Plant Genetic Resources: Characterization and Utilization

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Genetic variability, trait inter-relationships, third and fourth degree statistics based genetics for fruit quality and yield traits governing shelf life in tomato (*Solanum lycopersicum L.*)

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Research Article

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Abstract

Knowledge on genetic architecture and inheritance of tomato shelf life contributing traits in different genetic backgrounds is a key issue for shelf life improvement. An investigation was undertaken to estimate the nature and magnitude of variability, traits inter-relationships, third and fourth degree statistics to unravel the genetics of 18 fruit quality and yield traits governing shelflife in F_2 population of 'Arka Vikas' × 'Red ball' cross. The wider standardized range and higher estimates of phenotypic coefficient of variation indicated prevalence of adequate variability for fruit quality and yield traits. Fruit firmness and pericarp thickness ranged from 1.20–3.44 kg/cm^2 and 2.44–5.31 mm respectively. Pulp content and shelflife ranged from 58.59–94.70% and 10.60–26.40 days respectively. Significant positive correlation with direct effect on fruit shelf life was exhibited by fruit firmness, pericarp thickness, TSS, titratable acidity, pulp content, fruit length and locule number. Positive skewness with platykurtic distribution recorded for TSS, lycopene, ascorbic acid, titratable acidity, fruit length, weight, pericarp thickness, plant height and number of branches. Negatively skewed with platykurtic distribution observed for pH, fruit diameter, firmness, pulp content, locule number, shelf life and number of clusters which signified duplicate epistasis of dominant genes in traits inheritance. The transgressive segregants for fruit quality traits indicated complementary effects of dispersed allele combinations between parents. Additive and dominance components could be exploited in the advanced segregating population by evaluating large number of families. In addition to additive effects, predominance of dominance effects of genes are important in inheritance of fruit quality traits governing shelflife.

Introduction

Tomato (*Solanum lycopersicum* L.), is one of the widely cultivated and consumed vegetable crops in the world. It is a significant dietary source of antioxidants like lycopene, β-carotene, ascorbic acid and flavonoids which have blood purification and anti-cancerous properties (Arab and Steck, 2000). It is a perishable fruit crop with relatively short shelf life after ripening thus experiences remarkable post-harvest losses (Zewdie *et al.*, 2022). Globally post-harvest losses of tomatoes estimated upto 25–42% (Arah *et al.*, 2015) and upto 50% in developing countries (Delina and Mahendran, 2009).

The fruit development and maturation is the final phase of floral development. Tomato is a climacteric fruit which shows a burst of ethylene biosynthesis and an increase in respiration during ripening (Lelievre *et al.*, 1997). The ripening is accompanied by many structural and biochemical changes in fruit. These changes include cell wall ultrastructure and textural modification, conversion of starch to sugars, alterations in pigment biosynthesis and accumulation of increased levels of flavour and aromatic volatiles and increased susceptibility to post-harvest pathogens (Seymour *et al.*, 1993). The activation of cell wall degrading enzymes such as polygalacturonase and b-galactosidase at the climacteric is a major cause of fruit softening.

The fruits perishability is the cumulative effects of sub-standard post-harvest operations such as improper storage, inadequate transportation and insufficient processing, preservation facilities. This resulted in chemical and physical changes in the fruits such as loss of weight, sugar and acid contents, respiration, transpiration, softening of pulp and microbial decay which greatly contributes to high post-harvest losses (Garcia *et al.*, 2019; Zewdie *et al.*, 2022).This leads to glut in the market and interns' farmers fail to avail expected returns for their produce (Delina and Mahendran, 2009). Consequently, large volumes of low quality

tomatoes sold at throw-away prices and interns the farmers, processors and traders fail to get expected return for their produce (Sinha *et al*., 2019).

The post-harvest shelf life is one of the most important fruit quality traits for commercially grown tomatoes. Prolonging the keeping quality of tomatoes is very essential for both successful marketing and alleviates great losses in quality and quantity. This will enhance sufficient time for farmers to market their produce before fruit quality degraded (Osei *et al*., 2020). Minimizing these losses can increase their supply without bringing additional land under cultivation. Therefore, need for reduction of post-harvest losses is paramount important.

A number of post-harvest treatments of fruits with vinegar, salicylic acid (Chavan and Sakhale, 2020), calcium chloride and modified atmosphere packaging i.e. storage in plastic films are efficient methods in prolonging keeping quality. Through the advanced RNA interference technique it is possible to down regulate the ethylene biosynthesis enzymes gene expression such as ACC synthase and ACC oxidase, SAM-synthase and cell wall degrading enzymes such as endo-polygalacturonase and pectin methylesterase (Carrari *et al*., 2007). This resulted in the extension of shelf life of tomato fruit.

The transgenic approaches to improve tomato shelf life focused on delaying over ripening, silencing of genes encoding cell wall degrading enzymes and silencing inducers of ripening or over expressing inhibitors of ripening. Flavr Savr was the first genetically engineered food crop to be granted a license for human consumption. It had increased fungal resistance and improved shelf life. It contains two genes i.e. a reversed antisense polygalacturonase gene which interferes with the production of the enzyme Beta polygalacturonase and a gene responsible for the creation ofAminoglycoside-3'-phosphotransferase which confers resistance to kanamycin and neomycin (Redenbaugh *et al*., 1992). But these technologies are laborious, need greater financial assistance, unfeasible in farmer's field and need social acceptance. Therefore, genetic improvement through conventional plant breeding is the best option and safest way (Yogendra and Gowda, 2013).

