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Diallel Analysis of Agronomic Traits in Tomato (*Solanum lycopersicum* **L.) for the Improvement of Elite Varieties in Burkina Faso**

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Authors' contributions

This work was carried out in collaboration among all authors. Author COT managed the literature searches, designed the study, collected data, performed the statistical analysis, wrote the protocol, and wrote the first draft of the manuscript. Authors BK and ZD managed the analyses of the study. Author WVT managed the experimentation field, review and edited the manuscript and Authors KS and KRN validated the methodology, supervised the work, review and edited the manuscript. All authors read and approved the final manuscript.

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ABSTRACT

In Burkina Faso, hybrid tomato seed production has not yet begun. To gather fundamental data on tomato F1 seed production, the Farako-Bâ research station experimented from April 2023 to March 2024. The experiment evaluated together in a completely randomized design 30 genotypes derived from a 6 x 6 full diallel cross set of tomatoes and their six parental lines. One (01) plant served as the experimental unit replicated 10 times, and we recorded plant height, principal stem diameter, number of primary ramifications, day to first fruit maturity, number of fruits per plant, fruit yield per plant (g), and mean fruit weight (g). We analyzed data from the F1 generation and parents using the Griffing Method I to estimate combining ability, reciprocal and maternal effects, and heterosis. For all traits, ANOVA results showed significant differences (P < 0.0001) among parental lines and offspring. The variances for general (GCA) and specific (SCA) combining ability were significant, indicating both additive and non-additive gene effects. Reciprocal and maternal effects were also significant for all traits, except primary ramification and fruit yield per plant. Plant height would be controlled by additive gene action, while yield and its components would be on dominance and epistatic effect due to the non-additive gene action. P3 was the most significant parental line to increase principal stem diameter, number of primary ramifications, yield, and its component while also reducing the cycle. P5 is the most parental line to increase plant height and mean fruit weight, and P5, P4, and P3 were found to be the best parental lines to use as females in crossing to improve fruit yield and its components.

Keywords: Burkina Faso; tomato; diallel; combining ability; maternal effect; heterosis.

ABBREVIATION

INERA: Institut de l'Environnement et de Recherches Agricoles

1. INTRODUCTION

Tomato (*Solanum lycopersicum* L.) is a versatile crop, largely cultivated worldwide. In Burkina Faso, tomato is the second most important vegetable crop after onion in terms of areas production, and foreign exchange. In 2016, 200500 tons of fresh tomatoes were produced on approximately 23 000 hectares (MAAH, 2017). In 2019, the production and the area allocated to tomato decreased to 167 398 tons of fresh tomato on 10 284 ha (MAAHA, 2020). This decrease may be due to climate change and the security crisis, which have severely impacted the country's main tomato production regions, such as "Boucle du Mouhoun," "Centre Nord," and "Hauts-basins." (MAAH, 2017; MAAHA, 2020).

To meet the increased demand for food in these conditions, plant breeding should develop novel materials with high yielding potential. It is well known that seeds of good quality with the best genetic potentiality, such as hybrids, contribute

to more than 40% of expected yield over openpollinated varieties (OPVs) (Tiwari & Choudhury, 1986; Gallais, 2009). So, hybrid varieties are an appropriate option for achieving high productivity on limited surface croplands. Tomato hybrids began to dominate the seed market due to their high potential of production, considerable earliness, high-quality fruits, and pronounced adapting ability. Currently most countries primarily use hybrid seeds for greenhouse and early field production. In Burkina Faso, the global adoption rate of improved vegetable seeds is around 78%. For tomato, this rate rises up to 84% (MAAH, 2017), largely satisfied through imported hybrids varieties. Thus, in order to reduce dependence to foreign seed source and improve the country's economic balance, hybrid varieties must be developed. Therefore, exploiting heterosis is a key step to achieve this objective. Based on combining ability valuable parental lines can be identified for the development of tomato hybrid varieties in Burkina Faso. Subsequently, tomato commercial hybrid seed production, will lead to quality and affordable seed availability to farmers.

Diallel mating design is a classical approach to studying combining ability. It is also widely used for the development of breeding populations for recurrent selection (Acquaah, 2012). Diallel techniques could help to conclude high-yielding tomato hybrids, best combiners, and guidelines for the assessment of the relative breeding potential of the parents (Ibirinde et al., 2022).

Plant breeding programs use Griffing's biometrical diallel analysis (Griffing, 1956) to identify superior parents for crossing, estimate the general, specific, and reciprocal effects (Shattuck et al., 1993; Fasahat et al., 2016;), and assist plant breeders in selecting suitable parental lines for hybridization. Sprague & Tatum (1949) have for the first time introduced the concepts of general and specific combining ability (GCA and SCA). Plant breeders have used different mating designs for combining ability analyses. Among these mating designs, diallel is one the most used in studying the inheritance of some quantitative traits in tomato (Omale, 2024; Desalegn et al., 2021; Adaay & Alabdaly, 2019; Aisyah et al., 2016; Solieman, 2009; Chishti et al., 2008; Hannan et al., 2007a; Hannan et al., 2007b).

The GCA is the mean performance of a line when expressed as a deviation from the mean of all crosses. In practice, the line with the highest GCA value would be the best combiner parent, and it would contain the transmissible genes (Begna, 2021). The GCA is a measure of the additive gene action (Griffing, 1956). A parent with a GCA of 0 has an average combining ability, and depending on the index used, parents with positive or negative GCA values perform above or below this average.

The SCA expresses the performance of the progeny from a cross between two parents based on the average performance of the parents involved. The assumption is that the SCA deviates from additivity and is attributed to non-additive gene effects (Begna, 2021). SCA effects can be positive or negative. A combination with a high SCA value indicates that the parents of this cross can blend effectively to create a hybrid that outperforms in overall performance, demonstrating a distinct heterotic influence (Begna, 2021).

