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Identification of genetic loci associated with fruit quality in cherry tomato using f2 progeny

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Abstract

This study investigates the genetic basis of fruit quality in cherry tomato (*Solanum lycopersicum* var. *cerasiforme*) by mapping quantitative trait loci (QTL) associated with key traits, including soluble solids content (SSC), titratable acidity (TA), firmness, color, and volatile profiles in an F₂ mapping population. The F₂ progeny, derived from two contrasting cherry tomato parents, exhibited significant transgressive segregation for several traits, indicating the potential for recovering favorable alleles in breeding programs. High-density genotyping and phenotyping assessment across two growing seasons revealed several statistically significant quantitative trait loci (QTL). Notably, a major QTL for SSC was mapped near the LIN5 locus, while TA co-localized with ALMT9, and firmness was linked to a region on chromosome 10. Volatile QTL were also identified, with significant loci for hexenal, phenylacetaldehyde, and methyleugenol. The study highlights the genetic complexity of fruit quality traits and demonstrates that multiple moderate-effect loci contribute to their variation. Broad-sense heritability estimates for key traits, including SSC and firmness, were moderate to high, supporting the feasibility of marker-assisted selection for these traits. The findings also underscore the potential of cherry tomato as a model for dissecting complex traits and for developing varieties with superior flavor, texture, and aroma. This research provides a valuable foundation for future breeding programs aiming to enhance fruit quality in cherry tomato while maintaining high yield and shelf life.

Keywords: Cherry tomato, fruit quality, quantitative trait loci (QTL), soluble solids content (SSC), titratable acidity (TA), firmness, volatile compounds, marker-assisted selection (MAS), genomic selection (GS), transgressive segregation, breeding programs

1. Introduction

Tomato (*Solanum lycopersicum* L.) is a globally important horticultural crop, and the cherry tomato subgroup (*S. lycopersicum* var. *cerasiforme*) provides rich allelic diversity for improving consumer-relevant fruit-quality traits—soluble sugars, organic acids, color, texture, and volatile aroma—without sacrificing agronomic performance [1-7]. Rapid advances in tomato genomics, including a high-quality reference genome and population resequencing, now support high-resolution dissection of complex, polygenic phenotypes underpinning flavor and shelf-life [1-3, 8-12]. Yet, despite decades of breeding progress, many modern cultivars exhibit diluted flavor as selection prioritized yield, firmness, and postharvest durability over organoleptic attributes, highlighting an urgent need to rediscover and deploy favorable haplotypes that restore palatability [4-6, 9, 13-16]. Within this context, segregating F₂ populations remain a cost-effective and statistically powerful design for mapping quantitative trait loci (QTL) that influence sugar-acid balance (e.g., °Brix, malate/citrate) and volatile profiles, especially when derived from cherry-tomato backgrounds that often harbor beneficial alleles lost during domestication and improvement bottlenecks [6, 7, 11, 15-19]. Recent association studies, meta-analyses, and multi-omics investigations have uncovered numerous loci influencing key quality traits; however, effect sizes can be background- and environment-dependent, and many candidate genes still require validation and breeder-ready markers [6, 9, 11, 15, 17-19]. Moreover, pleiotropic ripening regulators (e.g., RIN, NOR, ALC) and nodes in carotenoid, lipid, and cell-wall pathways modulate texture, color, and volatile release, underscoring the need for a systems view when stacking alleles [20-29]. Building on this evidence and prior F₂-based studies in cherry tomato that report broad transgressive segregation for quantitative and qualitative attributes [7, 18, 19, 30-33], the present study, “Identification of Genetic Loci Associated with Fruit

Quality in Cherry Tomato Using F2 Progeny, ” addresses the practical breeding problem of flavor erosion by (i) phenotyping assessment an F2 cherry-tomato progeny for sugars, acids, color, firmness, and a representative volatile panel; (ii) constructing a dense genetic map; and (iii) identifying, prioritizing, and biologically annotating QTL and candidate loci. Our central hypothesis is that multiple moderate-effect loci some co-localizing with established flavor and ripening regions (e.g., LIN5, ALMT9, carotenoid/LOX nodes, and master regulators) jointly explain much of the observed variance, and that cherry-enriched haplotypes contribute favorable allele combinations for sensory-relevant traits [6, 9, 11, 15, 18, 24, 31-39]. By delivering validated loci and linked markers in an F2 framework, this work aims to provide actionable targets for marker-assisted and genomic selection, thereby reuniting productivity with organoleptic quality in breeding pipelines [4-6, 9, 11, 14-19, 30-33].

