



HAL
open science

The effects of diurnal temperature rise on tomato fruit quality. Can the management of the greenhouse climate mitigate such effects?

Juan Ruiz-Nieves, Oscar Ayala-Garay, Valérie Serra, Doriane Dumont, Gilles Vercambre, Michel Génard, Hélène Gautier

► To cite this version:

Juan Ruiz-Nieves, Oscar Ayala-Garay, Valérie Serra, Doriane Dumont, Gilles Vercambre, et al.. The effects of diurnal temperature rise on tomato fruit quality. Can the management of the greenhouse climate mitigate such effects?. *Scientia Horticulturae*, 2021, 278, pp.109836. 10.1016/j.scienta.2020.109836 . hal-03118905

HAL Id: hal-03118905

<https://hal.science/hal-03118905v1>

Submitted on 2 Jan 2023

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution - NonCommercial 4.0 International License

1 **The effects of diurnal temperature rise on tomato fruit quality. Can the**
2 **management of the greenhouse climate mitigate such effects?**

3

4 **Juan M. Ruiz-Nieves¹, Oscar J. Ayala-Garay¹, Valérie Serra², Doriane Bancel²,**
5 **Gilles Vercambre², Michel Génard², Hélène Gautier^{2*}**

6

7 ¹Programa de Recursos Genéticos y Productividad, Colegio de Postgraduados. 56230,
8 Texcoco, México.

9 ²INRAE, UR1115 Plantes et Systèmes de Cultures Horticoles, 228, route de
10 l'aérodrome, Domaine St Paul, Site Agroparc, CS 40 509, F-84914 Avignon, France.

11 *Corresponding author: helene.gautier@inrae.fr.

12

13 **Abstract**

14 In the present study, tomatoes were grown under control conditions (CT), a
15 moderate (MT, up to 2 °C) or a higher rise in temperature (HT, up to 5 °C), and a
16 moderate rise followed by a lower air temperature at the end of the day (ED), in order to
17 analyze the effects of increased temperature as well as management system impact on
18 fruit quality.

19 Rising temperatures up to 5 °C reduced the fruit growth duration by five days
20 and greatly reduced the fresh (29.7%) and dry matter (30%) accumulation rate.
21 Increasing the temperature during the day and lowering it at the end of the day increased
22 citric and malic acid concentrations in the fruit, therefore reducing the sugar/acid ratio.
23 The ascorbate concentration and carotenoids increased in the fruits grown under high
24 temperature, while, phenolics concentrations did not change. Fruit water conductance
25 was strongly reduced under HT (-37%), and so was starch accumulation, in contrast to

26 hexoses. Dropping the air temperature at the end of the day could help mitigate HT
27 impacts as it slightly increased the pericarp dry matter content. It could also improve
28 seeds quality as it increased their dry matter content. It would be interesting to consider
29 broader changes in ED temperature to confirm its potential role in improving fruits dry
30 matter content.

31

32 **Keywords:** *Solanum lycopersicum* L., fruit growth, temperature, fruit quality, fruit
33 composition, climate change scenario.

34

35 **1. Introduction**

36 Under glasshouse, different cultural practices and climate management strategies
37 can be used to modulate plant growth conditions in order to obtain the required fruit
38 yield and quality. Among those, temperature control is a useful method for growers to
39 modulate plant growth when other factors such as light, nutrients and water are not
40 limiting (Guichard et al. 2001).

41 Over the last few decades, several studies have been devoted to identifying the
42 minimal temperatures allowing a high yield of tomatoes while limiting the energy costs
43 of heating. Night temperature has long been known to be the determining factor in
44 tomato fruit setting, with optimum temperatures ranging from 15 °C to 20 °C.. In
45 addition, the variation of daily temperature patterns may affect the plant and fruit
46 growth and metabolism, and ultimately, the fruit quality (Adams et al. 2001; Hurd and
47 Graves, 1985; Truffault et al. 2015; Van der Ploeg and Heuvelink, 2005). In the near
48 future, climate change will cause an increase in temperature, which can affect crop
49 yield, due to a reduced fruit set, and change fruit quality (Garg and Cheema, 2011).
50 Increasing temperature generally increases the fruit growth rate but also accelerates fruit

51 maturation and ripening so that fruit weight at harvest can be reduced (Adams et al.
52 2001; Fleisher et al. 2006). Temperatures at the daily scale can affect water and carbon
53 fluxes within the plant. Walker and Ho (1977) reported that increasing fruit temperature
54 favored sugars allocation to the fruits. Similarly, a rapid decrease in air temperature at
55 the end of the day is used by growers to favor assimilate partitioning to the fruits. The
56 tomato fruits dry matter content is not affected by temperature increase from 18 °C to
57 23 °C (Heuvelink, 1995). However, growing plants at higher temperatures (increasing
58 temperature from 25/14 °C to 30/12 °C, day/night respectively) enhances the tomato
59 fruits dry matter content (Rosales et al. 2011). These changes in dry matter content also
60 reflected changes in the tomato fruits composition (Dorais et al. 2010; Rivero et al.
61 2001). Rosales et al. (2011) reported that sugars content increased at high temperatures
62 (30-35 °C) while organic acids decreased. Robertson et al. (1995) found a maximum
63 plateau of tomato lycopene concentration between 18 and 26 °C. Similarly, Brandt et al.
64 (2006), Krumbein et al. (2006), and Dannehl et al. (2012) reported that the lycopene
65 content in tomatoes increases with increasing temperature and reaches its maximum
66 concentration at 25 °C. Temperatures below 12 °C strongly inhibit lycopene
67 biosynthesis and temperatures above 32 °C stop the process (Dumas et al. 2003),
68 affecting the activities of enzymes in the metabolic pathway and consequently, the fruit
69 carotenoid composition (Gautier et al. 2008). Likewise, phenolic compounds (e.g.
70 chlorogenic acid, rutin and naringenin) increase with increasing mean temperatures
71 (Dannehl et al. 2012). In contrast, increasing the temperature from 27 to 32 °C reduces
72 ascorbate accumulation (Gautier et al. 2008). Thus, high temperature could also have a
73 significant impact on the quality of fruits due to changes in primary or secondary
74 metabolism (Moretti et al. 2010).

75 In this sense, in the present work, we intend to study the consequences of
76 different climates (moderate to larger temperature increase) in order to mimic a possible
77 future scenario under climate change. The data obtained may help in the interpretation
78 of the effects of diurnal temperatures in the development and dry mass allocation as
79 well as in the quality and composition of tomatoes. It is imperative to acquire such
80 knowledge since a moderate or larger temperature increase may have different effects.

81

82 **2. Materials and methods**

83 **2.1. Tomato plant culture and treatments**

84 In June 2013, tomato seeds (*Solanum lycopersicum* L. cv. “Moneymaker”) were
85 sown into seed trays containing a peat-moss and vermiculite (50/50 v/v) and were
86 germinated in a glasshouse at 25 °C in Avignon (Southern France, 44° N). Ninety plants
87 with five growing leaves were transplanted per treatment into 15 cm diameter pots
88 containing 5 L of potting soil, in a multispan Venlo-type greenhouse, N-S oriented.
89 Plant nutrition, pests and diseases control were carried out in accordance with
90 commercial practices. Water was supplied to the plants using a drip irrigation system to
91 maintain a 20-30% drainage. The flowers were pollinated by vibration once a day
92 during the anthesis phase, the inflorescences of each truss were pruned to six flowers,
93 and lateral shoots were removed as soon as they appeared.

94 Plants were grown in four different compartments, and temperature treatments
95 started on September 2013. The air temperature and humidity inside the different
96 compartments of the greenhouse were measured using ventilated shelters equipped with
97 temperature and humidity probes (HD 9817T1, Delta ohm, France). Temperatures were
98 regulated by various techniques: heating, free ventilation by opening the aeration vents,
99 forced ventilation, and evaporative cooling (cool box). These systems were gradually

100 implemented by the automaton that manages the greenhouse climate. The side walls of
 101 the compartments had been bleached to homogenize the radiation and the temperature
 102 of each compartment.