Several biochemical and genetic studies in tomato resulted in the identification and characterization of tomato ripening mutants such as alcobaca (*alc*), ripening-inhibitor (*rin*) and non-ripening (*nor*) which contain genes located on chromosomes 10, 10 and 5 respectively. These mutant genes encode for delayed ripening. The *alc* mutant gene governs uniform ripening in fruits while the fruits of *nor* and *rin* fail to ripen and do not exhibit any climacteric rise. During ripening all three mutants exhibit little or no activity of polygalactouranase enzyme. Through conventional breeding, the *alc*, *nor* and *rin* genes can be utilized for development of longer shelf life lines and varieties (Kopeliovitch *et al*., 1979).

In hybridization programme, selection of parents based on per se performance alone is not sound procedure since superior lines identified on this basis may yield poor recombinants in the segregating generations (Garg *et al*., 2007). Hence, effectiveness of tomato breeding hinges on comprehensive information on genetics of target traits.

Many earlier studies reported that the fruit shelf life is a ripening-associated complex trait affected by several low inherited quantitative fruit biochemical, morpho-physiological and yield traits. Genetics of quantitative traits could be unravelled at first, second, third and fourth degree statistics levels. Skewness, the third degree statistics and kurtosis, the fourth degree statistics are more powerful and useful than first (mean) and second degree (variance) statistics and their derivatives, especially for detecting and characterizing nature of epistasis. The information elicited from nature and magnitude of variability, traits inter-relationships and genetic analysis of economic traits in F_2 population guide plant breeders in identifying the transgressive segregants which can be tested for their combining ability to isolate best parental lines for hybridization in development of heterotic hybrids. There is a popular saying that 'A ton of fruits and vegetables saved is equivalent to two tons produced'. With this justified focus, we had attempted to unravel genetics of more important but less pursued shelf life and its contributing traits at third and fourth degree statistics levels.

Materials and method

The experiment consists of two steps, i.e. 1. Development of F_1 and F_2 generations and 2. Evaluation of parents, F_1 and F_2 generation.

Experimental site

The present investigation was carried out by conducting field and lab experiments during 2017 summer, rainy seasons and 2018 summer at Department of Genetics and Plant Breeding, College of Agriculture, Keladi Shivappa Nayaka University of Agricultural and Horticultural Sciences (KSNUAHS), Navule, Shivamogga (13.9739^{0}N, 75.5791^{0}E), Karnataka, India.

Basic genetic material

The basic material for the study involved two parents contrasting for shelf life such as 'Arka Vikas' (P_1) and 'Red ball' (P_2). 'Arka Vikas' is high yielding low shelf life popular publically bred tomato variety released from ICAR-Indian Institute of Horticultural Research, Bengaluru, Karnataka, India. 'Red ball' is high shelf life low yielding genotype maintained in KSNUAHS, Shivamogga (Pavan *et al*., 2018).

Development of experimental material

The crosses were affected during 2017 summer by pollinating pollens from male parent, 'Red ball' to the stigmas of emasculated flowers of seed parent, 'Arka Vikas'. The crossing was done between 6–8 A.M. in protected polyhouse condition and developed the first filial generation, F_1 hybrid (Arka Vikas × Red ball). The seeds of F_1 were sown during 2017 rainy season, raised healthy plants and were selfed. The selfed seeds were harvested individually and bulked which constituted the second filial generation i.e. the F_2 population which was the experimental material.

Evaluation of experimental material

The non-segregating, homogeneous P_1, P_2 and F_1 generations were planted in two separate contiguous blocks in Randomized Complete Block Design with two replications. The segregating, heterogeneous F_2 population was planted without replications. Standard crop production and protection practices were followed to raise healthy plants. The P_1, P_2, F_1 and F_2 generations were evaluated for fruit quality and yield traits governing shelf life during 2018 summer.

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Sampling of plants and collection of data

The data were recorded on five randomly selected plants (avoiding border plants) in each of P_1, P_2 and F_1 generations. All 223 plants in F_2 generation were considered for data recording since each plant in F_2 generation acts as a unique genotype. The 18 fruit quality traits governing shelf life such as 5 fruit biochemical traits TSS (%) (using Erma hand refractometer), pH (using Siemens pH meter), lycopene (mg/100 g) (Lichtenthaler spectrophotometric method, Lichtenthaler 1987), ascorbic acid (mg/100 g) (2,6-Dichlorophenol indophenol method, Association of Official Analytical Chemists, 2006), titratable acidity (%) (AOAC titration method, Association of Official Analytical Chemists 2000), 8 morpho-physiological traits fruit length (cm), diameter (cm) and pericarp thickness (mm) were measured with digital vernier-caliper, fruit weight (g) (using digital weighing), firmness (kg/cm2) (using fruit penetrometer), pulp content (%), 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 fruit surface) and 5 yield attributing traits plant height (cm), number of branches, number of clusters, number of fruit/cluster, yield/plant (cm) 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. The mean for each trait in each plant was estimated and then the mean of five plants was computed.

Statistical analysis

The collected data on fruit bio chemical, morpho-physiological and yield characters were analysed for descriptive statistics which are as follows.

Mean: By using all the individual plant observations, the population mean for each character was computed as $\bar{x} = (\sum x/n)$, where, $\bar{x}$ = Mean value, n = Number of observations.

Absolute range: The lowest and the highest values by individual plant observation were used to indicate the range for a given character.

