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Expression of MYB transcription factors and target genes and its association with phenolic content and antioxidant activity of selected *Solanum lycopersicum* var. *cerasiforme* accessions from Mexico

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ABSTRACT

Eight *Solanum lycopersicum* var. *cerasiforme* accessions from Mexico were evaluated for total phenolics (TP) and flavonoids (TF), phenolic profiles (UPLC-DAD-MS), antioxidant capacity (AC) (ABTS, DPPH, and FRAP), and expression of transcription factors (*MYB12* and *MYB14*) and target genes (*PAL, CHS* and *CHI*) by RT-qPCR. The AC (mmol TE/kg fw; TE, Trolox Equivalents) by ABTS (5.27–11.81), DPPH (1.43–3.67), and FRAP (4.41–9.22) correlated with TP (0.53–1.20 g GAE/kg fw; GAE, Gallic Acid Equivalents), TF (1.03–2.10 g QE/kg; QE, Quercetin Equivalents), and the levels of chlorogenic and dicaffeoylquinic acids and rutin. The expression of *MYB12* and *MYB14* correlated with that of *PAL* and *CHS*, while *CHI* was only associated with *MYB12*. The accessions Tumbisca and Kilim showed the highest gene expression, phenolics content, and AC, suggesting they can be used in breeding programs to produce tomatoes with better AC.

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PALABRAS CLAVE
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Expresión de factores de transcripción MYB y genes diana y su asociación con el contenido de fenólicos y actividad antioxidante en una selección de accesiones de *Solanum lycopersicum* var. *cerasiforme* de México

RESUMEN

Ocho accesiones de *Solanum lycopersicum* var. *cerasiforme* de México se evaluaron en contenido de fenólicos totales (FT), flavonoides totales (FLT), perfil de fenólicos (UPLC-DAD-MS), capacidad antioxidante (CAox) (ABTS, DPPH y FRAP) y expresión de factores de transcripción (*MYB12* y *MYB14*) y genes diana (*PAL, CHS* y *CHI*) por RT-qPCR. La CAox (mmol ET/kg pf; ET, Equivalentes de Trolox) por ABTS (5.27-11.81), DPPH (1.43-3.67) y FRAP (4.41-9.22) se correlacionó con FT (0.53-1.20 g EAG/kg pf; EAG, Equivalentes de Ácido Gálico), FLT (1.03-2.10 g EQ/kg; EQ, Equivalentes de Quercetina) y los niveles de ácido clorogénico y dicafeoilquínico y rutina. La expresión de *MYB12* y *MYB14* correlacionó con la de *PAL* y *CHS*, mientras que *CHI* solo mostró asociación con *MYB12*. Las accesiones Tumbisca y Kilim mostraron la mayor expresión génica, contenido de fenólicos y CAox, sugiriendo que pueden ser usadas en programas de mejoramiento para producir tomates con mejor CAox.

1. Introduction

The wild cherry tomato *Solanum lycopersicum* var. *cerasiforme* represents an important source of compounds with nutritional and biological activities (Adalid et al., 2010; Boches et al., 2011; Hanson et al., 2004). *S. lycopersicum* var. *cerasiforme* is widely distributed in Mexico and the accessions show significant variations in fruit quality (*e.g.*, color, lycopene and vitamin C content) (Crisanto-Juárez et al., 2010; Juárez-López et al., 2009), as well as in the content of phenolic compounds and antioxidant and antimutagenic activities (Delgado-Vargas et al., 2018), characteristics that can be used to improve nutraceutical characteristics of tomato cultivars.

The synthesis of phenylpropanoids is regulated by MYB transcription factors and several researchers have used biotechnological strategies to improve the levels of bioactive compounds in tomato. The overexpression of *At*MYB12 (Luo et al., 2008; Pandey et al., 2015) and *At*MYB11 (Li et al., 2015) in tomato fruit increased significantly the synthesis of caffeoyl quinic acids and flavonols, which has been associated with the up-regulation of genes involved in the synthesis of phenylpropanoids (Ding et al., 2022; Li et al., 2021; Pandey et al., 2015).

Delgado-Vargas et al. (2018) previously showed that the levels of phenolic compounds in some *S. lycopersicum* var. cerasiforme accessions from Mexico were close to those of transgenic tomato fruit overexpressing MYB transcription factors (Li et al., 2015; Luo et al., 2008), suggesting that the synthesis of phenylpropanoids is up-regulated in these tomato genotypes. The aim of this study was to analyze the expression of MYB transcription factors and target genes and its association with the levels of phenolic

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Table 1. Total phenolics and flavonoids content and antioxidant capacity of the methanol extracts from the pericarp of *Solanum lycopersicum* var. *cerasiforme* accessions[z].

