Increased Temperature Affects Tomato Fruit Physicochemical Traits at Harvest Depending on Fruit Developmental Stage and Genotype

Victoria A Delgado-Vargas, Oscar J Ayala-Garay, Ma. de Lourdes Arévalo-Galarza, Hélène Gautier

horticulturae

MDPI

Article

Increased Temperature Affects Tomato Fruit Physicochemical Traits at Harvest Depending on Fruit Developmental Stage and Genotype

Victoria A. Delgado-Vargas [1], Oscar J. Ayala-Garay [1], Ma. de Lourdes Arévalo-Galarza [1] and Hélène Gautier [2,*]

[1] Colegio de Postgraduados, Programa de Recursos Genéticos y Productividad, Carretera México-Texcoco km. 36.5, Texcoco 56230, Mexico
[2] INRAE, UR1115, Plantes et Systèmes de Culture Horticoles, Domaine St. Paul, Site Agroparc, 84914 Avignon, France
* Correspondence: helene.gautier@inrae.fr; Tel.: +33-(0)4-32-72-23-45

Abstract: In this study, we investigated how increasing temperature affects tomato fruit physicochemical traits and looked for genetic variability to help maintain fruit quality in the context of climate change. High temperature (HT: +3 °C) was applied at four fruit developmental stages, from anthesis and 15, 30 or 45 days after anthesis until ripening to three genotypes, a commercial cultivar (Money Maker, "MM") and two genotypes likely more tolerant to HT (Campeche 40 "C40", a landrace from a warm, humid region, and a hybrid Chapingo F1, "F1", resulting from crossbreeding landraces tolerant to high temperature). Increasing average diurnal temperature (from 27.0 to 29.9) reduced fruit firmness and size and affected fruit composition according to genotype. Sugar and acid contents were highly impacted in MM and C40 fruits, especially when HT was applied during the rapid fruit growth period. The application of HT at different fruit developmental stages revealed that HT could enhance acid accumulation and degradation (rate and/or duration), resulting in different effects on fruit acidity between genotypes. The F1 genotype appeared to be more adapted to HT, producing larger fruits with higher sugar, lower acid and increased vitamin C and calcium content. These results provide interesting directions for breeding programs that want to maintain future tomato fruit yields and quality.

Keywords: temperature; tomato quality; nutrients; phenolic compounds; carotenoids; minerals

Citation: Delgado-Vargas, V.A.; Ayala-Garay, O.J.; Arévalo-Galarza, M.d.L.; Gautier, H. Increased Temperature Affects Tomato Fruit Physicochemical Traits at Harvest Depending on Fruit Developmental Stage and Genotype. *Horticulturae* **2023**, *9*, 212. https://doi.org/10.3390/horticulturae9020212

Academic Editor: Qiaomei Wang

Received: 5 January 2023
Revised: 27 January 2023
Accepted: 2 February 2023
Published: 5 February 2023

1. Introduction

Global temperature increases are a challenge for agricultural production because they limit crop yields and quality [1]. The latest Intergovernmental Panel on Climate Change report [2] warns of an increase in global temperature of 1.5 °C in a few years, which would have huge impacts on plants' abiotic and biotic environment due to changes in temperature and rainfall regimes, consequently affecting plant development, production, quality, and yield. On a global scale, if we do not reduce greenhouse gas emissions, we could expect a +3 °C increase (compared to 1986–2005, RCP 8.5) in 2070 [3]. Agronomic species are susceptible to over-optimal temperatures affecting different physiological processes and modifying plant growth, development, and biochemical organ characteristics. With the observed climate change, it is thought that the optimal thermal threshold of plant growth will be exceeded, especially in tropical regions [4]. Multiple processes impairing fruit yield, including seed germination, plant growth and development, morphology, physiology, and biochemistry, will be drastically affected by high temperatures. For instance, pollen production and viability limit tomato plant growth at temperatures exceeding 35 °C [5]. Thus, if the fruit set is inhibited, despite parthenocarpic fruit development, tomato fruit production (fruit growth and quality) could be drastically affected in the future.

Once the best conditions in which to grow the plants are known [6,7], additional work will be required to identify accessions with improved heat tolerance. Different tomato

accessions have been evaluated to help select genes to be introduced into breeding programs focused on improving heat tolerance. Previous studies have assessed the effect of temperature on the number of flowers, fruits and fruit sets [8,9], primarily considering indicators of fruit quality instead of fruit composition (e.g., fruit color, pH or soluble sugar content estimate) [10]. However, less is known about the potential impact of heat stress on the tomato fruit's physicochemical traits. Hernández et al. [11] reported that vitamin C, phytoene, phytofluene, lycopene, γ-carotene, and violaxanthin concentrations were significantly attenuated when the temperature was increased to 32 °C during tomato fruit ripening. However, they did not observe increased concentrations when the temperature was increased during earlier fruit developmental stages, indicating specific temperature-sensitive metabolic steps may exist or that the plant may adapt its metabolism to high temperature (HT). Additionally, primary metabolic enzyme activities lead to the accumulation and/or degradation of sugars and acids depending on the temperature [12]. Such alterations may influence tomato composition at maturity, as in the case for the sugar/acid (SU/AC) ratio that defines the taste of the fruit.

According to FAO [13], one way to mitigate the adverse effects of HT on crop production and quality is through using plants' genetic resources. In the present study, we compared three genotypes to increase our knowledge of the possible deleterious effects of HT on tomato fruit cultivation. We applied increased temperature (+2.9 °C) during the fruit development stages to determine whether genotypes adapted to warmer climates, as evidenced by maintained growth and composition under HT conditions. Furthermore, the changes in fruit physicochemical traits and common or specific HT responses were monitored.

2. Materials and Methods

2.1. Plant Material and Location

In February 2020, seeds of three tomato genotypes (*Solanum lycopersicum* L.) were sown:

- Money Maker (MM), with indeterminate growth, taken as a tomato reference genotype [14], had an intermediate production compared to others when grown above 33 °C [15]; therefore, it was used as a control in our experiment. It is usually grown under a glasshouse or plastic tunnel, producing round-shape fruits.
- Campeche 40 (C40), a native variety originating from Campeche, a warm-humid region with indeterminate growth, is usually cultivated in an open field for local consumption, producing kidney-shaped fruits.
- ChapingoF1 (F1), an experimental hybrid whose parents are L52 and L47, a variety with indeterminate growth, known to be HT tolerant, is cultivated in a greenhouse producing saladette-type fruits.

The sowing was performed in 200-cavity polystyrene trays containing a substrate of peat moss-based Sunshine Mix #3 for 40 days inside a greenhouse located in Texcoco, Mexico (19°27′51″ N and 98°54′15″ W, at 2250 m.a.s.l.).

2.2. Crop Management

The seedlings were then transplanted into 25-L black polyethylene bags containing natural pozzolan. Tomato plants were managed according to conventional commercial practices. Plant density was 3.5 plants m^{-2}. The nutrient solution was applied by drip irrigation with Steiner's [16] solution with an electrical conductivity of 3.5 dSm^{-1} and a pH of 5.5 to 6.0. Nine irrigations were applied at one hour intervals during the day, and their volume was gradually increased to maintain drainage. Throughout the experiment, successive floral clusters were thinned to obtain only six fruits in each cluster.

2.3. Experimental Design and Temperature Treatments

Two tunnel-type greenhouses with overhead ventilation and polyethylene covers were used, one equipped with fans to generate the temperature control condition (CT), and the other with an electric heating system to generate the higher temperature condition (HT)

and produce a difference in the daytime (7:00 to 19:00 h) temperature (Figure 1). The air temperature was recorded every 10 min inside the greenhouses with Hobo® sensors (Onset Computer Corporation).

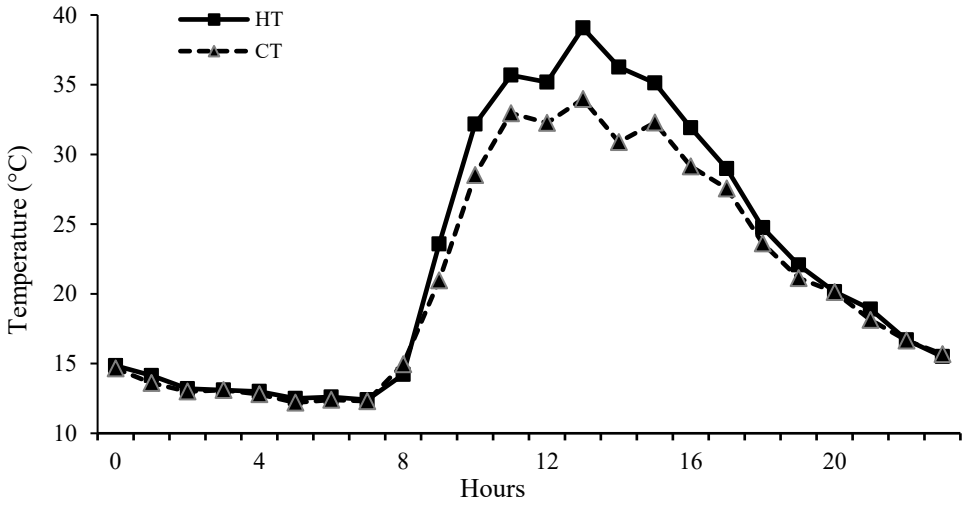

Figure 1. A typical daily evolution of temperature (recorded on 12 May 2020) within the two greenhouse compartments depending on the two treatments applied: control treatment (CT); higher temperature (HT).