Standardized range: The variability among the traits was compared by using the standardised range which was computed as follows

$$\text{Standardized range} = \frac{(\text{Highest value} - \text{Lowest value})}{\text{Mean}}$$

Coefficient of variability: The phenotypic coefficients of variability (PCV) for all the characters were computed (Burton and De vane, 1953) and expressed as per cent.

$$\text{PCV (\%)} = \frac{\sigma_p}{\bar{x}} \times 100$$

where, $\bar{x}$ = Grand mean of the character, σ_p = Phenotypic standard deviation

PCV values were further categorised as low, moderate and high as indicated by Sivasubramanian and Madhavamenon (1973) given as Low = 0–10%, Moderate = 10.1–20% and High = >20%.

Correlation coefficient analysis: The correlation coefficients among fruit bio chemical, morpho-physiological and yield characters at phenotypic (r_p) level were estimated (Al-Jibourie *et al.*, 1958).

$$\text{Phenotypic correlation} = r_{xy}(p) = \frac{\text{Cov}_{(xy)}(p)}{\sqrt{\sigma^2(x)_p \times \sigma^2(y)_p}}$$

where, $\text{Cov}_{(xy)}$ (p) = Phenotypic covariance's between 'x' and 'y' characters, $(x)_p$ = Phenotypic variances of 'x' character, $(y)_p$ = Phenotypic variances of 'y' character. The significance of correlation co-efficient was tested by comparing Table 'r' values for n-2 error degrees of freedom.

Path coefficient analysis: Path coefficient is a standardised partial regression coefficient. It is a measure of the direct and indirect effect of component characters as a dependent variable such as fruit shelf life. Direct and indirect effect of component characters on fruit shelf life was computed using appropriate correlation coefficient of different component characters (Wright, 1921, Dewey and Lu, 1959). Thus the correlation coefficient of any character with fruit shelf life was split into direct and indirect effects by adopting the standard formula

$$R_{isl} = r_{1i}P_1 + r_{2i}P_2 + r_{3i}P_3 + \ldots\ldots\ldots + r_{ni}P_n + \ldots\ldots r_{ii}P_1$$

where, R_{isl} = Correlation of the character on fruit shelf life, r_{1i} = The indirect effect of ith character on fruit shelf life through the first character, $r_{ni}P_n$ = Correlation between nth character and ith character, n = Number of independent variables, P_i = The direct effect of i^{th} character on fruit shelf life. The direct effect of component character on fruit shelf life was obtained by solving the following equations. $rry = [p_{1y}]\ [r_{ij}]$, Where, $[Pi] = [r_{ij}]^{-1}$ $[r_{ij}]$. The following formula obtained the residual effect

Residual effect = $P_R = \sqrt{1 - (P_{ij}r_{iy})}$, Where, P_{ij} and r_{iy} are as given above.

Frequency of transgressive segregants: The frequency of transgressive segregants indicates the occurrences in F_2 of individuals with a higher or lower intensity of a character than those present in the parents involved in the cross and it was expressed in per cent. For lower parent, the frequency of transgressive segregants = Total number of plants in F_2 segregating generation having trait means less than or equal to lower parent traits means and multiplied by 100. Similarly the frequency of transgressive segregants for higher parent was calculated. The analysis of descriptive statistics and frequency of transgressive segregants analysis was performed using 'WINDOSTAT'statistical package.

Skewness: Skewness is a measure of the extent to which the distribution of the respective variable skewed to the left (negative value) or right (positive value), relative to the standard normal distribution (for which the skewness is 0). The measure of skewness is related to the third moment of the distribution. The skewness defined as $\text{Skewness} = n \times \mu_3 \ / \ [(n-1) \times (n-2) \times \sigma^3]$, Where, '$\mu_3$' is equal to $\Sigma\ (Xi - \bar{x}) \times 3$, 'n' is the valid number of cases, 'σ^3' is the standard deviation (sigma) raise to the third power.

Kurtosis: The kurtosis is a measure of how 'wide' or skinny ('Flat' or 'Peaked') the distribution is for the respective variable relative to the standard normal distribution (for which the kurtosis is equal to 0). It is also sometimes referred to as the fourth moment of the distribution. The kurtosis defined as:

$$\text{Kurtosis} = [n\ x\ (n+1)x\ (\mu_4 - 3)x\ \mu_2 x\ \mu_2 x\ (n-1)]/$$
$$[(n-1)x\ (n-2)x\ (n-3)x\ \sigma^4]$$

Where, 'μ_4' is equal to $\Sigma\ (Xj - \bar{x}) \times j$, 'n' is the valid number of cases, 'σ^4' is the standard deviation (sigma) raise to the fourth power. The skewness and kurtosis were estimated (Snedecor

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and Cochran, 1994) using 'SPSS 16.0' (Statistical Package for Social Sciences) software program developed by Microsoft Corporation .

Results

Perse performance of parents, F_1 and F_2 segregating generation for fruit quality and yield traits

The mean values of both non-segregating and segregating generations were comparable to each other for all quantitative fruit quality traits (Table 1). The parents exhibited observable differences for all studied traits except for TSS, pH, lycopene and number of fruits/cluster. The P_1 exhibited superior performance for fruit biochemical (TSS, lycopene, ascorbic acid, titratable acidity) and yield traits (number of clusters, number of fruit/cluster, yield/plant). Similarly, P_2 was superior for morpho-physiological traits (fruit length, diameter, weight, firmness, pericarp thickness, pulp content, locule number, shelf life, plant height and number of branches). The trait means of first filial generation (F_1) were intermediate to those of their parents for ascorbic acid, titratable acidity, fruit length, weight, firmness, pericarp thickness, pulp content, shelf life, number of branches, number of clusters and higher for lycopene, diameter, locule number, plant height and yield/plant.