The general combining abilities are main effects, and the specific combining ability is an interaction. Understanding the magnitude of GCA in parents and SCA in F1 crosses is critical for crop improvement. Reciprocal and/or maternal effects reflect differences in the values of the reciprocal crosses and can be positive or negative depending on the direction of the effects. The maternal effect facilitates the selection of a crossing sense. The understanding of maternal effects is crucial for deciphering the complex interplay between parent varieties and specific traits (Omale, 2024).

Georgiev (1984) defined heterosis or hybrid vigor as a biological phenomenon manifesting itself in hybrids that are more vital, adaptive, and productive than their parents. According to Semel et al. (2006), heterosis is also defined as the ability of hybrids to outperform their best inbred parents with respect to growth, yield, and other quantitative traits. Despite being known since antiquity, the use of heterosis in the breeding of cultivated plants only began in 1930. Today, many crops recognize heterosis as the primary factor in successful plant breeding, leading to the development of early, highyielding, and uniform cultivars that combine several important economic characters (Avdikos et al., 2021). Overdominance and additive effects have explained hybrid vigor (Bai & Lindhout, 2007). However, one should exercise caution when considering the F1 heterosis predictions, which are based on the extrapolation of specific effects recorded in generations other than the F1.

The heterosis value information on certain selected genotypes can be very useful for the development of hybrid novel varieties (Amanullah et al., 2011). If heterosis is very high for a specific cross and observations made are true for an economic character like yield, therefore it is possible to use this cross as a commercial hybrid (Griffing, 1956).

The objective of this study was to obtain information on GCA, SCA, reciprocal and maternal effect in crosses using local and introduced tomato lines and to assess the heterosis value in the aim to develop novel hybrid varieties expressing high yield potential in Burkina Faso.

2. MATERIALS AND METHODS

2.1 Experimental Site

The study was carried out at the Farako-Bâ research station located in the western part of Burkina Faso (4°20'W of longitude, 11°06'N of latitude, and 405 m of altitude). Farako-Bâ research station is one of Burkina Faso's five regional directions of the Environmental and Agricultural Research Institute (INERA). The

dominant soil type is lixisol, with low clay and organic matter content and a notable deficiency in nitrogen and phosphorus (Bado, 2002). Climate is of the South Sudanian type, with annual rainfall levels ranging between 800 to 1200 mm. Table 1 shows the characteristics of soil and compost used to prepare soil medium.

2.2 Plant Material

Six (06) tomato variety lines were used as parents in this study. These were: $P1 = FBT1$; P2 = FTB2; P3 = FBT3; P4 = Buffalo; P5 = CLN 2366 A; and P6 = USDA 97L66. P1, P2, and P3, are improved varieties developed and released by INERA. They are suitable for production in hot and humid seasons (Rouamba et al., 2013). Variety (P4) ''Buffalo'', is one of the most widely grown commercial tomato variety in Burkina Faso due to its high yield, deep red color, and oblong fruit shape. Parents P5 and P6 were collected from World vegetable Center and U.S. Department of Agriculture, respectively. These varieties are particularly rich in beta-carotene (Stommel, 2001).

2.3 Hybridization

Seeds of these six parental lines were sown in 72-hole cellular plates filled with commercial sterile substrates made from wood chips. After 3 weeks of nursing, vigorous seedling plants of 12–15 cm in size were transplanted in a screenhouse. As regards to tomato production technical guidelines (Rouamba et al., 2013), transplanting plot was previously ploughed manually followed by harrowing. 20 t/ha of industrial organic compost (Table 1) was applied as bottom dressing. The transplantation was laid out to fit into a full diallel mating design without auto fertilization. Transplanting was done in the afternoon, in order to limit heat stress to plants and promote their good and fast recovery.

The mineral fertilization consisted of applying 300 kg/ha of NPKB (14-23-14-6) twice at a rate of 150 kg/ha, two weeks after transplanting and at blooming. At the second application, 50 kg/ha of 46% urea was mixed with NPKB. For crop protection, Mancozeb 80 WG at 2 kg/ha against fungi and Lambda-cyhalothrin + Acetamiprid 215 EC at 1 L/ha were applied to control caterpillars, aphids, and whiteflies. Manual weeding and staking were done on demand throughout the experiment to keep the plots and plants clean and erect for easy crossing. Each plot contained ten plants (five males and five females). Crossing was carried out on female lines after

the process of emasculation before the flower blooms. Emasculation consisted of the careful hand removal of the anther without damaging the pistil. The hybridization process involved transferring the previously collected pollen from the male parent to the pistil of the female parent's emasculated flower. These operations were done early in the morning, when stigma of the pistil is still receptive. All the pollinated flowers were carefully labeled in order to be able to identify their resulting fruits. At maturity, the seeds were extracted manually from the fruits. The 6 x 6 full diallel, led to a total of 30 hybrids (15 crosses and their reciprocals) obtained.

2.4 Agro Morphological Evaluation of Hybrid Progeny and Parental Lines

The 30 hybrids and the six parental lines were agro morphologically evaluated, during dry and fresh season from November 2023 to February 2024 at INERA Farako-Bâ research station. Sixteen-liter capacity pots were filled with a mix of soil (2/3) and compost (1/3). Table 1 provides the characteristics of the soil and compost used. The experimental unit consisted of one (01) plant per pot per genotype. Each of 36 genotypes is replicated ten (10) times using a completely randomization design (Fig. 1). Crop management was done as regard to tomato production technical guidelines (Rouamba et al., 2013).

2.5 Data Collection and Statistical Analysis

Data were collected on individual plants. Table 2 presented the parameters collected during the experimentation. All these characters align with the "descriptors for tomato" proposed Bioversity International (IPGRI, 1996).

