

Morphological characterization of native mexican tomato populations (*Solanum lycopersicum* (L.) Mill.)

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ABSTRACT

Objective: To characterize native populations of tomato (*Solanum lycopersicum* (L.) Mill.) collected from different regions of Mexico in order to determine their morphological diversity and potential use in breeding.

Design/methodology/approach: One hundred native tomato populations originating from 17 climatic regions in central and southern Mexico, along with two commercial hybrids, were cultivated in a completely randomized block design with two replications under greenhouse conditions. The crop was grown up to the tenth cluster, and morphological evaluation was carried out on the sixth cluster by measuring 28 variables. The statistical analysis included descriptive statistics, univariate analysis of variance, and mean comparison tests. Multivariate analyses included cluster analysis and principal component analysis.

Results: In the descriptive analysis, the variables with intermediate variability were average fruit weight and number of locules. Based on fruit shape, fruits were classified into the following types: kidney, squash, irregular shapes, pear, bell, round, flattened round, saladette, and cherry. In the principal component analysis, native populations were dispersed into eight groups according to their degree of domestication, earliness, and geographic origin. In the cluster analysis, the populations were distributed into 14 groups; Group 13 was shared by populations from Puebla, Guerrero, and the commercial hybrids, indicating that they share common traits.

Limitations of the study/Implications: Studies on culinary and nutritional quality in native tomato populations could be conducted to complement the information obtained.

Findings/Conclusions: Fruits from native tomato populations from Mexico exhibited considerable variability. This diversity is manifested in different fruit types, sizes, and number of locules. Understanding morphological variability opens the possibility for their inclusion in genetic improvement programs.

Keywords: tomato, native, diversity, variability, shape

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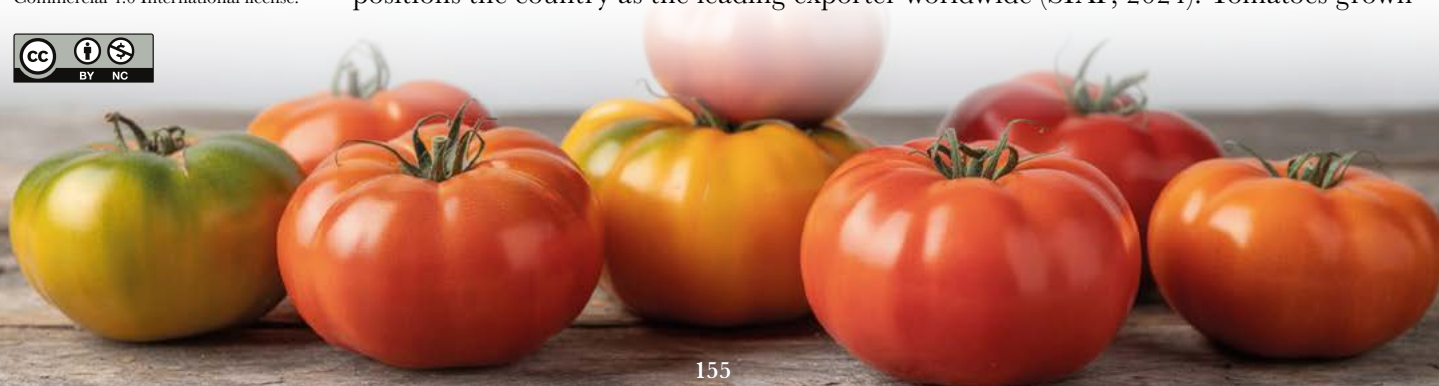
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INTRODUCTION

The tomato (*Solanum lycopersicum* (L.) Mill) holds agricultural importance in Mexico due to the area cultivated (49,461 ha) and the production volume (3,636,927 t), which positions the country as the leading exporter worldwide (SIAP, 2024). Tomatoes grown



in Mexico originate from improved varieties, and the types (or shapes) marketed include: large round, flattened round, squash, guaje, pear, bell, grape, cocktail, cherry, saladette, and Raf (Maldonado-Peralta *et al.*, 2016). However, in regional markets of Campeche, Guerrero, Puebla, Oaxaca, Tlaxcala, Veracruz, and Yucatán, tomatoes from native and wild populations are sold and highly valued due to their superior organoleptic and nutraceutical quality (Figure 1), comparable to modern varieties (Urrieta-Velázquez *et al.*, 2012). This has been corroborated in collections from Campeche, Chiapas, State of Mexico, Guerrero, Hidalgo, Oaxaca, Puebla, Veracruz, and Yucatán (Bonilla-Barrientos *et al.*, 2014; Berrospe-Ochoa *et al.*, 2018; Figueroa-Cares, 2018; Leana-Acevedo *et al.*, 2022).

The center of origin of tomato is the Andean region in northern Peru and southern Ecuador (Blanca *et al.*, 2012; Peralta *et al.*, 2008). The center of domestication remains controversial; however, recent genomic studies indicate that tomato pre-domestication began in Ecuador and Peru approximately 80,000 years ago with the wild species *Solanum pimpinellifolium* L., giving rise to the wild species *Solanum lycopersicum* var. *cerasiforme*. This species was subsequently re-domesticated in Mexico, and after a process of 7,000 years, it gave rise to *S. lycopersicum* L. (Blanca *et al.*, 2012; Razifard *et al.*, 2020; Wang *et al.*, 2020). Therefore, the tinguaraque or cherry tomato (*S. lycopersicum* var. *cerasiforme*) is the direct ancestor of the tomatoes currently cultivated. In Mexico, the regions with the highest genetic diversity of native tomato are the Sierra of Veracruz and Puebla (Long, 1995), where *S. lycopersicum* L. and *S. lycopersicum* var. *cerasiforme* predominate (Nuez *et al.*, 1996).

The genetic diversity of a species is determined by the different populations that comprise it within a specific geographic area. These populations are dynamic, have a historical origin, and possess a distinctive identity.

In Mexico, tomato was cultivated by the Mexica people since pre-Hispanic times using the chinampa system (Estabrook, 2011; Long, 1995) and became integrated into local



Figure 1. Regional market in Tehuacán, Puebla, Mexico, where native tomato populations are sold to their high quality.

gastronomy (López-Terrada, 2015). The tomatoes used by the Mexica exhibited diverse shapes and a range of colors, including yellow, pink, and red (Sahagún, 1961). Following the conquest of Mexico, tomato was introduced to Spain and from there dispersed worldwide (Blanca *et al.*, 2012; Estabrook, 2011). Today, tomato and cherry tomato are widely cultivated and valued across countries on all continents (Prasanna *et al.*, 2023).

