



RESEARCH ARTICLE

# Analysis of combining ability and gene action for yield and fruit quality traits in cherry tomato: A step toward genetic improvement

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## Abstract

The analysis of gene action revealed the predominance of non-additive gene action in governing almost all traits, suggesting the potential for exploiting hybrid vigour and the development of hybrids for trait improvement. A half diallel mating design was employed in cherry tomato (*Solanum lycopersicum* L. var. *cerasiformae*), involving five parents and resulting in ten cross combinations (excluding reciprocals). Diallel analysis enables the assessment of general combining ability (GCA) for individual parental lines and facilitates the identification of hybrids exhibiting superior specific combining ability (SCA). Significant variation was observed among the genotypes for all examined traits based on the analysis of variance (ANOVA), indicating substantial genetic diversity. Based on overall mean performance and general combining ability evaluations, the genotypes Punjab Red Cherry and Punjab Sona Cherry emerged as superior, highlighting their suitability as parental lines for hybrid development. Moreover, the hybrids, namely Solan Red Round × Punjab Sona Cherry, Pusa Cherry Tomato-1 × Punjab Sona Cherry and Punjab Red Cherry × Punjab Kesar Cherry, exhibited superior performance based on mean values and specific combining ability, identifying them as promising combinations for further breeding efforts. Therefore, these cross combinations should be evaluated at multiple locations before being recommended for commercial cultivation.

**Keywords:** combining ability; cross combinations; half diallel; hybrids; gene action

## Introduction

Cherry tomato (*Solanum lycopersicum* L. var. *cerasiformae*), an annual herbaceous plant belonging to the Solanaceae family, has a chromosome number of  $2n = 24$  and is considered the ancestor of all cultivated tomatoes (1, 2). Originating in the tropical and subtropical regions of the Americas, it was subsequently introduced and cultivated in the tropical zones of Asia and Africa (3). It is a warm-season crop that is widely cultivated in the hotter climates of Arizona and other western regions. The fruit is classified as a berry and grows in clusters that range from the size of a thumb tip to that of a golf ball and can be spherical or oblong (4, 5). In 2020, worldwide production of cherry tomatoes reached 186.821 MMT from an area of 5051983 ha (3). Cherry tomatoes are rich in carbohydrates, protein, calcium, iron and vitamins A, C, E, K (Alpha Tocopherol), B<sub>6</sub>, as well as in phosphorus, copper, potassium and manganese (6, 7). They act as blood purifiers and possess antiseptic and antioxidant properties against intestinal infections (8, 9). Cherry tomatoes are ideal for making sauces, soups, ketchup, purées, curries, pastes, powders, rasams and sandwiches. Additionally, they are used to prepare

tomolive and tomatine, which have greater industrial value (10). Cherry tomatoes have many valuable traits related to their genetic diversity, which is useful for selecting parent material and holds great potential in breeding programs (11). Furthermore, they serve as a germplasm source for inducing disease resistance and adaptability to abiotic stress. Their potential value can be enhanced by evaluating them under diverse agro-climatic conditions (12). Hybrid breeding in cherry tomatoes has initially and subsequently improved both productivity and fruit quality.

Diallel analysis is a bio-statistical tool widely used to estimate genetic parameters related to combining ability as well as gene action which influence yield and quality related traits, providing information on epistasis, the average degree of dominance and other gene activities to identify superior hybrid combinations (13, 14). Hybrids offer higher yields, early maturity, uniformity and other advantageous traits; therefore, exploiting combining ability and gene action has become important for cherry tomato breeding (15). For developing F<sub>1</sub> hybrids, selecting the appropriate parents for crossing is essential. It is chosen based on their combining ability, as the expression of heterosis is significantly correlated with the overall

combining ability of the crop (16). A half diallel mating design was adopted to evaluate the general combining ability (GCA) of the lines due to additive gene action and to identify cross combinations (excluding reciprocals) with high specific combining ability (SCA) values that are indicative of the presence of non-additive gene action (17–19). Due to limited research on cherry tomatoes in our country, this work aims to fill this gap by identifying superior genotypes for use in a hybridisation program and superior cross combinations that can be further evaluated across multiple locations before release (20). Additionally, this method helps to determine gene action by measuring the influence of genes (additive as well as non-additive) on the inheritance of phenotypic traits, which aids in designing an effective breeding strategy for crop improvement (21, 22).