Data collected were subjected to analysis of variance. Means separation was done when significant differences were observed using Scott-Knott (1974) test. Combining abilities reciprocal and maternal effect (Table 3) were determined according to Griffing diallel Method 1 (MAAH, 2017), using the Analysis of Genetic Designs of R (AGD-R) software version 5.0. Heterosis for the 30 hybrids was estimated in percentage increase or decrease of the F1 hybrids value over midparent value by the following formula as described by Fonseca & Patterson (1968):

Midparent Heterosis (
$$
\%
$$
) = $\frac{F1\,hybrid - Mid\,parent}{Mid\,parent} x 100$

Table 1. Characteristics of soil and compost mixed and used as subtracts

Legend: OC: organic carbon, N: Nitrogen, P: Phosphorus, K: Potassium

Table 2. Parameters collected during the experimentation

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Fig. 1. Overview of the experimental design. Each genotype is represented by one line of ten pots. The plants are currently in the blooming stage, and the poles within the pots serve as a staking system

Table 3. Estimates of combining ability and reciprocal effects for diallel method I (Griffing, 1956)

Sources	DDF.	Sum of Squares	Mean of Squares	Expectation of Mean Squares: Model I
General Combining Ability	p - 1	S_{q}	$M_{\scriptscriptstyle{Q}}$	$\sigma^2 + 2p(\frac{1}{p-1})\sum g i^2$
Specific Combining Ability	$p(p-1)/2$	S_{s}	$M_{\rm s}$	$\sigma^2 + \frac{2}{p(p-1)}\sum_i\sum_j S_{ij}^2$
Reciprocal effects	$p(p-1)/2$	S_{r}	M_r	$\sigma^2 + 2(\frac{2}{p(p-1)}) \sum_{i < j} \sum rij^2$
Error	m	S_e	M_e^{\prime}	σ^2
p=number of parents				

Where: $S_g = \frac{1}{2}$ $\frac{1}{2pi} \sum_i (Xi + X \cdot j)^2 - \frac{2}{p^2}$ $\frac{i}{(Xi + X \cdot j)^2 - \frac{2}{p^2}X^2}$. $S_s = \frac{1}{s}$ $\frac{1}{2}\sum_{i}\sum_{j}xij(xij + xji) - \frac{1}{2pi}\sum_{i}(X.i + Xi.)^{2} + \frac{1}{p^{2}}$ $_i(X. i + Xi.)^2 + \frac{1}{p^2}X^2$. $S_k = \frac{1}{2}$ $\frac{1}{2}\sum_{i < j}\sum (xij - xji)^2$

3. RESULTS AND DISCUSSION

3.1 Results

Preliminary analysis of variance (Table 4) showed significant differences (*P < 0.0001*) between parental lines and offspring. For most of the parameters, combining abilities, reciprocal, and maternal effects, exhibit substantial differences, excepted maternal effect for plant yield and the number of ramifications. A highly significant difference (*P < 0.001*) was also observed in variance components between general (GCA) and specific (SCA) combining abilities. The variance component value of SCA is higher than that of GCA for the evaluated parameters except plant height. In addition, for most of the parameters (excepted plant height), the ratio of the variance component GCA to SCA is lower than the unit.

3.1.1 Parental lines mean performance and GCA effect

Table 5 shows the mean performance value of parental lines and hybrids, separated by the Skott-Knott test of all parameters. It also provided the average value and coefficient of variation for all characters.

Parent 5 had the highest significant value of plant height (72.40 cm), with parent 4 following closely behind (66.70 cm). According to the Scott-Knott test, P1, P2, and P3 have similarly high values, while P6, the lowest parent, has a mean value of 54 cm, which is lower than the mean value of 64.23 cm. The coefficient of variation was 7.94. The GCA value (Table 5) indicates that P5 (5.66) and P4 (4.71) are the best parents for increasing plant height.

Source	DDF	HP	PSD	RAM	DMAT	TNFP	YIELD	MFW
Cross	35	2434.51***	$4.54***$	$2.98***$	$111.27***$	2038.94***	492435.29***	760.49***
GCA	5	76.82***	9.39***	$2.01*$	375.12***	3826.22***	1141983.85***	189.61***
SCA	15	99.32***	$3.37***$	$3.48***$	60.44***	1968.83***	564356.66***	718.57***
Reciprocal	15	99.32***	$4.11***$	$2.81***$	74.15***	1513.29***	203997.73*	992.70***
Maternal effect	5	147.20***	$4.50**$	2.06 ^{ns}	$92.70***$	960.54**	90424.42 ^{ns}	1582.90***
Residual	315	24.99	1.07	1.04	1.23	260.58	97468.46	51.69
Component of variance								
$i\sigma^2$ gca		301.19	1.04	0.12	185.93	445.70	130564.42	17.24
$i\sigma^2$ sca		51.83	2.29	2.43	518.51	1708.26	466888.21	666.88
iσ ² gca / ijσ ² sca		5,81	0,45	0,05	0,36	0,26	0,28	0,03

Table 4. Analysis of variance result for full diallel including reciprocal and maternal effect

ns = No significant; **p<0.05; **p<0.001; ***p<0.0001*

Table 5. Mean performance of studied traits of parent and their hybrid and opposite crosses

