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Fruit quality of Mexican native tomato accessions and wild relatives

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ABSTRACT

Tomato (*Solanum lycopersicum* L.) is a crop of global economic relevance. Mexico, as a center of diversification for the species, harbors extensive genetic variability across native wild, semi-domesticated, and cultivated populations, whose potential for genetic improvement remains underexplored. This study assessed the phenotypic diversity of 50 accessions, including 10 wild relatives, based on 14 fruit quality traits. The observed variability reflected evolutionary and domestication patterns, with a morphological and chromatic transition from small green fruits to pigmented and commercially desirable forms. Multivariate analyses—principal component analysis and hierarchical clustering via heatmap—revealed a genetic architecture shaped by the selection of visual and structural traits, while phenotypic correlations highlighted functional associations between nutritional pigments and optical parameters, such as the relationship between total carotenoids and the a^* value (green-red axis). Wild relatives and traditional varieties emerged as valuable sources of functional alleles for improving organoleptic and nutritional quality. The genetic independence between external and internal traits suggests feasibility for designing ideotypes that combine yield and quality without phenotypic drag. This phenotypic framework provides a reproducible basis for guiding the targeted introgression of functional alleles into elite backgrounds, with visual traceability and biochemical congruence.

Key words: Fruit quality traits, phenotypic diversity, phytochemical profiling, *Solanum lycopersicum*, tomato wild relatives.

INTRODUCTION

Tomato (*Solanum lycopersicum* L.) is the second most economically valuable vegetable crop worldwide (FAOSTAT, 2024). In 2024, Mexico was the world's leading exporter, capturing 28% of the global market with exports valued at USD 3331.8 million (Trade Map, 2024). Its versatility drives high demand for both fresh consumption and processed products like canned goods, paste, purée, juice, and sauces. Mexico is recognized as the center of domestication and a primary center of diversification for tomato (Blanca et al., 2012). Native, cultivated, and wild populations persist in the country; however, their physical, chemical, and nutritional traits remain poorly documented (Méndez et al., 2011). Beyond their invaluable cultural legacy, these local varieties represent a key source of genetic diversity for crop improvement.

The tomato has been consolidated as a platform for metabolic engineering, oriented toward enrichment with antioxidant bioactive compounds such as carotenoids, flavonoids, and anthocyanins. In modern tomato breeding programs, fruit quality is a relevant focus, particularly for improving flavor (Tieman et al., 2017). For both fresh-market and processing tomatoes, the main quality attributes include size, shape, total soluble solids, lycopene, β-carotene, firmness, nutritional value, pH, titratable acidity, and color (Grierson and Kader, 1986).

Studies on Mexican tomato landraces have reported wide variation in physicochemical traits, including vitamin C content (4-9 mg·100 g^{-1} fresh weight), total phenolics (180-320 mg GAE·100 g^{-1} fresh weight), antioxidant activity (950-1450 µmol TE·100 g^{-1} fresh weight) (Vera-Guzmán et al., 2025), lycopene content (135-262 mg·100 g^{-1} dry weight), soluble solids totals (5-6 °Brix), pH (4.14), and titratable acidity (~ 0.4%

citric acid) (Montesinos-Cortés et al., 2026). Evidence from nutritional studies indicates that bioactive compounds such as lycopene, β-carotene, quercetin, and kaempferol are consistently associated with reduced risks of cancer and cardiovascular disease (Ali et al., 2021).

Therefore, characterizing and evaluating tomato genetic diversity is a fundamental step for its conservation and strategic use in breeding programs targeting fruit quality. In this regard, the present study aimed to assess selected physicochemical and morphological fruit attributes in a collection of Mexican native tomato accessions and wild relatives.

MATERIALS AND METHODS

Genetic material

A total of 50 tomato accessions were evaluated, representing diverse biological statuses: 10 Wild relatives, *Solanum pennellii* Correll LA0716 (S1), *S. pimpinellifolium* L. LA1576 (S2), *S. arcanum* Peralta LA2172 (S3), *S. corneliomulleri* J.F. Macbr. LA1677 (S4), *S. habrochaites* S. Knapp & D.M. Spooner LA1777 (S5), *S. chilense* (Dunal) Reiche LA2748 (S6), *S. chmielewskii* (C.M. Rick et al.) D.M. Spooner et al. LA2695 (S7), *S. huaylasense* Peralta LA1360 (S8), *S. peruvianum* L. LA0446 (S9), and *S. neorickii* D.M. Spooner et al. LA2133 (S10), obtained from the C.M. Rick Tomato Genetics Resource Center (TGRC); 7 native wild types (C1-C4, U1-U2, E1), 10 semi-domesticated accessions (O1-O2, E2-E4, U3-U7); 21 advanced F_6 lines (A1-A4, P1-P3, T1-T7, B1, B2, B4, R1, R3, M1-M2) developed within the Tomato Conservation and Breeding Program-COLPOS, and two cultivars: 'Kumato' (B3) and 'JL-5' (R2) from Nicaragua.

Experimental design and agronomic management

The experiment was conducted during the spring-autumn 2024 cycle in a greenhouse at Colegio de Postgraduados, Texcoco, Mexico. A randomized complete block design (RCBD) was implemented with three replicates, each consisting of four plants as the experimental unit. Transplanting was performed 35 d after sowing into 12 L polyethylene bags filled with red tezontle substrate. Plants were grown under a drip hydroponic system supplied with Steiner's nutrient solution, adjusted to pH 6.0. Greenhouse conditions were maintained at 23-26 °C with relative humidity ranging from 70%-80%.

Phenotypic characterization

Fruit quality traits were assessed following international tomato descriptors (IPGRI, 1996). Selected descriptors were grouped into quantitative and qualitative variables. Quantitative traits included: Total soluble solids (°Brix), measured with a digital refractometer (MA871, Milwaukee Instruments, Rocky Mount, North Carolina, USA); fruit acidity (pH), determined with a pH meter (HI 8314-1, Hanna Instruments, Woonsocket, Rhode Island, USA); fruit firmness (N, 6 mm probe), measured with a fruit hardness tester (FR-5120, Lutron Electronic Enterprise Co., Taipei, Taiwan); fruit color expressed as CIELab coordinates (L*, a*, b*), measured using a MiniScan EZ 4500L spectrophotometer; and biochemical composition (mg g^{-1} DM, including total carotenoids, lycopene, chlorophyll *a*, and chlorophyll *b*), quantified according to the LAN-CRO-P11 analytical protocol of the Laboratorio Nacional de Investigación y Servicio Agroalimentario y Forestal (LANISAF) with a UV-Vis microplate spectrophotometer (Multiskan Go, Thermo Fisher Scientific, Vantaa, Finland). Qualitative traits comprised external color, epidermis color, fruit size (polar/equatorial diameter ratio), and fruit shape.

Statistical analysis

Data were subjected to ANOVA using the RCBD linear model, followed by mean separation with Tukey's HSD test ($p \leq 0.05$). Pearson correlation coefficients were estimated among variables, and Principal Component Analysis (PCA) was performed to identify traits contributing most to phenotypic variation. All statistical analyses were performed in R (version 4.5.1; R Foundation for Statistical Computing, Vienna, Austria) using the packages car, agricolae, ggplot2, and corrplot.

