



RESEARCH ARTICLE

Heat stress effects on physiological, biochemical and fruit quality traits of tomato (*Solanum lycopersicum* L.) genotypes at the late fruit maturation stage

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Abstract

Heat stress during late fruit maturation can impair physiological efficiency and fruit quality in tomato (*Solanum lycopersicum* L.). The present study evaluated 12 genotypes under natural field heat stress conditions (maximum temperature 36–38 °C) during the late fruit maturation stage using a randomised complete block design (RCBD) with five replicates. Gas exchange parameters, chlorophyll fluorescence (Fv/Fm), pigment composition, membrane thermostability, proline accumulation and fruit quality attributes were quantified and analysed using ANOVA ($p \leq 0.05$). Significant genotypic variation was observed in net photosynthetic rate (1.08–21.01 $\mu\text{mol m}^{-2} \text{s}^{-1}$), Fv/Fm (0.424–0.662), electrolyte leakage (EL; 76.59–99.15 %) and carotenoid retention. Genotypes VRT 101 A, EC 538380 and EC 620438 maintained comparatively higher photosynthetic performance and membrane stability, whereas EC 620-1, INDAM 2102, EC 620568 and EC 620419 exhibited superior fruit quality retention, including higher lycopene (up to 0.522 mg 100 mL⁻¹), β -carotene and total soluble solids (TSS). Sensitive genotypes showed reduced photosynthetic efficiency and higher membrane injury under prolonged exposure to elevated temperatures. The findings highlight genotype-dependent heat tolerance strategies and identify physiological and biochemical markers useful for selection under terminal heat stress conditions.

Keywords: climate resilience; fruit quality; heat stress; membrane stability; photosynthetic efficiency; PSII fluorescence; tomato genotypes

Introduction

Tomato (*Solanum lycopersicum* L.) is one of the most important vegetable crops cultivated worldwide, occupying nearly 5 million hectares globally (1). Its economic value derives not only from yield but also from fruit quality attributes such as lycopene, β -carotene, ascorbic acid, organic acids and soluble sugars. However, increasing global temperatures and recurrent heat waves pose a serious constraint to tomato productivity, particularly in tropical and subtropical regions. Tomato tissues are highly sensitive to temperatures above 35–38 °C and sustained exposure beyond this threshold leads to physiological injury and deterioration of fruit quality (2).

Heat stress influences multiple physiological processes in tomato, including photosynthesis, respiration, membrane stability and metabolic regulation (3). Most previous studies have focused on the reproductive phase—especially flowering and fruit set, because these stages are extremely temperature-sensitive and directly determine yield (4–7). The effects of high temperature on pollen viability, floral morphology and fruit set are well documented (4, 5, 7). Similarly, heat-induced alterations in vegetative-stage processes such as photosynthetic activity (8), nutrient uptake (9), mesophyll resistance (10) and membrane disorganisation (11) have also been reported. Nevertheless, comparatively limited attention has been

given to the late fruit maturation stage, despite its direct influence on marketable fruit quality.

Photosynthesis is one of the most heat-sensitive processes in plants. Elevated temperature reduces CO₂ assimilation through both stomatal limitation and non-stomatal impairment of mesophyll biochemical capacity (8, 12). Thermal stress destabilises photosystem II (PSII), leading to reduction in maximum quantum efficiency (Fv/Fm) and cause photoinhibition (13, 14). Structural damage to the D1 protein of PSII and disruption of electron transport can enhance reactive oxygen species (ROS) generation (14, 15). Excess ROS induces lipid peroxidation and compromises membrane integrity, which is commonly assessed through electrolyte leakage (EL) (16, 17). Maintenance of carotenoids plays a protective role under such conditions by scavenging ROS and preventing photo-oxidative injury (14, 18).

Heat stress during fruit ripening further affects biochemical composition. Lycopene biosynthesis is highly temperature-sensitive and exposure to elevated temperatures inhibits its accumulation and may accelerate oxidative degradation (19, 20). Prolonged heat, often accompanied by intense solar radiation, results in sunscald injury and pigment discoloration (21). Similarly, ascorbic acid content and soluble sugars are influenced by high temperature exposure (22–25). Alterations in pH and titratable acidity further

modify fruit flavour and processing quality (26, 27). Therefore, heat-induced physiological impairments at the leaf level can translate into significant deterioration in fruit biochemical attributes.

