Genomics and Applied Biology 2026, Vol.17, No.4, 200-212
http://bioscipublisher.com/index.php/gab

Research Insight Open Access

Effects of Temperature Regulation on Growth and Yield of Tomato

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Genomics and Applied Biology, 2026, Vol.17, No.4 doi: 10.5376/gab.2026.17.0016
Received: 02 Jun., 2026
Accepted: 04 Jul., 2026
Published: 15 Jul., 2026
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Preferred citation for this article:
Lin X.X., 2026, Effects of temperature regulation on growth and yield of tomato, Genomics and Applied Biology, 17(4): 200-212 (doi: 10.5376/gab.2026.17.0016)

Abstract Temperature is one of the most critical environmental factors regulating tomato (*Solanum lycopersicum* L.) growth, physiological processes, and yield formation. With the increasing frequency of extreme temperature events and the expansion of protected cultivation systems, effective temperature regulation has become essential for achieving stable and high-quality tomato production. This review summarizes the effects and mechanisms of temperature regulation on tomato growth, photosynthesis, reproductive development, fruit quality, and yield formation. Appropriate temperature management promotes seed germination, vegetative growth, root development, and biomass accumulation by optimizing plant metabolic activities and resource utilization efficiency. Temperature regulation also improves photosynthetic performance, antioxidant defense capacity, and nutrient metabolism, thereby enhancing plant adaptation to thermal stress. During reproductive growth, suitable temperature conditions facilitate flowering, pollen viability, fruit set, and fruit expansion, while temperature extremes can cause flower abortion, reduced fruit quality, and yield losses. Furthermore, this review discusses the physiological and molecular mechanisms involved in temperature responses, including hormonal regulation, heat shock proteins, cold-responsive pathways, and temperature-sensitive gene expression. A case study is presented to evaluate the practical effects of different temperature management strategies in greenhouse tomato production. Future research should focus on integrating intelligent environmental control systems, crop growth models, and multi-factor regulation approaches to develop precise and climate-resilient temperature management strategies for sustainable tomato production.
Keywords Temperature regulation; Tomato production; Growth and yield; Thermal stress; Greenhouse cultivation

1 Introduction

Tomato production depends strongly on temperature regulation because tomato is widely cultivated across open-field and greenhouse systems, yet its growth, reproductive success, and fruit quality decline when temperatures move beyond the crop's favorable range. Tomato is one of the world's most important horticultural crops, and rising temperatures are increasingly recognized as a major threat to its productivity under climate change (Luo et al., 2023; Graci and Barone, 2024). This sensitivity is agronomically important because tomato performs best within a relatively narrow thermal window: optimal growth has been placed broadly between 18°C-32°C, while optimal average day and night temperatures for reproductive performance are narrower, around 21°C-30°C and 18°C-21°C, respectively (Luo et al., 2023). As temperatures rise above or fall below these optima, the effects are expressed not only as general stress but also as direct constraints on flowering, fruit set, and marketable yield, making temperature regulation a central component of stable tomato production rather than a secondary environmental concern (Lee et al., 2022).

The importance of regulating temperature is further underscored by evidence that both heat stress and sub-optimal low temperature impair the formation of yield at multiple developmental stages. Temperature has a large effect on all aspects of tomato development, with declining temperatures reducing leaf and truss initiation rates, while sub-optimal conditions also reduce fruit set because of poorer pollen quality At the high-temperature end, reproductive development is especially vulnerable: exposure above 32/20°C day/night during the reproductive phase reduces fruit set and fruit weight, and temperatures above 35°C can further suppress fruit set and delay normal fruit coloration (Miller et al., 2021; Vijayakumar et al., 2021). These responses explain why temperature regulation is not simply about maintaining vegetative growth, but about protecting the sequence of processes—from floral initiation to successful fertilization and fruit enlargement—that ultimately determines yield.

