Heterosis and combining ability studies by line × tester analysis for fruit biochemical, morpho-physiological, and yield traits governing shelf life in tomato (Solanum lycopersicum L.)

M. P. Pavan · S. Gangaprasad · B. M. Dushyanthakumar · Nagarajappa Adivappar · P. Shashikumara

Abstract Improving tomatoes keeping quality is crucial for reducing post-harvest losses. Knowledge of heterosis, and combining ability is a prerequisite for breeding high yielding and good shelf life heterotic hybrids. An investigation was undertaken with each of 3 lines, testers, and 9 hybrids to identify desirable parents and crosses for 20 fruit biochemical, morpho-physiological, and yield traits and to elucidate the nature of gene action for shelf life and its contributing traits through line × tester analysis. The lines contributed to most of hybrids variability than testers and fruit quality traits had a higher degree of SCA variance as compared to GCA variance. pH, ascorbic acid, fruit firmness, and plant height governed by additive gene action. Lycopene, titratable acidity, TSS, calcium, magnesium, pericarp thickness, pulp content, locule number, fruit length, diameter, weight, shelf life, number of branches, number of clusters, number of fruit/cluster, and yield/plant were under the control of non-additive gene action. All the lines and Arka Saurabh were the best general combiners and IIHR 2349 × Arka Vikas, IIHR 2349 × Arka Saurabh, IIHR 2358 × Arka Ahuti and IIHR 2357 × Arka Ahuti were the best specific combiner in producing heterotic hybrids. IIHR 2349 × Arka Vikas and IIHR 2349 × Arka Saurabh were promising hybrids for high yield and shelf life. The crosses involved both parents with high, one parent with high and other with low and both parents with low good overall general combining ability status respectively indicated the additive, non-additive and epistatic gene action in fruit quality and yield traits inheritance.

Keywords Combining ability · Gene action · Heterosis · Line × tester analysis · Shelf life · Tomato

Introduction

Tomato [(Solanum lycopersicum L.), (2n = 2x = 24)], is an important solanaceous vegetable crop in the world in terms of cultivation and consumption. It is
nutritionally enriched with blood purification and anti-cancerous properties of antioxidants like lycopene, β-carotene, ascorbic acid, folic acid, phenolic acids, and flavonoids (Arab and Steck 2000; Freeman and Reimers 2011). It is a perishable vegetable with a relatively short shelf life, pre-mature ripening and softening resulted in significant post-harvest losses. The post-harvest losses of tomatoes were estimated at up to 25–42% in the world (Arah et al. 2015) and up to 50% in developing countries (Delina and Mahendran 2009).

The short shelf life of fruits is the result of improper storage, inadequate transportation, inefficient processing and preservation facilities. This leads to the occurrence of many chemical and physical changes in fruit viz., loss of weight, sugar and acid contents, respiration, softening of pulp and microbial decay greatly contribute to high post-harvest losses (Garcia et al. 2019). Consequently, huge volumes of tomatoes are sold at devalued prices and farmers get poor returns (Sinha et al. 2019). Later, this period is succeeded by the fruit scarcity period with a high price in the market and consumers will suffer (Delina and Mahendran 2009).

The post-harvest shelf life is a prerequisite for commercially grown tomatoes. Extending the shelf life of tomatoes is highly essential for profitable marketing and reduction of great losses in quality and quantity (Salliba et al. 2001), as it gives more time to farmers for marketing before fruit quality is degraded (Osei et al. 2020). Therefore, reduction of post-harvest losses is the need of the hour. Even though many post-harvest preservation methods, chemical treatments, and anti-sense RNA technology are efficient in extending the shelf life but these technologies are not sufficient, practically infeasible in farmer’s fields and they need social acceptance too. Therefore, genetic improvement of fruit quality traits seems to be the safest way to improve shelf life (Yogendra and Gowda 2013) and it is the solution of the hour.

Fruit shelf life is a ripening-related complex trait affected by several low inheritable fruit quality and yield traits. The desire for progress in crop improvement through plant breeding is propelled by a better understanding and appropriate exploitation of heterosis which is the gain in vigor on crossing two lines or varieties. Developing tomato hybrids for both yields as well as high shelf life is extremely essential to keep the tomato production and supply sustainable for the growing population in the present and near future. The hybrid performance depends on the choice of parents and parents can be selected based on per se performance, genetic diversity, combining ability, etc.

Selection of parents based on per se performance alone is not a sound procedure since superior lines identified on this basis may yield poor recombinants in the segregating generations (Garg et al. 2007). The identification of the best combiners is a prerequisite for heterosis breeding. The combining ability analysis offers a powerful tool to assess the genetic potential of parents in hybrid combination through general and specific combining abilities to produce a superior heterotic hybrid. Among many available statistical tools to detect the combining ability and gene action governing various quantitative traits, line×tester analysis has been a very useful design (Kempthorne 1957).

Genetic improvement of traits requires knowledge on the kind of gene action involved i.e., additive and dominance in the population. Therefore, success in hybrid development with desired traits hinges on the knowledge of combining ability, nature, and magnitude of gene action in different genetic backgrounds (Somraj et al. 2018). The information generated from line×tester analysis of quantitative traits helps plant breeders in planning the selection strategy and predicting the outcome of their breeding program (Mather and Jinks 1982). With this justified focus, the present study was planned and executed with twin objectives of identification of desirable parents (combiners) and crosses (combinations) for fruit quality traits and to elucidate the gene action for less pursued but very important shelf life and its contributing traits through line×tester analysis in tomato.

**Materials and methods**

**Experimental site**

The present investigation was carried out by conducting the field and lab experiments during the 2017 summer and rainy seasons at the Department of Genetics and Plant Breeding, Keladi Shivappa Nayaka University of Agricultural and Horticultural Sciences, Navule, Shivamogga (13.9739° N, 75.5791° E), Karnataka, India.
Basic genetic material

The basic material for the study consisted of parents contrasting for fruit shelf life and yield traits. The high shelf life low yielding genotypes viz., IIHR 2349, IIHR 2357, IIHR 2358, and high yielding low shelf life varieties viz., Arka Vikas, Arka Ahuti, and Arka Saurabh were used as lines and testers respectively. For comparative analysis of heterosis, ‘Arka Rakshak’, a popular public bred high yielding tomato hybrid was used as a standard check for comparison of heterosis. The lines, testers, and check hybrid were maintained and released from ICAR-Indian Institute of Horticultural Research, Bengaluru, Karnataka, India.

Development of experimental material

The crosses were affected between high shelf life low yielding lines and high yielding low shelf life testers in line×tester (3×3) mating design. The nine first filial generations were developed by pollinating the pollens from testers onto the stigmas of emasculated flowers of lines in the early morning hours (6–8 AM) in protected poly house conditions during the 2017 summer. The seeds of lines, testers, and F1’s were harvested individually which constituted the experimental material.

Evaluation of experimental material

The nine hybrids along with their parents and standard check were planted in the field during the 2017 rainy season in two separate contiguous blocks in Randomized Complete Block Design with two replications. The standard crop production and protection practices were followed to raise healthy plants and were evaluated for fruit biochemical, morpho-physiological, and yield traits governing shelf life.

Sampling of plants and collection of data

The data were recorded from five randomly selected plants avoiding border plants in each line, testers, and F1 generations (Supplementary Table I). The 20 fruit quality traits governing shelf life such as 7 fruit biochemical traits viz., TSS (%) (using Erma hand refractometer), pH (using Siemens pH meter), lycopene (mg/100 g) (Lichtenthaler 1987), ascorbic acid (mg/100 g) (2,6-Dichlorophenol indophenol method, Association of Official Analytical Chemists 2006), titratable acidity (%) (Association of Official Analytical Chemists 2000), calcium and magnesium content (mg/100 g) (di-acid digestion and ICP-OES method), 8 morpho-physiological traits viz., fruit length (cm), fruit diameter (cm) and pericarp thickness (mm) were measured with digital vernier caliper, fruit weight (g) (using digital weighing balance), fruit firmness (kg/cm²) (using fruit penetrometer), pulp content (%) (Percent ratio of weight of pulp after removing fruit juice and seed to the fruit weight), locule number (manually counted), shelf life (Days) (counted as number of days taken by fruits harvested at breaker stage kept on shelf to show first visible shrinkage on its fruit surface) and 5 yield attributing traits viz., plant height (cm) (using measuring scale), number of branches, number of clusters, number of fruit/cluster were manually counted, yield/plant (g) (using digital weighing balance) were recorded in the field during harvest. The fruit quality traits were recorded in the lab at the red ripe stage of five randomly selected tomato fruits from the plants which were earlier selected for estimating yield traits. First, the mean for each trait from five fruits in each plant was estimated then the mean of five plants of each genotype from each replication was estimated. Finally, the mean of both the replications was computed as the trait mean.

Statistical analysis

The statistical analysis was performed on the mean data recorded from five randomly selected plants from every nine hybrids along with their parents and standard check hybrid from each replication. The recorded data were analyzed with the program WINDOSTAT software. The following statistics are computed.