Although genotypic variability in heat tolerance has been reported, most classifications are based primarily on yield performance or reproductive traits. However, an integrated evaluation linking photosynthetic efficiency, membrane stability, osmolyte accumulation and fruit biochemical retention under terminal heat stress remains insufficiently explored. Such an integrative approach is essential under current climate change scenarios, where elevated temperatures frequently coincide with late fruit maturation.

We hypothesised that tomato genotypes capable of maintaining higher photosynthetic efficiency (Pn, Fv/Fm), membrane stability and antioxidant protection under late-stage heat stress would exhibit improved retention of fruit pigments and quality traits. Accordingly, the objectives of this study were to: (i) evaluate the physiological responses of diverse tomato genotypes under natural field heat stress during late fruit maturation stage; (ii) quantify associated changes in membrane stability and proline accumulation; and (iii) assess fruit biochemical and quality attributes to identify physiological markers associated with terminal heat tolerance.

By integrating physiological and fruit biochemical responses, this study aims to provide a mechanistic framework for genotype selection under prolonged high-temperature environments.

Materials and Methods

Experimental site and climatic conditions

The field experiment was conducted from January to July during 2012–2014 at the Indian Institute of Vegetable Research (IIVR), Varanasi, India. The experimental site is located at 25°18' N latitude and 83°03' E longitude, at an altitude of 128 m above mean sea level. During the late fruit maturation stage (24–30 weeks after transplanting), air temperature ranged from 21.2 to 36.1 °C and relative humidity ranged from 38.5 % to 78.2 %. The soil was classified as sandy loam with near-neutral pH.

Plant material and experimental design

Twelve tomato (*Solanum lycopersicum* L.) genotypes (EC 620431, VRT 101 A, EC 620-1, EC 620571, EC 620421, INDAM 2102, EC 620568, EC 620438, EC 620419, EC 538380, EC 625659 and EC 625652) were evaluated under natural field heat stress conditions.

The experiment was laid out in a randomised complete block design (RCBD) with five replications. Each plot maintained a uniform plant spacing of 60 × 45 cm. Standard agronomic practices, including irrigation, fertilisation and plant protection measures, were uniformly applied across all treatments.

Soil characteristics

Prior to transplanting, composite soil samples were collected from a depth of 0–15 cm depth and analysed for physico-chemical properties using standard soil analysis procedures. The soil was sandy loam with near-neutral pH and moderate fertility status. Organic carbon, available nitrogen, phosphorus, potassium, sulphur and micronutrient contents were within the recommended range for tomato cultivation. Detailed soil nutrient status is presented in Table 1.

Table 1. Initial physico-chemical properties of the experimental soil (0–15 cm depth). Values are presented as mean ± SD (*n*=3)

Parameter	Mean ± SD	Unit
Soil texture	Sandy loam	–
pH (1:2.5)	7.21 ± 0.08	–
EC	0.34 ± 0.02	dS m ⁻¹
Organic carbon	0.62 ± 0.03	%
Available N	268 ± 12.4	kg ha ⁻¹
Available P ₂ O ₅	21.5 ± 1.1	kg ha ⁻¹
Available K ₂ O	246 ± 9.6	kg ha ⁻¹

Gas exchange measurements

Net photosynthetic rate (Pn), stomatal conductance (gs) and intercellular CO₂ concentration (Ci) were measured using a portable infrared gas analyser (LI-6200, LI-COR Inc., USA). Measurements were recorded between 09:00 and 11:00 hr under ambient light conditions on fully expanded upper canopy leaves. Three plants per replication were measured and the values were averaged.

Chlorophyll fluorescence analysis

Maximum quantum efficiency of PS II (Fv/Fm) was determined using a portable chlorophyll fluorometer. Leaves were dark-adapted for 30 min prior to measurement. Fv/Fm was calculated as (Fm - Fo)/Fm following standard methodology (13).

Chlorophyll and carotenoid estimation

Chlorophyll a, chlorophyll b and total chlorophyll were extracted in 80 % acetone and quantified spectrophotometrically following the method described by Lichtenthaler and Buschmann (28). Carotenoid content was calculated using specific absorption coefficients and expressed as µg mL⁻¹ extract.

Membrane thermostability (electrolyte leakage)

Membrane stability was assessed as electrolyte leakage (EL) following the method described by Liu and Huang (16). Leaf discs were incubated in deionised water and electrical conductivity was measured before and after autoclaving. Electrolyte leakage (EL) was expressed as percentage conductivity.