A factorial experiment of 15 treatments was established and was made up of two factors: increased temperature (five conditions) and tomato genotype (three genotypes), which was analyzed in a completely randomized experimental design with 10 repetitions (plants). Forty-five days after sowing, 60 plants of each genotype were transplanted in the CT control condition and 10 plants of each genotype in the HT condition. These 10 plants per genotype were used to maintain a density of plantation of 3.5 plants m^{-2} in the HT greenhouse and were not used in this experiment. The plants that kept growing under CT temperature control were monitored daily until the opening of the second flower of their 4^{th} floral cluster. Once this phenomenon occurred, plants were tagged with labels, and the treatments of the plants under high temperature conditions began as follows: plants were transferred from the CT to the HT greenhouse during the growth of the 4^{th} cluster at different stages of development, expressed as days after anthesis (DAA). Five different treatments were considered:

- T1: 10 plants with the 4th floral cluster at anthesis were transferred from the control growing condition (CT) to the greenhouse at a higher temperature (HT).
- T2: 10 plants with the 4th floral cluster at 15 DAA were transferred from CT to HT.
- T3: 10 plants with the 4th floral cluster at 30 DAA were transferred from CT to HT.
- T4: 10 plants with the 4th floral cluster at 45 DAA were transferred from CT to HT.
- CT, control treatment: plants remained growing in the CT.

The HT plants were randomly distributed and settled alongside other plants growing to maintain a constant plant density.

There was no change in night temperature between the CT and HT treatments (Table 1). During the experiment, the average night temperature remained within the optimal values. In contrast, the average diurnal temperature of the HT treatment was 2.9 °C higher than CT, and the maximal temperature of HT was 3.4 °C higher than the CT, reaching 38.6 °C. Consequently, the average difference between day and night temperatures was 11.9 °C for the CT and 14.6 °C for HT treatments.

Table 1. Air temperature recorded during fruit development according to the treatments (conditions). Data are average value ± standard deviation.

Temperature °C	CT	HT
Maximal	35.2 ± 3.1	38.6 ± 3.1
Minimal	19.1 ± 2.2	19.2 ± 2.0
Average diurnal	27.0 ± 2.6	29.9 ± 2.5
Average nocturnal	15.1 ± 2.1	15.3 ± 2.2

2.4. Fruit Traits

From 5 to 16 June 2020, fruits from the 4th truss of plants grown on the control treatment were harvested at three ripening stages (green turning pink, pink, and red mature) to characterize fruit composition changes during ripening and differences between genotypes. During the same period, fruits from the 4th truss of the plants transferred from the CT to HT greenhouse reached the red ripe stage and were harvested to analyze the effect of temperature on fruit traits at maturity. For each genotype and treatment, 10 fruits at the red ripe stage were harvested (from the 10 corresponding plants). They were randomly pooled to constitute three replicates per genotype and treatment of 3–4 fruits per replicate for biochemical analyses.

The physical characteristics of the fruits were measured individually on five fruits per treatment. Fruit size was determined by measuring the polar and equatorial diameter of the fruits with a digital vernier (Truper), with values expressed in mm. Fruit weight was measured on a digital scale (Esnova SE-2000), with values expressed in g.

The external fruit color was measured with a colorimeter (Shenzhen NR20XE), recording the luminosity values (L*) and the coordinates *a* and *b*, which are used to calculate chromaticity (*Cr**) and hue angle (*Hue*) [17].

The fruit firmness was determined with a texturometer (Wagner Instruments Force Five FDV-30) with a 7 mm diameter punch. The force to penetrate the fruit was expressed in newtons (N). To estimate the dry matter weight, two opposite slices of fruit were sampled, weighed, and dried at 70 °C for 72 h in a conventional oven (Thelco 3480). The dry matter content was then calculated as the dry and fresh weight ratio.

The content of total soluble solids (TSS) was measured on one slice of pericarp with a refractometer (Atago Palette PR-32). For titratable acidity (TA), the readings were performed on 5 g of fruit juice placed in an Erlenmeyer flask with three drops of phenolphthalein, titrated with 0.1 N NaOH. The TA, expressed as meq of citric acid per g of tomato juice, was obtained with the Formula (1):

$$\mathrm{TA} = \frac{\mathrm{V\ NaOH} \times \mathrm{N\ NaOH}}{5} \quad (1)$$

where V is the volume (mL), and N is the normality of NaOH.

2.5. Biochemical Analyses

The three batches of 3–4 fruits of each treatment were dissected. The jelly was removed, and the placenta and seeds were extracted. The pericarp sample was homogenized, frozen in liquid nitrogen (N_2), and immediately stored in a freezer (Cryonext) at −80 °C. The frozen samples were ground in liquid N_2, freeze-dried for subsequent biochemical analysis and sent to INRAE-PACA, in Avignon.

An aliquot of 10 mg of ground freeze-dried tomato powder was extracted and separated from a methanol–chloroform–water solution to determine soluble sugars, starch, and organic acids, following the methodology described by Gomez et al. [18,19]. The soluble sugars and organic assays were estimated using HPLC. Soluble sugars were analyzed with a Sugar-Pack I pre column and column (Waters) and an EDTA solution (50 mg/L) as mobile phase. Organic acids were analyzed with an RSpak KC g precolumn and an RSpak KC-811 column (Shodex), utilizing an acid mobile phase (0.1% H_3PO_4). Starch was hydrolyzed into

glucose molecules, and the determination of the NADH formed during the reaction was measured with a microplate reader (Multiskan Ascent V1.24) at 340 nm, which corresponds to NADH absorption.

The ascorbic acid assay is based on reducing ferric ions to ferrous ions and on the measurement of absorbance of the dipyridyl-Fe^{2+} complex at 550 nm, following the method reported by Stevens et al. [20], with an additional measurement to subtract away other reducing compounds. Three aliquots were assessed per sample to determine the reduced ascorbate and the total ascorbate after adding DL-dithiothreitol to reduce the oxidized form of vitamin C, or after adding ascorbate oxidase to estimate other reducing compounds that could bias the assay.

The carotenoids were extracted according to Sérino et al. [21]. The assay was performed using HPLC with a DAD UV–vis detector (Thermo Finnigan Surveyor PDA Detector Plus, Riviera beach, USA) with four working wavelengths: 474 nm for lycopene, 454 nm for β-carotene, 286 nm for phytoene, and 448 nm for lutein.

The polyphenols were extracted from cold-dried fruit powder using a solution of methanol/water (70:30 v/v, as previously described) [14]. The assay was performed using HPLC with a DAD UV-vis detector (Thermo Finnigan Surveyor PDA Detector Plus, Riviera Beach, USA). The spectral data for all the peaks were accumulated in the range of 200–800 nm, and the chromatograms were recorded at 330 and 356 nm, with specific retention times for rutin, naringenin chalcone and chlorogenic acid.

The minerals were determined by an X-ray spectrometer (Bruker S1 Titan portable XRF spectrometer) from the freeze-dried powder. The sample was bombarded with photons emitted from an X-ray tube. Thus, the ionized atoms of the material were in an unstable state. As the atoms move towards a more stable state, they release energy as a characteristic photon for each atom. The photons detected by the counter are used to identify the atom according to its energy.

2.6. Statistical Analyses

Statistical differences among assayed variables were determined by analyses of variance, considering the experiment as a complete randomized design and the development stage, the genotypes, and their interactions as explanatory factors. The means were compared using Tukey's test ($\alpha = 0.05$ unless specified). The statistical analyses were performed with XLSTAT (Addinsoft Inc., New York, NY, USA).

3. Results

3.1. Diversity of Tomato Fruit Physicochemical Traits Linked to Genotypes and Ripening Stage

The three genotypes evaluated in this experiment produced fruits with significantly different quality traits at maturity (Table 2). From a visual point of view, the tomato fruits of F1 have the largest size and weight, followed by the MM fruits, and the smallest fruits were obtained from C40. The fruits' equatorial diameters were similar among the genotypes; thus, differences in fruit size were due to the fruits' polar diameters. The smaller fruit size of C40 also corresponds to the lower time taken to reach the red ripe stage (51.2 DAA) compared to MM (60.3 DAA) and F1 (70.7 DAA). This result indicates that the tomato fruit size was positively related to the duration of fruit growth (Table 3).

Table 2. Physical characterization of tomato fruits of genotypes C40, MM and F1 during ripening.

	Ripening stage	PD (mm)	ED (mm)	FW (g)	DM (%)	F (N)	TSS °Brix	TA meq H^+	Color				
									L	a	b	Cr*	°Hue
RS		0.18	0.78	0.60	0.98	**<0.001**	**<0.01**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	0.98	**<0.001**
G		**<0.001**	0.76	**<0.001**	**<0.001**	**0.017**	0.16	**<0.001**	**<0.001**	**<0.001**	**0.001**	**0.02**	0.15
RS*G		0.51	0.93	0.96	1.00	0.21	**<0.01**	**<0.001**	**<0.001**	**<0.001**	**<0.01**	0.22	**<0.001**
C40	Green	36.8	64.0	85.7	7.15	2.20	3.94 c	10.65 ab	88.25 a	−19.11 e	42.71 ab	47.09	104.08 a
	Pink	38.3	62.3	89.5	7.15	0.59	5.56 ab	12.86 a	60.73 bc	27.85 b	23.26 ef	40.01	38.97 c
	RM	39.7	63.8	103.2	6.96	0.38	6.46 a	11.09 ab	54.52 bc	35.82 ab	18.06 f	40.54	26.49 c