RESULTS AND DISCUSSION

Physical and visual fruit attributes

The panel of 50 tomato accessions exhibited high phenotypic diversity. They were classified into three genetic groups: Ten wild relatives, 14 *Solanum lycopersicum* var. *cerasiforme* (SLC), and 26 *S. lycopersicum* var. *lycopersicum* (SLL). The panel was further categorized into 10 fruit-type groups according to commercial types, specialties, and local varieties. Accessions of SLC corresponded to 'Cherry' (C1-C4, 8%), 'Cocktail' (E1, 2%), 'Ojo de venado' (O1-O2, 4%), and 'Grape' (U1-U7, 14%). In SLL, accessions were distributed among 'Kidney' (A1-A4, 8%), 'Globe' (B1-B4, 8%), 'Pumpkin' (P1-P3, 6%), 'Chili' (M1-M2, 4%), 'Chino criollo' (T1-T7, 14%), 'Cocktail' (E2-E4, 6%), and 'Roma' (R1-R3, 6%). Wild relatives (S1-S10, 20%) were grouped as wild type. In Mexico, commercial tomato production is concentrated in 'Roma' (75%), 'Globe' (20%), and, to a lesser extent, specialty types (5%).

Fruit color distribution across groups revealed patterns associated with domestication stages. In wild relatives, green fruits predominated (90%), with a single red-fruited accession (S2), reflecting ancestral traits. In SLC, red fruits were most frequent (69%), while orange (23%) and yellow (15%) variants were also observed. The SLL exhibited the greatest color diversity, with red fruits being most common (53%). Fruit size showed a clear gradient across genetic groups, consistent with the enlargement pattern observed during tomato domestication and breeding. All wild relatives' accessions (100%) bore very small fruits. In SLC, very small fruits accounted for 64.29% and small fruits for 35.71%. In contrast, in SLL, 19.23% of accessions produced small fruits, 73.08% medium fruits, and 7.69% large fruits.

Quispe-Choque et al. (2022) reported similar findings across 50 accessions, encompassing wild relatives, introduced varieties, and breeding lines, exhibiting variation in fruit shape, size, and color. Consistent with Lobato et al. (2012), native tomato populations in Mexico display notable diversity in fruit size, shape, and color, highlighting their variability. Red, yellow, and orange fruit pigmentation is synthesized through the carotenoid biosynthetic pathway (Sun and Li, 2020). In contrast, the brown pericarp coloration observed in accessions P2, T4, B3, and B4 results from carotenoid interactions modulated by specific mutations (Mes et al., 2008), rather than anthocyanin accumulation as seen in accessions E2 and E4.

The observed gradient in fruit size is a hallmark of the tomato domestication syndrome, largely driven by the cumulative effect of mutations in major QTLs such as *fw2.2* and *fas*, which were strongly selected for during the transition from the wild *S. pimpinellifolium* to the semi-domesticated SLC and finally to the fully domesticated SLL (van der Knaap et al., 2014). Furthermore, the wider morphological diversity observed in SLL, including shapes like 'Chili' and 'Pumpkin', suggests a post-domestication diversification driven by QTLs associated with fruit weight and shape variation in tomato (van der Knaap et al., 2014).

Fruit forms—classified into 13 types—and epidermis coloration varied according to descriptors (Figure 1). Wild relatives' accessions exhibited rounded (S2, S3, S7, S9, and S10), oblate (S1, S5, and S8), round-elongated (S4) or flattened (S6) forms, with 90% showing a colorless epidermis and 10% a yellow epidermis. Both SLC and SLL groups displayed greater morphological diversity, including forms absent in the wild relatives. In SLC, 36% of accessions exhibited a colorless epidermis and 64% a yellow epidermis. Fruit forms included rounded (50%), ovate (22%), elongated (7%), pyriform (7%), oval (7%), and elliptic (7%). In SLL, 50% exhibited a colorless epidermis, 42% a yellow epidermis, and 8% a yellow epidermis with anthocyanin accumulation (E2 and E4). Fruit forms included oblong (26%), flattened (15%), rounded (15%), oblate (12%), obovate (12%), round-elongated (8%), elliptic (4%), cylindric (4%), and ovate-elongated (4%), representing the most variable group.

According to Blanca et al. (2012), yellow epidermis is most frequent in cherry and traditional tomato types, followed by colorless; in modern materials, yellow epidermis predominates. This pigmentation is associated with the accumulation of naringenin chalcone, while colorless epidermis reflects reduced flavonoid deposition. In the latter, anthocyanin presence is rare, though some cultivars have been developed through backcrossing with wild relatives or via transgenesis (Mes et al., 2008). The presence of anthocyanins in accessions E2 and E4 likely reflects their classification as local 'Indigo' types, comparable to 'Indigo Rose' and 'Indigo Sun'. These accessions accumulated anthocyanins in the fruit epidermis (yellow in both), while pulp color remained red (E2) or yellow (E4). Additionally, wild relatives S4, S8, and S9 exhibited two longitudinal, opposite epidermal streaks with anthocyanins of pink or purple hue, depending on the accession.

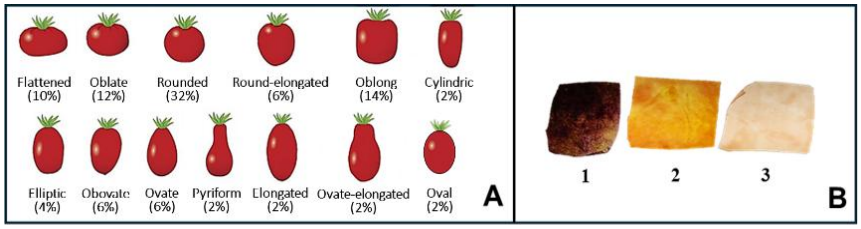

Figure 1. External characteristics of tomato fruits. (A) Fruit shapes and (B) fruit epidermis color: Yellow with anthocyanin accumulation (1), yellow (2), and colorless (3).

Significant differences ($p \leq 0.05$) were found for fruit firmness (Table 1). On average, wild relatives' accessions exhibited 7.99 N, with the highest value recorded in *S. huaylasense* (13.89 N) and the lowest in *S. pennellii* (4.40 N). In SLC, 'Cherry', 'Ojo de venado', 'Cocktail', and 'Grape' types registered values of 7.25, 7.84, 6.28, and 9.74 N, respectively. In contrast, within SLL, 'Kidney', 'Pumpkin', 'Cocktail', 'Globe', 'Roma', 'Chili', and 'Chino criollo' types showed values of 7.49, 8.51, 13.79, 11.71, 14.98, 16.11, and 11.71 N, respectively. The SLC group was the most homogeneous, while within wild relative and SLL accessions with high firmness were identified, making them suitable for use in elite cultivar breeding programs.

Fruit firmness is a trait determined by multiple factors, including skin resistance and internal fruit structure, which vary among cultivars; therefore, selecting cultivars with prolonged firmness allows harvesting at more advanced ripening stages, consequently improving flavor (Grierson and Kader, 1986). In this context, mutations conferring elongated or blocky fruit shapes offer greater firmness without compromising quality, as observed in chili-type accessions (M1 and M2).

In comparative studies of 'Cherry' tomato cultivars, Baek et al. (2024) reported that black-colored fruits exhibited the highest firmness (17.09 N), significantly surpassing green (13.38 N), orange (10.88 N), red (10.82 N), and yellow (10.44 N) fruits. Conversely, Chang et al. (2024) identified that brown-colored fruits showed the highest firmness (10.1 N), in contrast to yellow (7.1 N), red (6.9 N), and green (6.3 N) fruits. These results are consistent with those obtained in this study; however, some accessions in our panel exhibited superior firmness, highlighting their promising potential for breeding programs.