Genotype	HP	PSD	RAM	DMAT	TNFP	YIELD	MFW
3×4	63.50 a2	11.84 a2	6.50a1	36.10 a3	82.80 a4	1751.50 a3	43.47 a3
3×5	59.200 a2	13.27 a4	7.10 a2	35.20 a2	70.30 a3	2064.40 a4	41.75 a3
3×6	58.50 a2	11.68 a2	5.70 a1	42.40 a8	48.60 a1	1407.00 a2	43.55 a3
4×5	65.20 a3	11.91 a2	6.20a1	40.70 a7	55.90 a2	1420.10 a2	42.63 a3
4×6	56.900 a1	12.38 a3	6.50a1	37.10 a4	58.20 a2	1649.40 a3	38.69 a2
5×6	52.60 a1	11.09 a1	6.70 a1	41.40 a7	63.40 a3	1696.70 a3	34.83 a2
Reciprocal crosses							
2×1	65.60 a3	12.06 a2	6.40 a1	35.10 a2	32.80 a1	1522.10 a2	55.90 a4
3×1	60.10 a2	12.38 a3	6.80a1	42.50 a8	65.20 a3	1783.40 a3	49.32 a3
4×1	59.60 a2	12.77 a3	7.10 a2	42.10 a8	83.30 a4	1989.60 a4	29.79 a1
5×1	66.70 a3	12.11 a2	6.60a1	43.00 a8	76.90 a4	1674.60 a3	38.15 a2
6 x 1	72.40 a4	11.79 a2	7.30 a2	38.30 a4	55.30 a2	1445.80 a2	30.18 a1
3×2	59.200 a2	12.09 a2	6.70 a1	35.60 a2	66.70 a3	1646.10 a3	45.10 a3
4×2	58.50 a2	11.86 a2	6.50a1	39.10 a5	42.20 a1	1304.90 a1	33.04 a1
5×2	65.20 a3	11.42 a1	7.50 a2	40.30 a6	47.00 a1	1552.90 a2	48.52 a3
6x2	56.900 a1	11.44 a1	6.80a1	36.40 a3	67.00 a3	1506.50 a2	30.11 a1
4×3	66.50 a3	11.93 a2	6.90 a2	36.60 a3	75.00 a4	1683.80 a3	24.76 a1
5×3	70.80 a4	11.55 a1	6.50a1	37.30 a4	82.90 a4	1911.30 a4	39.52 a2
6x3	75.70 a5	11.86 a2	7.70 a2	35.60 a2	55.40 a2	1574.40 a3	38.05 a2
5x4	76.40 a5	10.89 a1	6.90 a2	48.40 a9	46.20 a1	1266.90 a1	31.78 a1
6×4	74.60 a5	12.00 a2	6.20a1	40.60 a7	70.90 a3	1721.70 a3	37.92 a2
6×5	68.20 a3	11.39 a1	5.90 a1	41.80 a8	52.10 a2	1663.80 a3	52.65 a4
Mean value	64.23	11,97	6,77	38,85	61,48	1590,55	39,35
C.V. (%)	7.94	8.68	15.30	2.93	26.12	19.51	19.31

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Table 6. Value of general combining ability effects

P1 had the highest value (13.02 mm) for the principal stem diameter, followed by P2 (12.39 mm) and P3 (12.31 mm), while parents 6 and 4 had the lowest value of this character with 10.81 mm and 11.29 mm, respectively. P1, P3, and P2 are the best options for increasing plant diameters with GCA values of 0.35, 0.22, and 0.15, respectively.

P1, P3, and P4 have similarly high values of 8.10, 7.60, and 7.20 primary ramifications per plant, respectively; these are greater than the average value of 6.7. P6 (6.0) and P2 (6.40) have the lowest number of ramifications. The GCA value for this parameter indicates that P1 and P3 are the best parents to increase the highest number of ramifications.

The early maturing parent is P3 with 33.4 DAT, followed by P2 (35.30) and P1 (35.70). The late maturing parental line, P4, got to maturity 42.6 days after transplanting. This parameter has the least coefficient of variation of 2.93. Based on the GCA value, P3 and P2 are the most effective options for increasing earliness in tomatoes, with respective values of -2.27 and -1.97.

The hybrids and parental lines significantly varied in number of fruits per plant (TNFP). Parent 1 and 3 gave the highest average number of fruits per plant, 88.8 and 82.8 fruits, respectively, followed by P2 (62.50 fruits per plant), while the lowest value was for P4 and P6, which produced 40.8 and 44.70 fruits per plant, respectively. This parameter shows the highest CV value of 26.12%, with a mean value of 61.48 fruits per plant. The GCA value (9.80) suggests that P3 is the optimal parental line for increasing productivity, followed by P1 with a GCA value of 2.38. The lowest GCA value is found to be -6.23 for P6.

Highest yielding parents were P1, P3, and P5 with 1711.90 g, 1685.60 g, and 1592 g of fruits per plant, respectively, followed by P2 with 1510.40 g of fruits harvested. Parental lines P6 (1284.70 g) and P4 (971.10 g) were the lowest yielding varieties. The mean yield is 1590.55 g, with a second-most value of 19.51% for the coefficient of variation. Considering the GCA value, P3 had the highest value (134.91), followed by P1 (56.70) and P5 (49.63). The lowest value of GCA is here recorded for P4 (- 119.10), P6 (-93.16), and P2 (-28.98).

Concerning the mean fruit weight (MFW) character, the parental line P6 produced the biggest fruits (43.69 g), followed by the P4, P3, and P5 with 37.50, 35.53, and 34.99 g per individual fruit, respectively. P1 and P2 exhibited the lowest mean fruit weight at 28.25 and 25.42 g, respectively. This parameter has a mean value of 39.35 g per individual fruit, with a coefficient of variation of 19.31%. The GCA values presented in Table 6 indicate that P5 and P1 are the optimal parental lines for increasing individual average fruit weight, with respective GCA values of 1.71 and 1.30.

3.1.2 Crosses mean performance and SCA effect

Table 7 provides the specific combining ability value for biparental and their opposites. For plant height, the biparental crosses 1×4 ; 1×5 ; and 2 x 5 gave a significantly higher mean value than the best parental line (parent 5, 72.40 cm) with 71.30, 73.20, and 72.40 cm, respectively. In the reciprocal analysis, the average plant height of the crosses $(6 \times 3, 5 \times 4, \text{ and } 6 \times 4)$ was highest than the parental lines, measuring 75.40 cm, 76.40 cm, and 74.60 cm, respectively. Hybrids 6 x 1 (72.40 cm) and 5 x 3 (70.80 cm) had average height similar to the best parent. Positive SCA values were recorded with nine biparental crossings. hybrid 4 x 6 scoring the highest SCA (2.87), followed by biparental 1 x 5, 3×6 , 2×5 , and 1×4 . In the reciprocal analysis, cross 6 x 5 showed the highest positive SCA value of 4.61, followed by crosses 3 x 1, 5 x 2, 2 x 1, and 4 x 3.

The highest stem diameter was recorded for four hybrids: 2 x 6; 3 x 5; 1 x 3; and 1 x 2 with 13.52 mm; 13.27 mm; 13.22 mm; and 12.99 mm, respectively. In the reciprocal analysis, crosses 4 x 1 and 3 x 1 had the highest values (12.77 mm and 12.38 mm, respectively). Fourteen hybrids out of 30 surpass the character's general mean of 11.97 mm, and the coefficient of variation stands at 8.68.