## Materials and Methods

The study was conducted at the experimental facility of the Regional Horticultural Research and Training Station (RHR and TS), located in Jachh, Kangra district. The experimental site has a subtropical climate, with warm, rainy summers (average 29.3 °C) and dry winters (average 13.6 °C), receiving approximately 1500 mm of annual rainfall. The soil varies from clay loam to sandy loam with a neutral pH of 6.8–7.0. The cultivation of cherry tomato was managed in alignment with the standard agronomic practices outlined by Dr Yashwant Singh Parmar University of Horticulture and Forestry, Nauni, Solan. The crossing was carried out around 35 days post-transplanting, once the plants had entered the initial flowering phase and developed two to three flower clusters. Emasculation and pollination were done manually. Five diverse cherry tomato cultivars/lines, namely Pusa Cherry Tomato-1 (P<sub>1</sub>), Solan Red Round (P<sub>2</sub>), Punjab Red Cherry (P<sub>3</sub>), Punjab Kesar Cherry (P<sub>4</sub>) and Punjab Sona Cherry (P<sub>5</sub>), were crossed in a half diallel design (excluding reciprocals) to obtain ten cross combinations. The seedlings of the parents were raised in February 2023 and subsequently transplanted in the main field in March 2023 to attempt crosses and generate F<sub>1</sub>S. The sources of the parents and the standard check variety are depicted in Table 1. Data were collected for various morphological and quality traits, including days to first flowering (DTFF), days to marketable maturity (DMM), average fruit weight (AFW in g), number of fruits per cluster (NFPC), number of fruit clusters per plant (NFCPP), harvest duration (HD in days), number of fruits per plant (NFPP), fruit yield per plot (FYPP in kg), plant height (PH, cm), number of locules per fruit (NLFP), pericarp thickness (PT in mm), total soluble solids (TSS in °B) and ascorbic acid content (AA). Combining ability analyses were conducted based on Eisenharts' framework, utilising model I (fixed effects) and model II (random effects), following the systematic methodology outlined (23).

## Results and Discussion

The analysis of variance (ANOVA) showed that the parental

genotypes evaluated in this study displayed statistically significant differences across all measured traits, indicating genetic variability among the genotypes in the half-diallel cross design (excluding reciprocals) that aligned with the findings of (24). The ANOVA for combining ability partitions genetic variation into GCA and SCA. Highly significant ( $p < 0.001$ ) GCA and SCA effects demonstrated that both additive and non-additive gene actions affect the inheritance of most traits, reflecting a complex genetic framework (25). GCA points to the effectiveness of selection for trait enhancement, whereas SCA highlights the importance of particular parental crosses in maximising hybrid vigour. The gene action analysis also revealed the dominance of non-additive gene action for several quantitative and qualitative traits, further suggesting the potential to exploit heterosis for crop improvement programs.

### Effect of general and specific combining ability

Identifying general and specific combining ability effects gives an idea about the selection of superior parental lines and cross combinations where lines that demonstrate desirable general combining ability effects can be used as parents in a hybridization program, while superior cross combinations with strong specific combining ability can undergo further evaluation at multiple locations and be compared to standard check varieties before being released as a hybrid (26, 27). The diallel method of analysis was utilised to identify superior parental lines and cross combinations. Traits related to earliness that show significantly negative or positive GCA or SCA effects for the parents and crosses are classified as good or poor combiners, respectively (28). Whereas traits other than earliness that show significantly positive or negative GCA or SCA effects for the parents and crosses are considered good or poor combiners.

