

Phenotypic diversity of wild tomato (*Solanum lycopersicum* L.) populations

Alvarado-Rodríguez, Rommel I.¹; Legaria-Solano, Juan Porfirio^{2*}

¹ Postgrado en Biotecnología Agrícola, Universidad Autónoma Chapingo, Carretera Federal México-Texcoco km 38.5, Chapingo, Estado de México, México, C. P. 56230.

² Universidad Autónoma Chapingo, Carretera Federal México-Texcoco km 38.5, Chapingo, Estado de México, México, C. P. 56230.

* Correspondence: legarias.juan@yahoo.com

ABSTRACT

Objective: To produce information about the morpho-agronomic variability of 15 wild tomato populations from different areas of Mexico.

Design/Methodology/Approach: A completely experimental design was used, comprised of 17 treatments (15 wild tomato populations and two commercial tomato populations) and 10 repetitions (individuals). The experimental unit was a plant (individual) which was subjected to an evaluation of 65 morpho-agronomic descriptors, proposed by Biodiversity International. An analysis of variance using repeated measurements was carried out and the mean differences were compared with Tukey's multiple comparison test ($p \leq 0.05$). The quantitative and qualitative variables were subjected to a main component and multiple correspondence analyses, respectively.

Results: A wide variability of the morphological traits and the quality attributes of the fruits —such as consistency and total soluble solids— was recorded. The main component and multiple correspondence analyses accounted for 67.41 and 42.06% of the phenotypic variation, respectively, in the first three components and dimensions. The more discriminatory characteristics belonged to fruits and cymes, based on which the populations were divided into four groups. The first group was made up of heirloom tomatoes with multiparous cyme, and red, small, and medium fruits; the second group was made up of cherry and grape tomatoes with uniparous and multiparous cymes, and yellow, orange, red, and very small fruits; the third group was made up of beef and cocktail tomatoes with uniparous and bifurcated cymes and red, orange, yellow, and small and medium fruits; finally, the fourth group was made up of purple beef tomatoes with uniparous cymes and medium size tomatoes.

Study Limitations/Implications: A molecular characterization must be carried out in order to better understand the variability of these populations.

Findings/Conclusions: All wild tomato populations show a wide genetic heritage. Fruits characteristics —such as size, shape, and color, as well as all types of cymes, and flowering days— contributed to the discrimination of the accessions. Indeterminate plants and red fruits showed higher °Brix than semi-determined plants and orange, yellow, and purple fruits; however, the latter had a better flavor. A new type of tomato leaf that had not been previously reported among the tomato descriptors was found; the leaf was described as “with sprout”.

Key words: *Solanum lycopersicum* L., native populations, morpho-agronomic characterization.

Citation: Alvarado-Rodríguez, R. I., & Legaria-Solano, J. P. (2022). Phenotypic diversity of wild tomato (*Solanum lycopersicum* L.) populations. *Agro Productividad*. <https://doi.org/10.32854/agrop.v15i5.2173>

Academic Editors: Jorge Cadena Iñiguez and Libia Iris Trejo Téllez

Received: October 3, 2020.

Accepted: April 19, 2022.

Published on-line: May 25, 2022.

Agro Productividad, 15(5). May. 2022. pp: 41-53.

This work is licensed under a Creative Commons Attribution-Non-Commercial 4.0 International license.



INTRODUCTION

Tomato (*Solanum lycopersicum* L.) is considered the most important vegetable at domestic and international level (FAOSTAT, 2020). Currently, Mexico is the main exporter of tomato. The country holds a 26.5% share of the market, out of which 99.8% is exported to the USA, amounting to US\$2,601,163,000 (TRADE MAP, 2021). Mexico is considered as the center of domestication and genetic diversity of tomato (Peralta and Spooner, 2007). Recent studies confirm that tomato crops have lost genetic variability, as a result of the constant selection carried out by domestication processes, promoting autogamy (Chen and Tanksley, 2004). Additionally, other factors that have influenced autogamy include the genetic improvement of specific features, such as: higher productivity, shelf life, self-pruning, plant height, precociousness, and adaptation to different cultivation systems (Bai and Lindhout, 2007). Meanwhile, the fruit quality attributes have been left aside (Klee and Tieman, 2018). This reduced genetic base has made tomato crops very sensitive to biotic and/or abiotic stress; therefore, efforts have been made to recover and preserve wild germplasms, because they have a wide genetic variability, as a result of the extreme conditions they have endured during long periods, in their agroecology environment. Consequently, these plants constitute a genetic heritage of new genes of interest. They can also be used to recover lost genes which could take part of an introgression in modern cultivars —through conventional and/or biotechnological techniques. Likewise, they can help to develop new varieties capable of facing climate change, the new challenges posed by productive systems, and the market demand for innocuous products, which must have higher sensorial and nutritional values. Therefore, the aim of this study was to evaluate the variability of wild tomato populations, based on their morphological traits, with their immediate accession in time and space in mind, in order to develop a program for the improvement of the genetic features of agronomic and commercial interest.

MATERIALS AND METHODS

Biological material

Fifteen wild tomato populations samples (from different areas of Mexico) and two commercial varieties (control) were evaluated (Table 1).

Experimental design and agronomic management

A completely randomized experimental design, with 17 treatments (15 wild tomato populations and 2 commercial tomato populations) and 10 repetitions (individuals), was used in the experiment. The experimental unit was one plant per bag. The plants were transplanted 35 days after the sow (dds) in a hydroponic system; there was 40 cm of separation between them and 1 m between rows. The nutrient solution proposed by Sánchez and Escalante (1989) was used. The plants were put under greenhouse conditions, with a 21-24 °C temperature and 60-70% relative humidity.

