Effects of genotype and cultivation environment on lycopene content in red-ripe tomatoes

Joseph O Kuti* and Hima B Konuru

Horticultural Crops and Food Research Laboratory, Texas A&M University-Kingsville, PO Box 5475, Kingsville, TX 78364-5475, USA

Abstract: Lycopene, a natural red pigment found in tomato, is correlated with reduced incidence of some cancers. Forty tomato varieties, including cluster F_1 hybrid tomatoes, round breeding line tomatoes (*Lycopersicon esculentum* Mill) and cherry tomato types (*L esculentum* var *cerasiforme*), grown under greenhouse and field conditions were evaluated for their lycopene content using high-performance liquid chromatography (HPLC) and spectrophotometry. Lycopene content varied significantly among the tomato varieties, with cherry tomato types having the highest lycopene content. Greenhouse-grown cluster and round tomatoes contained more lycopene (mean = 30.3 mg kg^{-1}) than field-grown tomatoes (mean = 25.2 mg kg^{-1}), whereas cherry tomato types had a higher lycopene content in field-grown (mean = 91.9 mg kg^{-1}) than in greenhouse-grown (mean = 56.1 mg kg^{-1}) fruits. HPLC analysis of lycopene isomeric forms revealed a higher content of all-*trans* isomers in all tomato genotypes examined. However, the *cis* isomeric form was exceptionally higher in the field- and greenhouse-grown cherry tomato *L esculentum* var *cerasiforme* cv Gardener's Delight, which contained ~9.3 and 9.9 mg kg^{-1} cis isomers respectively. Results indicate that genetics and choice of cultivation environment may have a strong influence on tomato lycopene content.

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Keywords: *Lycopersicon esculentum*; tomato typology; growth environment; genotype; lycopene content; lycopene isomers

INTRODUCTION

Tomato (*Lycopersicon esculentum*) is an important horticultural crop grown commercially worldwide and available all-year-round. Tomato has assumed the status of a functional food when one considers the overwhelming epidemiological evidence for tomato and tomato product consumption in prevention of chronic diseases such as cancers and cardiovascular diseases.¹⁻⁴ Tomato contains diverse nutrient and disease-preventing molecules, including ascorbic acids, vitamin E, flavonoids and phenolic acids, and carotenoids.⁵

The two main carotenoids in tomato fruits are lycopene (ψ , ψ -carotene), which imparts the red colour of tomato, and β -carotene, which accounts for approximately 7% of tomato carotenoid content.⁶ Tomatoes and related products are a major source of dietary lycopene compounds and an important source of carotenoids in the human diet.⁷ Lycopene is a phytochemical nutrient that is found in many fruits and vegetables, especially in tomatoes and tomato products.⁸ Lycopene pigment has attracted substantial interest among researchers owing to its biological and physiochemical properties, especially related to its effect as a natural antioxidant⁹ and various benefits for human health.¹⁰ Although it has no provitamin A activity, lycopene exhibits a physical quenching rate constant with singlet oxygen almost twice as high as that of β -carotene.¹¹ Lycopene is regarded as a bioantioxidant with high biological activity in various tissues of the human body.¹² Lycopene has drawn considerable attention as a result of epidemiological and clinical evidence linking regular consumption of lycopene to decreased incidence of prostate cancer,¹³ lung cancer,¹⁴ digestive tract cancer¹⁵ and cardiovascular disease.¹⁶ In addition, lycopene has been shown to induce cell-to-cell communication, modulate hormones and immune systems and affect other metabolic pathways.¹⁷

The main causes of tomato lycopene degradation during processing are isomerisation and oxidation.¹⁸ Isomerisation converts all-*trans* isomers to *cis* isomers owing to additional energy input, resulting in an unstable, energy-rich station.¹⁹ Lycopene in fresh tomato fruits occurs essentially in the all-*trans* configuration. The bioavailability of lycopene is influenced by many factors, including isomerisation. The bioavailability of *cis* isomers in processed tomato products is higher

^{*} Correspondence to: Joseph O Kuti, Botanicals and Phytotherapy Research Laboratory, Department of Natural Sciences, Fayetteville State University of North Carolina, 223 Lyons Science Building, 1200 Murchison Road, Fayetteville, NC 28301-4298, USA E-mail: josephk@sbcglobal.net

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than in unprocessed fresh tomatoes.²⁰ Lycopene concentrations in fruits may depend on genetics,²¹ and consequently the choice of cultivated variety is important; the influence of major factors of environment and cultivation techniques on the lycopene content in tomato fruits must also be known.