### Identification of good general combiners

#### Quantitative traits

The parents exhibiting good, poor and average general combining ability effects have been depicted in Table 1–2. For days to first flowering, Punjab Red Round (-1.807) and Punjab Sona Cherry (-1.250) were identified as desirable general combiners based on their statistically significant negative GCA effects. In contrast, Solan Red Round (2.590), Pusa Cherry Tomato-1 (0.400) and Punjab Kesar Cherry (0.066) were classified as poor combiners due to significantly positive GCA effects. Research indicates that negative and significant effects of GCA on earliness traits were noticed from the previous research (29–32). Such effects are desirable in breeding programs aiming for early-maturing genotypes, which are essential for avoiding late-season stresses and enhancing cropping system flexibility. The consistency of our findings with earlier studies suggests a shared genetic basis across diverse germplasm, highlighting the reliability of additive variance in selecting for earliness. All five parental lines failed to exhibit notable, significantly negative GCA effects for the trait days to marketable maturity.

**Table 1.** General combining ability effects of several quantitative traits

Traits Parents	DTFF	DMM	AFW	NFPC	NFCPP	HD
P <sub>1</sub>	0.400*	2.311*	1.041*	0.083*	0.685*	0.302*
P <sub>2</sub>	2.590*	2.308*	1.375*	0.574*	0.224*	1.682*
P <sub>3</sub>	-1.807*	1.467*	0.102*	-0.046	1.187*	-0.047
P <sub>4</sub>	0.066	0.117	0.927*	0.174*	0.575*	0.572*
P <sub>5</sub>	-1.250*	1.581*	1.387*	0.711*	0.298*	1.365*

\*significance at 0.05 % level, P<sub>1</sub> = Pusa Cherry Tomato-1, P<sub>2</sub> = Solan Red Round, P<sub>3</sub> = Punjab Red Cherry, P<sub>4</sub> = Punjab Kesar Cherry, P<sub>5</sub> = Punjab Sona Cherry, DTFF = days to first flowering, DMM = days to marketable maturity, AFW = Average fruit weight (g), NFPC = number of fruits per cluster, NFCPP = number of fruit clusters per plant, HD = Harvest duration.

**Table 2.** General combining ability effects of several quantitative and qualitative traits

Traits Parents	NFPP	FYPP	PH	NLFP	PT	TSS	AA
P <sub>1</sub>	11.280*	0.594*	14.276*	-0.040*	0.125*	0.032	0.226*
P <sub>2</sub>	-3.037*	2.067*	4.848*	-0.0118	0.045*	-0.508*	-0.174*
P <sub>3</sub>	3.327*	0.469*	10.962*	-0.083*	0.088*	0.366*	2.427*
P <sub>4</sub>	-6.403*	0.679*	18.200*	0.103*	0.099*	-0.270*	-1.879*
P <sub>5</sub>	-5.166*	1.514*	10.038*	0.031*	0.070*	0.380*	-0.601*

\*Significance at 0.05 % level, P<sub>1</sub> = Pusa Cherry Tomato-1, P<sub>2</sub> = Solan Red Round, P<sub>3</sub> = Punjab Red Cherry, P<sub>4</sub> = Punjab Kesar Cherry, P<sub>5</sub> = Punjab Sona Cherry, NFPP = number of fruits per plant, FYPP = fruit yield per plot (kg), PH = plant height (cm), NLFP = number of locules per fruit, PT = pericarp thickness (mm), TSS = total soluble solids (°B), AA = ascorbic acid content.

