^{ns}	0.16^{ns}	0.43*	-0.016^{ns}	0.53^{ns}
M1	13.5**	0.5^{ns}	6.0**	0.95^{ns}	0.35^{ns}	2.5*	0.16^{ns}	0.29^{ns}	0.64^{ns}	-0.08^{ns}	1.15*
M2	3.83**	0.5^{ns}	0.16^{ns}	-0.11^{ns}	0.22^{ns}	-0.75^{ns}	0.095^{ns}	0.003^{ns}	-0.12^{ns}	-0.025^{ns}	-0.2^{ns}
M3	-9.66**	-0.83**	-2.33**	-0.075^{ns}	-0.94^{ns}	-0.01^{ns}	-0.01^{ns}	-0.05^{ns}	0.001^{ns}	0.006^{ns}	-0.3^{ns}
M4	-1.16^{ns}	-0.00^{ns}	0.5^{ns}	-0.53^{ns}	0.1^{ns}	-1.66**	-0.12$_{ns}$	-0.19^{ns}	-0.34^{ns}	0.085*	-0.76**
M5	-6.5**	0.50^{ns}	-4.3**	-0.22^{ns}	0.26^{ns}	-0.12^{ns}	-0.12^{ns}	-0.04^{ns}	-0.18^{ns}	0.02^{ns}	0.11^{ns}
N12	-21.5**	-0.16^{ns}	-2.66^{ns}	-2.18^{ns}	-3.46^{ns}	0.55^{ns}	-0.83**	-0.53^{ns}	-0.61^{ns}	0.086^{ns}	-1.5^{ns}
N13	22.0**	1.166^{ns}	-1.16^{ns}	-0.53^{ns}	1.6^{ns}	-2.53^{ns}	-0.2^{ns}	-0.07^{ns}	-0.52^{ns}	0.084^{ns}	0.04^{ns}
N14	-4.33^{ns}	-0.50^{ns}	-5.33*	2.4*	4.43^{ns}	5.42**	0.48^{ns}	0.81*	1.615*	-0.24^{ns}	3.008**
N15	3.8^{ns}	-1.5^{ns}	9.1**	0.31^{ns}	-2.5^{ns}	-3.44^{ns}	0.55^{ns}	-0.19^{ns}	-0.48^{ns}	0.07^{ns}	-1.52^{ns}
N23	-11.5**	0.83^{ns}	-2.33*	0.42^{ns}	0.92^{ns}	1.32^{ns}	0.075^{ns}	0.14^{ns}	0.3^{ns}	0.042^{ns}	-0.09^{ns}
N24	-3.0^{ns}	0.66^{ns}	2.33*	-1.53^{ns}	-3.39*	-1.86*	-0.53**	-0.56*	-0.97**	0.052^{ns}	-1.11**
N25	-7**	0.83^{ns}	-2.6*	-1.06*	-0.99^{ns}	1.1^{ns}	-0.37**	-0.11^{ns}	0.06^{ns}	0.0^{ns}	-0.31^{ns}
N34	7.33**	-0.33^{ns}	-1.5^{ns}	0.035^{ns}	1.31^{ns}	-1.1^{ns}	-0.01^{ns}	0.05^{ns}	-0.04^{ns}	0.11^{ns}	-0.47^{ns}
N35	3.16^{ns}	0.50^{ns}	-2.00^{ns}	-0.15^{ns}	1.21^{ns}	-0.10^{ns}	-0.10^{ns}	0.00^{ns}	-0.18^{ns}	0.01^{ns}	0.42^{ns}
N45	0^{ns}	0.16^{ns}	-4.5**	0.90^{ns}	2.34^{ns}	2.44^{ns}	-0.07^{ns}	0.30^{ns}	0.56*	-0.08^{ns}	1.41**

*, **, and ns indicate significance at P≤0.05, P≤0.01, and non-significance, respectively.

X1: Days to fruit formation (NDF), X2: Fruit number per plant (NFP), X3: Days to fruit maturity (NDM), X4: Fruit weight (FWE), X5: Fruit length (FL), X6: Fruit width (FW), X7: Fruit rind thickness (FRT), X8: Fruit rind weight (FRW), X9: Fruit flesh weight (FFW), X10: pH, X11: Fruit sugar content (FSC).

