ESTIMATION OF COMBINING ABILITY AND GENE ACTION FOR MORPHOLOGICAL AND YIELD-RELATED TRAITS IN TOMATO (*Solanum lycopersicum* L.)

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Abstract. Tomato (*Solanum lycopersicum* L.) is the second most consumed vegetable. Its yield is highly affected by sudden climate changes. This study aimed to evaluate parents and cross combinations based on the combining ability (GCA and SCA) for yield and quality-related traits and gene actions by line × tester analysis. Good-quality but low-yielding lines (L; seven) and their contrasting testers (T; three) were crossed following the line × tester mating design. Twenty-one hybrids were evaluated for morphological and yield-related traits. The analysis revealed that these lines contributed more significantly to the variance of genotypes compared to testers, particularly for traits such as total soluble solids and fruit color. L_6, L_3, and L_4 were identified as good general combiners for yield traits due to their high positive General Combining Ability (GCA) values among the genotypes. High GCA values increased the potential and adaptation of parental lines for developing hybrids. Among the cross combinations, $L_7 \times T_2$, $L_4 \times T_1$, $L_1 \times T_2$, $L_5 \times T_3$, and $L_6 \times T_2$ showed high positive specific combining ability (SCA) for yield traits and total soluble solids. $L_4 \times T_3$ and $L_3 \times T_3$ had positive SCA values for fruit color and number of fruits/plant. Non-additive gene action was identified for all the traits except fruit color which indicates that genotypes should be tested for hybrid development.
Keywords: *climate change, non-additive, breeding, hybridization, line × tester, Solanum lycopersicum*

Introduction

Tomato (*Solanum lycopersicum* L.) is one of the most economically and nutritionally important vegetable crops globally, valued for its richness in essential minerals, vitamins A, B, C, and lycopene (Chadha, 2006; Kun et al., 2006). As a temperate to subtropical crop, tomato cultivation spans diverse climatic regions, which presents challenges in

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maintaining consistent productivity (Shukla et al., 2023). It is cultivated globally with a total production of approximately 186.1 million tons across 4.92 million hectares as of 2022 (FAOSTAT, 2022). In the global context, Pakistan ranks 34th in tomato production and 11th in terms of cultivation area (GOP, 2015). From 2016 to 2021, tomato production area in Pakistan increased from 52.9 to 57.9 thousand hectares with corresponding yield rising modestly from 583.5 to 605 thousand tons. However, the average yield per hectare has remained relatively stagnant (Soomro et al., 2020). To fulfill domestic tomato demand, the country imported between 240 to 371 thousand tons of tomatoes during 2019-2021, primarily from Iran and Afghanistan (MNFSR, 2023). One major bottleneck in Pakistan's tomato value chain is the lack of processing infrastructure which causes market fluctuations, farmers face price crashes during peak harvests while consumers encounter high prices during off seasons (Kirby et al., 2016). Furthermore, climate change poses a significant threat to tomato production due to increased pest and disease outbreaks (Anley et al., 2007; Sushma et al., 2024).

Given the rapidly growing population, there is an urgent need to develop tomato varieties that are not only high-yielding but also climate-resilient and nutritionally superior (Sushma et al., 2024). Although conventional breeding methods, such as mass selection and pedigree breeding, have led to improvements in yield and quality (Patil et al., 2016). These approaches are often insufficient against the pressures of modern climatic stressors. To address this gap, contemporary breeding programs are now incorporating advanced techniques, including hybridization, marker-assisted selection (MAS), genetic engineering, and quantitative trait loci (QTL) mapping (Lin et al., 2014). Breeding programs typically follow three integrated phases: screening, hybridization, and genetic transformation (Iqbal et al., 2019; Hu and Ziong, 2014).

Adopting modern approaches to produce hybrids that can tolerate stress conditions and also have good yield and quality is important (Solankey et al., 2015). The application of modern tools such as CRISPR/Cas9 genome editing (Chaudhary et al., 2015), male sterility systems (Zhang et al., 2023), haploid induction (Du et al., 2020), and genomic selection (Li et al., 2021) holds great promise for developing stress-tolerant, high-quality tomato cultivars with enhanced productivity.

The selection of suitable parents, effective cross-combinations, and a thorough understanding of combining abilities, and genetic components are essential for the genetic improvement of agricultural plants through the exploitation of heterosis (Fu et al., 2022; Kansouh and Zakher, 2011). These traits are governed by specific genes and their mode of action, which help in developing the best breeding strategy for improving the genetic makeup of plants for desired traits. Gene action is commonly assessed by estimating combining ability which includes general combining ability (GCA) and specific combining ability (SCA) as well as analyzing genetic components (Mohanty, 2003). GCA reflects additive gene effects and is crucial for identifying parental lines that consistently transmit favorable traits such as fruit size, total soluble solids (TSS), and disease resistance (Griffing, 1956; Kumar et al., 2013). In contrast, SCA captures the non-additive gene effects, such as dominance and epistasis, which are essential for detecting hybrid combinations exhibiting heterosis or hybrid vigor, particularly for traits like fruit yield and plant vigor (Patil and Madalageri, 2013). Integrating both GCA and SCA allows breeders to select not only superior parents but also exceptional hybrid combinations, thereby accelerating the genetic improvement of both yield and fruit quality traits in tomato. To achieve effective genetic gains, a variety of breeding techniques are required to effectively transfer favorable genes into high-yielding and commercially viable cultivars (Dou et al., 2021).

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To estimate these combining abilities and genetic components, line × tester mating design is the simplest yet powerful mating design, which provides detailed information regarding general and specific combining abilities for each cross, tester, and line. It can evaluate a larger set of germplasm and provide information for the selection of suitable parents for crossing in the breeding program (Anushma et al., 2018). It has been used in tomatoes for estimating the combining abilities for yield and quality-related traits in greenhouse (Fasahat et al., 2016; Zengin et al., 2015). This method helps to identify the best combiners through the evaluation of germplasm that could further be used to develop better genotypes (Saeed et al., 2014).

This study planned to screen genotypes that could be used for producing good yield and quality hybrids. We aimed to evaluate parents and cross combinations based on the combining ability (GCA and SCA) for yield and quality-related traits and gene actions by line × tester analysis. The analysis identified several good general and specific combiners and revealed a predominant role of non-additive gene action in trait expression.