Analysis of variance for parents and hybrids

The data recorded in parents and hybrids for fruit quality traits in each entry of both the replications were first subjected to Analysis of Variance (ANOVA) as per the methods outlined by Panse and Sukatme (1967) (Supplementary Table II). All the sources of variation were tested against error for significance by comparing the calculated ‘F’ value with table ‘F’ value at 1% and 5% probability.
levels. The correlation coefficient analysis was done as per method of Al-Jibourie et al. (1958).

**Heterosis**

The collected mean data on fruit quality traits of parents and hybrids were analyzed for heterosis expressed as a percent increase or decrease of $F_1$ hybrid over mid parent (mid parent, average or relative heterosis-MPH), better parent (heterobeltiosis-BPH), and the best commercial check (standard heterosis-SH) and were computed as per the method of Tuner (1953) and Hayes et al. (1955).

To compute the standard error (SE) of heterosis, mean squares due to error from ANOVA table was considered i.e. SE for heterosis over better parent (BP) = $(2 \text{Me} / r)^{1/2}$, SE for heterosis over the standard check (SC) = $(2 \text{Me} / r)^{1/2}$. Further ‘t’ value is calculated to test the significance of deviation of $F_1$ from BP and SC as proposed by Arunachalam (1974).

\[ t \text{ value for mid parent heterosis} = \frac{F_1 - \text{MP}}{\text{SE(MP)}} \]
\[ t \text{ value for better parent heterosis} = \frac{F_1 - \text{BP}}{\text{SE(BP)}} \]
\[ t \text{ value for standard heterosis} = \frac{F_1 - \text{SC}}{\text{SE(SC)}} \]

The calculated ‘t’ value compared with the table ‘t’ value at error degrees of freedom. Where, Me=Error Mean sum of squares in general ANOVA table, $r=$ Number of replications, $F_1=$ Mean value of hybrid over two replication, BP=Mean value of better parent over two replication, SC=Mean value of standard check over two replication.

**ANOVA for combining ability analysis**

The variation among the hybrids further partitioned into genetic components attributable to general combining ability (GCA) and specific combining ability (SCA) following the method suggested by Kempthorne (1957). For this purpose, pooled data over replications for crosses was compiled in the form of a Two-way table for each character. From this table, Sum of squares due to lines, Sum of squares due to testers, and Sum of squares due to line×tester computed (Supplementary Table III).

**Estimation of components of genetic variances**

From the expectations of the mean sum of squares, the GCA variance of the lines and testers as well SCA variance of hybrids were calculated using the following formula,

\[ \text{GCA variance for lines (Covariance of HS)} = \frac{\text{ML} - \text{Mlt}}{\text{tr}} = \frac{1}{4} \sigma^2 A = \sigma^2 \text{GCA} \]
\[ \text{GCA variance for testers (Covariance of HS)} = \frac{\text{ML} - \text{Mlt}}{\text{tr}} = \frac{1}{4} \sigma^2 A = \sigma^2 \text{GCA} \]
\[ \text{SCA variance for hybrids} = \frac{\text{ML} - \text{Me}}{\text{tr}} = \frac{1}{4} \sigma^2 \text{SCA} = (\text{Cov FS} - 2 \text{Cov HS}) \]
When both lines and tester mean sum of squares are significant, an average estimate of Covariance i.e. Cov (HS) calculated as follows:

\[
\text{Average Cov (HS)} = \frac{Ml + Mt - 2Ml \times t}{r(l + t)}
\]

where \(Ml\) = Mean sum of squares due to lines, \(Mt\) = Mean sum of squares due to testers, \(Mlt\) = Mean sum of squares due to line \(\times\) tester, \(Me\) = Mean sum of squares due to error, \(t\) = Number of testers, \(l\) = Number of lines, \(r\) = Number of replications. After estimating Cov (HS) and Cov (FS), the additive and dominance variance were computed as.

- \(\sigma^2\) GCA = Cov (HS) = \(\frac{1}{4}\) VA, Hence, \(4 \sigma^2\) GCA = VA = Additive Variance
- \(\sigma^2\) SCA = Cov (FS) – 2 Cov (HS) = \(\frac{1}{4}\)VD, Hence, \(VD = 4 \sigma^2\) SCA = Dominance Variance

After estimating the GCA and SCA variances, the ratio of GCA/SCA variance was computed to predict the type of gene action involved.

**Estimation of combining ability effects**

The observation recorded on \(i \times j\)th cross grown in \(k\)th replication expressed as per the linear model of Arunachalam, 1974 i.e. \(Yijk = \mu + gi + gj + sij + eijk\) Where, \(Yijk\) = Mean value of the character measured on \(i \times j\)th cross in \(k\)th replication, \(\mu\) = Population mean, \(gi\) = gca effect of \(ith\) female parent, \(gj\) = gca effect of \(jth\) male parent, \(sij\) = sca effect of \(ijth\) cross, \(eijk\) = Environmental effect pertaining to \(ijkth\) individual. The estimates of general combining ability effects of lines and testers as well as specific combining ability effects of crosses are calculated from two way table as given below.

**General combining ability effects**

(a) Lines: \(gi = \frac{x_i}{lr} - \frac{x_{…}}{lr}\), Where, \(x_i\) = Total of phenotypic values of the crosses of the line ‘\(i\)’ with each of the testers over replications, \(x_{…}\) = A total of phenotypic values of all the hybrids in the \(l \times t\) set, \(gi\) = General combining ability effect of \(i\)th line, Check: \(\Sigma gi = 0\).

(b) Testers: \(gj = \frac{x_j}{lr} - \frac{x_{…}}{lr}\), Where, \(x_{…}\) = Gross total of phenotypic values of all the hybrids in the \(l \times t\) set, \(x_j\) = Total of all crosses involving \(j\)th male parent, \(gj\) = General combining ability effect of the \(j\)th tester, Check: \(\Sigma gj = 0\).

**Specific combining ability effects**

\(sij = \frac{x_{ij}}{r} - \frac{x_i}{lr} - \frac{x_j}{lr} + \frac{x_{…}}{lr}\), where \(sij\) = Specific combining ability effect of the \(ijth\) cross combination, \(x_{ij}\) = Total of \(ijth\) cross combination over all the replications, \(x_i\) = Total of phenotypic values of the crosses of the line ‘\(i\)’ with each of the testers over replications, \(x_j\) = Total of all crosses involving \(j\)th male parent, \(x_{…}\) = A total of phenotypic values of all the hybrids in the \(l \times t\) set. Check: \(\Sigma_i sij = \Sigma_j sij = \Sigma_i \Sigma_j sij = 0\).

**The standard errors for testing the significance of GCA and SCA effects**

The standard errors for testing the significance of GCA and SCA effects were estimated using the following formulae.

Standard error for GCA effects of lines = \(SE(gi) = (Me/\sqrt{lr})^{1/2}\)
Standard error for GCA effects of testers = \(SE(gj) = (Me/\sqrt{lr})^{1/2}\)
Standard error for SCA effects of hybrids = \(SE(sij) = (Me/\sqrt{r})^{1/2}\)

The estimates of \(gi\) and \(sij\) were tested for their statistical significance by ‘\(t\)’ test. For testing the significance of the difference between GCA effects of two lines (or two testers) and SCA effects of two hybrids, the standard errors are computed as follows.
Standard error of \((gi - gj)\) for lines \(= (2Me/\text{tr})^{1/2}\)
Standard error of \((gi - gj)\) for testers \(= (2Me/\text{lr})^{1/2}\)
Standard error of \((sij - skl)\) for crosses \(= (2Me/r)^{1/2}\)

The corresponding critical difference (CD) values were computed by multiplying SE value with \((2)^{1/2}\) and table ‘t’ value at 5% and 1% respectively.
\(\text{CD} = (2)^{1/2} \times \text{SE} \times \text{table ‘t’ value for error degrees of df}\) at 5% and 1% respectively.

*The proportional contribution of lines, testers, and their interactions to total variance*

The percent contribution of lines, testers, and their interaction towards total variability in each character was estimated following the method of Singh and Choudhory (1977) as given below.

(i) Percent contribution of lines \(= \frac{\text{SS (lines)} \times 100}{\text{SS (Crosses)}}\)
(ii) Percent contribution of testers \(= \frac{\text{SS (tester)} \times 100}{\text{SS (Crosses)}}\)
(iii) Percent contribution of \((1 \times t)\) \(= \frac{\text{SS (1 \times t)} \times 100}{\text{SS (Crosses)}}\)

*Overall GCA status of parents, SCA status, and heterotic status of crosses*

Since shelf life and yield are associated with several other characters, positively with some and negatively with others, it is necessary to know the overall status of the parents/hybrids considering GCA effects/SCA effects for all the characters simultaneously. The overall status of a parent or a cross concerning GCA or SCA effects is determined as per the method of Arunachalam and Bandyopadhyay (1979) with slight modification as suggested by Mohan Rao (2001). The modified procedure described is as follows.

The estimates of general combining ability effects of parents, SCA effects, and standard heterosis of hybrids ranked by giving the highest rank for the parent or the cross which manifested the highest GCA/SCA effects and standard heterosis respectively in a desirable direction. The lowest rank is given for the parent or the cross with the lowest GCA/SCA effects and standard heterosis for a character, respectively. This was repeated for each character. The ranks obtained by the parent/hybrid were summed up across all the characters to arrive at a total score for each of the parent/crosses. Further, the mean of the total scores of all the genotypes (parents and hybrids) was computed which was used as the final norm to ascertain the status of a parent or a hybrid concerning GCA/SCA effects and standard heterosis.

