Research Article Electronic Journal of Plant Breeding, Vol.17(4):

Combining ability and gene action analysis for fruit yield and associated traits in hot pepper (*Capsicum annuum* L.) using a Line × Tester mating design

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https://doi.org/10.37992/2026.1704.048

Abstract

Combining ability analysis is an effective methodology for selecting superior parents and crosses for hybrid development in hot pepper (*Capsicum annuum* L.). The present experiment was undertaken to assess general combining ability (GCA), specific combining ability (SCA) and nature of gene action governing fruit yield and associated traits. A total of 72 F_1 hybrids were produced by crossing eight testers with nine elite lines in a Line × Tester mating design. The hybrids along with their 17 parents were evaluated in a randomized complete block design with three replications in three environments (Bengaluru, Munugudu and Satthanapalle) during *kharif* 2025-2026. The combined analysis of variance indicated significant ($P \leq 0.01$) effect of environment for all the studied traits indicating considerable genetic variability and differential genotypic responses across environments. Line × Tester analysis identified several parents with good GCA effects for fruit yield and associated traits. Significant positive SCA effects for fruit yield per plant were observed in the hybrids H17, H65, H8, H67 and H55 indicating the importance of specific parental combinations for the exploitation of heterosis. The relative importance of SCA variance over GCA variance for all the studied traits indicated the major role of non-additive gene action in trait inheritance. The superior general combiners and promising hybrids identified in the present study provide valuable genetic resources for the breeding of high-yielding commercial hot pepper hybrids and future breeding programmes.

Keywords: *Capsicum annuum*, combining ability, gene action, hybrid breeding, Line × Tester.

INTRODUCTION

Hot pepper (*Capsicum annuum* L.) is one of the most important vegetable and spice crops and belongs to the family Solanaceae (Lata *et al.,* 2023). It is commonly cultivated in the tropical and subtropical regions for its culinary, nutritional and medicinal importance. The fruits are rich in vitamins A and C, carotenoids, phenolic compounds and capsaicinoids and are important for fresh consumption, processing, pharmaceutical applications and food industry (Tarinta *et al.,* 2023). Intensified breeding efforts are required to develop high-yielding hybrids with superior fruit quality and wider adaptability, due to increasing demand for hot pepper. Hybrid breeding has been found an effective strategy for improvement of yield and other economic important traits in hot pepper. The success of a hybrid breeding programme depends largely on the identification of genetically superior parents with good combining ability (Sprague and Tatum, 1942). Line × Tester analysis developed by Kempthorne (1957) is one of the most reliable mating designs for estimation of general combining ability (GCA) and specific combining ability (SCA) for parental performance evaluation. GCA mainly represents additive gene action, while SCA indicates non-additive gene action, which is important for exploiting heterosis (Griffing, 1956). Recent studies have reported the preponderance of non-additive gene action for fruit yield and associated traits in chilli which highlights the need for identification of superior parental combinations for hybrid development (Deepthi *et al.,* 2024; Komala *et al.,* 2024; Saengarun *et al.,* 2025). Hence, the present investigation was undertaken to estimate the combining ability of selected parental lines, to identify the promising cross combinations and to elucidate the nature of gene

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How to cite this artilce: Basavaraj Kodihalli, Gopal Wasudeo Narkhede and Shabir H. Wani. 2026. Combining ability and gene action analysis for fruit yield and associated traits in hot pepper (*Capsicum annuum* L.) using a Line × Tester mating design. *Electronic Journal of Plant Breeding,* **17**(4): doi:10.37992/2026.1704.048

Received: 26.07.2026 **Accepted**: 28.10.2026 **Online**: 31.10.2026

action governing fruit yield and its contributing traits in hot pepper using Line × Tester mating design.

MATERIALS AND METHODS

The experimental material comprised of nine elite lines (L1-L9) and eight testers (T1-T8) of hot pepper from the breeding programme of Agroisia Seeds Pvt. Ltd., Bengaluru, Karnataka, India (**Table 1**). The parents were crossed during the *kharif* 2025-2026 following a Line × Tester mating design as suggested by Kempthorne (1957) and 72 F_1 hybrids were developed. The 72 F_1 hybrids along with 17 parents and 3 checks (Armour, Jini-2626 & Navtej) were evaluated in Randomized Complete Block Design (RCBD) with three replications at diverse locations *viz;* E1 – Bengaluru; E2 – Munugudu, E3 – Satthanapalle during *kharif* 2025-2026. Recommended agronomic and plant protection practices were followed uniformly across all genotypes to ensure healthy and vigorous crop growth with plot size of 1.5 x 3.5 ft. Observations were recorded in five randomly selected competitive plants per plot on days to 50% flowering, fruit length (cm), fruit diameter (mm), stalk length (cm), fresh fruit weight (g), number of seeds per fruit, plant height (cm), number of branches per plant and fruit yield per plant (g). The mean data recorded across the three environments were subjected to combined analysis of variance to estimate the effects of environment, genotype and genotype × environment interaction.