Proline estimation

Free proline content was estimated using the acid ninhydrin method described by Claussen (29). Absorbance was recorded at 520 nm and proline concentration was calculated using a standard curve and expressed as µg g⁻¹ fresh weight.

Fruit sampling and biochemical analysis

Fully ripened red fruits were harvested and analysed for quality parameters.

Lycopene and β-carotene

Lycopene and β-carotene were estimated spectrophotometrically following the method of Nagata and Yamashita (30). Pigment concentrations were expressed as mg 100 mL⁻¹ extract.

Ascorbic acid

Ascorbic acid content was determined using standard AOAC procedures (31) and expressed as mg 100 g⁻¹ fresh weight.

Total soluble solids (TSS)

Total soluble solids were measured using a digital refractometer and expressed as percentage (°Brix).

pH and titratable acidity

Fruit pH was measured using a digital pH meter. Titratable acidity

was determined by titration against 0.1 N NaOH and expressed as percentage citric acid equivalent (32).

Statistical analysis

All data were subjected to analysis of variance (ANOVA) under RCBD design using standard statistical procedures. Treatment means were compared using the least significant difference (LSD) test at $p \leq 0.05$.

Pearson correlation coefficients were computed to determine relationships among physiological and fruit quality parameters. Levels of significance were set at $P \leq 0.05$ (*), $p \leq 0.01$ (**) and $p \leq 0.001$ (***) (Fig. 1).

Principal component analysis (PCA) was performed using standardised data to identify major sources of variation and genotype clustering patterns. Eigenvalues > 1 were considered significant contributors to the total variance.

Results

Gas exchange parameters

Significant genotypic variation ($p \leq 0.05$) was observed in Pn, stomatal conductance (gs) and intercellular CO₂ concentration (Ci) under late-stage heat stress (Table 2). Pn ranged from 1.08 to 21.01 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Genotype VRT 101 A recorded the highest photosynthetic rate (21.01 $\mu\text{mol m}^{-2} \text{s}^{-1}$), followed by EC 538380

(16.20 $\mu\text{mol m}^{-2} \text{s}^{-1}$) and EC 620438 (9.46 $\mu\text{mol m}^{-2} \text{s}^{-1}$). In contrast, EC 625659 and EC 625652 exhibited significantly lower Pn values (1.79 and 2.62 $\mu\text{mol m}^{-2} \text{s}^{-1}$, respectively), indicating strong photosynthetic inhibition under elevated temperature.

Stomatal conductance (gs) varied significantly among genotypes ($\text{CD}_5\% = 0.353$). EC 620571 (2.80 $\text{mmol m}^{-2} \text{s}^{-1}$) and EC 620421 (2.26 $\text{mmol m}^{-2} \text{s}^{-1}$) exhibited comparatively higher gs values, whereas EC 625652 showed the lowest conductance (0.315 $\text{mmol m}^{-2} \text{s}^{-1}$).

Intercellular CO₂ concentration (Ci) values ranged from 275.75 to 560.40 $\mu\text{mol mol}^{-1}$. Elevated Ci in low-performing genotypes suggests the predominance of non-stomatal limitations contributing to reduced CO₂ assimilation.

Chlorophyll fluorescence and leaf pigments

The maximum quantum efficiency of PSII (Fv/Fm) differed significantly among genotypes ($p \leq 0.05$). Values ranged from 0.424 (INDAM 2102) to 0.662 (EC 620431). Genotypes maintaining higher Fv/Fm values exhibited comparatively lower photosynthetic decline.

Chlorophyll a content ranged from 1.79 to 7.60 $\mu\text{g mL}^{-1}$ extract. EC 620438 (7.60 $\mu\text{g mL}^{-1}$), EC 620431 (7.37 $\mu\text{g mL}^{-1}$) and VRT 101 A (7.29 $\mu\text{g mL}^{-1}$) retained higher chlorophyll a content under heat stress (Table 3). The chlorophyll a/b ratio varied between 1.62 and 2.64, with INDAM 2102 showing the highest ratio (2.64).