The relationship between temperature conditions and tomato growth and yield formation is therefore both physiological and developmental. Temperature alters metabolic efficiency, respiration, membrane stability, photosynthesis, and carbon use, and these whole-plant effects interact with stronger reproductive sensitivity during flowering and fruiting (Alsamir et al., 2020; Elazazi et al., 2024). Experimental and modeling studies show that yield losses under heat stress are driven mainly by reductions in fruit number, fruit set, seed set, and individual fruit mass rather than by a simple decline in total biomass. In South Florida simulations, yield decreased as air temperature increased, with losses of 52°C-85% above current conditions, primarily because fruit production declined, even though biomass accumulation and leaf area index increased with temperature (Ayankojo and Morgan, 2020). Likewise, controlled studies of fruit development found that both low (14°C) and high (26°C) temperature regimes tended to produce small parthenocarpic fruits and low fruit yields, while newer modeling work showed that 30-34°C reduces pollen viability, germination, seed set, and fruit mass, and that 14°C lowers yield by reducing both fruit set and fruit size (Zepeda et al., 2026). Together, these findings indicate that tomato yield formation is shaped not only by mean temperature but by the timing, duration, and amplitude of thermal stress, especially during sensitive reproductive stages.

Against this background, the objective of this review is to synthesize current knowledge on how temperature regulation affects tomato growth, reproductive development, and final yield, and to identify practical and biological factors that can improve resilience under fluctuating thermal environments. Recent work has shown that even within commercial greenhouses, local canopy microclimates can vary by up to 3°C in daily average temperature and can measurably influence stem growth, fruit growth, and truss mass, indicating that “temperature regulation” must be understood at the crop-canopy scale rather than only at the level of a central climate setting (Šalagovič et al., 2024). At the same time, advances in genetics and molecular physiology show that thermotolerance can be improved through targeted trait selection and mechanistic understanding: quantitative trait loci linked to fruit set, yield, and soluble solids have been identified under high temperature, and heat-responsive reproductive regulators such as the TSP4a/TSP4b module have been shown to help maintain fruit set and fruit sugar levels under warming conditions (Elazazi et al., 2024; Lu et al., 2025). Accordingly, this review focuses on three linked themes: the importance of temperature regulation in tomato production systems, the mechanisms by which temperature shapes growth and yield formation, and the emerging management, breeding, and monitoring strategies that can support high yield and fruit quality under climate warming.

2 Temperature Requirements and Environmental Regulation in Tomato Production

2.1 Optimal temperature ranges during different growth stages

Tomato temperature requirements vary by developmental stage, and reproductive performance is generally more temperature-sensitive than vegetative growth. Broadly, optimal growth has been placed between 18°C and 32°C, but fruit set and yield respond best within a narrower mean temperature window, with daily average temperatures of 21°C-24°C, 22°C-25°C, or 22°C-26°C repeatedly identified as favorable for reproductive success (Luo et al., 2023). Night temperature is also important during flowering and fruit set, because night temperatures of 15°C-20°C increase marketable yield, while a night temperature of 13°C can still maintain good fruit set under some conditions (Alsamir et al., 2020; Lee et al., 2022).

Stage-specific thresholds further show that tomato should not be managed with a single thermal target throughout the crop cycle. Seedling emergence can already be damaged at 30°C, whereas temperatures above 35°C significantly inhibit germination, vegetative growth, flowering, fruit set, and ripening; by contrast, lower developmental thresholds for tomato are often placed near 15°C, below which growth and development largely cease (Lee et al., 2022). During fruit development, increasing temperature accelerates ripening, with fruits ripening 95, 65, 46, and 42 days after flower opening at 14°C, 18°C, 22°C, and 26°C, respectively, but both high and low temperature regimes also tend to produce small parthenocarpic fruits and lower yields when flower number or fruit set is impaired.

2.2 Effects of temperature fluctuations on plant development

Temperature fluctuations affect tomato development not only through mean temperature but also through the timing, duration, and amplitude of thermal stress. Sub-optimal temperatures reduce leaf and truss initiation rates

and increase the time from anthesis to ripening, while high temperatures above the optimum alter vegetative and reproductive growth, including flower and pollen development, and thereby reduce fruit set and final yield (Graci and Barone, 2024). Experimental evidence also shows that tomato can integrate day-night temperature variation only within limits: early- and late-summer regimes with average day/night temperatures of 28.1°C/24.3°C and 30.1°C/26.5°C supported more clusters, flowers, fruits, and better quality than the hotter 32.4°C/28.5°C mid-summer regime (Talukder et al., 2025).

