

Effect of temperature perturbations on tomato (*Lycopersicon esculentum* Mill.) quality and production scheduling

By DAVID H. FLEISHER^{1*}, LOGAN S. LOGENDRA², CATALIN MORARU³, AREND-JAN BOTH⁴, JAMES CAVAZZONI⁴, THOMAS GIANFAGNA², TUNG-CHING LEE³ and HARRY W. JANES²

¹Crop Systems and Global Change Laboratory, USDA-ARS, BARC-West Building 1 Room 342, 10300 Baltimore Avenue, Beltsville, MD 20705, USA

²Department of Plant Biology and Pathology, Rutgers, The State University of New Jersey, 59 Dudley Road, New Brunswick, NJ 08901, USA

³Department of Food Science, Rutgers, The State University of New Jersey, 63 Dudley Road, New Brunswick, NJ 08901, USA

⁴Bioresource Engineering, Department of Plant Biology and Pathology, Rutgers, The State University of New Jersey, 20 Ag Extension Way, New Brunswick, NJ 08901, USA

(e-mail: dfleishe@asrr.arsusda.gov)

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SUMMARY

Controlled environment experiments were conducted to evaluate the effect of a 2-week change in air temperature imposed after first fruit-set on tomato production scheduling and on the quality of vine-ripened fruit. Experiments were conducted with hydroponically-grown tomato (*Lycopersicon esculentum* Mill., cv. 'Laura'). Air temperature was altered from control day/night temperature values of 23°/18°C for a 2-week period starting 10 d after fruit-set. Plants were returned to the 23°/18°C temperature and a minimum of eight fruits per treatment were harvested at three ripening stages, breaker (when 25% of the fruit skin had acquired a red tint), breaker plus 3 d, and breaker plus 6 d. A perturbation of $\pm 5^\circ\text{C}$ (28°/23°C and 18°/13°C) was used in two Experiments (E1 and E2) and $\pm 7^\circ\text{C}$ (30°/25°C and 16°/11°C) was used in a third Experiment (E3). Fruits were more responsive to an increase than to a decrease in temperature. Reductions in days to harvest (from 3.1 – 8.5 d) and fruit fresh weight at later stages of vine-ripening were observed for the high temperature treatments. Colour indices, soluble solids contents (SSC), acidity and viscosity at each ripening stage were significantly affected by high temperature treatments. The results indicate that short-term temperature perturbations following first fruit-set can influence the rates at which changes occurred in the external appearance of fruit (colour) and in their internal characteristics. The results can be used to improve environmental control and management strategies for tomato growers.

Tomato is one of the most commonly grown greenhouse crops in the United States and is also a candidate for the National Aeronautics and Space Administration (NASA) Advanced Life Support (ALS) research programme (Henninger, 1989). For ALS applications, crops will be grown in controlled environments on-board future space stations to satisfy the nutritional needs of the crew and to facilitate resource recycling (Barta *et al.*, 1999). Environmental control and management systems are essential to obtain satisfactory and predictable crop growth rates, yield and fruit quality. Mathematical relationships between daily light integral and days to flowering have been developed for single-truss tomato production systems (Chiu *et al.*, 1996; Giniger *et al.*, 1988; McAvoy *et al.*, 1989) to help growers make better management decisions. However, environmental control strategies can be improved through more detailed knowledge of crop growth and developmental responses to the environment (e.g., Challa and van Straten, 1993; Sigrimis and Rerras, 1996; Van Pee and Berckmans, 1998; Volk *et al.*, 1997).

Air temperature is known to influence tomato production scheduling and, during commercial production, the timing, magnitude and duration of temperature changes can be significant. Higher growth temperatures result in shorter crop production times [i.e., number of days to harvest; (DTH)], but with smaller fruit and lower yield (Sawheny and Polowick, 1985; Rylski, 1979). Differences in temperature during vegetative growth influence the rate of development and timing to first flower (Grimstad, 1995; Sauser, 1998). Hurd and Cooper (1970) reported that application of a short 2-week chilling temperature prior to anthesis delayed crop development, but resulted in larger individual fruit size. Abdalla and Verkerk (1968) and El Ahmadi and Stevens (1979) showed fruit set could be severely inhibited by short- and long-term exposure to temperatures in excess of 30°C in certain cultivars. Other research indicated that the duration, magnitude and timing of short-term temperature pulses during the growing season influenced fruit development time (Adams and Valdes, 2002), firmness and yield (Mulholland *et al.*, 2003).