Materials and methods

Plant material, growth, and yield parameters evaluation

A set of forty-six genotypes was collected from Germplasm Plant Genetic Resources Institute, National Agricultural Research Center, Islamabad Pakistan. Genotypes were sown in a walk-through tunnel and irrigated every five days. Thirty-days old seedlings of tomato genotypes were transplanted to the field. These genotypes were evaluated for morphological and yield traits that include number of days to first flower, number of clusters/plant, number of flowers/cluster, number of days to first harvesting, plant height (cm), fruit length (mm), fruit diameter (mm), individual fruit weight (g), number of fruits/plant, fruit yield/plant (kg) and quality traits include fruit shape (flattened, round, ellipsoid), fruit color (brown, orange, red), and total soluble solids (%).

Experimental design, field location, and cultural practices

Genotypes were screened during 2020 and 2021 at the research farm of MNS University of Agriculture, Multan (MNSUAM), Pakistan. Total Soluble Solids (TSS) were measured by hand refractometer (Mondal et al., 2009). Data from nine plants of each genotype were collected. Out of 10 screened genotypes, three were used as testers and seven as lines to produce 21 hybrids following the line × tester mating design developed by Cox and Pearson (1962). Based on their performance, seven genotypes with desirable morphological and fruit quality traits (e.g., high total soluble solids, fruit shape, size) were selected as lines, while three genotypes that excelled in yield-related traits (e.g., number of fruits per plant, fruit yield per plant) were chosen as testers. The rationale behind this contrasting selection was to ensure the inclusion of genetic diversity in the breeding material, targeting two major breeding goals: yield improvement and fruit quality enhancement in terms of color, shape and size. These lines and testers were used to produce hybrids. These hybrids along with their parents were sown in seedling trays to develop 30 days old seedlings by using reverse osmosis (RO) water. RO water reduces the effect of salts and other heavy metals present in the water and it increases plant germination and growth (Kempthorne, 1957). Seedlings were transplanted in the field during 2021 and 2022 in a Randomized Complete Block Design (RCBD) with three replicates with a spacing of 45 cm between plants and 75 cm between rows. According to the meteorological data recorded at the MNS University of

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Agriculture weather station, the average temperature during the crop season was 19 to 33°C while the relative humidity was 48 to 76%. The soil texture was loamy with an electrical conductivity of 2.47 and with pH value of 7.9. The soil was 33% saturated. The P and K concentrations were 8.4 mg/kg and 202.5 mg/kg, respectively. Irrigation was applied based on crop requirements mainly after 10-12 days. Proper weeding and crop protective measures were adopted for efficient crop growth.

Statistical analysis

Recorded data were subjected to analysis of variance to test differences among genotypes for various morphological and fruit traits following the method described by Munns and Tester (2008). Additionally, correlation analysis was conducted using the approach by Steel et al. (1997) to evaluate interrelationships among the studied traits. To visualize genotype performance and trait association, a biplot analysis was performed based on the method of Kwon and Torrie (1964) which enabled the evaluation of 46 tomato genotypes and the identification of ten best-performers for further crossing.

The selected three testers, seven lines, and their resulting 21 hybrids were further analyzed using the line × tester mating design to estimate the general combining ability (GCA), and specific combining ability (SCA) as outlined by Cox and Pearson (1962) and Anushma et al. (2018). This analysis is also used for the identification of underlying genetic components, and the nature of gene action (additive vs. non-additive). The variance ratio of GCA to SCA was used to interpret the predominance of gene action for each trait. All these statistical computations were conducted using RStudio version 2022.12.0 employing the Agricolae package (RStudio team, 2020) for ANOVA and combining ability analysis.

Results

Evaluation of tomato genotypes

Highly significant variations ($p < 0.01$) were identified across all the evaluated traits as shown in *Table 1*. The biplot analysis effectively illustrated the performance of different genotypes for yield and quality-related parameters. Genotypes G32, G42, and G46 exhibited the greatest deviation from the origin for fruit yield and fruit shape, indicating their superior potential for these traits. Similarly, genotypes G32, G31, and G25 exhibited the longest OP distance for key fruit characteristics such as fruit diameter, fruit length, and individual fruit weight, showcasing their potential in these parameters. Additionally, genotype G9 excelled in the number of fruits per plant, while genotypes G18 and G19 demonstrated the highest plant height. In terms of fruit quality, genotypes G15 and G22 demonstrated the highest levels for total soluble solids, highlighting their strong potential for enhancing fruit sweetness and flavor (*Fig. 1*). Slight difference in fruit shape (FS) and color (FC) of genotypes were also identified. Genotype G18, had a round shape and yellow color, genotype 44 displayed an ellipsoid shape and orange color, G45 had a round shape and orange color, genotype 50 exhibited a flattened shape and red color, and genotype 55 had an ellipsoid shape and red fruit color. All other genotypes predominantly displayed round fruit shapes and red fruit color.

Based on genotype performance, three testers (Genotypes 32, 45, 46) and seven lines (Genotypes 18, 29, 30, 36, 37, 42, 43) were selected for hybridization. The selected testers were characterized by high yield but poor quality whereas the lines exhibited lower yield

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but good quality traits. These contrasting genotypes were chosen to create hybrids with a balance of yield and quality traits.

Correlation analysis revealed that plant height (PH) had a highly significant negative correlation with fruit diameter (FD), fruit length (FL), individual fruit weight (IFW), and fruit yield (FY). In contrast, important yield traits like FL had a significant positive correlation with FD, IFW and FY. While FD showed a highly significant positive correlation with IFW. NOF, and TSS had a significant negative correlation with FL, FD, and IFW. Finally, FY was positively correlation with FD, FL, and IFW emphasizing their collective role in determining productivity (*Fig. 2*).