Table 2. *Cont.*

	Ripening stage	PD (mm)	ED (mm)	FW (g)	DM (%)	F (N)	TSS °Brix	TA meq H^+	Color				
									L	a	b	Cr*	°Hue
MM	Green	56.5	63.2	129.2	6.63	2.52	4.84 bc	11.35 ab	64.38 b	0.09 d	43.79 a	49.45	90.37 a
	Pink	51.0	60.5	115.7	6.65	0.59	4.74 bc	7.38 c	54.5 bc	40.30 a	29.56 de	49.99	36.31 c
	RM	54.8	61.6	123.7	6.64	0.28	5.42 ab	10.65 ab	56.66 bc	37.04 ab	31.23 de	48.52	40.24 c
F1	Green	77.1	61.9	180.6	8.01	2.33	4.86 bc	9.48 bc	60.04 bc	15.47 c	41.28 ab	44.71	68.29 b
	Pink	73.7	62.9	167.9	8.00	0.92	4.80 bc	5.14 d	54.63 bc	40.83 a	31.77 cde	51.79	38.00 c
	RM	76.8	66.0	188.5	8.01	0.93	4.78 bc	7.27 c	51.47 c	36.96 ab	33.14 bc	51.42	44.05 c
C40		38.2 c		92.8 b	7.09 a	1.05 b						42.6	
MM		50.7 b		122.9 b	6.64 b	1.13 ab						49.3	
F1		75.9 a		179.0 a	8.01 a	1.37 a						49.3	
	Green					2.35 a							
	Pink					0.70 b							
	RM					0.53 b							

PD = polar diameter; ED = equatorial diameter; FW = fruit weight; DM = dry matter content; F = firmness; TSS = content of total soluble solids; TA = titratable acidity; (L) = brightness; a = color coordinate varying from green to red color; b = color coordinate varying from blue to yellow; Cr* = Tonus Chroma; °Hue = hue angle; RS = ripening stage; G = genotype; RS*G = interaction between ripening stage and genotype. Different letters in the same column indicate significant differences between means according to Tukey's test ($p = 0.05$). Significant differences are indicated in bold. Values are expressed as the means of at least five measurements.

Table 3. Changes in the physical fruit characteristics of C40, MM and F1 tomato genotypes during fruit development at HT.

G	TT	Days to harvest	PD (mm)	ED (mm)	FW (g)	DM (%)	F (N)	TSS °Brix	TA meq H^+	Color				
										L	a	b	Cr*	°Hue
Statistics														
T		**<0.001**	**<0.001**	**0.047**	**0.01**	0.86	**<0.01**	**<0.01**	**<0.01**	**0.012**	0.53	0.41	0.72	**<0.01**
G		**<0.001**	**<0.001**	**<0.01**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	0.20	**<0.01**	**<0.001**	**<0.001**	**<0.001**
T*G		**<0.001**	0.10	0.05	0.23	0.95	**0.03**	0.37	**<0.001**	**0.03**	0.647	0.94	0.97	**0.04**
C40	CT	51.2 d	39.7	63.8	103.2	6.96	0.38 ef	6.46	11.09 ab	54.52 ab	35.82	18.06	40.54	26.49 d
	T1	43.4 e	38.5	67.1	100.4	6.77	0.20 f	5.86	10.76 ab	54.12 ab	34.23	17.97	37.95	26.97 d
	T2	52.4 d	37.1	69.3	107.0	6.34	0.27 ef	4.74	10.76 ab	54.11 ab	35.29	18.15	39.71	27.20 d
	T3	40.4 e	36.2	63.5	80.4	7.22	0.25 f	5.88	9.44 bcd	54.42 ab	34.55	17.52	38.79	27.10 d
	T4	40.6 e	35.7	61.3	86.9	7.15	0.42 def	6.24	12.38 a	55.44 ab	37.51	18.7	41.48	26.81 d
MM	CT	60.3 c	54.8	61.6	123.7	6.64	0.28 ef	5.42	10.65 ab	56.66 b	37.04	31.23	48.51	40.24 abc
	T1	63.6 b	56.6	61.3	130.4	6.64	0.58 bcde	5.04	9.99 ab	54.66 ab	37.22	30.05	47.88	39.02 abc
	T2	64.4 b	50.7	59.9	106.4	6.64	0.33 ef	4.18	6.72 ef	54.73 ab	38.22	31.14	49.34	39.32 abc
	T3	60.5 c	49.3	53.7	82.5	6.75	0.57 cdef	5.52	9.15 bcd	55.13 ab	40.29	30.46	50.53	37.00 bc
	T4	58.1 c	56.0	62.3	126.7	6.65	0.50 def	5.12	8.49 bcd	56.68 b	38.41	31.85	50.01	39.64 abc
F1	CT	70.7 a	76.8	66.0	188.5	8.01	0.93 ab	4.78	7.27 cde	51.47 ab	36.96	33.14	51.42	44.05 a
	T1	68.6 a	79.2	65.1	198.8	8.29	0.88 ab	4.76	4.59 f	48.84 a	40.12	35.45	50.79	41.54 abc
	T2	70.9 a	76.6	60.9	152.2	8.01	0.87 abcd	4.58	6.06 ef	56.44 b	37.72	34.2	50.99	42.55 abc
	T3	71.3 a	68.2	58.9	152.5	8.01	0.68 bcd	5.80	6.06 ef	56.6 b	41.16	33.07	52.86	34.97 cd
	T4	68.6 a	82.4	69.7	202.6	7.99	1.13 a	4.46	5.8 f	57.18 b	38.21	36.72	51.19	44.07 a
C40			37.4 c	64.5 a	95.6 b	6.89 b		5.84 a			35.48 b	18.08 c	39.70 b	
MM			53.5 b	64.1 a	113.9 b	6.66 b		5.06 b			38.27 a	30.95 b	49.26 a	
F1			76.6 a	59.7 b	178.9 a	8.06 a		4.88 b			38.83 a	34.52 a	51.60 a	
	CT		57.1 a	63.8	138.5 ab			5.73 a						
	T1		58.1 a	64.5	143.2 a			5.22 ab						
	T2		54.8 ab	63.4	121.9 ab			4.50 b						
	T3		51.2 b	58.7	105.2 b			5.73 a						
	T4		58.0 a	64.4	138.2 ab			5.27 ab						

G = genotype; TT = temperature treatment: CT = control treatment; T1 = plants transferred to HT at anthesis, T2 = plants transferred to HT 15 DAA; T3 = plants transferred to HT 30 DAA; T4 = plant transferred to HT 45 DAA; For other abbreviations, please refer to the caption of Table 2. Different letters in the same column indicate significant differences between means according to Tukey's test ($p = 0.05$). Values are expressed as the means (n = 10). Bold indicates a significant difference.

There was no change in the fruits' polar or equatorial diameter or fruit fresh weight during ripening (Table 2), indicating that the fruit stopped growing. In contrast, the Brix level significantly increased in C40 fruits during ripening (Table 2). A similar tendency was observed in MM fruits but did not change in F1 fruits.

Fruit firmness was similar between genotypes, decreasing during ripening, mainly between the green and pink developmental stages (Table 2).

Fruit luminosity decreased from the green to pink stage, especially for C40 fruits. The "a" coordinate increased, indicating a change from green to red, while the "b" coordinate decreased, which is characteristic of bluer and less yellow fruits. Consequently, the hue angle decreased from the green to pink stage, whereas the chroma value was unchanged.

At maturity, F1 fruits had a lower Brix level (4.78) compared to C40 fruit (6.46), whereas the value for MM fruits was intermediate (5.42). Interestingly, the Brix level was not a good indicator of the fruit dry matter (DM) content at maturity. The FI fruits had the highest DM content (8.01%) compared to C40 and MM (6.96 and 6.64%, respectively; Table 2, $p < 0.001$), whereas the C40 and MM fruits had higher Brix levels. This result is related to C40 and MM fruits having higher titratable acidity than those from F1 (11.09, 10.65 and 7.27, respectively).

3.2. Effect of Increased Temperature on Physical Fruits Characteristics and Growth

As shown in Table 3, the variation in fruit color was less affected by the HT treatment than by the genotype (Table 3). There was only a slight difference in T1 luminance and the T3 hue angle of F1 fruits, and a slight difference in firmness between T3 and T4 fruits in F1.

Whatever the genotype, increasing the temperature during fruit development had a similar effect on the fruit fresh weight, polar growth, and fruit Brix content. When the increased temperature occurred from 30 DAA until the RR stage (T3), fruit fresh weight was reduced, primarily due to reduced fruit polar growth. In contrast, there were significant interactions between genotype and treatment on fruit firmness and titratable acidity (TA). TA was reduced in F1 fruit when the temperature was increased at anthesis (T1) or during the later stage of fruit ripening (T4). In MM, the treatment with increased temperature from 30 DAA until ripening was the only one that significantly reduced fruit TA.

HT increased the time to reach the RR stage in MM fruits (from 60.3 DAA for the control to 63.6 DAA for T1 fruits or 64.4 DAA for T2 fruits). It did not affect F1 fruits; regardless of when the HT was applied, their developmental duration remained similar (between 68.5 and 71 DAA to reach the red ripe (RR) stage). Additionally, C40 fruits displayed an opposite response to temperature, in which increasing temperature from anthesis or 30 DAA (T3 or T4) reduced the time taken to reach the RR stage, from 51.2 DAA for the control to 43.4, 40.4 and 40.6 for T1, T3 or T4 fruits, respectively. It is interesting to note that the HT treatments did not significantly modify the dry matter content.

3.3. Changes in Sugar and Acid Contents Depending on Genotype, Ripening Stage, and Temperature

F1 fruits have the highest sugar values due to a higher content of fructose and glucose, the main sugars accumulating in tomatoes besides sucrose (Table 4, see data on RM fruits). C40 fruits have the lowest sugar levels due to lower glucose and fructose content, despite higher sucrose content. MM fruits have an intermediate sugar content that is significantly different from C40 and F1.

Irrespective of the genotype, citric acid is the main acid that accumulates in tomato fruits, compared to malic acid (Table 4), with MM fruits containing the highest citric acid content, followed by F1 and C40. The highest and lowest malic acid concentrations were detected in the C40 and F1 fruits, respectively.