Short periods of temperature extremes during reproductive stages can be especially damaging because they directly impair pollen quality, seed set, fruit set, and fruit mass. In a controlled modelling study, 30°C and 34°C reduced pollen viability and germination, lowering seed set and fruit mass, while 14°C and 34°C reduced fruit set; the predicted yield loss at 14°C came from both fewer fruits and smaller fruits, whereas at 30°C it came mainly from smaller fruits (Zepeda et al., 2026). Field and greenhouse comparisons likewise showed that yield losses near 70% under high temperature were linked to poorer fruit set, and that maximum or minimum temperature during sensitive reproductive periods can matter more than season-long mean temperature because even short exposure above the optimum can sharply reduce reproductive success (Ro et al., 2021).

2.3 Temperature management strategies in greenhouse tomato production

Greenhouse temperature management should aim to maintain stable crop-level conditions rather than relying only on compartment-wide averages. Commercial greenhouse monitoring has shown spatial temperature gradients of up to 3°C and vapour pressure deficit differences of up to 0.6 kPa within the same canopy, and these local microclimate differences measurably altered stem growth, fruit growth, and truss mass at harvest (Šalagovič et al., 2024). This supports the use of denser sensor networks, because local microclimate effects on plant growth were larger than bulk climate variation recorded by a single central sensor, making whole-greenhouse sensor grids more suitable for climate control than one-point monitoring (Šalagovič et al., 2024).

In hot-season protected cultivation, cooling strategies should be adjusted to reproductive thermal thresholds rather than fixed to a single seasonal set point. Mean daily temperatures of 25°C-26°C appear to be the upper limit for proper fruit set and fruit yield in protected tomato during Mediterranean summer, and reducing mean daily temperature by only 1°C-1.5°C with fogging, together with increasing daytime relative humidity from 50% to 70%, improved pollen viability. Evidence from passive solar greenhouse systems also suggests that low-cost protection can buffer unfavorable field conditions and raise marketable yield, but shading must be used cautiously because although greenhouse production increased yield 1.8-fold over open field, added shading delayed flowering and reduced marketable yield by 48% (Angmo et al., 2021).

3 Effects of Temperature Regulation on Tomato Vegetative Growth

3.1 Effects on seed germination and seedling establishment

Temperature regulation strongly determines the success of tomato seed germination and early seedling establishment because these stages are among the most temperature-sensitive phases of the crop life cycle. Controlled experiments showed that the most suitable germination temperatures were 24°C-28°C, whereas germination rate and seedling vigor declined above 28.5°C, only about half of the seeds germinated at 31.5°C, and no germination occurred at 36°C (Tokić et al., 2023). Classic thermal analysis similarly found that germination occurred between 6.0°C and 37.5°C, with the optimum range for germination kinetics centered around 25.9°C-29.5°C, indicating that both excessively low and excessively high temperatures constrain rapid and uniform emergence.

High temperature not only suppresses germination percentage but can also trigger physiological inhibition that compromises subsequent establishment. In one genetic study, prolonged exposure of imbibed seeds to elevated temperature induced thermo-dormancy in the cultivar ‘Moneymaker’, with induction beginning after about 33 h and germination falling to 0% after roughly 100 h of exposure. Variety comparisons also showed that 33°C significantly reduced germination rate, vigor, germination index, and vitality index, and that early seedling roots were inhibited more strongly than shoots, with larger effects in less thermotolerant genotypes.

3.2 Effects on plant morphology and biomass accumulation

Temperature regulation also reshapes tomato morphology during vegetative growth, often by altering elongation patterns, leaf traits, and whole-plant partitioning. Seedlings developed at 28.5°C and 31.5°C showed significant hypocotyl elongation, while stronger heat exposure caused more severe visible injury, including chlorosis, leaf wilting, and stem bending in both seedlings and adult plants (Tokić et al., 2023). Under greenhouse lighting systems with different thermal properties, warmer leaf conditions were associated with thinner and smaller leaves and with a higher fraction of biomass allocated to vegetative tissues, indicating that temperature interacts with canopy energy balance to shape plant form and dry-matter distribution.