General combining ability (GCA) and specific combining ability (SCA) effects were estimated using the Line × Tester method of Kempthorne (1957). The nature of gene action controlling the inheritance of the studied traits was inferred from the relative magnitudes of GCA and SCA variances following the concepts of Sprague and Tatum (1942) and Griffing (1956). All statistical analyses were performed using RStudio (Posit Team, 2025).

RESULTS AND DISCUSSION

The combined analysis of variance revealed significant differences among genotypes and environments for all nine traits evaluated across three environments (**Table 2**), indicating substantial genetic variability and environmental influence on trait expression. The genotype × environment (G × E) interaction was significant for days to 50% flowering and fruit yield per plant but non-significant for the remaining traits. This suggests that flowering time and fruit yield were more sensitive to environmental variation, emphasizing the importance of evaluating promising hybrids across different growing conditions. Shumbulo *et al.* (2018) reported significant genetic variation and combining ability effects in hot pepper evaluated across six environments in Ethiopia. Similarly, Lata *et al.* (2023) demonstrated the importance of combining ability analysis for green fruit yield and associated traits in chilli under wet temperate conditions. The present findings further highlight the need to consider environmental responses when selecting superior hybrids for fruit yield.

The general combining ability (GCA) analysis revealed significant differences among parental lines and testers for fruit yield and associated traits (**Table 3**). Among the lines, L2 recorded the highest positive GCA effect for fruit yield per plant (209.19), followed by L1 (189.14), L8 (146.57), L9 (119.33), L3 (112.09) and L4 (77.87). Among the testers, T8 exhibited the highest positive GCA effect (217.50), followed by T1 (120.09) and T2

Table 1. List of genotypes used in the present study and their sources

S.No.	Genotypes	Source name	Source code	Collected from
1	L1	2402038	AHP-001	Agroisia Seeds Pvt. Ltd. Bengaluru, Karnataka
2	L2	2402062	AHP-002	
3	L3	2402084	AHP-003	
4	L4	2402106	AHP-004	
5	L5	2402110	AHP-005	
6	L6	2402206	AHP-006	
7	L7	2402164	AHP-007	
8	L8	2402500	AHP-008	
9	L9	2402516	AHP-009	
10	T1	2402002	AHP-010	
11	T2	2402006	AHP-011	
12	T3	2402043	AHP-012	
13	T4	2402059	AHP-013	
14	T5	2402066	AHP-014	
15	T6	2402108	AHP-015	
16	T7	2402216	AHP-016	
17	T8	2402233	AHP-017	

Table 2. Combined analysis of variance (ANOVA) for fruit yield and associated traits of hot pepper evaluated across three environments

Source	Df	Days to 50% flowering	Fruit length	Fruit diameter	Stalk length	Fresh fruit weight	Number of seeds per fruit	Plant height	Number of branches per plant	Fruit yield per plant
ENV	2	5112.54**	11.55**	0.11**	0.01*	5.25**	5211.91**	1548.94**	107.38**	257185.12**
ENV:REP	6	2.44	9.16**	13.17**	0.93**	3.76**	1081.77**	580.05**	0.84	36948.74**
GEN	91	444.79**	16.33**	14.81**	0.91**	37.11**	2406.95**	1542.66**	6.25**	509888.35**
ENV:GEN	182	38.46**	0.01	0.0003	0.0001	0.01	1.83	22.57	0.42	81056.44**
Residuals	546	2.64	0.01	0.0024	0.0010	0.01	2.57	25.78	0.44	119.88

*, ** Significant at 5% and 1%, respectively

Table 3. General combining ability (GCA) effects of lines and testers for yield and contributing traits in hot pepper