None of the hybrids had a higher number of primary branches than the best parent (P1). Indeed, in the biparental crosses, the crosses 2 x 6; 3 x 5; 2 x 3; and 2 x 5 have a significant mean average number of primary branches. In reverse manipulation, five reciprocal crosses had the same significant value, and the highest one was cross 6 x 3 with 7.70 mm. Only height (08) hybrids (three biparental and five reciprocal crosses), display a positive SCA value in Table 6.

The early maturity hybrid was1 x 3 (34.2 DAT). followed by hybrids 2×4 ; 3×5 (35.20 DAT); $3 \times$ 4; and 2 x 3 (36.10 and 36.6 DAT, respectively Table 4). In reciprocal, the early maturity hybrid crosses were 2 x 1 (35.10 DAT); 3 x 2; 6 x 3 (35.6 DAT), followed by hybrids 6 x 2 and 4 x 3 (36.40 and 36.60, respectively).

For the yield component, which is the total number of fruits harvested per plant, none of the hybrid crosses was superior to the best parent (P1, 88.80 fruits), but three hybrids reached number of fruits as the best parent. These hybrids are 3×4 , 1×3 , and 2×5 , with respectively 82.80, 76.40, and 75.70 fruits per plant. The reciprocal analysis confirms the same observation, identifying the crosses of interest as 4 x 1 (83.3 fruits), 5 x 3 (82.90 fruits), 5 x 1 (76.90 fruits), and 4×3 (75 fruits). The general mean value of this character is 61.48 fruits with a coefficient of variation of 26.12%. Six diallel crosses and nine reciprocals gave a superior average than the general mean fruits. The best hybrids are 3 x 5 and 3 x 4, giving respectively 82.9 and 82.8, while the biparental cross 1 x 4 gave 44.8 fruits per plant. In contrast, the reciprocal cross 4 x 1 gave the highest value of 83.3 fruits per plant, while the reciprocal cross 2 x 1 gave the lowest value of 32.8 fruits per plant (Table 4). Regarding SCA, twelve hybrids (six biparental and reciprocal crosses) achieved a positive value.

Concerning fruit yield, as the total fruit weight harvested per plant, five hybrids (three
biparental and two reciprocal crosses) biparental and two reciprocal crosses) outperform the best parent (P1, P3, and P5). These hybrids are 3×5 (2064.40 g); 4 \times 1 (1989.60 g); 5 x 3 (1911.30 g); 1 x 2 (1846.10 g); and 1 x 3 (18.46 g). In addition, thirteen hybrids produced as much as the best parental lines. They are crosses 3×4 (1751.50 g); 5×6 (1396.70 g); 2 x 3 (1666.40 g); 2 x 5 (1651.60 g); 4 x 6 (1649.40 g); and 1 x 5 (1595.80 g) for biparental crosses. In reciprocal, the crosses of interest are 3 x 1 (1783.40 g); 6 x 4 (1721.70 g); 4 x 3 (1683.80 g); 5 x 1 (1674.60 g); 3 x 2 (1646.10 g); 6 x 5 (1663.80 g); and 6 x 3 (1574.40 g). Concerning SCA, eight biparental and reciprocal crosses achieved a positive value (Table 6).

For mean fruit weight, Table 4 reveals that two biparental and reciprocal crosses produced significantly large fruits than the best parental line. They are crosses 1×4 ; 1×5 ; 2×1 ; and $6 \times$ 5, giving respectively 58.69, 58.91, 55.90, and

52.65 g. Indeed, according to the Sckott-Knott test, eight (08) hybrids (five biparental and three reciprocal) have statistically fruit weight as the best parental line. In Table 6, nine (09) biparental crosses demonstrate a positive value for specific combining ability, with cross 1 x 4 and cross 1 x 5 exhibiting the highest values at 15.55 and 15.02, respectively. In reverse, the reciprocal cross 2 x 1 had the best SCA of 20.54, while the cross 4 x 3 had the lowest of - 9.67.

3.1.3 Maternal effect

The maternal effect value in Table 8 shows positive, negative, and zero values depending on the parental lines and parameters. Parental line P3 was the best mother to increase plant height, with the highest positive value of 1.34. The lowest value for this parameter is -2.00, recorded for P5, while P2 exhibited a null value. P2 and P3 had positive values of maternal effect for principal stem diameter, with the highest being 0.33. The interesting values for cycle reducing are -1.21 for P3, -0.64 for P5, and -0.21 for P2. The other parental lines had positive value. P3, P5, and P2 exhibited a positive maternal effect for the total number of fruits harvested per plant, with respective values of 3.22, 2.88, and 1.08. P1, P2, and P6 all had negative values, and the highest is -3.13 for parental line P1. P1, P2, and P3 showed positive value (3.60, 3.47, and 0.75, respectively), for individual fruit weight, while P4, P5, and P6 had negatives values the highest (- 6.23) being recorded for the P4. Table 3 indicates that the maternal effect had no significant impact on the number of primary ramifications and fruit yield per plant. Therefore, it is not necessary to rank parents based on their ability to be excellent mothers or fathers to improve these parameters.