Wild populations are species that grow naturally in a specific region, having evolved and adapted to the local ecosystem without human intervention. These populations maintain a close genetic relationship with cultivated populations and are known as wild relatives (Majeed *et al.*, 2021). Native or local populations are materials that have been cultivated and selected by farmers over several generations, resulting in populations with specific traits according to the preferences of local consumers.

These native populations are adapted to the conditions of their environment and retain considerable genetic variation, which provides stability under environmental changes, making them of interest for genetic improvement. They also hold significant historical, cultural, and economic value for local communities, making their preservation and understanding essential (Ruíz *et al.*, 2016; FAO, 2020).

In Mexico, native tomato populations are diverse, locally adapted, and associated with traditional cultivation systems (Camacho *et al.*, 2005). Currently, the characterization of these native populations has advanced through collections from Campeche, Chiapas, State of Mexico, Guanajuato, Guerrero, Hidalgo, Jalisco, Michoacán, Morelos, Oaxaca, Puebla, San Luis Potosí, Tabasco, Veracruz, and Yucatán (Canul-Hu *et al.*, 2022; Juárez-López *et al.*, 2012; Maldonado-Peralta *et al.*, 2016; Marín-Montes *et al.*, 2016; Matos-Canul *et al.*, 2018).

Knowledge of the diversity and genetic structure of native tomato populations is still limited, making a systematic study—including their characterization—necessary to harness their genetic potential for inclusion in breeding programs. In this study, we conducted a morphological characterization of native Mexican tomato populations from different regions of Mexico to determine their morphological diversity and expand knowledge about these native populations.

MATERIALS AND METHODS

Genetic material

Information on the native populations and tomato controls is presented in Table 1. This research is part of the project “Comprehensive Assessment of the Diversity of Native Mexican Tomato” (CP-CONACYT), which focuses on native tomato populations. A total of 100 native populations from 17 climatic regions in central and southern Mexico, located across seven states, were selected. The controls were the commercial hybrids Reserva (H1) and Sun-7705 (H2). For characterization, the original seeds from the collections were used.

Experimental design

The experiment was established during the Spring-Summer cycle in a complete randomized block design (CRBD) with two replications under greenhouse conditions at the Colegio de Postgraduados, Montecillo Campus, Texcoco, Mexico. The experimental unit consisted of four pots.

Table 1. Origin of native tomato (*Solanum lycopersicum* (L.) Mill.) populations collected in seventeen climatic regions of Mexico.

Origin	Populations by climatic region
Puebla	Region 1: P1, P2, P4, P5, P6, P7, P8, P9, P10, P11, P12, P13, P14, P15, P16, P17, P18, P19, P20, P21, P22, P23, P25, P26, P27, P28, P29, P30, P31, P32, P33; Region 2: P3; Region 3: P24
Guerrero	Region 4: G1, G3, G4, G5, G6, G7, G8, G9, G11, G12, G13, G14; Region 5: G10; Region 6: G2
Oaxaca	Region 7: O5, O6, O8, O9, O10, O11, O12, O13, O14, O15, O16, O17, O18, O19, O20, O21, O22; Region 8: O1; Region 9: O3; Region 10: O2; Region 11: O4; Region 12: O7
Campeche	Region 13: C1, C2, C3, C4, C5, C6, C7, C8, C9, C10
Yucatán	Region 14: Y1, Y2, Y3, Y4, Y5, Y6, Y7, Y8, Y9, Y10
México	Region 15: M1, M2, M3, M4, M5, M6, M8; Region 16: M7
Veracruz	Region 17: V1, V2, V3
Híbridos	Region 18: H1; Region 19: H2

Experimental Management

The seeds received a pre-germination treatment (0.2% KNO₃) and were germinated in trays with peat-moss. Seedlings at 40 days of germination were transplanted in December 2011 into 10-L black polyethylene bags filled with red tezontle as substrate (particle diameter ≤ 12 mm). One tomato seedling was placed per pot.

Nutrition, Pest Control, and Cultural Practices

Plant nutrition was provided using Steiner solution adjusted to pH 5.5, osmotic pressure 0.072, and electrical conductivity 2.0-2.5 dS·m⁻¹, supplemented with micronutrients. The crop was stimulated with Bioengorda[®], Agromil Plus[®], Boramin Ca[®], natural extracts, plant hormones, vitamins, and diluents. Whitefly (*Bemisia tabaci*) and tomato russet mite (*Aculops lycopersici*) were controlled with the insecticides Nimicide[®], Engeo[®], and Agrimec[®]. Preventive control of gray mold (*Botrytis cinerea* Pers.), late blight (*Phytophthora infestans*), bacterial spot (*Pseudomonas syringae*), and powdery mildew (*Leveillula taurica*) was carried out using Mancozeb[®], Cupravit[®], Ridomil Gold[®], Serenade[®], Kasumin[®], and Fungimycin[®]. Cultural practices included preparation of nutrient solutions, irrigation, foliar applications of biofertilizers, fungicides, and insecticides, staking, and pruning of lateral shoots and mature leaves.

Quantitative Variables

The crop was grown up to the tenth cluster, after which the plant was topped above the third leaf. Morphological evaluation was carried out on the sixth cluster. The variables were: PH1C=plant height to first cluster, SD6C=stem diameter at sixth cluster, NI=number of internodes, ID=internode distance, LC4=length of the fourth cluster, DC4=diameter of the fourth cluster, NS=number of fruit-bearing shoots, LL3C=leaf length before third cluster, NL6C=number of leaflets on the leaf before sixth cluster, LL6C=leaflet length on the leaf before sixth cluster, LW6C=leaflet width on the leaf before sixth cluster, LCR=leaf chroma, LHUE=leaf hue measured with Hunter Lab

D25-PC2 colorimeter, DF=days to flowering, DM=days to maturation, FS%=fruit set percentage at the third cluster, NS=number of sepals, PL=petal length, SCL=staminal column length, GL=gynoecium length, SE=stigma exertion, TNF=total number of fruits, AFW=average fruit weight measured with a granatary balance, FL=fruit length, FW=fruit width, FS=fruit shape, PT=pericarp thickness measured with a Truper vernier caliper, and NL=number of locules.