*Author for correspondence.

The quality of the harvested fruit is of major concern to growers because fruit is graded according to external attractiveness (e.g., colour, size, shape and skin defects) or internal characteristics such as taste and texture (Guichard *et al.*, 2001; Shi *et al.*, 2002). Researchers have evaluated the influence of the electrical conductivity (EC) of the nutrient solution (Dorais *et al.*, 2000; Shi *et al.*, 2002) or its calcium concentration (Paiva *et al.*, 1998) on tomato fruit quality factors such as soluble solids content (SSC) and sugar content. Gautier *et al.* (2005) reported decreases in sugar and lycopene content in cherry tomato when fruit temperatures were increased by approximately 1°C following fruit-set through harvest under high fruit load. However, the majority of studies on the influence of temperature on fruit quality parameters have focussed on post-harvest fruit ripening (e.g., Dala *et al.*, 1968; Lurie *et al.*, 1996). In the United States, most tomato fruits are harvested either at the breaker stage and ripened during storage, or allowed to ripen on the fruit cluster for several days following the breaker stage ('vine-ripened'). However, Arias and Lee (2000) identified significant differences in fruit quality between these two harvest approaches, indicating that additional research on the influence of temperature on vine-ripened fruit is warranted.

The use of short-term temperature changes during the growing season may be a viable method for growers to exert additional control over production scheduling and fruit quality (Adams and Valdés, 2002; Gautier *et al.*, 2005). The rate of starch biosynthesis, which influences sink-strength, and thus final fruit size and yield, is potentially at its highest levels the first 10–35 d following fruit set (Ho, 1996; Walker *et al.*, 1978). Temperature changes during this time may also affect fruit maturation and growth by influencing regulation of the enzymes acid invertase and sucrose synthase, or cell expansion and division (Guichard *et al.*, 2001; Ho and Hewitt, 1986) and regulation of sugar transport into the fruit (Ho, 1996).

The objective of this study was to determine if temperature could be manipulated during tomato fruit

development, following first fruit-set, to provide an additional level of control over fruit scheduling and vine-ripened fruit quality. Three controlled-environment experiments were conducted using hydroponically grown tomatoes. Each experiment included a 2-week high (HT) and low temperature (LT) perturbation applied 10 d after first fruit-set, and the effects on production scheduling factors (DTH, harvest window, fruit yield and fruit diameter) and fruit quality factors at different stages of fruit ripening were evaluated.

MATERIALS AND METHODS

Data collection

Five EGC growth chambers (Environmental Growth Chambers Inc., Chagrin Falls, OH, USA), four reach-in chambers and a "walk-in" chamber were used for each experiment (E1, Experiment 1; E2, Experiment 2; E3, Experiment 3). Chambers were modified to include a Campbell 21x data logger to record canopy microclimate data automatically at 15 min intervals, a recirculating hydroponic nutrient delivery system with drip irrigation, and atmospheric carbon dioxide control (Sausser, 1998). The growth area in each reach-in chamber was 1.2 m², while the area was limited to four 1.2 m² production trays in the "walk-in" growth chamber. Cool white fluorescent lamps provided 95% of incident photosynthetically active radiation (PAR) and incandescent bulbs provided the remaining 5%. The environmental conditions are summarised in Table I.

Tomato seeds (*Lycopersicon esculentum* Mill., cv. 'Laura') were sown in 3.5 × 3.5 × 4.0 cm rockwool plugs (Grodan Inc., Pine, CO, USA) and covered with a thin layer of 1:1 (v/v) peat-vermiculite mixture. The cubes were incubated in a reach-in growth chamber with a 16 h photoperiod (0600–2200 h) and environmental set points of 400 µmoles m⁻² s⁻¹ photosynthetic photon flux (PPF), 23°C day/night temperature, 75% relative humidity and a CO₂ concentration of 1 ml l⁻¹ (Table I). Light intensity and temperature were increased or decreased over a

TABLE I
Environmental conditions ± standard deviations (SD) in Experiments 1, 2 and 3