The F_2 plants were taller with more number of clusters and fruits had higher TSS, lycopene, diameter and locule number compared to parents. However, mean TSS, ascorbic acid, fruit length, weight, firmness, number of clusters and number of fruit/cluster was higher than F_1. The F_2 mean was lower than $F_1$for pH, lycopene, titratable acidity, pericarp thickness, plant height, yield/plant, locule number, shelf life, number of branches, fruit diameter and pulp content.

Variability in segregating generation for fruit quality and yield traits

Among F_2plants, TSS ranged from 2.10–6.20% (Table 2). pH ranged from 2.60–5.60.Lycopene ranged from 0.09–6.91 mg/100 g. Ascorbic acid ranged from 1.75 −29.65 mg/100 g.Titratable acidity ranged from 0.01–1.60%. The fruit length and diameter ranged from 31.20–49.43 cm and 36.98–70.52 cm respectively. Fruit weight ranged from 26.80–116.00 g. Fruit firmness and pericarp thickness ranged from 1.20–3.44 kg/cm^2 and 2.44–5.31 mm respectively.

Pulp content ranged from 58.59–94.70%. Locule number ranged from 2.00–6.60. Shelf life ranged from 10.60–26.40 days. The plant height and number of branches ranged from 35.60–122.30 cm and 2.30–8.30 respectively. Number of clusters, number of fruit/cluster and yield/plant ranged from 5.30–21.30, 3.00–35.00 and 345.60–2101.20 g respectively.

Among fruit quality and yield traits, the standardized range varied from 0.46–7.75. Wider standardized range and higher PCV manifested for number of fruit/cluster followed by titratable acidity, ascorbic acid, yield/plant, lycopene and number of fruit/cluster. Further, narrow standardized range and PCV recorded for rest of traits. The fruit length, pulp content and fruit diameter were weekly varied among F_2 plants.

Table 1. Estimates of fruit quality and yield traits means of parents, F_1 and F_2 segregating generation

		Mean ± SE			
Sl.No.	Fruit quality and yield traits	P_1	P_2	F_1	F_2
1	TSS (%)	3.24 ± 0.02	3.18 ± 0.11	2.98 ± 0.06	3.42 ± 0.05
2	pH	5.29 ± 0.02	5.30 ± 0.04	5.15 ± 0.05	4.23 ± 0.03
3	Lycopene (mg/100 g)	2.65 ± 0.09	2.60 ± 0.07	4.36 ± 0.09	2.68 ± 0.09
4	Ascorbic acid (mg/100 g)	25.05 ± 0.57	1.77 ± 0.04	4.56 ± 0.08	9.77 ± 0.31
5	Titratable acidity (%)	2.43 ± 1.60	0.63 ± 0.03	0.71 ± 0.02	0.57 ± 0.02
6	Fruit length (cm)	38.74 ± 0.69	43.58 ± 1.47	39.43 ± 0.48	39.89 ± 0.24
7	Fruit diameter (cm)	42.59 ± 1.50	45.64 ± 1.43	52.36 ± 0.44	51.90 ± 0.37
8	Fruit weight (g)	46.78 ± 1.40	70.20 ± 0.51	55.94 ± 1.94	56.81 ± 0.92
9	Fruit firmness (kg/cm^2)	1.67 ± 0.02	3.40 ± 0.05	2.01 ± 0.07	2.30 ± 0.03
10	Pericarp thickness (mm)	4.39 ± 0.22	7.27 ± 0.05	4.41 ± 0.09	3.59 ± 0.05
11	Pulp content (%)	71.95 ± 0.49	81.90 ± 0.45	80.73 ± 0.89	76.92 ± 0.58
12	Locule number	3.90 ± 0.29	4.34 ± 0.11	5.64 ± 0.23	5.03 ± 0.08
13	Shelf life (Days)	16.90 ± 0.37	38.16 ± 0.68	27.85 ± 0.62	19.01 ± 0.26
14	Plant height (cm)	66.88 ± 1.55	73.77 ± 1.08	101.34 ± 2.50	74.82 ± 1.07
15	Number of branches	4.52 ± 0.12	5.46 ± 0.20	4.84 ± 0.43	4.76 ± 0.08
16	Number of clusters	11.86 ± 0.20	6.16 ± 0.12	11.52 ± 0.17	15.03 ± 0.20
17	Number of fruit/cluster	4.54 ± 0.09	4.12 ± 0.15	3.60 ± 0.10	4.27 ± 0.20
18	Yield/plant (g)	1260.83 ± 47.12	561.30 ± 5.77	1336.57 ± 43.06	667.14 ± 23.19

Where, P_1 - 'Arka Vikas', P_2 - 'Red ball', F_1 - 'Arka Vikas Red ball', F_2 - F_1 F_1, SE: Standard error.

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Table 2. Estimates of descriptive statistics, third and fourth degree statistics for fruit quality and yield traits in F_2 segregating generation

