



International Journal of Research in Agronomy

E-ISSN: 2618-0618
P-ISSN: 2618-060X
© Agronomy
NAAS Rating (2025): 5.20
www.agronomyjournals.com
2025; 8(11): 804-808
Received: 20-09-2025
Accepted: 26-10-2025

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Dissecting genetic variability and trait interactions underlying yield improvement in tomato (*Solanum lycopersicum* L.)

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DOI: <https://www.doi.org/10.33545/2618060X.2025.v8.i11k.4580>

Abstract

Genetic improvement of tomato yield requires a clear understanding of the magnitude of genetic variability and the causal relationships among yield-contributing traits. The present study evaluated seventy-five tomato (*Solanum lycopersicum* L.) genotypes to assess genetic variability, heritability, trait associations and direct and indirect effects of key yield and quality attributes. The experiment was conducted in a randomized complete block design with three replications and observations were recorded for Pericarp Thickness (PT), Total Soluble Solids (TSS), Per Plant Yield (PPY) and Average Fruit Yield (AFY). Analysis of variance revealed highly significant genotypic differences for all traits, indicating substantial genetic variability. Phenotypic coefficients of variation exceeded genotypic coefficients for all traits, although relatively narrow differences for PPY and AFY suggested predominant genetic control. High heritability coupled with high genetic advance was observed for PPY and AFY, indicating the predominance of additive gene action and the effectiveness of phenotypic selection. Genotypic correlation analysis showed a significant positive association of PT with AFY and TSS with PPY. Genotypic path coefficient analysis identified PPY as the major determinant of AFY, exerting the highest positive direct effect, while PT and TSS contributed positively through direct and indirect effects. The results indicate that PPY and PT are priority traits for yield improvement, while TSS may be improved through integrated selection approaches. Overall, the study provides a robust genetic framework for trait prioritization in tomato breeding programmes.

Keywords: Genetic variability, heritability, correlation analysis, path coefficient analysis, yield components, *Solanum lycopersicum*

Introduction

Tomato (*Solanum lycopersicum* L.) is a globally cultivated vegetable crop of high economic and nutritional importance, serving as a rich source of vitamins, antioxidants, and dietary minerals (Rasheed *et al.* 2023) ^[5]. Despite its wide cultivation, improvement of fruit yield and associated quality traits remains a major breeding objective due to the quantitative nature of yield, which is controlled by multiple interacting traits influenced by both genetic and environmental factors (Zannat *et al.* 2023) ^[6]. A rigorous understanding of genetic variability and trait interrelationships is therefore essential to enhance selection efficiency in tomato breeding programmes. Genetic variability is the cornerstone of crop improvement, enabling breeders to exploit differences among genotypes for desirable traits. Estimation of genotypic and phenotypic coefficients of variation (GCV and PCV), heritability, and genetic advance (GA) provides insight into the degree of variability and the expected response to selection (Rasheed *et al.* 2023) ^[5]. High heritability combined with high genetic advance suggests the predominance of additive gene effects and greater probability of effective selection based on phenotypic performance (Eshwar *et al.* 2023) ^[3]. Conversely, traits with moderate heritability and low genetic advance may be influenced significantly by environmental factors or non-additive gene effects, limiting direct selection response, as reported earlier in tomato and other solanaceous crops (Podlesakova *et al.* 2019) ^[10].

Interrelationships among yield components and quality traits offer additional guidance for indirect selection. Correlation analysis quantifies the magnitude and direction of associations between traits, which aids breeders in identifying key attributes that contribute positively to yield improvement (Eshwar *et al.* 2023) ^[3]. However, correlation coefficients alone do not distinguish between direct and indirect influences of component traits on yield. To further dissect the nature of these interrelationships, path coefficient analysis partitions correlation coefficients into direct and indirect effects, elucidating causal relationships among traits (Dewey & Lu 1959) ^[2]. This analytical approach has been widely employed in tomato genetic studies to prioritize traits that exert strong direct effects on yield, even when their phenotypic correlations may be weak (Kadyan *et al.* 2024; Zannat *et al.* 2023) ^[4, 6]. Understanding these causal pathways is particularly important for breeding strategies aimed at simultaneous improvement of yield and quality in complex trait systems. Recent studies in tomato have reported significant genetic variability and strong inter-trait associations among yield and quality attributes, underscoring the potential for selection based on both primary and secondary traits (Kadyan *et al.* 2024; Eshwar *et al.* 2023) ^[3, 4]. For instance, traits such as fruit number, fruit weight, and biochemical quality parameters have shown significant direct and indirect effects on yield performance, providing practical selection targets (Kadyan *et al.* 2024; Zannat *et al.* 2023) ^[4, 6]. Nonetheless, trait contributions can be population-specific owing to genetic background and environmental interactions, necessitating population-specific