The objectives of this study were to determine the lycopene content in various indeterminate cluster and round tomato genotypes, including cherry tomatoes, grown under greenhouse and field conditions by means of spectrophotometric analysis and to compare lycopene isomeric forms in the tomato varieties using high-performance liquid chromatography (HPLC).

MATERIALS AND METHODS Plant materials

Thirty-six L esculentum Mill varieties (30 clustertype F₁ hybrid tomatoes and six round-type breeding lines) and four L esculentum var cerasiforme cherry-type tomatoes were used for greenhouse and field study.

Greenhouse plant establishment

Seeds of each tomato genotype were sown in flats filled with premixed soil. The flats were placed in a walk-in growth chamber at 20°C and 70% relative humidity (RH) under artificial illumination (photosynthe tically active radiation (PAR) = $280 \,\mu \text{mol}\,\text{m}^{-2}\,\text{s}^{-1}$). Ten seedlings of each tomato genotype were then transplanted in 7 gallon pots containing 900 l of field soil amended with appropriate fertiliser (NPK) and irrigation regimens before being placed in the Horticultural Crops research greenhouse. The greenhousegrown tomato plants were arranged in a randomised complete block design with four replications, and the experiment was repeated twice over 2 years. To ensure similar shading conditions for all tomato plants, border plants were placed at the east, south and west sides of the greenhouse. Plants were trained around bamboo stakes, and suckers were pruned every week. Bees were used for pollination.

Field plant establishment

Tomato plants were also established under field conditions in Horticultural Crops experimental vegetable plots (agricultural soil consisting of Victoria clay, fine montmorillonitic, hyperthermic Udic Pellusterts, with clay or silt clay texture, irrigation with a total of 120 mm and traditional NPK fertilisation regimens) in a 2 year study. Four replications were established in each year, each with a single plot of 20 plants for each tomato genotype.

Tomato fruit harvest

Healthy tomato fruits were hand harvested from each plant when they had reached the mature red-ripe stage. Harvested tomatoes were washed and cut into halves, the seeds were removed and the pericarp and mesocarp were ground to a homogeneous paste in a blender for 1 min before being used for lycopene content analysis. Approximately 25 g samples of red-ripe tomato fruit were taken in triplicate from each tomato variety, pooled and stored at -18 °C before being processed for lycopene extraction. Before lycopene extraction the raw tomato extracts were exposed to a microwave hot break, which employs simultaneous high shear, high temperature (100 °C) and evaporation to extract tomato juice. The evaporation was carried out in a vacuum kettle equipped with a scrape surface agitator and a steam jacket, and the total heating time was 40 s. The hot break process simulates commercial hot break procedures used in tomato canning and produces a tomato extract with better colour and consistency and which is more stable because of deactivation of enzymes by the procedure.²²

Reagents and standards

All organic solvents (methanol, methyl *t*-butyl ether (MTBE), butylated hydroxytoluene (BHT), hexane, acetone and ethanol) used for separation of tomato lycopene were of HPLC grade and purchased from Fisher Scientific (Pittsburgh, PA, USA). Lycopene standard was purchased from Sigma-Aldrich Chemicals (St Louis, MO, USA).

Lycopene extraction

With minor modifications, the lycopene extraction procedure used was similar to a published procedure for carotenoid extraction from vegetables and fruits.²³ Approximately 2 g of homogeneous tomato paste was extracted repeatedly with 20 ml of extraction solvent (hexane, acetone and ethanol in 50:25:25 ratio). All procedures were performed under reduced light.