103 Temperature scenarios were applied one week before truss flowering and until
 104 fruit harvest, by heating the glasshouse during the warmest hours of the day, from 11:00
 105 to 19:00, thus increasing diurnal temperature (+2 or +5 °C). We also used cooling to
 106 rapidly decrease temperature at the end of the day and study the possibility to mitigate
 107 the consequences of increased temperatures on fruit growth, physiology and quality.

108 The control treatment (CT) was similar to the outdoor climate, and the three
 109 other treatments had higher diurnal temperature:

110 - the High temperature Treatment (HT), achieved by heating from 11:00 to 19:00
 111 with an average offset of 2.6 °C up to 5 °C for maximum diurnal temperature (Table 1),

112 - the Moderate temperature Treatment (MT), achieved by heating from 11:00 to
 113 19:00 with an average offset of 0.5 °C up to 2 °C for maximum diurnal temperature,

114 - the ‘end-of-day’ treatment (ED), which was similar to MT except at the end of
 115 the day, from 19:00 to 22:00, when the temperature was reduced by 3°C in order to
 116 favor sugar allocation to the fruits (Walker and Ho, 1977).

117

118 **Table 1.** Air temperature and relative humidity recorded during the fourth truss
 119 development.

Treatments (conditions) and standard deviation				
Temperature (°C)	CT	MD	ED	HT
Maximal	25.3 ± 1.5	26.2 ± 1.6	26.1 ± 1.5	29.4 ± 1.5
Average diurnal	21.7 ± 2.3	22.2 ± 3.1	22.1 ± 2.4	24.3 ± 2.5
Average nocturnal	17.5 ± 2.9	17.5 ± 3.0	17.0 ± 2.8	18.0 ± 2.8

Minimal	16.6 ± 1.5	16.6 ± 1.5	16.4 ± 1.4	17.0 ± 1.6
Relative humidity (%)	CT	MD	ED	HT
Maximal	92 ± 3	90 ± 2	92 ± 3	89 ± 3
Average	82 ± 6	80 ± 4	81 ± 5	78 ± 5
Minimal	66 ± 10	61 ± 7	63 ± 7	63 ± 7

120 CT = Control; MT = moderate increased temperature (from 11:00 to 19:00); ED =
 121 moderate increased temperature (from 11:00 to 19:00) followed by a decreased
 122 temperature applied at the end of the day (from 19:00 to 22:00); HT = High temperature
 123 (from 11:00 to 19:00).

124

125 **2.2. Fruit sampling for biochemical analysis**

126 The flowers of the fourth cluster of each plant were tagged at anthesis. Then,
 127 tagged fruits were harvested from nine days after anthesis (DAA) until ripeness (light
 128 red fruits), at nine development stages named A-09, A-16, A-23, A-30, A-37, A-44, A-
 129 51, O, R, corresponding to 9, 16, 23, 30, 37, 44 and 51 DDA, orange stage, and red
 130 stage, respectively. At each development stage, at least three fruits were harvested and
 131 pooled to form a replicate per treatment; four replicates were collected per stage and per
 132 treatment. Fruits were rinsed and dried on blotting paper, then each fruit was weighed,
 133 and equatorial and distal diameter were measured to determine fruit volume.

134 Fruits from a replicate were dissected, the jelly was removed, the placenta and
 135 seeds were extracted, and two opposite quarters of pericarp were weighed and dried in a
 136 stove at 70 °C during 72 hours to determine the percentage of dry weight as well as its
 137 partitioning between pericarp and seeds. The two other quarters were pooled and
 138 immediately frozen in liquid nitrogen, and stored at -80 °C for biochemical analyses.
 139 Then, tomato fruits were ground in liquid nitrogen to obtain a fine powder and stored at
 140 -80 °C before analyses.

141 An aliquot of 10 mg of ground freeze-dried tomato powder was used to
142 determine soluble sugars, starch, and organic acids, following the methodology
143 described by Gomez et al. (2002, 2007), with extraction and separation from a
144 methanol-chloroform-water solution. The soluble sugars and organic assays were
145 estimated using HPLC. Starch was hydrolyzed into glucose molecules, and the
146 determination of NADH formed during the reaction was measured with a micro-plate
147 reader (Multiskan Ascent V1.24) at 340 nm, which corresponds to NADH absorption.

148 The ascorbic acid (AsA) assay is based on the reduction of ferric ions to ferrous
149 ions and the measurement of absorbance at 550 nm, following the method reported by
150 Stevens et al. (2006), with an additional measurement to subtract other reducing
151 compounds. Three aliquots were assessed per sample to determine the reduced
152 ascorbate and the total ascorbate, after the addition of DTT (DL-Dithiothreitol) to
153 reduce the oxidized form of vitamin C, or after the addition of ascorbate oxidase to
154 estimate other reducing compounds that could bias the assay.

155 The carotenoid extraction was performed according to Sérino et al. (2009). The
156 assay was performed using HPLC with a DAD UV-visible detector (UV6000LP,
157 Thermo Separation Products, Rivera Beach, FL), with four working wavelengths, 474
158 nm for lycopene, 454 nm for β -carotene, 286 nm for phytoene, and 448 nm for lutein.

159 The polyphenols extraction was performed on 20 mg of cold-dried fruit powder
160 and a mix solution of methanol/water (70:30 v/v), the samples were agitated (grinder
161 vibrant–oscillating, Retsch GmbH, Rheenische, StraBe 36, 42781 Haan, Germany, with
162 microtube adaptor) for 1 min at 30 osc/s. Then, the samples were centrifuged for 5 min
163 (4 °C; 13200 rpm), and finally, the supernatant was filtered (GHP 0.2 μ m, 13 mm of
164 diameter). The assay was performed using HPLC (Uptisphere, UP3HDO\$15QK, L =
165 150 mm, \emptyset = 3 mm, particles = 3 μ m). The spectral data for all the peaks were

166 accumulated in the range 200-800 nm and the chromatograms were recorded at 330 and
167 356 nm, with specific retention time for rutin, naringenin chalcone, caffeic acid
168 glucoside, chlorogenic acid, caffeic acid derivative 1, and caffeic acid derivative 2 at
169 330 nm.

170 Structural dry matter (sDM) was calculated by subtracting the reducing sugars
171 and organic acids to fruit dry matter. Consequently, fluctuations in water, sugar or acid
172 contents do not influence the estimate of the fruit content of other components when
173 expressed on a sDM basis (Rahmati et al. 2015).

174

175 **2.3. Fruit sampling for conductance measurement**

176 The skin fruit conductance was assessed for ten fruits per treatment at light red
177 ripe stage. Ten fruits per treatment were harvested at 09:00, and after the pedicles were
178 sealed with paraffin, the fruits were allowed to freely transpire in a controlled
179 environment under forced and large ventilation, i.e. with a negligible boundary layer
180 resistance. Subsequently, measuring the fruit water loss against time allowed the
181 estimation of the fruit surface conductance according to Fishman and Génard (1998).