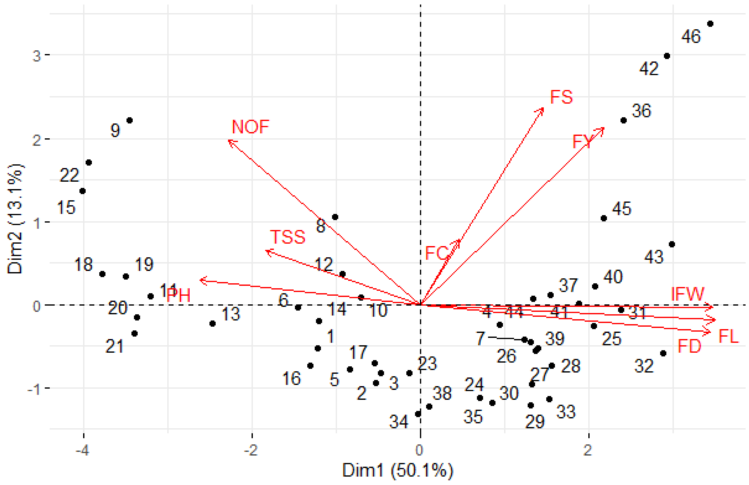

Figure 1. *Biplot analysis of morphological and yield related traits in tomato. Dim1 and 2 represent PC1 and PC2, respectively. NFP: number of fruits per plant, TSS: total soluble solids, PH: plant height, FY: fruit yield per plant, IFW: individual fruit weight, FD: fruit diameter, FL: fruit length*

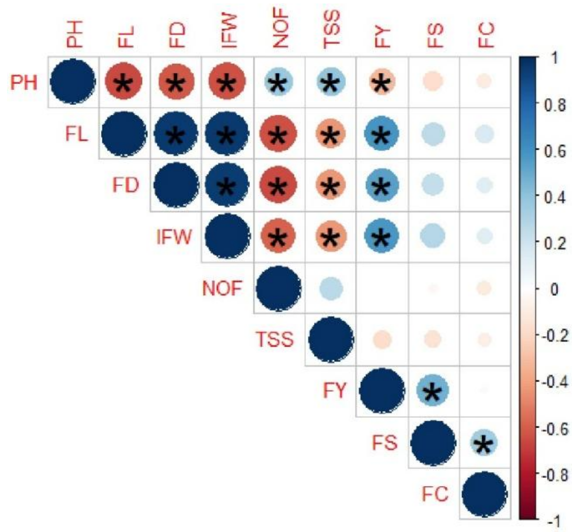

Figure 2. *Correlation analysis of morphological and yield related traits of tomatoes. The blue color represents the positive correlation, red color represents the negative correlation and (*) indicates the significance level p < 0.05. PH: plant height, FD: fruit diameter, FL: fruit length, IFW: individual fruit weight, FY: fruit yield, NOF: No. of fruits/plant, TSS: total soluble solids, FS: fruit shape and FC: fruit color*

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Table 1. *Mean square values of morphophysiological traits of tomatoes*

SOV	Df	PH	FD	FL	IFW	FY	NOF	TSS	FS	FC
Rep	2	795.1	8.4	29.0	67.9	0.27	163.1	0.3	1.205E-33	3.349E-33
Var	45	3114.9**	235.5**	354.7**	457.2**	0.33**	5265.18**	6.14**	0.19**	0.56**
Error	90	264.9	8.7	10.9	30.36	0.08	195.40	0.91	3.841E-34	1.158E-33

*, ** indicates significant differences at $p \leq 0.05$, $p \leq 0.01$ while ns indicates non-significant ($p \geq 0.05$), SOV: indicates source of variance, df: degree of freedom, PH: plant height, FD: fruit diameter, FL: fruit length, IFW: individual fruit weight, FY: fruit yield, NOF: No. of fruits/plant, TSS: total soluble solids, FS: fruit shape and, FC: fruit color

Mean performance of tomato hybrids and their parents

The hybrid $L_4 \times T_1$ showed the highest performance among all hybrids based on OP distance, recording the number of cluster/plant (55.5), number of flowers/clusters (6.9), individual fruit weight (57.2 g), fruits yield/plant (4.1 kg), and total soluble solids (10.8%). However, another hybrid $L_3 \times T_2$ also demonstrated strong performance with a fruit yield of 3.74 kg/plant, 47.21 number of clusters/plant, and the highest individual fruit weight (58.9 g) along with a round shape and red fruit color (*Table 2*).

Table 2. *Mean performance of tomato hybrids*

Hybrids	DF	CPP	FPC	DP	PH	FL	FD	IFW	NOF	TSS	FY	FS	FC
$L_1 \times T_1$	18.36	27.38	4.29	52.17	57.81	36.22	32.25	33.03	55.18	7.43	2.04	Round	Red
$L_2 \times T_1$	17.34	33.12	6.08	54.18	77.74	41.17	36.24	48.15	47.16	9.53	1.80	Round	Red
$L_3 \times T_1$	20.40	42.18	3.49	56.19	100.66	44.67	50.04	52.55	53.18	10.33	2.58	Flattened	Red
$L_4 \times T_1$	22.44	55.50	6.93	60.2	69.77	44.5	39.92	57.16	78.26	10.83	4.10	Round	Red
$L_5 \times T_1$	16.32	17.01	4.19	50.17	98.67	40.71	37.01	55.20	40.13	10.63	1.95	Round	Red
$L_6 \times T_1$	19.38	53.25	5.58	54.18	61.79	55.95	49.69	44.74	63.21	9.33	2.40	Round	Red
$L_7 \times T_1$	22.44	34.13	3.39	56.19	121.59	26.77	24.48	44.54	42.14	9.53	1.60	Round	Red
$L_1 \times T_2$	20.40	32.11	4.98	53.18	75.75	46.50	39.92	47.86	48.66	9.83	2.00	Round	Red
$L_2 \times T_2$	18.36	22.05	4.98	51.17	69.77	41.33	35.42	31.71	46.66	7.12	1.40	Round	Red
$L_3 \times T_2$	21.42	47.21	7.08	58.19	74.75	44.17	39.75	58.90	68.73	10.53	3.74	Round	Red
$L_4 \times T_2$	16.32	41.17	3.99	49.16	76.74	36.06	31.66	fi36.63	66.72	8.83	2.10	Round	Red
$L_5 \times T_2$	19.38	37.15	4.98	57.19	77.74	40.09	32.69	48.61	47.66	9.33	1.90	Round	Red
$L_6 \times T_2$	18.36	57.28	6.78	53.18	68.77	52.13	44.76	56.92	50.67	9.83	2.83	Round	Red
$L_7 \times T_2$	20.40	43.49	3.69	57.19	86.71	35.26	29.79	39.66	56.69	9.83	1.96	Round	Red
$L_1 \times T_3$	17.34	30.10	3.99	52.17	62.79	44.29	37.31	55.33	46.66	10.23	2.20	Ellipsoid	Red
$L_2 \times T_3$	20.40	38.15	5.98	54.18	79.73	44.03	34.16	49.33	39.63	9.13	1.85	Ellipsoid	Red
$L_3 \times T_3$	21.42	44.19	4.98	54.18	69.77	41.74	40.03	52.33	69.73	8.33	3.32	Round	Red
$L_4 \times T_3$	16.32	28.09	2.99	53.18	61.79	36.02	30.14	43.17	66.22	9.13	2.62	Round	Red
$L_5 \times T_3$	19.38	39.16	5.98	55.18	72.76	36.90	29.58	59.76	56.69	10.74	3.20	Round	Red
$L_6 \times T_3$	18.36	55.27	6.98	51.17	74.75	53.79	47.10	41.04	81.57	9.13	3.19	Ellipsoid	Red
$L_7 \times T_3$	26.52	46.41	4.19	55.18	79.73	35.12	26.18	37.22	58.70	9.63	1.94	Ellipsoid	Red