It was determined that C40 fruits (with lower sugar content) continue to hydrolyze starch and accumulate sugars during ripening. In contrast, the sugar content of F1 fruits (which have a higher glucose and fructose content) hardly increases during ripening (Table 4). Green MM fruits contain a small amount of starch hydrolyzed during ripening, likely contributing to the slight increase in sugar accumulation in RM fruits. Simultaneously, the citric and malic acid content decreases for all three genotypes. Thus, while glucose and fructose content increase and citric and malic acid content decrease, the SU/AC ratio increases during ripening, which is a good indicator of improved fruit taste upon ripening. Interestingly, the SU/AC ratio varied between genotypes. At the beginning of ripening, F1 fruits had the highest ratio, and then at the RR stage, C40 and F1 had higher SU/AC ratios than MM, indicating a higher quality fruit.

As shown in Table 5, the effects of HT depend on the fruit's developmental stage. These differences are probably related to the kinetics of metabolite accumulation during fruit development. In addition, the significant G*TT interactions (Table 5) indicate that these genotypes do not respond similarly to increased temperature.

Table 4. Changes in sugars and acids content during fruit ripening of three tomato genotypes (C40, MM and F1). Data are expressed per 100 g of dry matter (DM).

		SU (g/100 g DM)	Sta (g/100 g DM)	GLU (g/100 g DM)	FRU (g/100 g DM)	CA (g/100 g DM)	MA (g/100 g DM)	SU/AC
Statistics								
	G	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
	RS	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
	G*RS	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
C40	Green	0.803 c	4.95 c	13.06 a	14.72 a	5.40 c	4.32 h	2.94 a
	Pink	1.057 c	7.15 d	14.90 b	16.36 b	4.42 a	3.26 f	4.21 c
	RM	0.430 b	1.41 b	18.09 cd	21.49 ef	4.28 a	1.45 d	6.98 g
MM	Green	0.263 ab	1.13 b	17.00 c	17.43 bc	6.33 e	3.78 g	3.43 b
	Pink	0.257 ab	0.33 a	17.58 cd	18.32 cd	6.21 de	1.78 e	4.52 d
	RM	0.245 ab	0.31 a	18.63 d	19.20 d	5.83 d	1.89 e	4.94 e
F1	Green	0.253 ab	0.46 a	21.56 f	22.09 ef	6.23 e	1.03 c	6.05 f
	Pink	0.100 a	0.46 a	20.14 e	21.30 e	4.85 b	0.65 b	7.55 h
	RM	0.150 a	0.45 a	21.67 f	22.55 f	6.05 de	0.37 a	6.89 g

G = genotype; RS = ripening stage; SU = sucrose; Sta = starch; GLU = glucose; FRU = fructose; CA = citric acid; MA = malic acid; SU/AC = sugars/acids ratio; RM = red mature stage. Different letters in the same column indicate significant differences between means according to Tukey's test ($p = 0.05$). Bold font indicates a significant difference.

Table 5. Changes in sugars and acids content during fruit development at HT of tomato genotypes (C40, MM and F1). Data are expressed per 100g of dry matter (DM).

		SU (g/100 g DM)	GLU (g/100 g DM)	FRU (g/100 g DM)	CA (g/100 g DM)	MA (g/100 g DM)	SU/AC
Statistics							
	G	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
	RS	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
	G*RS	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
C40	CT	0.430 b	18.09 c	21.49 c	4.28 a	1.45 a	6.98 e
	T1	0.407 b	17.28 bc	21.19 c	6.14 d	1.95 b	4.81 b
	T2	0.317 a	15.45 a	18.72 a	5.47 c	2.73 c	4.21 a
	T3	0.313 a	16.46 b	21.51 c	5.15 b	1.59 a	5.68 d
	T4	0.270 a	17.48 c	20.03 b	5.26 bc	1.83 b	5.33 c
MM	CT	0.245 c	18.63 b	19.20 a	5.83 a	1.89 a	4.94 d
	T1	0.243 c	17.51 ab	18.81 a	5.75 a	2.04 a	4.69 cd
	T2	0.190 b	17.28 a	19.39 a	6.66 c	2.99 c	3.82 a
	T3	0.150 a	17.75 ab	18.35 a	6.14 ab	1.86 a	4.50 bc
	T4	0.263 c	18.55 b	19.40 a	6.42 bc	2.37 b	4.35 b
F1	CT	0.150 a	21.67 a	22.55 a	6.05 a	0.37 a	6.89 b
	T1	0.150 a	20.67 a	21.62 a	5.85 a	0.62 c	6.55 a
	T2	0.210 bc	20.33 a	21.19 a	5.70 a	0.54 b	6.68 a
	T3	0.250 cd	21.17 a	21.23 a	5.73 a	0.38 a	6.97 b
	T4	0.150 a	20.58 a	21.08 a	5.74 a	0.71 d	6.48 a

G = genotype; TT = temperature treatment; SU = sucrose; GLU = glucose; FRU = fructose; CA = citric acid; MA = malic acid; SU/AC = sugars/acids ratio; CT = control treatment; T1 = plants transferred to HT in anthesis, T2 = plants transferred to HT 15 DAA; T3 = plants transferred to HT 30 DAA; T4 = plant transferred to HT 45 DAA. Different letters in the same column indicate significant differences between means according to Tukey's test ($p = 0.05$). Bold font indicates a significant difference.

It was found that the HT treatment tends to reduce the sugar content of the tomato. For example, the glucose content of C40 fruits increased up to 15% when the HT was applied during T2 (i.e., 15 DAA) and 9% during T3 (i.e., 30 DAA). Moderate increases of around 6–7% were observed in MM and F1 fruits subjected to HT during T2 or T3. However, this result was not significant for F1. When HT is applied during the 15 days following flower

anthesis, the sugar content of the tomato fruit is not affected, but if it is applied later during rapid fruit growth (i.e., 15 to 45 DAA), which usually corresponds to the period of rapid accumulation of sugars, it reduces the fruit sugar content (Table 5).

Malic acid systematically increases with elevated temperature regardless of genotype. An 88% accumulation was observed when HT was applied between 15 and 30 DAA for MM fruits. Moreover, malic acid content increased by 58% in C40 fruits subjected to HT during T2. The F1 fruits had the lowest malic acid content but still responded to the elevated temperature with an increase of 66%, 46% and 90% when HT was applied during T1, T2 and T4, respectively. It is worth noting that the smallest increase in malic acid content occurs when HT is applied from 30 to 45 DAA (Table 5).

Thus, HT significantly decreases the SU/AC ratio of the fruits, reducing taste quality. Interestingly, there are strong divergences between genotypes: C40 is the most affected, with a decrease of 31%, 40%, 19% and 24% when HT is applied during (T1, T2, T3, or T4, respectively). MM fruits also show a reduction in SU/AC ratio of 23%, 8%, and 12% during (T2, T3 and T4). In contrast, F1 fruits are less affected, with 5%, 3% and 6% reductions during T1, T2 and T4, respectively. Under controlled conditions, F1 and C40 fruits have an almost similar SU/AC ratio (6.98 and 6.90, respectively), which is significantly higher than that of C40 fruits (4.94). Under HT, F1 fruits almost retain their values, indicating that their taste quality is less affected (Table 5).

3.4. Genetic and Environmental Factors Affecting the Content of Antioxidants and Minerals as Indicators of the Nutritional Quality of Fruit

Whatever the genotype, the same trends were observed during ripening. Few compounds decrease during ripening (e.g., lutein, chlorogenic acid) while many increase (e.g., lycopene, beta-carotene, phytoene, caffeic acid glucoside (cag), cryptochlorogenic acid (cry), and others). Similarly, vitamin C accumulates during ripening, mainly due to the accumulation of the reduced form (Table 6). The mineral content does not change much during ripening, but K and Cl increased, while Ca, Fe and Cu decreased, with slight differences between genotypes, with higher K, Cl and Ca contents in MM fruits, P in C40 fruits and Cu and Zn in F1 fruits (Table 7).

Nevertheless, at maturity, the antioxidant composition of tomato fruit is very different between genotypes. The MM red fruits contained high levels of carotenoids (lutein +210%, lycopene +274%, β-carotene +158%, phytoene +382%) compared to F1 fruits, which had the lowest carotenoid content. The C40 fruits also contained high carotenoid values, with higher phytoene and lower β-carotene content than MM. Vitamin C content was lower in fruits from MM (−17%) and C40 (−27%) compared to F1. In addition, the content in the active form of vitamin C (reduced form) is lower in MM (−26%) and C40 (−48%) fruits compared to F1 fruits (Table 6). In general, the MM and C40 fruits contained more phenolic compounds compared to F1 fruits, but it was determined that the composition was genotype specific. For example, C40 lacks chalcone naringenin.

Lycopene content increased by 66% for C40 and 80% for F1 fruits when HT was applied immediately after the anthesis. However, this response was not observed in MM fruits. Additionally, lutein, β-carotene and phytoene also increased in C40 fruits (+302%, +39% and +50%, respectively), lutein and phytoene in F1 fruits (+71% and +86%, respectively) and lutein and phytoene in MM fruits (13% and 29%, respectively). When the HT was applied during the early (T1) or later (T3 or T4) phases of fruit development, we observed an increase in carotenoid content.

On the other hand, when the high temperature occurs between 15 and 30 DAA, the lycopene content becomes attenuated (−28% in C40, −51% in MM, and −19% in F1 fruits). In this sense, HT has different effects depending on the fruits' developmental stage.