studies for efficient breeding. In the present investigation, a diverse set of tomato genotypes was evaluated to estimate the magnitude of genetic variability, heritability and genetic advance, and genetic and phenotypic correlations among key yield and quality traits. Additionally, genotypic and phenotypic path coefficient analyses were conducted to elucidate direct and indirect effects of yield-contributing traits. The findings provide a comprehensive genetic architecture of tomato yield components and inform evidence-based selection strategies for enhanced yield and quality improvement.

Materials and methods
Plant material and experimental layout

The experimental material comprised seventy-five tomato (*Solanum lycopersicum* L.) genotypes, representing a broad spectrum of genetic diversity. The field experiment was conducted during the *Kharif*-2023. The trial was laid out in a randomized complete block design (RCBD) with three replications to minimize environmental heterogeneity.

Trait phenotyping and data collection
Phenotypic evaluation was performed for four key yield and fruit quality traits selected for their direct relevance to productivity and market acceptability in tomato. All observations were recorded on fully developed, marketable fruits following standardized protocols to ensure accuracy and reproducibility.

Table 1: A detailed description of the traits evaluated, measurement protocols and units used for phenotypic assessment in tomato

Trait	Abbreviation	Description	Instrument / method	Unit
Pericarp thickness	PT	Thickness of fruit pericarp measured at the equatorial region	Digital vernier caliper	cm
Total soluble solids	TSS	Soluble sugar content of fruit juice	Digital refractometer (calibrated with distilled water)	°Brix
Per plant yield	PPY	Cumulative weight of marketable fruits harvested per plant	Field weighing at each harvest	kg plant ⁻¹
Average fruit yield	AFY	Mean fruit weight per plant (yield ÷ number of fruits)	Derived from yield and fruit count	g fruit ⁻¹

Statistical Analysis
Analysis of Variance

The recorded data were subjected to analysis of variance (ANOVA) following the linear model appropriate for RCBD:

$$Y_{ij} = \mu + g_i + r_j + e_{ij}$$

Y_{ij} is the observation of the I_{th} genotype in the j_{th} replication, μ is the overall mean, g_i is the effect of the I_{th} genotype, r_j is the effect of the j_{th} replication and e_{ij} is the experimental error. Significance of genotypic effects was tested against the error mean square at 5% and 1% probability levels.

Estimation of Genetic Variability Parameters

Genotypic variance (σ^2_g), environmental variance (σ^2_e), and phenotypic variance (σ^2_p) were estimated from ANOVA mean squares. Genotypic coefficient of variation (GCV) and phenotypic coefficient of variation (PCV) were calculated to assess the magnitude of variability following Burton and DeVane (1953). Broad-sense heritability (h^2) was estimated as the ratio of genotypic variance to phenotypic variance. Genetic advance (GA) and genetic advance as percentage of mean (GAM) were calculated following Johnson *et al.* (1955) ^[7], assuming a selection intensity of 5%. Classes of heritability and genetic advance were categorized according to the criteria suggested by Singh and Narayan *et al.*,1993 ^[8].

Correlation analysis
Genotypic and phenotypic correlation coefficients among traits were estimated to quantify the degree of association between yield and its component traits. Genotypic correlations were computed using variance and covariance components derived from ANOVA, whereas phenotypic correlations were calculated from observed trait values. The statistical significance of correlation coefficients was tested using a two-tailed *t*-test.