Sl. No.	Fruit quality and yield traits	Absolute range		Standardized range	Standard deviation	PCV (%)	Skewness	Kurtosis
		Low	High					
1	TSS (%)	2.1	6.2	1.21	0.7	20.73	1.43	2.85
2	pH	2.6	5.6	0.71	0.46	10.94	−1.32	1.89
3	Lycopene (mg/100 g)	0.09	6.91	2.59	1.33	50.59	0.55	0.1
4	Ascorbic acid (mg/100 g)	1.75	29.65	2.82	4.66	47.15	0.22	0.52
5	Titratable acidity (%)	0.01	1.6	2.84	0.24	44.43	0.52	0.66
6	Fruit length (cm)	31.2	49.43	0.46	3.62	9.06	0.08	−0.19
7	Fruit diameter (cm)	36.98	70.52	0.64	5.31	10.21	−0.13	0.59
8	Fruit weight (g)	26.8	116	1.56	1.34	23.44	0.34	1.04
9	Fruit firmness (kg/cm^2)	1.2	3.44	0.98	0.48	21.24	−0.16	−0.45
10	Pericarp thickness (mm)	2.44	5.31	0.8	0.7	19.64	0.36	−0.98
11	Pulp content (%)	58.59	94.7	0.47	8.59	11.13	−0.77	−0.12
12	Locule number	2	6.6	0.91	1.15	22.95	−0.89	−0.27
13	Shelf life (Days)	10.6	26.4	0.83	3.97	20.87	−0.27	−1.06
14	Plant height (cm)	35.6	122.3	1.16	1.62	21.6	0.15	−0.05
15	Number of branches	2.3	8.3	1.26	1.15	24.18	0.33	−0.21
16	Number of clusters	5.3	21.3	1.06	3.06	20.32	−0.18	−0.38
17	Number of fruit/cluster	3	35	7.75	2.16	52.51	13.1	187.18
18	Yield/plant (g)	345.6	2101.2	2.66	3.53	53.47	2.46	7.62

Quantitative traits inter-relationships

Association of fruit quality and yield attributing traits with shelf life

Significant and positive correlation with shelf life recorded for fruit firmness, pericarp thickness, titratable acidity, pulp content, TSS, yield/plant, locule number and fruit length (Table 3).

Path co-efficient analysis for fruit quality and yield attributing traits with shelf life

Direct effect: Twelve out of eighteen traits had positive direct effect on fruit shelf life at phenotypic level (Table 3). The traits which had positive direct effect were fruit firmness, pericarp thickness, TSS, titratable acidity, pulp content, lycopene, pH, number of branches, ascorbic acid, fruit length, plant height and locule number. However, fruit diameter, number of clusters, yield/plant, number of fruits/cluster and fruit weight had negative direct effect on shelf life.

Indirect effect: Fruit firmness influenced shelf life indirectly in positive direction through titratable acidity, locule number, pulp content, yield/plant, pericarp thickness and fruit length at phenotypic levels. Pericarp thickness recorded positive indirect effect on shelf life via yield/plant, titratable acidity, fruit firmness and TSS whereas, through other traits, it had negligible indirect effects. The residual effect was moderate.

Third and fourth degree statistics based genetics for fruit quality and yield traits

The F_2 population manifested positive skewness with platykurtic distribution for TSS, lycopene, ascorbic acid, titratable acidity, fruit length, weight, pericarp thickness, plant height and number of branches. Negatively skewed and platykurtic distribution was exhibited by pH, fruit diameter, firmness, pulp content, locule number, shelf life and number of clusters. Two traits *viz.*number of fruits/cluster and yield/plant showed leptokurtic and positively skewed distribution.

Transgressive segregants for fruit quality and yield traits

The frequency of plants that transgressed higher scoring parent 'Arka vikas' was higher for TSS and number of cluster (Table 4).Similarly, frequency of segregants that surpassed 'Red ball' was more for fruit diameter, pulp content, locule number and plant height (Fig. 1).

Discussion

Perse performance of parents, F_1 and F_2 segregating generation for fruit quality and yield traits

Observable differences exhibited between the parents which were further validated though the contrasting nature of parents for fruit quality and yield traits (Renna *et al.*, 2019, Grozeva *et al.*, 2021). An intermediate and higher trait means of hybrid compare to their parents highlighted an overall heterosis for traits (Pavan *et al.*, 2022). The higher F_2 generation mean than F_1 generation mean for TSS, ascorbic acid, fruit length, weight, firmness, number of clusters and number of fruit/cluster were contrast to the findings of Garg *et al.*, 2008, Gaikwad and Cheema, 2009. The lower F_2 mean compared to F_1 indicated the role of dominance gene action in the inheritance of pH, lycopene, titratable acidity,

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Table 3. Estimates of phenotypic correlation coefficients, direct and indirect effects of fruit quality and yield traitson shelf life