Measurement of total lycopene content by spectrophotometry

Approximately 3 g samples of tomato fruit were ground in liquid nitrogen and extracted with 10 ml of hexane/methanol/acetone (2:1:1) containing 25 g l^{-1} BHT. The suspension was centrifuged at $5000 \times g$ for 10 min in 50 ml Corex tubes. The upper hexane layer was removed with a Pasteur pipette, and the absorbance at 505 (A_{505}) of a 1:10 dilution of the extract was determined using a UV-vis spectrophotometer (Beckman Instruments Inc, Irvine, CA, USA) against a hexane blank. The concentration of total lycopene was calculated from the data using a specific extinction coefficient of $3400.^{24}$ Results were expressed as mg kg⁻¹ fresh weight.

HPLC analysis of lycopene isomers

A Hewlett Packard (Palo Alto, CA, USA) series 1100 high-performance liquid chromatograph with autosampler and software ('HP Chemistation for LC' Rev.A.05.02 (273)) was used for sample analyses. Isomer separation was performed on a $5 \,\mu m \, C_{30}$ column stationary phase ('Suplex' pkb-100, 5-8934) that gives superior resolution and produces unique

 Table 1. Presumptive identification of HPLC peaks in extracts of red-ripe tomato fruits

| HPLC peak | Carotenoid(s) | Absorbance maxima (nm) ^a | Ref |
|-----------------|---|---------------------------------------|-----|
| (1 + 1′ + 1″) | All- <i>trans</i> -lutein, <i>cis</i> -lutein and 5,6-dihydroxy- 5,6-dihydrolycopene (lycopene-5,6-diol) | 473, 446, 424, 483, 453, 432 | 27 |
| (2, 3, 4, 5, 6) | Lycopene epoxides | | 27 |
| 7 | <i>cis</i> -Lycopenes | | 27 |
| 8 | All-trans-lycopene | 504, 473, 446 | 28 |
| 9 | 5,5'-Di-cis-lycopene | 504, 473, 446, 360 | 27 |
| 10 | All-trans- β -carotene and cis- β -carotene | 480, 454, (430), 480, 454, (430), 343 | 28 |
| 11 | <i>cis</i> -Phytofluene | 368, 350, 333, 258 | 27 |
| 12 | trans-Phytofluene | 368, 350, 333 | 27 |
| 13 | trans-Carotene | 427, 401, 380 | 27 |
| 14 | Phytoene | (278), 287, (289) | 27 |
| 15 | 15-Mono- <i>cis</i> -lycopene | 499, 467, 440, 360 | 28 |

^a Photodiode array detector data as described in the text. Values in parentheses represent inflection points.

separations.²⁵ Lycopene isomer separation was carried out at 1 mlmin^{-1} flow rate using a linear slope 40-50% methanol and MTBE mobile phase for 35 min. Reverse phase liquid chromatography was used to optimise the separation of the geometric isomers (*cis* and all-*trans* isomers) of lycopene according to Emenhiser *et al*;²⁶ this method allows for better separation between very similar compounds. Detection was monitored with a Hewlett Packard 1040A diode array absorbance detector that also stored spectral data over the range 190–600 nm for spectrophotometric peak identification. Presumptive peak identification was based on HPLC retention times and published absorbance spectral data (Table 1).^{27,28}

Statistical analysis

Statistical analyses were performed using SPSS (Chicago, IL, USA) for Windows v10.0. One-way analysis of variance (ANOVA) was carried out to determine values of least significant difference (LSD) and degree of significance between varieties and cultivation environments at significance level $p \leq 0.05$.