Covariance analysis
Analysis of covariance was performed to partition genotypic, phenotypic, and environmental covariances among trait combinations. This analysis enabled identification of shared genetic control and environmental influence underlying trait associations, thereby strengthening the interpretation of correlation results.

Path coefficient analysis
To elucidate the causal relationships among yield-contributing traits, genotypic and phenotypic path coefficient analyses were conducted following Wright (1921) ^[9] as outlined by Dewey and Lu (1959) ^[2]. Average fruit yield was considered the dependent variable, while pericarp thickness, total soluble solids, and per plant yield were treated as independent variables. Correlation coefficients were partitioned into direct and indirect effects, and residual effects were computed to estimate the contribution of

unmeasured factors influencing yield.

Statistical software

All statistical analyses, including estimation of genetic parameters, correlation coefficients, covariance and path coefficients were performed using R statistical software with appropriate packages for quantitative genetic analysis.

Results

Detection of Significant Genetic Variability Among Tomato Genotypes

The analysis of variance revealed highly significant ($p < 0.01$) differences among genotypes for all the evaluated traits, including pericarp thickness (PT), total soluble solids (TSS), per plant yield (PPY) and average fruit yield (AFY), indicating the presence of substantial genetic variability in the experimental population (Table 1). The mean squares due to replications were non-significant for all traits, suggesting uniform experimental conditions and minimal environmental variation across replications. The significance of genotype effects confirms the adequacy of the experimental material for assessing genetic variability and selection potential.

Table 1: Analysis of variance (ANOVA) for yield and quality traits in tomato genotypes

Trait	Source	df	Mean Square	F-value	Significance
PT	Replication	2	0.0141	2.97	NS
	Genotype	74	0.0269	5.67	**
	Error	151	0.0047		
TSS	Replication	2	0.2490	0.87	NS
	Genotype	74	0.9246	3.24	**
	Error	151	0.2853		
PPY	Replication	2	0.1322	0.33	NS
	Genotype	74	5.6271	14.09	**
	Error	151	0.3994		
AFY	Replication	2	220.92	2.10	NS
	Genotype	74	1942.92	18.51	**
	Error	151	104.95		

Magnitude and Partitioning of Phenotypic and Genotypic Variability

Estimates of phenotypic and genotypic coefficients of variation revealed that phenotypic variability exceeded genotypic variability for all traits indicating environmental influence on trait expression (Table 2). Among the studied traits, per plant yield exhibited the highest magnitude of variability, with genotypic and phenotypic coefficients of variation of 56.71% and 62.87%, respectively. Moderate variability exhibited by average fruit yield (GCV: 34.56%; PCV: 37.41%). Low levels

of variability were observed for pericarp thickness and total soluble solids.

The relatively narrow differences between GCV and PCV for PPY and AFY indicate limited environmental influence and a greater contribution of genetic factors, suggesting favourable prospects for effective selection.

Table 2: Genetic variability parameters

Trait	Mean	GCV (%)	PCV (%)	Heritability (%)	GA	GA (%)
PT	0.47	18.38	23.50	61.16	0.14	29.61
TSS	4.07	11.34	17.34	42.76	0.62	15.27
PPY	2.33	56.71	62.87	81.35	2.45	105.37
AFY	71.61	34.56	37.41	85.37	47.11	65.79

Heritability and expected genetic gain for Yield and Quality Traits

Broad-sense heritability estimates ranged from 42.76% for total soluble solids to 85.37% for average fruit yield (Table 2). High heritability coupled with high genetic advance as a percentage of the mean was recorded for per plant yield (81.35% heritability; 105.37% genetic advance) and average fruit yield (85.37% heritability; 65.79% genetic advance), indicating the predominance of additive gene action and the effectiveness of selection based on phenotypic performance.

In contrast, total soluble solids exhibited moderate heritability associated with relatively low genetic advance, suggesting the involvement of non-additive gene effects and greater environmental influence, thereby limiting the efficiency of direct selection for this trait.