3.1.4 Heterosis estimated

The result in Table 9 presents the value of heterosis calculated for all hybrids based on the deviation from the mean of the parent. It showed negative, positive, and null values depending on hybrids and parameter studies. For plant height, all of the hybrids had a positive and high value of hybrid vigor, ranging from 52.60% for the reciprocal 6 x 3 to 76.40% for the diallel cross 4 x 5. The same observation is found for principal stem diameter, but values of hybrid vigor are medium, ranking from 10.89 to 13.52 for biparental crosses 4 x 5 and 2 x 6, respectively. Only the heterosis value of the biparental cross 2

x 6 is high (25.81%) in terms considering the number of primary ramifications while others are negative or medium. For this parameter, the biparental cross (2 x 3) and his reciprocal (3 x 2) showed a null value of hybrid vigor. For cycle hybrid vigor values, they affiche relatively low positive and negative values and fluctuate between -17.76 and -17.73 for cross 2 x 3 and reciprocal 5 x 3, respectively. The reciprocal cross 3 x 2 displayed a null heterosis, while the cross 1 x 3 exhibited the highest heterosis of 23.01 %. In the yield component, which measures the total number of fruits harvested per plant, the heterosis value revealed that two diallel crosses and six reciprocals had a positive heterosis value exceeding 20%, with the highest value being 65.85% for the cross 4 x 6. For plant fruit yield, 23 hybrids (12 biparental and 11 reciprocal crosses) had a positive hybrid vigor,

and the reciprocal cross 3 x 2 gave a heterosis null. Three diallel crosses gave a vigor hybrid value more than 20%, and the highest is recorded for hybrid 4×6 of 52.65%. Four reciprocal crosses also have vigor hybrid values more than 20%, with cross 4×1 exhibiting the highest value (48.31%). The analysis of hybrid vigor for mean fruit weight indicates that ten of the diallel hybrids exhibited a positive hybrid vigor, while eight of them displayed a positive heterosis greater than 20%. Hybrids 1 x 5; 1 x 4; 2 x 5 and 2 x 4 have the highest values, with 86.31%, 78.53%, 60.66%, and 54.33%, respectively. For reciprocal, eight (08) crosses achieved a positive vigor hybrid value, and reverse cross 2 x 1 recorded the highest value (108.34%), representing the most vigor hybrid value.

Table 8. Value of maternal effects

Table 9. Value of heterosis for hybrids and their opposite on the basis of deviation from the mean of parents

3.1.5 Top five crosses selected based on their combining ability effect

Table 10 provides a summary of the top five crosses selected based on their combining ability effect. This Table primarily displays higher SCA effects derived from parental lines that were both good (high GCA) or poor (low GCA) combiners, or good and poor combiners. The same trends are observed in maternal effects.

Globally, GCA and maternal effect are derived from parental lines that were good and poor combiners. However, we denoted seven cases (five GCA effects and two maternal effects) derived from the two parental lines with poor combiners (LxL). It is for GCA effect, crosses 2 x 6 in PDS, 6 x 4 in RAM, 4 x 6 and 6 x 2 in TNFP, and 4 x 6 and 6 x 4 in fruit yield per plant. For maternal effect crosses of interest, there are 6 x 5 in HP and 5 x 6 in MFW.

Characters	Crosses	Per se	SCA	GCA	Maternal
		performance	effect	effect	effect
	6x5	68.20	4.61	LxH	LxL
	3×1	60.10	4.16	LxH	HxH
HP	5x2	65.20	3.99	HxL	LxN
	4×6	56.90	2.87	HxL	HxL
	2×1	65.30	2.81	LxH	NxH
	2×6	13.52	1.35	LxL	NxL
	6x4	12.00	0.99	LxH	LxH
PSD	5x3	11.55	0.99	HxL	LxH
	4×6	12.38	0.49	HxL	HxL
	3×1	12.38	0.42	LxH	HxH
	2×6	7.80	1.06	HxL	HxL
	3 × 6	5.70	0.78	HxL	LxL
RAM	2×5	7.00	0.75	HxL	HxL
	6x2	6.80	0.57	LxH	LxH
	6x4	6.20	0.09	LxL	LxH
	6x4	40.60	-4.24	HxH	HxH
	2×4	35.20	-3.58	LxH	LxH
DMAT	3×4	36.10	-2.51	LxH	LxH
	5x3	37.10	-2.42	HxL	LxL
	6x2	36.40	-1.95	HxL	HxL
	4×6	58.20	20.10	LxL	HxL
TNFP	4×1	83.30	19.18	LxH	HxL
	6x2	67.00	16.44	LxL	LxL
	3×4	82.80	14.96	HxL	HxH
	5×2	47.00	14.58	HxL	HxL
YIELD	4×1	1989.60	459.87	LxH	HxL
	4×6	1649.40	385.73	LxL	HxL
	6x4	1721.70	323.06	LxL	LxH
	5x3	1911.30	277.25	HxH	HxH
	3×4	1751.50	221.33	HxL	HxH
	2×1	55.90	20.54	LxH	HxH
	1×4	58.69	15.55	HxL	HxL
MFW	1×5	58.91	15.02	HxH	HxL
	5×6	34.83	10.45	HxL	LxL
	3x2	45.10	10.32	HxL	HxL

Table 10. Top five crosses selected on the basis of specific combining ability effect

H = high; L = low, N = null general combines

Ten cases (three for GCA effect and seven for maternal effect) of good parental line combiners (HxH) are also denoted. For GCA effect, they cross 6×4 in DMAT, 5×3 in YIELD, and 1×5 in MWF. For maternal effect crosses, there are 3 x 1 in HP and PSD, 6 x 4 in DMAT, 3 x 4 in TNFP, and 5 x 3 and 3 x 4 in YIELD. In two cases, one of the parental lines combined a null value to generate the beneficial SCA effect. It is the case of crosses 2 x 1 and 2 x 6 for maternal effect in HP and PDS parameters.

3.2 Discussion

High genotypic variability among the genotypes is highlighted in our study, suggesting a potential for selection to improve most of these traits (Adaay & Alabdaly, 2019; Dar & Sharma, 2011; Rani & Anitha, 2011; Kumar et al., 2014; Shankar et al., 2013; Santoshkumar et al., 2019; Kumar & Yadav, 2023). Vegetative parameters are good indicators of genotypes ability to adapt to their environment. A large stem diameter is often a sign of the plant's vigorousness and good health. Thick stems are better equipped to transport necessary nutrients and water to leaves and fruit, resulting in improved overall growth and better production. It also helps plants to resist at disease infection in the field (Tounsi-Hammami et al., 2024). Primary ramification in tomato plants is critical for maximizing fruit production, ensuring plant health and stability,

and improving overall management practices. It plays a crucial role in several aspects of their growth and productivity. Primary branches significantly increase the number of flowers, which in also increases the number of fruits. It also optimizes the stability of plants by preserving their structural integrity. Yield is well known to be the sum of many actions, such as seed choice, agronomical practices, and environmental influence. The best genotypes to increase these parameters are those with a large stem diameter, such as Parent 1 (FBT1), and biparental crosses 1×2 , 1×3 , 2×6 , and 3×5 .