Parents	Days to 50% flowering	Fruit length	Fruit diameter	Stalk length	Fresh fruit weight	Number of seeds per fruit	Plant height	Number of branches per plant	Fruit yield per plant
Lines									
L1	2.77 **	0.06 **	0.01	0.02 **	0.19 **	-4.80 **	-3.84 **	-0.75 **	189.14 **
L2	7.29 **	-0.74 **	0.22 **	-0.09 **	-0.45 **	-0.44 **	-3.64 **	-0.41 **	209.19 **
L3	-3.54 **	0.78 **	0.33 **	-0.04 **	1.69 **	-7.77 **	1.27 *	-0.35 **	112.09 **
L4	-3.14 **	0.32 **	0.42 **	-0.01 *	-0.58 **	4.53 **	-12.54 **	0.62 **	77.87 **
L5	-1.86 **	-1.03 **	0.36 **	-0.09 **	-0.30 **	3.75 **	2.09 **	0.12	29.08 **
L6	-1.71 **	-0.25 **	-0.45 **	0.20 **	-0.29 **	11.36 **	11.15 **	-0.05	-60.62 **
L7	2.99 **	-0.47 **	-0.75 **	0.14 **	-0.66 **	1.01 **	3.15 **	0.25 **	-25.98 **
L8	1.02 **	-0.39 **	-0.57 **	-0.13 **	-0.80 **	-6.87 **	-2.18 **	0.03	146.57 **
L9	-3.81 **	1.72 **	0.44 **	-0.00 ns	1.21 **	-0.77 **	4.53 **	0.56 **	119.33 **
SE±	**0.309**	**0.021**	**0.011**	**0.003**	**0.022**	**0.233**	**0.833**	**0.115**	**1.404**
CD @ 5%	**0.606**	**0.041**	**0.022**	**0.007**	**0.043**	**0.458**	**1.632**	**0.224**	**2.752**
CD @ 1%	**0.798**	**0.054**	**0.029**	**0.009**	**0.057**	**0.602**	**2.148**	**0.295**	**3.623**
Testers									
T1	-2.48 **	0.40 **	1.21 **	-0.14 **	1.33 **	10.14 **	1.83 **	0.03 ns	120.09 **
T2	3.71 **	-0.17 **	-1.29 **	-0.05 **	-1.36 **	-12.54 **	7.77 **	0.28 **	110.85 **
T3	-1.17 **	-0.69 **	-0.18 **	0.02 **	-0.85 **	-6.90 **	-7.75 **	0.06 ns	-58.49 **
T4	-2.57 **	-0.43 **	-0.55 **	0.01 *	-0.96 **	-4.15 **	-3.87 **	-0.26 **	-94.22 **
T5	2.31 **	0.94 **	0.80 **	0.26 **	1.32 **	5.47 **	-0.57	0.16 *	1.67
T6	-0.82 **	-0.61 **	-0.77 **	-0.10 **	-0.93 **	7.20 **	-5.36 **	-0.34 **	-63.54 **
T7	2.80 **	0.54 **	0.26 **	0.01 **	0.18 **	1.03 **	6.54 **	-0.05	-12.15 **
T8	-1.78 **	0.02	0.52 **	0.00	1.28 **	-0.25	1.41 *	0.11	217.50 **
SE±	**0.291**	**0.020**	**0.011**	**0.003**	**0.021**	**0.220**	**0.785**	**0.108**	**1.324**
CD @ 5%	**0.571**	**0.039**	**0.021**	**0.006**	**0.041**	**0.431**	**1.539**	**0.212**	**2.595**
CD @ 1%	**0.752**	**0.051**	**0.027**	**0.008**	**0.053**	**0.568**	**2.025**	**0.279**	**3.415**

*, ** Significant at 5% and 1%, respectively

(110.85). These parents may serve as useful genetic resources for developing high-yielding hybrids. Lata *et al.* (2023) identified DPChMS 9-2 as a promising general combiner for marketable green fruit yield in chilli, while Rizvi *et al.* (2025) reported trait-specific differences in combining ability for morphological, biochemical and yield-related characteristics in chilli. These findings support the importance of selecting parents based on their combining ability for targeted breeding objectives.