Evaluated variables

The characterization was based on 65 morpho-agronomic descriptors, proposed by Biodiversity International (1996): 19 vegetative types and 46 reproductive types, and 29 quantitative and 36 qualitative types.

Statistical analysis

The quantitative data were subject to an analysis of variance and a mean comparison test (Tukey, $p \leq 0.05$), using the SAS statistical software (version 9.4); in addition, the Pearson coefficient was estimated and a correlation matrix was developed to carry out a main component analysis, using the RStudio software (version 4.0.4). A description of the features of the qualitative data was carried out and the result was subjected to a multiple correspondence analysis, using the RStudio software (version 4.0.4).

RESULTS AND DISCUSSION

All the wild tomato populations showed a high phenotypic variability during the vegetative and reproductive stages (Table 1). The results were: 53.33% had an indetermined habit, while 46.67% showed a semi-determined habit.

The cymes of semi-determined plants were mostly finished in flower (71.43%) and the cymes of indetermined plants reverted to a vegetative shape (87.50%) with leaves

Table 1. Qualitative traits of tomato populations.

POP	Accessions	GH	LT	TI	SP	FS	FSM	FF	Fruit type	Fruit colour
1	LBCh 76	S	S	VL	S	S	I	VF	Ball	Yellow
2	LBCh 231	S	S	EF	S	S	I	I	Ball	Red
3	LBCh 301	S	S	EF	I	R	S	VF	Ball	Orange
4	LBCh 188	I	S	VS	S	R	V	S	Cherry	Red
5	LBCh 86	S	S	EF	S	H	V	F	Grape	Red
6	LBCh 82	S	S	VS	S	R	V	VS	Ball	Red
7	LBCh 75	I	S	VS	E	F	S	VS	kidney	Red
8	LBCh 71	I	W	VS	S	R	V	I	Cherry	Yellow
9	LBCh 67	I	W	VS	S	S	V	I	Cherry	Orange
10	LBCh 61	I	S	VL	E	F	S	VS	kidney	Red
11	LBCh 2da 28	I	W	VS	S	R	V	F	Cherry	Orange
12	LBCh 2da 18	I	S	VS	S	F	S	VS	kidney	Red
13	LBCh 2da 11	S	P	EF	S	S	S	I	Ball	Purple
14	LBCh 2da 02	I	S	EF	S	C	V	F	Grape	Orange
15	LBCh 2da 09	S	P	EF	S	S	S	I	Ball	Purple
16	Rio Grande	D	S	EF	S	H	I	I	Saladette	Red
17	Floradade	D	S	EF	S	S	I	I	Ball	Red

POP=population; GH=growth habit, S=semi-determinate, I=indeterminate, D=determinate; LT=leaf type, S=standard, W=with sprout, P=potato leaf; TI=terminal meristem of inflorescence, EF=ended in flower, VL=vegetative reverted to leaf, VS=vegetative reverted to sprout; SP=stigma position, S=same level as anthers, I=inserted, E=exserted; FS=fruit shape, F=flattened, S=slightly flattened, R=rounded, H=high rounded, C=cylindrical; FSM=fruit size at maturity, I=intermediate, S=small, V=very small; FF=fruit firmness, VF=very firm, F=firm, I=intermediate, S=soft, VS=very soft. Rio Grande y Floradade correspond to control varieties.

and sprouts, after a certain number of flowers were formed. Most populations showed flowers with stigma at the same level of the stem cone; however, some were also slightly or excessively projected. These results match the change of position from exerted to inserted stigma during domestication, which favored self-fertilization (Chen and Tanksley, 2004); however, the inserted or same-level stigma are more common in modern materials (Blanca *et al.*, 2012).

The most frequent type of leaves was the standard (66.67%), followed by the leaves “with sprouts” (20.00%) (Figure 1) —which had not been reported among the tomato descriptors— and, to a lesser degree, potato leaves (13.33%) —which are related to high anthocyanin populations.

These results differ from those obtained by Agudelo *et al.* (2011), who reported a greater frequency of potato leaves (69.56%) than standard leaves (30.43%). Blanca *et al.* (2012) pointed out that standard leaves prevail in the cultivated species.

Most of the fruits were very small (46.67%) (Figure 2) and had rounded, slightly flattened, and oblong-elongated shapes (indetermined plants) or rounded and roundish-elongated shapes (semi-determined plants). There were also small fruits (40%) with flattened shapes (indetermined plants) and slightly flattened and rounded shape (semi-determined plants). To a lesser degree, there were medium-sized fruits (13.33%), with slightly flattened shapes (semi-determined plants). Therefore, slightly flattened (33.33%) and rounded (33.33%) shapes were most frequent than flattened (20%), roundish-elongated (6.67%), and oblong-elongated (6.67%) shapes. One of the major consequences of domestication is the increase of fruit size (Díez and Nuez, 2008).

The populations with an indetermined growth habit bore red, orange, and yellow fruits; additionally, semi-determined plants bore more purple fruits (Figure 2). The native tomato populations of Mexico have a high variability in fruit size, shape, and color (Lobato-Ortiz *et al.*, 2012). Consequently, the color and pigment content of tomato fruits would be a very interesting area of research that would improve its nutraceutical quality and/or meet the preferences of the consumers.



Figure 1. Leaves “with sprouts” in tomato populations 8, 9, and 11.