Tabla 1. Contenido de fenólicos y favonoides totales y capacidad antioxidante de extractos metanólicos del pericarpio de accesiones de *Solanum lycopersicum* var. *cerasiforme*[z].

				Fruit weigth	Phenolics content		Antioxidant capacity (mmol TE/kg)		
Accession code[y]	Common name	State of origin	Fruit color	(g)	(g GAE/kg)	Flavonoids content (g QE/kg)	ABTS	DPPH	FRAP
TS09118	Altamirano	Guerrero	Red	**3.24 ± 0.17a**	0.81 ± 0.03^{d}	1.77 ± 0.13^{b}	8.02 ± 0.29^{c}	2.03 ± 0.01^{cd}	6.72 ± 0.19^{c}
SLC0082	Cartagena	Chiapas	Red	2.45 ± 0.09^{c}	0.87 ± 0.02^{c}	1.32 ± 0.05^{c}	8.04 ± 0.25^{c}	1.69 ± 0.14^{ef}	6.42 ± 0.25^{c}
TS09150	Francisco	Tabasco	Red	2.76 ± 0.17^{b}	**0.53 ± 0.04**^{e}	**1.03 ± 0.05**^{d}	**5.27 ± 0.58**^{d}	**1.43 ± 0.09**^{f}	**4.41 ± 0.15**^{e}
SLC0085	Kilim	Yucatán	Red	**2.22 ± 0.14d**	0.94 ± 0.04^{b}	1.09 ± 0.08^{d}	9.23 ± 0.49^{b}	2.47 ± 0.15^{b}	7.58 ± 0.40^{b}
SLC0102	Placharosa	Sinaloa	Yellow	2.48 ± 0.06^{c}	0.81 ± 0.04^{d}	1.09 ± 0.05^{d}	7.67 ± 0.67^{c}	1.75 ± 0.09^{de}	5.51 ± 0.31^{d}
TS09129	Rincon	Oaxaca	Red	2.74 ± 0.13^{b}	0.81 ± 0.04^{d}	1.45 ± 0.08^{c}	7.87 ± 0.43^{c}	2.21 ± 0.05^{bc}	6.75 ± 0.25^{c}
TS09125	Tumbisca	Michoacán	Red	2.50 ± 0.06^{c}	**1.20 ± 0.02**^{a}	**2.10 ± 0.20**^{a}	**11.81 ± 1.15**^{a}	**3.67 ± 0.44**^{a}	**9.22 ± 0.71**^{a}
TS09128	Villamaza	Sinaloa	Yellow	2.54 ± 0.02^{c}	0.94 ± 0.01^{b}	**1.03 ± 0.05**^{d}	7.92 ± 0.29^{c}	1.84 ± 0.11^{de}	6.39 ± 0.20^{c}
	Moneymaker		Red	68.87 ± 6.91	0.44 ± 0.02	0.54 ± 0.02	2.99 ± 0.78	0.96 ± 0.03	3.32 ± 0.18

[z]Values are the mean ± standard deviation of three replicates (50 fruit each). The phytochemicals content and antioxidant capacity are expressed on a fresh weight basis. The lowest and highest values of the accessions are in bold type. [y]Codes starting with TS and SLC correspond to accessions provided by the germplasm banks of University of Guadalajara and Autonomous University of Sinaloa, respectively. GAE, gallic acid equivalents; QE, quercetin equivalents. Different letters in a single column indicate significant differences between the accessions (Fisher, α = 0.05).

[z]Los valores son la media ± desviación estándar de tres réplicas (50 frutos cada una). El contenido de fitoquímicos y la capacidad antioxidante están expresados en peso fresco. Los valores más bajos y más altos de las accesiones están en negritas. [y]Los códigos que inician con TS y SLC corresponden a accesiones proporcionadas por los bancos de germoplasma de la Universidad de Guadalajara y la Universidad Autónoma de Sinaloa, respectivamente. GAE, equivalentes de ácido gálico; QE, equivalentes de quercetina. Letras diferentes en una misma columna indican diferencias significativas entre las accesiones (Fisher, α = 0.05).