182

183 **2.4. Statistical analyses**

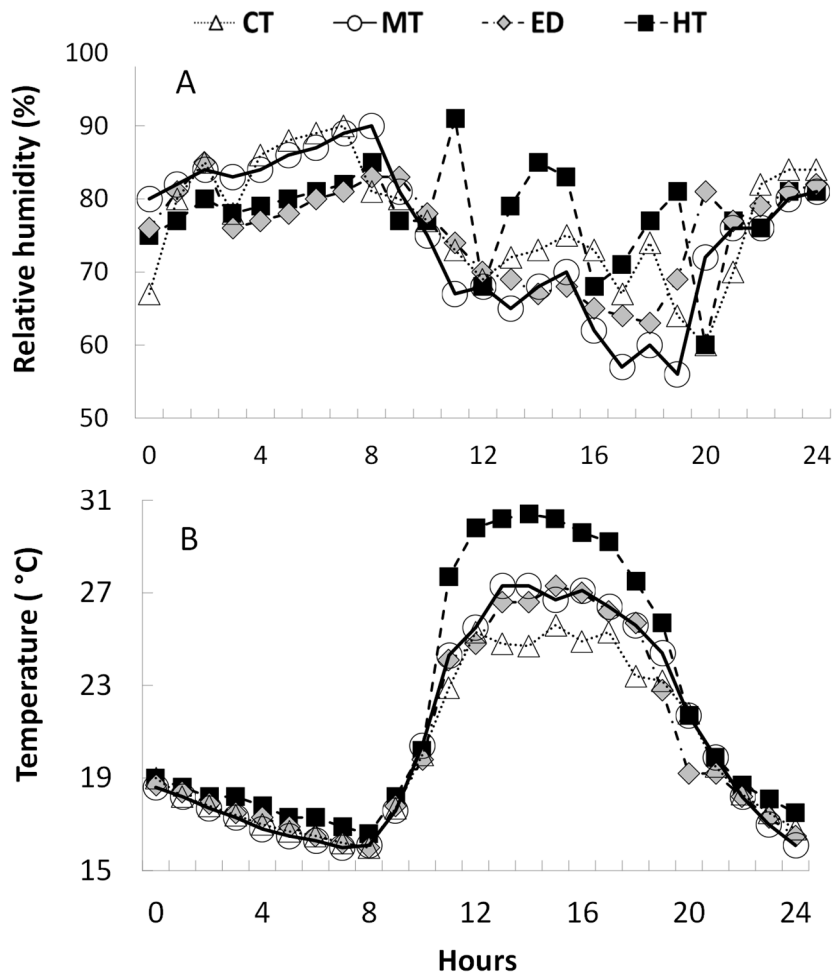
184 Statistical differences among assayed variables were determined by analyses of
185 variance, considering the experiment as a complete randomized design, and the
186 development stage, the treatments, and their interactions as explanatory factors. The
187 comparison between means was carried out using Tukey's test ($\alpha = 0.05$ unless
188 specified). The statistical analyses were performed with XLSTAT (Addinsoft Inc. Long
189 Island City, USA).

190

191 **3. Results**

192 In the present experiment, the mean temperatures were of 21.7 °C (CT) and 24.3
193 °C (HT) during the day, and of 17.0 °C (ED) and 18.0 °C (HT) during the night (Table
194 1). The average maximal temperatures were 25.3 °C (CT) and 29.4 °C (HT). On a daily
195 scale, the various climate management systems allowed differentiating the treatments
196 with increased temperatures from CT to HT, MT, and ED, showing intermediate
197 temperature variations (Figure 1A). The impact of the end-of-day treatment (ED) was
198 only visible in air temperature at 20:00. Relative humidity ranged from 61 to 92%, with
199 a night and day cycle and a mean value around 80% (Figure 1B, Table 1).

200



201

202 **Figure 1.** Example of a typical daily evolution of relative humidity (recorded on
203 September 22, 2013) (A) and air temperature (B) within the four greenhouse

204 compartments depending on the four treatments applied: control treatment (CT);
205 moderate temperature increase (MT); high temperature increase (HT); and temperatures
206 similar to those of the MT treatment during the day and night, with the exception of a
207 rapid drop in temperature at the end of the day (ED).

208

209 Fruit under HT started ripening sooner on a daily basis compared to other
210 treatments. The fruit growth duration, defined as the time between anthesis and the fruit
211 light red stage, was reduced by five days from 63.1 to 58.5 days (Table 2) from CT to
212 HT. The fruits grown under the intermediate temperature treatments (ED, MT) showed
213 an intermediate maturation time of around 60 days. We calculated the fruit growth
214 duration (from anthesis to red ripe stage) on a thermal time basis, considering a thermal
215 time basis (TTB) of 5.7 °C according to Adams et al. [4], 10 °C according to Calado
216 and Portas (1987) and Okello et al. (2014), or 0 °C (Table 2). Considering a thermal
217 time basis of 0 °C was the only way to find a constant fruit growth duration whatever
218 the temperature treatment was (average value 1191 °C d).

219

220 **Table 2.** Changes in physical and biochemical traits of ripe tomato fruits (stage R) according to treatment. Data are mean + SE.

Fruit quality traits	CT	MT	ED	HT	P value
Days to reach maturity	63.10 ± 1.12 a	60.16 ± 0.98 ab	60.72 ± 1.18 ab	58.50 ± 1.01 b	0.03
GDD ^a to reach maturity (TTB 0 °C)	1185 ab	1173 ab	1165 a	1239 b	0.142
GDD to reach maturity (TTB 5.7 °C)	826 a	830 a	819 a	906 b	0.021
GDD to reach maturity (TTB 10 °C)	554 a	571 a	558 a	655b	0.003
Fruit fresh weight (FW g)	96.0 ± 7.3 b	84.2 ± 6.1 ab	77.1 ± 3.2 a	78.1 ± 4.3 a	0.05
Fruit water conductance (cm/h)	35.34 ± 0.04 a	32.49 ± 0.05 a	31.81 ± 0.04 a	22.31 ± 0.06 b	0.028
Pericarp fresh weight (g)	72.97 ± 3.74 b	64.03 ± 4.16 ab	60.20 ± 3.85 a	58.57 ± 3.50 a	0.09
Pericarp dry weight content (% FW)	4.57 ± 0.13 a	4.60 ± 0.55 a	4.84 ± 0.13 a	4.54 ± 0.13 a	0.39
Seeds fresh weight (g)	20.69 ± 2.53 a	18.97 ± 2.33 a	18.77 ± 1.86 a	17.40 ± 1.87 a	0.44
Seeds dry weight content (% FW)	6.77 ± 0.81 b	6.45 ± 0.79 ab	6.82 ± 0.65 b	6.22 ± 0.75 a	0.04
<u>Macro compounds (g kg⁻¹ FW)</u>					
Glucose	7.54 ± 0.45 a	7.26 ± 0.33 a	7.80 ± 0.32 a	7.81 ± 0.32 a	0.60
Fructose	8.51 ± 0.49 a	8.00 ± 0.30 a	8.64 ± 0.30 a	8.89 ± 0.33 a	0.28
Sucrose	0.15 ± 0.04 a	0.19 ± 0.05 a	0.26 ± 0.06 a	0.24 ± 0.04 a	0.33
Starch	0.30 ± 0.03 a	0.37 ± 0.08 a	0.36 ± 0.04 a	0.25 ± 0.02 a	0.20
Citric acid	1.93 ± 0.08 a	2.08 ± 0.09 ab	2.20 ± 0.07 b	1.95 ± 0.09 a	0.10

Malic acid	1.40 ± 0.04 a	1.72 ± 0.12 b	1.73 ± 0.09 b	1.45 ± 0.08 a	0.01
Structural dry weight (g g ⁻¹ DW)	0.568 ± 0.012 a	0.573 ± 0.009 a	0.567 ± 0.010 a	0.547 ± 0.009 a	0.22
<u>Micro compounds (mg kg⁻¹ FW)</u>					
AsA + DHA	89.70 ± 5.46 ab	93.72 ± 6.02 ab	87.62 ± 6.21 b	104.27 ± 5.17 a	0.14
AsA	78.55 ± 5.39 a	81.03 ± 4.06 a	77.52 ± 6.57 a	103.08 ± 5.47 b	0.002
Lutein	0.39 ± 0.03 b	0.49 ± 0.04 ab	0.41 ± 0.04 ab	0.51 ± 0.04 a	0.06
Lycopene	11.96 ± 2.28 b	14.59 ± 2.55 b	15.20 ± 2.94 b	32.66 ± 5.84 a	0.0001
β-Carotene	2.40 ± 0.11 a	2.52 ± 0.11 a	2.46 ± 0.11 a	2.51 ± 0.09 a	0.85
Phytoene	3.34 ± 0.71 b	3.53 ± 0.72 b	3.54 ± 0.64 b	7.96 ± 1.48 a	0.0008
Caffeic acid glucoside	5.28 ± 0.47 a	4.74 ± 0.26 a	5.77 ± 0.50 a	5.12 ± 0.52 a	0.45
Chlorogenic acid	11.34 ± 1.53 a	11.88 ± 1.62 a	9.19 ± 1.25 a	13.31 ± 1.33 a	0.23
Chlorogenic acid derivative 1	1.78 ± 0.16 a	1.50 ± 0.10 a	1.70 ± 0.18 a	1.85 ± 0.10 a	0.21
Chlorogenic acid derivative 2	1.30 ± 0.13 a	1.08 ± 0.09 a	1.34 ± 0.19 a	1.23 ± 0.09 a	0.45
Rutin	7.17 ± 0.69 a	6.19 ± 0.78 a	6.68 ± 0.50 a	7.84 ± 0.77 a	0.34
Naringenin chalcone	74.58 ± 12.07 a	63.40 ± 9.84 a	67.12 ± 8.86 a	83.00 ± 9.11 a	0.44