RESULTS AND DISCUSSION

Total lycopene contents in tomato varieties

Data in Table 2 represent total lycopene contents in the 40 tomato varieties. There were significant differences in total lycopene content between greenhouseand field-grown tomato varieties. The total lycopene content in fresh market tomato varieties (L esculentum Mill) grown in the greenhouse ranged from 5.7 mg kg^{-1} in cv Dona to 47.8 mg kg^{-1} in cv Red Plum, while in those tomatoes grown in the field the content ranged from $4.3 \,\mathrm{mg \, kg^{-1}}$ in cv Dona to 31.5 mg kg^{-1} in cv Red Plum. The total lycopene content in cherry tomatoes (L esculentum var cerasiforme) grown in the greenhouse ranged from $48.9 \,\mathrm{mg \, kg^{-1}}$ in cv Gardener's Delight to 63.6 mg kg^{-1} in cv Sugar Lump, while in those tomatoes grown in the field the content ranged from 73.8 mg kg^{-1} in cv Gardener's Delight to 116.7 mg kg⁻¹ in cv Sugar Lump. Generally, among the cluster and round tomato types (Lesculentum Mill), greenhouse-grown tomatoes consistently contained more total lycopene (mean = 30.3 mg kg^{-1}) than field-grown tomatoes (mean = 25.2 mg kg^{-1}). However, among the cherry tomato types (L esculentum var cerasiforme) there was significantly more lycopene in field-grown (mean = 91.9 mg kg^{-1}) than in greenhouse-grown (mean = 56.1 mg kg^{-1}) fruits. Differences in carotenoid content among tomato varieties had been previously reported.^{29,30} The large variation in total lycopene content of greenhouseand field-grown tomato cultivars may be attributed to differences in genotype, environmental factors such as the amount of sun exposure, and cultivation regimens such as the fertiliser and water used,³¹ which together may markedly affect the biosynthesis of carotenoids.²⁹ Total lycopene content on average constitutes about 80-90% of the total carotenoid content of redripe tomatoes.9 The carotenoid content of tomatoes depends on genetic factors,³² and the choice of variety cultivated may affect the content at harvest.33 The results obtained with cherry tomatoes, which contained significantly higher amounts of lycopene, agreed with previous reports on antioxidant contents in tomato as a function of genotype.33 It has been suggested that cherry tomatoes may be useful varieties for processing and for improvement of nutritional and health benefits in tomato breeding programmes.³⁴

Red-ripe tomato fruits accumulate large amounts of the linear carotene lycopene and small amounts of its orange cyclisation product β -carotene (provitamin A). Lycopene is transformed into β -carotene by the action of lycopene β -cyclase (β -Lcy),³⁵ and tomato cultivars which contain the crimson gene (cg) are usually found to have higher lycopene contents than those cultivars lacking the gene.³⁶ The cyclisation of lycopene is an important branching point in the carotenoid biosynthetic pathway,³⁷ and lycopene begins to accumulate at the 'breaker' stage of fruit ripening after the fruit has reached the 'mature green' stage.³⁸

Analysis of lycopene isomers in tomatoes

Characteristic chromatographic peaks were identified on the basis of their HPLC retention times and

| Table 2. Total lycopene contents in raw red-ripe samples of 40 |
|--|
| tomato varieties grown under greenhouse and field environments |
| (<i>n</i> = 3) |

| | | Lycopene content (mg kg ⁻¹ fresh weight) | | |
|------|------------------------------|--|---------------|--|
| Code | Variety | Greenhouse | Field | |
| | Round tomato type (L | | | |
| | esculentum Mill) | | | |
| 01 | Golden Jubilee | 30.4 | 23.3 | |
| 02 | Early Cascade | 29.6 | 20.2 | |
| 03 | First Lady | 37.2 | 26.5 | |
| 04 | Better Boy | 19.9 | 14.0 | |
| 05 | Early Girl | 23.9 | 20.2 | |
| 06 | Super Steak | 8.4 | 6.2 | |
| 07 | Early Pick | 18.0 | 12.6 | |
| 08 | Fantastic | 35.1 | 16.2 | |
| 09 | Monte Carlo | 8.3 | 6.1 | |
| 10 | Dona | 5.7 | 4.3 | |
| 11 | Italian Beefsteak | 30.6 | 29.6 | |
| 12 | Terrific | 23.4 | 11.7 | |
| 13 | Mar Globe Select | 26.1 | 21.3 | |
| 14 | Stupice | 45.9 | 27.5 | |
| 15 | Druzba | 29.7 | 23.6 | |
| 16 | Red Brandywine | 37.3 | 17.6 | |
| 17 | Miracle Sweet | 30.6 | 28.8 | |
| 18 | Sweet Cluster | 34.2 | 16.2 | |
| 19 | Big Beef | 27.4 | 13.5 | |
| 20 | Saint Pierre | 39.6 | 27.2 | |
| 21 | Boxcar Willie | 31.5 | 19.8 | |
| 22 | Goliath Bush | 23.8 | 20.5 | |
| 23 | Red Plum | 47.8 | 31.5 | |
| 24 | Husky Red | 33.6 | 10.8 | |
| 25 | Bonny Best | 26.4 | 16.2 | |
| 26 | Polish Giant | 9.7 | 5.3 | |
| 27 | Keepsake | 27.2 | 18.3 | |
| 29 | Kada | 35.1 | 19.9 | |
| 30 | Sun Master | 27.8 | 20.1 | |
| 00 | Cluster tomato type (L | 21.0 | 20.1 | |
| | esculentum Mill) | | | |
| 31 | ALMA-01 | 34.4 | 27.9 | |
| 32 | GS-111 | 21.9 | 15.3 | |
| 33 | GS-114 | 33.3 | 12.6 | |
| 34 | TMT-510 | 30.6 | 23.4 | |
| 35 | TMT-521 | 35.4 | 21.6 | |
| 36 | TMT-555 | 29.6 | 14.3 | |
| | Mean | 30.3 | 25.2 | |
| | Cherry tomato type (L escul- | | | |
| 07 | entum var cerasiforme) | | 045 | |
| 37 | Juliet Hybrid | 54.7 | 94.5 | |
| 38 | Gardener's Delight | 48.9 | 73.8 | |
| 39 | Sugar Lump | 63.6 | 116.7 | |
| 40 | Sun Cherry | 57.3 | 82.5 | |
| | Mean | 56.1 | 91.9 | |
| | LSD _{5%} | 6.2 | 4.8 | |
| | Р | ≤0.05 | <u>≤</u> 0.05 | |