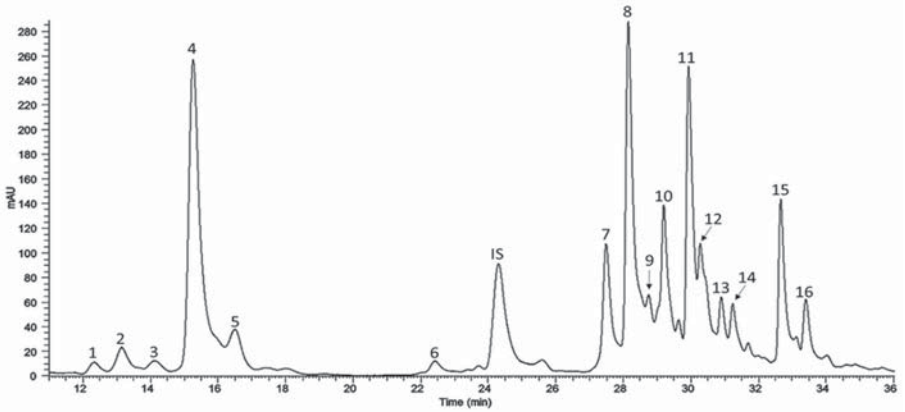

Figure 1. UPLC-DAD phenolic profile of the methanol extract from the pericarp of *Solanum lycopersicum* var. *cerasiforme* accession Rincon. Similar profiles with quantitative variations were obtained for the other accessions. Peaks were identified as caffeoyl hexose I (1), *cis*-*p*-coumaric hexose acid (2), *trans*-*p*-coumaric hexose acid (3), chlorogenic acid (4), dicaffeoylquinic acid II (5), rutin hexose (6), rutin pentoside (7), rutin (8), quercetin dihexose pentoside deoxyhexose (9), naringenin chalcone hexose I (10), dicaffeoylquinic acid III (11), naringenin-*O*-hexose (12), naringenin chalcone hexose II (13), naringenin chalcone hexose III (14), tricaffeoylquinic acid (15), naringenin chalcone (16). Sinapic acid was used as internal standard (IS).

Figura 1. Perfil de fenólicos por UPLC-DAD del extracto metanólico del pericarpio de la accesión Rincon de *Solanum lycopersicum* var. *cerasiforme*. Todas las accesiones mostraron perfiles similares con variaciones cuantitativas. Los picos fueron identificados como cafeoil hexosa I (1), ácido *cis*-*p*-coumárico hexosa (2), ácido *trans*-*p*-coumárico hexosa (3), ácido clorogénico (4), ácido dicafeolquinico II (5), rutina hexosa (6), rutina pentósido (7), rutina (8), quercetina dihexosa pentósido desoxihexosa (9), naringenina chalcona hexosa I (10), ácido dicafeoilquínico III (11), naringenina-*O*-hexosa (12), naringenina chalcona hexosa II (13), naringenina chalcona hexosa III (14), ácido tricafeoilquínico (15), naringenina chalcona (16). El ácido sinápico fue usado como estándar interno (IS).

the phenylpropanoids pathway, the expression of the transcription factors *MYB12* and *MYB14* and the target genes *PAL*, *CHS* and *CHI* was evaluated (Figure 3). The expression of *MYB12* varied significantly among the accessions and was higher than that of the Moneymaker variety; Kilim and Tumbisca showed the highest expression levels and corresponded with the highest phenolic and flavonoid content in these materials (Tables 2 and 3). *AtMYB12* is a key regulator of flavonoid biosynthesis in *Arabidopsis thaliana* and its expression in tomato increases significantly the content of phenylpropanoids such as chlorogenic acid and caffeoylquinic acids (Luo et al., 2008; Pandey et al., 2015). These results correspond with the correlation observed in the present study between the expression levels of *MYB12* and the content of the main phenolic compounds: chlorogenic acid ($r = 0.41$; $p \leq 0.05$) and dicaffeoylquinic acid I ($r = 0.45$; $p \leq 0.05$). The expression of *MYB12* also correlated with the AC by the three methods ($r = 0.43–0.51$; $p \leq 0.05$) (Supplementary Table S2).

Wang et al. (2018) overexpressed *SlMYB12* in three cherry tomato varieties and observed significant increases in the content of flavonols and the expression of genes involved in their biosynthesis, suggesting the potential use of *SlMYB12* as a marker for the accumulation of flavonoids in tomato.

MYB14 showed, in general, lower relative expression values than *MYB12* in the accessions (Figure 3). The highest transcript levels were observed in Kilim, followed by Tumbisca and Altamirano, which corresponded with the high content of the major phenolics observed in these accessions (Tables 2 and 3). The expression levels of *MYB14* correlated significantly with the content of chlorogenic acid ($r = 0.73$; $p \leq 0.001$), rutin ($r = 0.68$; $p \leq 0.001$) and dicaffeoylquinic acids ($r = 0.58–0.65$; $p \leq 0.01$) and the AC ($r = 0.44–0.49$; $p < 0.05$) in the tomato accessions (Supplementary Table S2). Consistent with the possible role of *MYB14* in the modulation of phenylpropanoids pathway, the overexpression of this gene in tomato plants increased the transcript levels of several genes associated with flavonoid biosynthesis (Li et al., 2021).