Genetic and phenotypic interrelationships among yield and quality components

Genotypic correlation coefficients were generally higher in magnitude than their phenotypic counterparts, reflecting stronger inherent genetic associations among traits (Table 3). At the genotypic level, pericarp thickness exhibited a significant and positive association with average fruit yield ($r = 0.6877$), indicating that increased pericarp thickness contributes favourably to yield improvement. Total soluble solids showed a strong positive genotypic correlation with per plant yield ($r = 0.7618$), whereas its association with average fruit yield was non-significant.

At the phenotypic level, average fruit yield displayed a significant positive correlation with pericarp thickness but showed significant negative correlations with total soluble solids and per plant yield. The observed discrepancies between genotypic and phenotypic correlations suggest that environmental factors modify the expression of genetic associations among yield-related traits.

Table 3: Genotypic (above diagonal) and phenotypic (below diagonal) correlations

Trait	PT	TSS	PPY	AFY
PT	-	0.6865**	-0.2975**	0.6877**
TSS	-0.3155**	-	0.7618**	0.0498NS
PPY	-0.4843**	-0.0268NS	-	-0.0966NS
AFY	0.2258**	-0.3808**	-0.2887**	-

Partitioning of Genotypic and Environmental Covariances Among Traits

Covariance analysis revealed significant genotypic covariance between pericarp thickness and per plant yield, as well as between per plant yield and average fruit yield, indicating shared genetic control among these traits (Table 4). Positive genotypic

covariance between pericarp thickness and average fruit yield further substantiates their favourable genetic association. Conversely, negative environmental covariance observed for certain trait combinations suggests antagonistic environmental effects on trait expression.

Table 4: Covariance analysis

Trait combination	Genotypic	Phenotypic	Environmental
PT × TSS	0.0272	-0.0246	-0.0518
PT × PPY	-0.0338	-0.0781	-0.0443
PT × AFY	1.4633	0.6664	-0.7969
TSS × PPY	0.4642	-0.0277	-0.4919
TSS × AFY	0.5686	-7.2013	-7.7699
PPY × AFY	-3.1558	-11.3173	-8.1615

Direct and indirect genetic effects on fruit yield revealed by path analysis

Genotypic path coefficient analysis demonstrated that per plant yield exerted the highest positive direct effect on average fruit yield (2.4156), followed by average fruit yield itself (2.0462), total soluble solids (0.7173), and pericarp thickness (0.5792) (Table 5). Despite some traits exhibiting weak or negative correlations with average fruit yield, their substantial direct effects indicate that indirect effects mediated through other traits may obscure their true contribution to yield. The relatively high residual effect suggests that additional yield-determining traits not included in the present study may also influence fruit yield expression.

Table 5: Genotypic path coefficients

Trait	Direct effect on AFY
PT	0.5792
TSS	0.7173
PPY	2.4156
AFY	2.0462

Phenotypic causal relationships governing fruit yield expression

Phenotypic path coefficient analysis revealed that average fruit yield had the highest positive direct effect (0.9041) on itself, followed by pericarp thickness (0.2260) (Table 6). In contrast, total soluble solids (−0.3808) and per plant yield (−0.2887) exhibited negative direct effects on average fruit yield at the phenotypic level. The low residual effect (0.0959) indicates that a substantial proportion of phenotypic variation in fruit yield was explained by the traits included in the analysis. The integrated interpretation of variability parameters, heritability estimates, correlation coefficients, covariance structure, and path analysis clearly identifies per plant yield and pericarp thickness as priority traits for yield improvement in tomato. Their high heritability, substantial genetic advance, favourable genetic correlations, and strong direct effects on yield suggest that simultaneous selection for these traits would be highly effective in tomato breeding programmes.

Table 6: Phenotypic path coefficients

Trait	Direct effect on AFY
PT	0.2260
TSS	-0.3808
PPY	-0.2887
AFY	0.9041

Discussion

The significant genotypic variation observed for all studied traits confirms the presence of substantial genetic diversity among the evaluated tomato genotypes, providing a strong basis for selection. Although phenotypic coefficients of variation exceeded genotypic coefficients for all traits, the relatively small differences between PCV and GCV for per plant yield and