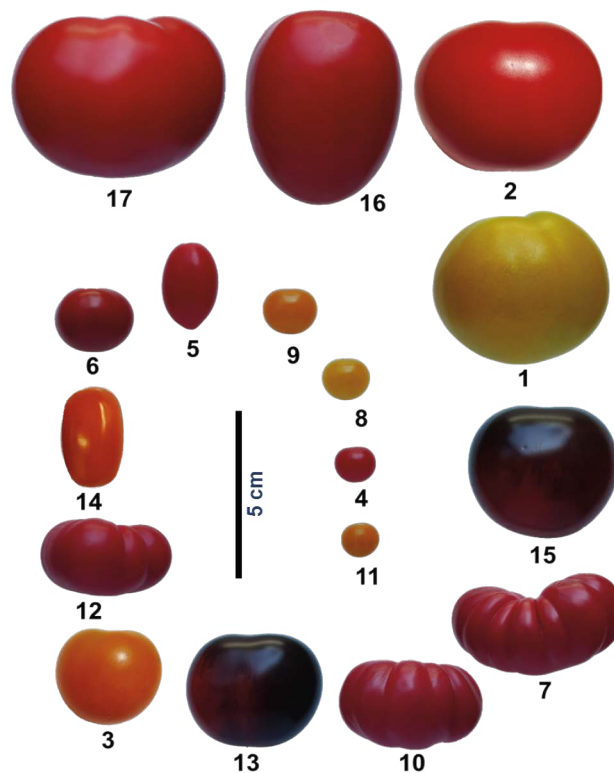


Figure 2. Size, shape and color of fruits for seventeen populations. Numbers indicate tomato populations. The bar (5 cm) indicates a reference measurement.

Additionally, populations with high fruit consistency were found. On the one hand, after 20 days, the consistency of populations 5, 3, and 14 reached a medium point and turned soft after 40 days; likewise, the consistency of population 1 changed to medium after 60 days. On the other hand, the consistency of populations 13 and 15—which were pigmented with anthocyanin—turned soft after 20 days; nevertheless, the integrity of their epidermis remained constant up to 30-40 days of shelf life. Control and other wild varieties showed an opposite behavior. Bonilla-Barrientos *et al.* (2014) reported a higher frequency of hard fruits (pepper-type) than medium fruits (cherry tomatoes) and soft fruits (kidney-shaped); these results are very similar to those obtained in this study.

Analysis of variance

There were significant differences ($p \leq 0.05$) in all the evaluated variables. All the wild populations showed high phenotypic variability; however, the characteristics that helped to achieve a better discrimination were fruits and cymes (Table 2). Precocious materials and flowering were detected in populations 12, 8, 9, 14, and 7 (45-48 dds) and in populations 6, 2, and 3 (49-51 dds). Other populations behaved similarly to control—such as populations 5, 10, 15, and 13 (55-62 dds). Regarding fruit ripening, the populations were classified as early (8 and 9); medium, before control (12, 14, 7, and 6); and medium, similar to control (2 and 3); medium, after control (5, 10, 15, 13, 4, and 11); and late ripening (1).

Table 2. Quantitative traits of tomato populations.

POP	FT	FRT	HC	NFI	IL	FW	NL	PD	ED	NSF	TSS
1	73	105	44.75 a	11.70 b	46.60 b	71.76 bc	2.70 cd	4.70 b	5.50 ab	109.80 b	6.90 cdef
2	50	86	30.19 b	7.00 b	12.94 b	105.67 b	3.50 bc	5.00 a	6.10 a	102.70 bc	8.10 abc
3	51	85	20.50 bcd	17.70 b	30.25 b	24.12 efg	2.00 d	3.40 bcd	3.50 cdef	66.40 cde	8.10 abc
4	64	80	21.24 bcd	7.10 b	16.85 b	1.49 g	2.00 d	1.30 e	1.40 g	40.40 efg	9.70 a
5	55	78	29.70 b	78.30 a	117.10 a	7.92 fg	2.00 d	3.10 bcd	2.00 efg	23.60 fg	9.50 ab
6	49	80	15.70 cd	7.50 b	20.30 b	11.26 fg	2.00 d	2.50 cde	2.70 defg	67.00 cde	9.00 abc
7	48	80	22.50 bcd	12.20 b	33.50 b	44.31 de	6.90 a	3.20 bcd	5.00 bc	149.50 a	8.10 abc
8	46	62	24.00 bcd	6.00 b	11.70 b	2.43 g	2.00 d	1.60 de	1.60 fg	52.90 def	8.00 abc
9	46	64	21.00 bcd	5.90 b	17.25 b	3.56 g	2.00 d	1.70 de	1.90 efg	52.10 def	8.00 abc
10	60	87	44.10 a	8.20 b	28.30 b	53.90 cd	7.00 a	3.40 bcd	4.80 bc	62.70 cde	7.90 bcd
11	64	85	12.13 d	12.38 b	9.75 b	1.37 g	2.00 d	1.30 e	1.30 g	41.40 efg	7.80 bcd
12	45	81	17.25 bcd	12.13 b	30.88 b	27.16 def	7.40 a	2.50 cde	4.20 bcde	53.40 cdef	9.00 abc
13	62	80	22.88 bcd	16.13 b	45.75 b	36.82 def	2.00 d	3.80 bc	4.20 bcde	41.30 efg	5.60 defg
14	47	82	24.70 bcd	74.60 a	146.40 a	8.00 fg	2.00 d	3.50 bcd	2.20 efg	19.90 g	9.10 abc
15	60	81	28.30 bc	17.60 b	48.90 b	42.69 de	2.00 d	3.90 bc	4.40 bcd	84.70 bcd	5.50 efg
16	57	84	22.50 bcd	7.70 b	16.85 b	76.33 bc	2.30 d	6.00 a	5.10 bc	65.70 cde	4.70 fg
17	60	90	22.30 bcd	6.20 b	8.15 b	145.27 a	4.30 b	5.80 a	6.80 a	176.70 a	4.20 g
Media	55	82	24.93	18.14	39.04	39.06	3.18	3.34	3.69	71.19	7.60
C. V.	-	-	32.40	73.97	68.08	44.24	23.02	32.11	28.17	28.96	20.52
HSD	-	-	13.20	22.11	42.33	26.74	1.15	1.84	1.75	32.42	2.51