Phenylalanine ammonia-lyase (PAL), chalcone synthase (CHS), and chalcone isomerase (CHI) catalyze key steps in the phenylpropanoid pathway and the genes encoding these enzymes are targets of MYB transcription factors. The fruit-specific expression of *At*MYB12 in tomato increased up to 18, 16 and 10 times the transcript levels of *PAL*, *CHS* and *CHI*, respectively (Ding et al., 2022; Zhang et al., 2015). In this regard, the expression of *PAL* varied significantly among the accessions (Figure 3) and correlated with the transcript levels of *MYB12* ($r = 0.69$; $p \leq 0.001$) and *MYB14* ($r = 0.59$; $p \leq 0.01$). The expression levels of *PAL* also correlated with the content of chlorogenic acid ($r = 0.58$; $p \leq 0.01$), dicaffeoylquinic acids ($r = 0.69–0.79$; $p \leq 0.001$), rutin ($r = 0.54$; $p \leq 0.01$) and naringenin chalcone (0.84; $p \leq 0.001$), and the AC by the three methods ($r = 0.68–0.71$; $p \leq 0.001$) (Supplementary Table S2).

CHS is the first committed enzyme in flavonoid biosynthesis and its coding gene is activated by AtMYB12, which binds directly to the promoter region (Zhang et al., 2015). The expression of *CHS* in the accessions Kilim and Tumbisca was 3.1 and 4.2 times higher than that of Moneymaker (Figure 3). The transcript levels of this gene correlated with those of *MYB12* ($r = 0.61$; $p \leq 0.001$) and *MYB14* ($r = 0.57$; $p \leq 0.001$). The expression of *CHS* also showed a highly significant correlation with the content of naringenin chalcone ($r = 0.80$; $p \leq 0.001$) and the AC ($r = 0.79–0.88$; $p \leq 0.001$) (Supplementary Table S2). These results agree with the key role of CHS in the synthesis of flavonoids.

CHI catalyzes the conversion of naringenin chalcone to naringenin and its expression appears to be modulated by *MYB12* since the silencing of this transcription factor decreased the accumulation of naringenin chalcone in tomato fruit (Ballester et al., 2010). In this study, the expression of *CHI* varied significantly among the accessions (Figure 3) and correlated with the levels of *MYB12* ($r = 0.46$; $p \leq 0.05$) and the AC ($r = 0.57–0.63$; $p \leq 0.001$) (Supplementary Table S2). The content of naringenin chalcone also correlated with the transcript levels of *MYB12* (r

Table 2. Phenolic acids content in the methanol extracts from the pericarp of *Solanum lycopersicum* var. *cerasiforme* accessions[z].

Tabla 2. Contenido de ácidos fenólicos en extractos metanólicos del pericarpio de accesiones de *Solanum lycopersicum* var. *cerasiforme*[z].

Accession	Caffeoyl hexoside I	*cis-p*-Coumaric acid hexoside	*trans-p*-Coumaric acid hexoside	Chlorogenic acid	Dicaffeoylquinic acid I	Dicaffeoylquinic acid II	Tricaffeoylquinic acid
Altamirano	3.8 ± 0.3^{d}	5.50 ± 0.5^{b}	3.37 ± 0.3^{a}	137.97 ± 12.8^{b}	20.76 ± 1.9^{c}	74.25 ± 5.2^{c}	42.11 ± 3.4^{de}
Cartagena	5.46 ± 0.5^{c}	4.50 ± 0.2^{c}	**3.71 ± 0.2a**	66.45 ± 4.6^{c}	12.12 ± 0.1^{e}	59.44 ± 4.6^{de}	39.2 ± 3.9^{ef}
Francisco	**1.77 ± 0.1e**	2.71 ± 0.2^{e}	**1.29 ± 0.1d**	73.44 ± 1.2^{c}	12.00 ± 0.9^{e}	**49.15 ± 2.6e**	**32.57 ± 3.4f**
Kilim	**8.21 ± 0.1a**	**7.05 ± 0.3a**	3.45 ± 0.1^{a}	182.83 ± 17.4^{a}	24.66 ± 2.4^{b}	**125.85 ± 1.4a**	58.99 ± 5.2^{c}
Placharosa	8.18 ± 0.6^{a}	3.64 ± 0.3^{d}	1.75 ± 0.2^{c}	**43.5 ± 3.8d**	**8.24 ± 0.7f**	53.72 ± 3.6^{e}	47.29 ± 1.9^{d}
Rincon	2.02 ± 0.1^{e}	**2.45 ± 0.1e**	2.84 ± 0.2^{b}	131.95 ± 11.2^{b}	16.06 ± 1.1^{d}	69.23 ± 5.3^{cd}	34.66 ± 3.2^{f}
Tumbisca	3.45 ± 0.3^{d}	6.50 ± 0.4^{a}	3.63 ± 0.3^{a}	**193.38 ± 8.9a**	**35.94 ± 3.1a**	120.81 ± 13.1^{ab}	72.28 ± 4.7^{b}
Villamaza	6.21 ± 0.5^{b}	5.42 ± 0.5^{b}	2.63 ± 0.1^{b}	73.75 ± 5.8^{c}	12.59 ± 1.1^{e}	112.95 ± 4.3^{b}	**106.64 ± 6.3a**
Moneymaker	7.12 ± 0.4	7.23 ± 0.4	7.1 ± 0.7	23.89 ± 1.9	4.46 ± 0.1	16.68 ± 1.1	15.56 ± 0.9
LOD	1.025	0.430	0.430	39.770	3.179	0.607	0.548
LOQ	3.105	1.302	1.302	120.516	9.634	1.840	1.662