Fruit shape and firmness are not only morphological descriptors but critical traits influencing consumer acceptance and market segmentation. Comparative analyses of cherry and fresh market tomatoes have shown that variation in size, height/width ratio, and firmness is strongly associated with consumer preferences and defines distinct commercial categories. In this context, the broad diversification of fruit forms observed in SLC and SLL, together with differences in pigmentation, underscores the relevance of these materials not only for understanding post-domestication variability but also for breeding programs aimed at specific market niches.

For both fresh-market and processing tomatoes, color is an important fruit quality parameter, determined primarily by carotenoid and flavonoid compounds (Ballester et al., 2010). Tomato quality is typically assessed visually combined with colorimetric methods (Li et al., 2018). In this study, significant differences ($p \leq 0.05$) in fruit color among accessions were compared using CIELab parameters (L*, a*, b*) (Table 1). The highest L* (lightness) value in wild relatives was S8 (*S. huaylasense*) at 85.97, and in SLC it was U5 (yellow 'Grape'-type) at 53.15; the lowest in SLL was B4 (brown 'Globe'-type) at 19.91. The lowest a* (green-red axis) value in wild relatives was S5 (*S. habrochaites*) at -26.31; whereas the highest values in SLC and SLL were C2 (red 'Cherry') at 76.78 and R1 (red 'Roma') at 77.01, respectively. The highest b* (blue-yellow axis) value in PS was S1 (*S. pennellii*) at 74.50, and the lowest was S6 (*S. chilense*) at 20.53; in SLC, the highest was U5 (yellow 'Grape') at 83.58, and in SLL, the lowest was E4 (purple-yellow 'Cocktail') at 1.34.

These results are consistent with those reported by Chang et al. (2024) and Baek et al. (2024) for 'Cherry' tomato cultivars of different colors; however, our accession panel exhibited broader and more extreme ranges. Chang et al. (2024) observed that L* values were highest in yellow and green fruits, in contrast to red and brown ones. Regarding the a* value, red and brown fruits showed the highest values, just above 20 and 10, respectively. The b* value was notably higher in yellow fruits, approaching 40—nearly double that recorded in the other cultivars. Similarly, Baek et al. (2024) recorded CIELab values of 51.08,-3.32, and 34.75 in yellow fruits; 49.41, 10.59, and 38.32 in orange fruits; 37.56, 14.42, and 19.04 in red fruits; 36.92, 1.46, and 16.48 in black fruits; and 44.09, -8.86, and 18.55 in green fruits.

Table 1. Tukey HSD mean comparison ($p \leq 0.05$) for 50 tomato accessions. AC: Accession; TSS: total soluble solids content (°Brix); FA: fruit acidity as hydrogen potential (pH); FF: fruit firmness (N); L: lightness in CIELab space; a: green-red axis in CIELab space; b*: blue-yellow axis in CIELab space; Chlor_*a*: chlorophyll *a* content (mg g^{-1}); Chlor_*b*: chlorophyll *b* content (mg g^{-1}); Lyc: lycopene content (mg g^{-1}); TotCar: total carotenoids content (mg g^{-1}); SD: standard deviation; CV: coefficient of variation (%); HSD: Tukey's honestly significant difference test. Letters indicate significant differences among means ($p \leq 0.05$).