DF: Days to flowering, CPP: No. of clusters/plant, FPC: No. of flowers/cluster, DP: No. of days to 1st picking, PH: Plant height (cm), FL: Fruit length (mm), FD: Fruit diameter (mm), IFW: Individual fruit weight (g), NOF: No. of fruits/plant, TSS: Total soluble solids (%), FY: Fruit yield/plant (kg)

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Among the parental lines, L7 recorded the highest value for DF, and L6 was superior in CPP, while in case of IFW, and fruit yield, L3 and F5 and F6 outperformed the remaining lines. Among the testers, T2 and T3 outperformed in most of the studied traits (*Table 3*).

Table 3. *Mean performance of tomato hybrids*

Parents		DF	CPP	FPC	DP	PH	FL	FD	IFW	NOF	TSS	FY	FS	FC
Lines	L1	18.76	29.96	4.46	52.68	65.89	42.48	36.61	45.56	50.5	9.25	2.08	Round	Red
	L2	18.76	31.21	5.74	53.36	76.26	42.32	35.39	43.2	44.78	8.68	1.68	Ellipsoid	Orange
	L3	21.15	44.68	5.23	56.38	82.27	43.68	43.41	54.77	64.3	9.86	3.22	Flattened	Red
	L4	18.42	33.36	4.5	54.36	69.89	38.99	34.02	45.14	70.87	9.22	2.94	Round	Red
	L5	18.42	31.21	5.1	54.36	83.61	39.36	33.2	54.7	48.48	10.33	2.35	Round	Red
	L6	18.76	55.45	6.52	53.02	68.9	54.14	47.34	47.73	65.58	9.53	2.81	Ellipsoid	Red
	L7	23.2	41.48	3.8	56.38	96.65	32.49	26.91	40.61	52.86	9.76	1.83	Round	Red
Testers	T1	19.59	34.05	4.82	54.93	84.56	41.57	38.65	47.78	54.54	9.56	2.35	Round	Red
	T2	19.29	40.2	5.26	54.36	76.26	42.36	36.4	45.91	55.48	9.43	2.27	Round	Red
	T3	20.03	40.34	5.06	53.79	72.1	41.84	35.05	48.47	60.29	9.57	2.62	Ellipsoid	Red

Some hybrids like $L_5 \times T_3$ and $L_3 \times T_1$ showed favorable performance for traits like DF, DP, TSS, and IFW but exhibited relatively low OP distance. Long OP vector in biplot indicates greater variation for that specified trait and genotypes with a greater OP distance are considered better performers for that specified trait. TSS had a short vector length suggesting the less variation among hybrids for that trait. In contrast, hybrids such as $L_6 \times T_2$, $L_6 \times T_1$ and $L_6 \times T_3$ performed well for FPC, NOF, FD, and FL with high OP distance while $L_3 \times T_3$ showed low performance with less OP distance. All other hybrids positioned on the negative side of the biplot were considered poor about the traits studied (*Fig. 3*).

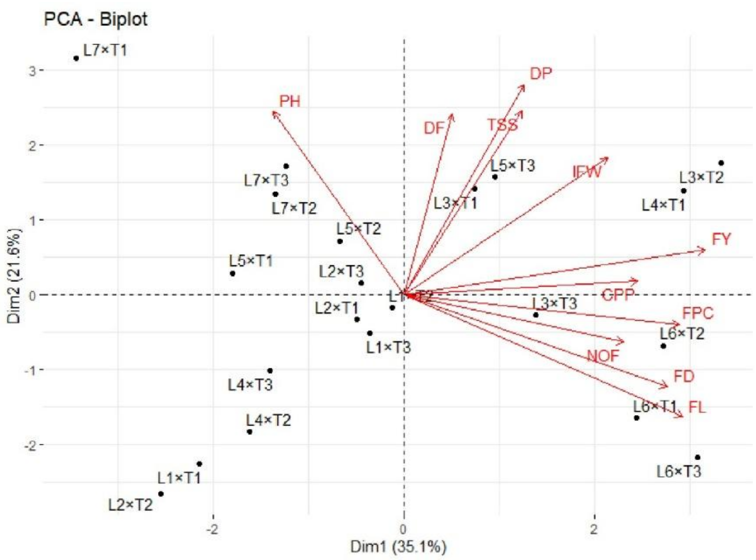

Figure 3. *Biplot analysis of morphological and yield-related traits in tomato hybrids. Dim1 and 2 represent PC1 and PC2, respectively. PH: plant height, DF: days to first flowering, DP: days to 1st picking, TSS: total soluble solids, IFW: individual fruit weight, FY: fruit yield/plant, CPP: number of clusters/plant, FPC: number of flowers/cluster, NOF: number of fruits/plant, FD: Fruit diameter FL: Fruit length*

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Evaluation of the F_1 population and proportional contribution of lines and testers in variance

Significant variations were observed in the mean square values of both parents, and hybrids. Analysis of variance revealed that mean square values for all traits showed significant differences among crosses for all the traits except FC. This indicates substantial genetic variability among the breeding materials for yield and quality-related traits. The parental genotypes also differed significantly for all the studied traits except DP. However, lines × testers interaction was significant for all the characters except FC highlighting the presence of specific combining ability effects across most traits. Similarly, the crosses also showed significant differences for all the traits except one trait FC while lines were significant only for CPP, FL, and FD. While in the case of parent vs crosses and testers, non-significant variations were identified (*Table 4*).