Biomass accumulation responds to temperature in a more complex way than morphology because higher temperature can stimulate growth processes while reducing final dry matter if respiratory or assimilate costs become too high. In growth-chamber experiments, a daily mean temperature of 30°C increased relative growth rate, net assimilation rate, and leaf area ratio, and gas-exchange at the later stage was about twice that at 20°C (Yamaura et al., 2021). However, the same study found that total dry matter was lower at 30°C and that non-structural carbohydrate accumulation in leaves and stems decreased, showing that supra-optimal temperature can accelerate carbon use and short-term growth while limiting biomass storage and final vegetative accumulation (Yamaura et al., 2021).

3.3 Effects on root development and nutrient uptake

Root systems are highly temperature-sensitive, and both low and high root-zone temperatures restrict root development and nutrient capture. Under heat stress, tomato seedlings showed inhibited primary root length at both 37°C and 45°C, while lateral root number was significantly suppressed under 37°C, demonstrating that root architecture is modified even before severe aboveground damage becomes apparent (Tokić et al., 2023). Low root-zone temperature had similarly negative effects: at 7°C and 13°C, root development was delayed and the number and diameter of ducts in root and stem were reduced, which limited mineral absorption and transport capacity (Miao et al., 2023).

Temperature effects on roots translate directly into nutrient uptake efficiency and shoot nutrition. Across six root-zone temperature treatments, nutrient uptake for most mineral elements peaked at 26.7°C, and root dry weight, shoot dry weight, shoot growth, plant height, and water use all peaked near 25°C, indicating a clear physiological optimum for root-mediated support of vegetative growth (Tindall et al., 1990). Additional evidence from low-temperature and nutrient-composition studies showed that increasing root temperature increased shoot total N, P, Mg, and K, whereas low root temperature caused nitrate and potassium to accumulate in roots because ion translocation was hindered, helping explain why cool root zones slow tomato growth even when nutrients are supplied adequately.

4 Effects of Temperature Regulation on Photosynthesis and Physiological Processes

4.1 Temperature effects on photosynthetic performance

Temperature regulation directly controls tomato photosynthetic capacity because both chilling and heat stress impair the efficiency of the photosynthetic apparatus. Under sub-optimal temperature, tomato showed reduced chlorophyll content and declines in Y(II), Fv/Fm, qP, and ETR, with larger reductions in the cold-sensitive cultivar than in the tolerant one, indicating that genotype influences the extent of photochemical damage (Gao and Wu, 2024). Heat stress similarly depressed gas exchange and photosynthesis by lowering P_Nmax and SPAD values, while increases in internal CO_2 concentration indicated that the limitation was mainly non-stomatal and associated with photosystem and Rubisco impairment (Luo et al., 2023).

Evidence from fluorescence-based studies shows that temperature stress acts strongly on electron transport, especially within PSII. In tomato leaf and fruit, OJIP fluorescence parameters clearly distinguished heat from chilling injury, and heat had a greater effect on the PSII electron transport chain than chilling, with fruit tissues showing stronger changes than leaves. Day/night temperature regime also matters: at the fruiting stage, positive DIF increased chlorophyll content, net photosynthetic rate, stomatal conductance, Fv/Fm, and ϕPSII, whereas negative DIF reduced these traits and increased non-photochemical quenching.

4.2 Regulation of water and nutrient metabolism under temperature changes

Temperature changes regulate tomato water relations largely through root hydraulic function and stomatal behavior. Under suboptimal soil temperature, root hydraulic conductivity and conductance declined, stomatal conductance decreased, and plant biomass was reduced, showing that cool root zones restrict water transport even when aboveground conditions are more favorable (Bristow et al., 2021). Heat stress also altered leaf water relations: high temperature reduced water-use efficiency, while salicylic acid pretreatment improved leaf water potential, osmotic potential, and stomatal function, indicating that water balance is a major component of thermal adaptation (Luo et al., 2023).

Temperature effects on nutrient metabolism are closely linked to photosynthesis and root performance. High temperature reduced nitrogen metabolism through lowered photosynthesis and nutrient loss, while moderate nitrogen supply helped maintain nitrate reductase, glutamine synthetase, soluble protein, and free amino acid levels under thermal stress (Luo et al., 2023). Under suboptimal soil temperature, nutrient uptake was also selectively constrained, with phosphorus uptake identified as especially inadequate because of low solubility and dependence on root surface activity, whereas greater phosphorus uptake was associated with improved photosynthetic performance (Bristow et al., 2021).