Nr	AC	TSS	FA	FF	L*	a*	b*	Chlor_*a*	Chlor_*b*	Lyc	TotCar
1	S1	5.96^{p-u}	4.13^{p}	4.40^{v}	76.04^{ef}	-19.59^{s}	74.50^{c}	0.2974	0.1018	0.0000	0.2875
2	S2	10.04^{cde}	5.21^{a}	5.16^{u}	37.91^{uv}	55.26^{j}	48.34^{nop}	0.0082	0.0065	1.6247	1.9839
3	S3	6.81^{l-p}	4.39^{no}	8.75^{mn}	80.22^{bcd}	-13.93^{qrs}	45.45^{opq}	0.1348	0.0450	0.0000	0.0568
4	S4	7.58^{i-m}	4.79^{b-f}	7.03^{q}	82.97^{abc}	-10.78^{q}	52.37^{i-n}	0.1654	0.0534	0.0000	0.0739
5	S5	9.98^{cde}	5.33^{a}	12.39^{fg}	71.53^{g}	-26.31^{t}	69.15^{de}	0.1162	0.0286	0.0000	0.0510
6	S6	7.46^{j-m}	4.38^{o}	11.24^{hi}	74.28^{efg}	-2.86^{p}	20.53^{w}	0.0354	0.0114	0.0000	0.0554
7	S7	10.08^{cd}	4.93^{bc}	5.91st	83.85^{a}	-16.37^{qrs}	58.52^{fgh}	0.0903	0.0343	0.0000	0.0467
8	S8	9.45^{def}	4.64^{f-l}	13.89^{cd}	85.97^{a}	-16.86^{rs}	55.67^{f-j}	0.0637	0.0298	0.0000	0.0421
9	S9	8.57^{f-i}	4.86^{b-e}	6.11^{s}	79.90^{cd}	-14.63^{qrs}	54.52^{g-l}	0.1345	0.0536	0.0000	0.0641
10	S10	8.39^{g-j}	4.57^{j-n}	5.00^{uv}	85.19^{a}	-13.50^{qr}	38.30^{r-u}	0.1921	0.0857	0.0000	0.1084
11	A1	9.06^{e-h}	4.58^{i-m}	7.00^{qr}	54.77^{jkl}	62.73^{i}	39.36^{rst}	0.0228	0.0370	0.7376	1.6411
12	A2	11.53^{b}	4.85^{b-e}	5.92st	52.96^{k-n}	65.42^{f-i}	43.44^{pqr}	0.0088	0.0052	0.7243	1.2668
13	P1	7.84^{ijk}	4.75^{c-i}	7.24^{q}	72.99^{fg}	14.60^{n}	76.19^{bc}	0.0105	0.0139	0.0416	0.3149
14	P2	7.24^{k-o}	4.73^{d-k}	8.58^{n}	29.99^{w}	37.20^{l}	28.30^{v}	0.0678	0.0318	0.4352	0.6747
15	C1	6.42^{n-r}	4.78^{b-h}	5.23^{tu}	53.15^{k-n}	76.48^{ab}	52.34^{i-n}	0.0248	0.0287	0.3492	0.5913
16	A3	9.34^{d-g}	4.43^{mno}	6.10^{s}	49.64^{nop}	70.99^{b-f}	49.92^{k-o}	0.0098	0.0070	0.4389	0.7669
17	A4	4.49^{w-A}	4.61^{g-m}	10.94^{ij}	46.01^{qrs}	65.45^{f-i}	53.62^{h-m}	0.0061	0.0175	0.8294	1.1186
18	O1	6.59^{m-q}	4.59^{i-m}	8.07^{nop}	50.94^{mno}	73.21^{abc}	51.56^{j-n}	0.0126	0.0092	0.7383	1.2058
19	O2	5.63^{q-v}	4.43^{mno}	7.60^{opq}	44.50^{rst}	66.78^{e-i}	47.85^{nop}	0.0110	0.0153	0.7146	1.4237
20	C2	7.74^{i-l}	4.80^{b-f}	8.32^{no}	53.15^{k-n}	76.78^{a}	54.32^{h-l}	0.0143	0.0166	0.8625	1.4536
21	C3	8.45^{f-j}	4.80^{b-f}	7.30^{q}	48.82^{opq}	64.85^{hi}	49.83^{l-o}	0.0147	0.0073	0.6171	1.1340
22	U1	9.66^{cde}	4.95^{b}	12.60^{ef}	64.05^{h}	50.25^{jk}	71.37^{cde}	0.0098	0.0064	0.0613	0.3599
23	U2	13.88^{a}	4.95^{b}	9.63^{kl}	65.51^{h}	46.48^{k}	72.65^{cd}	0.0076	0.0076	0.0812	0.3967
24	C4	6.30^{o-s}	4.78^{b-g}	8.15^{nop}	42.56st	61.83^{i}	45.03^{opq}	0.0019	0.0090	0.9528	1.5722
25	E1	7.34^{k-n}	4.60^{h-m}	6.28^{rs}	54.00^{klm}	76.75^{a}	58.69^{fgh}	0.0135	0.0221	0.7419	1.2806
26	E2	9.11^{d-h}	4.55^{k-o}	14.75^{b}	23.36^{xy}	2.20^{op}	2.40^{x}	0.0451	0.0147	0.8671	1.4387
27	U3	9.86^{cde}	4.86^{b-e}	12.23^{fg}	65.91^{h}	46.96^{k}	72.09^{cde}	0.0087	0.0073	0.0915	0.4565
28	U4	8.12^{h-k}	4.59^{i-m}	7.47^{pq}	51.22^{l-o}	73.63^{abc}	58.61^{fgh}	0.0214	0.0294	0.4275	0.6683
29	U5	5.58^{r-v}	4.58^{i-m}	7.05^{q}	83.77^{ab}	5.19^{o}	83.58^{a}	0.0045	0.0249	0.0476	0.5076
30	U6	6.73^{l-p}	4.60^{h-m}	9.42^{lm}	76.95^{de}	17.88^{n}	80.54^{ab}	0.0161	0.0230	0.0582	0.1106
31	E3	6.31^{o-r}	4.73^{d-j}	10.92^{ij}	40.95^{tu}	65.21^{ghi}	48.45^{m-p}	0.0120	0.0209	0.6248	1.0143
32	E4	9.91^{cde}	4.68^{e-k}	15.71^{a}	24.06^{x}	1.15^{op}	1.34^{x}	0.0647	0.0296	0.0358	0.1844
33	U7	10.65^{bc}	4.79^{b-f}	9.78^{kl}	56.37^{ijk}	63.28^{i}	66.88^{e}	0.0286	0.0515	0.0993	0.3923
34	T1	5.20^{t-y}	4.81^{b-f}	10.34^{jk}	58.95^{i}	65.87^{f-i}	38.52^{r-u}	0.0072	0.0169	0.9526	1.6209
35	T2	4.28^{yzA}	4.78^{b-g}	10.81^{ij}	57.68^{ij}	62.07^{i}	34.43^{tu}	0.0202	0.0328	0.7390	1.6006
36	T3	5.26^{t-y}	4.79^{b-f}	12.61^{ef}	56.15^{ijk}	70.86^{b-g}	36.49^{stu}	0.0141	0.0090	0.8464	1.4934
37	T4	5.29^{s-x}	4.72^{e-k}	13.24^{de}	35.10^{v}	46.87^{k}	34.36^{tu}	0.0234	0.0148	0.6317	0.9903
38	T5	6.13^{p-t}	4.68^{e-k}	11.82^{gh}	53.16^{k-n}	66.08^{f-i}	36.84^{stu}	0.0145	0.0211	0.5272	0.8582
39	T6	3.56^{A}	4.80^{b-f}	11.11^{hi}	53.05^{k-n}	62.24^{i}	33.79^{u}	0.0103	0.0269	0.5345	0.8500
40	T7	4.15^{zA}	4.83^{b-e}	12.02^{fg}	54.06^{klm}	71.88^{a-e}	39.27^{rst}	0.0100	0.0269	0.7198	1.3058
41	B1	4.83^{v-z}	4.50^{l-o}	10.83^{ij}	48.08^{opq}	67.33^{d-i}	54.26^{h-l}	0.0099	0.0321	0.9351	1.5336
42	B2	5.03^{u-z}	4.49^{l-o}	10.60^{ij}	48.38^{opq}	72.35^{a-e}	55.76^{f-j}	0.0053	0.0131	0.6389	1.3067
43	B3	4.53^{w-A}	4.78^{b-h}	13.17^{de}	20.66^{xy}	30.00^{m}	28.24^{v}	0.0452	0.0080	0.6213	1.1103
44	B4	5.45^{r-w}	4.90^{bcd}	12.24^{fg}	19.91^{y}	26.09^{m}	27.16^{v}	0.0312	0.0195	0.5296	0.9556
45	P3	4.33^{x-A}	4.50^{l-o}	9.70^{kl}	49.99^{nop}	72.66^{a-d}	59.75^{fg}	0.0105	0.0250	0.6385	1.0054
46	R1	4.68^{v-z}	4.60^{h-m}	14.84^{b}	54.08^{klm}	77.01^{a}	60.62^{f}	0.0120	0.0295	0.6374	1.3810
47	R2	4.18^{zA}	4.55^{k-o}	14.51^{bc}	47.84^{o-r}	70.72^{c-g}	55.16^{g-k}	0.0092	0.0208	0.9282	1.6223
48	M1	4.36^{x-A}	4.93^{bc}	16.24^{a}	49.60^{nop}	69.11^{c-h}	55.11^{g-k}	0.0107	0.0058	0.8420	1.5358
49	R3	4.72^{v-z}	4.80^{b-f}	15.60^{a}	47.26^{pqr}	69.43^{c-h}	57.42^{f-i}	0.0087	0.0145	0.6437	1.1521
50	M2	4.44^{w-A}	4.59^{i-m}	15.98^{a}	52.46^{lmn}	67.40^{d-i}	41.52^{qrs}	0.0143	0.0040	0.3275	0.6138
Mean		7.05	4.71	10.04	55.40	43.47	49.49	0.0386	0.0241	0.4779	0.8736
Minimum		3.56	4.13	4.40	19.91	-26.31	1.34	0.0019	0.0040	0.0000	0.0421
Maximum		13.88	5.33	16.24	85.97	77.01	83.58	0.2974	0.1018	1.6247	1.9839
SD		2.34	0.21	3.29	17.14	34.09	17.42	0.0575	0.0192	0.3776	0.5680
CV		33.21	4.38	32.81	30.95	78.42	35.20	148.80	79.68	79.01	65.02
HSD		1.02	0.18	0.74	3.57	5.69	5.28	–	–	–	–

Phytochemical fruit attributes

The total soluble solids (TSS) content ranged from 3.56 °Brix (T6 of SLL) to 13.88 °Brix (U2 of SLC) (Table 1). On average, wild relatives' accessions exhibited 8.43 °Brix, while SLC and SLL accessions showed values of 8.07 and 5.97 °Brix, respectively (Figure 2). Notably, the SLL group displayed the greatest diversity. Within SLC, 'Cherry', 'Ojo de venado', 'Cocktail', and 'Grape' types had mean values of 7.23, 6.11, 7.34, and 9.21 °Brix, respectively. Among SLL, 'Kidney', 'Pumpkin', 'Cocktail', 'Chino criollo', 'Globe', 'Roma', and 'Chili' types obtained mean values of 8.61, 6.47, 8.44, 4.84, 4.96, 4.52, and 4.40 °Brix, respectively. In contrast, within wild relatives, the highest values were recorded in *S. chmielewskii* (10.08 °Brix) and *S. pimpinellifolium* (10.04 °Brix), followed by *S. habrochaites* (9.98 °Brix) and *S. huaylasense* (9.45 °Brix).