221 GDD^a: Growing Degree Day; TTB: Thermal time basis ; AsA: ascorbic acid; DHA: dehydroascorbic acid; CT= Control conditions; ED = End-of-day temperature conditions

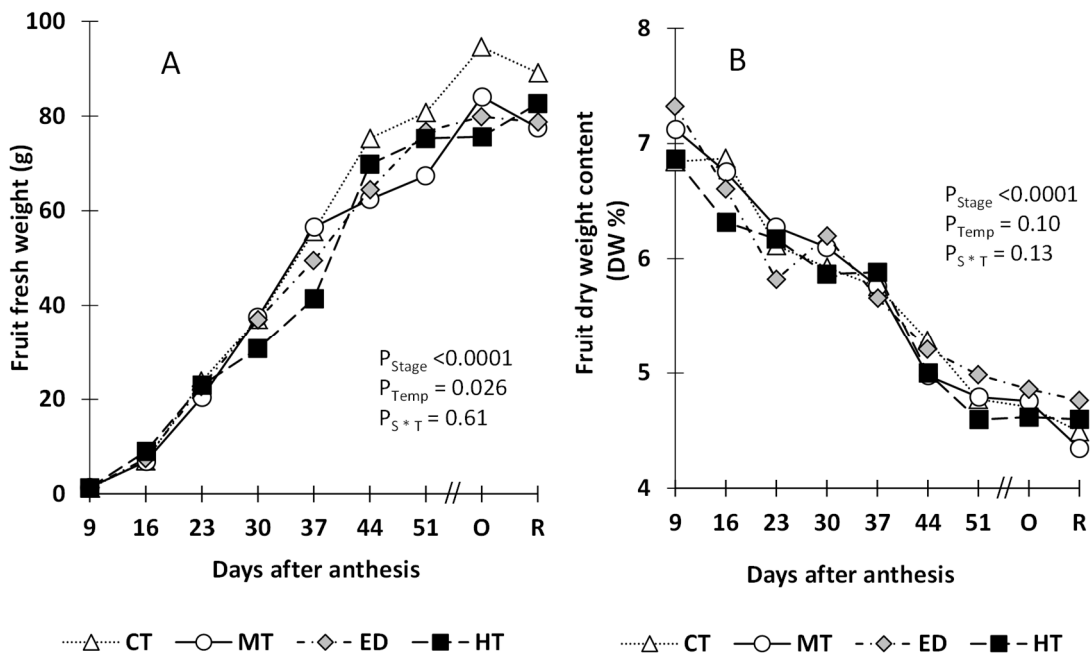
222 (from 19:00 to 22:00); HT = High temperature conditions (from 11:00 to 19:00); LT = Low temperature condition (11:00 to 19:00); FW = Fruit fresh weight (g); DW: Dry

223 weight. Different letters in the same column indicate a significant difference between means according to Tukey's test ($\alpha = 0.1$), significant differences are highlighted in bold.

224

225

226 The slight reduction of growth duration, corresponding to a reduction of 7%, had
227 a strong and larger impact on the fruit fresh weight accumulation. The fruit fresh mass
228 decreased by 18.6%, from 96 g to 78 g. Such fruit growth reduction was mostly due to a
229 decreased pericarp fresh weight (minus 20%, Figure 2A), and to a minor extent, to a
230 decrease in the seeds (-16%, Table 2). As usually observed, the pericarp dry weight
231 (DW) decreased during fruit development. However, the pericarp DW remained slightly
232 greater under the ED treatment ($\alpha = 0.1$, Figure 2B) and until maturity (Table 2, $\alpha =$
233 0.09). Moreover, it decreased with increasing temperature. The fruit surface
234 conductance was significantly modified by temperature treatments (Table 2).
235



236

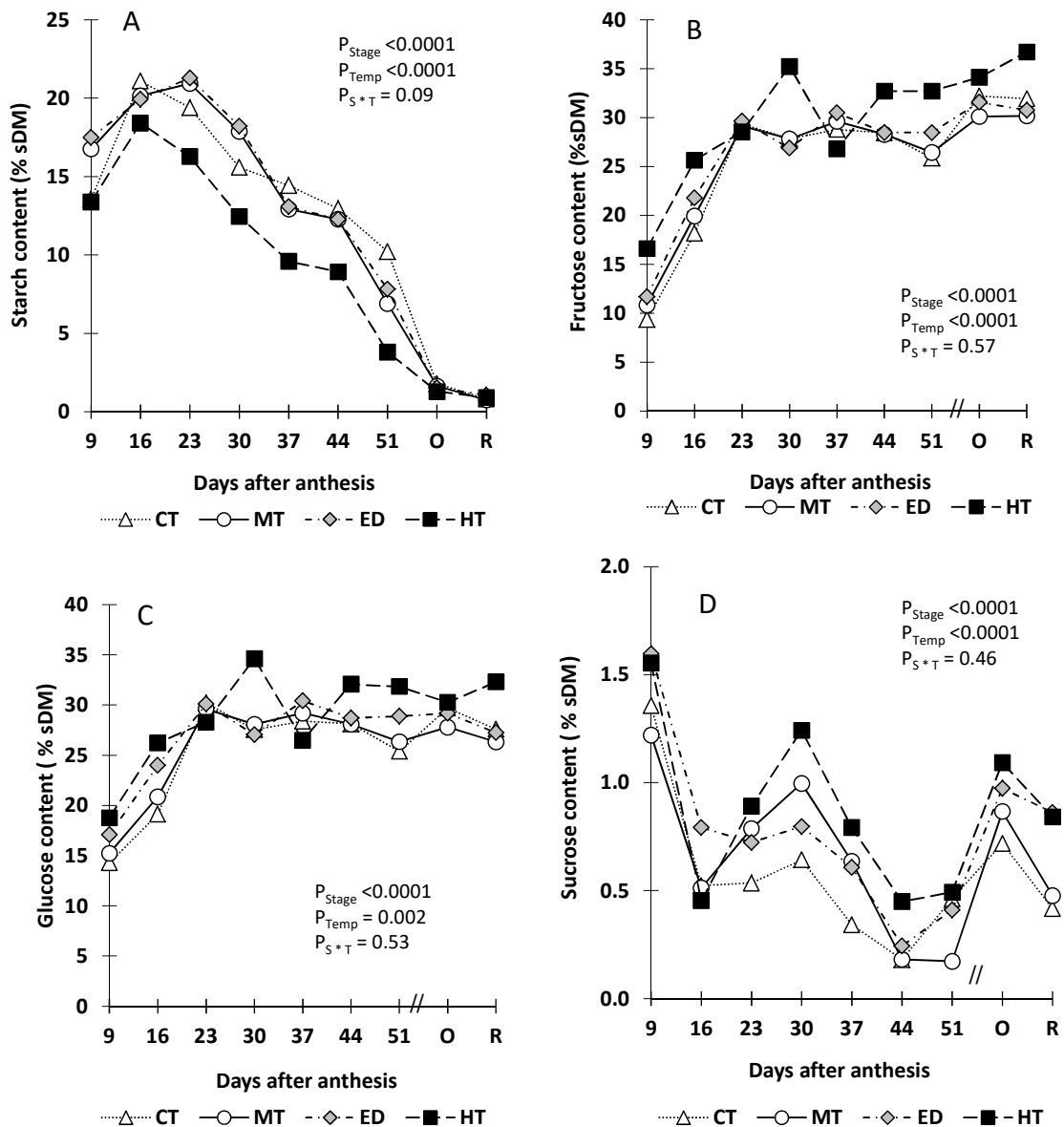
237 **Figure 2.** Evolution of fruit fresh weight (A) and fruit dry weight (B) contents as the
238 fruits develop from nine days after anthesis (to light red stage) depending on the four
239 temperature treatments applied (for treatments legends, please refer to Figure 1 caption).
240 The fruits (a total of 290 fruits) were harvested from nine to 51 days after anthesis,

241 orange (O) and red (R) stages. The data represent average values. p-values were
242 obtained from an ANOVA considering the effect of fruits development stage (Stage),
243 the temperature of each treatment (Temp) and the interaction between fruit Stage and
244 Treatment (S * T).