 $\mathsf{LSD}_{5\%} = \mathsf{least}$ significant difference at 5% probability; $\mathit{P} = \mathsf{probability}$ level.

absorbance spectra (Table 1). Data in Table 3 represent concentrations of lycopene isomers (*cis* and all-*trans*) in the 40 tomato varieties. The all-*trans* lycopene isomer content was significantly higher than

the *cis* isomer content in greenhouse- and field-grown tomato varieties. Generally, among the cluster and round tomato types (L esculentum Mill), greenhousegrown tomatoes consistently had a higher content of all-*trans* lycopene isomers than field-grown tomatoes. However, in the cherry-type tomatoes (L esculentum var cerasiforme) there was a higher content of all-trans lycopene isomers in field-grown than in greenhousegrown fruits. While there are significant differences in all-trans isomers, there is no significant difference in cis isomers among the tomato varieties. However, the cis isomeric form was exceptionally higher in the field- and greenhouse-grown cherry tomato cv Gardener's Delight (\sim 9.3 and 9.9 mg kg⁻¹ respectively). Processing of fresh tomatoes causes lycopene degradation, resulting in irreversible isomerisation of all-trans lycopene to cis isomers.³⁹ In fresh tomatoes, relative concentrations of all-trans lycopene isomers may depend on different factors such as agronomic and physicochemical parameters of the crop cycle in the field, temperature, sun exposure, fertiliser and irrigation regimens, method of analysis, and equipment.⁴⁰

Based on the standard HPLC procedure, the all-trans isomer content was assumed to be considerably higher than the cis isomer content, because the standard method does not separate 5-cis and all-trans isomers; consequently, all-trans isomer contents have been overestimated in many previous studies. However, in this study a higher-resolution method confirmed the findings of previous studies that the range of content of all-trans isomeric forms of lycopene in tomato was extremely variable.⁴¹ The degree of lycopene isomer separation and purification using HPLC may be determined by the choice of stationary and mobile phases.²³ The use of C₃₀ stationary phase gives superior resolution and unique separation of cis-trans isomers,²⁶ and the length of the column may be the reason for this unique separation, because it allows efficient separation of long molecules such as $C_{40}H_{56}.^{25}$

While all tomato varieties examined in the present study contained substantial amounts of total lycopene, significant variations among cultivars and types were evident. The lycopene content of tomatoes was also affected by environmental factors and agronomic techniques used. Given that environment sometimes obscures genetic differences, breeding progress of functional tomatoes will require estimates of lycopene content and other antioxidants that distinguish genotypic differences among varieties of red-fruited tomatoes. The results of the present study should provide useful preliminary data for detecting small isomeric differences among genotypes in lycopene content and studying genotype \times environment variation sources.