[z]Values are the mean ± standard deviation of three replicates (50 fruit each) and are expressed in mg/kg on a fresh weight basis. The lowest and highest values of the accessions are in bold type. Different letters in a single column indicate significant differences between the accessions (Fisher, α = 0.05). LOD: Limit of detection (µg/mL); LOQ: Limit of quantification (µg/mL).

[z]Los valores son la media ± desviación estándar de tres réplicas (50 frutos cada una) y están expresados en mg/kg en peso fresco. Los valores más bajos y más altos de las accesiones están en negritas. Letras diferentes en la misma columna indican diferencias significativas entre las accesiones (Fisher, α = 0.05). LOD: Límite de detección (µg/mL); LOQ: Limite de cuantificación (µg/mL).

Table 3. Flavonoids content in the methanol extracts from the pericarp of *Solanum lycopersicum* var. *cerasiforme* accessions[z].

Tabla 3. Contenido de flavonoides en extractos metanólicos del pericarpio de accesiones de *Solanum lycopersicum* var. *cerasiforme*[z].

Accession	Rutin hexoside	Rutin pentoside	Rutin	Rutin *O*-hexoside-pentoside	Naringenin chalcone hexose I	Naringenin *O*-hexoside	Naringenin chalcone hexose II	Naringenin chalcone hexose III	Naringenin chalcone
Altamirano	5.34 ± 0.4^{b}	47.73 ± 4.6^{a}	132.17 ± 7.3^{b}	6.03 ± 0.2^{c}	6.13 ± 0.2^{c}	6.82 ± 0.6^{b}	5.26 ± 0.4^{b}	4.57 ± 0.3^{d}	6.54 ± 0.4^{c}
Cartagena	2.60 ± 0.3^{de}	35.31 ± 1.5^{c}	50.39 ± 3.8^{e}	5.54 ± 0.4^{a}	**10.15 ± 0.4a**	5.17 ± 0.4^{d}	3.43 ± 0.4^{d}	6.44 ± 0.5^{c}	2.93 ± 0.3^{d}
Francisco	**1.83 ± 0.2f**	**20.63 ± 1.7d**	61.13 ± 2.8^{de}	ND	**3.52 ± 0.3d**	**2.32 ± 0.2e**	**2.22 ± 0.1e**	7.43 ± 0.3^{c}	**0.94 ± 0.1d**
Kilim	**8.58 ± 0.6a**	53.24 ± 3.6^{a}	141.33 ± 12.9^{b}	7.8 ± 0.5^{a}	8.07 ± 0.4^{b}	6.04 ± 0.6^{c}	5.69 ± 0.5^{b}	15.76 ± 1.2^{a}	2.38 ± 0.1^{d}
Placharosa	2.14 ± 0.2^{ef}	36.46 ± 2.3^{c}	**36.87 ± 1.6f**	4.40 ± 1.6^{a}	6.07 ± 0.4^{c}	**7.81 ± 0.3^{a}**	3.77 ± 0.2^{cd}	4.92 ± 0.3^{d}	37.41 ± 2.0^{b}
Rincon	2.9 ± 0.2^{d}	33.67 ± 1.6^{c}	87.42 ± 6.9^{c}	**7.55 ± 4.9^{a}**	7.72 ± 0.6^{b}	7.78 ± 0.6^{a}	4.15 ± 0.4^{c}	8.69 ± 0.7^{b}	6.54 ± 0.4^{c}
Tumbisca	4.47 ± 0.3^{c}	**46.52 ± 3.9b**	**159.74 ± 9.0a**	ND	9.54 ± 0.4^{a}	NQ	**7.11 ± 0.4^{a}**	**15.90 ± 0.1^{a}**	2.82 ± 0.2^{d}
Villamaza	5.23 ± 0.3^{b}	34.09 ± 2.5^{c}	66.25 ± 6.3^{d}	5.09 ± 0.1^{a}	3.89 ± 0.2^{d}	4.48 ± 0.4^{d}	3.51 ± 0.3^{d}	**2.94 ± 0.2e**	**52.01 ± 4.7^{a}**
Moneymaker	1.28 ± 0.1	9.73 ± 1.0	16.79 ± 1.1	1.99 ± 0.1	0.86 ± 0.1	1.59 ± 0.1	1.66 ± 0.1	4.66 ± 0.3	ND
LOD	0.349	12.744	0.321	0.111	0.512	0.704	0.704	1.768	2.014
LOQ	1.057	38.617	0.974	0.337	1.553	2.133	2.133	5.357	6.104