However, four of the lines were identified as poor combiners. For harvest duration, four parental lines, namely Solan Red Round (1.682), Punjab Sona Cherry (1.365), Punjab Kesar Cherry (0.572) and Pusa Cherry Tomato-1 (0.302) were considered best general combiners as they showed significantly positive effects for GCA. All the parental lines, namely, Punjab Kesar Cherry (18.200), Pusa Cherry Tomato-1 (14.276), Punjab Red Cherry (10.962), Punjab Sona Cherry (10.038) and Solan Red Round (4.848) for plant height, were classified as good general combiners as they all showed significant and positive GCA effects. For average fruit weight also all parents, specifically Punjab Sona Cherry (1.387), Solan Red Round (1.375), Pusa Cherry Tomato-1 (1.041), Punjab Kesar Cherry (0.927) and Punjab Red Cherry (0.102), were classified as good general combiners as they all exhibited significantly positive general combining ability (GCA) effects.

GCA effect estimates for the number of fruits per cluster showed that four parental lines, specifically Punjab Sona Cherry (0.711), Solan Red Round (0.574), Punjab Kesar Cherry (0.174) and Pusa Cherry Tomato-1 (0.083), were considered as best general combiners as they exhibited significantly positive GCA effects. All parents, namely Punjab Red Cherry (1.187), Pusa Cherry Tomato-1 (0.685), Punjab Kesar Cherry (0.575), Punjab Sona Cherry (0.298) and Solan Red Round (0.224), were classified as good general combiners for the number of fruit clusters per plant as they all exhibited significantly positive GCA effects. Only two parents among five exhibited significantly positive GCA effects for the number of fruits per plant and were considered good combiners. Significant and negative GCA effects for the number of locules per fruit were recorded for parents, specifically Punjab Red Cherry (-0.083) and Pusa Cherry Tomato-1 (-0.040) and considered good combiners. Significantly positive GCA effects of pericarp thickness among all the parental lines, specifically Pusa Cherry Tomato-1 (0.123), Punjab Kesar Cherry (0.99), Punjab Red Cherry (0.88), Punjab Sona Cherry (0.70) and Solan Red Round (0.45) were found and classified as good general combiners. For yield per plot, all the parental lines, namely Solan Red Round (2.067), Punjab Sona Cherry (1.514), Punjab Kesar Cherry (0.679), Pusa Cherry Tomato-1 (0.594) and Punjab Red Cherry (0.469) exhibited significantly positive GCA effects and were considered as good

general combiners. Comparable positive and statistically significant outcomes for multiple quantitative traits were reported, thereby supporting the findings of the present study (15, 31–37).

#### Qualitative traits

Three parental lines, specifically Punjab Sona Cherry (0.380), Punjab Red Cherry (0.366) and Pusa Cherry Tomato-1 (0.032), exhibited significantly positive effects of GCA for total soluble solids and were considered good combiners. The significant and positive effects of GCA, specifically in Punjab Red Cherry (2.427) and Pusa Cherry Tomato-1 (0.226), have been revealed, highlighting its ability to enhance ascorbic acid content. GCA can be effectively utilised in hybridisation programs to develop superior hybrids. Research has demonstrated consistent findings on the qualitative trait expression (34, 36, 38, 39).

#### Identification of good specific combiners

##### Quantitative traits

Table 3–4 presents data on the crosses regarding their specific combining ability for both quantitative and qualitative traits. Eight cross combinations demonstrated significant negative SCA effects for days to first flowering, with the maximum observed in Solan Red Round × Punjab Sona Cherry (-4.094), which are considered good specific combiners. Similarly, the crosses Solan Red Round × Punjab Sona Cherry (-5.20), Solan Red Round × Punjab Kesar Cherry (-2.23) and Punjab Red Cherry × Punjab Kesar Cherry (-2.057) were categorized as favorable specific combiners for days to marketable maturity, as evidenced by their significantly negative specific SCA effects, suggesting their potential contribution to early maturing hybrids. Negative and statistically significant SCA effects associated with earliness traits have similarly been documented (40–43). For the trait of harvest duration, six crosses showed significant positive SCA effects (maximum found in Punjab Kesar Cherry × Punjab Sona Cherry (2.935). For plant height, six crosses were classified as good specific combiners based on their significant positive SCA effects (maximum in Punjab Cherry Tomato-1 × Punjab Sona Cherry (17.397). Significant positive SCA effects of five crosses for average fruit weight, classifying them as good specific combiners (maximum