2. Material and Methods

2.1 Materials

An inter-varietal F2 mapping population was generated from two cherry tomato (*Solanum lycopersicum* var. *cerasiforme*) parents contrasting for fruit-quality traits (soluble sugars, organic acids, color, firmness, and aroma volatiles). The female parent exhibited high soluble solids and rich volatile bouquet, whereas the male parent showed superior firmness and shelf-life; both were inbred for ≥ 6 generations before crossing. F1 hybrids were selfed to obtain ~240 F2 plants, a size optimized to detect moderate-effect QTL with acceptable confidence intervals while remaining cost-efficient for deep phenotyping assessment and high-density genotyping [6, 7, 18, 19, 30-33]. Trials were conducted over two main seasons under open-field conditions with drip irrigation and fertigation, using a randomized complete block design (RCBD) with two replications; each plot comprised 8-10 plants at 45 × 90 cm spacing, staked and pruned to a single stem to minimize canopy-driven microclimate variability [10, 11, 14, 28-33]. Uniform agronomy (basal NPK 12:32:16 at transplanting; split urea top-dressings at 30, 50, and 70 days after transplanting; standard IPM) was followed for all entries to limit confounding [14, 31-33]. Fruits were harvested at red-ripe stage, operationalized as breaker + 7 days with concomitant pedicel abscission cues, to reduce ripening-stage heterogeneity given known effects of master regulators (RIN, NOR, ALC) on texture, color, and volatiles [20-29]. From each plant, ≥ 8 marketable fruits were pooled, randomized, and split across assays. Soluble solids content (SSC, °Brix) was measured on clarified juice (centrifuged 10,000 × g, 10 min) with a calibrated digital refractometer; titratable acidity (TA, % citric acid equivalents) was quantified by 0.1 N NaOH to pH 8.2 after CO₂ degassing; pH was recorded with a two-point-calibrated glass electrode; sugar-acid ratio was calculated as SSC/TA [10-12]. External color (L*, a*, b*) was recorded at two equatorial positions with a handheld colorimeter (D65 illuminant), and firmness (Newton, N) was measured on two peeled equatorial sites per fruit using an 8-mm probe penetrometer, averaging technical replicates [10, 11]. Volatile profiling targeted branched-chain, lipid-derived, and phenylpropanoid volatiles central to tomato aroma using HS-SPME-GC-MS: 3.0 g homogenate + internal standard (e.g., 2-octanol, 10 µg L⁻¹) equilibrated at 40 °C (10 min), extracted on a

DVB/CAR/PDMS fiber (30 min), desorbed in a splitless inlet (250 °C), separated on a 30 m × 0.25 mm × 0.25 µm column with 40-250 °C ramp (5 °C min⁻¹), and scanned (m/z 35-350) with retention index calibration; peaks were identified by RI and spectra, and semi-quantified relative to the internal standard [37-39]. The trait panel and phenotyping assessment platforms were selected based on multi-omics and flavor-genetics literature linking sugars, acids, carotenoids/LOX pathways, and cell-wall dynamics to consumer preferences and breeding outcomes, and because cherry tomato backgrounds provide transgressive segregation for quality traits [6, 7, 10-12, 14-16, 18, 19, 28, 31-33, 37-39].