P2×P3 had the minimum (93 days). ANOVA confirmed significant differences among genotypes, with both GCA and SCA, as well as maternal and non-maternal variances, being significant. P3 (95.33 days) showed the highest positive GCA effect (11), while hybrids P3×P5 (28.3) and P1×P3 (25.5) exhibited high positive SCA effects, making them strong candidates for reducing maturity duration. P1 (107.33 days) and P2 (103 days) showed the highest negative GCA effects (-9 and -3.16, respectively), while P2×P5 (-13.6) and P2×P3 (-11.3) exhibited the most negative SCA effects. Statistically significant maternal and non-maternal effects were observed, with P1 showing positive maternal effects, while P3 and P5 displayed negative effects (Tables 4 and 5).

Fruit number

The number of fruits per plant (NFP) ranged from 1 to 2.66 (Table 2). The highest values were observed in P3×P2, P4×P3, and P5×P3, while the lowest were seen in P1×P3 and P1×P4. While GCA and SCA variances were not significant, reciprocal maternal variance was significant. P1 and P3 (2.66) ranked highest for this trait, with P3 showing the highest positive maternal effect (Table 5).

Fruit weight

Fruit weight (FWE) ranged from 1.60 to 7.49 kg (Table 2). The highest value was seen in P3×P1 (7.49 kg), while P4×P3 had the lowest (2.73 kg). GCA, SCA, and reciprocal variances were significant, indicating both additive and non-additive gene effects in its inheritance. P5 (2.4 kg) showed the highest positive GCA effect (0.49), making it a strong candidate for breeding larger fruit. P2×P4 exhibited the highest positive SCA effect (1.94). Non-maternal effects were highly significant, with maternal effects strongest in P3 and P5, and significant positive and negative non-maternal effects observed in P1×P4 and P2×P5 (Tables 4 and 5).

Fruit flesh weight

Fruit flesh weight (FFW) ranged from 0.94 to 4.85 kg. P3×P1 (4.85 kg) had the highest value, while P4 (0.94 kg) and P4×P3 (1.91 kg) had the lowest (Table 2). P1 (1.44 kg) ranked highest among parents, and P2×P4 showed the highest positive SCA effect (1.16). Significant positive and negative non-maternal effects were observed in P4×P5 and P2×P4, respectively (Tables 4 and 5).

Fruit rind weight

Fruit rind weight (FRW) ranged from 0.50 to 2.64 kg. P3×P1 (2.64 kg) showed the highest value, while P2 (0.50 kg) and P4×P3 (0.65 kg) had the lowest (Table 2). Watermelon genotypes were distributed across all three rind thickness groups defined by Gusmini *et al.* (2004). P5 (1.31 kg) ranked highest among parents, with P2 and P4 showing negative GCA effects (-0.34 and -0.44, respectively). P1×P2 and P2×P4 exhibited the most significant negative (-1.73) and positive (0.77) SCA effects, respectively. Significant negative non-maternal effects were observed in P1×P2, P2×P4, and P2×P5 (Tables 4 and 5).

Fruit length and width

Fruit length (FL) ranged from 15.13 to 36.92 cm. The highest value was seen in P3×P1 (36.92 cm), while P2 (15.13 cm) and P4 (15.95 cm) had the lowest (Table 1). SCA variance was significant, indicating non-additive gene effects. The highest negative non-maternal value was found in P2×P4 (-3.39) (Tables 4 and 5).

Fruit width (FW) ranged from 14.76 to 30.3 cm, with P5×P4 showing the highest value (30.3 cm). The lowest values were seen in P2 (14.76 cm), P3 (14.85 cm), and P3×P5 (15.6 cm) (Table 2). P5 (18.70 cm) and P1 (16.90 cm) ranked highest among parents, while P1 and P2 showed the most positive (6.43) and negative (-2.94) GCA effects. P2×P3 (4.79) and P2×P4 (4.022) had the highest positive SCA effects, whereas P1×P2 (-13.9) had the most negative. Significant maternal effects were observed in P1 and P4, with notable non-maternal effects in P1×P4 and P2×P5 (Tables 4 and 5).

Fruit sugar content

Fruit sugar content (FSC), measured as total soluble solids, is a key determinant of watermelon taste. The studied genotypes had an average sugar content ranging from 4.00 to 6.93. The highest sugar content was observed in parent P4 (6.93), followed by hybrids P5×P3 (6.86) and P3×P4 (6.66), while P1×P4 had the lowest value (Table 2).