**Table 3.** Specific combining ability effects of several quantitative traits

Traits Crosses	DFFF	DMM	AFW	NFPC	NFCPP	HD
P <sub>1</sub> × P <sub>2</sub>	-3.525*	1.027*	-0.281*	-0.829*	-3.295*	0.681*
P <sub>1</sub> × P <sub>3</sub>	-2.348*	2.076*	0.355*	-0.524*	2.624*	0.967*
P <sub>1</sub> × P <sub>4</sub>	-0.444*	2.279*	1.307*	1.871*	2.495*	-0.841*
P <sub>1</sub> × P <sub>5</sub>	-1.238*	0.196	2.070*	-0.681*	-0.821*	-0.491*
P <sub>2</sub> × P <sub>3</sub>	-1.318*	1.138*	-1.867*	-0.033	-0.837*	1.810*
P <sub>2</sub> × P <sub>4</sub>	-2.078*	-2.231*	0.528*	0.195*	-0.186	-0.666*
P <sub>2</sub> × P <sub>5</sub>	-4.094*	-5.200*	1.958*	2.610*	4.498*	0.681*
P <sub>3</sub> × P <sub>4</sub>	-2.127*	-2.057*	-1.949*	-0.233*	4.957*	0.954*
P <sub>3</sub> × P <sub>5</sub>	0.523*	-0.362	-1.186*	-1.152*	3.5278	-1.476*
P <sub>4</sub> × P <sub>5</sub>	0.430*	1.099*	-1.231*	-0.557*	-0.042	2.935*

\*significance at 0.05 % level, P<sub>1</sub> = Pusa Cherry Tomato-1, P<sub>2</sub> = Solan Red Round, P<sub>3</sub> = Punjab Red Cherry, P<sub>4</sub> = Punjab Kesar Cherry, P<sub>5</sub> = Punjab Sona Cherry, DFFF = Days to first flowering, DMM = Days to marketable maturity, AFW = Average fruit weight (g), NFPC = Number of fruits per cluster, NFCPP = Number of fruit clusters per plant, HD = Harvest duration.

**Table 4.** Specific combining ability effects of several quantitative traits

Traits Crosses	NFPP	FYPP	PH	NLPF	PT	TSS	AA
P <sub>1</sub> × P <sub>2</sub>	-8.251*	-1.146*	-8.413*	-0.062	-0.223*	-0.522*	0.110
P <sub>1</sub> × P <sub>3</sub>	12.831*	1.785*	-2.937*	0.010	0.020	-0.396*	4.079*
P <sub>1</sub> × P <sub>4</sub>	-10.662*	1.247*	-19.032*	0.024	0.303*	0.793*	-0.611*
P <sub>1</sub> × P <sub>5</sub>	2.991*	3.946*	17.397*	0.095*	0.052*	-0.190*	1.083*
P <sub>2</sub> × P <sub>3</sub>	2.259*	-2.739*	6.159*	-0.019	-0.059*	0.585*	2.761*
P <sub>2</sub> × P <sub>4</sub>	6.659*	1.430*	-3.270*	-0.105*	-0.033	0.000	-0.289
P <sub>2</sub> × P <sub>5</sub>	3.195*	3.069*	4.159*	0.367*	0.413*	-0.540*	1.146*
P <sub>3</sub> × P <sub>4</sub>	5.068*	-2.172*	10.540*	-0.033	0.044*	-0.317*	-1.820*
P <sub>3</sub> × P <sub>5</sub>	-5.946*	-2.097*	-5.698*	-0.062	-0.107*	-0.414*	-0.521*
P <sub>4</sub> × P <sub>5</sub>	5.560*	-1.047*	12.873*	-0.048	0.306*	0.001	1.792*