Table 2. Physiological traits of tomato genotypes under high temperature stress

Genotype	Pn ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	gs ($\text{mmol m}^{-2} \text{s}^{-1}$)	Ci ($\mu\text{mol mol}^{-1}$)	Fv/Fm	EL (%)	Proline ($\mu\text{g g}^{-1} \text{FW}$)
EC 620431	3.25 ^{ef}	1.14 ^{cd}	326.60 ^f	0.662 ^a	91.15 ^{bc}	0.986 ^b
VRT 101 A	21.01 ^a	1.76 ^{bc}	501.10 ^b	0.448 ^{de}	87.23 ^{ab}	0.196 ^c
EC 620-1	2.37 ^f	0.94 ^d	314.80 ^f	0.509 ^{cd}	88.69 ^{ab}	0.804 ^b
EC 620571	6.24 ^{cd}	2.80 ^a	275.75 ^f	0.525 ^{cd}	91.75 ^{bc}	0.226 ^c
EC 620421	5.10 ^{de}	2.26 ^{ab}	318.55 ^f	0.446 ^{de}	97.84 ^d	1.307 ^a
INDAM 2102	1.08 ^f	1.23 ^{cd}	459.45 ^c	0.424 ^e	95.05 ^{cd}	1.177 ^a
EC 620568	7.14 ^{cd}	2.04 ^b	392.35 ^d	0.554 ^{bc}	94.74 ^{cd}	0.634 ^b
EC 620438	9.46 ^c	0.82 ^d	560.40 ^a	0.551 ^{bc}	96.63 ^d	0.201 ^c
EC 620419	3.47 ^{ef}	0.97 ^d	342.40 ^e	0.586 ^{ab}	99.15 ^d	0.228 ^c
EC 538380	16.20 ^b	1.15 ^{cd}	483.80 ^c	0.456 ^{de}	76.59 ^a	1.056 ^a
EC 625659	1.79 ^f	0.66 ^d	556.80 ^a	0.505 ^{cd}	94.57 ^{cd}	0.306 ^c
EC 625652	2.62 ^f	0.32 ^e	489.00 ^c	0.437 ^e	91.44 ^{bc}	0.941 ^b
CD ($P \leq 0.05$)	4.579	0.353	6.081	0.247	13.724	0.734
SEm $\pm$	1.471	0.114	1.954	0.079	4.409	0.236

Means followed by the same letter within a column are not significantly different at $p \leq 0.05$ (LSD test).

Pn: net photosynthetic rate; gs: stomatal conductance; Ci: intercellular CO₂ concentration; Fv/Fm: maximum quantum efficiency of PS II; EL: electrolyte leakage.

Table 3. Chlorophyll and pigment traits of tomato genotypes under high temperature stress

Genotype	Chl a ($\mu\text{g mL}^{-1}$)	Chl b ($\mu\text{g mL}^{-1}$)	Total Chl ($\mu\text{g mL}^{-1}$)	Chl a/b	Carotenoids ($\mu\text{g mL}^{-1}$)
EC 620431	7.37 ^a	3.12 ^{ab}	10.49 ^a	2.36 ^{bc}	1.421 ^{ab}
VRT 101 A	7.29 ^a	2.76 ^{bc}	10.05 ^a	2.64 ^a	1.681 ^a
EC 620-1	5.86 ^{bc}	2.88 ^{bc}	8.74 ^{bc}	2.03 ^{cd}	1.503 ^{ab}
EC 620571	4.90 ^{cd}	2.44 ^{cd}	7.34 ^{cd}	2.01 ^{cd}	1.102 ^{bc}
EC 620421	3.48 ^{de}	1.87 ^{de}	5.35 ^{de}	1.86 ^{de}	0.933 ^{cd}
INDAM 2102	2.95 ^{ef}	1.12 ^f	4.07 ^{ef}	2.64 ^a	1.595 ^a
EC 620568	6.42 ^{ab}	3.02 ^{ab}	9.44 ^{ab}	2.13 ^c	1.280 ^b
EC 620438	7.60 ^a	2.98 ^{ab}	10.58 ^a	2.55 ^{ab}	1.402 ^{ab}
EC 620419	4.26 ^d	2.14 ^d	6.40 ^d	1.99 ^{cd}	0.874 ^{cd}
EC 538380	6.98 ^{ab}	3.21 ^a	10.19 ^a	2.17 ^c	1.350 ^{ab}
EC 625659	2.47 ^f	1.52 ^{ef}	3.99 ^f	1.62 ^e	0.433 ^e
EC 625652	3.10 ^{ef}	1.66 ^e	4.76 ^{ef}	1.86 ^{de}	0.589 ^{de}
CD ($P \leq 0.05$)	1.12	0.84	1.95	0.41	0.27
SEm $\pm$	0.36	0.27	0.63	0.13	0.09

Means followed by the same letter within a column are not significantly different at $p \leq 0.05$ according to LSD test.