Experiment 1 (LT = 18°/13°C, CT = 23°/18°C, HT = 28°/23°C)												
Time (DAS)	Group*	T (day) (°C)	SD	T (night) (°C)	SD	PAR (µmoles m ⁻² s ⁻¹)	SD	RH (%)	SD	CO ₂ (ml l ⁻¹)	SD	
0–14	ALL	23.0	0.35	21.7	1.04	418	10.8	83	6	637	136.9	
15–55	ALL	22.7	0.35	17.9	0.84	420	96.0	84	5	1091	65.9	
56–69	HT	27.1	1.69	22.3	1.87	489	39.5	90	6	950	286.9	
56–69	LT	18.8	0.50	12.8	0.41	486	31.1	92	4	1057	388.3	
56–69	CT	23.0	0.42	17.9	0.57	506	7.1	84	5	1109	115.8	
70–114	ALL	23.3	0.37	17.8	0.24	516	34.9	84	5	1125	124.1	
Experiment 2 (LT = 18°/13°C, CT = 23°/18°C, HT = 28°/23°C)												
0–14	ALL	23.3	0.17	22.2	1.15	346	28.7	95	6	984	81.3	
15–58	ALL	22.4	0.66	16.3	0.76	409	20.7	89	9	1091	231.6	
59–72	HT	28.5	0.22	23.6	0.67	357	40.3	79	3	1012	221.6	
59–72	LT	18.6	1.84	13.1	1.55	386	33.5	92	3	1107	318.2	
59–72	CT	22.8	0.48	17.2	0.55	412	10.3	87	1	1148	92.5	
72–108	ALL	22.7	0.59	17.9	0.65	393	55.9	90	2	858	209.1	
Experiment 3 (LT = 16°/11°C, CT = 23°/18°C, HT = 30°/25°C)												
0–9	ALL	22.6	0.26	21.6	1.82	454	14.3	83	12	1116	209.5	
10–56	ALL	22.2	0.53	17.2	1.14	364	50.3	78	2	1086	157.3	
57–70	HT	30.0	0.51	25.3	0.40	346	48.9	81	5	950	150.0	
57–70	LT	16.0	0.34	11.5	0.49	333	46.7	91	2	1006	113.3	
57–70	CT	23.03	0.18	18.7	0.43	325	5.6	78	2	923	105.4	
71–116	ALL	22.9	0.21	17.9	0.17	303	9.9	78	4	970	57.8	

*HT, high temperature treatment; LT, low temperature treatment; CT, control temperature treatment; ALL, common conditions for all treatment groups; DAS, days after sowing.

30 min interval to the desired value at the start and end of each photoperiod. Seeds were hand-watered with tap water until germination, after which a dilute nutrient solution (EC 1.1 mS cm⁻¹) consisting of tap water, Peter's Professional Hydrosol Formula 5-11-26 (The Scotts Company, Columbus, OH, USA), and solution-grade calcium nitrate 15.5-0-0 (Hydro-Gardens Inc., Colorado Springs, CO, USA) was used [0.58 g l⁻¹ Hydrosol and 0.36 g l⁻¹ Ca(NO₃)₂]. Germination of 50% of the seeds occurred 6 d after sowing (DAS) for all experiments.

Seedlings were selected for uniformity based on stem height, transplanted into 15 cm green plastic pots filled with perlite (super coarse grade; Whittemore Company Inc., Grayslake, IL, USA), moved into the "walk-in" growth chamber, assigned to one of the four production trays and fitted with an irrigation drip emitter. Seedlings were transplanted with 1 cm of perlite above the top of the rockwool cube. Each pot was covered with white on black polyethylene film (white-side up) to prevent algal growth starting at 14 DAS using 80 seedlings during E1 and E2, and at 9 DAS using 60 seedlings during E3. Mylar screening was used (installed 24, 24 and 28 DAS during E1, E2 and E3, respectively) to minimise side-lighting and delineate production areas. At this time, plants in E1 and E2 were removed to provide planting densities of 13.3, 13.3 and 12.5 plants m⁻² in E1, E2 and E3, respectively. At the time of first flower appearance (37, 36 and 36 DAS in E1, E2 and E3), a hand-held hair dryer (with the heating element disabled) was used for 5 min d⁻¹ to facilitate pollination. Plants were pruned to a single truss at 39 DAS (McAvoy and Giacomelli, 1986), with the main stem cut above the second true leaf above the first fruit cluster. Side-shoots were removed once per week. Plants in all growth chambers were irrigated eight times d⁻¹ (750 ml per plant) from the same nutrient solution that was stored in a 530 l reservoir tank. Nutrient solution was maintained at an EC of 2.1 mS cm⁻¹ prior to flowering and 2.3 mS cm⁻¹ after flowering. The nutrient solution pH ranged from 5.5 to 6.5. Water and make-up nutrient solution were added to the reservoir tank twice per week to maintain the desired EC levels and to minimise possible effects of preferential nutrient uptake on solution ion composition. Approximately 50–75% of the reservoir tank volume had to be replaced each week due to tank leakage and water uptake by the tomato plants.