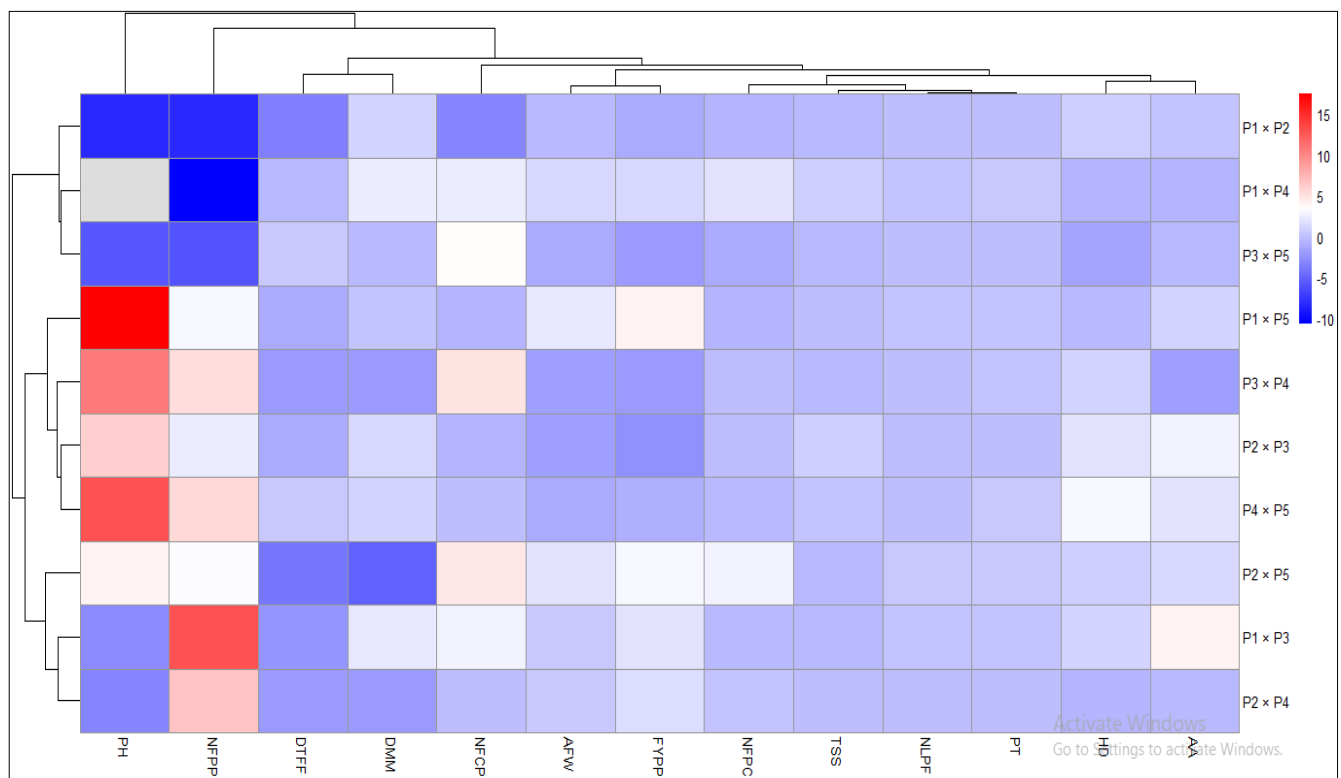
\*Significance at 0.05 % level, P<sub>1</sub> = Pusa Cherry Tomato-1, P<sub>2</sub> = Solan Red Round, P<sub>3</sub> = Punjab Red Cherry, P<sub>4</sub> = Punjab Kesar Cherry, P<sub>5</sub> = Punjab Sona Cherry, NFPP = Number of fruits per plant, FYPP = Fruit yield per plot (kg), PH = Plant height (cm), NLPF = Number of locules per fruit, PT = Pericarp thickness (mm), TSS = Total soluble solids (°B), AA = Ascorbic acid content.