The effect of HT on vitamin C depends on both the genotype and fruit developmental stage. The vitamin C content of F1 fruits was systematically reduced by HT, whereas it increased for C40 and MM fruits when it occurred either within the 15 days after anthesis or during T3 or T4 (Table 8).

Table 6. Changes in sugars and acids content during fruit ripening of three tomato genotypes (C40, MM and F1).

		Lu	Ly	Bc	Phy	t-Vc	r-Vc	rV/tV
Statistics								
	G	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
	RS	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
	G*RS	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
C40	Green	1.191 bc	25.29 ab	8.27 a	15.58 a	1145 b	416 b	0.366 b
	Pink	2.735 e	49.14 abc	11.45 ab	35.78 c	743 a	125 a	0.169 a
	RM	0.517 ab	330.16 d	21.26 c	108.69 e	1884 d	1134 c	0.602 c
MM	Green	2.535 e	12.36 a	8.70 a	5.88 a	1830 d	1139 c	0.623 c
	Pink	1.599 c	290.08 d	18.71 c	88.41 d	1843 d	1369 e	0.742 de
	RM	1.783 cd	338.46 d	35.51 d	88.08 d	2120 e	1614 f	0.762 e
F1	Green	2.376 de	36.69 abc	11.56 ab	9.87 a	1789 d	1277 d	0.714 d
	Pink	0.346 a	103.11 c	8.12 a	32.90 bc	1460 c	1133 c	0.775 e
	RM	0.573 ab	90.57 bc	13.79 b	18.27 ab	2566 f	2189 g	0.853 f
		Cag	**Cry**	**Chl**	**Ru**	**unk 1**	**NC**	
Statistics								
	G	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	
	RS	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	
	G*RS	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	
C40	Green	155.3 c	43.4 b	375.5 f	51.4 de	993.9 e	0.0 a	
	Pink	111.5 a	74.4 c	466.4 g	67.0 f	959.4 d	0.0 a	
	RM	239.7 d	137.5 e	311.2 d	56.5 ef	1501.2 g	0.0 a	
MM	Green	247.2 d	30.9 a	619.5 h	52.5 de	654.7 c	46.7 b	
	Pink	394.8 f	69.4 c	217.0 c	35.5 c	1109.3 f	39.0 b	
	RM	339.9 e	94.4 d	354.6 e	51.2 de	972.7 de	54.8 b	
F1	Green	122.5 ab	23.2 a	314.9 d	23.3 b	271.3 a	129.5 c	
	Pink	133.2 b	25.0 a	39.2 a	2.5 a	316.1 b	42.5 b	
	RM	244.1 d	46.6 b	124.2 b	42.0 cd	288.5 ab	47.6 b	

Data are expressed as mg/kg DM (except the ratio rV/tV, without unit). G = genotype; RS = ripening stage; Lu = lutein; Ly = lycopene; Bc = beta-carotene; Phy = phytoene; t-Vc: total vitamin C; r-Vc: reduced vitamin C; rV/tV = ratio between reduced and total vitamin C; Cag = caffeic acid glucoside; Cry = cryptochlorogenic acid; Chl = chlorogenic acid; Ru = rutin; unk1 = unknown phenolic compounds; NC = naringenin chalcone. Bold font indicates a significant difference. Different letters in the same column indicate significant differences between means according to Tukey's test ($p = 0.05$).

Table 7. Fruit mineral content during the ripening of three tomato genotypes (C40, MM and F1). Data are expressed as g per 100 g dry matter (DM).

		K	P	Cl	S	Ca	Fe	Cu	Zn	Rb	Mn
Statistics											
	G	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
	RS	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
	G*RS	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
C40	Green	3.07 e	0.318 f	0.176 cd	0.129 f	0.139 d	0.017 b	0.001 a	0.003 bc	0.002 bc	0.004 abc
	Pink	2.71 cd	0.299 ef	0.188 de	0.118 e	0.128 b	0.010 ab	0.001 a	0.002 a	0.002 ab	0.003 a
	RM	2.69 c	0.289 e	0.176 cd	0.120 ef	0.126 b	0.010 a	0.001 a	0.002 ab	0.002 ab	0.004 abc
MM	Green	2.73 cd	0.217 bc	0.193 e	0.097 bc	0.130 bc	0.034 c	0.012 d	0.004 d	0.002 ab	0.005 de
	Pink	2.76 cd	0.231 c	0.185 cde	0.104 cd	0.138 d	0.017 ab	0.004 b	0.003 c	0.002 c	0.003 ab
	RM	2.86 d	0.252 d	0.196 e	0.108 d	0.136 cd	0.016 ab	0.002 a	0.003 bc	0.002 bc	0.004 bc
F1	Green	2.18 b	0.219 bc	0.149 b	0.094 b	0.130 bc	0.030 c	0.013 d	0.003 d	0.002 ab	0.005 cd
	Pink	1.94 a	0.203 ab	0.102 a	0.074 a	0.117 a	0.045 d	0.007 c	0.004 d	0.001 a	0.006 e
	RM	2.32 b	0.191 a	0.170 c	0.098 bc	0.128 bc	0.017 ab	0.005 b	0.003 c	0.002 a	0.004 bc

K = potassium; P = phosphorus; Cl = chloride; S = sulfur; Ca = calcium; Fe = iron; Cu = copper; Zn = zinc; Rb = rubidium; Mn = manganese. Bold font indicates a significant difference. Different letters in the same column indicate significant differences between means according to Tukey's test ($p = 0.05$).

Table 8. Fruit antioxidant content during fruit development at high temperature of tomato genotypes (C40, MM and F1).

		Lu	Ly	Bc	Phy	t-Vc	r-Vc	rV/tV
Statistics								
	G	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
	TT	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
	G*TT	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
C40	CT	0.517 a	330.16 a	21.26 a	108.69 ab	1884 b	1134 b	0.602 a
	T1	2.078 c	547.21 bc	29.54 ab	163.41 c	2274 c	1292 c	0.568 a
	T2	1.499 abc	237.57 a	23.11 a	82.48 a	1696 a	991 a	0.586 a
	T3	0.815 ab	375.75 ab	25.13 ab	141.32 bc	2388 c	1572 d	0.658 b
	T4	1.639 bc	575.74 c	33.01 b	154.79 c	1712 a	1029 ab	0.600 a
MM	CT	1.783 b	338.46 b	35.51 b	88.08 b	2120 b	1614 b	0.762 b
	T1	2.015 b	318.04 b	32.51 b	113.47 c	2376 c	1897 c	0.798 bc
	T2	0.456 a	164.62 a	19.08 a	50.35 a	1729 a	1119 a	0.646 a
	T3	4.002 c	475.52 c	35.68 b	113.27 c	2083 b	1585 b	0.761 b
	T4	4.674 c	378.39 b	31.77 b	112.49 c	2596 d	2119 d	0.816 c
F1	CT	0.573 ab	90.57 ab	13.79 b	18.27 a	2566 c	2189 d	0.853 ab
	T1	0.980 b	163.18 c	12.86 b	33.91 c	2046 b	1815 c	0.887 bc
	T2	0.133 a	73.16 a	8.03 a	17.57 a	2004 b	1631 b	0.810 a
	T3	0.187 a	122.09 b	8.94 a	24.68 b	1983 b	1821 c	0.920 c
	T4	0.940 b	74.01 a	10.77 ab	17.77 a	1720 a	1413 a	0.820 a
		Cag	**Cry**	**Chl**	**Ru**	**unk 1**	**NC**	
Statistics								
	G	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	
	TT	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	
	G*TT	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	
C40	CT	239.7 b	137.5 c	311.2 d	56.5 b	1501.2 bc	0.0	
	T1	274.9 c	140.2 c	281.8 c	43.5 a	1388.3 a	0.0	
	T2	216.9 a	99.8 a	272.9 bc	33.2 a	1425.7 ab	0.0	
	T3	272.4 c	133.8 c	194.6 a	80.9 c	1529.3 c	0.0	
	T4	247.1 b	121.0 b	258.3 b	69.2 c	1452.4 abc	0.0	
MM	CT	339.9 a	94.4 b	354.6 c	51.2 a	972.7 b	54.8 a	
	T1	358.9 b	95.1 b	327.5 b	77.3 b	893.0 a	79.3 a	
	T2	443.9 d	129.8 d	359.2 c	155.6 d	1014.8 c	113.1 bc	
	T3	332.4 a	86.5 a	291.1 a	173.6 e	1024.2 c	136.4 c	
	T4	387.6 c	105.8 c	385.2 d	126.7 c	1272.5 d	84.9 ab	
F1	CT	244.1 d	46.6 c	124.2 d	42.0 b	288.5 a	47.5 ab	
	T1	179.3 b	36.5 b	81.8 a	10.9 a	329.8 b	64.1 bc	
	T2	197.3 c	44.3 c	80.1 a	33.5 b	426.9 c	79.2 c	
	T3	190.1 bc	47.4 c	93.0 c	38.7 b	404.2 c	46.1 a	
	T4	148.1 a	29.9 a	87.5 ab	21.4 a	268.3 a	64.0 bc	

Data are expressed as mg/kg DM (except the ratio rV/tV, without unit). G = genotype; TT = temperature treatment; Lu = lutein; Ly = lycopene; Bc = beta-carotene; Phy = phytoene; t-Vc: total vitamin C; r-Vc: reduced vitamin C; rV/tV = ratio between reduced and total vitamin C; Cag = caffeic acid glucoside; Cry = cryptochlorogenic acid; Chl = chlorogenic acid; Ru = rutin; unk1 = unknown phenolic compounds; NC = naringenin chalcone. Bold font indicates a significant difference. Different letters in the same column indicate significant differences between means according to Tukey's test ($p = 0.05$).