POP=population; FT=flowering time (days); FRT=fruit ripening time (days); HC=height of the first fruit cluster (cm); NFI=number of flowers per inflorescence; IL=inflorescence length (cm); FW=fruit weight (g); NL=number of locules per fruit; PD=polar diameter of fruit (cm); ED=equatorial diameter of fruit (cm); NSF=number of seeds per fruit; TSS=total soluble solids (°Brix); C. V.=coefficient of variation; HSD=Tukey's honestly significant difference test. Letter indicate significant differences between the means ($P \leq 0.05$).

The characterization of wild materials and semi-domestic plants shows a high diversity in days to the beginning of flowering (Carrillo and Chávez, 2010) and ripening time of the fruit (Chávez-Servia *et al.*, 2011). On this regard, Mejía- Betancourt (2020) pointed out that precocious and compact modern materials are very helpful, as a result of the efficient use of greenhouse space and time, handling high sow densities, shortening the crop cycle, and obtaining a higher number of cycles per year. Additionally, they help to reduce the production costs, as a result of the reduced use of phytosanitary and nutrimental supplies.

For practical purposes, the populations were grouped in four categories, based on the height of the first bunch. The first group was formed by populations 1 and 10 (>40 cm); the second included populations 2, 5, and 15 (28-31 cm); the third included populations 14, 8, 13, 7, 16, 17, 4, 9, 3, and 12 (17-25 cm); finally, the fourth included populations 6 and 11 (12-16 cm).

These results are similar to those obtained by Bonilla-Barrientos *et al.* (2014) in pepper, cherry, and kidney-shaped native varieties, which reached a 1.96-45.41 cm height. We must highlight those materials with bunches at very low heights (<20 cm) suffer disadvantages, because they can be impacted by pathogens in open field production systems. This is not

an undesirable quality in intensive greenhouse crop systems, where making the best of the space, reducing the crop cycle, and obtaining higher yields is fundamental.

The flower quantity was directly related to the cyme length ($r=0.95$) and the cyme type. Populations 5 and 14 stood out with 4.7 bunches in average, a >115 cm length, and >70 flowers per cyme; the rest had simple, bifurcated, and trifurcated bunches, a 9-49 cm length, and 5-18 flowers per cyme, depending on the population. Other studies have found a high variability in cherry tomatoes regarding the number of flowers—from 7.4 to 177 (Boada *et al.*, 2010)—and cyme length—from 58.5-77.6 cm in progenitors to 147.3 cm in hybrids (Yanokuchi *et al.*, 1994).

For practical purposes, the populations were regrouped according to fruit weight. The group with highest weight included populations 1, 2, and control (72-145 g); the medium group included populations 3, 12, 13, 15, 7, and 10 (24-54 g); and, finally, the lower group included populations 11, 4, 8, 9, 5, 14, and 6 (1-11 g). Chávez-Servia *et al.* (2011) obtained similar results using wild and semi-domesticated materials, recording 5.6-128.7 g per fruit.

The populations were also divided in groups, according to the number of loculus per fruit. The first group included populations 7, 10, and 12 (5-10 loculus); the second group was comprised of population 2 and Floradade (3-6 loculus); the third group included population 1 and Río Grande (2 or 3 loculus); and populations 3, 4, 5, 6, 8, 9, 11, 13, 14, and 15 made up the final group (2 loculus).

Wild species have less loculus per fruit (2-3) than modern varieties—which usually have 2.6-36 loculus, although the actual figure can range from 2 to 30 (Grandillo and Tanksley, 1996).

Polar and equatorial diameter characteristics had a positive relation ($r=0.86$), with values from 1.3 to 5.0 and 1.3 to 6.1, respectively. These results are higher than those recorded by Chávez-Servia *et al.* (2011) in wild and semi-domesticated populations: a 1.4- to 3.1-cm polar diameter and a 1.4- to 3.7-cm equatorial diameter. According to the reports of Bai and Lindhout (2007), we can conclude that all populations that show high values of loculus, as well as of fruit weight and diameter, are semi-domesticated biological materials.

Regarding total soluble solids, all the wild populations obtained more °Brix (5.5-9.7) than Rio Grande and Floradade control plants (4.7 and 4.2, respectively). Overall, indetermined plants show higher °Brix (8.45 average) than semi-determined plants (7.52 average). Regarding the fruits, red tomatoes had the highest °Brix (8.76 average), followed by yellow (7.45 average), and purple (5.55 average); however, purple tomatoes had a better flavor. Additionally, very small tomatoes had 8.73 °Brix, the medium tomatoes, 7.50 °Brix, and small tomatoes, 7.37 °Brix. Crisanto-Juárez *et al.* (2010) recorded similar values for wild harvested fruits (4.5-9.3 °Brix). These results prove that these materials have excellent quality features for the improvement of modern materials.