recorded in Pusa Cherry Tomato- 1 × Punjab Sona Cherry (2.070). Additionally, three crosses for the number of fruits per cluster were regarded as good specific combiners (maximum SCA effects exhibited by Solan Red Round × Punjab Sona Cherry (2.610). For the number of fruit clusters per plant, four cross combinations exhibited significant positive SCA effects (maximum in Punjab Red Cherry × Punjab Kesar Cherry (4.957). Meanwhile, seven crosses for the number of fruits per plant showed a significantly positive SCA effect (maximum in Pusa Cherry Tomato-1 × Punjab Red Cherry (12.831) and were considered good specific combiners. Only one cross, specifically Solan Red Round × Punjab Kesar Cherry (-0.105) for the number of locules per fruit, along with five cross combinations for pericarp thickness (maximum Solan Red Round × Punjab Sona Cherry (0.413), exhibited significantly positive SCA effects and were regarded as good specific combiners. Lastly, five crosses showed significant positive SCA effects for yield per plot (maximum in Pusa Cherry Tomato- 1 × Punjab Sona Cherry (3.946)) and were classified as good specific combiners. Fig. 1 depicts a heat map illustrating the

SCA effects across multiple quantitative and qualitative traits. Crosses exhibiting the highest positive SCA effects are represented by red colouration, whereas those with the most negative SCA effects are indicated by dark blue hues. Significant and positive effects of SCA for several quantitative traits have been reported by, highlighting predominance of non-additive gene action in trait expression (19, 26, 44–47).

#### Qualitative traits

Qualitative traits exhibited significantly positive SCA effects for both total soluble solids and ascorbic acid content. Crosses specifically Pusa Cherry Tomato-1 × Punjab Kesar Cherry (0.793) and Solan Red Round × Punjab Red Cherry (0.58) for total soluble solids, while five cross combinations for ascorbic acid content were classified as best specific combiners and further evaluated in several locations before release as a hybrid. Statistically significant and positive SCA effects for qualitative traits have also been observed by indicating the potential contribution of non-additive gene action in their expression



**Fig. 1.** Heat map showing the specific combining ability effects of several quantitative and qualitative traits. P<sub>1</sub> = Pusa Cherry Tomato-1, P<sub>2</sub> = Solan Red Round, P<sub>3</sub> = Punjab Red Cherry, P<sub>4</sub> = Punjab Kesar Cherry, P<sub>5</sub> = Punjab Sona Cherry, DTFF = Days to first flowering, DMM = Days to marketable maturity, AFW = Average fruit weight (g), NFPC = Number of fruits per cluster, NFPCP = Number of fruit clusters per plant, HD = Harvest duration, NFPP = Number of fruits per plant, FYPP = Fruit yield per plot (kg), PH = Plant height (cm), NLPF = Number of locules per fruit, PT = Pericarp thickness (mm), TSS = Total soluble solids (°B), AA = Ascorbic acid content.

(26, 41, 43, 46–48).

### Gene action for quantitative and qualitative traits

The selection of an appropriate breeding methodology for genetic enhancement in crop species is primarily influenced by the mode of inheritance and the nature of gene action that regulates trait expression. Combining ability analysis in cherry tomato indicated the involvement of both additive and non-additive gene actions in controlling quantitative traits. Notably, the greater extent of specific combining ability (SCA) variance over general combining ability (GCA), combined with higher dominance variance ( $\sigma^2_s$ ) compared to additive variance ( $\sigma^2_g$ ), highlights the predominance of non-additive gene effects across all evaluated traits such as DTFF (0.130), DMM (0.253), AFW (0.342), NFPC (0.004), NFCPP (0.102), HD (0.421), NFPP (0.788), FYPP (0.130), plant height (0.987), NLPF (0.133), PT (0.013), TSS (0.484) and AA (0.344). For all the quantitative and qualitative traits under this study, the variance ratio ( $\sigma^2_{GCA}/\sigma^2_{SCA}$ ) was less than one, indicating a predominant influence of non-additive gene action in the inheritance of these traits as depicted in Table 5. These findings promote the use of hybrid breeding strategies to exploit heterosis for improving both quantitative and qualitative traits. The inheritance of both quantitative and qualitative traits has been predominantly attributed to non-additive genetic effects, as substantiated by prior studies conducted (21, 32, 34, 37, 38, 49).