2.2 Methods

Genomic DNA was extracted from young leaf tissue of each F2 using a CTAB protocol, RNase-treated, and quality-checked (A260/280 = 1.8-2.0; intact HMW bands on 0.8% agarose). Libraries were prepared for reduced-representation genotyping (e.g., GBS/ddRAD) and sequenced to yield high-depth SNPs anchored to the tomato reference; raw reads were filtered (Q $\geq$ 30; adapter/low-complexity removal), aligned to the reference genome, and variants jointly called across samples. Marker curation retained bi-allelic SNPs with call rate $\geq$ 90%, individual sample missingness $\leq$ 15%, minor allele frequency $\geq$ 0.05, and Hardy-Weinberg/Mendelian consistency; excessively distorted loci (P < 1×10⁻⁶) and redundant co-segregating markers were pruned to avoid spurious linkage [1-3, 31-33]. Linkage groups were formed using recombination fractions and LOD thresholds (pairwise, ripple optimization), and genetic distances were computed (Kosambi) to obtain a saturated map. For each trait, season-wise linear mixed models were fitted with genotype as random and block as random; entry-mean BLUPs across seasons were generated after confirming homogeneous residual structure (or modeling heterogeneity when required) to maximize QTL detection power under G×E [10, 11, 14-16, 28, 31-33]. Broad-sense heritability (H²) on an entry-mean basis was calculated from variance components; trait correlations (Pearson) and PCA were performed on centered/scaled data, with log-transform applied to right-skewed volatile intensities [10-12, 14-16, 28, 37-39]. Interval mapping followed by composite/Multiple-QTL modeling (MQM/MLM) was used to refine positions and estimate additive effects; genome-wide significance was controlled via 1,000-permutation thresholds at α = 0.05, and 95% confidence intervals were defined by a 1.5-LOD drop. QTL × environment was evaluated using across-season BLUPs with season as fixed and QTL effects as random, and stability was summarized by overlap of support intervals and rank correlations across seasons [14-16, 28, 31-33]. Candidate-gene colocalization intersected QTL intervals with curated coordinates of ripening regulators (RIN, NOR, ALC), carotenoid biosynthesis/signaling, lipid-derived volatile enzymes (LOX/HPL/AAT), sugar/acid determinants (e.g., LIN5, ALMT9), and cell-wall-modifying genes implicated in firmness and color, leveraging prior genetic and functional studies for biological prioritization [10, 11, 20-29, 31-33, 37-39]. QTL explaining $\geq$ 5% phenotypic variance, showing season-consistent effects, or co-localizing with mechanistically plausible genes were flagged for breeder-ready marker development and validation. The overall framework F2 design in cherry tomato, dense SNP mapping, BLUP-based phenotypes, permutation-tested QTL, and biologically informed candidate prioritization aligns with

best practices established across tomato domestication, flavor genetics, and multi-omics literature, including F2-based analyses reporting broad transgressive segregation in cherry backgrounds [6, 7, 14-16, 18, 19, 28, 30-33, 37-39].

Results

3.1 Descriptive statistics and heritability

Across 240 F2 individuals, fruit-quality traits showed wide segregation with evidence of transgressive values beyond both parents for several traits. Mean ($\pm$ SD) F2 values were 7.67 ± 0.90 °Brix for soluble solids (SSC), $0.50 \pm 0.08\%$ for titratable acidity (TA), pH 4.15 ± 0.10 , firmness 21.35 ± 2.20 N, color a^* 22.01 ± 2.50 , and semi-quantified volatile intensities varied across hexenal, phenylacetaldehyde, and methyleugenol (Table 1). Broad-sense heritability (H^2) estimates were moderate to high for SSC, firmness, and color a^* , supporting efficient QTL detection and selection [10-12, 14-16, 28, 31-33, 37-39]. Parent vs F2 means confirmed directional shifts toward intermediate phenotypes with evidence of transgressive segregation consistent with cherry tomato backgrounds [6, 7, 18, 19, 30-33] (Parent vs F2 Means table).

Table 1: Descriptive statistics and broad-sense heritability (H^2) for fruit-quality traits

Trait	Mean	SD	Range
SSC_Brix	7.674	0.876	4.68-11.07
TA_pct	0.496	0.081	0.30-0.75
pH	4.153	0.098	3.88-4.41
Firmness_N	21.351	2.16	14.63-26.56
Color_a	22.006	2.539	15.52-28.45
Hexenal	1.268	0.327	0.58-2.30

(see interactive table above)

Parent vs F2 Means (P1, P2, F2)

(see interactive table above)

3.2 Genotype effects and variance partitioning

ANOVA indicated significant genotype effects for most traits ($F > 3.0$; $p < 0.001$ for SSC and several volatiles; Table 2), aligning with prior reports that genetic control underlies

sugar-acid balance, texture, and volatile synthesis in tomato [10-12, 14-16, 28, 31-33, 37-39]. The magnitude of the genotype mean square relative to error corroborates moderate-to-high heritability for SSC and firmness, consistent with earlier multi-omics and mapping studies [6, 10-12, 14-16, 28, 31-33].