Multiple correspondence analysis

Taking into account the 34 morpho-agronomic qualitative characteristics, the analysis showed that the first three dimensions (Dim1, Dim2, and Dim3) accounted for 42.06% of

the total phenotypic variability. However, Garzón (2011) reported that the total variation of 36 accessions of cherry tomato accounted for 76.98% of the three first dimensions. The phenotypic variability of the populations was mainly represented by the characteristics of the fruit and the cyme; Chime *et al.* (2017) reported similar results.

Four features with the highest contribution to the two first dimensions were selected, subsequently, the populations were classified in four groups (Figure 3, Table 3). Dim1 accounted for 17.17% of the variation and was represented by shape, firmness, multiparous characteristics, and style projected position; meanwhile, Dim2 accounted for 13.02% and was represented by the type of leaves, growth habit, color intensity of the hypocotyl, and fruit size and color. Group I was comprised of populations 7 (G), 10 (J), and 12 (L), which had irregular transversal shaped features (iFT), low firmness in shelf life (dFE), flattened shape (aFF), colorless epidermis (iCE), ‘cat-face’ appearance (pACF), slightly projected style (IPE), and multiparous bunch (mPI). Group II was more diverse and included populations 1 (A), 2 (B), 3 (C), 4 (D), 5 (E), 6 (F), 14 (N), and the Rio Grande (P) and Floradade (Q) control plants; they were characterized by a high fruit firmness in shelf life (fFE), semi-determined growth (sHC), and medium-sized plants (iTP). Group III included populations 13 (M) and 15 (O), which had the usual features for greenish-purple unripe fruits (vmCF), purple ripe fruits (mCFM), potato leaves (ppTH), and

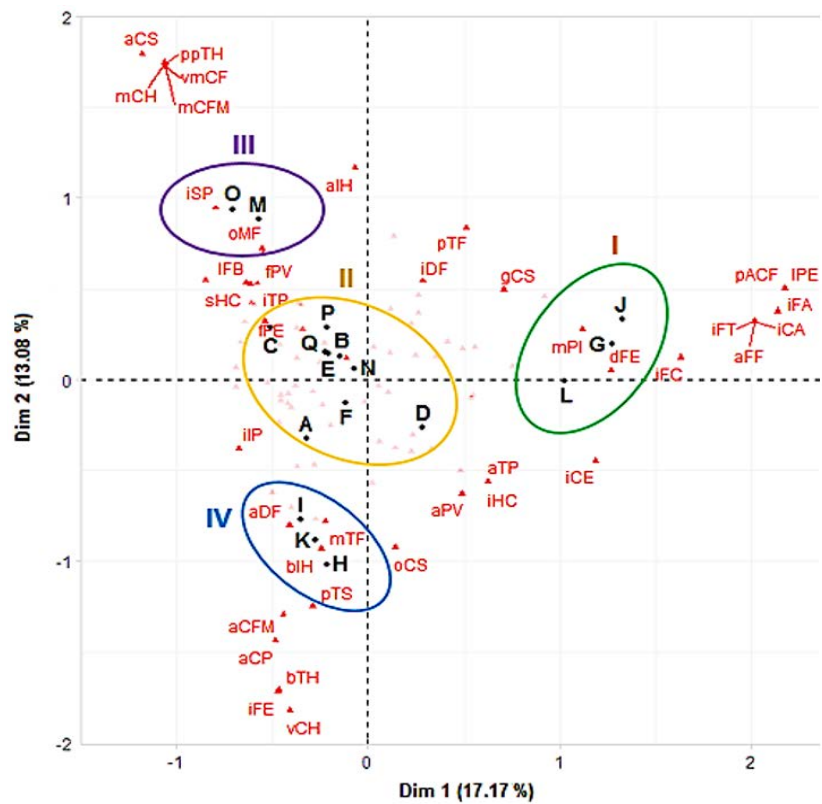


Figure 3. Qualitative traits associated with 15 wild tomato populations. A) vectors and eigenvalues; B) biplot with Dim1 and Dim2.

Table 3. Qualitative characteristics of 15 wild tomato populations. A) vectors and values provided by the authors; B) biplot Dim1 and Dim2.