[z]Values are the mean ± standard deviation of three replicates (50 fruit each) and are expressed in mg/kg on a fresh weight basis. The lowest and highest values of the accessions are in bold type. Different letters in a single column indicate significant differences between the accessions (Fisher, α = 0.05). LOD: Limit of detection (µg/mL); LOQ: Limit of quantification (µg/mL). ND: Not detected; NQ: Not Quantified.

[z]Los valores son la media ± desviación estándar de tres réplicas (50 frutos cada una) y están expresados en mg/kg en peso fresco. Los valores más bajos y más altos de las accesiones están en negritas. Letras diferentes en la misma columna indican diferencias significativas entre las accesiones (Fisher, α = 0.05). LOD: Límite de detección (µg/mL); LOQ: Limite de cuantificación (µg/mL). ND: No detectado; NQ: No cuantificado.

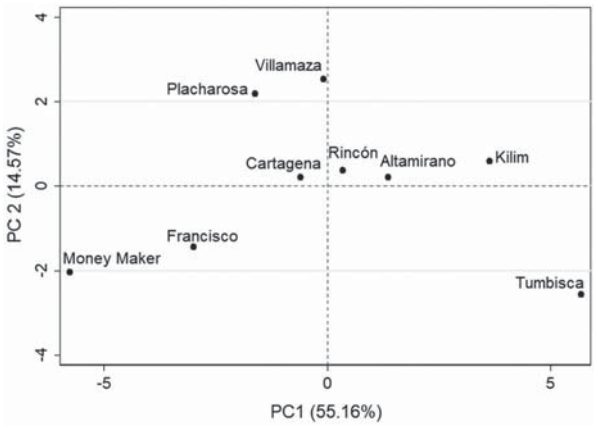

Figure 2. Principal component analysis of eight wild tomato (*Solanum lycopersicum* var. cerasiforme) accessions and the commercial variety Moneymaker using the content of phenolics and the antioxidant activity (ABTS, DPPH, FRAP).

Figura 2. Análisis de componentes principales de ocho accesiones de tomate silvestre (*Solanum lycopersicum* var. cerasiforme) y la variedad comercial Moneymaker usando el contenido de compuestos fenólicos y la actividad antioxidante (ABTS, DPPH, FRAP).