Fruit length was measured as the polar diameter, and fruit width as the equatorial diameter, both determined using a digital caliper. Fruit shape (FS) was calculated as the ratio of fruit length to fruit width (FL/FW); fruits with a ratio less than 1 were considered flattened, fruits with a ratio equal to 1 were considered round, and fruits with a ratio greater than 1 were considered elongated. The number of locules was determined by cutting the fruit in half and counting the cavities.

Statistical Analysis

Each variable was evaluated using descriptive statistics and univariate analysis of variance based on the Complete Randomized Block (CRB) model with two replications. Mean differences were determined using Tukey's test ($p \leq 0.05$). Similarity relationships among native populations were calculated using the Euclidean distance coefficient (data not shown). Multivariate analyses included cluster analysis and principal component analysis (PCA). Cluster analysis was performed using the unweighted pair-group method with arithmetic mean (UPGMA).

PCA was used to identify relationships among materials based on proximity and to determine the variables that contributed most to the variation (informative variables). Statistical analyses were performed using InfoStat statistical software (Di Rienzo *et al.*, 2008).

RESULTS AND DISCUSSION

Morphological Characterization

Table 2 presents the descriptive statistics of the variables and the analysis of variance. Dispersion statistics indicate the variation among the observed data; high values for range, variance, and standard deviation suggest dispersed data with greater variability, while low values indicate homogeneous data. Quantitative variables exhibiting a wide range were related to plant architecture (plant height to first cluster, length of the fourth cluster, leaflet length on the leaf before the sixth cluster, leaflet width on the leaf before the sixth cluster), phenology (days to flowering, days to maturation), yield (fruit set percentage at the third cluster, total number of fruits), and fruit quality (average fruit weight, fruit length, fruit width).

The coefficient of variation (CV) expresses the variability of a dataset relative to its mean and is used to compare the dispersion of two or more datasets. Variables with intermediate dispersion ($30\% < CV < 70\%$) were related to the fruit and included average fruit weight, number of locules, number of fruit-bearing shoots, and total number of fruits. Variables with low dispersion ($CV < 30\%$) were associated with plant architecture, flower characteristics, and phenology.

Analysis of variance detected significant differences for all variables, except for the diameter of the fourth cluster and the leaflet length on the leaf before the sixth cluster. In terms of phenology, populations C9, Y8, and P2 stood out, averaging 20 days to flowering. These populations were earlier than those from Guanajuato, Puebla, Guerrero, Hidalgo, Oaxaca, and Yucatán, which required 25 to 32 days (Vázquez-Ortiz *et al.*, 2010), and earlier than populations from Puebla, Michoacán, Oaxaca, and Chiapas, which required 55 days (Alvarado-Rodríguez *et al.*, 2022).

For days to maturation, populations P1, P2, and P3 stood out with 69 days, showing earlier maturity than populations from Puebla and Oaxaca, which required 100 days (Bonilla-Barrientos *et al.*, 2014). However, there are native populations from Guanajuato, Puebla, Guerrero, Hidalgo, Oaxaca, and Yucatán that are even earlier, reaching maturity in 46 days (Vázquez-Ortiz *et al.*, 2010). These results highlight the wide variation in earliness present in native Mexican tomato populations, providing useful information for the development of improved varieties.

In terms of number of locules, population Y4 stood out with 17 locules per fruit. This value is higher than that of populations from Oaxaca, which have 11 locules (Leana-Acevedo *et al.*, 2022), and the CAM25 population from Campeche, which has 13 locules (Maldonado-Peralta *et al.*, 2022). Regarding fruit weight, populations G4 and O5 stood out with 265 g and 219 g, respectively. These weights are much higher than those of populations LBCh231 and PUE10 from Puebla, with 145.27 g and 147.8 g, respectively; OAX100 from Oaxaca with 154.8 g; and the varieties Floradade and Cid F1 with 105.67 g and 112.6 g, respectively (Alvarado-Rodríguez *et al.*, 2022; Maldonado-Peralta *et al.*, 2022).

Regarding pericarp thickness, populations P13, P16, and P24 exhibited thickness similar to the hybrid H2, at 7 mm. These fruits had greater thickness than populations from Guerrero, Puebla, Oaxaca, Yucatán, Campeche, Veracruz, and the State of Mexico, which averaged 3.8 mm (Maldonado-Peralta *et al.*, 2016), but lower than population PUE100 from Puebla with 8.9 mm and the hybrid Cid F1 with 9.9 mm (Maldonado-Peralta *et al.*, 2022). In terms of petal length, populations P15, P30, P32, and Y2 stood out with 21 mm. These values are higher than those of populations collected in Morelos, Puebla, Oaxaca, Tabasco, and Veracruz, which averaged 16.75 mm (Canul-Ku *et al.*, 2022).

Regarding variables related to plant architecture, in breeding programs it is desirable for the position of the leaf before the third cluster to be semi-drooping, so that the plant is compact and receives light throughout the canopy. For the clusters, a larger peduncle diameter provides greater strength and prevents fruit drop, while cluster length is associated with more branching and a higher number of fruits.

Modern commercial varieties exhibit little variation (Miller and Tanksley, 1990), whereas native populations possess considerable morphological variability, as identified in this study, which allows for the exploitation of the outstanding traits of these native populations.

Figure 2 shows the fruit shapes or types identified in the native tomato populations. Fruit shape (FS) exhibited wide variability, allowing native populations to be classified into

Table 2. Descriptive statistics and analysis of variance for 28 quantitative variables evaluated in native tomato (*Solanum lycopersicum* (L.) Mill.) populations.