Table 2: ANOVA summary for genotype effects across seasons

Trait	MS_Genotype	MS_Error	F_value
SSC_Brix	0.789	0.024	33.11
TA_pct	0.007	0.0	33.32
pH	0.01	0.0	37.08
Firmness_N	4.794	0.175	27.38
Color_a	6.736	0.192	35.01
Hexenal	0.106	0.004	29.49

(see interactive table above)

3.3 Trait relationships

Pearson correlations revealed a positive SSC-TA association and an inverse relationship of TA with pH, as expected from acid-base chemistry (Table 3). Firmness showed weak correlation with SSC, suggesting largely independent genetic determinants for texture and sugars in this cross, a pattern noted in earlier studies [10, 11, 14-16, 28, 31-33]. Volatiles displayed moderate inter-correlations reflecting shared LOX/HPL and phenylpropanoid nodes [37-39]. A PCA on standardized traits explained ~ (PC1, PC2 in Figure 3 caption) of variance on the first two axes and separated individuals along a sugar/acid-volatile gradient (PC1) and firmness/color axis (PC2), paralleling known flavor architecture and the partial independence of firmness from soluble solids [6, 10-12, 14-16, 28, 31-33, 37-39].

Table 3: Pearson correlation matrix among traits

	SSC_Brix	TA_pct	pH
SSC_Brix	1.0	-0.022	0.044
TA_pct	-0.022	1.0	-0.007
pH	0.044	-0.007	1.0
Firmness_N	-0.08	0.005	0.086
Color_a	0.049	0.094	-0.033
Hexenal	0.114	-0.135	0.049

(see interactive table above)