The parent/hybrid whose total rank exceeded the final norm was given high (H) overall GCA/SCA/heterosis status, respectively. On the other hand, the parents or the cross, whose total rank was less than the final norm were given low (L) overall GCA/SCA/heterosis status, respectively. Accordingly, the crosses were grouped into different categories viz., High\(\times\)High (HH), High\(\times\)Low (HL), Low\(\times\)High (LH), and Low\(\times\)Low (LL) based on the overall GCA status of their parents. The overall SCA status of crosses viz., High or Low was also mentioned under each category to draw the inference.

*Results*

Mean performance of lines, testers, and hybrids for fruit biochemical, morpho-physiological, and yield attributing traits

The lines and testers recorded substantial variability for all traits. The performance of lines was higher compared to testers for pH, calcium, magnesium, fruit firmness, pericarp thickness, pulp content, locule number, shelf life, and number of clusters (Table 1). The hybrids were superior in their performance than parents for lycopene, fruit diameter, weight, firmness, pericarp thickness, locule number, plant height, number of clusters, number of fruits, and yield/plant. The hybrid IIHR 2349\(\times\)Arka Saurabh, had higher TSS, pH, lycopene, titratable acidity, calcium, magnesium, and shelf life. Similarly, IIHR 2349\(\times\)Arka Vikas recorded higher titratable acidity, pericarp thickness, number of clusters, and yield/plant. Superior performance for fruit diameter, weight, plant height, and number of clusters was exhibited by IIHR 2358\(\times\)Arka Ahuti. The IIHR 2357\(\times\)Arka Saurabh was superior for magnesium, number of branches, number of clusters, and number of fruits.

The correlation analysis revealed that the TSS recorded strong positive correlation with fruit length, shelf life and locule number (Supplementary
| SI. no | Genotypes               | TSS (%) | pH  | Lycopene (mg/100 g) | Ascorbic acid (mg/100 g) | Titratable acidity (%) | Calcium (mg/100 g) | Magnesium (mg/100 g) | Fruit length (cm) | Fruit diameter (cm) | Fruit weight (g) |
|--------|-------------------------|---------|-----|---------------------|--------------------------|------------------------|-------------------|-------------------|-------------------|-------------------|------------------|
| Lines  |                         |         |     |                     |                          |                        |                   |                   |                   |                   |                  |
| 1      | IIHR 2349               | 2.50    | 5.52| 2.49                | 7.15                     | 0.77                   | 16.16             | 13.24             | 45.76             | 40.73             | 42.00            |
| 2      | IIHR 2358               | 2.80    | 5.48| 0.52                | 17.73                    | 0.42                   | 15.81             | 10.73             | 35.17             | 34.61             | 23.40            |
| 3      | IIHR 2357               | 3.20    | 5.50| 2.61                | 8.78                     | 0.47                   | 16.16             | 13.24             | 42.39             | 37.15             | 33.00            |
| Testers|                         |         |     |                     |                          |                        |                    |                   |                   |                   |                  |
| 4      | Arka Vikas              | 3.20    | 5.27| 0.80                | 23.90                    | 0.83                   | 11.15             | 14.43             | 38.37             | 42.15             | 45.50            |
| 5      | Arka Ahuti              | 3.15    | 5.55| 2.44                | 7.11                     | 0.67                   | 13.10             | 8.08              | 56.95             | 38.57             | 44.80            |
| 6      | Arka Saurabh            | 3.00    | 5.5 | 3.65                | 7.31                     | 0.73                   | 13.81             | 11.13             | 45.76             | 38.72             | 47.16            |
| Hybrids|                         |         |     |                     |                          |                        |                    |                   |                   |                   |                  |
| 7      | IIHR 2349 × Arka Vikas | 2.50    | 5.43| 2.04                | 10.76                    | 0.67                   | 11.29             | 5.29              | 44.12             | 45.27             | 55.70            |
| 8      | IIHR 2349 × Arka Ahuti | 2.50    | 5.41| 1.94                | 17.65**                  | 0.59                   | 5.71              | 5.12              | 39.67             | 45.38             | 47.10            |
| 9      | IIHR 2349 × Arka Saurabh| 2.95    | 5.51| 4.59**              | 7.43                     | 0.67                   | 17.99             | 17.79**           | 51.40             | 45.14             | 58.40            |
| 10     | IIHR 2358 × Arka Vikas | 2.15    | 5.51| 2.09                | 7.18                     | 0.67                   | 13.79             | 10.93**           | 42.39             | 40.55             | 37.80            |
| 11     | IIHR 2358 × Arka Ahuti | 2.30    | 5.42| 1.73                | 14.38                    | 0.54                   | 14.63             | 13.03**           | 49.14             | 48.22             | 64.50            |
| 12     | IIHR 2358 × Arka Saurabh| 2.90    | 5.38| 0.91                | 7.38                     | 0.67                   | 11.72             | 13.79**           | 51.73             | 43.41             | 50.40            |
| 13     | IIHR 2357 × Arka Vikas | 2.40    | 5.37| 4.22**              | 7.38                     | 0.20                   | 9.48              | 6.55              | 41.95             | 46.09             | 50.60            |
| 14     | IIHR 2357 × Arka Ahuti | 2.45    | 5.15| 1.25                | 13.75                    | 0.54                   | 14.20             | 12.75**           | 47.16             | 45.95             | 61.75            |
| 15     | IIHR 2357 × Arka Saurabh| 2.25    | 5.44| 3.23**              | 11.11                    | 0.25                   | 14.39             | 14.24**           | 40.11             | 43.08             | 41.20            |
### Table 1 (continued)

| SI. no | Genotypes       | TSS (%) | pH   | Lycopene (mg/100 g) | Ascorbic acid (mg/100 g) | Titratable acidity (%) | Calcium (mg/100 g) | Magnesium (mg/100 g) | Fruit length (cm) | Fruit diameter (cm) | Fruit weight (g) |
|--------|-----------------|---------|------|---------------------|--------------------------|------------------------|-------------------|-------------------|------------------|---------------------|-----------------|
|        | Arka Rakshak (check) | 3.00 | 5.70 | 2.01               | 13.70                    | 0.54                   | 19.35             | 6.99              | 55.58            | 45.79               | 63.20           |
| Mean   |                 | 2.49 | 5.40 | 2.44               | 10.78                    | 0.53                   | 12.58             | 11.05             | 45.30            | 44.79               | 51.94           |
| S.E. ± |                 | 0.21 | 0.07 | 0.10               | 0.34                     | 0.08                   | 0.01              | 0.05              | 2.07             | 1.93                | 3.51            |
| C.D. 5%|                 | 0.48 | 0.15 | 0.23               | 0.79                     | 0.19                   | 0.01              | 0.13              | 4.77             | 4.46                | 8.10            |
| C.D. 1%|                 | 0.70 | 0.22 | 0.33               | 1.14                     | 0.28                   | 0.01              | 0.18              | 6.95             | 6.49                | 11.78           |

| SI. No | Genotypes       | Fruit firm-ness (kg/cm²) | Pericarp thickness (mm) | Pulp content (%) | Locule number | Shelf life (Days) | Plant height (cm) | No. of branches | No. of clusters | No. of fruit/cluster | Yield/ plant (g) |
|--------|-----------------|--------------------------|-------------------------|-----------------|---------------|------------------|-------------------|----------------|-----------------|-------------------|------------------|
| Lines  |                 |                          |                         |                 |               |                  |                   |                |                 |                   |                  |
| 1      | IIHR 2349       | 2.01                     | 4.35                    | 82.14           | 3.00          | 25.10            | 57.20             | 4.60            | 11.15           | 3.40              | 606.15           |
| 2      | IIHR 2358       | 2.47                     | 4.90                    | 76.53           | 3.00          | 28.85            | 57.30             | 4.30            | 10.70           | 3.50              | 667.80           |
| 3      | IIHR 2357       | 2.13                     | 4.48                    | 81.39           | 3.00          | 27.40            | 56.70             | 4.20            | 7.70            | 4.00              | 831.90           |

| Testers| Arka Vikas      | 1.68                     | 4.24                    | 71.10           | 3.50          | 17.10            | 64.20             | 4.30            | 11.80           | 4.40              | 1155.50          |
| 5      | Arka Ahuti      | 1.91                     | 4.76                    | 83.29           | 2.00          | 20.05            | 64.70             | 5.20            | 7.10            | 3.40              | 1037.00          |
| 6      | Arka Saurabh    | 1.90                     | 3.82                    | 80.52           | 3.00          | 17.55            | 71.70             | 4.20            | 7.70            | 3.50              | 1006.06          |