Variable	Range		AVG	SD	CV	Analysis of variance	
	Max	Min				SS (Region)	MS (Error)
PH1C	57.38	19.75	33.89	8.71	25.70	4425.81**	36.79
SD6C	15.77	10.24	13.00	1.24	9.53	88.55 **	0.75
NI	33.38	12.38	25.59	2.65	10.35	226.16**	5.49
ID	8.17	4.84	6.25	0.76	12.10	24.29**	0.38
LC4	60.50	16.75	32.18	8.63	26.83	3417.17**	46.73
DC4	11.65	4.67	7.89	0.96	12.20	12.36	0.92
NS	6.62	1.00	2.77	1.05	37.83	63.02**	0.54
LL3C	47.13	21.38	35.61	5.21	14.62	1825.79**	10.38
NL6C	8.00	5.00	6.89	0.50	7.28	7.92**	0.20
LL6C	161.78	84.17	124.51	13.90	11.16	3326.34	183.86
LW6C	81.19	40.14	59.33	8.04	13.56	1590.25**	56.18
LCR	17.77	9.61	12.30	2.12	17.23	341.13**	1.28
LHUE	-48.15	-53.89	-51.46	1.27	-2.47	53.77**	1.24
DF	45.38	19.25	32.15	6.68	20.79	2808.69**	19.35
DM	109.50	69.25	89.83	9.53	10.61	6289.49**	32.84
FS%	96.41	57.73	81.52	8.04	9.87	1401.02**	58.32
NS	9.38	5.25	7.11	0.93	13.03	55.11**	0.36
PL	21.67	12.43	17.00	2.26	13.28	299.73**	2.45
SCL	10.87	6.95	8.64	0.77	8.96	22.76**	0.43
GL	10.99	6.75	8.90	1.03	11.62	64.88**	0.49
SE	1.46	0.78	1.05	0.13	12.60	0.77**	0.01
TNF	123.13	25.50	63.64	23.07	36.25	33,240.31**	233.06
AFW	265.15	5.11	74.95	37.97	50.66	40,729.84**	1191.85
FL	106.25	16.13	44.08	10.91	24.76	4473.26**	85.89
FW	1.29	0.46	0.87	0.20	22.71	2.30**	0.02
FS	93.52	19.43	53.06	10.52	19.83	4847.78**	71.99
PT	8.02	2.09	5.22	1.22	23.36	100.03**	0.57
NL	17.13	2.25	6.45	2.79	43.21	486.48**	3.37

** Significant differences, Max: maximum, Min: minimum; AVG: average, SD: standard deviation, CV: coefficient of variation, PH1C: plant height to first cluster, SD6C: stem diameter at sixth cluster, NI: number of internodes, ID: internode distance, LC4: length of the fourth cluster, DC4: diameter of the fourth cluster, NS: number of fruit-bearing shoots, LL3C: leaf length before third cluster, NL6C: number of leaflets on the leaf before sixth cluster, LL6C: leaflet length on the leaf before sixth cluster, LW6C: leaflet width on the leaf before sixth cluster, LCR: leaf chroma, LHUE: leaf hue, DF: days to flowering, DM: days to maturation, FS%: fruit set percentage at third cluster, NS: number of sepals, PL: petal length, SCL: staminal column length, GL: gynoecium length, SE: stigma exertion, TNF: total number of fruits, AFW: average fruit weight, FL: fruit length, FW: fruit width, FS: fruit shape, PT: pericarp thickness, NL: number of locules.

the following types: kidney, squash, irregular shapes (with a higher number of locules), pear, bell, round, flattened round, saladette, and cherry.

Flattened round, squash, ribbed bell, and kidney-type fruits had a flattened shape ($FL/FW < 1$). Round fruits included the ball and cherry types ($FL/FW = 1$). Saladette, pear, and bell-type fruits exhibited an elongated shape ($FL/FW > 1$).



Figure 2. Fruit types of native Mexican tomato (*Solanum lycopersicum* (L.) Mill). Source: prepared by the autor with support from Ramiro Maldonado.

Kidney-shaped fruits had a higher number of locules than cherry, ball, bell, and saladette-type fruits. Locules are cavities that protect the seeds and derive from the carpels of the flower. The number of locules is associated with fruit shape and larger size, and this variability is genetically determined (Muños *et al.*, 2012).

These ribbed and flattened tomato variants are frequently observed in native populations and occur at low frequency in modern cultivars. These shapes are associated with multilocular ovaries and abnormal fusion of floral organs (Barrero and Tanksley, 2004).

Fruits with similar shapes have been reported in native populations from Campeche, State of Mexico, Guanajuato, Guerrero, Hidalgo, Oaxaca, Puebla, Veracruz, and Yucatán (Vásquez-Ortiz *et al.*, 2010; Maldonado-Peralta *et al.*, 2016; Bonilla-Barrientos *et al.*, 2014).

Table 3 presents the contribution of the variables to the Principal Component Analysis (PCA). The first two principal components explained 39% of the variation. PC1 accounted for 25% of the variation, with positive contributions from days to flowering, days to maturation, and pericarp thickness, and negative contributions from the number of locules and leaf length before the third cluster. PC2 accounted for 14% of the variation, with positive contributions from length of the fourth cluster, diameter of the fourth cluster, and number of internodes, and a negative contribution from average fruit weight.

Figure 3 shows the spatial distribution of the populations across two principal components. The 100 native populations and the tomato controls were grouped into eight clusters based on the degree of domestication, earliness, and geographic origin. Early-flowering native populations were grouped in quadrant IV, intermediate-flowering populations in quadrants I and IV, and late-flowering native populations with specific fruit shapes in quadrants I and II.

Table 3. Variable contributions to principal components.

Variable	CP1	CP2
Height to first cluster	0.20	0.19
Stem diameter at the sixth cluster	-0.06	0.21
Number of internodes	0.11	0.30
Internode distance	-0.05	0.18
Length of the fourth cluster	-0.13	0.36
Diameter of the fourth cluster	-0.03	0.34
Number of fruit-bearing shoots	-0.25	0.20
Leaf length before third cluster	-0.26	-0.01
Number of leaflets on the leaf before sixth cluster	0.11	0.17
Leaflet length on the leaf before sixth cluster	0.17	0.15
Leaflet width on the leaf before sixth cluster	0.20	0.22
Leaf chroma	-0.12	-0.01
Leaf hue	0.17	-0.09
Days to flowering	0.32	0.11
Days to maturation	0.30	0.03
Fruit set percentage at the third cluster	0.11	-0.08
Number of sepals	-0.25	-0.05
Petal length	0.29	0.16
Staminal column length	0.24	-0.03
Gynoecium length	0.13	0.22
Stigma exertion	-0.05	0.19
Total number of fruits	-0.22	0.26
Average fruit weight	0.12	-0.28
Fruit length	0.11	-0.23
Fruit width	0.09	-0.23
Fruit shape (Length/width ratio of the fruit)	0.02	-0.05
Pericarp thickness	0.26	-0.10
Number of locules	-0.28	-0.11
Explained variation (%)	25.00	14.00

Group A consisted of populations from Puebla (P10, P11, P12, P13, P14, P15, P17, P18, P19, P20, P21, P23, P24, P25, P26, P27, P28, P29, P30, P31, P32, P33) that produced ribbed bell-type fruits with four locules, thick pericarp, and intermediate fruit weight. The plants were low-growing with short leaves, long-petaled flowers, and late maturation.