CONCLUSION

Plant genotype and cultivation environment affect the biosynthesis of lycopene in tomatoes. The apparent difference in total lycopene content between cherry

| Table 3. Concentrations of lycopene isomers (cis and all-trans) in raw red-ripe samples of 40 tomato varieties grown under greenhouse and field |
|---|
| environments $(n = 3)$ |

| Code | Variety | Lycopene concentration (mg kg $^{-1}$ fresh weight) ^a | | | | |
|----------|---------------------------|--|----------------------------------|--------------------------------|----------------------------------|--|
| | | Gree | nhouse | Fie | Field | |
| | | Cis | All-trans | Cis | All-trans | |
| | Round tomato type (L eso | culentum Mill) | | | | |
| 01 | Golden Jubilee | 3.4 ± 0.1 | 26.9 ± 4.2 | 3.7 ± 0.5 | 19.6 ± 3.0 | |
| 02 | Early Cascade | 4.1 ± 0.3 | 25.5 ± 1.8 | 4.8 ± 0.5 | 15.4 ± 1.0 | |
| 03 | First Lady | 4.7 ± 2.8 | 32.5 ± 0.9 | 2.9 ± 6.2 | 23.6 ± 2.1 | |
| 04 | Better Boy | 2.6 ± 0.2 | 17.3 ± 1.6 | 3.4 ± 1.2 | 10.6 ± 0.4 | |
| 05 | Early Girl | 3.8 ± 1.6 | 20.1 ± 0.9 | 3.6 ± 1.0 | 16.6 ± 1.5 | |
| 06 | Super Steak | 2.9 ± 2.3 | 5.5 ± 1.7 | 2.7 ± 0.5 | 3.5 ± 1.2 | |
| 07 | Early Pick | 2.8 ± 0.9 | 7.2 ± 2.4 | 3.3 ± 1.7 | 9.3 ± 0.1 | |
| 08 | Fantastic | 4.2 ± 1.0 | 30.9 ± 3.6 | 3.5 ± 1.5 | 12.7 ± 0.9 | |
| 09 | Monte Carlo | 2.1 ± 0.1 | 6.3 ± 0.3 | 2.4 ± 2.2 | 3.7 ± 0.6 | |
| 10 | Dona | 2.0 ± 0.4 | 3.6 ± 0.5 | 1.8 ± 0.1 | 2.5 ± 0.5 | |
| 11 | Italian Beefsteak | 3.2 ± 2.2 | 27.4 ± 1.8 | 2.8 ± 0.4 | 26.8 ± 1.7 | |
| 12 | Terrific | 3.4 ± 0.6 | 20.0 ± 0.4 | 2.9 ± 1.1 | 8.8 ± 0.5 | |
| 13 | Mar Globe Select | 3.1 ± 0.9 | 23.0 ± 0.8 | 2.2 ± 1.5 | 19.1 ± 2.7 | |
| 14 | Stupice | 4.5 ± 2.5 | 41.4 ± 7.3 | 3.3 ± 1.2 | 28.2 ± 5.4 | |
| 15 | Druzba | 3.9 ± 1.8 | 25.8 ± 1.6 | 2.8 ± 0.8 | 20.8 ± 0.4 | |
| 16 | Red Brandywine | 4.7 ± 1.3 | 32.6 ± 3.8 | 3.1 ± 0.1 | 14.5 ± 0.5 | |
| 17 | Miracle Sweet | 3.3 ± 1.0 | 27.3 ± 5.2 | 2.6 ± 0.7 | 26.2 ± 2.4 | |
| 18 | Sweet Cluster | 4.2 ± 0.9 | 30.0 ± 1.3 | 3.2 ± 1.6 | 13.0 ± 2.2 | |
| 19 | Big Beef | 2.7 ± 1.6 | 24.7 ± 0.2 | 3.8 ± 1.5 | 9.7 ± 0.5 | |