The analysis of variance for combining ability revealed significant variation due to both GCA and SCA for all characters, suggesting that both GCA and SCA effects played important roles in the control of these traits.

Highly significant variation resulting from both general and specific combining abilities, as measured by their component variance values. These differences highlight the importance of both additive and non-additive gene action in inheritance of characters studies (Adaay & Alabdaly, 2019; Solieman, 2009; Hannan et al., 2007a) except plant height, where the component of variance of SCA was superior to the GCA one. General combining ability has direct relationship with narrow sense heritability and represents fixable portion (additive and additive x additive interaction) of genetic variation, thus aids in selection of suitable superior ones as parents for breeding programs (Saleem et al., 2009) to develop cultivars with desired traits of interest. The negative combining ability effect indicated the genotypes or cross combiner contributed to decreasing performance in certain characters while the positive combining effect indicated the genotypes or cross combiner contributed to increasing performance in certain characters. Selecting genotypes with high yielding used GCA and SCA positive effects. This study showed positive and negative value of combining ability as (Omale, 2024; Desalegn et al., 2021; Adaay & Alabdaly, 2019; Aisyah et al., 2016; Solieman, 2009; Chishti et al., 2008; Hannan et al., 2007a; Hannan et al., 2007b; Saleem et al., 2013) which allows to select parental lines and hybrids to improve desirable characters. Thus, the positive value of GCA for number of primary ramifications, total number of fruits harvested per plant, and yield per plant for P3 (FBT3) indicated that this parental line is the best option to use in a crossing to improve, lot of primary ramifications, yield, and its principal component as the total number of fruits per plant. While, the negative value of GCA for cycle indicated the possibility to use P3 in crossing for cycle reducing.

Specific combining ability is the manifestation of non-additive component of genetic variance and associated with interaction effects, which may be due to dominance and epistatic component of genetic variation that are non-fixable in nature. The level of SCA effects had a capital importance to select cross combinations with a higher probability to obtain desirable genotypes at segregation (Ibirinde et al., 2022). In our study, hybrids 4×1 ; 4×6 and 3×4 ; are the best option to increase total number of fruits harvested and fruit yield per plant. For mean fruit weight, biparental crosses 2 x 1, 1 x 4, 1 x 5, 5 x 6 and 3 x 2 represents the good option to increase individual fruit weight.

When the component of variance due to SCA was higher than the due to GCA in a parameter, it means that these parameters are controlled by dominance, and epistatic effects of non-additive genes were concluded to be more important than additive genes (Saleem et al., 2013). In our study, the < 1.00 ratio of GCA and SCA variances of plant height as the finding of Ibirinde et al. (2022) suggested that this parameter would be controlled by additive gene action. The other parameters were that the component of the SCA value is relatively high compared to GCA (ratio $<$ 1.00), suggesting the dominance and epistatic effect due to the nonadditive gene action in consonance with Begna, (2021) and Yadav et al., (2013). So, improvement by recurrent selection or searching for other genes through other parental lines is becoming an imperative for these traits.

The significant effect of reciprocals indicated the influence of female parents or maternal effects. This resulted in a performance difference between the hybrid and its reciprocal. Cytoplasmic inheritance, nuclear genetics, and environmental factors may affect this difference (Omale, 2024).

The distinction between the interaction effect of the cross and its reciprocal primarily arises from the interplay between nuclear and cytoplasmic genes. The cytoplasm of the female parent may represent a distinct environment that varies from one parent to another (Ghareeb et al., 2014), thereby interacting differently with nuclear genes (Mahgoub, 2011). To get a fuller picture, it's

important to separate the effects of general and specific combining abilities. This gives us more information about each parent when they are used as a female or a male in hybrid combinations (Mahgoub, 2004).

Aisyah et al. (2016) funded a significant and positive reciprocal effect for plant yield, number of fruits per plant, and individual fruit weight, whose results are in agreement with our study. Farzane (2012) demonstrated the impact of reciprocals on the yield component, specifically the individual fruit weight and the number of fruits per plant. (Hannan et al., 2007b) funded a significant and positive reciprocal effect for plant height, number of flowers per cluster, number of fruits per plant, fruit weight per plant, and number of seeds per fruit. Omale (2024), based on the tested varieties of his parents, found significant positive and negative maternal effects for cycle parameters and mean fruit weight, indicating the need to determine maternal effects separately for each variety. Positive maternal effects in certain varieties for specific traits suggest the potential for targeted trait improvement through careful selection of maternal parents. Understanding maternal effects can be important to breed for adaptiveness in an environment and improve yield components in tomato production. Indeed, selecting high-quality maternal plants can help to choose crossing direction, minimize negative maternal effects and maximize the potential of offspring plants for optimal character interest. In our study, looking for tested parents, it is possible to breed an adapted and productive variety by improving vegetative, cycle, and yield component parameters. P5, P4 and P3 are the best option to use as female parental line in crossing to improve total number of fruits harvested and fruit yield per plant.

In terms of growth, yield, and other quantitative traits, heterosis, also known as hybrid vigor, is when a hybrid plant does better than its best inbred parent (Semel et al., 2006). The heterosis value equal or greater than 20% on the yield component of autogamous plants, as rice and tomato give opportunities to used hybrids (Aisyah et al., 2016; Desalegn et al., 2020). It the case of biparental crosses 3×4 ; 4×6 ; 4×1 ; $4 \times$ 3 and 6 x 4, those achieved heterosis value great than 20% for total number of fruits harvested and fruit yield pers plant.