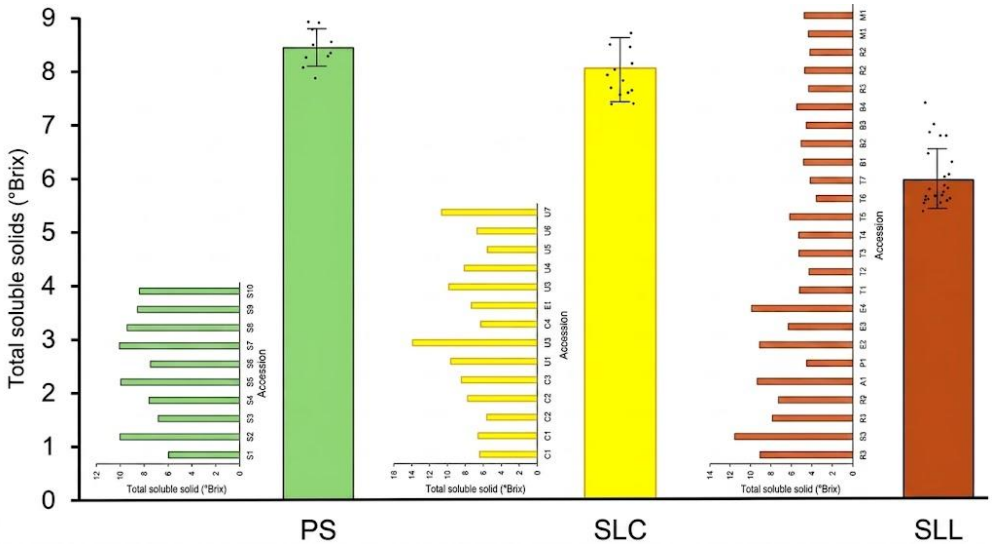

Figure 2. Mean total soluble solids content for three tomato groups: Wild relatives (PS), *Solanum lycopersicum* var. *cerasiforme* (SLC), and *Solanum lycopersicum* var. *lycopersicum* (SLL). Individual values for each group are shown in the inset.

On average, wild relatives and SLC groups exhibited a mean fruit pH of 4.72, while SLL averaged 4.69. Wild relatives showed the greatest variability, with the highest value recorded in *S. habrochaites* (pH 5.33) and the lowest in *S. pennellii* (pH 4.13). Within SLC, 'Cherry', 'Ojo de venado', 'Cocktail', and 'Grape' types had mean pH values of 4.79, 4.51, 4.60, and 4.76, respectively. In SLL, 'Kidney', 'Pumpkin', 'Cocktail', 'Chino criollo', 'Globe', 'Roma', and 'Chili' types produced fruits with mean pH values of 4.62, 4.66, 4.66, 4.77, 4.67, 4.65, and 4.76, respectively.

Baek et al. (2024), in five 'Cherry' tomato cultivars, reported high TSS values in yellow (10.75 °Brix), orange (8.66 °Brix), red (8.26 °Brix), green (7.84 °Brix), and black (7.43 °Brix) fruits. Similarly, Tripodi et al. (2023), in 60 tomato accessions, found that 'Cherry' (7.82 °Brix) and 'Globe' (7.38 °Brix) types exhibited the highest TSS contents compared to 'Beefsteak' (7.13 °Brix), 'Plum' (7.14 °Brix), and 'Oxheart' (6.79 °Brix). However, the latter two types exhibited higher pH values, though all showed less variation (pH < 5). Figàs et al. (2015) reported comparable results in eight Mediterranean cultivar groups. The 'Cherry' (7.68 °Brix) and 'Penjar' (6.57 °Brix) groups outperformed 'Borseta', 'Cor', 'Plana', 'Pruna', 'Redona', and 'Valenciana' (< 6.0 °Brix). The pH values in their study ranged from 4.16 to 4.33 and were nonsignificant. In contrast, Méndez et al. (2011), in a study of wild and cultivated Mexican tomatoes, found nonsignificant differences in TSS, whether in juice (4.38-8.01 °Brix) or pulp (5.18-7.88 °Brix), but did observe significant differences in pH (3.96-4.75).

The gradient in TSS from wild relatives and SLC to SLL is inversely related to the gradient in fruit size, consistent with the long-recognized negative correlation between fruit weight and sugar concentration that has constrained tomato breeding and domestication. It has been demonstrated that soluble solids and moisture content are negatively correlated, indicating that low °Brix in tomatoes results from dilution by high water levels. As fruit volume increases, sugar biosynthesis and phloem loading do not scale proportionally, leading to

reduced sugar concentration per unit of mass (Heuvelink et al., 2025). However, several studies have demonstrated that the negative correlation between fruit weight and °Brix can be broken through phenotype-guided selection. The high TSS values observed in the 'Grape' type of SLC and in the 'Kidney' and 'Cocktail' types of SLL indicate that these accessions retain favorable alleles capable of overcoming the dilution effect, making them valuable genetic resources for breeding programs aimed at enhancing fruit quality without compromising yield.

Variation in fruit acidity exerts a more pronounced effect on flavor than the limited variation in sugar content observed in most cultivars. Several studies demonstrate that the selection of certain traits has negatively impacted flavor. For example, modern commercial varieties contain significantly fewer biochemical compounds essential for flavor compared with older and wild varieties (Tieman et al., 2017).

Consumer preference indicates that a higher sugar-to-acid ratio produces a favorable taste in both fresh-market and processing tomatoes (Baldwin et al., 1998). Tomatoes with good flavor are those that achieve a balance of sugars, acids, and volatile compounds, preferably with high levels of the latter, which enhance the perception of sweetness beyond its actual concentration (Tieman et al., 2017). Grierson and Kader (1986) linked sour-tasting fruits to high acid and low sugar levels, mild flavor to high sugar and low acid levels, and bland flavor to low levels of both sugars and acids. However, soluble solids content is not necessarily correlated with perceived sweetness (Klee and Tieman, 2018).

During domestication, allele frequencies for flavor-related metabolites shifted: South American SLC increased citric acid alleles, Mesoamerican SLC gained a glucose allele, and cultivated SLL acquired a malic acid allele while the citric acid allele was lost (Razifard et al., 2020). Humans perceive fruits with higher fructose and citric acid content as sweeter and more acidic than those with higher glucose and malic acid content (Grierson and Kader, 1986).

Given that conventional phenotyping can be limited in detecting genetic variation among fruits with similar coloration, while traditional genetic approaches are often laborious and restricted in application, carotenoid profiling has emerged as an efficient alternative for identifying genes involved in fruit pigmentation (Yoo et al., 2017). In this study, chlorophyll *a*, chlorophyll *b*, lycopene, and total carotenoids were quantified, with mean contents varying across the three evaluated groups. Based on fruit color, wild relatives' accessions clustered into two categories. Green fruits showed elevated chlorophyll *a* (0.1366 mg g^{-1}) and chlorophyll *b* (0.0493 mg g^{-1}) contents but low total carotenoids (0.0873 mg g^{-1}), except for S1 (*S. pennellii*), and no detectable lycopene. In contrast, the only red-fruited accession, S2 (*S. pimpinellifolium*), exhibited the highest lycopene (1.6247 mg g^{-1}) and total carotenoid (1.9839 mg g^{-1}) contents among the 50 accessions.