Temperature treatments were introduced 10 d after at least two fruits on 50% of the plants had set (Table I). Thirty-two plants were removed from the "walk-in" growth chamber and assigned at random to one of the four reach-in growth chambers for 2 weeks. Two chambers were assigned to the HT-treatment and two to the LT-treatment. Four additional plants were also removed from the "walk-in" growth chamber at this time in E1 and E2, so that plant densities of 12.5 plants m⁻² were maintained

in all experiments during this stage. Set-points were 28°/23°C day/night for the HT-treatment chambers and 18°/13°C for the LT-treatment chambers in E1 and E2, and 30°/25°C and 16°/11°C for E3. Plants that remained in the "walk-in" chamber were kept under control temperatures (CT) of 23°/18°C. Following the 2-week treatment period, plants were returned to the "walk-in" chamber until the end of each experiment (Table I).

Fruits were harvested from each plant at one of three vine-ripened stages, breaker stage (B) (25% of the fruit skin showed a reddish hue), B plus 3 d (B+3) and B plus 6 d (B+6). During E1, fruits were harvested at random from plants in each treatment group, so that at least eight fruits were obtained at each stage. During E2 and E3, the entire fruit cluster from each plant was designated for harvest at a specific ripening stage. No fruits were harvested at the B+3 stage during E3. Fruit and plant numbers are summarised in Table II.

Fruit fresh weight (FW) and diameter were obtained following harvest. All analyses except lycopene and ascorbic acid content assays were performed within 3 d of harvest. Lycopene and ascorbic acid were measured following completion of all experiments on fruits that were frozen immediately following harvest. Physico-chemical indices were determined in duplicate, using two plants per treatment and three fruits per plant, unless stated otherwise. Tomato pH was measured at 25°C with a Corning 125 pH meter (Corning Science Products, Medfield, MA, USA) on fruit pulp that had been homogenised for 5 min in a Nova 1 blender (Waring Products, New Hartford, CT, USA) at the highest speed. Acidity was determined by titrating 5 g of homogenised fruit pulp, diluted in 50 ml distilled water, with 0.1 M NaOH to pH 8.1 ± 0.5 (Thakur *et al.*, 1996). Results are reported as % citric acid on a FW basis. Moisture contents were determined by drying 10 g of homogenised pulp sample in a Fisher Isotemp 282A vacuum oven (Fisher Scientific, Pittsburgh, PA, USA) at 70°C and 83 kPa for at least 10 h. Soluble solids contents (SSC) were determined by refractometry (Barrett *et al.*, 1998) using a portable refractometer (Leica Inc., Buffalo, NY, USA). The results were read directly in °Brix. Colour measurements were performed on ten points around the equatorial region of the fruit surface, using a Minolta CR-200 Chromameter (Minolta Camera Co., Osaka, Japan) with a CR-200 measuring head (Arias and Lee, 2000). The results were reported using the L*a*b* scale established by CIE (Commission Internationale de l'Eclairage). Fruit textures were determined using a TA.XT2 Texture Analyser and a 1.2 cm diameter spherical probe (Stable Micro Systems, Haslemere, UK). Fruit firmness was reported as the force (N) required to reach 5 mm compression at five points around the equatorial plane of the fruit at a speed of 1 mm s⁻¹. Homogenate viscosity was quantified by measuring the

TABLE II
Number of fruits harvested in Experiments 1, 2 and 3 after various temperature treatments at various vine-ripened stages

Stage	Experiment 1 ^a			Experiment 2 ^b			Experiment 3 ^b	
	B [*]	B+3	B+6	B	B+3	B+6	B	B+6
HT	16	14	15	21	25	22	30	29
LT	16	16	16	24	24	26	29	30
CT	16	8	8	25	19	20	36	32

^aIn Experiment 1, fruits from the same plant cluster were harvested at different vine-ripened stages.

^bIn Experiments 2 and 3, all fruits from the same plant cluster were harvested at the same stage.

*B = Breaker stage; B+3 and B+6 = Breaker plus 3 or 6 d, respectively.