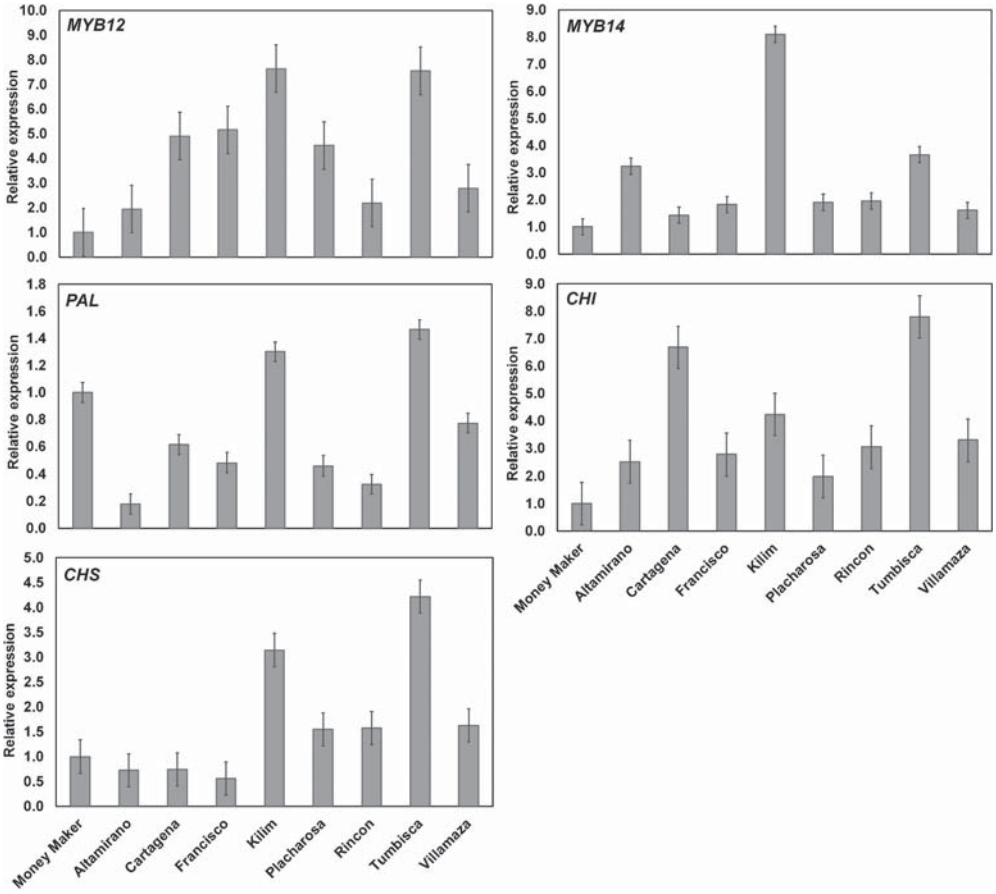

Figure 3. Relative expression of MYB transcription factors and target genes in the pericarp of *Solanum lycopersicum* var. *cerasiforme* accessions. The *UBI3* gene was used as control and the expression values are relative to that of the commercial tomato Moneymaker. Bars indicate the LSD ($\alpha = 0.05$). Means are significantly different when the bars do not horizontally overlap. *MYB12* and *MYB14*: Transcription factors; *PAL*: Phenylalanine ammonia-lyase; *CHS*: Chalcone synthase; *CHI*: Chalcone isomerase.

Figura 3. Expresión relativa de factores de transcripción MYB y genes diana en el pericarpio de accesiones de *Solanum lycopersicum* var. *cerasiforme*. Se usó el gen *UBI3* como control y los valores de expresión son relativos al de la variedad comercial de tomate Moneymaker. Las barras indican LSD ($\alpha = 0.05$). Las medias son significativamente diferentes cuando las barras no se traslapan horizontalmente. *MYB12* y *MYB14*: Factores de transcripción; *PAL*: Fenilalanina amonio liasa; *CHS*: Chalcona sintasa; *CHI*: Chalcona isomerasa.

Table 4. Antioxidant activity of phenolic standards evaluated at the concentration found in the methanol extract of Tumbisca and 50 µmol/L.

Tabla 4. Capacidad antioxidante de estándares de fenólicos evaluados a la concentración del extracto metanólico de Tumbisca y 50 µmol/L.