No.	Characteristics	Code	Dim1	Dim2	Dim3
1	Dark yellow seed	aCS	0.6684402	2.0297843	2.0881350
2	Purple hypocotyl	mCH	1.0915815	3.8292992	3.9739250
3	Potato leaf	ppTH	1.0915815	3.8292992	3.9739250
4	Purple color of ripe fruit	mCFM	1.0915815	3.8292992	3.9739250
5	Green-purple color of immature fruit	vmCF	1.0915815	3.8292992	3.9739250
6	Intermediate facility to separate the fruit	iSP	1.2132500	2.2585527	1.0104040
7	Leaflets with wavy margin	oMF	0.7440139	1.6607922	0.3125941
8	Hypocotyl with high intensity staining	aIH	0.0089196	3.4410878	1.7452220
9	Inflorescence ending in flower	iPV	1.1645026	2.4048689	0.8925949
10	Semi-determinate growth habit	sHC	1.2628357	1.2238481	0.0333420
11	Intermediate height plant	iTP	1.2944758	1.4165056	0.1365200
12	High firmness fruit on shelf (10 ds)	fFE	1.3976733	0.6467704	0.9987624
13	Fruit with slightly cleft base	IFB	0.9743000	0.9013400	0.9734923
14	Small size fruit	pTF	0.7561467	2.6603956	0.7735197
15	Intermediate foliage density	iDF	0.3894345	1.8728563	0.0277012
16	Gray seed	gCS	1.1993170	0.7731033	0.1997073
17	Multiparous inflorescence	mPI	3.0136009	0.2436924	0.4061571
18	Low firmness fruit on shelf (10ds)	dFE	3.8586452	0.0072673	0.3857630
19	Fruits of intermediate firmness at harvest	iFC	5.1271148	0.0381446	0.2380655
20	Fruit with irregular cross section	iFT	5.8700385	0.2078257	0.1033894
21	Flattened shaped fruit	aFF	5.8700385	0.2078257	0.1033894
22	Fruit with irregular apex scar	iCA	5.8700385	0.2078257	0.1033894
23	Fruit with indented apex	iFA	5.8708385	0.2078257	0.1033894
24	Slightly exerted style	IPE	4.5409601	0.3207046	0.0731773
25	Fruit with cat-face appearance	pACF	4.5409601	0.3207046	0.0731773
26	Large height plant	aTP	1.5123073	1.6146075	0.5467456
27	Fruit with colorless epidermis	iCE	2.0324658	0.3782076	0.8280825
28	Inflorescence ending in vegetative and/or flower	aPV	0.9250148	1.9872506	0.6346747
29	Indeterminate growth habit	iHC	1.5123073	1.6146075	0.5467456
30	Dark brown seed	oCS	0.0386171	2.1683382	1.3910380
31	Pericarp with intermediate intensity	iIP	1.3232791	0.5456709	2.8052140
32	High foliage density	aDF	0.4023615	2.0551404	0.0500720
33	Very small fruit size	mTF	0.1701719	2.7182851	0.0849405
34	Hypocotyl with low intensity staining	bIH	0.1710982	3.3076166	0.4143379
35	Small size seed	pTS	0.2033297	4.9517903	0.5795743
36	Yellow color of ripe fruit	aCFM	0.1893568	2.1148779	0.0718591
37	Yellow pericarp	aCP	0.4490272	5.2368754	0.4117801
38	Leaf type with sprout	bTH	0.3150106	5.5416175	1.2303180
39	Intermediate firmness fruit on shelf (10 ds)	iFE	0.2137655	3.7368020	1.5691100
40	Green hypocotyl	vCH	0.1599537	4.2070902	0.6804410
	Eigenvalue		0.34833078	0.26523764	0.23946287
	Percent variance		17.17	13.08	11.81
	Cumulative percent variance		17.17	30.25	42.06

purple hypocotyls (mCH). Group IV was comprised of populations 8 (H), 9 (I), and 11 (K), which had yellow pericarps (aCP), medium firmness in shelf life (iFE), green hypocotyls (vCH), and leaves “with sprouts” (bTH).

Main component analysis

Based on 28 morpho-agronomic quantitative characteristics, the analysis showed that the first three components (CP1, CP2, and CP3) accounted for 67.41% of the observed phenotypic variation. CP1 and CP2 contributed 55.48% and they were mainly related to fruit and cyme features; these results are similar to the findings of Carrillo and Chávez (2010) and Bonilla-Barrientos *et al.* (2014), who isolated a total variability of 68.5% and 77.03%, respectively. CP1 and CP2 were taken into account to associate the populations, which were divided into three groups (Figure 4, Table 4). Group I was divided into two subgroups, gathering all the colors of the fruits. The first included populations 3 (C), 13 (M), 15 (O), 2 (B), and Rio Grande (P), while the second subgroup was comprised of populations 1 (A) and Floradade (Q). Group II included populations 4 (D), 5 (E), 6 (F), 8 (H), 14 (N), 9 (I), and 11 (K). Finally, Group III was made up of populations 7 (G), 10 (J), and 12 (L).

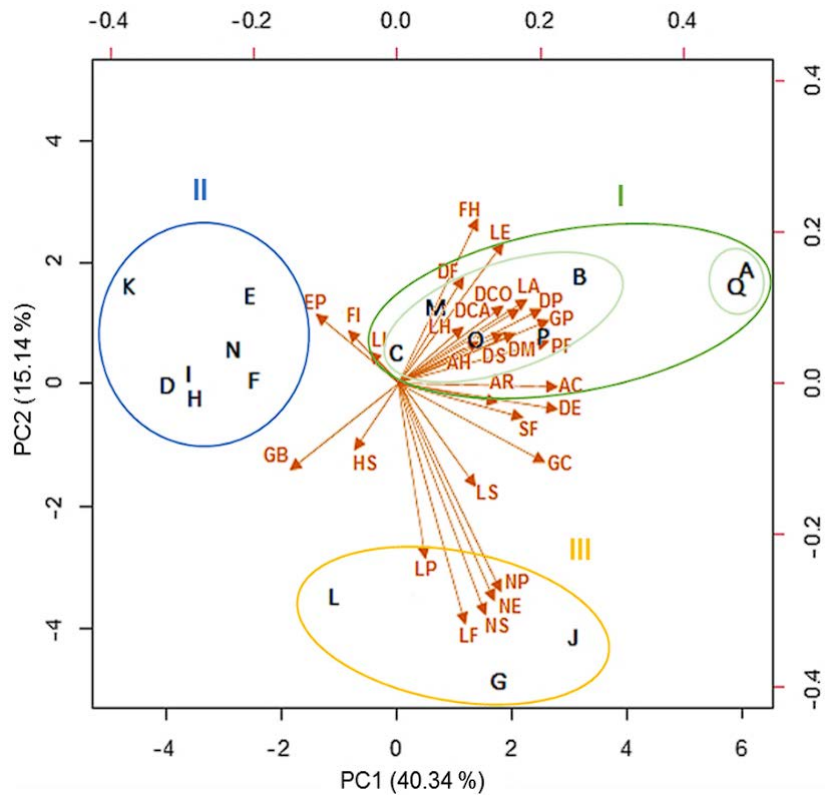


Figure 4. Quantitative traits associated with 15 wild tomato populations. A) vectors and eigenvalues; B) biplot with Dim1 and Dim2

Table 4. Quantitative characteristics of 15 wild tomato populations. A) vectors and values provided by the authors; B) biplot CP1 and CP2.