TABLE III

Effect of temperature perturbation on days to harvest for the breaker (B) stage expressed as fruit numbers per cluster

Fruit No.*	Stage	Experiment 1	Experiment 2	Experiment 3
		B	B	B
1	HT	82.1 b	81.3 b	74.2 b
	CT	86.9 a	86.3 a	82.7 a
	LT	88.7 a	86.5 a	85.3 a
	sig. ^z	***	***	***
2	HT	85.2 b	84.1 b	77.5 c
	CT	89.7 a	89.1 a	83.2 b
	LT	89.9 a	89.0 a	86.8 a
	sig. ^z	**	**	***
3	HT	88.3 b	88.0 a	80.3 b
	CT	95.6 a	91.1 a	87.6 a
	LT	93.1 a	91.5 a	89.4 a
	sig. ^z	***	NS	***

*Number of fruit (1, 2 or 3) sampled per treatment group (Experiment 1) or per cluster (Experiments 2 and 3).

^zNS, *, **, *** Non-significant, or significant at $P < 0.05$, $P < 0.01$, or $P < 0.001$.

distance the homogenate flowed in 30 s under its own weight along a level surface (Barrett *et al.*, 1998), using a standard Bostwick consistometer (CSC Scientific Co., Fairfax, VA, USA). The results were reported with a precision of ± 0.25 cm. Ascorbic acid contents were determined using the AOAC 967.21 procedure, based on 2,6-dichloro-indophenol reduction by ascorbic acid at low pH, with the corresponding colour change to persistent light rose (AOAC, 1990). Results were reported in mg ascorbic acid kg^{-1} . Lycopene contents were determined by extraction with solvents followed by HPLC analysis, using the method described by Moraru *et al.* (2004). The results are reported in mg all-*trans* lycopene kg^{-1} homogenate.

Data analysis

Data were grouped according to harvest stage and analysed using SAS statistical software (SAS Institute, Cary, NC, USA) for one-way analysis of variance (ANOVA) with temperature as the main treatment. Treatment means were separated based on an LSD (least square difference) approach at the 5% significance level. During E1, fruits were harvested at random from all plants in a given treatment. During E2 and E3, fruits were harvested from the same cluster from the same plant, so that fruit weight could be expressed on a per plant basis. During E3, no fruits were harvested at the B+3 stage because the differences were found to be more

significant for the B and B+6 stages during E1 and E2. DTH was based on DAS for the first, second and third fruits that reached the B stage of vine ripening. Harvest window was calculated for B stages (E2 and E3 only) and defined as the number of days elapsed between harvest of the first to third fruit. Fruit numbers used for each analysis are reported in Table II.

RESULTS

Days to harvest and harvest window

DTH for the B stage were significantly less for harvested fruit in the HT-treatment compared with the CT and LT groups (Table III). These trends were observed whether the time required for one, two or all three fruits to achieve B stage was considered (except for DTH for three fruits in E2). Thus, temperature treatment influenced the majority of the fruit cluster. DTH was reduced by 5.5, 4.3 and 7.2 d for HT-treated fruits compared to CT-treated fruits when values for all three fruits were averaged together in E1, E2 and E3, respectively. At a 10% significance level, DTH values for LT fruit were significantly longer than the CT group for all fruits in E3 (not shown). No significant differences in harvest window, which varied between 4.9–7.3 d, were observed between temperature treatments (data not shown).

Fruit diameter and yield

Similar patterns to those recorded for fruit FW were observed for fruit diameter. At the B stage, there were no significant differences between fruit FW between treatment means (Table IV). Significant differences between treatment groups in E1, E2 and E3 were observed for all harvested fruit per cluster at the B+3 and B+6 stages. Generally, fruit weights were lowest for HT-, intermediate for CT-, and highest for LT-treated fruits (Table IV). The average FW of the first three fruit was also larger than the average of all fruit in the cluster during E2 and E3 at all vine-ripening stages. No significant differences were found in the total number of fruit set per cluster (data not shown). The average fruit FW of LT-treated fruit continued to increase with vine-ripening stage for all experiments. HT-treated fruit either maintained the same FW throughout vine-ripening, or decreased.