Chl a: chlorophyll a; Chl b: chlorophyll b; total Chl: total chlorophyll; Chl a/b: chlorophyll a/b.

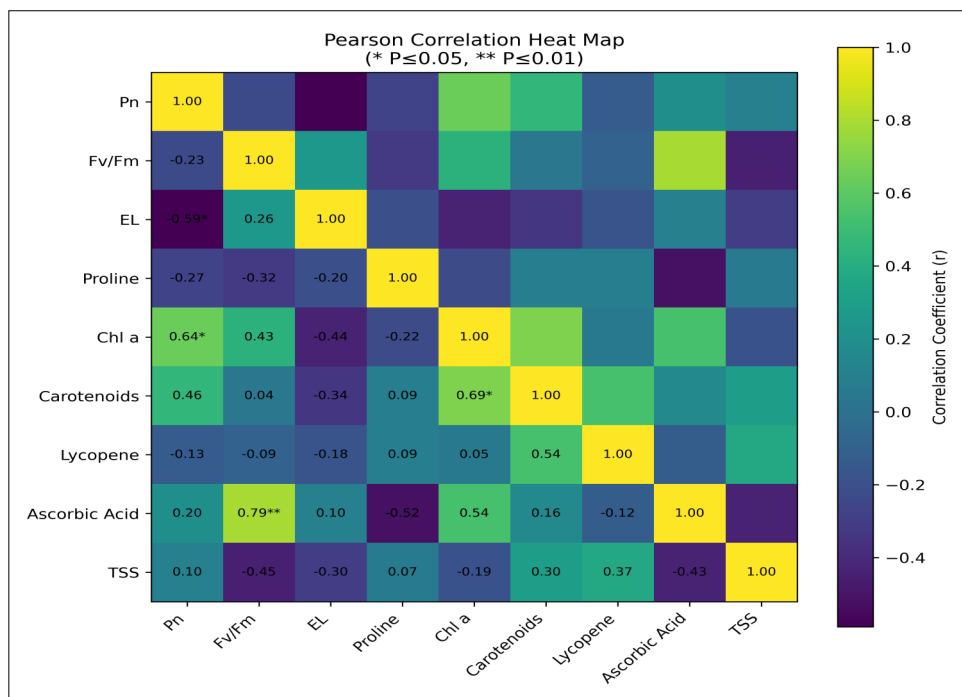


Fig. 1. Pearson correlation heat map illustrating relationships among physiological and fruit quality traits of tomato genotypes under late-stage heat stress. Red indicates positive correlations whereas blue indicates negative correlations, with colour intensity proportional to the strength of the correlation coefficient (r). Asterisks denote statistical significance (* $p \leq 0.05$; ** $p \leq 0.01$). Pn: net photosynthetic rate; Fv/Fm: maximum quantum efficiency of PSII; EL: electrolyte leakage; Chl a: chlorophyll a; TSS: total soluble solids.

Carotenoid content ranged from 0.433 to 1.681 $\mu\text{g mL}^{-1}$. VRT 101 A, INDAM 2102 and EC 620-1 exhibited comparatively higher carotenoid concentrations, suggesting enhanced photoprotective capacity.

Membrane stability and proline accumulation

Electrolyte leakage (EL) showed significant genotypic variation ($\text{CD}_5\% = 13.724$). The lowest EL was recorded in EC 538380 (76.59 %), indicating superior membrane thermostability. In contrast, EC 620419 exhibited the highest EL (99.15 %), reflecting greater membrane injury under high temperature conditions.

Proline content ranged from 0.196 to 1.307 $\mu\text{g g}^{-1}$ fresh weight (FW). EC 620421 (1.307 $\mu\text{g g}^{-1}$ FW) and INDAM 2102 (1.177 $\mu\text{g g}^{-1}$ FW) accumulated comparatively higher proline levels, indicating enhanced osmotic adjustment under stress.