In total variance, testers had contributed less as compared to lines for several traits like FPC, DP, PH, FL, FD, IFW, NOF, TSS, FY, and FC which were 2.18%, 3.05%, 12.61%, 0.24%, 4.45%, 1.73%, 4.5%, 0.39%, 4.21%, and 16.28%, respectively. While, in total variance, testers have a greater contribution compared with lines for DF (49.39%), CPP (71.28%), and FS (18.18%). The higher contribution of line × tester to the total variance was identified in the case of the number of days to first flowering (49.07%), number of flowers/cluster (51.87%), number of days to first harvesting/picking (69.84%), individual fruit weight (60.52%), total soluble solids (71.5%), fruit shape (66.67%), and fruit color (59.69%) (*Table 4*).

Table 4. *General combining ability of the lines and testers*

Parents	DF	CPP	FPC	DP	PH	FL	FD	IFW	NOF	TSS	FY	FS	FC
Lines													
Bumper	-0.874	-8.202	-0.579	-1.672	-11.675	0.554	-0.085	-1.823	-6.225	-0.262	-333.824	0.048	0.127
NBH-149	-0.874	-6.960	0.683	-1.003	-1.376	0.395	-1.303	-4.168	-11.911	-0.831	-731.826	0.048	0.238
NBH-204	1.506	6.462	0.186	2.007	4.604	1.744	6.698	7.363	7.487	0.338	798.619	0.381	-0.095
Super special	-1.214	-4.812	-0.547	0.000	-7.689	-2.921	-2.670	-2.242	14.008	-0.295	522.414	-0.286	-0.095
BH-327	-1.214	-6.960	0.052	0.000	5.933	-2.547	-3.483	7.293	-8.232	0.807	-67.602	-0.286	-0.095
HT-001	-0.874	17.2	1.448	-1.338	-8.685	12.175	10.605	0.336	8.758	0.005	391.299	0.048	-0.095
38113	3.546	3.273	-1.244	2.007	18.889	-9.400	-9.761	-6.760	-3.884	0.239	-579.081	0.048	0.016
Tester													
Nadir	-0.049	-4.127	-0.228	0.573	6.882	-0.355	1.941	0.394	-2.213	0.034	-62.087	0.000	-0.048
TO-1057	-0.0340	1.999	0.213	0.000	-1.376	0.439	-0.292	-1.476	-1.280	-0.081	-139.244	-0.286	0.143
TAI-14-6242	0.389	2.128	0.014	-0.573	-5.505	-0.084	-1.649	1.082	3.493	0.047	201.330	0.286	-0.095

DF: Days to flowering, CPP: No. of clusters/plant, FPC: No. of flowers/cluster, DP: No. of days to 1st picking, PH: Plant height (cm), FL: Fruit length (mm), FD: Fruit diameter (mm), FW: Individual fruit weight (g), NOF: No. of fruits/plant, TSS: Total soluble solids (%), FY: Fruit yield/plant (kg)

Estimation of general and specific combining ability (GCA, SCA) of lines, testers and hybrids

The results of general combining ability effects indicated that HT-001 (L_6) and NBH-204 (L_3) both were identified as good general combiners for traits like CPP, FL, FY, and FD due to high positive GCA values. However, for the traits like PH, NOF, TSS, and FY only NBH-204 (L_3) had high GCA values compared with other lines. Super special (L_4) also showed the highest positive GCA value for FY, confirming its potential as a promising parent for improved yield traits. Whine NBH-149 (L_2) had high negative GCA values for 40% of studied traits suggesting limited suitability as a combiner. Among the testers, TAI-14-6242 (T_3) showed the highest values of GCA for yield related traits like

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FY, NOF, and CPP, while Nadir (T_1) and TO-1057 (T_2) showed negative GCA values for most of the studied traits (*Table 5*). Overall, from the parents, two lines and one tester were identified as good general combiners.

***Table 5.** Estimation of specific combining ability of hybrids*

Hybrids	DF	CPP	FPC	DP	PH	FL	FD	IFW	NOF	TSS	FY	FS	FC
$L_1 \times T_1$	-0.291	1.643	0.095	-0.908	-14.523	-5.760	-6.186	-12.772	7.229	-1.772	21.489	-0.333	-0.175
$L_2 \times T_1$	-1.311	6.141	0.627	0.430	-4.888	-0.652	-0.974	4.692	4.888	0.904	178.891	-0.333	-0.286
$L_3 \times T_1$	-0.631	1.778	-1.466	-0.573	12.055	1.496	4.821	-2.435	-8.490	0.535	-567.861	1.333	0.048
$L_4 \times T_1$	4.129	1.376	2.153	5.447	-6.550	5.997	4.072	9.780	10.072	0.268	1218.821	0.000	0.048
$L_5 \times T_1$	-1.991	-9.966	-0.636	-4.587	8.733	1.834	1.979	0.285	-5.815	0.366	-340.573	0.000	0.048
$L_6 \times T_1$	0.729	2.114	-0.635	0.764	-13.526	2.345	0.564	-3.221	0.272	-0.135	-340.241	-0.333	0.048
$L_7 \times T_1$	-0.631	-3.086	-0.139	-0.573	18.699	-5.260	-4.277	3.671	-8.156	-0.166	-170.525	-0.333	0.270
$L_1 \times T_2$	2.040	0.250	0.351	0.669	11.675	3.725	3.721	3.928	-0.225	0.750	59.709	-0.048	0.302
$L_2 \times T_2$	0.000	-11.09	-0.911	-2.007	-4.604	-1.283	0.436	-9.880	3.454	-1.391	-146.279	-0.048	0.524
$L_3 \times T_2$	0.680	0.686	1.680	2.007	-5.600	0.202	-3.229	5.778	6.130	0.950	665.366	-0.381	-0.143
$L_4 \times T_2$	-1.700	5.920	-0.678	-5.017	8.685	-3.240	-1.954	-6.883	-2.398	-0.220	-699.689	0.286	-0.143
$L_5 \times T_2$	1.360	4.041	-0.280	3.010	-3.939	0.420	-0.111	-4.435	0.779	-0.822	-308.343	0.286	-0.143
$L_6 \times T_2$	0.000	0.014	0.118	0.334	1.709	-2.263	-2.129	10.826	-13.201	0.483	162.206	-0.048	-0.143
$L_7 \times T_2$	-2.380	0.148	-0.280	1.003	-7.926	2.439	3.267	0.665	5.461	0.249	267.029	-0.048	-0.254
$L_1 \times T_3$	-1.749	-1.893	-0.447	0.239	2.848	2.035	2.464	8.844	-7.004	1.022	-81.198	0.381	-0.127
$L_2 \times T_3$	1.311	4.918	0.285	1.577	9.492	1.934	0.539	5.188	-8.342	0.487	-32.612	0.381	-0.238
$L_3 \times T_3$	-0.049	-2.464	-0.214	-1.433	-6.455	-1.698	-1.592	-3.343	2.360	-1.485	-97.505	-0.952	0.095
$L_4 \times T_3$	-2.429	-7.296	-1.475	-0.430	-2.136	-2.757	-2.118	-2.897	-7.674	-0.048	-519.132	-0.286	0.095
$L_5 \times T_3$	0.631	5.925	0.916	1.577	-4.793	-2.254	-1.868	4.150	5.036	0.456	648.917	-0.286	0.095
$L_6 \times T_3$	-0.729	-2.128	0.517	-1.099	11.818	-0.083	1.564	-7.605	12.929	-0.348	178.035	0.381	0.095
$L_7 \times T_3$	3.011	2.938	0.419	-0.430	-10.773	2.822	1.010	-4.336	2.695	-0.083	-96.505	0.381	-0.016