The SLC group was subdivided into red, orange, and yellow fruits. For chlorophyll *a*, no differences were observed, with values of 0.0143, 0.0137, and 0.0103 mg g^{-1}, respectively. Chlorophyll *b* content in yellow fruits (0.0240 mg g^{-1}) was 1.40 times higher than in red (0.0172 mg g^{-1}) and 1.32 times higher than in orange fruits (0.0182 mg g^{-1}). Lycopene concentration in red fruits (0.6755 mg g^{-1}) was 8.11 times greater than in orange (0.0833 mg g^{-1}) and 12.77 times greater than in yellow fruits (0.0529 mg g^{-1}). For total carotenoids, red fruits (1.1662 mg g^{-1}) contained 2.91 times more than orange (0.4014 mg g^{-1}) and 3.77 times more than yellow fruits (0.3091 mg g^{-1}).

The SLL group was subdivided into five fruit colors. Chlorophyll *a* was highest in brown (0.0419 mg g^{-1}) and purple (0.0549 mg g^{-1}) fruits compared with red (0.0105 mg g^{-1}), pink (0.0129 mg g^{-1}), and yellow (0.0105 mg g^{-1}). Chlorophyll *b* remained relatively stable in red (0.0190 mg g^{-1}), pink (0.0197 mg g^{-1}), brown (0.0185 mg g^{-1}), and yellow (0.0139 mg g^{-1}) fruits, with a maximum in purple (0.0222 mg g^{-1}). Lycopene contents were highest in purple-red (0.8671 mg g^{-1}) and red fruits (0.7182 mg g^{-1}), followed by pink (0.6639 mg g^{-1}) and brown (0.5545 mg g^{-1}), while the lowest values were recorded in yellow (0.0416 mg g^{-1}) and purple-yellow fruits (0.0358 mg g^{-1}). For total carotenoids, maximum contents were found in purple-red (1.4387 mg g^{-1}) and red fruits (1.2787 mg g^{-1}), with a gradual reduction in pink (1.1918 mg g^{-1}) and brown (0.9327 mg g^{-1}). The lowest values were observed in yellow (0.3149 mg g^{-1}) and purple-yellow fruits (0.1844 mg g^{-1}).

Green tomato fruits contain high chlorophyll levels, while red and orange fruits are characterized by elevated concentrations of lycopene and β-carotene, respectively (Li et al., 2018). They also accumulate other carotenoids such as phytoene, violaxanthin, and lutein (Ballester et al., 2010).

According to Górecka et al. (2020), lycopene content depends on product type and harvest date. In their study with 'Grandimat', they reported dry-weight concentrations of 0.4645-0.5997 mg g^{-1} in fresh tomato, 0.8433-1.3979 mg g^{-1} in dehydrated tomato, and 1.8429-2.1173 mg g^{-1} in tomato paste. These values were higher than those obtained in the present study, likely because their quantification was performed in fully ripe fruits, in contrast to the optimal consumption stage considered here. In contrast, Aono et al. (2021), in a broad

panel of 157 tomato accessions encompassing diverse forms, sizes, and colors, quantified chlorophyll *a*, chlorophyll *b*, lycopene, and total carotenoids with ranges of 0.000-0.204, 0.001-0.104, 0.007-1.298, and 0.037-2.142 mg g^{-1}, respectively—values like those quantified in this study. Chang et al. (2024), in 'Cherry' tomatoes, determined that the highest lycopene contents were in red (0.048 mg g^{-1}) and brown fruits (0.034 mg g^{-1}), whereas in yellow and green fruits it was not detected. Ballester et al. (2010) reported that lycopene content did not differ significantly between red and pink fruits, indicating that variation in coloration is mainly due to the accumulation of naringenin chalcone in the epidermis, findings that are consistent with those obtained in the present study.

The green-fruited phenotype of wild tomatoes results from multiple blocks in the ripening program rather than a single mutation. For example, *S. habrochaites* retains chloroplasts and photosynthetic activity, fails to degrade chlorophyll, and does not form chromoplasts, preventing carotenoid accumulation (Kilambi et al., 2017). Reduced PSY1 protein abundance and mutations in *SlPSY1*, *SlSGR1*, and *SlMYB12* further impair pigmentation (Cui et al., 2024).

Variation in lycopene content among red, orange, and yellow fruits in SLC and SLL reflects differences in the functionality of key carotenogenic genes. A 4906-bp deletion near *PSY1* reduces its expression and carotenoid accumulation (Liu et al., 2024), explaining the low lycopene levels in yellow fruits of our panel (0.0529 mg g^{-1} in SLC; 0.0416 mg g^{-1} in SLL). Orange fruits (0.0833 mg g^{-1} lycopene in SLC) likely carry mutations in *SlLCYB*, which converts lycopene to β-carotene, as described in the tangerine mutant (Ronnen et al., 2024). Red fruits (0.6755-0.7182 mg g^{-1} lycopene) retain functional *PSY1* alleles and low *LCYB* activity, enabling lycopene accumulation. Thus, the color gradient from yellow to orange to red reflects progressive restoration of *PSY1* function and modulation of downstream carotenogenic genes.

Principal component analysis

Based on 14 quantitative and qualitative fruit quality attributes, principal component analysis (PCA) showed that the first two components captured 50.93% of the total phenotypic variability. The clustering of the 50 accessions was performed according to fruit type, displaying a progressive distribution from left to right in the biplot, ranging from very small fruits (wild relatives) to large fruits (domesticated) (Figure 3). The low variance explained by the first two components reflected the weak correlation among the evaluated phenotypic attributes, resulting in information dispersed across multiple dimensions. Jolliffe and Cadima (2016) noted that when variables are partially independent, the covariance matrix approximates a diagonal form and eigenvalues are more evenly distributed, preventing the first components from concentrating most of the variability.

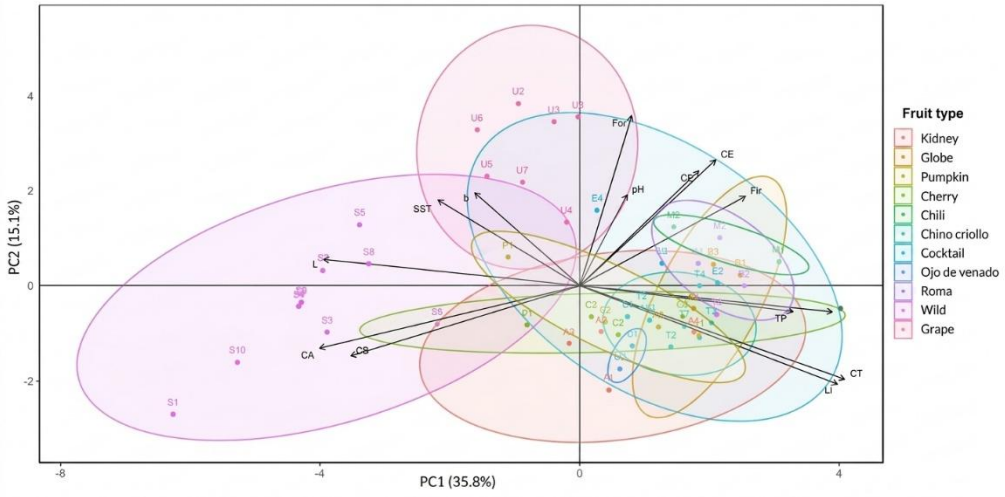

Figure 3. Principal component analysis for 50 tomato accessions based on 14 fruit quality attributes. L: Lightness (L*); a: green-red axis (a*); b: blue-yellow axis (b*); CA: chlorophyll *a* (mg g^{-1}); CB: chlorophyll *b* (mg g^{-1}); LI: lycopene (mg g^{-1}); CT: total carotenoids (mg g^{-1}); pH: hydrogen potential; SST: total soluble solids (°Brix); Fir: fruit firmness (N); CE: fruit epidermis color; CF: fruit color; For: fruit shape; TF: fruit size.