Considerable variation was also observed in GCA effects for individual yield components. L9 exhibited favourable effects for fruit length (1.72), fruit diameter (0.44), plant height (4.53) and number of branches per plant (0.56), whereas L3 recorded a positive effect for fresh fruit weight (1.69). L4 showed desirable effects for number of seeds per fruit (4.53) and branches per plant (0.62). Among the testers, T5 was a promising general combiner for fruit length (0.94), fruit diameter (0.80), stalk length (0.26), fresh fruit weight (1.32) and seeds per fruit (5.47). T1 also exhibited favourable effects for fresh fruit weight (1.33) and seeds per fruit (10.14). For days to 50% flowering, significant negative GCA effects were recorded for L9 (-3.81), L3 (-3.54), L4 (-3.14), T4 (-2.57), T1 (-2.48) and T8 (-1.78), indicating their usefulness for improving early flowering. Notably, L9 and T8 combined favourable effects for flowering time and fruit yield. Siddappa *et al.* (2019) identified promising general combiners for earliness and green fruit yield in chilli, supporting the value of trait-specific parental selection. However, early flowering does not necessarily indicate early fruit maturity. The specific combining ability (SCA) analysis identified several promising hybrid combinations for fruit yield and associated traits (**Table 4**). H17 recorded the highest significant positive SCA effect for fruit yield per plant (489.28), followed by H65 (435.08), H8 (341.34), H67 (306.26) and H55 (284.39). These results indicate favourable specific interactions between parental combinations, suggesting the importance of non-additive genetic effects in fruit yield expression. Malavika *et al.* (2025) reported predominantly non-additive gene action for most traits in cytoplasmic-genic male sterility-based chilli hybrids and identified promising combinations based on combining ability and *per se* performance. Similarly, Janaki *et al.* (2017) reported greater SCA than GCA variance for fruit yield per plant and several associated traits in chilli. The present results support the potential of exploiting heterosis, although superior SCA effects

Table 4. Top five cross combinations exhibiting significant specific combining ability (SCA) effects in the desirable direction for yield and contributing traits in hot pepper

Trait	Rank 1	Rank 2	Rank 3	Rank 4	Rank 5
Days to 50% flowering	H8 (2402038 × 2402233) (-12.75**)	H50 (2402164 × 2402006) (-11.03**)	H16 (2402062 × 2402233) (-8.13**)	H23 (2402084 × 2402216) (-7.11**)	H71 (2402516 × 2402216) (-6.85**)
Fruit length	H10 (2402062 × 2402006) (2.50**)	H33 (2402110 × 2402002) (2.19**)	H7 (2402038 × 2402216) (1.76**)	H19 (2402084 × 2402043) (1.41**)	H25 (2402106 × 2402002) (1.41**)
Fruit diameter	H8 (2402038 × 2402233) (1.96**)	H55 (2402164 × 2402216) (1.39**)	H70 (2402516 × 2402108) (1.37**)	H41 (2402206 × 2402002) (1.34**)	H9 (2402062 × 2402002) (1.27**)
Stalk length	H63 (2402500 × 2402216) (0.78**)	H4 (2402038 × 2402059) (0.76**)	H43 (2402206 × 2402043) (0.68**)	H49 (2402164 × 2402002) (0.56**)	H69 (2402516 × 2402066) (0.53**)
Fresh fruit weight	H24 (2402084 × 2402233) (7.48**)	H25 (2402106 × 2402002) (2.51**)	H7 (2402038 × 2402216) (2.18**)	H8 (2402038 × 2402233) (1.99**)	H10 (2402062 × 2402006) (1.73**)
Number of seeds per fruit	H22 (2402084 × 2402108) (36.13**)	H9 (2402062 × 2402002) (24.72**)	H3 (2402038 × 2402043) (23.92**)	H49 (2402164 × 2402002) (19.74**)	H69 (2402516 × 2402066) (18.09**)
Plant height	H4 (2402038 × 2402059) (42.25**)	H10 (2402062 × 2402006) (24.21**)	H17 (2402084 × 2402002) (24.03**)	H48 (2402206 × 2402233) (20.68**)	H13 (2402062 × 2402066) (16.15**)
Number of branches per plant	H49 (2402164 × 2402002) (1.29**)	H57 (2402500 × 2402002) (1.20**)	H9 (2402062 × 2402002) (1.17**)	H11 (2402062 × 2402043) (1.17**)	H45 (2402206 × 2402066) (1.05**)
Fruit yield per plant	H17 (2402084 × 2402002) (489.28**)	H65 (2402516 × 2402002) (435.08**)	H8 (2402038 × 2402233) (341.34**)	H67 (2402516 × 2402043) (306.26**)	H55 (2402164 × 2402216) (284.39**)

*, ** Significant at 5% and 1%, respectively

Table 5. Estimates of genetic variance components, GCA and SCA variances, and the nature of gene action for yield and contributing traits in hot pepper

Characteristics	Lines	Tester	Lines x Tester	σ2 gca	σ2 sca	σ2 gca / σ2 sca	Gene action
Days to 50% flowering	26.78	11.86	61.36	0.36	36.97	0.01	Non additive
Fruit length	36.99	17.57	45.44	0.03	1.00	0.03	Non additive
Fruit diameter	13.16	43.07	43.78	0.02	0.82	0.03	Non additive
Stalk length	10.48	12.32	77.21	0.00	0.10	0.00	Non additive
Fresh fruit weight	18.53	32.24	49.23	0.05	2.34	0.02	Non additive
Number of seeds per fruit	14.56	22.55	62.90	1.59	182.55	0.01	Non additive
Plant height	20.82	14.20	64.98	1.14	153.59	0.01	Non additive
Number of branches per plant	23.15	4.92	71.92	0.00	0.67	0.00	Non additive
Fruit yield per plant	31.36	22.96	45.68	719.57	28927.72	0.02	Non additive

alone do not establish high absolute yield or commercial superiority.