	TSS	pH	LYC	ASA	TA	FL	FD	FW	FF	PT	PC	LN	PHT	NOB	NOC	NOF	YPP	CC
TSS	**0.200**	0.016	−0.002	−0.030	0.017	0.009	−0.011	−0.009	0.005	0.037	0.005	−0.018	−0.017	−0.013	0.024	−0.006	−0.006	0.279**
pH	0.004	**0.057**	−0.003	0.005	−0.009	−0.003	−0.006	−0.003	0.001	−0.008	0.003	0.005	0.002	−0.002	0.002	−0.001	0.005	0.011
LYC	−0.001	−0.004	**0.070**	−0.006	−0.007	0.001	0.001	0.001	−0.001	0.008	0.002	0.001	−0.004	0.004	−0.006	0.004	−0.002	0.088
ASA	−0.005	0.003	−0.003	**0.031**	0.001	0.006	0.003	0.002	−0.003	−0.001	−0.003	−0.002	0.007	0.001	−0.003	−0.001	0.003	−0.051
TA	0.013	−0.024	−0.015	0.003	**0.156**	0.035	0.008	0.008	0.069	0.036	0.029	0.022	0.009	−0.007	0.006	−0.016	0.040	0.448**
FL	0.002	−0.001	0.001	0.005	0.006	**0.027**	0.018	0.019	0.004	0.002	−0.001	0.001	0.004	0.001	−0.001	0.001	0.005	0.139*
FD	0.001	0.003	−0.001	−0.003	−0.001	−0.021	**−0.032**	−0.026	−0.001	0.002	0.002	−0.004	−0.002	−0.002	0.003	−0.002	−0.003	−0.031
FW	0.001	0.001	−0.001	−0.001	−0.001	−0.006	−0.007	**−0.008**	−0.001	0.001	0.001	−0.001	−0.001	−0.001	0.001	−0.001	−0.001	−0.016
FF	0.012	0.003	−0.005	−0.044	0.196	0.066	0.017	0.015	**0.444**	0.087	0.116	0.118	0.013	0.020	0.042	−0.016	0.101	0.608**
PT	0.060	−0.046	0.037	−0.006	0.074	0.029	−0.020	−0.013	0.062	**0.316**	0.051	0.026	−0.028	−0.011	0.037	−0.017	0.085	0.487*
PC	0.003	0.007	0.004	−0.011	0.023	−0.003	−0.007	−0.004	0.032	0.020	**0.122**	0.016	0.001	0.008	0.003	0.009	0.014	0.326**
LN	−0.001	0.001	0.001	−0.001	0.002	0.001	0.001	0.001	0.003	0.001	0.002	**0.011**	0.001	0.001	0.001	0.001	0.003	0.169**
PHT	−0.001	0.001	−0.001	0.003	0.001	0.002	0.001	0.001	0.001	−0.001	0.001	0.001	**0.014**	0.002	−0.001	0.001	0.001	0.004
NOB	−0.003	−0.001	0.001	0.001	−0.002	0.001	0.004	0.002	0.002	−0.002	0.003	0.002	0.005	**0.050**	−0.004	0.002	0.003	0.049
NOC	−0.004	−0.001	0.003	0.003	−0.002	0.001	0.003	0.002	−0.003	−0.004	−0.001	−0.002	0.003	0.003	**−0.034**	0.002	−0.001	0.071
NOF	0.001	0.001	−0.001	0.001	0.002	−0.001	−0.001	−0.002	0.001	0.001	−0.001	−0.001	−0.001	−0.001	0.001	**−0.018**	0.001	−0.057
YPP	0.001	−0.002	0.001	−0.003	−0.007	−0.005	−0.002	−0.001	−0.006	−0.008	−0.003	−0.006	−0.003	−0.002	−0.001	0.001	**−0.029**	0.218**

TSS, TSS (%); TA, Titratable acidity (%); FF, Fruit firmness (Kg/cm^2); PHT, Plant height (cm); YPP, Yield/plant (g); pH, pH; FL, Fruit length (cm); PT, Pericarp thickness (mm); NOB, No. of branches; SL, Shelf life (Days); LYC, Lycopene (mg/100 g); FD, Fruit diameter (cm); PC, Pulp content (%); NOC, No. of clusters; CC, Correlation coefficient with fruit shelf life; ASA, Ascorbic acid (mg/100 g); FW, Fruit weight (g); LN, Loculenumber; NOF, No.of fruit/cluster.
*Significant at $p = 0.05$ **Significant at $p = 0.01$ Bold figures: Direct effect, Residual effect = 0.63.

Table 4. Estimates of frequency of transgressive segregants for fruit quality and yield traits in F_2 population

Sl. No.	Fruit quality and yield traits	Lower parent (%)	Higher parent (%)	Sl. No.	Fruit quality and yield traits	Lower parent (%)	Higher parent (%)
1	TSS	33.18	42.60	10	Pericarp thickness	84.15	0.00
2	pH	99.55	0.45	11	Pulp content	21.60	30.60
3	Lycopene	60.08	39.91	12	Locule number	20.25	75.60
4	Ascorbic acid	0.45	0.45	13	Shelf life	32.40	0.00
5	Titratable acidity	65.25	0.00	14	Plant height	31.05	51.75
6	Fruit length	39.15	17.17	15	Number of branches	50.40	27.00
7	Fruit diameter	3.15	86.85	16	Number of clusters	0.45	85.95
8	Fruit weight	25.20	14.40	17	Number of fruit/cluster	54.00	34.20
9	Fruit firmness	16.20	2.25	18	Yield/plant	43.65	4.50

pericarp thickness, plant height, yield/plant (Das *et al.*, 2020), locule number, shelf life (Garg *et al.*, 2008), number of branches, fruit diameter and pulp content (Pavan *a*nd Gangaprasad, 2022). The contrasting results of additive gene action were reported for lycopene (Suo *et al.*, 2010), locule number, shelf life (Rodriguez *et al.*, 2010) and yield/plant (Katoch and Vidyasagar, 2004).

Variability in segregating generation for fruit quality and yield traits

TSS and acidity are the critical elements of consumers' demand and chief determinants of yield, consistency and overall quality of finished product (Athinodorou *et al.*, 2021). TSS of 5.0–6.5% is preferable for industrial tomatoes. The pH below 4.5 is desirable for processing, because it halts the proliferation of microorganisms in final product. Higher lycopene is essential for processing to compensate for loss of antioxidant activity due to chemical, physical and biological factors (Siddiqui *et al.*, 2015). Lycopene alleviate the oxidative stress, delay ripening during storage period and thus extends shelf life of fruits. Ascorbic acid >20 mg/100 g is desirable for processing. Titratable acidity is an important quality attribute for tomato processing. The higher value (>0.35%) of which controls microbial deteriorations in canned tomato products (Renna *et al.*, 2019). Vijayakumar *et al.*, 2021 in their studies recorded TSS and titratable acidity of 2.32–5.72% and 0.33–0.76% respectively under normal conditions. Fruit length and diameter are less important for processing but important for table purpose.