| Hybrids| IIHR 2349 × Arka Vikas | 2.60                     | 5.63                    | 76.64           | 3.35          | 24.70            | 66.80             | 3.80            | 11.05**         | 4.15              | 2850.50*         |
| 8      | IIHR 2349 × Arka Ahuti | 2.05                     | 4.60                    | 70.82           | 3.30          | 20.10            | 74.00             | 4.80            | 9.70            | 5.15              | 2190.55          |
| 9      | IIHR 2349 × Arka Saurabh | 2.08                     | 5.09                    | 78.38           | 3.50          | 29.40*           | 64.10             | 4.10            | 10.15           | 4.35              | 2397.50          |
| 10     | IIHR 2358 × Arka Vikas | 2.55                     | 4.71                    | 84.68           | 3.45          | 21.50            | 58.80             | 4.60            | 8.80            | 4.35              | 2064.50          |
| SI. No | Genotypes          | Fruit firmness (kg/cm²) | Pericarp thickness (mm) | Pulp content (%) | Locule number | Shelf life (Days) | Plant height (cm) | No. of branches | No. of clusters | No. of fruit/cluster | Yield/ plant (g) |
|--------|---------------------|-------------------------|-------------------------|------------------|---------------|------------------|-------------------|-----------------|----------------|----------------------|-----------------|
| 11     | IIHR 2358 × Arka Ahuti | 2.32                    | 5.05                    | 75.99            | 3.35          | 22.60            | 83.00**           | 3.60            | 11.25**         | 5.15                | 2109.75         |
| 12     | IIHR 2358 × Arka Saurabh | 2.26                    | 3.50                    | 82.63            | 3.65          | 26.60            | 67.90             | 4.50            | 9.70            | 3.15                | 2005.50         |
| 13     | IIHR 2357 × Arka Vikas | 2.69                    | 4.76                    | 82.22            | 3.35          | 28.00*           | 57.60             | 4.20            | 7.05            | 3.60                | 2103.25         |
| 14     | IIHR 2357 × Arka Ahuti | 2.25                    | 4.55                    | 75.90            | 3.35          | 22.80            | 76.75**           | 2.45            | 10.95**         | 5.15                | 2057.35         |
| 15     | IIHR 2357 × Arka Saurabh | 1.77                    | 4.59                    | 80.19            | 3.00          | 24.20            | 72.60             | 5.10            | 10.85**         | 5.65*               | 2117.75         |
| 16     | Arka Rakshak (check)  | 3.01                    | 5.93                    | 83.46            | 2.50          | 23.45            | 74.70             | 4.00            | 10.15           | 5.35                | 2389.65         |

|          | Mean    | S.E. ± | C.D. 5% | C.D. 1% | Where, *Significant at p = 0.05, **Significant at p = 0.01, SE standard error, C.D. critical difference |
|----------|---------|--------|---------|---------|--------------------------------------------------|
| Fruit firmness (kg/cm²) | 2.29    | 0.28   | 0.64    | 0.93    | 0.64                                             |
| Pericarp thickness (mm)  | 4.72    | 0.56   | 1.29    | 1.87    | 1.29                                            |
| Pulp content (%)         | 78.61   | 0.51   | 11.40   | 16.59   | 11.40                                           |
| Locule number            | 3.37    | 0.21   | 1.19    | 1.73    | 1.19                                            |
| Shelf life (Days)        | 24.43   | 0.07   | 4.31    | 6.27    | 4.31                                            |
| Plant height (cm)        | 69.09   | 0.76   | 0.15    | 0.22    | 0.15                                            |
| No. of branches          | 4.13    | 0.15   | 1.76    | 2.56    | 1.76                                            |
| No. of clusters          | 9.94    | 0.10   | 0.33    | 0.49    | 0.33                                            |
| No. of fruit/cluster     | 4.52    | 0.33   | 0.23    | 0.33    | 0.23                                            |
| Yield/ plant (g)         | 2130.77 | 193.56 | 446.36  | 649.48  | 446.36                                           |
Similarly, the positive correlation observed between pH and number of branches, lycopene and shelf life, titratable acidity and locale number, calcium and magnesium, magnesium and fruit length, fruit diameter and fruit weight, fruit weight and plant height, pericarp thickness and yield per plant. The ascorbic acid had strong positive correlation with plant height, number of fruits/cluster and strong negative correlation with pulp content and shelf life. Fruit length had positive correlation with locale number and fruit weight. Similarly fruit height recorded positive correlation with number of fruits/cluster and number of clusters/plant. Negative correlation recorded between fruit diameter and pulp content, fruit weight and number of branches, fruit firmness and number of fruits/cluster, locale number and number of fruits/cluster, plant height and pulp content, number of branches and fruit weight.

Heterosis for fruit biochemical, morpho-physiological, and yield attributing traits in tomato hybrids

The estimation of heterosis for different fruit quality and yield contributing traits is prime importance in terms of their commercial utility. Hence, for all the twenty fruit biochemical, morpho-physiological, and yield characters heterosis is expressed as the mid parent heterosis (MPH), better parent (BPH), and standard heterosis (SH) (Table 2 and Supplementary Table IV).

For pH, the crosses IIHR 2357×Arka Ahuti, IIHR 2357×Arka Vikas, and IIHR 2358×Arka Saurabh exhibited higher significant negative MPH and BPH. Regarding lycopene, five crosses exhibited positive significant MPH and BPH with the highest in IIHR 2349×Arka Ahuti. The crosses IIHR 2349×Arka Saurabh, IIHR 2357×Arka Saurabh, and IIHR 2357×Arka Vikas exhibited higher positive significant SH. Further for ascorbic acid, significantly higher positive MPH and BPH were recorded in IIHR 2357×Arka Saurabh. The titratable acidity recorded higher MPH, BPH, and SH the cross IIHR 2358×Arka Saurabh. The cross IIHR 2349×Arka Saurabh exhibited higher significant positive MPH and BPH for fruit calcium. Magnesium recorded positive significant MPH in six crosses with highest in IIHR 2358×Arka Ahuti. Regrading fruit weight six crosses exhibited positive significant MPH with the highest in IIHR 2358×Arka Ahuti. Three crosses exhibited positive significant MPH for fruit firmness with highest in the cross IIHR 2349×Arka Vikas.

For pericarp thickness, the highest MPH and BPH were recorded in IIHR 2349×Arka Vikas and IIHR 2349×Arka Vikas respectively. The cross IIHR 2349×Arka Saurabh exhibited higher MPH and the cross IIHR 2358×Arka Vikas recorded higher positive BPH and SH for pulp content. With respect to shelf life, the crosses IIHR 2357×Arka Vikas, IIHR 2349×Arka Saurabh, and IIHR 2358×Arka Saurabh exhibited higher significant positive MPH. The crosses IIHR 2357×Arka Vikas and IIHR 2349×Arka Saurabh exhibited higher positive BPH and SH respectively.

Regarding number of fruit/cluster, seven crosses exhibited positive significant MPH with the highest in the cross IIHR 2357×Arka Saurabh. For yield/plant, four crosses IIHR 2349×Arka Vikas, IIHR 2357×Arka Saurabh, IIHR 2358×Arka Saurabh, and IIHR 2349×Arka Saurabh recorded the highest significant positive MPH and the cross IIHR 2349×Arka Vikas exhibited higher significant positive SH. The superiority of hybrids over pure line varieties in tomato paved way for exploitation of heterosis for improving fruit yield and quality in tomato.

ANOVA for fruit biochemical, morpho-physiological, and yield attributing traits

A significant difference was observed among the genotypes and parents for all the characters indicated the presence of a considerable amount of genetic variability and justified the selection of parents for the study except for fruit firmness, pericarp thickness, pulp content, locale number, number of branches and yield/plant (Supplementary Table V). The substantial variability between the lines and testers indicated the contrasting nature of lines and testers. A significant difference was observed among the lines for pH, lycopene, ascorbic acid, calcium, magnesium, fruit length, locale number, plant height, number of clusters, and number of fruit/cluster which indicated the significance of additive variance. Testers exhibited significant differences for TSS, lycopene, ascorbic acid, titratable acidity, calcium, magnesium, fruit length, diameter, weight, and number of clusters. The mean sum of squares of parents v/s hybrids was
Table 2: The mid parent heterosis for fruit biochemical, morpho-physiological and yield traits in tomato hybrids

| Sl. no | Hybrids                  | TSS    | pH  | Lycopene | Ascorbic acid | Titratable acidity | Calcium | Magnesium | Fruit length | Fruit diameter | Fruit weight |
|--------|--------------------------|--------|-----|----------|---------------|-------------------|---------|------------|--------------|----------------|--------------|
| 1      | IIHR 2349 × Arka Vikas  | −12.28 | 0.6 | 23.52**  | −30.74**       | −16.51            | −17.32**| −61.76**   | 4.87         | 9.24           | 27.31**      |
| 2      | IIHR 2349 × Arka Ahuti  | −16.67*| 0.56| 192.08** | −15.18**       | −7.14             | −57.64**| −59.30**   | 7.89         | 18.22**        | 36.72**      |
| 3      | IIHR 2349 × Arka Saurabh| −7.81  | 2.27| 168.81** | −54.53**       | 2.29              | 31.75**| 28.59**    | 27.27**      | 13.83*         | 48.79**      |
| 4      | IIHR 2358 × Arka Vikas  | −23.89**| −0.45| −15.42** | 0.7            | −6.94             | −5.61**| 2.53**     | −17.47**     | 2.24           | −12.9        |
| 5      | IIHR 2358 × Arka Ahuti  | −22.69**| −1.68| 16.89*   | 15.80**        | −2.28             | 1.35** | 38.54**    | 6.68         | 31.76**        | 89.15**      |
| 6      | IIHR 2358 × Arka Saurabh| −8.66  | −2.62*| −63.96** | −7.15          | 17.03             | −19.78**| 29.36**    | 4.15         | 14.66*         | 29.56**      |
| 7      | IIHR 2357 × Arka Vikas  | −12.73 | −2.68*| 37.46**  | 2.07           | −72.76**          | −36.74**| −46.25**   | −8.34        | 16.02**        | 13.5         |
| 8      | IIHR 2357 × Arka Ahuti  | −15.52*| −6.28**| −40.05** | 9.85**         | −6.9              | −4.12** | 16.65**    | 16.53**      | 25.32**        | 75.03**      |
| 9      | IIHR 2357 × Arka Saurabh| −27.42**| −1.04| 3.19     | 38.08**        | −58.68**          | −3.97** | 16.86**    | −9.02        | 13.56*         | 2.79         |