Among the yield-contributing traits, H10 exhibited the highest positive SCA effect for fruit length (2.50), H8 for fruit diameter (1.96), H63 for stalk length (0.78), H24 for fresh fruit weight (7.48), H22 for seeds per fruit (36.13), H4 for plant height (42.25) and H49 for branches per plant (1.29). For days to 50% flowering, H8 recorded the highest significant negative SCA effect (-12.75), followed by H50 (-11.03), H16 (-8.13), H23 (-7.11) and H71 (-6.85). H8 was particularly promising because it combined desirable SCA effects for early flowering, fruit diameter and fruit yield. Istiqlal *et al.* (2018) investigated combining ability for yield-related traits in big- and curly-fruited chilli lines, while Sahid *et al.* (2020) examined combining ability and heterotic effects for yield components and capsaicin content in chilli pepper. These studies demonstrate the importance of identifying hybrid combinations suited to specific breeding objectives. Nevertheless, the promising crosses identified here require further evaluation for mean performance, heterosis and adaptability.

The variance component analysis revealed that SCA variance exceeded GCA variance for all nine traits (**Table 5**), indicating the predominance of non-additive genetic effects in the evaluated population. For fruit yield per plant, SCA variance (28927.72) was considerably higher than GCA variance (719.57), with a GCA/SCA ratio of approximately 0.02. Similar trends were observed for days to 50 % flowering (0.36 and 36.97), seeds per fruit (1.59 and 182.55) and plant height (1.14 and 153.59). The GCA/SCA ratios ranged from approximately 0.00 to 0.03 across traits, with values reported as 0.00 reflecting rounding of very small estimates. The relative contributions of lines, testers and line × tester interactions to fruit yield per plant were 31.36, 22.96 and 45.68 %, respectively. Line × Tester interactions also contributed substantially to stalk length (77.21 %), branches per plant (71.92 %), plant height (64.98 %) and seeds per fruit (62.90 %). These findings further indicate the importance of specific parental combinations in determining hybrid performance. However, the predominance of SCA variance does not independently distinguish dominance from epistatic effects.

The predominance of non-additive genetic effects agrees with Janaki *et al.* (2017) and Malavika *et al.* (2025), who reported substantial non-additive genetic contributions to yield and associated traits in chilli. However, Komala *et al.* (2024) observed higher SCA variance for most traits except fruit yield per plant in chilli hybrids. In contrast, Patil *et al.* (2018) reported predominantly additive gene action for most traits in chilli, with non-additive effects for flowering-related characters. These differences may be associated with variations in parental genetic backgrounds, mating designs and experimental conditions. Thus, the predominance of non-additive effects observed in the present investigation should be interpreted in relation to the evaluated breeding population rather than generalized to all chilli germplasm.

Overall, L2 and T8 were identified as promising general combiners for fruit yield, while L9, L3, L4, T5 and T1 contributed favourable effects for several yield-related traits. Among the hybrids, H17, H65, H8, H67 and H55 exhibited superior positive SCA effects for fruit yield per plant, with H8 also showing desirable effects for early flowering and fruit diameter. The predominance of SCA variance and the substantial contribution of line × tester interactions indicate that heterosis breeding may be a useful strategy for improving fruit yield and associated traits in hot pepper. Further, multi-environment evaluation of the promising hybrids for *per se* performance, standard heterosis, fruit quality and yield stability is necessary before their commercial potential can be established.

Significant environmental, genotypic, and genotype × environment interaction effects, coupled with substantial genetic variability, were observed among the parental lines and hybrids for fruit yield and its associated traits in hot pepper. The parents L2, L1, L8, L9, T8, T1 and T2 were identified as superior general combiners for fruit yield and other desirable traits. The hybrids H17, H65, H8,

H67 and H55 showed significant specific combining ability for fruit yield per plant. The predominance of non-additive genetic effects across all the studied traits indicated the potential of exploiting heterosis through superior parental combinations for improving fruit yield and associated traits in hot pepper. The identified superior combiners and promising hybrids can be effectively utilized for commercial hybrid development and future breeding programmes for improvement of productivity and yield related traits.

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