No.	Trait	Code	PC1	PC2	PC3
1	Seedling emergence	EP	-0.14198804	0.11521405	-0.12579729
2	Sympodium length	LS	0.13320737	-0.17528546	0.35529871
3	Sympodium diameter	DS	0.18321171	0.08319585	0.00757643
4	Leaves per sympodium	HS	-0.07523910	-0.10923667	0.25064273
5	Leaflets per leaf	FH	0.14068266	0.27455916	-0.12154306
6	Leaf length	LH	0.11393586	0.09477567	0.20869656
7	Leaf width	AH	0.14493577	0.07362487	0.13757391
8	Height of the first fruit cluster	AR	0.17529247	-0.02925165	0.31747032
9	Flowering time	OF	0.11597196	0.17869755	-0.00578613
10	Flowers per inflorescence	FI	0.08574209	0.08963171	0.36935312
11	Inflorescence length	LI	-0.04857321	0.05337954	0.42025007
12	Number of petals	NP	0.17782611	-0.33828452	0.02959308
13	Number of sepals	NS	0.15265601	-0.37798700	-0.02001142
14	Corolla diameter	DCO	0.21288692	0.12456773	0.20616778
15	Calyx diameter	DCA	0.18580503	0.12907483	0.23916102
16	Stamen length	LE	0.18568266	0.23435240	0.06262061
17	Number of stamens	NE	0.16737826	-0.35399539	-0.06575172
18	Total length of the pedicel	LP	0.05029053	-0.28628617	0.15991232
19	Abscission zone length	LA	0.22620119	0.13930400	0.08418366
20	Ripening time	DM	0.20394520	0.08432035	0.09869649
21	Pedicel scar width	AC	0.27931441	-0.00396691	-0.12167903
22	Fruit weight	PF	0.26249150	0.07044068	-0.13380377
23	Polar diameter of fruit	DP	0.25179816	0.12224396	0.01619772
24	Equatorial diameter of fruit	DE	0.27961214	-0.03989131	-0.08083599
25	Number of locules per fruit	LF	0.11858295	-0.39097791	-0.03009091
26	Pericarp thickness	GP	0.26439998	0.10644528	-0.02280295
27	Columella thickness	GC	0.25827506	-0.12926713	-0.12077907
28	Number of seeds per fruit	SF	0.21938254	-0.05610109	-0.17912647
29	Total soluble solids	GB	-0.18806195	-0.14116580	0.25398408
	Eigenvalue		11.69699	4.39148	3.45959
	Standard deviation		3.4204	2.0956	1.8800
	Percent variance		40.34	15.14	11.93
	Cumulative percent variance		40.34	55.48	67.41

CONCLUSIONS

Wild populations showed a high phenotypic variability in the vegetative and reproductive stages; the fruit and cyme characteristics made the most important contribution to their discrimination. We discovered a type of leaf that had never been reported among tomato descriptors and called it “with sprouts”. Materials with high °Brix values, high firmness in shelf life, and intense red and purple colors were detected. These elements are related to

bioactive compounds with high antioxidant capacity with great potential for the genetic improvement of modern varieties.

ACKNOWLEDGMENTS

The authors would like to thank El Consejo Nacional de Ciencia y Tecnología for its economic support, which facilitated the RIAR studies, and the Universidad Autónoma Chapingo for providing the opportunity to be included in its postgraduate program. Additionally, the authors would like to thank the advisory committee, which took part in their scientific education, and to Mr Noé Alarcón Cruz (PhD), who provided the accessions.