Tomato fruits with high firmness and thicker pericarp keep well for long distance transport (Siddiqui *et al.*, 2015). Thicker pulp enhances firmness and ultimately fruit shelf life (Chakraborty *et al.*, 2007). The fruit firmness is one of the critical components of internal fruit quality and it is the final index on which the consumer's perception and decision to purchase a given batch of tomatoes depends. With advancement in fruit ripening, changes in fruit texture, structure and composition of their cell walls by breakdown of insoluble protopectin into soluble pectin takes place leads to softening of fruits which considerably influences post-harvest performance. Pericarp thickness assumes prime importance among parameters which condition fruit firmness. Thick pericarp fruits would stand long-distance transport and keep well for longer days. Fruits with fewer locules, ≤4 are desirable for fresh market (Siddiqui *et al.*, 2015).

Longer shelf life cultivars had slower phase of biochemical reactions which would stand for long-distance markets. When fruit is harvest at breakers stage, the respiration rate of fruit slowly goes on increasing i.e. climacteric rise with number of days elapsed from harvesting. The ethylene is rapidly produced in fruit at breaker stage, drives series of reactions that together define fruit ripening process (Moneruzzaman *et al.*, 2008). There is natural tendency for perishable fruits and vegetables to degrade to simpler inorganic compounds such as Co_2, H_2O and NH_3 through spontaneous biochemical reaction which leads to loss of free energy and reduction in shelf life and other (Moneruzzaman *et al.*, 2008).

The higher rate of change in physiological loss in fruit weight signified the higher dehydration rate that happens in tender tissue of turning stage tomatoes. The slow physiological losses in fruit weight and slow pace in rate of change in physiological loss in weight may contribute to higher shelf life in F_2 tomato lines.

The high shelf life lines identified in the segregating generations can be forward to subsequent generations for development of pure line varieties. Cultivation of these varieties can be transported to long-distance markets and farmers can get good price for their produce during price crash periods in local markets (Dar and Sharma, 2011).

The probability of isolating genotypes with maximum number of 'plus' genes is remote considering economically important traits controlled by large number of genes. However, genotypes with short of perfection are common in segregating population (Palmer, 1953). Crossing together genotypes short of perfection selected from cross is expected to uncover higher frequency of near perfection genotypes even from smaller F_2 populations which breeders normally handle. Wider standardized range for number of fruit/cluster, titratable acidity, ascorbic acid, yield/plant and lycopene indicated the prevalence of adequate variability among F_2 plants. The higher PCV for yield/plant, number of fruit/cluster, lycopene, ascorbic acid and titratable acidity suggested the possibility of exploiting variability for quality traits improvement in tomato. The estimates of PCV represent true reflection of variability, unlike standardized range which is biased by extreme values were relatively higher for traits with wider standardized range.

Thus, the estimates of wider standardized range followed by higher PCV and narrow standardized range followed by lower PCV indicated that the standardized range and PCV were complement each other in explaining the variability in F_2 generation.

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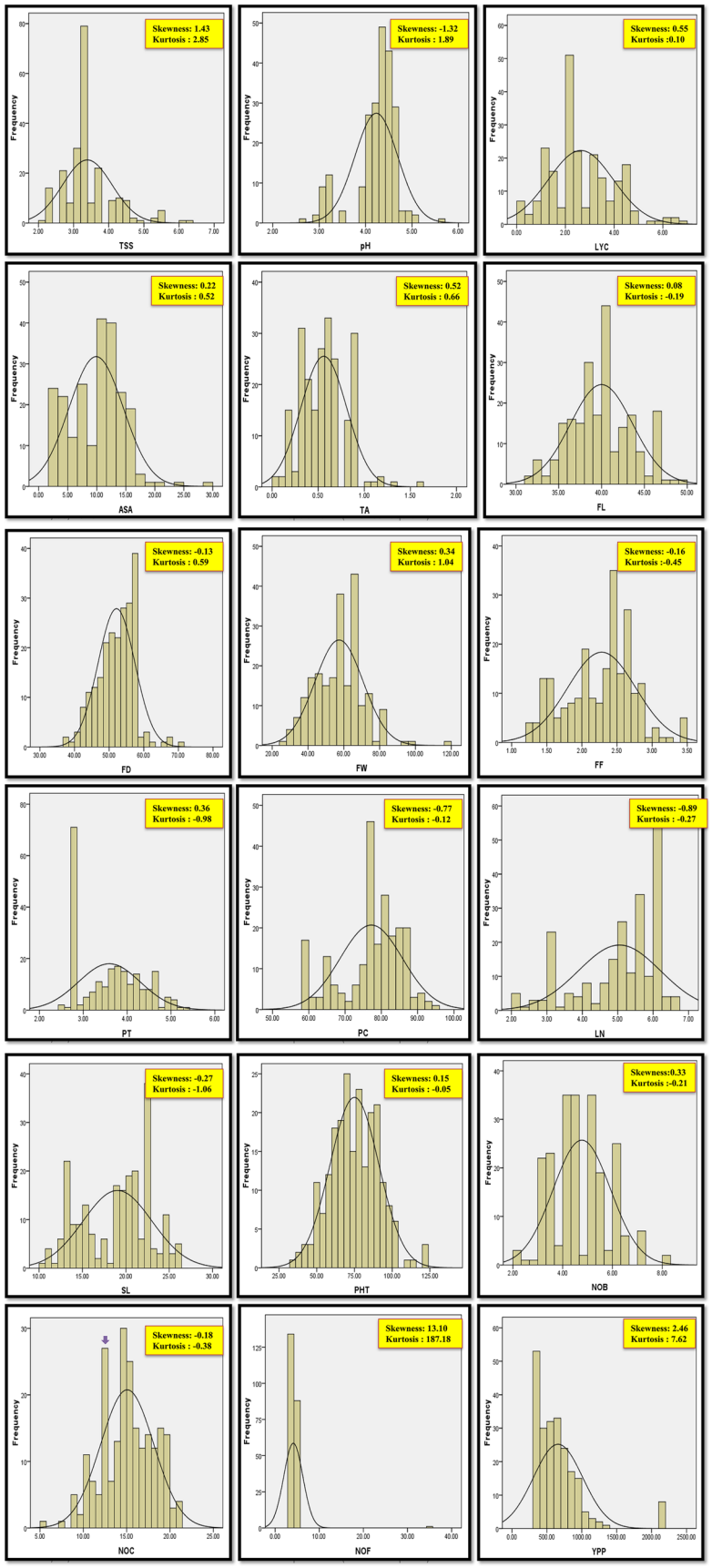