4.3 Antioxidant defense and stress adaptation mechanisms

A central consequence of temperature stress in tomato is the overproduction of reactive oxygen species, which disrupts redox balance and damages membranes, proteins, and photosynthetic systems. Heat stress is associated with toxic accumulation of ROS and broad physiological injury, and more general plant evidence shows that high temperature drives ROS overproduction, lipid peroxidation, membrane damage, and impairment of the oxygen-evolving and photochemical systems (Hasanuzzaman et al., 2020; Khan et al., 2024). In tomato exposed to drought, heat, and combined stress, both cultivars showed sharp increases in H_2O_2 and superoxide production, accompanied by higher oxidative damage markers and smaller canopy area and stem diameter under combined stress.

Tomato stress tolerance depends on activating both enzymatic and signaling-based antioxidant defenses. Under cold stress, trehalose pretreatment increased SOD, CAT, APX, and GR-related antioxidant capacity, reduced membrane lipid peroxidation, and acted through an H_2O_2-NO signaling pathway in which NO functioned downstream of H_2O_2 (Liu et al., 2020). Other studies support a similar redox-regulated adaptation model: exogenous ALA increased glutathione- and ascorbate-linked antioxidant defense at low temperature, while in heat stress, tomato thermotolerance was associated with higher APX and SOD activity, HSP40-mediated enzyme protection, and melatonin-related ROS scavenging (Fortunato et al., 2023).

5 Effects of Temperature Regulation on Flowering, Fruit Set and Yield Formation

5.1 Effects on flowering and reproductive development

Temperature regulation is especially critical during the reproductive stage because tomato flowering and fertilization respond to a narrower thermal range than vegetative growth. Optimal daily mean temperature for fruit set is generally around 21°C-24°C, whereas exposure to warmer conditions for successive days or weeks during reproductive growth markedly disrupts fruit set, and in protected cultivation 25°C-26°C appears to be the upper limit for proper fruit set and yield during hot Mediterranean summers. The reproductive damage is expressed through impaired anther and pollen function: mean daily temperatures near 29°C reduce fruit number, fruit set percentage (Dasgan et al., 2021), and fruit weight per plant, largely because elevated temperature disrupts pollen and anther development and lowers pollen viability.

Heat stress affects not only male fertility but the broader sequence of reproductive development from flower formation to post-pollination processes. Long-term moderate heat significantly reduced pollen viability, pollen number, female fertility, seeded-fruit set, and flower number per inflorescence, while only previously identified heat-tolerant cultivars maintained seeded fruit set under stress. Male-sterile experiments further showed that adequate pollen supply alone is not sufficient at high temperature, because as mean daily temperature increased from 25°C to 29°C, fruit set, total fruit number, total fruit weight, and seediness declined due to effects on ovule

development and post-pollen production processes, with sharp losses already evident from 25°C to 26°C and from 28°C to 29°C (Fortunato et al., 2023) (Figure 1).