REFERENCES

- Agudelo, A. A. G., Ceballos, A. N., & Orozco, F. J. (2011). Caracterización morfológica del tomate tipo cereza (*Solanum lycopersicum* Linnaeus). *Agronomía*, 19(2), 44-53.
- Bai, Y., & Lindhout, P. (2007). Domestication and breeding of tomatoes: what have we gained and what can we gain in the future? *Annals of Botany*, 100(1), 1085-1094. <https://doi.org/10.1093/aob/mcm150>
- Bioversity International. (1996). Descriptores para el tomate (*Lycopersicon* spp.). Recuperado el 22 de marzo de 2022, de https://www.bioversityinternational.org/fileadmin/_migrated/uploads/tx_news/Descriptores_para_el_tomate__Lycopersicon_spp._489.pdf
- Blanca, J., Cañizares, J., Cordero, L., Pascual, L., Díez, 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>
- Boada, H. M. Y., Mejía, R. J. L., Ceballos, A. N., & Orozco, F. J. (2010). Evaluación agronómica de treinta introducciones de tomate silvestre tipo cereza (*Solanum lycopersicum* L.). *Agronomía*, 18(2), 59-67.
- Bonilla-Barrientos, O., Lobato-Ortiz, R., García-Zavala, J. J., Cruz-Izquierdo, S., Reyes-López, D., Hernández-Leal, E., & 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. <https://doi.org/10.35196/rfm.2014.2.129>
- Carrillo, R. J. C., & Chávez, S. J. L. (2010). Caracterización agromorfológica de muestras de tomate de Oaxaca. *Revista Fitotecnia Mexicana*, 33(4), 1-6.
- Chávez-Servia, J. L., Carrillo-Rodríguez, J. C., Vera-Guzmán, A. M., Rodríguez-Guzmán, E., & Lobato-Ortiz, R. (2011). *Utilización actual y potencial del jitomate silvestre mexicano*. SINAREFI: Oaxaca, México. 72 p.
- Chen, K.-Y., & Tanksley, S. (2004). High-resolution mapping and functional analysis of se2.1: A major stigma exertion Quantitative Trait Locus associated with the evolution from allogamy to autogamy in the genus *Lycopersicon*. *Genetics*, 168, 1563-1573. <http://dx.doi.org/10.1534/genetics.103.022558>
- Chime, A. O., Aiwansoba, R. O., Osawaru, M. E., & Ogwu, M. C. (2017). Morphological evaluation of tomato (*Solanum lycopersicum* Linn.) cultivars. *Makara Journal of Science*, 21(2), 97-106. <https://doi.org/10.7454/mss.v21i2.7421>
- Crisanto-Juárez, A. U., Vera-Guzmán, A. M., Chávez-Servia, J. L., & Carrillo-Rodríguez, J. (2010). Calidad de frutos de tomates silvestres (*Lycopersicon esculentum* var. *cerasiforme* Dunal) de Oaxaca, México. *Revista Fitotecnia Mexicana*, 33(4), 7-13. https://doi.org/10.35196/rfm.2010.Especial_4.7
- Díez, M. J., & Nuez, F. (2008). *Tomato*. In: Vegetables II, Prohens, J. & Nuez, F., Eds.; Springer: Berlin, Germany. pp. 249-323. <https://doi.org/10.1007/978-0-387-74110-9>
- FAOSTAT. (2020). *Datos sobre alimentación y agricultura*. Organización de las Naciones Unidas para la Alimentación y la Agricultura. Recuperado el 2 de marzo de 2020, de FAOSTAT: <http://www.fao.org/faostat/es/#data/QC>
- Garzón, R. J. P. (2011). Caracterización y evaluación morfoagronómica de la colección de tomate tipo cherry de la Universidad Nacional de Colombia sede Palmira. Tesis de maestría, Universidad Nacional de Colombia, Palmira, Colombia. 56 p.
- Grandillo, S., & Tanksley, S. D. (1996). QTL analysis of horticultural traits differentiating the cultivated tomato from the closely related species *Lycopersicon pimpinellifolium*. *Theoretical and Applied Genetics*, 92(1), 935-951. <https://doi.org/10.1007/BF00224033>
- Klee, H. J., & Tieman, D. M. (2018). The genetics of fruit flavour preferences. *Nature Reviews Genetics*, 19, 347-356. <https://doi.org/10.1038/s41576-018-0002-5>

- Lobato-Ortíz, R., Rodríguez-Guzmán, E., Carrillo-Rodríguez, J. C., Chávez-Servia, J. L., Sánchez-Peña, P., & Aguilar-Meléndez, A. (2012). *Exploración, colecta y conservación de recursos genéticos de jitomate: avances en la Red de Jitomate*. SINAREFI: Texcoco, Estado de México, México. 56 p.
- Mejía-Betancourt, F. A. (2020). Manejo de esquejes enraizados para la producción de jitomate en alta densidad de población, bajo invernadero e hidroponía. Tesis de maestría. Universidad Autónoma Chapingo, Texcoco, Estado de México, México.
- Peralta, E. I., & Spooner, M. D. (2007). *History, origin and early cultivation of tomato (Solanaceae)*. In: Genetic Improvement of Solanaceous Crops, Razdan, M. & Mattoo, A., Eds.; Science Publishers: USA. pp. 1-24.
- Rodríguez-Valdés, A., Florido-Bacallao, M., Dueñas-Hurtado, F., Muñoz-Calvo, L. J., Hanson, P., & Álvarez-Gil, M. (2017). Caracterización morfoagronómica en líneas de tomate (*Solanum lycopersicum* L.) con resistencia a begomovirus. *Cultivos Tropicales*, 38(2), 70-79.
- Sánchez, F., & Escalante, E. (1989). *Hidroponía: un sistema de producción de plantas*. 3a ed.; Universidad Autónoma Chapingo: Texcoco, Estado de México, México.
- Tengö, M., & Belfrage, K. (2004). Local management practices for dealing with change and uncertainty: A cross-scale comparison of cases in Sweden and Tanzania. *Ecology and Society*, 9(3), 1-22. <https://doi.org/10.5751/ES-00672-090304>
- TRADE MAP. (2021). Datos comerciales mensuales, trimestrales y anuales. Estadísticas del comercio para el desarrollo internacional de las empresas. Consultado el 12 de marzo de 2021, en TRADE MAP: https://www.trademap.org/Country_SelProductCountry.aspx?nvpm=3%7c484%7c%7c%7c0702%7c%7c%7c4%7c1%7c1%7c2%7c1%7c%7c2%7c1%7c%7c1
- Yanokuchi, Y., Fujino, M., Ishii, T., & Uchiumi, T. (1994). Inheritance of the sideshootless character and the length of pedicel in cherry tomatoes. *Tohoku Agricultural Research*, 47, 277-278. <http://www.naro.affrc.go.jp/org/tarc/to-noken/DB/DATA/047/047-277.pdf>