Fruit pigment composition

Significant differences ($p \leq 0.05$) were observed for lycopene content among genotypes (Table 4). Lycopene ranged from 0.051 to 0.522 $\text{mg } 100 \text{ mL}^{-1}$. INDAM 2102 (0.522 $\text{mg } 100 \text{ mL}^{-1}$) and EC 620-1 (0.508 $\text{mg } 100 \text{ mL}^{-1}$) retained the highest lycopene concentrations. β -carotene ranged from 0.029 to 0.217 $\text{mg } 100 \text{ mL}^{-1}$. EC 620-1

showed the highest β -carotene content (0.217 $\text{mg } 100 \text{ mL}^{-1}$). Fruit chlorophyll content showed non-significant variation among genotypes (data not shown).

Fruit biochemical quality traits

Ascorbic acid content varied significantly ($p \leq 0.05$), ranging from 1.75 to 5.60 $\text{mg } 100 \text{ g}^{-1}$ fresh weight. EC 620568 retained the highest ascorbic acid concentration (5.60 $\text{mg } 100 \text{ g}^{-1}$ FW).

Total soluble solids (TSS) ranged between 1.55 % and 5.6 %. EC 620568 exhibited the highest TSS value (5.6 %), whereas EC 620421 recorded the lowest (1.55 %).

Fruit pH varied between 4.5 and 6.15, while titratable acidity ranged from 0.022 % to 0.056 % citric acid equivalent.

Correlation analysis

The correlation heat map revealed a strong positive association between Pn and chlorophyll a ($r = 0.64$, $p \leq 0.05$), indicating that maintenance of pigment stability contributes to sustained photosynthetic performance under heat stress. A significant negative correlation between Pn and EL ($r = -0.59$, $p \leq 0.05$) suggests that membrane integrity is closely linked to physiological resilience.

Table 4. Fruit quality traits of tomato genotypes under high temperature stress

Genotype	Lycopene (mg 100 mL ⁻¹)	β -carotene (mg 100 mL ⁻¹)	Ascorbic acid (mg 100 g ⁻¹ FW)	pH	Titratable acidity (%)	TSS (%)
EC 620431	0.208 ^{bc}	0.029 ^d	5.50 ^a	4.84 ^c	0.037 ^{bc}	7.0 ^c
VRT 101 A	0.248 ^{bc}	0.093 ^c	3.70 ^c	4.75 ^c	0.052 ^a	12.6 ^a
EC 620-1	0.508 ^a	0.217 ^a	1.75 ^e	5.45 ^b	0.030 ^c	11.4 ^a
EC 620571	0.143 ^{cd}	0.080 ^c	4.10 ^{bc}	5.59 ^b	0.046 ^b	12.6 ^a
EC 620421	0.051 ^d	0.076 ^c	1.55 ^e	6.15 ^a	0.022 ^c	7.8 ^c
INDAM 2102	0.522 ^a	0.110 ^b	2.30 ^d	6.00 ^a	0.022 ^c	11.7 ^a
EC 620568	0.224 ^{bc}	0.085 ^c	5.60 ^a	4.59 ^c	0.052 ^a	5.6 ^d
EC 620438	0.214 ^{bc}	0.098 ^{bc}	4.50 ^b	5.26 ^{bc}	0.045 ^b	2.8 ^e
EC 620419	0.219 ^{bc}	0.071 ^c	5.05 ^{ab}	4.93 ^c	0.056 ^a	6.1 ^d
EC 538380	0.272 ^b	0.206 ^a	3.55 ^c	5.24 ^b	0.024 ^c	7.5 ^c
CD ($P \leq 0.05$)	0.009	0.073	1.111	0.150	0.005	1.1
SEm $\pm$	0.003	0.023	0.384	0.048	0.002	0.357

Means followed by the same letter within a column are not significantly different at $p \leq 0.05$ (LSD test).

TSS: total soluble solids.

A strong positive relationship between Fv/Fm and ascorbic acid content ($r = 0.79$, $p \leq 0.01$) highlights the role of antioxidant protection in preserving PSII efficiency under elevated temperature conditions. Furthermore, chlorophyll a showed a positive correlation with carotenoids ($r = 0.69$, $p \leq 0.05$), reflecting coordinated pigment stability during stress.

Overall, the matrix indicated that thermotolerance is associated with integrated maintenance of photosynthetic efficiency, membrane stability and antioxidant metabolism, which collectively support fruit biochemical quality.

Principal component analysis (PCA)

Principal component analysis was performed to elucidate multivariate relationships among physiological and fruit quality traits under late-stage heat stress (Fig. 2). The first two principal components (PC1 and PC2) together explained a major proportion of total variance among genotypes.