DF: Days to flowering, CPP: No. of clusters/plant, FPC: No. of flowers/cluster, DP: No. of days to 1st picking, PH: Plant height (cm), FL: Fruit length (mm), FD: Fruit diameter (mm), FW: Individual fruit weight (g), NOF: No. of fruits/plant, TSS: Total soluble solids (%), FY: Fruit yield/plant (kg)

The cross combination of $L_7 \times T_2$, $L_4 \times T_1$, $L_1 \times T_2$, $L_2 \times T_3$, $L_5 \times T_3$, $L_3 \times T_2$, and $L_6 \times T_2$ showed high positive SCA values for the yield-related traits like the CPP, FD, FL, IFW, NOF, and FY except for one quality trait, TSS. While $L_4 \times T_2$ showed the highest negative SCA value for FY, following $L_3 \times T_1$ and $L_4 \times T_3$. $L_4 \times T_3$ and $L_3 \times T_3$ had negative SCA values for all the studied traits except FC for $L_4 \times T_3$ and FC, NOF for $L_3 \times T_3$ (*Table 6*).

Genetic components for yield and quality-related traits

The female parent (line) had the highest covariance for PH (64.3), FD (40.999), NOF (71.1) and FY (230678.8) while the male parents (tester) had the highest covariance value for the CPP (76.26), and PH (18.3) (*Table 7*). The dominance genetic variance showed a major contribution for the traits such as number of clusters/plants, plant height, individual fruit weight, number of fruits/plant, and fruit yield.

The variance of GCA (σ^2GCA) was identified as lower than the variance of SCA (σ^2SCA) which indicates the effect of non-additive gene action for studied traits that support heterosis breeding (*Table 7*). High dominance genetic variance was identified as compared to additive genetic variance for most of the studied traits. These results were supported by the ratio of the variances of general and specific combining ability (σ^2GC/σ^2SCA) which is below unity except for fruit color. For fruit color, the additive gene played a significant role because of the higher value of σ^2GC/σ^2SCA ratio than unity. Therefore, it is identified that the inheritance of studied traits was under the influence of non-additive gene effects except for fruit color.

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***Table 6.** Estimation of genetic components for yield and quality-related traits in tomato*

Genetic components	DF	CPP	FPC	DP	PH	FL	FD	IFW	NOF	TSS	FY	FS	FC
Cov. H.S. (line)	-0.578	7.204	0.357	-0.655	64.3	37.6	40.999	5.925	71.1	-0.076	230678.8	-0.064	-0.0044
Cov. H.S. (tester)	1.684	76.26	-0.144	-0.927	18.3	-1.94	1.317	-8.49	-2.5	-0.147	-15730.2	0.031	0.0062
Cov. H.S. (average)	0.087	5.75	0.016	-0.097	5.5	2.537	2.955	-0.048	4.9	-0.013	15359.4	-0.003	2.76e-05
Cov. F.S. (average)	5.295	131.44	1.341	2.792	249.8	47.44	57.595	56.408	145.9	0.6006	526195.4	0.345	0.0119
F = 0, Additive genetic variance:	0.347	23.02	0.066	-0.387	22.1	10.15	11.819	-0.191	19.5	-0.0534	61437.5	-0.0109	0.0001
F = 1, Additive genetic variance:	0.174	11.51	0.033	-0.194	11.1	5.075	5.909	-0.095	9.73	-0.027	30718.73	-0.0054	5.51e-05
F = 0, Variance due to dominance:	9.918	76.74	2.661	11.22	285.4	28.76	27.045	140.59	161.0	2.037	664440.5	0.67	0.0039
F = 1, Variance due to dominance:	4.959	38.37	1.331	5.610	142.6	14.38	13.523	70.292	80.5	1.019	332220.2	0.335	0.00195
σ^2GCA	0.103	27.923	0.003	-0.848	32.13	9.916	13.222	-4.166	19.633	-0.125	61333.33	0.003	0.003
σ^2SCA	4.94	38.375	1.33	5.622	142.71	14.381	13.523	70.297	80.5	1.017	328876.7	0.337	0.002
σ^2GCA/σ^2SCA	0.021	0.728	0.002	-0.151	0.225	0.69	0.978	-0.059	0.244	-0.123	0.186	0.009	1.367

DF: Days to flowering, CPP: Number of clusters/plant, FPC: Number of flowers/cluster, DP: Number of days to 1st picking, PH: Plant height (cm), FL: Fruit length (mm), FD: Fruit diameter (mm), FW: Individual fruit weight (g), NOF: No. of fruits/plant, TSS: Total soluble solids (%), FY: Fruit yield/plant (kg), σ^2GCA is for variance due to general combining ability, σ^2SCA is for variance due to specific combining ability