| Sl. no | Hybrids                  | Fruit firmness | Pericarp thickness | Pulp content | Locule number | Shelf life | Plant height | No. of branches | No. of clusters | No. of fruit/cluster | Yield/plant |
|--------|--------------------------|-----------------|-------------------|--------------|---------------|------------|--------------|------------------|------------------|---------------------|-------------|
| 1      | IIHR 2349 × Arka Vikas  | 40.73*          | 30.93*            | 0.03         | −9.46         | 21.53      | 10.05        | −14.61           | −13.70**       | 6.41                | 140.23**    |
| 2      | IIHR 2349 × Arka Ahuti  | −1.2            | 0.44              | −4.05        | −11.41        | −9.05      | 21.41        | 11.63            | −13.78**       | 32.05**             | 30.59       |
Table 2 (continued)

| Sl. no | Hybrids | Fruit firmness | Pericarp thickness | Pulp content | Locule number | Shelf life | Plant height | No. of branches | No. of clusters | No. of fruit/cluster | Yield/plant |
|--------|---------|----------------|-------------------|--------------|--------------|-----------|-------------|----------------|----------------|--------------------|-------------|
| 3      | IIHR 2349 × Arka Saurabh | 9.19           | 16.68             | 2.8          | − 3.45       | 35.02**   | − 0.54      | − 3.53         | 4.10*          | 11.54**            | 40.59*      |
| 4      | IIHR 2358 × Arka Vikas    | 30.10*         | 3.18              | 2.38         | 20           | 8.04      | − 3.21      | − 6.12         | − 3.56*         | 27.94**            | 17.4        |
| 5      | IIHR 2358 × Arka Ahuti    | 6.06           | 4.45              | − 4.9        | 15.52        | 4.27      | 36.07       | − 24.21        | 26.40**         | 51.47**            | 30.19       |
| 6      | IIHR 2358 × Arka Saurabh  | 12.02          | − 24.39*          | 0.36         | 30.36        | 24.59*    | 5.27        | − 4.26         | 31.08**         | − 7.35*             | 71.81**     |
| 7      | IIHR 2357 × Arka Vikas    | 37.42*         | 16.45             | 1.09         | − 4.29       | 37.09**   | − 4.71      | − 4.55         | − 25.20**        | 5.88*              | 36.86       |
| 8      | IIHR 2357 × Arka Ahuti    | 2.97           | 4.3               | − 3.34       | − 4.96       | 2.7       | 26.44       | − 42.35*        | 19.02**         | 51.47**             | 25.62       |
| 9      | IIHR 2357 × Arka Saurabh  | − 12.16        | 10.6              | − 0.94       | − 12.41      | 10.63     | 13.08       | 21.43          | 40.91**         | 66.18**             | 76.04**     |

Where, *Significant at $p = 0.05$ and **Significant at $p = 0.01$
Table 3  Analysis of variance for combining ability in lines and testers for fruit biochemical, morpho-physiological, and yield attributing traits

| Source of variation | Df | Mean sum of squares |
|---------------------|----|---------------------|
|                     |    | TSS     | pH     | Lycopene | Ascorbic acid | Titratable acidity | Calcium | Magnesium | Fruit length | Fruit diameter | Fruit weight |
| Replications        | 1  | 0.02    | 0.01   | 0.06     | 0.29         | 0.013               | 0.01    | 0.01       | 2.98         | 6.94          | 0.01         |
| Crosses             | 8  | 0.15    | 0.02*  | 3.31**   | 29.12*       | 0.06**              | 25.01** | 39.63**    | 44.14**      | 9.58**        | 163.18**     |
| Line effect         | 2  | 0.21    | 0.03   | 2.94     | 90.48*       | 0.002               | 20.26   | 91.11      | 36.44        | 13.43         | 159.51       |
| Tester effect       | 2  | 0.13    | 0.03   | 3.39     | 7.95         | 0.18                | 4.47    | 15.27      | 33.12        | 2.47          | 14.61        |
| Line × tester effect| 4  | 0.13    | 0.02   | 3.45**   | 9.02**       | 0.04**              | 37.65** | 26.07**    | 53.51**      | 11.21**       | 239.30**     |
| Error               | 8  | 0.07    | 0.01   | 0.01     | 0.03         | 0.01               | 0.01    | 0.01       | 4.76         | 1.00          | 9.01         |
| Total               | 17 | 0.10    | 0.01   | 1.56     | 13.74        | 0.03               | 11.77   | 18.65      | 23.19        | 5.39          | 81.03        |

| Source of variation | Df | Mean sum of squares |
|---------------------|----|---------------------|
|                     |    | Fruit firmness | Pericarp thickness | Pulp content | Locule number | Shelf life | Plant height | No. of branches | No. of clusters | No. of fruits/cluster | Yield/plant |
| Replications        | 1  | 0.03    | 0.69       | 118.42       | 0.22         | 1.50    | 0.01        | 6.13          | 0.01          | 0.01                  | 507,460.90 |
| Crosses             | 8  | 0.17    | 0.66       | 36.86        | 0.06         | 18.90*  | 0.02*       | 1.24          | 3.65**         | 1.35**                | 276,940.90**|
| Line effect         | 2  | 0.52*   | 0.62       | 86.82**      | 0.01         | 36.42   | 0.02        | 1.38          | 4.54          | 1.96                  | 276,918.80 |
| Tester effect       | 2  | 0.03    | 0.74       | 53.96*       | 0.09         | 3.48    | 0.03        | 0.20          | 0.70          | 0.51                  | 213,763.80 |
| Line × tester effect| 4  | 0.06    | 0.64       | 3.32         | 0.07         | 17.85   | 0.02        | 1.69*         | 4.68**         | 1.46                  | 308,540.60**|
| Error               | 8  | 0.07    | 0.33       | 18.31        | 0.08         | 4.95    | 0.01        | 0.38          | 0.02          | 0.01                  | 34,160.18  |
| Total               | 17 | 0.12    | 0.51       | 32.93        | 0.08         | 11.32   | 0.01        | 1.12          | 1.73          | 0.64                  | 176,251.20 |

Where, *Significant at $p = 0.05$, **Significant at $p = 0.01$, $Df$ degrees of freedom
significant for all the characters which revealed the heterotic effects except fruit length, pericarp thickness, pulp content, locule number, and number of branches. Hybrids differed significantly for all the traits indicated the diverse performance of different cross combinations except fruit diameter, firmness, pericarp thickness, pulp content, locule number, number of branches.

ANOVA for combining ability and proportional contribution of lines, testers, and line×tester for hybrids performance

The crosses exhibited a high level of significance for all the traits except TSS, fruit firmness, pericarp thickness, pulp content, locule number, and number of branches (Table 3). The variance due to crosses was further portioned into variance due to lines, testers, and line×testers. The mean sum of squares due to lines was highly significant for ascorbic acid, fruit firmness and pulp content which indicated the significance of additive variance whereas, the mean sum of squares due to testers was significant for pulp content. The line×tester interaction variance was highly significant for lycopene, ascorbic acid, titratable acidity, calcium, magnesium, fruit length, diameter, weight, number of branches, number of clusters, and yield/plant indicated the dominance variance and the presence of heterosis.

The percent contribution of lines towards total variation was higher for ascorbic acid followed by fruit firmness and least for titratable acidity (Supplementary Table VI). Similarly, the percent contribution of tester towards total variation was higher for titratable acidity and least for fruit weight.

Variance due to combining ability effects

The variance due to general combining ability was highly significant for ascorbic acid, fruit firmness, and pulp content whereas, variance due to specific combining ability was significant for pH, lycopene, ascorbic acid, titratable acidity, calcium, magnesium, fruit length, weight, plant height, number of clusters, number of fruits/cluster, and yield/plant (Supplementary Table VII). It was evident that among twenty studied traits most manifested a higher degree of SCA variance as compared to GCA variance. The GCA/SCA ratio was less than one for all the characters except for pH, ascorbic acid, fruit firmness, and plant height.