PC1 was positively associated with Pn, chlorophyll a and carotenoids and negatively associated with EL, representing the photosynthetic performance and membrane stability axis. PC2 was primarily influenced by fruit biochemical attributes, including lycopene, ascorbic acid and TSS, reflecting the fruit quality retention axis.

Genotypes VRT 101 A and EC 538380 clustered positively along PC1, indicating superior physiological resilience under heat stress. In contrast, INDAM 2102 and EC 620-1 were positioned along PC2, demonstrating stronger fruit biochemical retention. Sensitive genotypes grouped toward the negative PC1 region, characterised by reduced photosynthetic efficiency and increased membrane injury.

This separation demonstrates that heat tolerance involves distinct but interrelated physiological and metabolic dimensions. Similar multidimensional thermotolerance frameworks have been reported in recent crop stress studies (42, 43).

Discussion

Heat stress during the late fruit maturation stage significantly alters gas exchange and photochemical efficiency among tomato genotypes. The reduction in Pn in sensitive genotypes indicates both stomatal and non-stomatal limitations. Elevated temperatures impair Rubisco activase activity and electron transport efficiency, restricting carbon assimilation even when stomatal conductance is not severely constrained (12, 33). Thermal stress also disrupts transcriptional regulation of heat-responsive genes involved in photosynthetic stability (34).

The decline in Fv/Fm values in susceptible genotypes reflects damage to PSII. Heat stress destabilises the D1 protein and suppresses PSII repair mechanisms, promoting photoinhibition and excessive ROS generation (13, 14, 35). Maintenance of higher Fv/Fm in tolerant genotypes suggests improved thermal acclimation capacity. PSII stability has been widely recognised as a reliable physiological indicator of thermotolerance across crops (36, 37).

Increased EL in sensitive genotypes indicates compromised membrane integrity under prolonged high temperature. Heat-induced ROS accumulation triggers lipid peroxidation and membrane destabilisation (16, 38). Genotypes with lower EL values exhibited better membrane thermostability, suggesting stronger antioxidant defense systems.

Carotenoids contribute to photoprotection by scavenging singlet oxygen and minimising photo-oxidative damage (18, 36). Although variation in proline content was moderate, its accumulation may aid osmotic adjustment and cellular redox buffering under heat stress (29, 39). Multifactorial stress adaptation mechanisms involving coordinated antioxidant responses are increasingly recognised as central to thermotolerance (40).

A key outcome of this study is the positive association between maintenance of photosynthetic efficiency and retention of fruit quality attributes. Genotypes sustaining higher Pn and lower membrane injury exhibited improved lycopene and β -carotene