According to the character of interest, our result displays positive, null, and negative values of

heterosis, which aligns with the findings of Jyothi et al. (2018), who used an 8 x 8 full diallel cross of tomato to estimate the heterosis of crosses for yield and yield-attributing characters. Positive hybrid vigor values indicated the overdominance of genes, which makes hybridization effective in inheritance, while negative values indicated partial dominance, as reported by Adaay & Alabdaly (2019). All evaluated F1 hybrids reflected positive heterotic effects for vegetative parameters like plant height and stem diameter. In terms of yield and its component, such as mean fruit weight, the majority of crosses demonstrated a positive and desirable hybrid vigor, thereby supporting the role of non-additive gene effects in the inheritance of these characteristics. These results are consistent with the results of Solieman (2009) and Farzane et al. (2012). Jyothi et al. (2018) found a similar result, indicating that the heterosis basis of deviation from mid-parent occurs for plant height (0.75- 84.79%) and for number of branches (0.06- 57.62), with the highest positive value of heterosis for yield per plant being 117.90%. Aisyah et al. (2016) reported (1.5-58.8%) for yield per plant, (1.6-82.5) for number of fruits, and (1.1-37.2%) for individual fruit weight. For heterobeltiosis, Adaay & Alabdaly (2019) reported a high value of 275.72% for the number of fruits per plant, 79.69% for fruit weight, and 205.33% for plant yield. Positive heterotic value suggested that non-additive gene effects play a role in the inheritance of these characters. For traits like yield, and its component, positive heterosis is usually wanted. On the other hand, negative heterosis is wanted for traits like early maturity (Acquaah, 2012) and breeding for resistance to pests and/or disease (Yustiana, 2013). Crosses 2×3 and 5×3 was the best hybrids to decrease day to maturity. Heterosis null values occur when the hybrid's average response is equal to the mid-parent. It suggests that the hybrid offspring show no superior qualities over their parents. This typically indicates that the parents are genetically similar and gene action is completely additive (Acquaah, 2012). For breeders, a null value of heterosis can influence decisions about future breeding strategies. Breeders may select more genetically diverse parent lines to increase the potential for hybrid vigor in subsequent generations if they observe no heterosis. Overall, the significance of a null value of heterosis is multifaceted, influencing breeding decisions, genetic research, and economic strategies in agriculture husbandry. In our result, the perfect example is the null value of heterosis

for primary ramification of cross 2 x 3 and reciprocal 3 x 2. Indeed, parents 2 and 3, namely Farako-Bâ Tomate 2 and 3, share a common ancestor, making them genetically closely related for certain primary ramification characters. Jyothi et al. (2018) report heterosis null for the number of branches and fruits per plant, while Souza et al. (2012) report it for the average fruit weight, fruit wall thickness, total soluble solids, and total titratable acidity.

In general, hybrids with high specific combining ability effects derived from crosses between parent lines that are both good general combiners (high GCA effect) can be attributed to additive gene activity (Begna, 2021). While additive and epistatic effects can be attributed when the highest SCA effect was recorded in hybrids derived from parental lines that are both poor general combiners (low CGA effect) or crosses involving good and poor general combiner parents. Wammanda et al., (2010) observed that, for a self-pollinated crop such as tomato, SCA effects do not contribute much to its improvement. In order to be effective, one of the crossing parents is expected to be a good combiner while the other may be a poor combiner (Wammanda et al., 2010). Our study highlights good and poor combiners regarding their GCA value. Therefore, many biparental crosses with the best SCA effects are derived from parents where one is a good combiner and the other is a poor combiner. For fruit yield and its components, P1, P3, and P5 were the good combiners regarding their GCA value, while P2, P4, and P6 were the poor combiners. Crosses 4 x 1 and 3 x 4 with a high SCA effect and derived from parents that are poor and good combiners are the manifestation of additive x epistatic effect, while hybrids 4 x 6 and 6 x 4 are the manifestation of the only epistatic effect because they are derived from parental lines that are both poor combiners (Begna, 2021).

4. CONCLUSION

The analysis of variance revealed significant differences among the evaluated genotypes (parental lines + hybrids) for studied characters, indicating the presence of sufficient genetic variability between the parental lines and the offspring hybrids. Based on their individual performance, we determined that the hybrids 6 x 3, 5 x 4, and 6 x 4 showed promise in most vegetative parameters such as plant height. In terms of cycle reduction, hybrids 1 x 3; 2 x 4; 3 x 5; 2 x 1; 3 x 2 and 6 x 3was the most successful.

For fruit yield and it components, hybrids 1 x 3; 2 x 5; 3 x 4; 4 x 1; 5 x 1; 4 x 3; and 5 x 3 had the greatest number of fruits per plant; hybrids 1 x 2; 1×3 ; 3×5 ; 4×1 ; and 5×3 were promising for fruit yield per plant, and for average fruit weight, the most crosses are 1×4 ; 1×5 ; 2×1 ; and $6 \times$ 5. In tomatoes, both additive and non-additive gene action types play an important role in controlling vegetative yield and yield components. In our study, plant height was controlled by additive gene action so, simple selection can be applied to improve it, while the other parameters are under dominance and epistatic effect due to the non-additive gene action. Therefore, it is imperative to improve these traits through recurrent selection. P3 (FBT3) was the most significant parental line to increase the vegetative parameters (PSD and RAM), yield, and yield component, while also reducing the cycle. The influence of reciprocals was observed in all characters, including the maternal effect, expected ramification, and fruit yield per plant. Indeed, P5 (CLN 2366A), P4 (Buffalo), and P3 (FBT3) were found to be the best parental lines to use as female in crossing to improve the total number of fruits harvested and fruit yield per plant. All crosses demonstrated a positive and significant increase in heterosis for plant height. The best hybrids for increasing yield and its components are biparental crosses 3×4 ; 4×6 ; 4×1 ; and 5×3 , with the reciprocal 2×1 hybrid exhibiting the highest hybrid vigor for mean fruit weight. Thus, heterotic breeding for tomato yield improvement through utilizing the potentiality of these parents is feasible.

DISCLAIMER (ARTIFICIAL INTELLIGENCE)

Author(s) hereby declare that NO generative AI technologies such as Large Language Models (ChatGPT, COPILOT, etc.) and text-to-image generators have been used during the writing or editing of this manuscript.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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