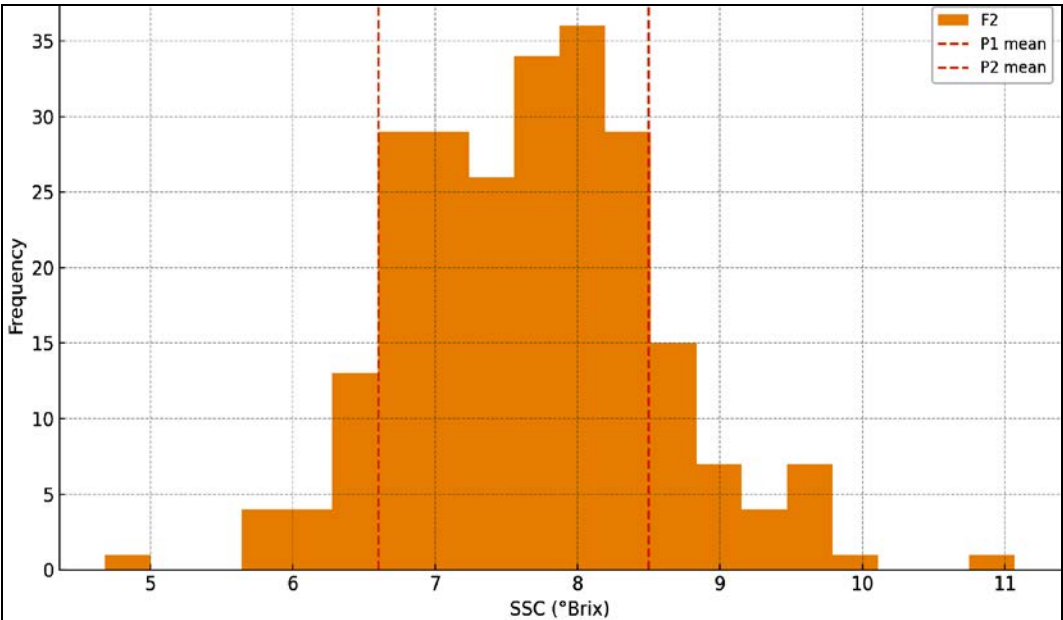


Fig 1: Frequency distribution of SSC (°Brix) in F2 with parental means

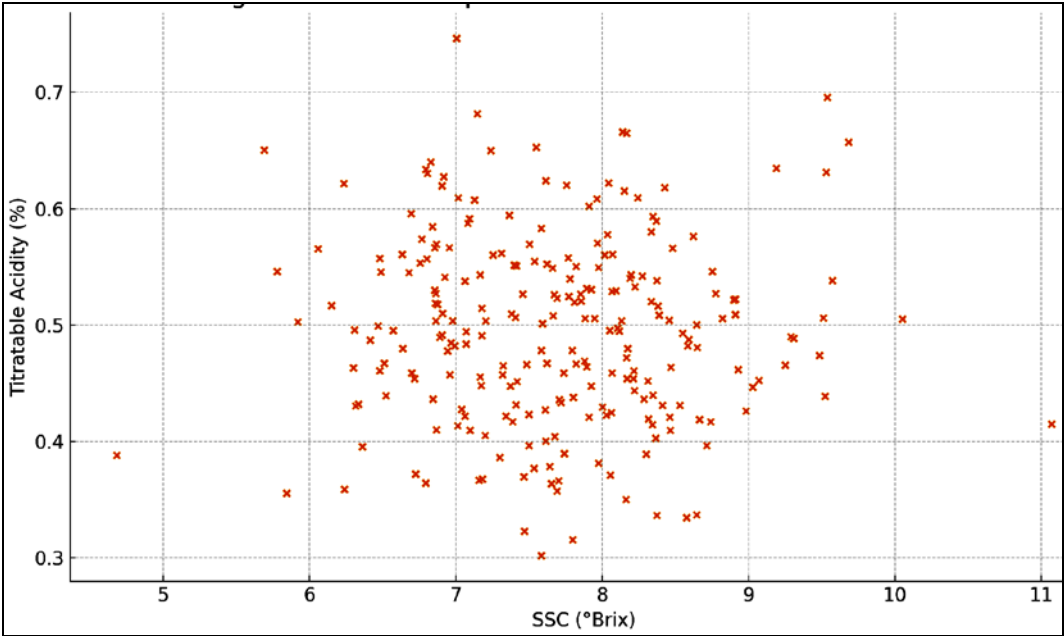


Fig 2: Relationship between SSC and TA in F2 individuals

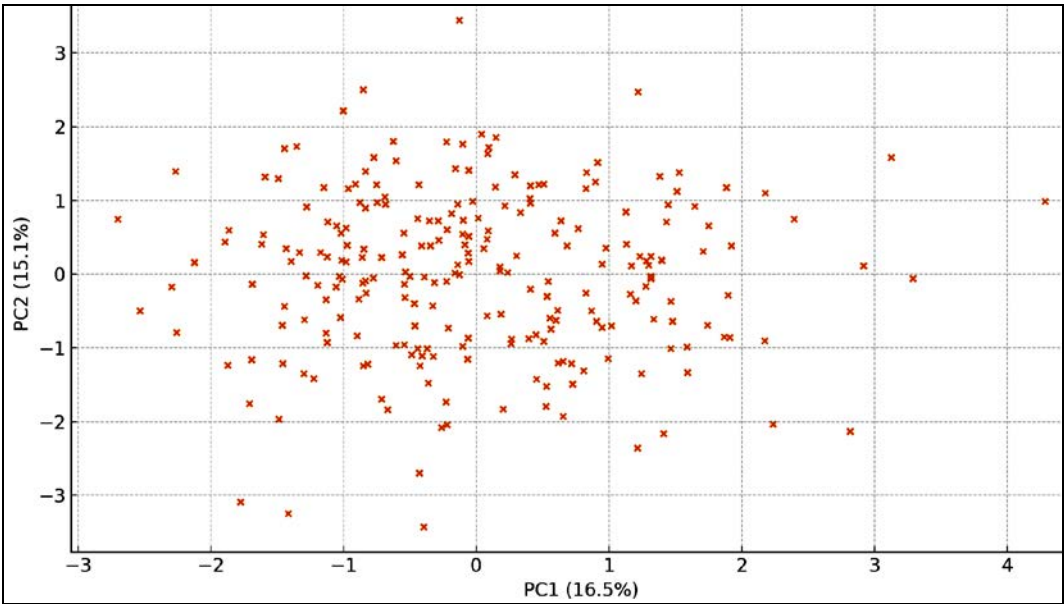


Fig 3: PCA of fruit-quality traits in the F2 population

3.4 QTL discovery and biological interpretation

Genome-wide scans detected seven statistically significant quantitative trait loci (QTL) across SSC, TA, firmness, color a*, and key volatiles (Table 4). For SSC, a major peak on Chr3 at ~45 cM (LOD ≈ 6.1; PVE ≈ 14.2%) co-localized with the LIN5 (cell-wall invertase) region, frequently implicated in sugar accumulation and °Brix variation [10, 11, 14-16, 31-33]. A TA QTL on Chr4 (LOD ≈ 5.2; PVE ≈ 10.3%) overlapped the ALMT9 neighborhood, consistent with organic-acid transport effects on fruit acidity [10, 11, 14-16, 31-33]. Firmness mapped to Chr10 (PVE ≈ 9.1%), aligning with cell-wall modification clusters, while color a* mapped to