Group B included populations from Guerrero (G3 and G4), Oaxaca (O4 and O5), Puebla (P16), and the controls H1 and H2. This group produced large fruits of the saladette and round types, with thick pericarp and high weight. The plants were low-growing with few internodes, short clusters, and late maturation. Within this group, population G4 stood out for producing round-type fruits with the highest weight.

Group C included populations from Campeche (C3, C4, C5, C7, C9), Yucatán (Y4, Y7, Y8), and Guerrero (G7) that produced round and flattened squash-type fruits with numerous locules (10 locules), thin pericarp, and high fruit weight. The plants had flowers with short petals and early maturation.

Group D consisted of populations from Puebla (P1, P2, P4, P6, P7, P8, P9), Veracruz (V1, V2, V3), and Oaxaca (O12) with characteristics similar to kidney-type native tomatoes. The fruits were squash- and kidney-shaped with numerous locules and thin pericarp. The plants had long leaves and early maturation. Kidney-type native tomatoes exhibit plants with longer internodes, small, flattened, and ribbed fruits (fruits with pronounced grooves). Group E included populations from Oaxaca (O1, O2, O3, O6, O8, O9, O10, O11, O14, O15, O16, O18, O19, O21, O22), Guerrero (G1, G5, G6, G8, G10, G14), and Campeche (C1, C8). These populations produced squash-, kidney-, and irregular-shaped fruits with high weight. The plants had long leaves, flowered at 30 days, and matured at 88 days.

Group F consisted of populations from Yucatán (Y1, Y2, Y3, Y5, Y6, Y10), Campeche (C2, C6), Guerrero (G2, G13), and Oaxaca (O20), producing squash-, pear-, and flattened round-type fruits with thick pericarp and intermediate weight (64.17 g). The plants had numerous internodes, long and wide clusters, and long-petaled flowers.

Group G included populations from the State of Mexico (M2, M3, M4, M5, M6, M7) and Guerrero (G11, G12) with pear- and squash-type fruits of intermediate weight (64.17 g) and thick pericarp. The plants exhibited late flowering and maturation.

Group H was represented by the population from the State of Mexico (M1), which produced cherry-type fruits with two or three locules, thin pericarp, and low weight. The plant had few internodes, long leaves, short-petaled flowers, early flowering at 23 days, and maturation at 80 days.

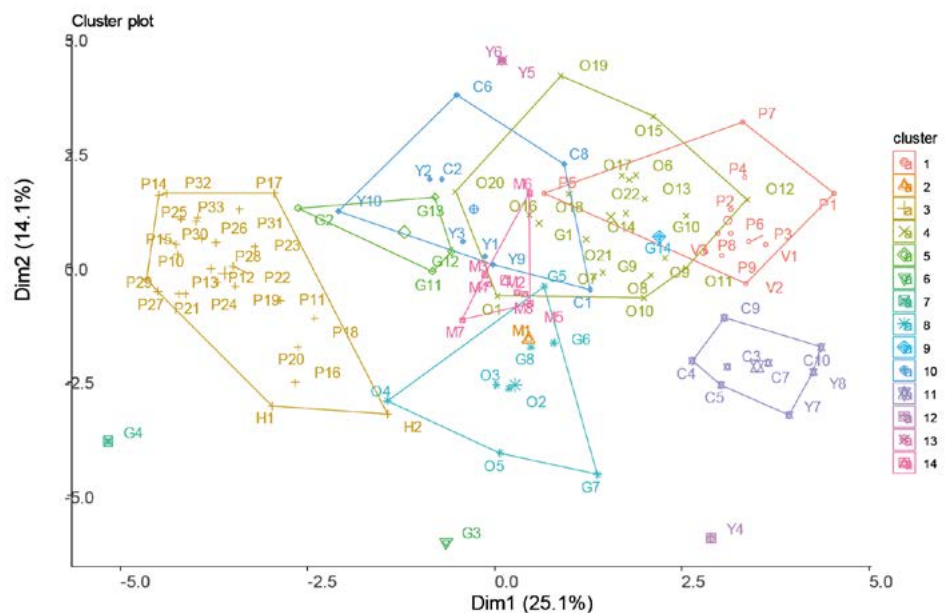


Figure 3. Principal Component Analysis diagram of 100 native tomato populations and two commercial hybrids (*Solanum lycopersicum* (L.) Mill.) based on quantitative morphological variables.

Hierarchical Cluster Analysis

Figure 4 shows the cluster analysis performed based on the 28 quantitative variables. A Euclidean distance cutoff of 1.19 defined 14 groups. Populations in groups 1 to 7 were separated individually according to their outstanding traits.

Group 1 included population Y2, which produced fruits with thick pericarp, long-petaled flowers, and long internodes. Group 2 included population Y4, which produced large round-type fruits with high weight and 17 locules; this population exhibited early flowering and flowers with short gynoecia and stigmas. Populations in groups 1 and 2 displayed traits of interest for breeding, as consumers prefer round and saladette-type tomatoes, which are large, have thick pericarp, and high fruit weight.

Group 3 included population C9, which exhibited early flowering and maturation, with flowers having short gynoecia. Group 4 included population G3, which produced fruits with few locules, short internodes, and flowers with long staminal columns; this trait may be associated with pollination efficiency. In tomato flowers, the stamens are fused by their anthers to form a staminal column (or cone) that releases pollen from the top through the buzzing of native bees, depositing it directly onto the pollinator's body (Vallejo-Marín *et al.*, 2022). A long staminal column ensures proper pollen deposition on pollinators but may limit self-pollination.