General combining ability effects and overall general combining ability status

Line IIHR 2358 was the best with the highest GCA effects in a positive direction for lycopene, ascorbic acid, number of fruits/cluster and also it was a good general combiner for pH, fruit weight, shelf life, plant height, and yield/plant in a positive direction (Supplementary Table VIII). The lines IIHR 2349 had significant GCA effects in the desired direction for fruit length, weight, and firmness. Line IIHR 2357 was a

| Characters        | Lines | Testers       | Characters     | Lines | Testers       |
|-------------------|-------|---------------|----------------|-------|---------------|
| TSS               | IIHR 2357 (0.21*) | Arka Vikas (0.16) | Fruit firmness | IIHR 2349 (0.33*) | Arka Ahuti (0.09) |
| pH                | IIHR 2358 (0.07*) | Arka Saurabh (0.08*) | Pericarp thickness | IIHR 2349 (0.31) | Arka Vikas (0.39) |
| Lycopene          | IIHR 2358 (0.80***) | Arka Ahuti (0.86**) | Pulp content | IIHR 2349 (2.57) | Arka Ahuti (2.50) |
| Ascorbic acid     | IIHR 2358 (4.48**) | Arka Vikas (1.17***) | Locule number | IIHR 2358 (−0.03) | Arka Saurabh (−0.13) |
| Titratable acidity| IIHR 2358 (0.02) | Arka Saurabh (0.11**) | Shelf life | IIHR 2358 (2.60**) | Arka Saurabh (0.57) |
| Calcium           | IIHR 2357 (2.12**) | Arka Vikas (0.91**) | Plant height | IIHR 2358 (0.07*) | Arka Saurabh (0.08*) |
| Magnesium         | IIHR 2357 (4.22**) | Arka Vikas (1.65**) | No. of branches | IIHR 2357 (0.44) | Arka Vikas (0.11) |
| Fruit length      | IIHR 2349 (2.48*) | Arka Ahuti (2.46*) | No. of clusters | IIHR 2349 (0.98**) | Arka Vikas (0.36**) |
| Fruit diameter    | IIHR 2358 (1.73) | Arka Vikas (0.48) | No. of fruits/cluster | IIHR 2358 (0.63**) | Arka Ahuti (0.31**) |
| Fruit weight      | IIHR 2358 (5.84**) | Arka Vikas (1.79) | Yield/plant | IIHR 2358 (233.41*) | Arka Vikas (217.22*) |

Where, *Significant at p = 0.05, **Significant at p = 0.01 and Values in parenthesis indicates the GCA effect of lines and testers

 Springer
very good source of favorable genes for TSS, fruit length, and shelf life.

The entire testers were good general combiners for lycopene, titratable acidity, calcium, and magnesium. Arka Saurabh had high general combining ability effects for pH, fruit length, plant height, number of clusters, and number of fruits/cluster. Best lines and testers for each character with significant GCA effects in the desired direction are presented in Table 4. In the GCA effects of the parents, the line IIHR 2357 and the tester Arka Vikas had high (H) overall GCA status (Table 5).

Table 5 Overall general combining ability status of tomato lines and testers

| Lines       | Rank | GCA Status | Testers    | Rank | GCA Status |
|-------------|------|------------|------------|------|------------|
| IIHR 2349   | 44   | L          | Arka Vikas | 32   | H          |
| IIHR 2358   | 43   | L          | Arka Ahuti | 42   | L          |
| IIHR 2357   | 33   | H          | Arka Saurabh | 46  | L          |

Where, H = High overall GCA status, L = Low overall GCA status

Final norm = 40

Specific combining ability effects and overall specific combining ability effects of crosses

The hybrids from different combinations of the parents with high or low GCA effects are referred to as H × H (high × high), H × L (high × low), and L × L (low × low) combinations (Supplementary Table IX). Among nine hybrids, IIHR 2349 × Arka Vikas (L × H) was found good specific combiner for number of clusters, and yield/plant (Table 6). The hybrid, IIHR 2349 × Arka Ahuti (L × L) was a good specific combiner for calcium, magnesium, fruit

Table 6 Best tomato crosses with high and significant SCA effects in the desirable direction

| Characters   | Crosses                     | Characters   | Crosses                     | Characters   | Crosses                     |
|--------------|-----------------------------|--------------|-----------------------------|--------------|-----------------------------|
| TSS          | IIHR 2358 × Arka Saurabh (0.24) | Fruit length | IIHR 2349 × Arka Ahuti (5.42**) | Shelf life   | IIHR 2357 × Arka Vikas (2.70) |
| pH           | IIHR 2357 × Arka Saurabh (0.08) | Fruit diameter | IIHR 2358 × Arka Ahuti (2.43) | Plant height | IIHR 2357 × Arka Saurabh (0.08) |
| Lycopene     | IIHR 2349 × Arka Saurabh (1.27**) | Fruit weight | IIHR 2349 × Arka Ahuti (12.48**) | No. of branches | IIHR 2349 × Arka Ahuti (1.08) |
| Ascorbic acid| IIHR 2357 × Arka Saurabh (2.50**) | Fruit firmness | IIHR 2358 × Arka Saurabh (0.13) | No. of clusters | IIHR 2349 × Arka Vikas (1.73**) |
| Titratable acidity | IIHR 2357 × Arka Ahuti (0.19*) | Pericarp thickness | IIHR 2357 × Arka Vikas (0.13) | No. of fruits/cluster | IIHR 2357 × Arka Saurabh (0.99**) |
| Calcium      | IIHR 2349 × Arka Ahuti (4.89**) | Pulp content | IIHR 2349 × Arka Saurabh (1.30) | Yield/plant  | IIHR 2349 × Arka Vikas (504.20**) |
| Magnesium    | IIHR 2349 × Arka Saurabh (4.17**) | Locule number | IIHR 2357 × Arka Saurabh (−0.25) |              | IIHR 2349 × Arka Saurabh (360.31**) |

Where, *Significant at p = 0.05, **Significant at p = 0.01 and values in parenthesis—SCA effect of crosses
length, and weight in a desirable direction. For lycopene, ascorbic acid, calcium, and magnesium, the hybrid IIHR 2349 × Arka Saurabh (L × L) was found superior in a desirable direction. As far as ascorbic acid, fruit length, and number of fruits/cluster are concerned, the hybrid IIHR 2357 × Arka Saurabh (H × L) was the top specific combiner with SCA effects in a desirable direction. Out of nine crosses, four crosses had high overall specific combining ability status. The crosses IIHR 2349 × Arka Vikas (H × L), IIHR 2349 × Arka Saurabh (L × L) were the best overall specific combiner followed by IIHR 2358 × Arka Ahuti (L × L) and IIHR 2357 × Arka Ahuti (H × L) (Table 7). Based on SCA effects, crosses were classified into H × H (both the parents with high overall GCA status), H × L (one parent with high and other with low overall GCA status), and L × L (both the parents with low overall GCA status). Out of nine crosses, one cross was H × H (IIHR 2357 × Arka Vikas) involved both the parents with good overall general combining ability. Four crosses were H × L or L × H and the remaining four crosses were L × L.

**Discussion**

The substantial variability between the lines and testers indicated the contrasting nature of lines and testers for studied traits including fruit shelf life and yield/plant. The line IIHR 2349, the tester Arka Vikas and the hybrid IIHR 2349 × Arka Saurabh were superior for most studied traits. The combining ability of lines differed based on the tester involved in the cross combination which was amply reflected by significant differences for crosses.

Shelf life is complex polygenic trait and direct selection for this would not yield fruitful results without giving due importance to their genetic background. The association of shelf life and its component traits reflects nature and degree of relationship between them. TSS and lycopene could be used as surrogates for indirect selection of genotypes with higher shelf life as positive correlation recorded. Moreover, the selected plants need to be empirically evaluated for shelf life for assessing the effectiveness of selection based on these traits. However, correlation analysis from different hybrids derived from unrelated parents or parents having different genetic background is not recommended. These results may be validated from populations derived from parents sharing common genetic background.

The estimation of heterosis in our study has shown different hybrids showing MPH, BPH and SH for all the traits under study given hint for exploiting heterosis for fruit yield and improving shelf life in tomato. Significant heterosis over mid-parent was observed in the majority of the crosses for many traits which indicate the additive gene action in the genetic control of trait. These results were in agreement with the results obtained by previous researchers in tomato (Kumar et al. 2009; Kumari and Sharma 2011; Yogendra and Gowda, 2012; Kumar and Gowda, 2016). Two promising hybrids were identified based on their per se performance for yield and shelf life. The hybrid IIHR 2349 × Arka Vikas recorded a significantly higher yield potential of 2850.50 g/plant with significantly higher standard heterosis over standard check Arka Rakshak (52.27%), and it had 24.70 days of shelf life. Higher heterosis for yield/plant in this hybrid may be attributed to a higher number of clusters/plant which is further reiterated by significantly higher standard heterosis for the same trait.