average fruit yield indicate predominant genetic control of these yield attributes, a trend consistently reported in recent tomato variability studies (Rasheed *et al.* 2023; Eshwar *et al.* 2023) [3, 5]. Similar observations have been documented across diverse genetic backgrounds, emphasizing the reliability of yield-related traits as effective targets for selection (Kadyan *et al.* 2024) [4]. High heritability coupled with high genetic advance for per plant yield and average fruit yield suggests the predominance of additive gene action, indicating that direct phenotypic selection for these traits would be highly effective. Comparable findings have been reported in recent global studies, where yield components showed rapid response to selection owing to their strong additive genetic control (Rasheed *et al.* 2023; Kadyan *et al.* 2024) [4, 5]. In contrast, total soluble solids exhibited moderate heritability with relatively low genetic advance, implying the involvement of non-additive genetic effects and greater environmental influence, a pattern commonly observed for fruit quality traits in tomato (Eshwar *et al.* 2023) [3]. Genotypic correlations were generally stronger than phenotypic correlations, highlighting the masking effect of environmental variation on observable trait associations. The significant positive genotypic association between pericarp thickness and average fruit yield suggests that genetic factors enhancing pericarp thickness may simultaneously contribute to increased fruit weight and yield stability. Similar positive relationships between pericarp thickness, fruit firmness, and yield stability have been reported in recent tomato studies, underscoring the importance of this trait for both productivity and post-harvest quality (Kadyan *et al.* 2024; Rasheed *et al.* 2023) [5]. The strong positive genotypic correlation observed between total soluble solids and per plant yield is particularly noteworthy, as yield and quality traits are often reported to be negatively associated. This favourable association indicates the presence of genotypes combining high productivity with improved soluble solids content, a finding also reported in population-specific studies where yield and quality improvement were not mutually exclusive (Eshwar *et al.* 2023). Recent physiological and genetic studies further suggest that such associations depend on the underlying genetic architecture and can be exploited through targeted selection (Li *et al.* 2025). Path coefficient analysis provided a clearer understanding of causal relationships among yield-related traits. Genotypic path analysis revealed that per plant yield exerted the highest direct positive effect on average fruit yield, confirming its primary role as a key determinant of productivity. Similar dominance of per plant yield and its components as major contributors to fruit yield has been consistently reported in recent path analysis studies in tomato (Eshwar *et al.* 2023; Kadyan *et al.* 2024) [3, 1]. Pericarp thickness and total soluble solids also contributed positively, either directly or indirectly, reinforcing their importance as secondary selection traits. In contrast, phenotypic path analysis showed negative direct effects of per plant yield and total soluble solids on average fruit yield, reflecting environmental influences and compensatory trade-offs such as fruit number versus fruit size under field conditions. Such discrepancies between genotypic and phenotypic path coefficients have been widely reported and highlight the importance of relying on genotypic parameters for selection decisions (Rasheed *et al.* 2023) [5]. The low phenotypic residual effect observed in the present study indicates that the included traits collectively explained most of the phenotypic variation in yield. Overall, the integrated interpretation of variability parameters, heritability estimates, correlation coefficients, and path analysis

identifies per plant yield as the most reliable primary selection criterion for yield improvement in tomato, with pericarp thickness serving as an important secondary trait contributing to yield stability and fruit quality. Total soluble solids, although genetically associated with yield, may require integrated phenotypic and molecular approaches for effective improvement, as suggested by recent advances in tomato genomics and marker-assisted breeding (Li *et al.* 2025). While the present findings are robust, validation across multiple environments and inclusion of additional yield components would further strengthen selection strategies, as emphasized in recent global tomato breeding studies (Rasheed *et al.* 2023; Kadyan *et al.* 2024) ^[4, 5].

Conclusion

The evaluated tomato germplasm exhibits substantial genetic variability for yield-related attributes, especially PPY and AFY, which display high heritability and genetic advance and act as major causal determinants of average fruit yield. Pericarp thickness and total soluble solids are promising secondary targets the former for yield stability and processing suitability, the latter requiring integrated Table 3. Genotypic (above diagonal) and phenotypic (below diagonal) correlations and molecular selection. These results provide a robust, population-specific basis for trait prioritization and breeding strategy design aimed at simultaneous yield and quality improvement.

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