Group 5 included population G4, which produced round-type fruits with high weight, few fruits per plant, short-gynoecium flowers, and late flowering. Group 6 included population M5, which produced long fruits with thick pericarp, flowers with long gynoecia, and late flowering. Populations in groups 5 and 6 also exhibited large fruits with thick pericarp, traits of interest for genetic improvement.

Group 7 included population C5, which exhibited long leaflets and flowers with short gynoecium and staminal column. Group 8 included populations M1 and G14, which produced cherry-type fruits with few locules, high fruit set, and plants with long leaves, few internodes, and limited branching. This group displayed traits of interest for the development of cherry-type populations.

Group 9 included twenty-two populations from Oaxaca (O1 to O22) and seven from Guerrero (G1, G5, G6, G7, G8, G9, G10) with large kidney- or squash-type fruits, flowers with long gynoecia, and 7 to 9 sepals. These populations have traits of interest for breeding, as kidney-type tomatoes are appreciated by consumers for their characteristic acidic taste and are also tolerant to pests and drought (Matos-Canul *et al.*, 2018).

Group 10 included nine populations from Puebla (P1 to P9) and three from Veracruz (V1, V2, V3), producing a high number of small fruits with thin pericarp, early flowering and maturation, and flowers with short staminal columns and gynoecia. These native populations exhibit traits similar to Cherry tomatoes.

Group 11 included four populations from Campeche (C3, C4, C7, C10) and two populations from Yucatán (Y7, Y8) with intermediate-sized and weighted fruits, plants with long leaves, and flowers with short staminal columns and gynoecia.

Group 12 consisted of six populations from the State of Mexico (M2, M3, M4, M6, M7, M8) and two populations from Puebla (P12, P24) producing pear-type fruits, branched clusters, and flowers with long gynoecia. Pear-type fruits are of interest for the European

market, as fruits with these characteristics are used in preparing the cold soup gazpacho (Campra *et al.*, 2019).

Group 13 included twenty-four populations from Puebla (P10 to P33), four populations from Guerrero (G2, G11, G12, G13), two populations from Yucatán (Y5, Y6), and the two commercial hybrids (H1, H2). These populations produced long fruits with higher weight and thick pericarp, plants with late flowering, and flowers with long petals, staminal columns, and gynoecia. These populations exhibited traits similar to the commercial hybrids, making them favorable for genetic improvement.

Group 14 consisted of populations from Campeche (C1, C2, C6, C8) and Yucatán (Y1, Y3, Y9, Y10) with intermediate-weight fruits, plants with intermediate flowering, and flowers with short staminal columns and gynoecia. The staminal column forms a cone around the stigma, and its height affects pollination. In flowers with short pistils and styles (gynoecia), self-pollination and wind pollination are limited; however, entomophilous pollination can ensure fertilization. The buzzing of bees releases pollen through the pores and deposits it on the thorax, facilitating contact with the stigma. Buzz pollination increases fruit size and weight by enhancing the number of fertilized seeds (fruit set), thereby impacting yield (Bashir *et al.*, 2017).

In the descriptive analysis, the variables average fruit weight and number of locules showed intermediate variability. Variables related to plant architecture, flower, and phenology exhibited low to intermediate variation. Fruits were classified into the following types: kidney, squash, irregular, pear, bell, round, flattened round, saladette, and cherry. The variables contributing most to the variation were days to flowering, days to maturation, pericarp thickness, length of the fourth cluster, diameter of the fourth cluster, and number of internodes. In the PCA diagram, native and cultivated populations were

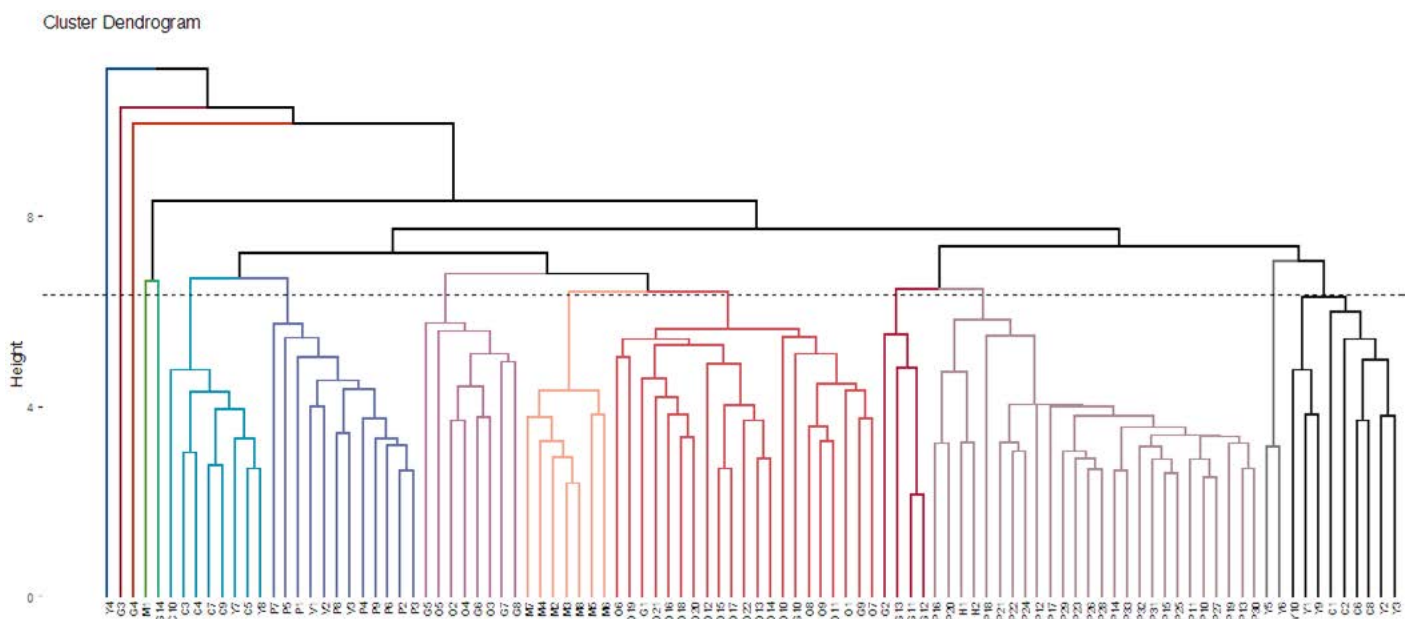


Figure 4. Hierarchical relationships among 100 native tomato (*Solanum lycopersicum* (L.) Mill.) populations using Euclidean distances from quantitative variables.

dispersed according to their degree of domestication, earliness, and geographic origin. In the cluster analysis, populations were distributed into fourteen groups, with group 13 shared by populations from Puebla, Guerrero, and the commercial hybrids, indicating they share common traits.