Principal component 1 (PC1) and principal component 2 (PC2) explained 35.79% and 15.14% of the total variation, respectively, revealing differentiated patterns in variable contributions (Table 2). The PC1 was mainly associated with total carotenoids, chlorophyll *a*, and lycopene, indicating its relationship with pigmentation attributes. In contrast, PC2 reflected characteristics related to fruit shape, epidermis color, and external color—attributes linked to consumer preferences.

Table 2. Percentage contribution of each variable to the first two principal components.

Nr	Variable	Code	PC1	PC2
1	Lightness	L*	12.43893	0.57211
2	Green-red axis	a*	12.08905	0.57759
3	Blue-yellow axis	b*	2.08145	7.18507
4	Chlorophyll *a*	CA	12.83838	3.29444
5	chlorophyll *b*	CB	9.95148	4.18767
6	Lycopene	LI	12.61172	8.21599
7	Total carotenoids	CT	13.27093	7.38717
8	Hydrogen potential	pH	0.41613	6.86291
9	Total soluble solids	SST	3.82073	6.09336
10	Fruit firmness	Fir	5.18819	6.66792
11	Fruit epidermis color	CE	3.48960	13.20219
12	Fruit color	CF	2.68498	11.00427
13	Fruit shape	For	0.50912	24.19691
14	Fruit size	TF	8.60930	0.55239
	Eigenvalues		5.01113	2.11901
	Standard deviation		2.23856	1.45568
	Percentage of variance		35.79377	15.13576
	Cumulative percentage of variance		35.79377	50.92953

Based on taxonomic classification, wild relatives' accessions (S1-S10, except S2) formed a well-defined group in the PCA, associated with lightness (L*) and chlorophyll *a* and chlorophyll *b* contents. The SLC' accessions occupied an intermediate position between wild relatives and SLL, with 'Grape'-type fruits (U_) forming a distinct subgroup that clustered with two SLL accessions: A yellow 'Pumpkin'-type (P1) and a purple-yellow 'Cocktail'-type (E4). This pattern is explained by the fact that most 'Grape'-type fruits exhibited orange or yellow coloration, associated with b* values and high soluble solids content. The remaining fruit types 'Cherry' (C_), 'Cocktail' (E1), and 'Ojo de venado' (O_) clustered with some SLL types.

All SLL' accessions clustered closely together, within which two subgroups were discernible. Subgroup 1 comprised 'Kidney' (A_), 'Pumpkin' (P2, P3), 'Globe' (B1, B2), and 'Chino criollo' (T_) fruit types of SLL, together with 'Cherry' and 'Ojo de venado' fruit types of SLC. This subgroup was associated with lycopene, fruit size, and total carotenoids. Subgroup 2 included 'Roma' (R_), 'Globe' (B3, B4), 'Chili' (M_), and one 'Chino criollo' accession (T4) of SLL, linked to firmness, fruit size, and a* values. 'Cocktail'-type fruits exhibited the greatest heterogeneity: One SLC accession (E1) clustered with subgroup 1, two SLL accessions (E2, E3) with subgroup 2, and one (E4) with 'Grape'-type fruits of SLC. Notably, accession S2 (*S. pimpinellifolium*) was distributed across both subgroups.

Barnett et al. (2023) captured 41.0% of the total variation with two components derived from 21 phenotypic traits (morphological, color, and nutritional) recorded in 38 accessions distributed across 13 wild species (*S. arcanum*, *S. lycopersicum* var. *cerasiforme*, *S. cheesmaniae* (L. Riley) Fosberg, *S. chilense*, *S. chmielewskii*, *S. corneliomulleri*, *S. galapagense* S.C. Darwin & Peralta, *S. habrochaites*, *S. huaylasense*, *S. neorickii*, *S. pennellii*, *S. peruvianum*, and *S. pimpinellifolium*). They determined that the first component was associated with fruit color, sugar composition (types), and malic acid, while the second was linked to fruit size, fruit weight, and total sugar concentration. Furthermore, they found that species separated into two groups: One comprising four species with colored fruits characterized by higher chroma, lower malic acid concentration, and elevated

glucose and fructose contents; and another comprising nine species with green fruits showing higher lightness and elevated sucrose and malic acid contents.

Baek et al. (2024) captured 80.42% of the total variation with two components derived from 43 physicochemical attributes associated with different fruit colors in five 'Cherry' tomato cultivars. The first principal component (PC1, 53.72% of variance) differentiated cultivars primarily by amino acid and organic acid contents, in contrast to higher levels of antioxidant compounds and sweetness. The second component (PC2, 26.69% of variance) was associated with fruit firmness and contents of anthocyanins, carotenoids, and phenolic compounds. These authors identified a clustering pattern based on fruit coloration: 'Gold Chance' (orange), 'Snacktom' (red), and 'BN Satnolang' (yellow) formed a group characterized by high antioxidant activity and sweetness, whereas 'Black Q' (black) and 'Jocheong' (green) constituted another group with elevated amino acid and gamma-aminobutyric acid (GABA) contents.

The progressive separation of wild relatives, SLC, and SLL along the PCA axes reflects the genomic structure of the tomato clade. Using SNP markers, Blanca et al. (2012) demonstrated that *S. pimpinellifolium* (SP) and *S. lycopersicum* var. *lycopersicum* (SLL) are genetically distinct, while *S. lycopersicum* var. *cerasiforme* (SLC) occupies an intermediate position, consistent with its role as a semi-domesticated transitional form. Razifard et al. (2020) estimated that SLC diverged naturally from SP in Ecuador ~ 78 ka, later spreading northward into Mesoamerica, where re-domestication events gave rise to modern cultivated tomato (SLL). This migration was accompanied by selection for fruit size and sugar content. The clear separation of wild relatives (associated with chlorophyll and lightness) from cultivated groups (associated with carotenoids and lycopene) illustrates the domestication bottleneck that reduced genetic diversity in cultivated tomatoes, as confirmed by super-pangenome analyses (Li et al., 2023). The heterogeneity observed within SLC is consistent with the high genetic diversity reported for South American accessions (Blanca et al., 2012; Razifard et al., 2020). Finally, the clustering of SP across both SLL subgroups underscores its role as the progenitor of cultivated tomato (Razifard et al., 2020; Li et al., 2023).