245 HT reduced the fruit surface conductance by 37% compared to CT, but there was
246 no significant effect for fruits harvested on plants grown under MT or ED. Expressed on
247 a fresh weight basis (FW), the pericarp sugars composition was not modified at harvest,
248 whatever the treatment. In contrast, organic acid concentrations were affected, with
249 lower concentrations of malic and citric acid under CT and HT, and higher
250 concentrations for fruits grown under the ED treatment (+24 %) compared to the
251 control. Temperature treatments also affected minor compounds accumulation. At
252 harvest, fruit grown under HT had a significant increased amount of ascorbate (+31%)
253 compared to fruits under control conditions. In contrast, moderate increased
254 temperatures (ED, MT) did not affect the fruit ascorbate content. Similarly, carotenoids
255 contents (except β -carotene) were higher under HT; lutein, phytoene and lycopene
256 contents increased by 31%, 138% and 173%, respectively under HT compared to CT,
257 but no significant changes were recorded under moderate temperature increase (ED or
258 MT). Additionally, whatever the temperature treatment, there was no significant effect
259 of moderate or stronger temperature increase on phenolic compounds.

260 We followed the kinetics of primary and secondary compounds accumulation of
261 within the fruits, expressed per structural dry matter. When expressed on a structural dry
262 matter basis, any change in primary or secondary metabolite content is related to
263 changes in the fruit metabolism and not to a dilution (or concentration) effect triggered
264 by the accumulation (or the shortage) of water or other compounds.

265 If the starch content evolution during fruit growth showed similar patterns
 266 whatever the treatment, the maximal content was affected by the treatments, and
 267 especially by the HT treatment, where there was a significant reduction in the starch
 268 accumulation (Figure 3A).
 269



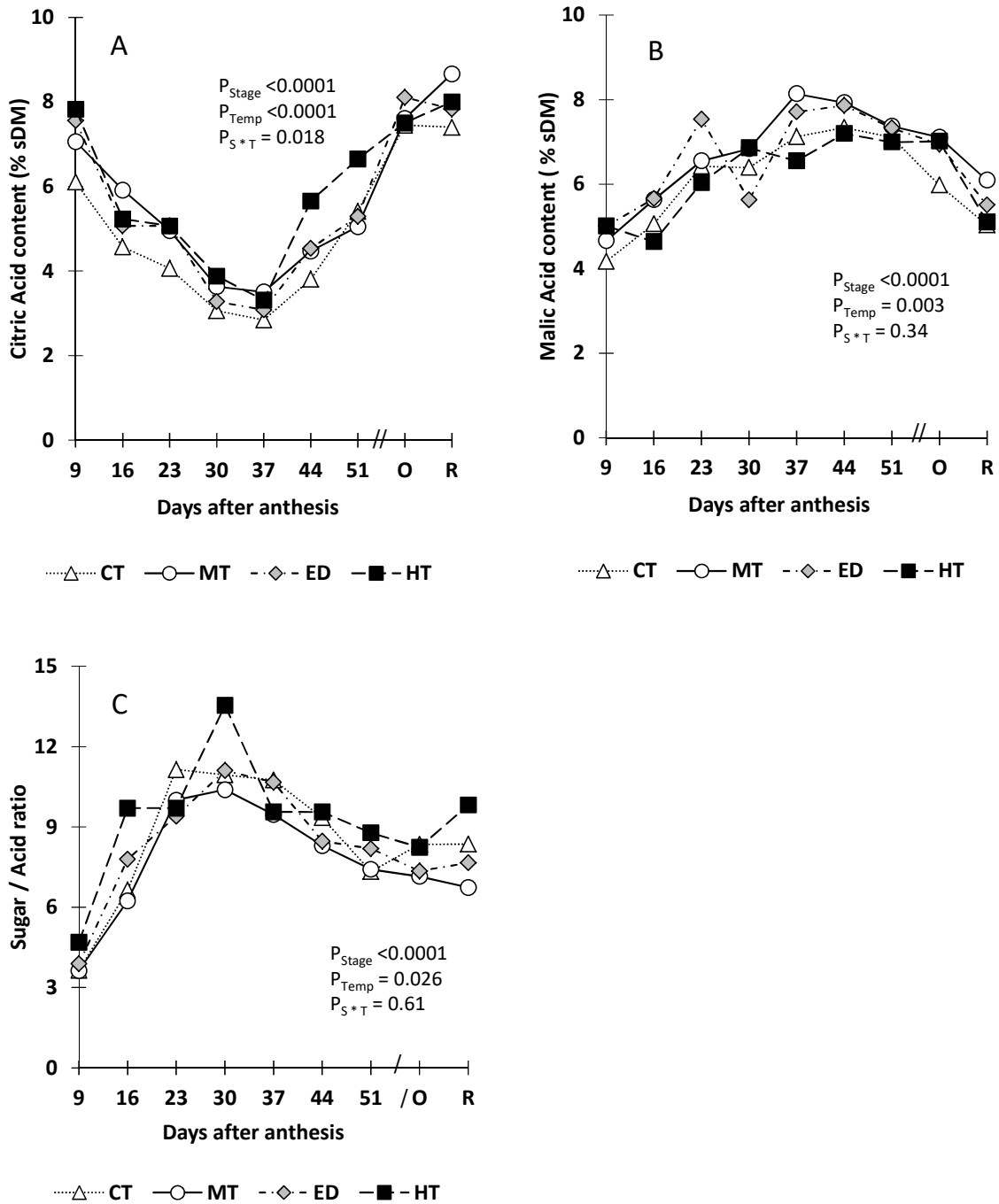
270
 271 **Figure 3.** Evolution of the contents of starch (A), fructose (B), glucose (C) and sucrose
 272 (D) to the structural dry weight content as the fruits develop from nine days after

273 anthesis (to light red stage) depending on the four temperature treatments applied (for
274 treatments legends, please refer to Figure 1 caption).

275

276 Glucose, fructose and sucrose contents increased in fruit growing under the HT
277 treatment (Figures 3B, C, D). Similarly, the time course of citric acid was affected by
278 HT, with an increased accumulation from 37 DAA. However, there was no difference at
279 maturity (Figure 4A). On the other hand, malic acid accumulation was reduced by the
280 HT treatment, also without significant difference at maturity (Figure 4B). Consequently,
281 the ratio between total soluble sugars and acids was greater under HT when compared to
282 the control (Figure 4C).

283

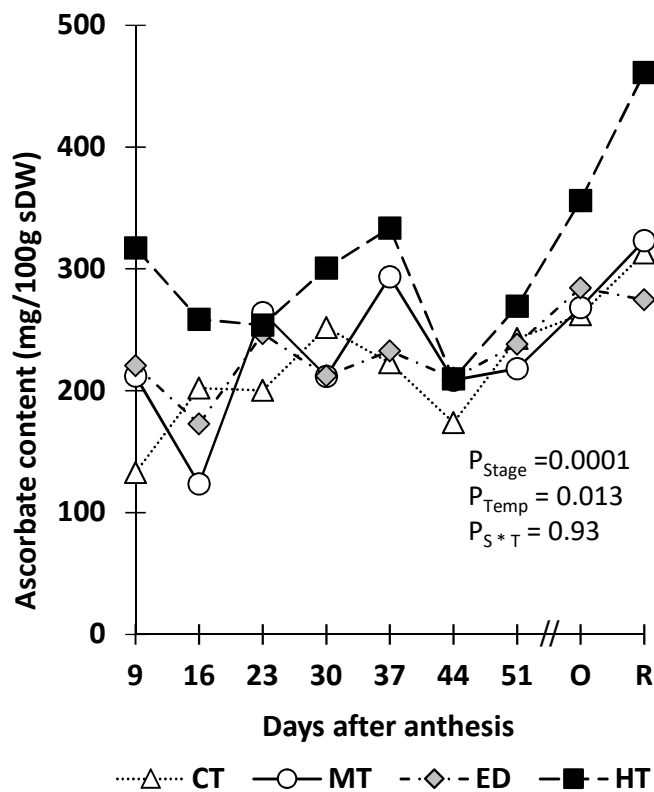


284

285 **Figure 4.** Evolution of the contents of citric acid (A), malic acid (B) and sugar/acid
 286 ratio (C) to the structural dry weight content as the fruits develop from nine days after
 287 anthesis (to light red stage) depending on the four temperature treatments applied (for
 288 treatments legends, please refer to Figure 1 caption).