CONCLUSIONS

Native and local Mexican tomato populations exhibited high variability in the quantitative traits evaluated. The observed variability opens the possibility for their inclusion in breeding programs for its utilization and preservation.

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REFERENCES

- Alvarado-Rodríguez, R. L. y Legaria-Soriano, J. P. (2022). Phenotypic diversity of wild tomato (*Solanum lycopersicum* L.) populations. *Agroproductividad*, 41-53. <https://doi.org/10.32854/agrop.v15i5.2173>
- Barrero, L.S. & Tanksley, S.D. (2004). Evaluating the genetic basis of multiple-locule fruit in a broad cross section of tomato cultivars. *Theoretical and Applied Genetics*, 109:669-679. <https://doi.org/10.1007/s00122-004-1676-y>
- Bashir, M. A., Alvi, A. M., Khan, K. A., Asif Rehmani, M. I., Ansari, M. J., Atta, S., Ghramh, H. A., Batool, T., & Tariq, M. (2018). Role of pollination in yield and physicochemical properties of tomatoes (*Lycopersicon esculentum*). *Saudi Journal of Biological Sciences*, 25(7): 1291-1297. <https://doi.org/10.1016/j.sjbs.2017.10.006>
- Berrospe-Ochoa, E. A., Saucedo-Veloz, C., Ramírez-Guzmán, M. A. y Saucedo-Reyes, D. (2018). Componentes del sabor y contenido de ácido ascórbico de tomates (*Solanum lycopersicum* L.) nativos e híbridos comerciales. *Agrociencia*, 52:623-638.
- Blanca J., Cañizares J., Cordero L., Pascual L., Diez M. J. & Nuez F. (2012) Variation revealed by SNP genotyping and morphology provides insight into the origin of the tomato. *Plos ONE*, 7(10):e48198. <https://doi.org/10.1371/journal.pone.0048198>
- Bonilla-Barrientos, O., Lobato-Ortiz, R., García-Zavala, J. J., Cruz-Izquierdo, S., Reyes-López, D., Hernández-Leal, E. y Hernández-Bautista, A. (2014). Diversidad agronómica y morfológica de tomates arriñonados y tipo pimiento de uso local en Puebla y Oaxaca, México. *Revista Fitotecnia Mexicana*, 37(2):129-139.
- Camacho-Villa. T.C., Maxted N., Sholten, M. & Ford-Lloyd. (2005). Defining and identifying crop landraces. *Plant Genetic Resources*, 3:373-384. <https://doi.org/10.1079/PGR200591>
- Campra, P., Aznar-Garcia, M. J., Ramos-Bueno, R. P., Gonzalez-Fernández, M. J., Khaldi, H. & Garrido-Cardenas, J. A. (2019). A whole-food approach to the *in vitro* assessment of the antitumor activity of gazpacho. *Food Research International*, 121:441-452. <https://doi.org/10.1016/j.foodres.2018.11.058>
- Canul-Ku, J., González-Pérez, E., Barrios-Gómez, E. J., Pons-Hernández, J. L., y Rangel-Estrada, S. E. (2022). Caracterización morfológica y agronómica de germoplasma de tomate nativo del sur de México. *Revista fitotecnia mexicana*, 45(1):23-31. <https://doi.org/10.35196/rfm.2022.1.23>
- Ruíz de G., J. I., Prohens, J. y Tierno, R. (2016). Las poblaciones locales en la mejora genética de plantas. Servicio Central de Publicaciones del Gobierno Vasco. España. <https://dialnet.unirioja.es/servlet/libro?codigo=769121>
- Di Rienzo, J., Casanoves, F., Balzarini, M., Gonzalez, L., Tablada, M., & Robledo, C. (2008). Manual InfoStat versión 2008. Grupo InfoStat, FCA, Universidad Nacional de Córdoba. Argentina. <https://www.infostat.com.ar/>
- Estabrook, B. (2011). *Tomatoland: How modern industrial agriculture destroyed our most alluring fruit*. Andrews McMeel Publisher, LCC. Kansas City, Missouri.
- FAO. (2020). Directrices voluntarias para la conservación y la utilización sostenible de poblaciones de los agricultores/ poblaciones locales. Roma. <https://doi.org/10.4060/ca5601es>