	ABTS [µmol/L TE]			DPPH [µmol/L TE]			FRAP [µmol/L TE]		
Compound	Extract[z]	50 µmol/L		Extract[z]	50 µmol/L		Extract[z]	50 µmol/L	
p-Coumaric acid (9.4 µmol/L)	7.1 ± 0.1	63.8 ± 1.1		17.4 ± 0.5	58.8 ± 4.3		22.7 ± 1.5	119.2 ± 10.6	
Chlorogenic acid (417.4 µmol/L)	584.0 ± 2.7	213.8 ± 10.6		89.0 ± 10.4	9.9 ± 0.5		1355.7 ± 67.4	118.2 ± 7.5	
Rutin (189.5 µmol/L)	543.1 ± 1.2	287.4 ± 8.2		426.8 ± 23.2	55.8 ± 3.6		666.3 ± 14.1	180.8 ± 10.2	
Naringenin (26.0 µmol/L)	107.9 ± 4.7	231.8 ± 17.2		29.8 ± 1.7	38.11 ± 2.1		19.2 ± 1.6	103.1 ± 1.4	
Mixture (50 µmol/L)	Observed	Expected	Interaction	Observed	Expected	Interaction	Observed	Expected	Interaction
Rutin-Chlorogenic acid	589.7 ± 27.3^{a}	501.3 ± 1.7^{b}	Synergistic	422.4 ± 2.6^{a}	65.8 ± 2.7^{b}	Synergistic	531.2 ± 49.9^{a}	298.9 ± 13.0^{b}	Synergistic
Rutin-*p*-Coumaric acid	255.2 ± 1.7^{b}	351.3 ± 6.4^{a}	Antagonistic	303.4 ± 2.3^{a}	114.6 ± 4.8^{b}	Synergistic	181.1 ± 12.6^{b}	299.9 ± 2.65^{a}	Antagonistic
Rutin-Naringenin	450.9 ± 30.9^{b}	519.3 ± 17.9^{a}	Antagonistic	355.7 ± 1.7^{a}	93.9 ± 4.0^{b}	Synergistic	187.3 ± 16.9^{b}	283.8 ± 10.8^{a}	Antagonistic
Chlorogenic-*p*-Coumaric acid	221.8 ± 13.6^{b}	277.7 ± 6.6^{a}	Antagonistic	311.9 ± 2.6^{a}	68.7 ± 2.8^{b}	Synergistic	201.3 ± 17.3^{b}	237.3 ± 8.9^{a}	Antagonistic
Clorogenic acid-Naringenin	235.9 ± 21.1^{b}	445.7 ± 4.7^{a}	Antagonistic	165.1 ± 3.2^{a}	48.02 ± 1.7^{b}	Synergistic	182.9 ± 18.4^{a}	221.3 ± 6.7^{a}	Additive
p-Coumaric acid-Naringenin	350.2 ± 3.7^{a}	295.7 ± 13.0^{b}	Synergistic	182.7 ± 1.3^{a}	96.87 ± 3.9^{b}	Synergistic	23.9 ± 3.40^{b}	222.2 ± 9.9^{a}	Antagonistic
Rutin-Chlorogenic-Coumaric	1005.9 ± 37.4^{a}	565.15 ± 1.8^{b}	Synergistic	251.6 ± 3.1^{a}	124.5 ± 4.8^{b}	Synergistic	307.9 ± 35.0^{b}	418.4 ± 2.9^{a}	Antagonistic
Rutin-Chlorogenic-Naringenin	457.1 ± 7.4^{b}	733.1 ± 10.5^{a}	Antagonistic	263.9 ± 3.2^{a}	103.9 ± 4.2^{b}	Synergistic	355.2 ± 10.4^{b}	402.1 ± 14.0^{a}	Antagonistic
Rutin-Coumaric-Naringenin	568.6 ± 17.8^{a}	583.1 ± 18.8^{a}	Additive	219.9 ± 2.9^{a}	152.7 ± 6.1^{b}	Synergistic	186.7 ± 14.3^{b}	402.9 ± 1.4^{a}	Antagonistic
Chlorogenic-Coumaric-Naringenin	498.2 ± 8.10^{a}	509.5 ± 5.5^{a}	Additive	229.6 ± 2.3^{a}	106.8 ± 3.9^{b}	Synergistic	323.2 ± 35.3^{a}	340.4 ± 8.9^{a}	Additive
Rutin-Chlorogenic-Coumaric-Naringenin	611.7 ± 1.3^{b}	796.9 ± 11.3^{a}	Antagonistic	279.4 ± 2.4^{a}	162.6 ± 6.2^{b}	Synergistic	432.7 ± 35.1^{b}	521.2 ± 4.3^{a}	Antagonistic

[z]Individual compounds evaluated at the concentration of the extract indicated in parenthesis. TE: Trolox equivalent. Different letters between observed and expected values in each method indicate significant differences ($P < 0.05$) according to the *t*-test.

[z]Compuestos individuales evaluados a la concentración del extracto indicado en paréntesis. TE: equivalente de Trolox. Letras diferentes entre valores observados y esperados en cada método indican diferencias significativas ($P < 0.05$) de acuerdo con la prueba *t*.

= 0.71; $p \leq 0.001$), *MYB14* (r = 0.90; $p \leq 0.001$) and *CHI* (r = 0.39; $p \leq 0.05$), suggesting that higher expression levels of *MYB12* and *MYB14* could be increasing the content of this compound as an intermediate for the synthesis of flavonoids.

6. Conclusions

The methanol extracts from the pericarp of *Solanum lycopersicum* var. *cerasiforme* accessions showed high antioxidant capacity mainly associated with caffeoylquinic acids and rutin. The phenolic content and antioxidant capacity of the accessions showed positive correlation with the expression levels of the transcription factors *MYB12* and *MYB14* and their target genes *PAL, CHS*, and *CHI*. In this regard, the accessions Tumbisca and Kilim showed the highest levels of gene expression and phenolics content, suggesting they can be used in breeding programs to produce functional tomatoes with high levels of phenylpropanoids derivatives and antioxidant capacity.

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