289

290 Total ascorbate concentrations (tAsA) tended to increase under HT treatments (α
 291 = 0.14, Table 2). This was due to the accumulation of the reduced form (ascorbic acid
 292 content, rAsA) which significantly increased under HT treatments, particularly from 51
 293 DAA until ripening stage (Figure 5). Thus, the proportion of vitamin C in a reduced
 294 form (rAsA/tAsA ratio) was significantly greater for fruits harvested under HT (Table
 295 2).



296
 297 **Figure 5.** Evolution of the content of reduced ascorbate to the structural dry weight
 298 content as the fruits develop from nine days after anthesis (to light red stage) depending
 299 on the four temperature treatments applied (for treatments legends, please refer to
 300 Figure 1 caption).

301

302 **4. Discussion**

303 Despite the fact that the average temperature differences were rather small and
304 close to climate projections for the near future in France, we observed that they affected
305 different processes and resulted in reduced fruit growth and changes in fruit quality
306 traits at harvest. In the present experiment, the most visible quality trait impacted by the
307 temperature treatments was the final fruit size at harvest. We observed that the fruit
308 growth duration decreased in a linear way with increased temperatures: the higher the
309 temperature, the lower the duration of fruit development (from anthesis until red ripe
310 stage). Similar findings have been reported with a reduced developmental duration to
311 reach ripe stage for tomato fruits grown under increased temperature, especially during
312 the fruit later stages of maturation (Adams et al. 2001; Fleisher et al. 2006; Hurd and
313 Graves, 1985). In other species like chili, heat stress following anthesis or from 30 DAA
314 until harvest also reduced the growth period of chili fruits by 15 and 10 days,
315 respectively (Pagamas and Nawata, 2008). High temperatures generally accelerate fruit
316 maturation and ripening, and this could be an adaptive mechanism to stress conditions,
317 enabling the plant to disperse its seeds faster when under stress (Mizhari, 1982).
318 Experiments using locally heated fruits showed that heating fruits reduced fruit size,
319 since it modified the cell division orientation (Fanwoua et al. 2012) and reduced cell
320 expansion (Okello et al. 2014). In another study, rising temperatures from 20/20
321 day/night to 25/25°C had no effect on tomato fruit size (Bertin, 2005). This might be
322 linked to the fact that i) the plant remains at optimal temperature regarding fruit growth,
323 or that ii) different processes are affected by increased temperatures, but they
324 compensate one another. Indeed, Bertin (2005) reported a compensatory effect between
325 a reduced duration of fruit cell division (which reduced the number of fruit cells per
326 fruit) and an increased period of cell expansion, where the cell expansion rate was not
327 affected. When the temperature further increases, some processes will not be at their

328 optimal temperature and will not be compensated. In addition, other processes can be
329 affected; so the reduction of fruit size could be related to other factors such as limited
330 assimilate supply, as it was reported for higher fruit load under HT (Gautier et al. 2005).
331 Indeed, the fruit dry weight accumulation was reduced under HT (Figure 2), which
332 could be linked to the increased carbohydrate loss by respiration. Furthermore, the
333 increase in temperature causes a higher vapor pressure deficit (VPD), which could lead
334 to a larger water loss by transpiration. However, this higher climatic demand could be
335 partly, fully, or over-compensated by the observed decrease of the fruit skin
336 conductance associated with the HT treatment. Similar findings have been reported for
337 leaves growing under water stress (Cameron et al. 2006), which could be the
338 consequence of changes in the cuticular wax composition or thickness (Vogg et al.
339 2004). If the water conductance of young growing fruits is also decreased, it will impair
340 fruits photosynthesis and transpiration (Blanke and Lenz, 1989). Even if their
341 photosynthetic activity remains low (Carrara et al. 2001), it can contribute to 10 or 15%
342 of the carbon skeleton of the fruits (Tanaka et al. 1974). Thus, reduced fruit
343 photosynthesis alters carbon allocation to seeds and may impact the seeds quality
344 (Lytovchenko et al. 2011).

345 In addition, reducing fruit transpiration helps maintaining fruit water pressure
346 and limits the entry of water and carbon into the fruits through the phloem. This could
347 partly explain the lower rate of fruit growth observed under HT. Similar data have been
348 reported by Li et al. (2001). in covered peach fruits: a decrease in transpiration,
349 respiration, and photosynthesis rates could contribute to reducing the quantity of
350 carbohydrates entering into the fruits, which in turn would result in reducing soluble
351 solids content. We observed a 37% reduction in fruit water conductance from the

352 control to the HT treatment (at red ripe stage), which parallels the 33% decrease in dry
353 mass accumulation.

354 In the present experiment, dry matter and structural dry matter contents were not
355 affected by HT applied during tomato fruits development (Figures 1C and D). However,
356 we observed that the ED treatment tended to increase the pericarp DM content. Under
357 moderate temperatures, Heuvelink (1995) reported no significant difference in the DM
358 content of fruits harvested on plants grown at 18 °C or 24 °C. In contrast, under higher
359 temperatures, Rosales et al. (2011) found increased dry matter contents in tomato fruits
360 produced at 30/12 °C compared to 25/14 °C (day/night respectively), which could also
361 be linked to water limitation in the summer conditions. In the present experiment, the
362 temperature decrease at the end of the day may have been too low, and it would be
363 interesting to consider broader changes in ED temperature to confirm its potential role
364 in improving fruits dry matter content. In addition, we observed that HT tended to
365 reduce both the carbon influx to the fruit and its partitioning to the seeds, and
366 consequently, seed storage and quality could be altered (Lytovchenko et al. 2011).

367 The present work gives a better understanding of the influence of HT on
368 processes linked to fruit quality traits, considering both visual traits, such as fruit size,
369 and fruit composition. In our study, the time course of starch accumulation and
370 degradation was significantly affected by temperature; the HT treatment reduced starch
371 accumulation particularly from 16 to 58 DAA (Figure 3A). The period during the first
372 10-30 DAA following the fruit set in tomato fruits is the one when the rate of starch
373 biosynthesis is potentially at its highest levels (Walker and Ho, 1977). Similar data were
374 obtained when increasing temperature in potatoes, which perturbs starch synthesis and
375 related enzymatic activities, increasing leaf respiration and carbon loss (Geigenberger et
376 al. 1998). These changes in starch metabolism were accentuated by the effect of HT on

377 fruits phenology, which accelerates fruit maturation and consequently starch
378 degradation. This more rapid degradation of starch is in agreement with our observed
379 increased soluble sugars content (glucose, fructose and sucrose content, Figures 3B, C
380 and D).

381 Rosales et al. (2011) reported that sugar contents increased at HT while organic
382 acids contents diminished. Similarly, Wang and Camp (2000) also reported increased
383 sucrose contents in two strawberry varieties when increasing temperatures from 18/12
384 to 25/22 °C day/night, respectively. In tomatoes, the effect of HT on organic acids
385 accumulation was different according to each acid: citric acid contents increased by the
386 HT treatment from 37 to 58 DAA, and then decreased at ripe stage (65 DAA) (Figure
387 4A). Malic acid contents were reduced by the temperature treatments applied during
388 tomato fruits growth (Figure 4B); consequently, the ratio between soluble sugars and
389 organic acids was increased by the HT treatment during tomato fruits growth (Figure
390 4C).

391 Ascorbic acid contents (AsA) increased in fruits grown under HT, and
392 particularly during ripening (Figure 5). At this stage, most of the vitamin C was
393 reduced, which is the active form that helps the plant to resist oxidative stress. Rosales
394 et al. (2009) reported similar findings when studying the seasonal change in tomato
395 oxidative compounds: they found the greatest amount of ascorbate during the hottest
396 period of the year.