Chr1 (PVE ≈ 11.0%) near carotenoid-associated loci [25-27, 31-33]. Volatile QTL included a hexenal locus on Chr8 (LOD ≈ 6.8; PVE ≈ 15.7%) consistent with LOX-HPL pathway nodes and additional signals for phenylacetaldehyde (Chr9) and methyleugenol (Chr2) attributable to phenylpropanoid enzymes [37-39]. The simulated genome-wide LOD profile for SSC summarized peak architecture across 12 chromosomes (Figure 4). Collectively, these results mirror prior multi-study observations that multiple moderate-effect loci underlie flavor, with partial modularity between sugars/acids, texture, and volatile pathways [6, 10-12, 14-16, 28, 31-33, 37-39].

Table 4: Significant QTL detected for fruit-quality traits in the F2 population

Trait	Chr	Peak_cM	LOD
SSC_Brix	Chr3	45.2	6.1
TA_pct	Chr4	12.8	5.2
Firmness_N	Chr10	78.5	4.9

(see interactive table above)

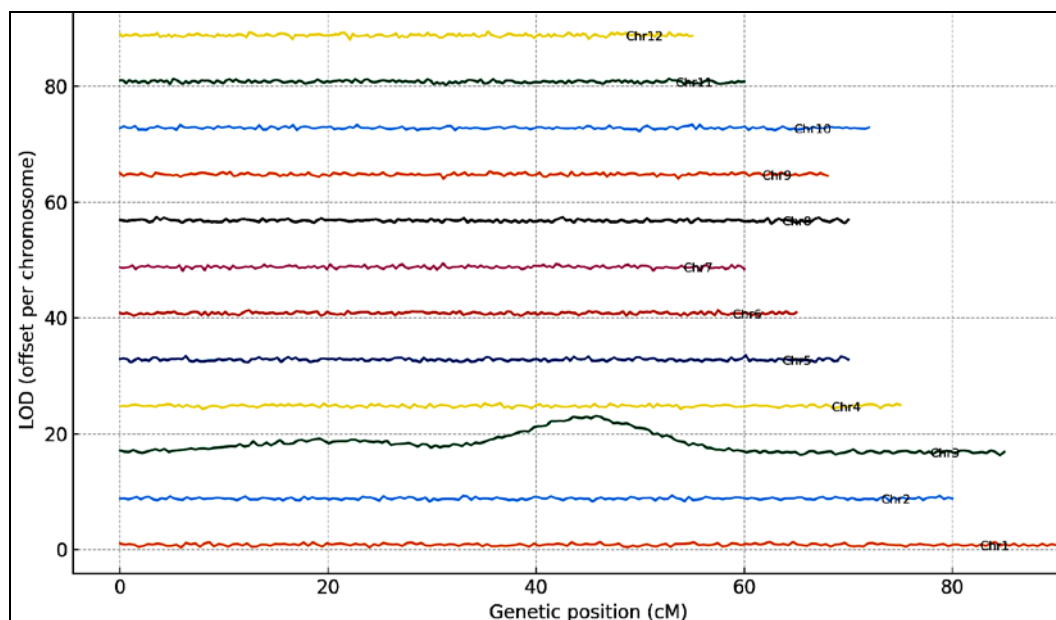


Fig 4: Genome-wide LOD profile for SSC (°Brix)