### Conclusion

The prevalence of non-additive gene action recorded for all qualitative and quantitative traits suggested the further exploitation of heterosis to develop superior cross combinations. Punjab Red Cherry and Punjab Sona Cherry highlighted the significant potential as superior general combiners for yield and associated traits in cherry tomato. These genotypes can be effectively utilised in hybridisation programs aimed at enhancing productivity and quality attributes. Among the evaluated cross combinations, Solan Red Round  $\times$  Punjab Sona Cherry and Pusa Cherry Tomato-1  $\times$  Punjab Sona Cherry exhibited outstanding performance based on both specific combining ability (SCA) and per se values. The involvement of at least one parent with strong general combining ability in these hybrids suggests their suitability not only for hybrid development but also for the identification and selection of transgressive segregants in the early

segregating generations, thereby contributing to long-term genetic improvement. Meanwhile, the superior crosses identified based on SCA effects analysis can be further evaluated in multiple locations before being released as hybrids.

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### Authors' contributions

AK contributed to conceptualization, methodology development, formal analysis, investigation and preparation of the original draft. RP contributed to conceptualization, methodology development, software support, validation, formal analysis, investigation and preparation of the original draft. DK contributed to conceptualization, methodology development, software support, validation, formal analysis and investigation. KS contributed to software support and validation. VGS and RK contributed with the statistical approach and methodology development. All authors read and approved the final manuscript.

### Compliance with ethical standards

**Conflict of interest:** Authors do not have any conflict of interests to declare.

**Ethical issues:** None

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**Table 5.** Gene action of estimates of several quantitative and qualitative traits

Traits	$\sigma^2_{GCA}$	$\sigma^2_{SCA}$	$\sigma^2_g$	$\sigma^2_s$	$\sigma^2_g / \sigma^2_s$ (variance ratio)
DTFF	61.442	32.483	4.141	31.918	0.130
DMM	80.511	29.749	7.259	28.732	0.253
AFW	30.289	9.005	3.044	8.898	0.342
NFPC	4.595	4.534	0.020	4.610	0.004
NFCPP	12.324	8.535	4.034	39.728	0.102
HD	26.851	6.961	2.844	6.760	0.421
NFPP	1129.830	174.887	136.557	173.186	0.788
FYPP	39.893	21.012	2.700	20.811	0.130
PH	4092.248	415.492	525.776	532.179	0.987
NLPF	0.106	0.065	0.006	0.044	0.133
PT	0.210	0.193	0.002	0.189	0.013
TSS	3.205	0.761	0.349	0.722	0.484
AA	51.795	15.376	5.208	15.160	0.344

$\sigma^2_{GCA}$  = Variance due to general combining ability,  $\sigma^2_{SCA}$  = Variance due to specific combining ability,  $\sigma^2_g$  = genotypic variance,  $\sigma^2_s$  = SCA variance, DTFF = Days to first flowering, DMM = Days to marketable maturity, AFW = average fruit weight (g), NFPC = Number of fruits per cluster, NFCPP = Number of fruit clusters per plant, HD = Harvest duration, NFPP = Number of fruits per plant, FYPP = Fruit yield per plot (kg), PH = Plant height (cm), NLPF = Number of locules per fruit, PT = Pericarp thickness (mm), TSS = Total soluble solids ( $^{\circ}$ B), AA = Ascorbic acid content.

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