397 Lutein contents in tomato fruits were not changed by temperature treatments and
398 decreased during fruit growth and ripening (Table 2). Lycopene, β -carotene and
399 phytoene were increased under the HT treatment (Table 2). Temperature may have
400 contrasting effects on carotenoids contents as previously reported by Dorais et al.
401 (2008), and a decrease in the content of carotenoids has been found under extreme

402 temperatures (either high above 32 °C or low below 12 °C) (Dumas et al. 2003). In our
403 experiment, temperatures were lower and close to optimal conditions around 22-26 °C.
404 Thus, lycopene and other carotenoids' syntheses were not inhibited.

405 This study reinforces our knowledge of the effects of temperature on the
406 different processes involved in building tomato quality. Even a moderate increase in
407 temperature can affect the accumulation of water and carbon in the fruit, the synthesis
408 and accumulation of starch, the transpiration of the fruit, and the primary and secondary
409 metabolism, so that the growth and quality of the fruit at maturity are affected. This
410 study also aimed to determine if crop and climate management can prevent the
411 detrimental effects of increased temperatures and help growers cope with consumers'
412 demand for tastier fruits. The ED treatment applied increased the pericarp dry matter
413 content, but the temperature drop at the end of the day was moderate and it did not
414 promote fruit growth duration, nor did it increase the sugar acid ratio. In a context of
415 climate change, crop species will have to undergo an adaption to temperature increases,
416 either through genetics, by investigating the variability of the sensitivity of these
417 processes to temperature, or through cultural practices that mitigate climate changes.

418

419 **Acknowledgments**

420 The authors would like to acknowledge the technical assistance of Béatrice
421 Brunel, Sylvie Sérino, and Emilie Rubio. The present work was financed by the
422 Metaprogram ACCAF (INRA). Juan M. Ruiz-Nieves would like to acknowledge the
423 Mexican Government for funding his PhD grant and for financing his stay at France.

424

425 **Conflict of interests**

426 The authors have no conflict of interest to declare.

427

428 **References**

- 429 Adams, S.R., Cockshull, K.E., Cave, C.R.J., 2001. Effect of temperature on the growth
430 and development of tomato fruits. *Ann. Bot.* 88, 869–877.
431 <https://doi:10.1006/anbo.2001.1524>
- 432 Bertin, N., 2005. Analysis of the tomato fruit growth response to temperature and plant
433 fruit load in relation to cell division, cell expansion and DNA endoreduplication.
434 *Ann. Bot.* 95, 439–447. <https://doi:10.1093/aob/mci042>
- 435 Blanke, M., Lenz, F., 1989. Fruit photosynthesis. *Plant Cell Environ.* 12, 31–46.
436 <https://doi.org/10.1111/j.1365-3040.1989.tb01914.x>
- 437 Brandt, S., Pék, Z., Barna, É., Lugasi, A., Helyes, L., 2006. Lycopene content and
438 colour of ripening tomatoes as affected by environmental conditions. *J. Sci. Food*
439 *Agric.* 86, 568–572. <https://doi.org/10.1002/jsfa.2390>
- 440 Calado, A.M., Portas, C.M., 1987. Base-temperature and date of planting in processing
441 tomatoes. *Acta Hortic.* 200, 185–193.
442 <https://doi.org/10.17660/ActaHortic.1987.200.17>
- 443 Cameron, K.D., Teece, M.A., Smart, L.B., 2006. Increased accumulation of cuticular
444 wax and expression of lipid transfer protein in response to periodic drying events in
445 leaves of tree tobacco. *Plant Physiol.* 140, 176–183.
446 <https://doi.org/10.1104/pp.105.069724>
- 447 Carrara, S., Pardossi, A., Soldatini, G.F., Tognoni, F., Guidi, L., 2001. Photosynthetic
448 activity of ripening tomato fruit. *Photosynthetica* 39, 75–78.
449 <https://doi.org/10.1023/A:1012495903093>
- 450 Dannehl, D., Huber, C., Rocks, T., Huyskens-Keil, S., Schmidt, U., 2012. Interactions
451 between changing climate conditions in a semi-closed greenhouse and plant

452 development, fruit yield, and health-promoting plant compounds of tomatoes. *Sci.*
453 *Hortic.* 138, 235–243. <https://doi.org/10.1016/j.scienta.2012.02.022>

454 Dorais, M., Ehret, D.L., Papadopoulos, A.P., 2008. Tomato (*Solanum lycopersicum* L.)
455 health components: from the seed to the consumer. *Phytochem. Rev.* 7, 231–250.
456 <https://doi.org/10.1007/s11101-007-9085-x>

457 Dorais, M., Papadopoulos, A.P., Gosselin, A., 2010. Greenhouse tomato fruit quality.
458 *Hortic. Rev.* 26, 239–319. <https://doi.org/10.1002/9780470650806.ch5>

459 Dumas, Y., Dadomo, M., Di Lucca, G., Grolier, P., 2003. Effects of environmental
460 factors and agricultural techniques on antioxidant content of tomatoes. *J. Sci. Food*
461 *Agric.* 83, 369–382. <https://doi.org/10.1002/jsfa.1370>

462 Fanwoua, J., de Visser, P.H.B., Heuvelink, E., Angenent, G.C., Yin, X., Marcelis,
463 L.F.M., Struil, P., 2012. Response of cell division and cell expansion to local fruit
464 heating in tomato fruit. *J. Am. Soc. Hortic. Sci.* 137, 294–301.
465 <https://doi.org/10.21273/JASHS.137.5.294>

466 Fishman, S., Génard, M., 1998. A biophysical model of fruit growth: simulation of
467 seasonal and diurnal dynamics of mass. *Plant Cell Environ.* 21, 739–752.
468 <https://doi.org/10.1046/j.1365-3040.1998.00322.x>

469 Fleisher, H.D., Logendra, S.L., Moraru, C., Aren-Jan, B., Cavazzoni, J., Gianfagna, T.,
470 Lee, T-C., Janes, H.W., 2006. Effect of temperature perturbations on tomato
471 (*Lycopersicon esculentum* Mill.) quality and production scheduling. *J. Hortic. Sci.*
472 *Biotechnol.* 81, 125–131. <https://doi.org/10.1080/14620316.2006.11512038>

473 Garg, N., Cheema, D.S.C., 2011. Assessment of fruit quality attributes of tomato
474 hybrids involving ripening mutants under high temperature conditions. *Sci. Hortic.*
475 131, 29–38. <https://doi.org/10.1016/j.scienta.2011.09.024>

476 Gautier, H., Diakou-Verdin, V., Benard, C., Reich, M., Buret, M., Bougaud, F., Poëssel,
477 J.L., Caris-Veyrat, C., Génard, M., 2008. How does tomato quality (sugar, acid, and
478 nutritional quality) vary with ripening stage, temperature, and irradiance? J. Agric.
479 Food Chem. 56, 1241–1250. <https://doi.org/10.1021/jf072196t>

480 Gautier, H., Rocci, A., Buret, M., Grasselly, D., Causse, M., 2005. Fruit load and fruit
481 position alters response to temperature and subsequently cherry tomato quality. J.
482 Sci. Food Agric. 85, 1009–1016. <https://doi.org/10.1002/jsfa.2060>

483 Geigenberger, P., Geiger, M., Stitt, M., 1998. High-Temperature Perturbation of Starch
484 Synthesis Is Attributable to Inhibition of ADP-Glucose Pyrophosphorylase by
485 Decreased Levels of Glycerate-3-Phosphate in Growing Potato Tubers. Plant
486 Physiol. 117, 1307–1316. <https://doi.org/10.1104/pp>.