Correlation analysis

Pearson correlation analysis (Figure 4) revealed significant phenotypic associations among the evaluated fruit quality attributes in the 50 accessions studied. Strong and highly significant positive correlations were identified between lycopene and total carotenoids ($r = 0.96$, $p < 0.001$), suggesting a shared biosynthetic regulation within the carotenoid pathway in pigmented fruits. This implies that selecting for either pigment drives co-selection of the other, offering a practical advantage for breeding by enabling simultaneous optimization of fruit color and nutritional value through a single trait. Likewise, the strong correlation between chlorophyll *a* and chlorophyll *b* ($r = 0.85$, $p < 0.001$) reflects a close relationship in the accumulation of photosynthetic pigments in fruits borne by wild relatives.

Moderate positive correlations were also observed between total carotenoids and a* values ($r = 0.73$, $p < 0.001$), as well as between lycopene and a* values ($r = 0.69$, $p < 0.001$), indicating that increased carotenoid pigments are consistently associated with more intense red coloration in the fruit. Other notable associations included the correlation between lightness and b* values ($r = 0.58$, $p < 0.01$), linked to joint variations in brightness perception and yellow hue, and a moderate correlation between firmness and fruit size ($r = 0.50$, $p < 0.01$), related to structural and developmental tissue characteristics.

On the other hand, highly significant negative correlations were detected. The strongest inverse association was between a* values and chlorophyll *a* ($r = -0.74$, $p < 0.001$), suggesting antagonism between the accumulation of red pigments (carotenoids) and green pigments (chlorophyll) during ripening. Negative correlations were also observed between lycopene and lightness (L*) ($r = -0.64$, $p < 0.001$), total carotenoids and lightness ($r = -0.61$, $p < 0.001$), and external fruit color with lightness ($r = -0.55$, $p < 0.01$), indicating that fruits with higher carotenoid contents tend to exhibit a less bright and darker surface. A notable trade-off was observed between fruit size and total soluble solids ($r = -0.58$, $p < 0.001$), possibly reflecting compensation between size attributes and organoleptic quality. Several variable pairs showed nonsignificant correlation ($p > 0.05$), particularly those involving morphological attributes such as fruit shape and epidermis color, which were not associated with most of the chemical and pigmentary parameters evaluated. The independence between external traits and internal composition—suggesting independent genetic control—enables ideotypes combining commercial appeal with nutritional quality, free from phenotypic drag, and offers opportunities for breeding novel quality combinations without compromising fruit appearance.

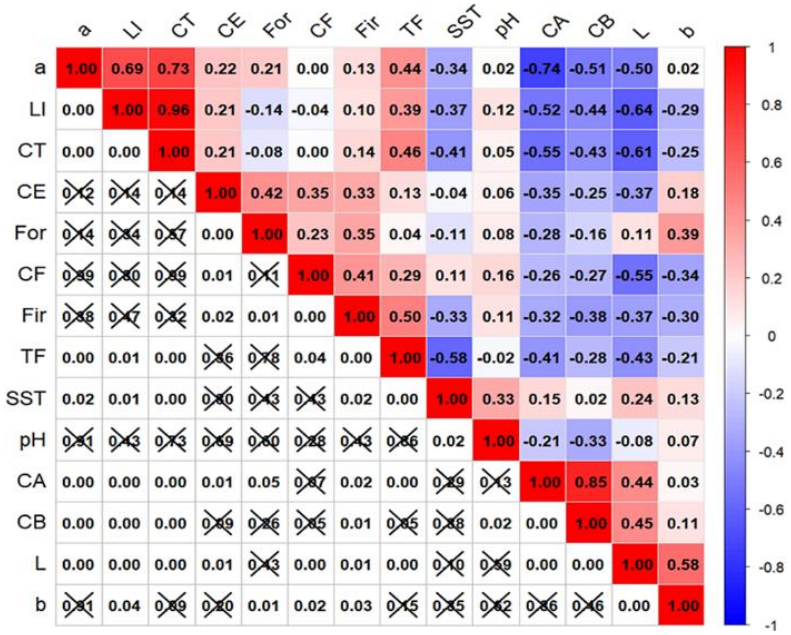

Figure 4. Correlation matrix for 50 tomato accessions based on 14 fruit quality attributes. Pearson correlation coefficients are presented above the diagonal, and statistical significances are below the diagonal. a: Green-red axis (a*); LI: lycopene (mg g^{-1}); CT: total carotenoids (mg g^{-1}); CE: fruit epidermis color; For: fruit shape; CF: fruit color; Fir: fruit firmness (N); TF: fruit size; SST: total soluble solids (°Brix); pH: hydrogen potential; CA: chlorophyll *a* (mg g^{-1}); CB: chlorophyll *b* (mg g^{-1}); L: lightness (L*); b: blue-yellow axis (b*). Magnitude: very strong: $|r| \geq 0.80$, strong: $0.60 \leq |r| < 0.80$, moderate: $0.40 \leq |r| < 0.60$, weak: $0.20 \leq |r| < 0.40$, very weak: $|r| < 0.20$.

Tripodi et al. (2023) reported an average negative correlation over 2 yr between fruit weight (an indirect indicator of size) and total soluble solids (-0.29) in a broad panel of 60 tomato accessions with diverse forms, colors, and sizes, grouped into 'Beefsteak', 'Cherry', 'Globe', 'Oxheart', and 'Plum' types. Although both this value and that obtained in the present study are negative, the twofold difference between them is attributed to the diversity of panels evaluated. Baek et al. (2024), in 'Cherry' tomato cultivars of different colors, reported a strong positive correlation between lycopene content and a* values, as well as between lightness and b* values, in agreement with the present study. However, they found a moderate negative correlation between chlorophyll *a* and total soluble solids, differing from our findings, which showed a low positive correlation. In their study, the correlation between lycopene and firmness was moderately positive, whereas in the present study it was low. In contrast, Barnett et al. (2023), in a study of different accessions from 13 wild tomato species, obtained a low positive correlation between total soluble solids and lightness, and between fruit weight and lightness. The latter contrasts with our findings of a moderate negative correlation, where fruit size served as a proxy for weight. They also reported a moderate negative correlation between fruit size and total soluble solids, whereas in this study the correlation was strongly negative.

CONCLUSIONS

The panel evaluated comprises a marked phenotypic diversity across accessions and taxonomic groups, spanning morphological traits (form, size, color) and distinctive physicochemical profiles. Wild and semi-domesticated genotypes exhibited greater phytochemical diversity, particularly in soluble solids and pigments, consolidating their role as strategic sources for reintroducing sensory attributes into elite germplasm. External fruit color proved to be an indirect indicator of the nutritional profile of accessions. The strong association between carotenoids and a* values, together with the inverse relationship between fruit size and sugar content, underscores both the potential and the challenges of balancing sensory quality and yield. Analyses confirmed that domestication and breeding have shaped the genetic architecture of the species, privileging

morphology and pigmentation as primary axes of diversification. The identification of specific accessions with superior quantitative traits provides a foundation for targeted breeding to enhance both nutritional quality and sensory attributes in modern tomato cultivars.

Author contribution

Conceptualization & Methodology: R.L-O., R.A.-R. Software: R.A-R. Validation: M.V-T., J.P.L-S., M.H.-R. Formal analysis: R.A-R., A.H-B., J.J.G-Z. Investigation: R.A-R. Resources: R.L-O. Data curation: R.A-R. Writing-original draft: R.A-R., R.L-O. Writing-review & editing: R.L-O., J.J.G-Z., M.V-T., J.P.L-S., A.H-B., M.H-R. Visualization: R.A-R. Supervision: R.L-O. Project administration: R.L-O. Funding acquisition: R.L-O., R.A.-R. All co-authors reviewed the final version and approved the manuscript before submission.

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