TABLE IV

Effect of temperature treatment on average fruit weight and diameter grouped by vine-ripening stage, in Experiments 1, 2 and 3

Parameter*	Temperature treatment	Experiment 1 ^a			Experiment 2			Experiment 3	
		B	B+3	B+6	B	B+3	B+6	B	B+6
FW-3 (g fruit ⁻¹)	HT	–	–	–	232 a	184 a	234 a	217 a	218 b
	CT	–	–	–	263 a	239 a	233 a	235 a	272 a
	LT	–	–	–	235 a	282 a	308 a	231 a	279 a
	sig. ^b	–	–	–	NS	NS	NS	NS	*
FW-all (g fruit ⁻¹)	HT	254 a	216 b	236 b	192 a	149 b	180 a	193 a	195 c
	CT	227 a	209 b	269 b	195 a	226 a	214 a	210 a	239 ab
	LT	260 a	283 a	320 a	186 a	198 ab	234 a	217 a	250 a
	sig. ^b	NS	***	***	NS	*	NS	NS	**
D (mm fruit ⁻¹)	HT	82.7 a	77.1 b	78.2 b	84.1 a	77.8 a	83.9 a	80.7 a	77.9 b
	CT	81.1 a	76.6 b	83.4 b	85.8 a	84.7 a	86.1 a	83.1 a	85.1 a
	LT	83.1 a	85.7 a	89.0 a	83.7 a	86.8 a	93.1 a	82.3 a	87.7 a
	sig. ^b	NS	***	***	NS	NS	NS	NS	**

*FW-3', average fresh weight of the first three fruits harvested per plant; 'FW-all', average fresh weight of all fruit harvested per plant during E2 and E3, or all fruit harvested per treatment during E1; 'D', average diameter of the first three fruit harvested per plant during E2 and E3, or the average diameter of all fruit harvested per treatment during E1.

^aSome data not available due to the fruit harvesting protocol used in this experiment.

^bNS, *, **, *** Non-significant, or significant at $P < 0.05$, $P < 0.01$, or $P < 0.001$.

Fruit quality parameters

Significant differences were observed between temperature treatments for several vine-ripening stages in each experiment for SSC, titratable acidity, Bostwick consistency, L* and a* colour indices, firmness and lycopene content (Table V). Titratable acidity, SSC and Bostwick consistency decreased with decreasing temperature. However, the differences between CT- and LT-treated fruit were not always significant. Fruit firmness values were generally lower in HT-treated fruit compared with LT-treated fruit at the B+3 and B+6 stages with the single exception of the B stage in E3. L* colour index had higher values for HT-treated fruit at the B stage in all experiments, but the difference was not observed between any treatment mean at the B+3 and B+6 stages. The a* colour index showed differences at the B+3 and B+6 ripening stages during E1, at B+3 during E2, and at B+6 during E3 for the HT-treatment vs. the CT- or LT-treatments. Lycopene contents were, in general, not significantly different between treatments in E1 and E2. However, at the B+6 stage in E2, HT-fruit had higher levels of lycopene than CT- or LT-fruit. During E3, the opposite finding was observed, as the

lycopene content was lowest for HT-treated fruit compared to LT-fruit. As the duration of vine-ripening increased from B to the B+6 stage, SSC, colour a* index, ascorbic acid and lycopene contents all increased. Conversely colour L* index and firmness measurements decreased as fruit ripened.

DISCUSSION

In re-circulating hydroponic systems, such as that used during the present study, preferential uptake of ions by plants can alter the mineral composition of plant tissues and of the nutrient solution over time. Previous research has indicated that fruit quality parameters can be influenced by nutrient composition (e.g., Paiva *et al.*, 1998). During all our experiments, approximately 50–75% of the nutrient solution (i.e., 530 l) that was shared by all growth chambers and treatments was replenished twice each week as a result of plant uptake and plumbing leakage. Any impact of preferential ion uptake on fruit quality measurements was therefore assumed to be minimal but, if present, would be confounded with treatment temperatures.