487 Gomez, L., Bancel, D., Rubio, E., Vercambre, G., 2007. The microplate reader: an
488 efficient tool for the separate enzymatic analysis of sugar in plant tissues–validation
489 of micro method. J. Sci. Food Agric. 87, 1893–1905.
490 <https://doi.org/10.1002/jsfa.2924>

491 Gomez, L., Rubio, E., Augé, M., 2002. A new procedure for extraction and
492 measurement of soluble sugars in ligneous plants. J. Sci. Food Agric. 82, 360–369.
493 <https://doi.org/10.1002/jsfa.1046>

494 Guichard, S., Bertin, N., Leonardi, C., Gary, C., 2001. Tomato fruit quality in relation to
495 water and carbon fluxes. Agronomie 21, 385–392.
496 <https://doi.org/10.1051/agro:2001131>

497 Heuvelink, E., 1995. Effect of temperature on biomass allocation in tomato
498 (*Lycopersicon esculentum*). Physiol. Plant 94, 447–452.
499 <https://doi.org/10.1111/j.1399-3054.1995.tb00952.x>

500 Hurd, R.G., Graves, C.J., 1985. Some effects of air and root temperatures on the yield
501 and quality of glasshouse tomatoes. *J. Hortic. Sci.* 60, 359–371.
502 <https://doi.org/10.1080/14620316.1985.11515640>

503 Krumbein, A., Schwarz, D., Kläring, H.P., 2006. Effects of environmental factors on
504 carotenoid content in tomato (*Lycopersicon esculentum* (L.) Mill.) grown in a
505 greenhouse. *J. Appl. Bot. Food Qual.* 80, 160–164.

506 Li, S.H., Génard, M., Bussi, C., Huguet, J.G., Habib, R., Besset, J., 2001. Fruit quality
507 and leaf photosynthesis in response to microenvironment modification around
508 individual fruit by covering the fruit with plastic in nectarine and peach trees. *J.*
509 *Hortic. Sci. Biotech.* 76, 61–69. <https://doi.org/10.1080/14620316.2001.11511328>

510 Lytovchenko, A., Eickmeier, I., Pons, C., Osorio, S., Szecowka, M., Lehmberg, K.,
511 Arrivault, S., Tohge, T., Pined, B., Antón, M.T.O., Hedtke, B., Lu, Y., Fisahn, J.,
512 Bock, R., Stitt, M., Grimm, B., Granell, A., Fernie, A.R., 2011. Tomato fruit
513 photosynthesis is seemingly unimportant in primary metabolism and ripening but
514 plays a considerable role in seed development. *Plant Physiol.* 157, 1650–1663.
515 <https://doi.org/10.1104/pp.111.186874>

516 Mizrahi, Y., 1982. Effect of salinity on tomato fruit ripening. *Plant Physiol.* 69, 966–
517 970. <https://doi.org/10.1104/pp.69.4.966>

518 Moretti, C.L., Mattos, L.M., Calbo, A.G., Sargent, S.A., 2010. Climate changes and
519 potential impacts on postharvest quality of fruit and vegetable crops: A review.
520 *Food. Res. Int.* 43, 1824–1832. <https://doi.org/10.1016/j.foodres.2009.10.013>

521 Okello, R.C.O., de Visser, P.H.B., Heuvelink, E., Lammers, M., de Maagd, R.A.,
522 Struik, P.C., Marcelis, L.F., 2014. A multilevel analysis of fruit growth of two
523 tomato cultivars in response to fruit temperature. *Plant Sci.* 153, 403–418.
524 <https://doi.org/10.1111/ppl.12247>.

525 Pagamas, P., Nawata, E., 2008. Sensitive stages of fruit and seed development of chili
526 pepper (*Capsicum annum* L. var. Shishito) exposed to high temperature stress. *Sci.*
527 *Hortic.* 117, 21–25. <https://doi.org/10.1016/j.scienta.2008.03.017>

528 Rahmati, M., Vercambre, G., Davarynejad, G., Bannayan, M., Azizi, M., Génard, M.,
529 2015. Water scarcity conditions affect peach fruit size and polyphenol contents
530 more severely than other fruit quality traits. *J. Sci. Food Agric.* 95, 1055–1065.
531 <https://doi.org/10.1002/jsfa.6797>

532 Rivero, R.M., Ruiz, J.M., García, P.C., López-Lefebvre, L.R., Sánchez, E., Romero, L.,
533 2001. Resistance to cold and heat stress: accumulation of phenolic compounds in
534 tomato and watermelon plants. *Plant Sci.* 160, 315–321.
535 [https://doi.org/10.1016/S0168-9452\(00\)00395-2](https://doi.org/10.1016/S0168-9452(00)00395-2)

536 Robertson, G.H., Mahoney, N.E., Goodman, N., Pavlath, A.E., 1995. Regulation of
537 lycopene formation in cell suspension culture of VFNT tomato (*Lycopersicon*
538 *esculentum*) by CPTA, growth regulators, sucrose, and temperature. *J. Exp. Bot.* 46,
539 667–673. <https://doi.org/10.1093/jxb/46.6.667>

540 Rosales, A.M., Rios, J.J., Cervilla, L.M., Rubio-Wilhelmie, M.M., Blasco, B., Ruiz,
541 J.M., Romero, L., 2009. Environmental conditions in relation to stress in cherry
542 tomato fruits in two experimental Mediterranean greenhouses. *J. Sci. Food Agric.*
543 89, 735–742. <https://doi.org/10.1002/jsfa.3500>

544 Rosales, M.A., Cevilla, L.M., Sánchez-Rodriguez, E., Rubio-Wilhelmi, M.M., Blasco,
545 B., Rios, J.J., Soriano, T., Castilla, N., Romero, L., Ruiz, J.M., 2011. The effect of
546 environmental conditions on nutritional quality of cherry tomato fruits: evaluation
547 of two experimental Mediterranean greenhouses. *J. Sci. Food Agric.* 91, 152–162.
548 <https://doi.org/10.1002/jsfa.4166>.

549 Sérino, S., Gomez, L., Costagliola, G., Gautier, H., 2009. HPLC assay of tomato
550 carotenoids: validation of a rapid microextraction technique. *J. Agric. Food Chem.*
551 57, 8753–8760. <https://doi.org/10.1021/jf902113n>.

552 Stevens, R., Buret, M., Garchery, C., Carretero, Y., Causse, M., 2006. Technique for
553 rapid, small-scale analysis of vitamin C levels in fruit and application to a tomato
554 mutant collection. *J. Agric. Food Chem.* 54, 6159–6165.
555 <https://doi.org/10.1021/jf061241e>

556 Tanaka, A., Fujita, K., Kikuchi, K., 1974. Nutrio-physiological studies on the tomato
557 plant. III. Photosynthetic rate on individual leaves in relation to dry matter
558 production of plants. *Soil Sci. Plant Nutr.* 20, 173–183.
559 <https://doi.org/10.1080/00380768.1974.10433240>

560 Truffault, V., Fifel, F., Longuenesse, J.J., Vercambre, G., Le Quillec, S., Gautier, H.,
561 2015. Impact of temperature integration under greenhouse on energy use efficiency,
562 plant growth and development and tomato fruit quality depending on cultivar
563 rootstock combination. *Acta Hortic.* 1099, 95–100.
564 <https://doi.org/10.17660/ActaHortic.2015.1099.7>

565 Van der Ploeg, D., Heuvelink, E., 2005. Influence of sub-optimal temperature on tomato
566 growth and yield: a review. *J. Hortic. Sci. Biotechnol.* 80, 652–659.
567 <https://doi.org/10.1080/14620316.2005.11511994>

568 Vogg, G., Fischer, S., Leide, J., Emmanuel, E., Jetter, R., Levy, A.A., Riederer, M.,
569 2004. Tomato fruit cuticular waxes and their effects on transpiration barrier
570 properties: functional characterization of a mutant deficient in a very-long-chain
571 fatty acid b-ketoacyl-CoA synthase. *J. Exp. Bot.* 55, 1401–1410.
572 <https://doi.org/10.1093/jxb/erh149>

573 Walker, A.J., Ho, L.C., 1977. Carbon translocation in the tomato: carbon import and
574 fruit growth. *Ann. Bot.* 41, 813–823. <https://www.jstor.org/stable/42753774>
575 Wang, S.Y., Camp, M.J., 2000. Temperatures after bloom affect plant growth and fruit
576 quality of strawberry. *Sci. Hortic.* 85, 183–199. <https://doi.org/10.1016/S0304->
577 4238(99)00143-0
578