***Table 7.** Mean square values of and proportional contribution of parents and F_1 populations of tomatoes against studied traits*

	Df	DF	CPP	FPC	DP	PH	FL	FD	IFW	NOF	TSS	FY	FS	FC
Replications	2	163.8	212.6	0.0069	62.93	223.86	6.068	3.56	46.78	21.50	0.287	2.6e + 04	0.043	0.38
Treatments	30	14.3**	281.9**	3.622**	16.56	519.3**	120.2**	131.4**	160.5**	352.2**	1.958**	1.2e + 06**	0.93**	0.3**
Parents	9	6.8**	188.4**	1.66**	4.80	258.5*	85.78**	93.99**	61.2**	206.4**	0.57**	7.2e + 05**	0.97**	1.26**
Parents vs. crosses	1	0.08	0.3356	0.0516	0.668	5.40	0.405	0.298	0.49	2.86	0.17	1.5e + 01	0.443	1.15
Crosses	20	18.3**	338.1**	4.685**	22.6**	662.3**	141.7**	154.81**	213.2**	435.2**	2.67**	1.6e + 06**	0.94**	0.2
Lines (L)	6	2.8	268.4*	7.174	20.47	1028.9	382.6**	410.34**	268.42	888.7	2.503	3.15e + 06	0.476	0.16
Testers (T)	2	30.1	803.5	1.024	6.903	835.4	3.42	69.01	36.8	196.7	0.105	6.7e + 05	1.714	0.33
Lines × testers	12	14.9**	117.1**	4.05**	26.4**	450.2**	44.27**	41.35**	215.1**	248.2**	3.18**	9.9e + 05**	1.05**	0.204
Error	60	0.08	1.974	0.059	9.535	22.07	1.126	0.78	4.21	6.7	0.129	3.37e + 03	0.04	0.198
Proportional contribution														
Contribution of lines (%)		1.54	7.94	45.94	27.11	46.6	81.01	79.51	37.76	61.25	28.1	58.04	15.15	24.03
Contribution of testers (%)		49.39	71.28	2.18	3.05	12.61	0.24	4.45	1.73	4.5	0.39	4.21	18.18	16.28
Contribution of L × T (%)		49.07	20.78	51.87	69.84	40.78	18.74	16.02	60.52	34.22	71.5	37.74	66.67	59.69

*, ** indicates significant differences at $p \leq 0.05$, $p \leq 0.01$ while ns indicates non-significant ($p \geq 0.05$), DF: Days to flowering, CPP: No. of clusters/plant, FPC: No. Of flowers/cluster, DP: No. of days to 1st picking, PH: Plant height (cm), FL: Fruit length (mm), FD: Fruit diameter (mm), FW: Individual fruit weight (g), NOF: No. of fruits/plant, TSS: Total soluble solids (%), FY: Fruit yield/plant (kg)

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Discussion

Tomato yield and quality are complex traits influenced by a combination of plant vegetative growth and development factors. Parameters such as fruit weight, number of fruits/plant, fruit length, and fruit diameter are major contributors to final yield (Yan et al., 2001). In the current study, the performance of forty-six tomato genotypes was evaluated under field conditions revealing highly significant variation in traits such as Plant height (PH), fruit shape (FS), fruit color (FC), total soluble solids (TSS), fruit length (FL), fruit diameters (FD), number of fruits (NOF), individual fruit weight (IFW), and fruit yield (FY) (*Table 1*). These findings are consistent with previous findings of Mohamed et al. (2018) which also identified significant differences for PH, NOF, TSS and FY. Variations in morphological traits such as fruit shape and color are likely influenced by both genotypic differences (Narasimhamurthy and Gowda, 2013) and environmental factors (Gautam et al., 2018b), indicating the importance of multi-environment testing. Some genotypes such as G18, G19, G11, and G20 showed high plant height compared to other genotypes based on OP) distance in the biplot (*Fig. 1*) but exhibited lower yield due to reduced number of fruits, fruit diameter, fruit length, and individual fruit weight. The traits have a high distance from the origin, indicating a high OP distance. Those genotypes which have high OP distance, are the best-performing genotypes for that specified trait. Correlation studies were performed to find out the association of traits (Narolia et al., 2012). Genotypes G45, and G46 exhibited high yield as compared to other varieties because of the high number of fruits/plant, fruit weight, fruit length, and fruit diameter. These results correlate with the findings of Manna and Paul (2012) who reported that yield-contributing traits like fruit weight and size significantly influence tomato productivity. The ability of these genotypes to produce high yields indicates the presence of better alleles that could be used in breeding programs.

Plant height tends to increase while fruit diameter, fruit length, and individual fruit weight decrease due to a significant negative correlation among these traits (Hasan et al., 2021) (*Fig. 2*). Specifically, plant height shows a strong negative correlation with fruit diameter, fruit length, individual fruit weight, and overall fruit yield. Genotypes G36, G40, G42, G43, G45, and G46 exhibited higher fruit diameter and length compared to other genotypes, which contributed to higher yield due to their strong positive correlation with individual fruit weight and total fruit yield (Hasan et al., 2021). Similar negative correlations between plant height and yield-related traits were also reported by Jilani et al. (2013). Conversely, Souza et al. (2012) observed a significant positive correlation between the number of clusters per plant (CPP) and fruit yield (FY), supporting the potential for effective selection strategies to enhance yield (Ara et al., 2009). These positive associations among yield-contributing traits suggest the possibility of achieving yield improvement (Tasisa et al., 2012). Although some genotypes demonstrate high individual fruit weight (IFW), they have fewer fruits per plant, resulting in lower yields. In contrast, genotypes with smaller fruit weights but higher fruit counts often achieve higher total yields. Independent traits such as plant height, fruit diameter, and fruit length play distinct roles in plant improvement and maintaining fruit quality (Haydar et al., 2007). Significant genetic variability in yield-related traits among tomato genotypes, consistent with these findings, was also confirmed by Al-Aysh et al. (2012).