Figure 1. The frequency distribution for fruit quality and yield traits in F_2 population.

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Association of fruit quality and yield attributing traits with shelf life

Fruit shelf life is complex quantitative trait and direct selection for this trait without giving due importance to their genetic background would not end with fruitful results. The correlation of shelf life and its component traits reflects the nature and degree of relationship between them. Fruit firmness, pericarp thickness, titratable acidity, pulp content, TSS, yield/plant, locule number and fruit length could be used as surrogates for indirect selection of genotypes with higher shelf life as significant and positive correlation recorded. However, for assessing the effectiveness of selection based on correlated traits, it necessitates the empirical evaluation of selected plants for shelf life (Pavan *et al.*, 2022). Chakraborty *et al.*, 2007 reported that higher fruit firmness, pericarp thickness and thicker pulp enhance shelf life of tomatoes.

Path co-efficient analysis for fruit quality and yield attributing traits with shelf life

The relationship between shelf life and its component traits may be negative or positive but it is the net result of direct effect of that particular trait and indirect effects via other traits. The path coefficients partitioned the observed correlation into direct and indirect effects and also revealed the cause and effect relationship between shelf life and related traits. The true relationship between shelf life with fruit firmness, pericarp thickness, TSS, titratable acidity, pulp content, lycopene, pH, number of branches, ascorbic acid, fruit length, plant height and locule number indicated that direct selection for these traits will be rewarding for shelf life improvement. The residual effect was moderate which indicated inclusion of some more traits beside studied traits which contribute to shelf life.

Third and fourth degree statistics based genetics for fruit quality and yield traits

The trait variation in F_2 population is by and large caused by additive and additive × additive epistasis as dominance and dominance-based epistasis will dissipate with increase in homozygosity (Xu, 2010). Therefore, genetic expectation of coefficient of skewness of the distribution of F_2 population is function of number of genes and parameters that specify their additive main genetic and their digenic additive × additive epistatic interaction effects (Pooni *et al.*, 1977). The skewed distribution of trait suggests that trait is under control of non-additive gene action, especially epistasis and influenced by environmental variables (Pooni *et al.*, 1977, Roy, 2000). Kurtosis indicates relative number of genes controlling the trait under investigation (Robson, 1956).

TSS, lycopene, ascorbic acid, titratable acidity, fruit length, weight, pericarp thickness, plant height and number of branches were controlled by large number of genes with complementary epistasis predominantly additive × additive type of gene interaction with increasing effects on trait expression as these traits recorded positive skewness with platykurtic distribution. This indicated that genetic gain could be rapid with mild selection and less rapid with intense selection in enhancing degree of corresponding trait (Roy, 2000).

Negatively skewed and platykurtic distribution for pH, fruit diameter, firmness, pulp content, locule number, shelf life and number of clusters signified the involvement of large number of dominant genes with majority of them had increasing effects and duplicate epistasis in their inheritance. The number of fruits/cluster and yield/plant controlled by few segregating genes with majority of them had decreasing effects and dominance based complementary type of interaction in their inheritance. Gaikwad and Cheema, 2009 reported contrasting results of additive and non-additive gene effects for fruit quality and yield traits. Das *et al.*, 2020 reported dominant gene action for pH, lycopene, titratable acidity, pericarp thickness, plant height and yield/plant. Contrasting findings of additive gene action were reported for locule number, shelf life (Rodriguez *et al.*, 2010) and yield/plant (Katoch and Vidyasagar, 2004).

Traits with positively skewed distribution require intense selection from available variability in order to maximize genetic gain (Roy, 2000). Simple selection may not be effective in improving genetic gain for pH, fruit diameter, firmness, pulp content, locule number and shelf life which were controlled by dominant genes with duplicate epistasis as dominance and dominance × dominance gene effects are non-fixable (Shalaby, 2013). Therefore large number of families should be evaluated in advanced segregating generations to identify desirable genotypes. Inter mating among selected segregates followed by one to two generations of selfing led to break of undesirable linkage and accumulation of favourable alleles. One to two cycles of biparental mating followed by intensive selection leads to dissipation of dominance and enhance frequency of genes with increasing effects on trait expression (Das *et al.*, 2020).

Transgressive segregants for fruit quality and yield traits

Occurrence of transgressive segregants could be attributed to constellation of completely or incompletely dominant genes that are dispersed between their parents. Genetic studies indicated that transgressive segregation resulted from the combinations of alleles from both parents that had complementary gene effects dispersed between parents (Risenberg *et al.*, 1999). That is, individuals that receives 'plus' alleles from both parents or 'minus' alleles from both parents are likely to have extreme phenotypes. The transgressive segregants for fruit firmness, pericarp thickness, titratable acidity, pulp content, TSS, yield/plant, locule number and fruit length that surpassed better parent inF_2 population suggested the possibility to identify and develop pure lines that outperform parental limits.

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