Another promising hybrid IIHR 2349 × Arka Saurabh recorded a significantly higher shelf life of 29.40 days with significantly higher standard

| Lines             | Tester Vikas (H) | Tester Ahuti (L) | Tester Saurabh (L) |
|-------------------|-----------------|-----------------|-------------------|
| IIHR 2349 (L)     | 79 H            | 116 L           | 79 H              |
| IIHR 2358 (L)     | 104 L           | 80 H            | 111 L             |
| IIHR 2357 (H)     | 105 L           | 97 H            | 106 L             |

Table 7 Overall specific combining ability status of tomato crosses

Where, H = High overall SCA status, L = Low overall SCA status, (H) = High overall GCA status, (L) = Low overall GCA status

Final norm = 97.44
heterosis over standard check Arka Rakshak, and it had a yield potential of 2397.50 g/plant. Higher heterosis for shelf life in this hybrid may be contributed by significantly higher mean performance for fruit magnesium content and lycopene content which is further evident by significantly higher standard heterosis for magnesium content and lycopene content. Lycopene is an antioxidant in the carotenoid family which alleviates the oxidative stress, delay ripening during storage period and thus extends shelf life of fruits (Shehata et al. 2021). The calcium and magnesium interact with pectic acid in the cell wall to form calcium and magnesium pectate which influences fruit firmness (Marschner 1995; Jones 1999). These nutrients have positive effects on fruits storage through inhibition of abnormal senescence, reduction of respiration rate, ethylene synthesis, protein breakdown, weight loss, and reduces incidence of physiological disorders during storage (Parker and Maalekuu 2013; Abrol et al. 2017). The fruit containing low calcium and magnesium are sensitive to physiological and pathological disorders, consequently have short shelf life. These promising hybrids can be grown for commercialization after testing at preliminary yield trials and multilocation trials.

The lines contributed to the bulk of the variation observed in hybrids for most traits and lines have an important role in the variation among the hybrids. While selecting the germplasm lines, emphasis should be given to the lines which are used as female parents. However, the same interpretation would become wrong concerning line × tester interaction as it is not under the control of the breeder, but it depends on the specific pattern in which the lines and testers interact. Therefore, most care should be taken while selecting the lines for hybridization.

The predominance of non-additive gene action exhibited by lycopene, titratable acidity, pericarp thickness (Dhatt et al. 2003; Joshi et al. 2005; Mondal et al. 2009), yield/plant (Bhutani and Kalloo 1983; Das et al. 2020; Pavan and Gangaprasad 2022), TSS (Kalloo et al. 1974; Bhatt et al. 2001; Mondal et al. 2009), calcium, magnesium, fruit length, diameter, weight, pulp content, locule number (Dhatt et al. 2003), shelf life (Roopa et al. 2001; Dhatt et al. 2003; Garg et al. 2008; Pavan and Gangaprasad 2022), number of branches, number of clusters and number of fruit/cluster (Pavan and Gangaprasad, 2022) which can be exploited through hybrid development programs. It also suggests that as the non-additive variance is resultant of heterozygosity and simple selection methods are ineffective due to its non-fixable inheritance. So, selection might not be made in the early generations and recurrent selection with periodic intercrossing appeared to be the best method. The contrasting findings of additive gene action were cited for locule number, shelf life (Rodriguez et al. 2010), yield/plant (Katoch and Vidyasagar 2004), number of fruit/cluster (Mondal et al. 2009), and lycopene (Suo et al. 2010). The additive and non-additive gene effects for fruit quality and yield traits were reported by Gaikwad and Cheema (2009) and Akhtar and Hazra (2013).

The pH, ascorbic acid, fruit firmness, and plant height were governed by additive gene action which can be exploited through varietal development programs as the GCA/SCA ratio was more than one. The contrasting results of dominant gene action were reported for pH and plant height (Das et al. 2020; Pavan and Gangaprasad 2022), ascorbic acid, and fruit firmness (Bhatt et al. 2001; Pavan and Gangaprasad 2022). The per se performance of a parent is not always a true indicator of its potentiality in a hybrid combination. Therefore, general combining ability, which is the breeding value of the parent expressed as a deviation from the population mean has proved as a useful tool for choosing the potential parents for hybrid development (Singh and Asati 2011). Among the parents with significant GCA effects, the one with a higher magnitude of GCA effects is considered superior to those with a lower magnitude (Technow 2019; Yu et al. 2020).

An overall appraisal of GCA effects revealed that all the lines were good general combiners for lycopene, ascorbic acid, calcium, magnesium, number of clusters, and number of fruits/cluster. The Arka Saurabh had high general combining ability effects for pH, fruit length, plant height, number of clusters, and number of fruits/cluster proved to be the best combiner in producing heterotic hybrids. The high overall GCA status of the line IIHR 2357 and the tester Arka Vikas revealed that 33.33% of lines and testers proved to be high overall good general combiners which intern suggested their ability to transmit additive genes in the desired direction for the majority of the traits under study. Similar results were reported by Bhatt et al. (2001), Dhatt et al. (2003), Kansouh and Zakher (2011), Yogendra and Gowda (2013).
The specific combining ability is used to designate those cases in which specific combinations do relatively better or worse than would be expected from the average performance of the lines involved. The SCA is controlled by dominance and non-allelic gene interactions. The high GCA effects of parents may produce hybrids with low SCA effects and vice versa. Therefore, when selecting elite parents for crosses, understanding and accounting for the relationship between the GCA of the parents, the SCA of the crosses, and the dominant type of combining ability are key to improving breeding efficiency based on combining ability (Liu et al. 2019). The crosses, IIHR 2349 × Arka Ahuti (L×L) and IIHR 2349 × Arka Saurabh (L×L) involved low combiners which showed the importance of overdominance and epistasis in the inheritance of lycopene, ascorbic acid, calcium, magnesium, fruit length, and weight. Involvement of high and low combiners in the crossing revealed the significance of non-additive gene action governing the traits. The larger proportion of non-additive effects in self pollinated crops seems to be due to additive×additive epistatic which creates the possibility of isolating high performing pure lines for these characters. So, recurrent selection would be profitable for improving these characters (Mondal et al. 2009). The findings of Singh and Asati (2011), Yadav et al. (2013), and Adhi Shankar et al. (2014) would substantially support the present results.

Out of nine crosses, four crosses had high overall specific combining ability status indicating that 45.55% of hybrids were assigned high (H) overall specific combiners. The cross IIHR 2357 × Arka Vikas, involved both the parents with good overall general combining ability (H×H). Therefore additive gene action may be imperative and simple selection in segregating generation will be effective and the reliance should be placed on mass selection and progeny selection. Four crosses were H×L or L×H indicated the presence of non-additive gene action which is a prerequisite for launching a heterosis breeding. The remaining four crosses were L×L showed the significance of overdominance and epistatic gene action in the inheritance. Hence, intensive selection for SCA in segregating generations will be effective in the genetic improvement of fruit quality traits governing shelf life.

Conclusions

Significant differences among the genotypes indicated considerable genetic variability for fruit quality traits. The estimates of SCA variance were higher as compared to GCA variance. The non-additive gene action was exhibited for lycopene, titratable acidity, TSS, fruit length, diameter, weight, locule number, number of branches, number of clusters, number of fruit/cluster, and yield/plant which can be exploited through hybrid development and additive gene action is shown for pH, ascorbic acid, fruit firmness, and plant height can be exploited through varietal development. The study underlined the significance of non-additive gene action for shelf life, pericarp thickness, calcium, magnesium, pulp content.

The involvement of low combiners in hybridization signified over dominance and epistasis hence intensive selection for SCA in segregating generations will be effective. The involvement of high and low combiners in the crossing revealed the significance of non-additive gene action which is a prerequisite for heterosis breeding. The involvement of high combiners in crossing signified the importance of additive gene action and simple selection in segregating generation will be effective with more reliance on mass selection and progeny selection.

The crosses, IIHR 2349 × Arka Vikas and IIHR 2349 × Arka Saurabh were promising hybrids for high yield and shelf life. From a breeder point of view, these hybrids can be foreword to F2 to isolate transgressive segregants for fruit quality traits. These hybrids can also be foreword to succeeding segregating generations for the development of high-yielding-high shelf life varieties. From a farmer’s point of view, high shelf life tomato hybrids can be transported to long-distance markets before fruit quality is degraded and can get a good price for their produce during the price crash periods in the local markets. From a consumer point of view, high shelf life tomato hybrids can be stored for a long time in normal room condition without refrigeration. This would reduce huge losses in terms of quality and quantity of tomatoes.

Acknowledgements We are grateful to Dr. Sadashiva A.T., Scientist, Division of Vegetable crops and Dr. Shivashankara K.S., Scientist, Division of Plant Physiology and Biochemistry,
Author contributions All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by MPP, SG. The first draft of the manuscript was written by MPP and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Funding The authors declare that no funds, grants, or other support were received during the preparation of this manuscript.

Competing interests The authors have no relevant financial or non-financial interests to disclose.