The effect of HT on phenolic compounds varies according to genotype and fruit developmental stage. For F1 fruits, phenolic compounds systematically decrease with HT, except for the unknown phenolic (unk1). On the other hand, rutin systematically increased in MM fruits when HT was applied (+51%, +204%, +239% and +148% during T1, T2, T3 and T4, respectively). Rutin content was less affected in C40 fruits compared to MM fruits. For F1 fruits, HT reduced rutin when applied during T1 and T4. Chlorogenic acid decreased systematically for C40 and F1 fruits, and only in MM fruits during T1 and T3. Naringenin chalcone increased when HT was applied during T2 (+107%) and T3 (+149%) in MM, and during T2 (+67%) in F1 fruits. This observation confirms that the phenolic content of tomato fruits is highly variable according to genotype and growing conditions (Table 8).

Similarly, mineral content varies with HT depending on genotype and fruit developmental stage. Potassium content increased in C40 and F1 fruits but decreased in MM fruits.

HT tended to increase major mineral content (K, P, S, Ca, Fe) except for Cl in F1 fruits. On the other hand, HT reduced P, S and Ca content (except during T2) in MM fruits (Table 9).

Table 9. Fruit mineral content depending on the temperature treatments applied during C40, MM and F1 fruit development. Data are expressed as g per 100 g dry matter (DM).

		K	P	Cl	S	Ca	Fe	Cu	Zn	Rb	Mn
Statistics											
	G	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
	TT	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
	G*TT	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
C40	CT	2.69 a	0.289 c	0.176 a	0.120 c	0.126 b	0.010 ab	0.001 a	0.002 a	0.002 a	0.004 a
	T1	3.00 c	0.265 b	0.228 c	0.102 a	0.123 b	0.014 b	0.013 c	0.003 b	0.002 c	0.004 a
	T2	2.92 bc	0.299 c	0.175 a	0.113 b	0.121 b	0.012 ab	0.003 b	0.002 a	0.002 bc	0.003 a
	T3	2.71 a	0.240 a	0.203 b	0.107 ab	0.126 b	0.015 b	0.001 a	0.002 a	0.002 a	0.004 a
	T4	2.83 b	0.257 b	0.208 b	0.121 c	0.111 a	0.009 a	0.001 a	0.003 a	0.002 ab	0.003 a
MM	CT	2.86 c	0.252 b	0.196 b	0.108 b	0.136 c	0.016 bc	0.002 a	0.003 a	0.002 a	0.004 a
	T1	2.51 a	0.207 a	0.174 a	0.095 a	0.121 b	0.017 c	0.003 b	0.003 ab	0.002 a	0.004 a
	T2	2.96 c	0.250 b	0.216 c	0.107 b	0.152 d	0.012 ab	0.006 d	0.003 b	0.002 a	0.004 a
	T3	2.69 b	0.252 b	0.180 a	0.104 b	0.125 b	0.011 a	0.004 c	0.002 a	0.002 a	0.003 a
	T4	2.51 a	0.217 a	0.173 a	0.098 a	0.109 a	0.013 abc	0.002 a	0.002 a	0.002 a	0.004 a
F1	CT	2.32 a	0.191 a	0.170 b	0.098 a	0.128 a	0.017 ab	0.005 ab	0.003 a	0.002 a	0.004 a
	T1	2.52 b	0.228 c	0.154 a	0.103 ab	0.140 b	0.026 c	0.006 b	0.003 ab	0.002 a	0.005 a
	T2	2.60 b	0.251 d	0.144 a	0.118 c	0.144 b	0.022 bc	0.012 c	0.003 bc	0.002 a	0.004 a
	T3	2.49 b	0.231 c	0.153 a	0.105 b	0.143 b	0.015 a	0.003 a	0.003 ab	0.002 a	0.004 a
	T4	2.36 a	0.207 b	0.153 a	0.116 c	0.145 b	0.026 c	0.014 d	0.004 c	0.002 a	0.005 a

K = potassium; P = phosphorus; Cl = chloride; S = sulfur; Ca = calcium; Fe = iron; Cu = copper; Zn = zinc; Rb = rubidium; Mn = manganese. Bold font indicates a significant difference. Different letters in the same column indicate significant differences between means according to Tukey's test ($p = 0.05$).

4. Discussion

Color in tomato fruit is one of the most critical characteristics for assessing ripeness. In the present experiment, as tomato fruits were harvested according to their exterior color, it is not surprising that fruit colors at harvest were very similar between treatments. Regarding the chroma value, the genotypes remained within the range of 35 to 50 units during maturation, which agrees with the values that Cantwell [22] reported in commercial tomato varieties, and those reported by Vela-Hinojosa et al. [23] in native varieties of Mexican tomato. The size, weight and firmness of ripe fruits were the physical traits modified by the increased temperature. It was interesting to note that the response to increased temperature was not linear, and that the more substantial effects on fruit size and weight were not observed throughout the fruits' development (T1 fruits), but rather in fruits subjected to HT during their period of rapid growth (from 30 DAA). The sudden increase in temperature reduced the time necessary for C40 fruits to ripen, explaining their lower weight and size at harvest. Hernández et al. [11] also found that fruit equatorial and longitudinal diameter decreased due to the increased temperature (32 °C). In contrast, the growth duration was not affected (in F1) or even increased (in MM) by HT, regardless of the application period. Nevertheless, while HT slightly reduced fruit fresh weight and size, the F1 fruits remained larger than MM or C40 fruits, whatever the HT treatment. Therefore, F1 fruits might be less sensitive to increased temperature, as their growth and visual aspects were modified less.

Tomato is considered a climacteric fruit in which ripening is accompanied by increased respiration and ethylene production, which implies a series of physicochemical changes, such as softening and color evolution [24]. Fluxomic analyses and modeling have brought new insight into the timeline of the different events during fruit ripening [25]. These authors demonstrated that the initiation of the climacteric respiration was related to an unbalanced carbon allocation, as carbon storage and synthesis decrease so that starch degradation is initiated. In the present study, the rapid temperature increase when the fruit growth rate has already declined (during T3) is likely to trigger unbalanced carbon allocation.

Indeed, the thermal stress will increase cell wall degradation and starch hydrolysis, both of which are enzymatic processes enhanced by high temperatures [14,26]. According to Colombié et al. [25], these responses will increase carbon availability and trigger climacteric respiration. In the present experiment, F1 fruits had a lower starch content than MM, and more than C40 at the green stage. Thus, the F1 fruits' carbon metabolism appears different from the others. It is plausible that their response to increased temperature is related to different carbon balances during fruit development.

Interestingly, the F1 fruits' growth time is longer than that of the other genotypes, and HT did not affect it. It would be interesting to assay alternative oxidase activity in these fruits to analyze further the origin of F1's different behavior and low sensitivity to higher temperatures. We hypothesize that the retarded ripening and the absence of an effect of increased temperature on it could be linked to reduced respiration, as previously reported by Xu et al. [27] in transgenic tomatoes with low alternative oxidase.

In addition, a decrease in fruit firmness during ripening and under increased temperature provides evidence of fruit aging and cell wall degradation. Tomato fruit firmness is a good quality indicator that is crucial for consumer acceptance, shelf life, and portability. This characteristic depends on several factors such as genotype, growth conditions, harvest, and postharvest conditions [28]. In the present study, we confirm that increased temperature also affected fruit firmness, altering its postharvest quality and reducing its shelf life.

The HT mainly modified the primary and secondary metabolite content in a genotype-dependent manner. In C40 and MM fruits, the soluble sugar content was reduced, and the acid content was increased in MM and C40, but not in F1 fruits. The total soluble solids (TSS) considers the soluble sugars (sucrose and hexoses), acids (citrate and malate) and other minor components (phenols, amino acids, soluble pectins, ascorbic acid and minerals) in tomato pulp [29]. In the present study, TSS increased during ripening for C40 and MM as sugars accumulated (Tables 2 and 4), confirming that, under control conditions, TSS is an indicator of sugar accumulation during ripening. We observed that HT had a negligible effect on TSS in MM and C40 fruits, decreasing sugar content, increasing acid content and consequently attenuating the SU/AC ratio. Thus, when plants are submitted to thermal stress, we observed that measuring TSS is not an accurate way of detecting changes in fruit composition or quality, as it does not discriminate between sugar and acid contents.

This study confirms that temperature is one of the environmental factors that act on the accumulation of organic acid, as was previously reviewed by Etienne et al. [30]. Citric acid content was higher in MM and C40 fruit under HT (Table 5), depending on the period of HT occurrence and the genotype. In C40, it accumulated up to 44% (28%, respectively) when the HT was applied from the anthesis (15 DAA, respectively). These periods (0–30 DAA) correspond to the period of citric acid synthesis, which seems to be enhanced by HT in MM and C40. During ripening, citric acid is catabolized (Table 4), and HT may limit this degradation in MM and C40, as there is still about 20% more citric acid in the fruit receiving high temperature in C40 (from 30 or 45 DAA). The higher citric acid content of C40 fruits could also be related to a direct effect of temperature that reduces fruit developmental duration, as already described [6,14]. HT did not affect the citric acid content of F1 fruits, which may be of interest to breeders for the selection of genotypes with lower acidic content and titratable acidity.

HT also increased malic acid accumulation depending on HT periods of occurrence. Previous studies have reported such variation depending on the balance between malic acid synthesis, degradation, or transport for vacuolar storage [30]. Our data show that HT enhanced malic acid accumulation during T1 or T2 and ripening, limiting its degradation. Sweetman et al. [31] also reported that grape sensitivity to HT depended on the grape berry stage of development. They observed an increased malate content when HT was applied during the earlier fruit development period (pre-veraison), and a decrease in malate content when HT occurred later, during ripening. An attenuated malate content when HT is applied during ripening has also been reported for kiwi [32]. These authors

hypothesized that this might be linked to more prolonged malate degradation and the use of acids as a carbohydrate source for respiration and secondary metabolites' synthesis. Malate and citrate are not the principal sources of carbohydrates in tomatoes compared to hexoses. Thus, the sugar content decrease triggered by HT could be related to their use as carbohydrate sources for respiration.