TABLE V
Summary of fruit quality parameters grouped by temperature treatment and ripening stage in Experiments 1, 2 and 3

Parameter	Temperature treatment	Experiment 1			Experiment 2			Experiment 3	
		B	B+3	B+6	B	B+3	B+6	B	B+6
Moisture content (%)	HT	93.08 a	93.24 a	93.21 a	93.02 a	93.36 a	93.01 b	92.88 a	92.82 b
	CT	93.39 a	93.62 a	93.54 a	93.00 a	93.05 a	93.70 a	93.08 a	93.29 ab
	LT	93.18 a	93.44 a	93.33 a	93.50 a	93.65 a	93.76 a	93.01 a	93.57 a
	sig.*	NS	NS	NS	NS	NS	***	NS	**
SSC (°Brix)	HT	6.00 a	6.33 a	6.73 a	5.80 a	6.16 a	6.11 a	5.24 a	5.94 a
	CT	5.70 b	6.11 a	6.31 b	5.43 ab	6.08 a	5.67 b	5.02 ab	5.49 a
	LT	5.69 b	6.18 a	6.33 b	5.32 b	5.42 b	5.81 ab	4.87 b	5.22 a
	sig.	*	NS	*	**	***	*	**	***
pH	HT	4.23 a	4.20 a	4.17 b	4.33 a	4.18 a	4.24 a	4.46 a	4.49 a
	CT	4.19 a	4.20 a	4.19 b	4.17 b	4.22 a	4.21 a	4.19 b	4.21 a
	LT	4.20 a	4.24 a	4.31 a	4.22 b	4.19 a	4.20 a	4.20 b	4.23 a
	sig.	NS	NS	***	**	NS	NS	**	NS
Titratable acidity (% citric acid)	HT	0.73 a	0.68 a	0.68 a	0.77 a	0.73 a	0.48 a	0.59 a	0.66 a
	CT	0.69 ab	0.65 ab	0.63 b	0.73 a	0.53 b	0.42 b	0.59 a	0.60 b
	LT	0.68 b	0.62 b	0.60 b	0.71 a	0.52 b	0.41 b	0.59 a	0.57 b
	sig.	NS	**	***	NS	***	**	NS	***
Bostwick consistency (cm)	HT	20.26 a	18.66 a	18.08 ab	18.70 a	24.00 a	23.22 a	15.13 a	22.50 a
	CT	15.94 b	19.10 a	18.13 a	16.71 ab	20.54 b	20.51 b	13.95 a	19.11 b
	LT	16.53 b	17.17 a	15.59 b	14.76 b	20.90 b	22.47 a	11.77 b	15.45 c
	sig.	***	NS	*	**	**	***	***	***
Colour index (L*)	HT	58.83 a	46.48 a	40.48 a	59.11 a	47.83 a	41.23 a	63.95 a	41.03 a
	CT	55.92 b	47.80 a	40.12 a	56.07 b	45.72 b	39.83 a	57.43 b	41.08 a
	LT	55.19 b	46.72 a	40.35 a	55.99 b	47.07 ab	40.92 a	55.20 b	39.98 a
	sig.	***	NS	NS	***	*	NS	***	NS
Colour index (a*)	HT	-0.82 a	22.90 a	29.84 a	-1.56 a	26.43 a	25.75 a	-4.46 a	30.97 a
	CT	-1.85 a	19.12 ab	27.69 ab	-5.16 a	20.25 b	25.75 a	-4.42 a	26.53 b
	LT	-4.30 a	17.96 b	26.47 b	-4.77 a	17.25 b	26.18 a	-5.39 a	25.56 b
	sig.	NS	*	***	NS	***	NS	NS	***
Firmness (N)	HT	25.53 a	14.19 b	11.32 b	26.95 a	12.40 b	9.92 a	34.39 a	10.55 b
	CT	27.23 a	14.63 b	11.58 b	27.03 a	15.36 a	10.38 a	28.98 b	11.84 a
	LT	28.93 a	17.01 a	12.98 a	27.63 a	14.68 a	10.14 a	29.29 b	11.04 ab
	sig.	NS	***	***	NS	**	NS	**	**
Ascorbic acid content (mg kg ⁻¹)	HT	-	-	-	-	-	-	18.94 a	73.58 a
	CT	-	-	-	-	-	-	20.59 a	33.74 a
	LT	-	-	-	-	-	-	17.07 a	39.93 a
	sig.	-	-	-	-	-	-	NS	NS
Lycopene content (mg kg ⁻¹)	HT	6.47 a	51.03 a	89.76 a	5.30 a	74.23 a	123.63 a	0.84 b	50.74 c
	CT	4.43 ab	57.05 a	92.60 a	4.61 a	53.78 b	119.51 a	1.64 ab	85.73 a
	LT	3.65 b	42.50 a	66.69 a	2.09 a	44.57 b	113.41 a	2.02 a	74.49 b
	sig.	*	NS	NS	NS	**	NS	**	***

*NS, *, **, *** Non-significant, or significant at $P < 0.05$, $P < 0.01$, or $P < 0.001$.