- Figueroa-Cares, I. E., Cruz-Álvarez, O., María Martínez-Damián, M. T., Rodríguez-Pérez, J. E., Colinas-León, M. T. y Valle-Guadarrama, S. (2018). Calidad nutricional y capacidad antioxidante en poblaciones y genotipos nativos de tomate (*Solanum lycopersicum* L.). *Revista de la Facultad de Agronomía de la Universidad del Zulia (LUZ)*, 35:63-84. <https://produccioncientificaluz.org/index.php/agronomia/article/view/27261>
- Juárez-López, P., Castro-Brindis, R., Colinas-León, T., Sandoval-Villa, M., Ramírez-Vallejo, P., Reed, W. D., Cisneros-Zevallos, L. y King, S. (2012). Evaluación de variables de interés agronómico de siete genotipos nativos de tomate (*Lycopersicon esculentum* Mill.) cultivados en hidroponía. *Revista Chapingo, Serie Horticultura*, 18(2):207-216.
- Leana-Acevedo, J. L., Juárez-López, P., Palemón-Alberto, F., Sainz-Aispuro, M. J., Alía-Tejacal, I., Avonce-Vergara, N., Damián-Nava, A. y Ortega-Acosta, S. A. (2022). Competitividad agronómica de ecotipos nativos de jitomate (*Solanum lycopersicum* L.) cultivados en invernadero. *Acta Agrícola y Pecuaria*, 8:e0081017. <https://doi.org/10.30973/aap/2022.8.0081017>
- Long, J. (1995). De tomates y tomatos en el siglo XVI. *Estudios de Cultura Náhuatl*, 25, 239-252. <https://nahuatl.historicas.unam.mx/index.php/ecn/article/view/78174>
- López-Terrada, M. (2015). La historia de la llegada del tomate a Europa: una primera aproximación. *Proyecto Traditom, European Union's Horizon 2020, Agreement No 634561*. <https://traditom.eu/es/proyecto/historia/>
- Majeed, S., Chaudhary, M. T., Hulse-Kemp, A. M., & Azhar, M. T. (2021). Introduction: Crop Wild Relatives in Plant Breeding. In: *Wild Germplasm for Genetic Improvement in Crop Plants*. Azhar, M. T. & Wani, S. H. (eds). Academic Press. Pakistan. ISBN 9780128221372. <https://doi.org/10.1016/B978-0-12-822137-2.00001-1>.
- Maldonado-Peralta, R., Ramírez-Vallejo, P., González-Hernández, V. A., Castillo-González, F., Sandoval-Villa, M., Livera-Muñoz, M. y Cruz-Huerta, N. (2016). Riqueza agronómica en colectas mexicanas de tomates (*Solanum lycopersicum* L.) nativos. *Agroproductividad*, 9(12):68-75.
- Maldonado-Peralta, R., Cruz-Huerta, N., Ramírez-Ramírez, I., Castillo-González, F., Livera-Muñoz, M. & González-Hernández, V. A. (2022). Desempeño agronómico y fisiológico de poblaciones nativas de tomate mexicano sometidas a deficiencias de agua y nutrientes. *Tecnociencia Chihuahua, Revista de Ciencia y Tecnología*, XVI(1)e 882. <https://doi.org/10.54167/tecnociencia.v16i1.882>
- Marín-Montes, I. M., Rodríguez-Pérez, J. E., Sahagún-Castellanos, J., Hernández-Ibáñez, L. y Velasco-García, Á. M. (2016). Morphological and molecular variation in 55 native tomato collections from Mexico. *Revista Chapingo. Serie horticultura*, 22(2), 117-132. <https://doi.org/10.5154/r.rchsh.2016.03.008>
- Matos-Canul, E. E., Gómez-Leyva, J. F., Alamilla-Magaña, J. C., Sandoval Gío, J. J. y Criollo-Chan, M. A. (2018). El Jitomate Rosapa'ak o Riñón, un ecotipo nativo de la península de Yucatán. *Temas de Ciencia y Tecnología*, 22(64):63-68.
- Miller, J. C. & Tanksley, S. D. (1990). RFLP analysis of phylogenetic relationships and genetic variation in the genus *Lycopersicon*. *Theoretical and Applied Genetics*, 80:437-448. <https://doi.org/10.1007/BF00226743>
- Muños, S., Ranc, N., Botton, E., Bérard, A., Rolland, S., Duffé, P., Carretero, Y., Le Paslier, M. C., Delalande, C., Bouzayen, M., Brunel, D., & Causse, M. (2011). Increase in tomato locule number is controlled by two single-nucleotide polymorphisms located near WUSCHEL. *Plant Physiology*, 156(4):2244-54. <https://doi.org/10.1104/pp.111.173997>
- Nuez, F., Díez, M. J., Picó, B. y Fernández de Córdova, P. (1996). Catálogo de semillas de tomate. Monografías INIA Núm. 95. Mapa, Madrid. España.
- Peralta, I. E., Spooner, D. M., y Knapp, S. (2008). Taxonomy of wild tomatoes and their relatives (*Solanum* sect. *Lycopersicoides*, sect. *Juglandifolia*, sect. (*Lycopersicon*; *Solanaceae*). *Systematic Botany Monographs* Vol. 84. American Society of Plant Taxonomists. USA. <https://www.jstor.org/stable/i25027970>
- Prasanna, H. C., Rai, N., Hussain, Z., Yerasu, S. R. y Tiwari, J. K. (2023). Tomato: Breeding and Genomics. *Vegetable Science*, 50:146-155. <https://doi.org/10.61180/vegsci.2023.v50.spl.02>
- Razifard H., Ramos A., Della Valle A. L., Bodary C., Goetz E., Manser E. J., Li X., Zhang L., Visa S., Tieman D., van der Knaap E., & Caicedo A. L. (2020). Genomic Evidence for Complex Domestication History of the Cultivated Tomato in Latin America. *Molecular Biology and Evolution*, 7(4):1118-1132. <https://doi.org/10.1093/molbev/msz297>
- Sahagún, B. (1961) Florentine Codex- The General History of The Tings of New Spain, traducido al inglés por A. J. O. Anderson & Dibble C., The School of American Research and The University of Utah, Santa Fe. USA.
- SIAP. (2024). Servicio de Información Agroalimentaria y Pesquera. Consultado: 8 de abril 2025. <https://www.gob.mx/siap/acciones-y-programas/produccion-agricola-33119>

- Urrieta-Velázquez, J. A., Rodríguez-Mendoza, M. N., Ramírez-Vallejo, P., Baca-Castillo, G. S., Ruiz-Posada, L. M., & Cueto-Wong, J. A. (2012). Variables de producción y calidad de tres selecciones de tomate de costilla (*Solanum lycopersicum* L.). *Revista Chapingo Serie Horticultura*, 18:371-381.
- Vallejo-Marín, M., Pereira-Nunes, C. E. & Russell, A.L. (2022). Anther cones increase pollen release in buzz-pollinated *Solanum* flowers, *Evolution*, 76,(5):931-945. <https://doi.org/10.1111/evo.14485>
- Vásquez-Ortiz., R., Carrillo-Rodríguez., J. C. y Ramírez-Vallejo, P. (2010). Evaluación morfo-agronómica de una muestra del tomate nativo del centro y sureste del México. *Revista Naturaleza y Desarrollo*, 8(2):49-64.
- Wang, X., Gao, L., Jiao, C., Stravoravdis, S., Hosmani, P. S., Saha, S., Zhang, J., Mainiero, S., Strickler, S. R., Catala, C., Martin, G. B., Mueller, L. A., Vrebalov, J., Giovanni, J. J., Wu, S., & Fei, Z. (2020). Genome of *Solanum pimpinellifolium* provides insights into structural variants during tomato breeding. *Nature Communications*, 11,5817. <https://doi.org/10.1038/s41467-020-19682-0>