The results of HT's effects on secondary metabolites also showed significant interactions between genotype and the temperature treatments, indicating that the metabolic responses to HT are genotype dependent. A good example is the evolution of rutin content, because it systematically increased with HT in MM fruits (by 51% when HT was applied from anthesis, and up to 239% when HT was applied after 30 DAA). This result agrees with similar reports in cherry tomatoes when the temperature was increased from 21 to 26 °C during fruit ripening [33]. In contrast, in F1 fruits, rutin content was lower, and it decreased or remained stable depending on the fruit's developmental stage. We observed intermediate effects in C40 fruits (decrease or increase depending on the fruit developmental stage).

Reimer et al. [34], observed rutin accumulation in leaves of cultivated tomatoes in contrast to wild species when submitted to different abiotic stresses. Such an accumulation of rutin has also been described in tomato leaves exposed to cold temperatures [35].

The change in the color of tomato fruits during ripening is due to the accumulation or degradation of various carotenoids (β-carotene, lycopene, and lutein, among others) under genetic and environmental control [36]. According to Cantwell [22], there is a correlation between reduced hue values and increased lycopene content during fruit ripening. However, we observed that fruits showed significant differences in carotenoid content depending on the temperature treatments, despite their almost similar color. In a previous experiment under controlled conditions, we observed reduced lycopene accumulation in fruits maintained at high temperatures during ripening (fruit ripened on-vine at 32 °C), and inhibition of lycopene synthesis [33]. Though the color development in tomatoes is temperature sensitive, with better plastid conversion occurring above 12 °C and below 30 °C [37], in this study, we did not observe the negative effect of high temperature on the red color or carotenoid accumulation. This observation might be because the fruits did not remain under high temperature throughout the day, and the mean temperature did not exceed 31 °C. In addition, the present study shows that increased temperature effects on carotenoids depend on the fruit's developmental stage.

Interestingly, lycopene, the primary carotenoid in ripe red tomatoes, accumulates during T4 but not T1 or T2 (Table 8). Therefore, the effect of HT during T1 and T2 could be related to the enhancement of oxidative stress, and may result from a complex interaction between temperature and sugar concentration, as was previously proposed by Fanciullino et al. [38], affecting the potential accumulation of carotenoids. During T3 and T4, the temperature may act directly on the carotenoid biosynthetic pathway and, depending on its level, promote or reduce it [39].

In higher plants, vitamin C plays different essential roles and is involved in physiological processes that help the plant adapt to different abiotic and biotic constraints [40,41]. We observed that increased temperature effects on vitamin C depended on the fruit's developmental stage. When HT was applied from anthesis until ripening, it increased the vitamin C in MM and C40 fruits but not in F1 (which contains higher amounts of vitamin C under control conditions). The increased vitamin C could be related to an adaptation, as vitamin C is necessary for cell division and growth. A similar increase has been reported by Hernandez et al. [11] in tomato cultivars. For Velasco fruits at anthesis, a decrease was observed at a later ripening stage when plants were subjected to increased temperature (from 24 to 32 °C). In our experiment, HT applied from 15 DAA (which corresponds to the fruit's rapid growth period, when most of the cell division is already achieved) lowers the reduced form of ascorbate, whatever the genotype. This result could be due to a lower ascorbate synthesis and/or a lower ascorbate recycling under high temperatures. This reduced recycling activity

has been reported by Massot et al. [42], with a lower dehydro-ascorbate reductase activity when the tomato fruit temperature was increased from 27 to 31 °C.

Fruit mineral content was modified by HT treatments and according to the genotype. Fruit calcium content was lower for MM and C40 fruits, especially when HT was applied during ripening. In contrast, HT increased fruit calcium content of F1 fruits, which could be critical for limiting physiological disorders due to low calcium fluxes in fruits and for limiting the appearance of blossom end rot.

5. Conclusions

In conclusion, the present study shows that the F1 genotype is better adapted to produce large fruits with high sugar content under HT. In contrast to MM and C40 fruits, HT treatments did not reduce F1 fruit growth duration, maintaining high sugar fluxes to the fruits and allowing acid catabolism before harvest so that the size and the SU/AC ratio of F1 ripe fruits are less affected under HT, and remain very high compared to C40 or MM. We confirmed that the synthesis and degradation of citric and malic acid are very sensitive to HT, and that both could be enhanced by HT; therefore, the resultant fruit acidity depends on their relative duration and the occurrence of the climacteric crisis, which could shorten fruit growth duration under HT. The differences between genotypes appeared to be related to carbon metabolism and balance. Future work must assess how F1 plant physiology is affected by changes in temperature. It is also important to determine the temperature threshold for maintaining carbon acquisition, allocation and/or fruit growth before inhibition. Furthermore, it would be interesting to study the productivity of this genotype when submitted to other production-limiting factors related to climate change such as water stress, in order to confirm its significance.

Author Contributions: Conceptualization, V.A.D.-V., O.J.A.-G. and H.G.; methodology, V.A.D.-V., O.J.A.-G., M.d.L.A.-G. and H.G.; validation, V.A.D.-V., O.J.A.-G. and H.G.; formal analysis, V.A.D.-V., O.J.A.-G. and H.G.; investigation, V.A.D.-V., O.J.A.-G. and M.d.L.A.-G.; resources, V.A.D.-V., O.J.A.-G. and M.d.L.A.-G.; data curation, V.A.D.-V., O.J.A.-G. and H.G.; writing—original draft preparation, V.A.D.-V., O.J.A.-G. and H.G.; writing—review and editing, V.A.D.-V., O.J.A.-G. and H.G.; visualization, V.A.D.-V., O.J.A.-G. and H.G.; supervision, O.J.A.-G. and H.G.; project administration, V.A.D.-V., O.J.A.-G., M.d.L.A.-G. and H.G. All authors have read and agreed to the published version of the manuscript.

Funding: This research received a funding from the Joint Technology Unit IQUAR (Innovating to improve the post-harvest quality of fresh fruit and vegetables, INRAE-Avignon University-CTIFL-CIRAD).

Data Availability Statement: The data presented in this study are available in article.

Acknowledgments: We thank Patricia Laugier, who carried out the biochemical analyses (sugars, acids, phenolics, carotenoids, vitamin C and minerals).

Conflicts of Interest: The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript; or in the decision to publish the results.

References

1. Xu, J.; Wolters-Arts, M.; Mariani, C.; Huber, H.; Rieu, I. Heat stress affects vegetative and reproductive performance and trait correlations in tomato (*Solanum lycopersicum*). *Euphytica* **2017**, *213*, 156. [CrossRef]
2. IPCC. *Summary for Policymakers, in Global Warming of 1.5 °C. An IPCC Special Report on the Impacts of Global Warming of 1.5 °C above Pre-Industrial Levels and Related Global Greenhouse Gas Emission Pathways, in the Context of Strengthening the Global Response to the Threat of Climate Change, Sustainable Development, and Efforts to Eradicate Poverty*; The Intergovernmental Panel on Climate Change: Geneva, Switzerland, 2018; pp. 1–24.
3. Wibig, J. Symptoms and driving factors of contemporary earth warming and projections for the future. *Pap. Glob. Chang.* **2016**, *23*, 37–57. [CrossRef]
4. Pio, R.; Souza, F.B.M.D.; Kalcsits, L.; Bisi, R.B.; Farias, D.D.H. Advances in the production of temperate fruits in the tropics. *Acta Sci. Agron.* **2018**, *41*, e39549. [CrossRef]
5. Pham, D.; Hoshikawa, K.; Fujita, S.; Fukumoto, S.; Hirai, T.; Shinozaki, Y.; Ezura, H. A tomato heat-tolerant mutant shows improved pollen fertility and fruit-setting under long-term ambient high temperature. *Environ. Exp. Bot.* **2020**, *178*, 104150. [CrossRef]