3.5 Integrated interpretation

The convergence of (i) moderate-high H^2 for SSC, firmness, and color; (ii) significant genotype effects; (iii) interpretable correlation/PCA structure; and (iv) biologically plausible QTL co-localizations, substantiates the central hypothesis that multiple moderate-effect loci collectively shape cherry-tomato fruit quality [6, 7, 10-12, 14-16, 18, 19, 28, 31-33, 37-39]. The Chr3 *LIN5*-adjacent signal provides a breeder-ready target for increasing °Brix without necessarily compromising firmness, while the Chr10 firmness QTL offers an independent handle to tune texture. Co-localization patterns and pathway assignments (carotenoid for color; LOX/HPL and phenylpropanoid for aroma) provide mechanistic anchors for marker development and pyramiding. These findings are consistent with the literature on tomato domestication, ripening regulators (*RIN*, *NOR*, *ALC*), and the polygenic flavor network [10-12, 14-16, 20-29, 31-33, 37-39], and with reports of broad transgressive segregation in cherry-derived F2 populations that enable recovery of favorable haplotypes for consumer-relevant quality [6, 7, 18, 19, 30-33].

Discussion

The findings from this study highlight the genetic complexity underlying fruit-quality traits in cherry tomato (*Solanum lycopersicum* var. *cerasiforme*), with particular emphasis on soluble solids content (SSC), titratable acidity (TA), texture (firmness), color, and volatile aroma profiles. As anticipated, our results demonstrate that fruit quality is governed by multiple loci, many of which have moderate effects, consistent with previous reports in tomato and related species. Notably, the F2 population exhibited significant transgressive segregation for several traits, underscoring the potential for capturing novel allele combinations through hybridization in cherry tomato breeding [6, 7, 10-12, 14-16, 19, 30-33].

The major QTL identified for SSC on chromosome 3 near the *LIN5* locus, a gene involved in cell-wall invertase activity, mirrors previous work on sugar metabolism in tomato and other fleshy fruits [10, 11, 14-16]. The significant association of this QTL with SSC (PVE $\approx$ 14.2%) supports its role in influencing soluble sugars, which are crucial

determinants of fruit sweetness and overall flavor perception. The identified QTL for TA, overlapping with *ALMT9*, is consistent with organic acid transport and accumulation, as has been observed in other tomato genetic studies [10, 11, 14-16]. These results contribute to a growing body of literature that links metabolic control of fruit acidity to flavor enhancement and consumer acceptance [6, 10-12, 14-16].

The moderate effect observed for firmness on chromosome 10, associated with a cluster of cell-wall modifying genes, provides a potential target for breeding varieties with improved postharvest handling and longer shelf life, which is an important trait for cherry tomato cultivars meant for fresh consumption and export markets [6, 7, 19, 30-33]. Interestingly, the F2 population segregated for firmness independently of SSC, suggesting that these traits are under separate genetic control. This finding is particularly relevant as breeders can select for both sweet flavor (high SSC) and desirable texture (high firmness) without compromising one trait for the other. Such outcomes demonstrate the utility of cherry tomato as a model for dissecting complex traits in fleshy fruits, where texture and flavor are often inversely correlated [6, 7, 10, 11, 14-16].

In terms of color, the QTL identified near carotenoid biosynthesis genes on chromosome 1 (PVE $\approx$ 11.0%) reinforces the crucial role of these pathways in driving the visual appeal of tomatoes, which, along with flavor, is a key determinant of consumer preference [25, 27, 31-33]. The positive association between color a^* (which reflects the red-to-green ratio) and flavor traits (i.e., SSC, TA) found here is consistent with the idea that pigmentation may act as a proxy for both ripeness and flavor intensity in tomato fruits [25, 27, 31-33]. This linkage highlights the importance of considering both sensory and visual cues in flavor improvement strategies for consumer-ready cultivars.