To improve complex traits like fruit quality and yield, the knowledge of combining abilities of parents, their crosses, their genetic components and gene action is necessary

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for breeders (Singh and Asati, 2011). In current study, non-additive gene action was predominantly observed aligning with previous findings that reported the presence of non-additive gene action in tomatoes for the traits like lycopene contents and vitamin C (Gautam et al., 2018a). Both additive and non-additive gene actions play significant roles in determining the yield and fruit quality emphasizing the need for balanced breeding strategies (Joshi and Kohli, 2006). Among the evaluated lines, L_6 and L_3 were identified as strong general combiners due to high positive GCA values. Notably, L3 showed superior GCA values as compared to other lines across multiple traits suggesting its potential as a reliable parent in breeding programs. López et al. (2012) also identified similar results which indicate, the positive GCA values of a line for polar diameter, average fruit weight, fruit weight per plant, number of fruits per plant and yield. These data also consistent with the findings of Kumar et al. (2013). High GCA values are useful for selecting parents with stable performance across environments.

In terms of specific combining ability, several hybrids demonstrated trait specific superiority. The cross $L_3 \times T_1$ exhibited the highest SCA value for fruit yield (FY) indicating its potential for enhancing productivity. Similarly, the hybrid $L_4 \times T_2$ showed elevated SCA values for fruit length (FL) and plant height (PH) while $L_5 \times T_3$ displayed superior SCA values for individual fruit weight (IFW), making a promising candidate for breeding work focused on increasing fruit size. SCA effects indicate the best cross combinations (Chishti et al., 2008). The ratio of GCA/SCA variance being less than one showed the importance of non-additive variance as compared to additive variance for all traits except FS. Our data correspond with the findings of Farzane et al. (2012) and Pandey et al. (2006). The non-additive gene actions indicate that the genotypes should be used for hybrid development that should contain improved traits.

Combining these genotypes with others having resistance to abiotic and biotic stress will lead to improved hybrids (Cebolla-Cornejo et al., 2013). The incorporation of genes controlling the yield traits can aid in marker-assisted selection. This method is very fast and reliable in developing better hybrids with improved traits (Liu et al., 2024).

Conclusions

Good general combiners play a crucial role in producing high-quality, high-yielding hybrids. In this study, parents L4, L6, and T3 emerged as strong general combiners, particularly for yield-related traits, indicating their potential as core parental lines in tomato breeding programs. These can be used to develop a base population with improved additive gene effects. Among the hybrids evaluated, such as $L_4 \times T_1$, $L_3 \times T_2$, and $L_5 \times T_3$, were identified as excellent specific combiners for fruit yield, while $L_2 \times T_1$ and $L_1 \times T_3$ were notable for total soluble solids (TSS) and fruit size (FS). These crosses combine non-additive effects with important traits from parents, making them suitable candidates for commercial hybrid development. Interestingly, the hybrids that showed poor combining ability for plant height (PH), a trait negatively correlated with yield, are considered favorable as reduced plant height may indirectly benefit yield potential through better source partitioning. The predominance of non-additive gene action for most traits except fruit color further supports the suitability of heterosis breeding in enhancing the tomato performance. The findings provide clear direction for tomato breeding programs aiming to enhance fruit yield, sweetness, and market traits. Plant breeders can achieve both short-term commercial and long-term genetic improvement by selecting high GCA parents for foundational breeding and exploiting high SCA crosses for hybrid release.

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APPENDIX

List of 46 genotypes

Sr. No.	Genotype name	Sr. No.	Genotype name
G1	17863	G24	T-10 F_1
G2	17873	G25	T-20 F_1
G3	17902	G26	Mehran-670
G4	17903	G27	AALA-F_1
G5	19289	G28	Goto
G6	19844	G29	Super special
G7	19852	G30	Bumper
G8	19850	G31	R10 Grande
G9	19888	G32	Nadir
G10	19891	G33	Naqeeb
G11	19898	G34	Four Seasons
G12	19903	G35	UGTH-1806
G13	19892	G36	NBH-149
G14	19893	G37	BH-327
G15	19897	G38	NBH-313
G16	19899	G39	NIAB-Gohar
G17	19900	G40	NBH-148
G18	38113	G41	NIAH Jauhar
G19	19905	G42	NBH-204
G20	19907	G43	HT-001
G21	19912	G44	NBH-5
G22	38036	G45	TO-1057
G23	LA-3847	G46	TAI-14-6242

The germplasm was collected from the Germplasm Plant Genetic Resources Institute, National Agricultural Research Centre Islamabad. From genotypes 1-22 were pure lines while the genotypes from 23-46 were the advanced genotypes that were to be tested for multilocation trials in different areas of Pakistan

List of tomato lines, testers and hybrids

Sr. No.	Names of lines and testers	Abbreviation	Sr. No.	Names of hybrids	Abbreviations
	Lines		5	BH-327 × Nadir	$L_5 \times T_1$
1	Bumper	L_1	6	HT-001 × Nadir	$L_6 \times T_1$
2	NBH-149	L_2	7	38113 × Nadir	$L_7 \times T_1$
3	NBH-204	L_3	8	Bumper × TO-1057	$L_1 \times T_2$
4	Super special	L_4	9	NBH-149 × TO-1057	$L_2 \times T_2$
5	BH-327	L_5	10	NBH-204 × TO-1057	$L_3 \times T_2$
6	HT-001	L_6	11	Super special × TO-1057	$L_4 \times T_2$
7	38113	L_7	12	BH-327 × TO-1057	$L_5 \times T_2$
	Testers		13	HT-001 × TO-1057	$L_6 \times T_2$
1	Nadir	T_1	14	38113×TO-1057	$L_7 \times T_2$
2	TO-1057	T_2	15	Bumper × TAI-14-6242	$L_1 \times T_3$
3	TAI-14-6242	T_3	16	NBG-149 × TAI-14-6242	$L_2 \times T_3$
Sr. No.	**Names of hybrids**	**Abbreviations**	17	NBH-204 × TAI-14-6242	$L_3 \times T_3$
1	Bumper × Nadir	$L_1 \times T_1$	18	Super special × TAI-14-6242	$L_4 \times T_3$
2	NBG-149 × Nadir	$L_2 \times T_1$	19	BH-327 × TAI-14-6242	$L_5 \times T_3$
3	NBH-204 × Nadir	$L_3 \times T_1$	20	HT-001 × TAI-14-6242	$L_6 \times T_3$
4	Super special × Nadir	$L_4 \times T_1$	21	38113 × TAI-14-6242	$L_7 \times T_3$

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