6. Adams, S.R.; Cockshull, K.E.; Cave, C.R.J. Effect of temperature on the growth and development of tomato fruits. *Ann. Bot.* **2001**, *88*, 869–877. [CrossRef]
7. Truffault, V.; Fifel, F.; Longuenesse, J.J.; Vercambre, G.; Le Quillec, S.; Gautier, H. Impact of temperature integration under greenhouse on energy use efficiency, plant growth and development and tomato fruit quality depending on cultivar rootstock combination. *Acta Hortic.* **2015**, *1099*, 95–100. [CrossRef]
8. Gonzalo, M.J.; Li, Y.-C.; Chen, K.-Y.; Gil, D.; Montoro, T.; Nájera, I.; Baixauli, C.; Granell, A.; Monforte, J.A. Genetic control of reproductive traits in tomatoes under high temperature. *Front. Plant Sci.* **2020**, *11*, 326. [CrossRef]
9. Gonzalo, M.J.; Nájera, I.; Baixauli, C.; Gil, D.; Montoro, T.; Soriano, V.; Olivieri, F.; Rigano, M.M.; Ganeva, D.; Grozeva-Tileva, S.; et al. Identification of tomato accessions as source of new genes for improving heat tolerance: From controlled experiments to field. *BMC Plant Biol.* **2021**, *21*, 345. [CrossRef]
10. Bineau, E.; Diouf, I.; Carretero, Y.; Duboscq, R.; Bitton, F.; Djari, A.; Zouine, M.; Causse, M. Genetic diversity of tomato response to heat stress at the QTL and transcriptome levels. *Plant J.* **2021**, *107*, 1213–1227. [CrossRef]
11. Hernández, V.; Hellín, P.; Fenoll, J.; Flores, P. Increased temperature produces changes in the bioactive composition of tomato, depending on its developmental stage. *J. Agric. Food Chem.* **2015**, *63*, 2378–2382. [CrossRef]
12. Moretti, C.L.; Mattos, L.M.; Calbo, A.G.; Sargent, S.A. Climate changes and potential impacts on postharvest quality of fruit and vegetable crops: A review. *Food Res. Int.* **2010**, *43*, 1824–1832. [CrossRef]
13. FAO (Food and Agriculture Organization of the United Nations). *Coping with Climate Change—The Roles of Genetic Resources for Food and Agriculture*; FAO Editions: Rome, Italy, 2015; pp. 1–129.
14. Ruíz-Nieves, J.M.; Ayala-Garay, O.J.; Serra, V.; Dumont, D.; Vercambre, G.; Génard, M.; Gautier, H. The effects of diurnal temperature rise on tomato fruit quality. Can the management of the greenhouse climate mitigate such effects? *Sci. Hortic.* **2021**, *278*, 109836. [CrossRef]
15. Kugblenu, Y.O.; Oppong Danso, E.; Ofori, K.; Andersen, M.N.; Abenney-Mickson, S.; Sabi, E.B.; Plauborg, F.; Abekoe, M.K.; Ofosu-Anim, J.; Ortiz, R.; et al. Screening tomato genotypes for adaptation to high temperature in West Africa. *Acta Agric. Scand. Sect. B Soil Plant Sci.* **2013**, *63*, 516–522. [CrossRef]
16. Steiner, A.A. The universal nutrient solution. In Proceedings of the 6th International Congress on Soilless Culture, Wageningen, The Netherlands, 29 April–5 May 1984; pp. 633–650.
17. Camelo, A.F.L.; Gómez, P.A. Comparison of color indexes for tomato ripening. *Hortic. Bras.* **2004**, *22*, 534–537. [CrossRef]
18. Gomez, L.; Rubio, E.; Augé, M. A new procedure for extraction and measurement of soluble sugars in ligneous plants. *J. Sci. Food Agric.* **2002**, *82*, 360–369. [CrossRef]
19. Gomez, L.; Bancel, D.; Rubio, E.; Vercambre, G. The microplate reader: An efficient tool for the separate enzymatic analysis of sugar in plant tissues–validation of micro method. *J. Agric. Food Chem.* **2007**, *87*, 1893–1905. [CrossRef]
20. Stevens, R.; Buret, M.; Garchery, C.; Carretero, Y.; Causse, M. Technique for rapid, small-scale analysis of vitamin C levels in fruit and application to a tomato mutant collection. *J. Agric. Food Chem.* **2006**, *54*, 6159–6165. [CrossRef]
21. Sérino, S.; Gomez, L.; Costagliola, G.; Gautier, H. HPLC assay of tomato carotenoids: Validation of a rapid microextraction technique. *J. Agric. Food Chem.* **2009**, *57*, 8753–8760. [CrossRef]
22. Cantwell, M. Optimum procedures for ripening tomatoes. In *Fruit Ripening and Ethylene Management*; Thompson, J.T., Crisosto, C., Eds.; UC Postharvest Horticulture Series; UC Postharvest: Davis, CA, USA, 2000; pp. 106–116.
23. Vela-Hinojosa, C.; Escalona-Buendía, H.B.; Mendoza-Espinoza, J.A.; Díaz de León-Sánchez, F.; Lobato-Ortíz, R.; Rodríguez-Pérez, J.E.; Ramírez-Aguilar, M.; Pérez-Díaz, F.; Villa-Hernández, J.M. Chemical and sensory analysis of native genotypes and experimental lines of tomato (*Solanum lycopersicum* L.). *Fruits* **2018**, *73*, 60–71. [CrossRef]
24. Dominguez, I.; Lafuente, M.T.; Hernandez-Muñoz, P.; Gavara, R. Influence of modified atmosphere and ethylene levels on quality attributes of fresh tomatoes (*Lycopersicon esculentum* Mill.). *Food Chem.* **2016**, *209*, 211–219. [CrossRef]
25. Colombié, S.; Beauvoit, B.; Nazaret, C.; Bénard, C.; Vercambre, G.; Le Gall, S.; Biais, B.; Cabasson, C.; Maucourt, M.; Bernillon, S.; et al. Respiration climacteric in tomato fruits elucidated by constraint-based modelling. *New Phytol.* **2017**, *213*, 1726–1739. [CrossRef]
26. Ramakrishna, W.; Deng, Z.; Ding, C.K.; Handa, A.K.; Ozminkowski, R.H., Jr. A novel small heat shock protein gene, vis1, contributes to pectin depolymerization and juice viscosity in tomato fruit. *Plant Physiol.* **2003**, *131*, 725–735. [CrossRef] [PubMed]
27. Xu, F.; Yuan, S.; Zhang, D.-W.; Lv, X.; Lin, H.-H. The role of alternative oxidase in tomato fruit ripening and its regulatory interaction with ethylene. *J. Exp. Bot.* **2012**, *63*, 5705–5716. [CrossRef] [PubMed]
28. Aurand, R.; Faurobert, M.; Page, D.; Maingonnat, J.F.; Brunel, B.; Causse, M.; Bertin, N. Anatomical and biochemical trait network underlying genetic variations in tomato fruit texture. *Euphytica* **2012**, *187*, 99–116. [CrossRef]
29. Beckles, D.M. Factors affecting the postharvest soluble solids and sugar content of tomato (*Solanum lycopersicum* L.) fruit. *Postharvest Biol. Technol.* **2012**, *63*, 129–140. [CrossRef]
30. Etienne, A.; Génard, M.; Lobit, P.; Mbeguié, A.; Mbéguié, D.; Bugaud, C. What controls fleshy fruit acidity? A review of malate and citrate accumulation in fruit cells. *J. Exp. Bot.* **2013**, *64*, 1451–1469. [CrossRef]
31. Sweetman, C.; Sadras, V.O.; Hancock, R.D.; Soole, K.L.; Ford, C.M. Metabolic effects of elevated temperature on organic acid degradation in ripening *Vitis vinifera* fruit. *J. Exp. Bot.* **2014**, *65*, 5975–5988. [CrossRef] [PubMed]
32. Richardson, A.C.; Marsh, K.B.; Boldingh, H.L.; Pickering, A.H.; Bulley, S.M.; Frearson, N.J.; Ferguson, A.R.; Thornber, S.E.; Bolitho, K.M.; Marcrae, E.A. High growing temperatures reduce fruit carbohydrate and vitamin C in kiwifruit. *Plant Cell Environ.* **2004**, *27*, 423–435. [CrossRef]

33. Gautier, H.; Diakou-Verdin, V.; Benard, C.; Reich, M.; Buret, M.; Bourgaud, F.; Poessel, J.L.; Caris-Veyrat, C.; Genard, M. How does tomato quality (sugar, acid, and nutritional quality) vary with ripening stage, temperature, and irradiance. *J. Agric. Food Chem.* **2008**, *56*, 1241–1250. [CrossRef]
34. Reimer, J.J.; Thiele, B.; Biermann, R.T.; Junker-frohn, L.V.; Wiese-Klinkenberg, A.; Usadel, B.; Wormit, A. Tomato leaves under stress: A comparison of stress response to mild abiotic stress between a cultivated and a wild tomato species. *Plant Mol. Biol.* **2021**, *107*, 177–206. [CrossRef]
35. Röhlen-Schmittgen, S.; Ellenberger, J.; Groher, T.; Hunsche, M. Boosting leaf contents of rutin and solanesol in bio-waste of *Solanum lycopersicum*. *Plant Physiol. Biochem.* **2020**, *155*, 888–897. [CrossRef] [PubMed]
36. Weingerl, V.; Unuk, T. Chemical and fruit skin colour markers for simple quality control of tomato fruits. *Croat. J. Food Sci. Technol.* **2015**, *7*, 76–85. [CrossRef]
37. Dumas, Y.; Dadomo, M.; Di Lucca, G.; Grolier, P. Effects of environmental factors and agricultural techniques on antioxidant content of tomatoes. *J. Sci. Food Agric.* **2003**, *83*, 369–382. [CrossRef]
38. Fanciullino, A.L.; Bidel, L.; Urban, L. Carotenoid responses to environmental stimuli: Integrating redox and carbon controls into a fruit model. *Plant Cell Environ.* **2004**, *37*, 273–289. [CrossRef]
39. Gautier, H.; Rocci, A.; Buret, M.; Grasselly, D.; Dumas, Y.; Causse, M. Effect of photoselective filters on the physical and chemical traits of vine-ripened tomato fruits. *Can. J. Plant Sci.* **2005**, *85*, 439–446. [CrossRef]
40. Gest, N.; Gautier, H.; Stevens, R. Ascorbate as seen through plant evolution: The rise of a successful molecule? *J. Exp. Bot.* **2013**, *64*, 33–53. [CrossRef] [PubMed]
41. Ntagkas, N.; Woltering, E.; Nicole, C.; Labrie, C.; Marcelis, L.F.M. Light regulation of vitamin C in tomato fruit is mediated through photosynthesis. *Environ. Exp. Bot.* **2019**, *158*, 180–188. [CrossRef]
42. Massot, C.; Bancel, D.; Lauri, F.L.; Truffault, V.; Baldet, P.; Stevens, R.; Gautier, H. High temperature inhibits ascorbate recycling and light stimulation of the ascorbate pool in tomato despite increased expression of biosynthesis genes. *PLoS ONE* **2013**, *8*, e84474. [CrossRef]