GCA variance was not significant, but SCA, maternal, and non-maternal variances were (Table 3). Parent P2 showed the highest positive GCA effect (0.66). Hybrid P1×P2 exhibited the highest positive SCA effect (4.72), while P2×P3 had the highest negative SCA effect (-1.45) (Tables 3 and 4). Statistically significant maternal effects were observed, with P1 contributing positively and P3 negatively. Significant non-maternal effects were found in P1×P4 and P4×P5, while P2×P4 displayed a notable non-maternal effect (Tables 4 and 5).

pH

The average pH of the studied genotypes ranged from 4.86 to 5.21, with the highest value in hybrid P5×P1 and the lowest in P1×P4 (Table 2). ANOVA revealed highly significant differences among genotypes for this trait. However, reciprocal, maternal, and non-maternal effects were not significant, indicating that pH is under strict nuclear control (Table 3).

Parents P3 (5.13) and P1 (5.12) ranked highest for this trait. Parent P2 exhibited the highest positive GCA effect (0.18). Hybrids P1×P2 (1.096) and P1×P3 (0.79) showed the highest positive SCA effects, whereas P2×P3 (-0.39) and P2×P4 (-0.24) had the most negative SCA effects (Tables 4 and 5).

DISCUSION

The results of this diallel cross highlight the potential of these lines for breeding programs aimed at developing high-yielding and quality-enhanced watermelon hybrids. The significant general combining ability (GCA) effects observed for key traits are instrumental in identifying superior parental lines with favorable alleles for fruit yield improvement (Singh *et al.,* 2022).

Parent P4 emerged as the best general combiner for fruit number, making it a strong candidate for breeding programs focused on increasing fruit production. Likewise, parent P2 was identified as the best general combiner for sugar content and pH, traits directly linked to fruit quality. These findings align with Santos *et al.* (2017), who observed similar trends for fruit number per plant (NFP) and fruit rind thickness (FRT), and Bahari *et al.* (2012), who reported comparable results for NFP, reinforcing the stability of these traits across different studies.

Significant GCA and specific combining ability (SCA) effects, along with maternal and non-maternal variances, were detected for days to fruit maturity (NDM), suggesting a complex inheritance pattern involving additive, non-additive, and maternal influences. This agrees with Bahari *et al.* (2012), who also found significant GCA, SCA, and reciprocal variances for NDM in watermelon genotypes.

For fruit number per plant (NFP), GCA and SCA variances were not significant, whereas reciprocal maternal variance was, indicating the crucial role of maternal effects in trait inheritance. This finding is consistent with Bahari *et al.* (2012) and Santos *et al.* (2017), who also reported non-significant GCA and SCA effects for NFP.

Fruit weight (FEW) demonstrated significant GCA, SCA, and reciprocal variances, confirming the involvement of both additive and non-additive gene effects in its inheritance. This agrees with previous studies (Singh *et al.,* 2009; Gvozdanovic-Varga *et al.,* 2011; Ahmed *et al.,* 2012; Bahari *et al.,* 2012; Singh *et al.,* 2022), which reported similar inheritance patterns for FEW in watermelon.

The predominance of non-additive gene effects in most traits suggests that exploiting heterosis or delaying selection to later generations could be advantageous for trait improvement (Fasahat *et al.,* 2016). The cross P2×P4 exhibited significant positive SCA effects for fruit weight, fruit width, rind thickness, and flesh weight, but a significant negative SCA effect for pH. This combination holds promise for developing high-yielding genotypes suited for commercial production.

Conversely, the cross P1×P2 showed significant positive SCA effects for days to fruit formation (NDF), pH, and sugar content but negative effects for days to fruit maturity, fruit width, rind thickness, and flesh weight. This indicates its potential for breeding high-quality genotypes with improved sweetness and early maturity, traits highly valued in commercial markets.

The significant non-additive gene actions observed underscore the potential of heterosis exploitation in watermelon breeding. By focusing on hybrid combinations that maximize non-additive genetic variance, breeders can develop superior cultivars with enhanced traits. Additionally, the detection of significant maternal and non-maternal effects for several traits highlights the complexity of their inheritance. Maternal influences suggest that female parent selection can significantly impact progeny performance, a critical factor in hybrid seed production.

Heterosis breeding strategies should therefore consider both parent selection and cross-direction to fully utilize these effects. A balanced approach that combines selection for additive effects (to fix favorable alleles) and hybridization to exploit non-additive effects would be the most effective strategy for watermelon cultivar improvement. By integrating genetic effects and maternal influences, breeding programs can more efficiently develop hybrids with improved yield, earliness, fruit quality, and other desirable horticultural traits.

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