Fruit growth rates increase with high air temperatures under non-limiting assimilate and water supply, but this increase is offset by a decrease in DTH, resulting in smaller fruit (Adams *et al.*, 2001; Papadopoulos and Hao, 2001; Peterson and Taber, 1991; Sawheny and Polowick, 1985; Rylski, 1979). Our results were consistent with this pattern, where DTH and fruit FW decreased with HT (Tables III, IV). DTH was more responsive to HT than to LT perturbations as increases in LT- vs. CT-treatments were rarely significant (Table III). Adams *et al.* (2001) reported a decline in DTH between 8.7 – 11.2 d when temperatures were increased by 7°C above a nominal value of 18°C for 3 weeks at 1, 2 or 7 weeks following fruit-set. For the same temperature increase, but for only a 2-week period (E3), a 7.3 d-decrease in DTH was observed. However, in contrast to Adams *et al.* (2001), who reported a longer harvest window at lower temperatures, significant differences in harvest window between treatments were not observed (data not shown). This discrepancy indicates that the time and duration, in addition to the magnitude, of temperature pulses influence the harvest window.

HT-fruit generally had lower FWs, and LT-fruit higher FWs at the B+6 stage (FW-all; Table IV). In E3, HT-fruit were significantly smaller than CT-fruit, presumably because DTH was reduced in the HT-treatments. LT-fruit and, to a lesser extent, CT-fruit also continued to increase in size and weight from the B to the B+6 stage (FW-all; Table IV). A significant increase in moisture content in LT- vs. HT- treated fruits was observed in E2 and E3 at B+6 (Table V). Temperature plays an important role in fruit metabolism and fruit expansion when photosynthesis, nutrients and water are not limiting factors. Cell number and cell size greatly influence the final size of tomato fruit (Guichard *et al.*, 2001). In our study, anthesis of the second flower during E1, E2, and E3 occurred 46 – 48 DAS and treatments were initiated 8 – 10 d after anthesis. The cell division phase in fruits generally occurs within 2 weeks following anthesis (Ho, 1996). Therefore, the increase in LT-treated fruit size was most likely due to cell expansion rather than to cell division. Similar results were also observed for analyses conducted with the first three fruits per cluster, and with all fruits per cluster (Table IV). Thus, the increase in LT-fruit FWs during the later stages of fruit ripening may have been the result of cell expansion or water intrusion *via* the xylem.

HT-treatment increased SSC, acidity, and viscosity (Bostwick consistency) at most vine-ripened stages in

E1, E2, and E3 compared with LT- and CT-treated fruit, although the results were not significantly different at all stages (Table V). Temperature influences assimilate transport and storage during fruit development (Guichard *et al.*, 2001; Pearce *et al.*, 1993). However, structural and functional compounds such as starch, and secondary metabolites that influence internal quality, are synthesised during the later stages of fruit ripening (Guichard *et al.*, 2001). The present results indicate that some of these pathways may be linked with assimilate transport and storage during fruit development. Lycopene biosynthesis is known to be inhibited by high temperatures (Tomes, 1963). Lycopene content at the B+6 stage of HT-treated fruit was significantly less than for CT- or LT-fruit in E3 only, indicating that the magnitude of a short-term increase in temperature prior to ripening can be significant. The decrease in lycopene content for HT-treated fruit during E3 was associated with an increased *a** colour index (Table V) compared to LT- or CT-treated fruit. This result indicates that surface colour alone cannot be used to grade internal fruit quality characteristics (Kaskitalo and Ormrod, 1972; Young *et al.*, 1993).

Previous studies have indicated that fruit quality and yield are sensitive to HT-pulses during ripening (Adams and Valdes, 2002; Gautier *et al.*, 2005; Mulholland *et al.*, 2003). The present work demonstrates that the period following fruit-set is also a point in fruit development during which growers can use temperature changes to influence production scheduling and fruit quality. For example, the flavour of tomato fruit has been shown to be related to the ratio of soluble sugar and acid contents (Dalal *et al.*, 1968; Guichard *et al.*, 2001). Thus, changes introduced by temperature perturbation can be used to alter flavour. Fruits were also more sensitive to HT- than to LT-pulses. Future work to elucidate the interactions between the magnitude, duration, and timing of temperature pulses at different points during fruit development can be used to formulate more effective control and management strategies for tomato growers.

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