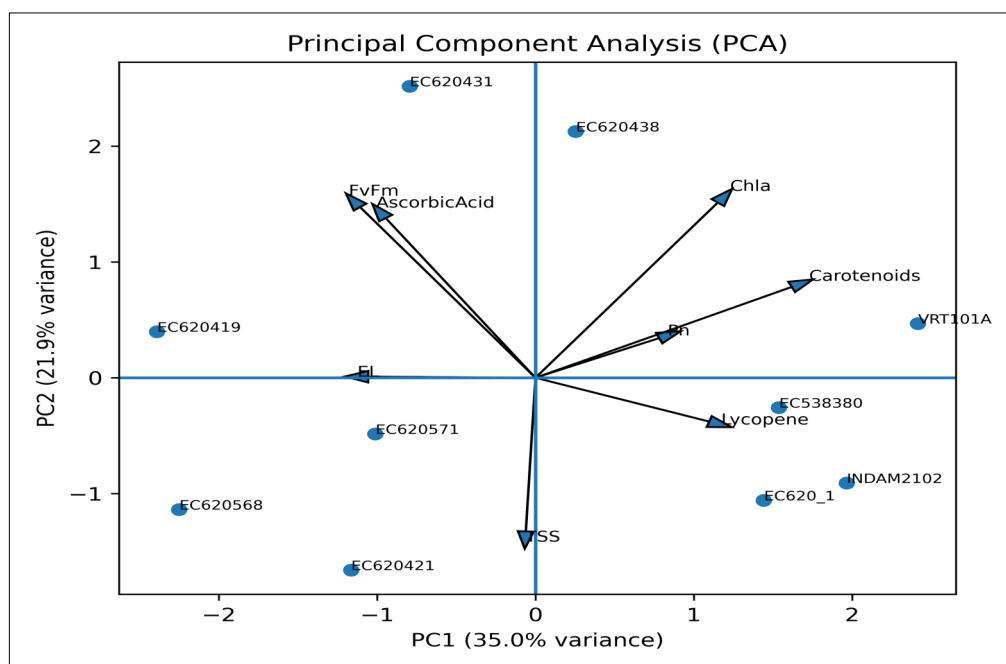


Fig. 2. Principal component analysis (PCA) biplot showing relationships among physiological and fruit quality traits of tomato genotypes under late-stage heat stress. PC1 represents photosynthetic performance and membrane stability, whereas PC2 reflects fruit biochemical attributes. Genotype clustering indicates distinct heat tolerance strategies involving coordinated regulation of photochemical efficiency and antioxidant retention.

concentrations. Lycopene biosynthesis is highly temperature-sensitive and exposure above 35 °C inhibits its accumulation through disruption of carotenoid pathway enzymes (19, 41). Oxidative degradation of pigments further exacerbates quality loss.

Declines in ascorbic acid and TSS in sensitive genotypes reflect metabolic perturbations under heat stress. Antioxidant depletion reduces the fruit's capacity to detoxify ROS generated during ripening (22–24, 38). These findings support the hypothesis that physiological resilience at the leaf level translates into improved fruit biochemical retention during terminal heat stress.

Distinct genotype-specific tolerance patterns were observed. Some genotypes maintained superior photosynthetic performance, whereas others showed better fruit biochemical retention. Heat tolerance is therefore a multidimensional trait involving coordinated regulation of photosynthesis, antioxidant defense and metabolic stability.

Recent molecular studies demonstrate that thermotolerance is governed by complex transcriptional networks and heat shock regulatory pathways (34, 42). Consequently, classification of heat tolerance based solely on yield or reproductive traits may underestimate physiological resilience. Integrating physiological markers such as Fv/Fm and membrane stability provides a more robust evaluation framework.

Projected increases in global temperatures are expected to reduce crop yields, including tomato, under future climate scenarios (42). Heat waves increasingly coincide with fruit maturation stages, intensifying quality losses. The present findings indicate that terminal heat stress not only reduces physiological efficiency but also compromises fruit biochemical attributes.

Breeding strategies should therefore prioritise:

- Maintenance of PSII efficiency.
- Reduced membrane injury.
- Stable carotenoid biosynthesis.
- Sustained antioxidant capacity.

Recent advances in crop thermotolerance emphasise the integration of physiological screening with genomic selection strategies (43, 44). Incorporating indicators such as Fv/Fm and EL into breeding pipelines may accelerate development of climate-resilient cultivars.

The collective evidence supports the following pathway:

High temperature → PSII disruption → ROS overproduction → Membrane injury → Pigment degradation → Fruit quality decline.

Genotypes capable of maintaining photochemical stability and redox balance exhibit improved fruit biochemical retention under prolonged heat exposure.

Conclusion

Heat stress during late fruit maturation significantly impaired photosynthetic efficiency, membrane stability and fruit biochemical quality in tomato. Genotypic variation was evident in maintenance of net photosynthesis, PSII integrity (Fv/Fm) and EL, confirming that thermotolerance is strongly associated with preservation of photochemical and membrane stability under elevated temperatures. Reduced membrane injury and sustained

carotenoid accumulation in tolerant genotypes suggest effective ROS detoxification mechanisms, consistent with current understanding of redox homeostasis in heat adaptation. Importantly, this study establishes a functional linkage between leaf-level physiological resilience and fruit quality retention. Genotypes maintaining higher photochemical efficiency exhibited superior lycopene and antioxidant preservation under thermal stress, reinforcing the concept that heat-induced disruption of photosynthesis directly influences fruit metabolic stability. Given projected global temperature increases and associated yield penalties, identification of physiological markers such as Fv/Fm, EL and carotenoid retention offers practical screening tools for climate-resilient breeding programs.

Future breeding strategies should integrate physiological phenotyping with molecular and genomic approaches to accelerate development of heat-tolerant cultivars. Collectively, the findings provide a mechanistic framework linking thermotolerance, oxidative balance and fruit quality preservation, contributing to sustainable tomato production under warming climatic scenarios.

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Authors' contributions

AC contributed to conceptualization, data curation, investigation, methodology and writing-original draft as well as review and editing. PKP involved in experimental design, investigation, data curation, analysis, visualization and writing-review and editing. All authors read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interest to declare.

Ethical issues: None

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