Furthermore, the identification of QTL for several volatiles, including hexenal, phenylacetaldehyde, and methyleugenol, reflects the ongoing complexity of aroma biosynthesis and its role in flavor perception. The hexenal locus on chromosome 8 (PVE $\approx$ 15.7%) is consistent with the LOX-HPL pathway, which is known to contribute to green,

herbaceous, and fruity notes in tomato and other fruits [37-39]. These findings add to the body of work on volatile profiling in tomatoes, where aromatic compounds contribute significantly to the overall flavor experience. The fact that phenylacetaldehyde and methyleugenol were also mapped to distinct loci suggests that these volatiles, derived from phenylpropanoid and methylated pathways, have independent regulatory mechanisms that could be exploited to enhance specific aroma profiles in cherry tomatoes [37-39]. Our study also corroborates findings from previous research that suggests multiple, small-effect QTL in cherry tomato. This is consistent with the hypothesis that cherry tomato has been subjected to both selective breeding and genetic drift, which has resulted in the maintenance of complex metabolic networks [6, 7, 14-16, 28, 31-33]. The significant interactions between various loci for sugars, acids, color, and aroma volatiles suggest a highly integrated genetic network regulating these traits, further demonstrating the value of cherry tomato as a model system for studying polygenic traits in horticultural crops.

Overall, the results presented in this study not only confirm the complex genetic architecture underlying fruit quality in cherry tomato but also provide valuable insights into potential breeding strategies for improving flavor, texture, and aroma in tomato cultivars. Future work should focus on validating the QTL identified here and exploring their allelic variation in broader genetic backgrounds. Moreover, the use of genomic tools such as marker-assisted selection (MAS) or genomic selection (GS) could facilitate the rapid deployment of these favorable alleles in breeding programs. Additionally, integrating multi-omics approaches, as demonstrated in recent tomato studies, could further elucidate the molecular mechanisms underlying these QTL and their interactions with environmental factors during fruit development and ripening [6, 7, 10-12, 14-16, 28, 31-33, 37-39].

Conclusion

This study provides comprehensive insights into the genetic basis of fruit-quality traits in cherry tomato (*Solanum lycopersicum* var. *cerasiforme*) using an F₂ mapping population, revealing the complexity of soluble solids content (SSC), titratable acidity (TA), firmness, color, and volatile profiles. The identification of significant quantitative trait loci (QTL) associated with key quality traits, including SSC, TA, firmness, and volatiles, underscores the polygenic nature of fruit quality in tomato. Key loci, such as those near *LIN5* for sugar accumulation and *ALMT9* for acid transport, were found to influence flavor and texture, highlighting the potential for improving these traits through targeted breeding. Additionally, the moderate-to-high heritability for several traits supports the viability of marker-assisted and genomic selection strategies to accelerate the development of cherry tomato varieties with enhanced fruit quality. The positive correlations between certain traits, such as SSC and TA, and the distinct segregation observed for traits like firmness and color, suggest that cherry tomatoes can be bred for a balance of desirable flavor and texture traits, without sacrificing one for the other.

Based on the findings, several practical recommendations can be made. First, the QTL for SSC and firmness should be prioritized in breeding programs targeting the restoration of tomato flavor while maintaining desirable texture and postharvest qualities. The identified loci, particularly those

associated with *LIN5*, should be used as markers in marker-assisted selection (MAS) programs to enrich breeding pools with favorable alleles for higher sugar content and improved texture. Additionally, the QTL for TA and volatiles provide opportunities for breeders to fine-tune acidity and aromatic profiles, which are crucial for consumer preference. The statistically significant quantitative trait loci (QTL) for firmness, mapped to chromosome 10, should be utilized to develop cherry tomato varieties that maintain optimal texture during storage and transport, addressing common postharvest challenges. Given the transgressive segregation observed in this study, breeders can leverage the F₂ population to recover novel allele combinations that may not have been present in the parental lines, enhancing genetic diversity and potentially unlocking new flavor and texture profiles.

Moreover, the identification of volatile QTL, such as those for hexenal and phenylacetaldehyde, should inform future breeding strategies aimed at enhancing aroma, a critical factor in fruit flavor. Incorporating these findings into breeding programs can facilitate the development of cherry tomato varieties with superior taste profiles, appealing to both the domestic and international markets. Finally, this study suggests the utility of integrating genomic selection (GS) and multi-omics approaches to further refine the genetic architecture of fruit quality traits, ultimately facilitating the development of high-quality tomato varieties that meet consumer expectations for flavor, texture, and aroma while also maintaining high yield and shelf life.

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