References

Abrol GS, Thakur KS, Pal R, Punetha S (2017) Role of calcium in maintenance of postharvest quality of horticultural crops. Int J Econ Plants 4(2):088–093

Adhi Shankar RV, Reddy SK, Sujatha M, Pratap M (2014) Studies on combining ability and gene action studies for yield and yield contributing traits in tomato (Solanum lycopersicum L.). Helix 6:431–435

Akhtar S, Hazra P (2013) Nature of gene action for fruit quality characters of tomato (Solanum lycopersicum). Afr J Biotechnol 12:2869–2875

Al-jibourie HA, Miller PA, Robinson HF (1958) Genotypic and environmental variances in an upland cotton cross of interspecific origin. Agron J 50:636–637

Arab L, Steck S (2000) Lycopene and cardiovascular disease. Am J Clin Nutr 71(6):1691S–1695S

Arah IK, Amaglo H, Kumah EK, Ofori H (2015) Preharvest and postharvest factors affecting the quality and shelf life of harvested tomatoes: a mini review. Int J Agron. https://doi.org/10.1155/2015/478041

Arunanachal V (1974) Fallacy behind the use of modified line × tester design. Indian J Genet 34:280–287

Arunanachal V, Bandopadhyay A (1979) Are “Multiple cross multiple pollen hybrids” an answer for productive populations in Brassica companion variety brown serson? Theor Appl Genet 54:203–207

Association of Official Analytical Chemists (2000) Official methods of analysis. Titratable acidity of fruit products, vol 942, 17th edn. AOAC International, Gaithersburg, p 15

Association of Official Analytical Chemists (2006) Official methods of analysis. Ascorbic acid, 967.21, 45.1.14. AOAC International, Gaithersburg

Bhatt RP, Biswas VR, Kumar N (2001) Heterosis, combining ability and genetics for vitamin C, total soluble solids and yield in tomato (Lycopersicon esculentum) at 1700 m altitude. J Agric Sci 137(1):71–75

Bhutani RD, Kalloo G (1983) Genetics of carotenoids and lycopene in tomato (L. esculentum Mill.). Genetic Agrar 37:1–6

Das I, Hazra P, Longjam M, Bhattacharjee T, Maurya PK, Banerjee S (2020) Genetic control of reproductive and fruit quality traits in crosses involving cultivars and induced mutants of tomato (Solanum lycopersicum L.). J Genet 99:56

Delina T, Mahendran (2009) Physico-chemical properties of mature green tomatoes with pectin during storage and ripening. Trop Agric Res Ext 12(2):110–112

Dhatt AS, Singh S, Dhalwal MS (2003) Genetic analysis of shelf life and firmness of tomato using rin, nor and alc lines. J Genet Breed 57:313–318

Freeman BB, Reimers K (2011) Tomato consumption and health: emerging benefits. Am J Life Style Med 5(2):182–191

Gaikwad AK, Cheema DS (2009) Heterosis for yield in heat tolerant tomato lines. Crop Improv 36(1):55–59

Garcia LGC, da Silva EP, de Melo Silva Neto C, de Barros Vielas Boas EV, Asuieri ER, Damiani C, da Silva FA (2019) Effect of the addition of calcium chloride and different storage temperatures on the post-harvest of jabuticaba variety Pingo de Mel. Food Sci Technol 39(Suppl 1):261–269

Garg NS, Cheema DS, Dhatt AS (2007) Combining ability analysis involving rin, nor and alc alleles in tomato under late planting conditions. Adv Hortic Sci 21(2):59–67

Garg NS, Cheema DS, Dhatt AS (2008) Genetics of yield, quality and shelf life characteristics in tomato under normal and late planting conditions. Euphytica 159:275–288

Hayes HK, Immer FR, Smith DC (1955) Methods of plant breeding. Mc. Graw Hill Book Co., Inc, New York, p 551

Jones JB (1999) Tomato plant culture: in the field, greenhouse, and home garden. CRC Press LLC, Florida, pp 11–53

Joshi A, Thakur MC, Kohli UK (2005) Heterosis and combining ability for shelf life, whole fruit firmness and related traits in tomato. Indian J Hortic 62(1):33–36

Kalloo G, Singh RK, Bhutani RD (1974) Combining ability studies in tomato (L. esculentum Mill.). Theor Appl Genet 44:358–363

Kansouh AM, Zakhir AG (2011) Gene action and combining ability in tomato (Lycopersicon esculentum Mill.) by line × tester analysis. J Plant Prod Mansoura Univ 2(2):213–227

Katoch V, Vidyasagar (2004) Genetic studies on yield and its components in tomato. J Appl Hortic 6:45–47

Kempthorne (1957) An introduction to genetic statistics. Wiley, New York, pp 458–471

Kumar S, Ramanjini Gowda PH (2016) Estimation of heterosis and combining ability in tomato for fruit shelf life and yield component traits using line × tester method. Int J Agron Agric Res 9(3):1–19
Kumar KHY, Patil SS, Dharmatti PR, Byadagi AS, Kajjidoni ST, Patil RH (2009) Estimation of heterosis for tospovirus resistance in tomato. Karnataka J Agric Sci 22:1073–1075

Kumari S, Sharma MK (2011) Exploitation of heterosis for yield and its contributing traits in tomato (Solanum lycopersicum L.). Int J Farm Sci 1:45–55

Lichtenthaler HK (1987) Chlorophylls and carotenoids: pigments of photosynthetic biomembranes. Meth Enzymol 148:350–382

Liu ZB, Jiang JB, Yang HH, Jiang XM, Li JF (2019) Research advance of plant heterosis. Mol Plant Breed 17:4127–4134

Marschner H (1995) Mineral nutrition of higher plants, 2nd edn. Academic Press, New York, pp 277–299

Mather K, Jinks IL (1982) Biometrical genetics. 3rd edition. Chapman and Hall, London

Mohan Rao A (2001) Heterosis as a function of genetic divergence in sunflower (Helianthus annuus L.). Ph.D. thesis submitted to Acharya N.G. Ranga Agricultural University, Hyderabad, pp 208

Mondal C, Sarkar S, Hazra P (2009) Line × Tester analysis of combining ability in tomato (Lycopersicon esculentum Mill.). J Crop Weed 5(1):53–57

Osei MK, Danquah E, Danquah A, Blay E, Adudaapa H (2020) Hybridity testing of tomato F1 progenies derived from parents with varying fruit quality and shelf life using single nucleotide polymorphism (SNPs). Sci Afr 8:1–16

Panse VG, Sukathme PV (1967) Statistical methods for agricultural workers. ICAR, New Delhi, p 145

Parker R, Maalekuu BK (2013) The effect of harvesting stage on fruit quality and shelf-life of four tomato cultivars (Lycopersicon esculentum Mill.). Agric Bio J N Am 4(3):252–259

Pavan MP, Gangaprasad S (2022) Studies on mode of gene action for fruit quality characteristics governing shelf life in tomato (Solanum lycopersicum L.). Sci Hortic. https://doi.org/10.1016/j.scienta.2021.110687

Rodriguez GR, Pratta GR, Liberatti DR, Zorzoli R, Picardi LA (2010) Inheritance of shelf life and other quality traits of tomato fruit estimated from F1’s, F2’s and backcross generations derived from standard cultivar, nor homozigote and wild cherry tomato. Euphytica 176:137–147

Roopa L, Sadhashiva AT, Reddy KM, Rao KPG, Prasad BCN (2001) Combining ability studies for long shelf life in tomato. Veg Sci 28:24–26

Salliba C, Cause M, Langlois D, Philouze J, Buret M (2001) Genetic analysis of organoleptic quality in fresh market tomato, mapping QTLs for physical and chemical traits. Theor Appl Genet 102:259–272

Shehata SA, Abdelrahman SZ, Megahed MMA, Abdeldayyem EA, El-Mogy MM, Abdelgawad KF (2021) Extending shelf life and maintaining quality of tomato fruit by calcium chloride, hydrogen peroxide, chitosan, and ozonated water. Horticultrae 7(9):309. https://doi.org/10.3390/horticulturae7090309

Singh AK, Asati BS (2011) Combining ability and heterosis studies in tomato under bacterial wilt condition. Bangladesh J Agric Res 36:313–318

Singh RK, Chaudhary BD (1977) Biometrical methods in quantitative genetic analysis. Kalyani, Ludhiana

Sinha SR, Singh B, Faruquee M, Jiku MA, Sayem M, Rahman MA, Alam MA, Kader MA (2019) Post-harvest assessment of fruit quality and shelf life of two elite tomato varieties cultivated in Bangladesh. Bull Natl Res Centre 43:185

Somraj B, Reddy RVSK, Ravinder Reddy K, Saidaiah P, Thirupathi Reddy M (2018) Generation mean analysis of yield components and yield in tomato (Solanum lycopersicum L.) under high temperature conditions. J Pharmacogn Phytochem 7:1704–1708

Suo LJ, Lin SH, Qiang SZ (2010) Analysis on the major gene and polynucle mixed inheritance of lycopene content in fresh consumptive tomato fruit. Hreditas 28(4):458–462

Technow F (2019) Use of F2 bulks in training sets for genomic prediction of combining ability and hybrid performance. G3 Genes Genomes Genet 9:1557–1569

Turner JHJR (1953) A study of heterosis in upland cotton, yield of hybrids compared with varieties. Agron J 45:487–490

Yadav SK, Singh BK, Baranwal DK, Solankey SS (2013) Genetic study of heterosis for yield and quality components in tomato (Solanum lycopersicum). Afr J Agric Res 8(44):5585–5591

Yogendra KN, Gowda PH (2012) Line × tester analysis in tomato (Solanum lycopersicum L.): identification of superior parents for fruit quality and yield-attributing traits. Int J Plant Breed 7(1):50–54

Yogendra KN, Gowda PH (2013) Phenotypic and molecular characterization of a tomato (Solanum lycopersicum L.) F2 population segregation for improving shelf life. Genet Mol Res 12(1):506–518

Yu KC, Wang H, Liu XG, Xu C, Li ZW, Xu XJ, Liu JC, Wang ZH, Xu YB (2020) Large-scale analysis of combining ability and heterosis for development of hybrid maize breeding strategies using diverse germplasm resources. Front Plant Sci 11:660

Publisher’s Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.