| 20 | Saint Pierre | 3.7 ± 1.0 | 35.9 ± 3.1 | 2.7 ± 0.7 | 24.5 ± 1.7 | |
| 21 | Boxcar Willie | 3.5 ± 0.6 | 28.0 ± 0.8 | 3.1 ± 0.1 | 16.7 ± 0.9 | |
| 22 | Goliath Bush | 2.7 ± 0.5 | 21.1 ± 2.6 | 2.2 ± 0.5 | 18.3 ± 0.8 | |
| 23 | Red Plum | 5.3 ± 1.6 | 42.5 ± 1.5 | 3.9 ± 0.7 | 23.6 ± 2.6 | |
| 24 | Husky Red | 3.5 ± 1.0 | 30.1 ± 0.3 | 2.5 ± 0.1 | 20.0 ± 2.0 8.3 ± 0.5 | |
| 25 | Bonny Best | 2.2 ± 0.1 | 24.2 ± 0.8 | 1.9 ± 0.4 | 14.3 ± 0.3 | |
| 26 | Polish Giant | 1.8 ± 0.4 | 7.9 ± 0.1 | 1.3 ± 0.2 | 4.0 ± 0.1 | |
| 27 | Keepsake | 3.2 ± 2.1 | 24.0 ± 3.1 | 2.5 ± 0.5 | 15.8 ± 0.3 | |
| 29 | Kada | 4.6 ± 1.0 | 30.5 ± 2.8 | 3.2 ± 0.3 | 10.0 ± 0.0 16.8 ± 1.1 | |
| 30 | Sun Master | 4.0 ± 1.0 2.8 ± 0.3 | 25.0 ± 0.7 | 3.2 ± 0.3 2.2 ± 0.4 | 10.0 ± 1.1 17.9 ± 2.5 | |
| | Cluster tomato type (L es | | 20.0 ± 0.1 | 2.2 ± 0.4 | 17.3 ± 2.0 | |
| 31 | ALMA-01 | 3.9 ± 2.1 | 30.5 ± 1.7 | 3.0 ± 1.4 | 24.9 ± 0.9 | |
| 32 | GS-111 | 5.5 ± 4.2 | 30.5 ± 1.7 16.4 ± 0.5 | 3.0 ± 1.4 6.7 ± 0.1 | 24.9 ± 0.9 8.6 ± 1.0 | |
| 33 | GS-114 | 5.5 ± 4.2 4.6 ± 6.1 | 10.4 ± 0.5 28.7 ± 1.9 | 0.7 ± 0.1 4.6 ± 0.7 | 8.0 ± 1.0 8.0 ± 0.4 | |
| 33 34 | | | 20.7 ± 1.9 30.9 ± 0.4 | | | |
| | TMT-510 | 3.7 ± 1.2 | | 7.6±1.3 | 15.8 ± 4.1 | |
| 35 | TMT-521 | 5.2 ± 1.7 7.2 ± 2.3 | 30.2 ± 3.2 | 8.4 ± 0.8 | 13.2 ± 3.3 | |
| 36 | TMT-555 | | 29.8 ± 1.4 | 6.4 ± 0.6 | 7.9 ± 0.5 | |
| 07 | Cherry tomato type (L eso | | | 15100 | 040154 | |
| 37 | Juliet Hybrid | 4.2 ± 1.5 | 50.5 ± 7.1 | 1.5 ± 6.3 | 84.6 ± 5.1 | |
| 38 | Gardener's Delight | 9.3 ± 4.5 | 39.6 ± 5.9 | 9.9 ± 1.8 | 72.3 ± 4.3 | |
| 39 | Sugar Lump | 2.7 ± 5.2 | 60.9 ± 6.3 | 7.2 ± 7.5 | 109.5 ± 7.0 | |
| 40 | Sun Cherry | 6.6 ± 4.6 | 52.7 ± 5.2 | 1.2 ± 5.2 | 81.3 ± 5.2 | |

^a Mean \pm standard deviation.

tomato types grown in the field (mean = 91.9 mg kg^{-1}) and in the greenhouse (mean = 56.1 mg kg^{-1}) may be due to inhibition of lycopene biosynthesis by occasional temperature build-up inside the greenhouse, which exceeded $32 \,^{\circ}$ C in most cases during this study.

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