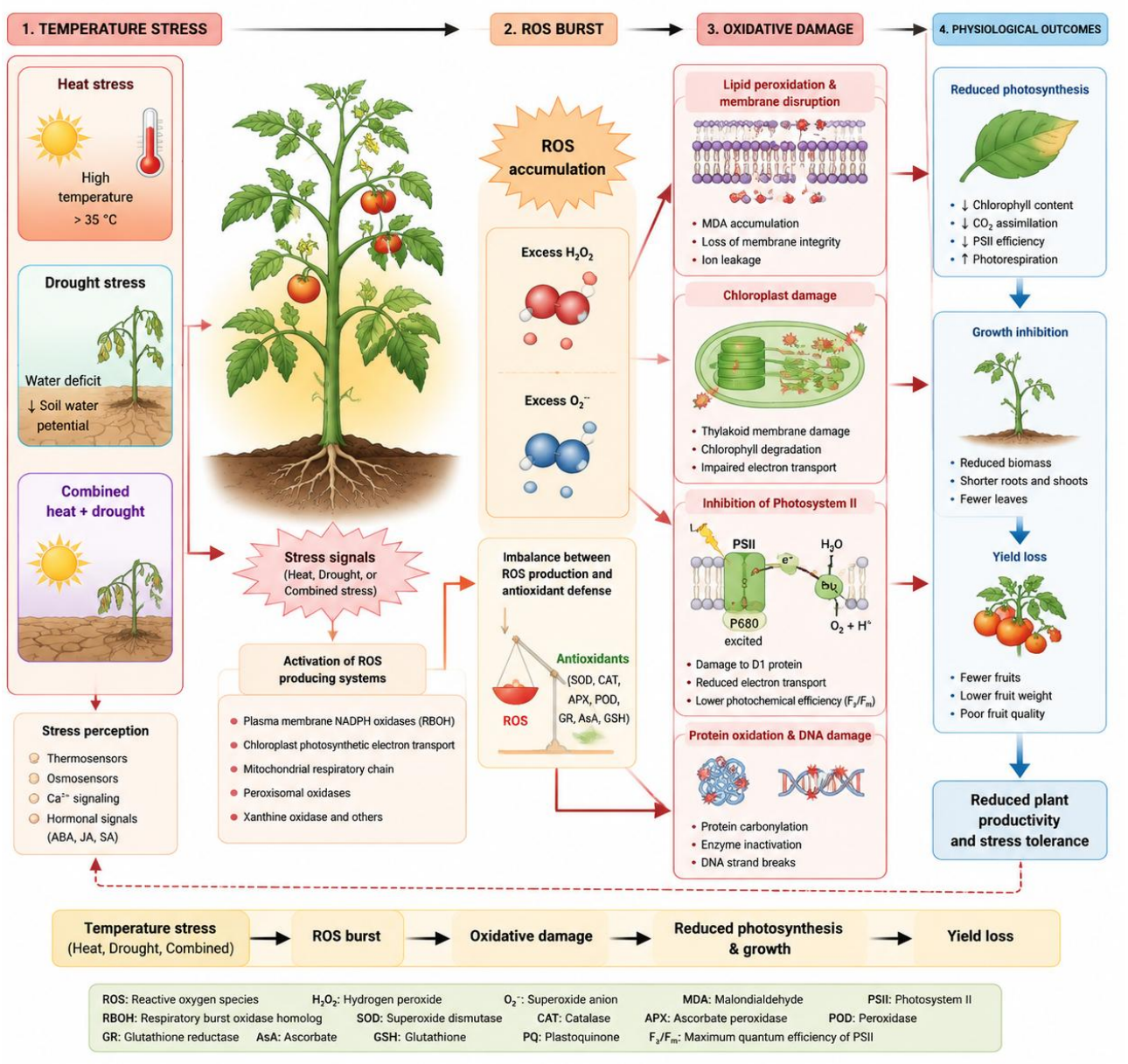

Figure 1 Mechanistic overview of temperature stress-induced reactive oxygen species (ROS) accumulation and antioxidant defense activation in tomato plants

5.2 Effects on fruit development and yield components

Temperature regulation strongly influences yield formation by altering fruit set, fruit number, seed formation, fruit growth rate, and fruit mass. In male-fertile tomatoes, a daily mean temperature of 29°C reduced fruit number, fruit weight per plant, and seed number per fruit to 10%, 6.4%, and 16.4% of the values observed at 25°C, showing how rapidly yield can collapse when reproductive heat stress persists. Genotype comparisons under elevated temperature likewise found that fruit number per plant, fruit set percentage, average fruit weight, and yield per plant all declined with rising temperature, although the extent of reduction differed among cultivars, indicating substantial genetic variation in reproductive heat tolerance (Vijayakumar et al., 2021).

Fruit development after set is also temperature-sensitive, and the direction of the response depends on both developmental stage and the thermal regime. Controlled-environment studies showed that fruits ripened much faster as temperature rose from 14°C to 26°C, but both low and high regimes tended to produce small

parthenocarpic fruits, and the combination of poor fruit set at 26°C, fewer flowers, and altered fruit growth resulted in low yield. Temperature also modifies the cellular basis of fruit growth: although fruit growth rate was lower at 20/20°C than at warmer regimes, final fruit size was maintained by compensation between cell number and cell size, whereas heavier fruit load reduced fruit size mainly by slowing cell expansion rather than by reducing cell number.

5.3 Effects on fruit quality characteristics

Temperature regulation affects tomato fruit quality as strongly as it affects yield, but the response is trait-specific. Elevated temperature often increases total soluble solids, titratable acidity, and ascorbic acid, while decreasing lycopene, and high-temperature field screening further showed increases in soluble solids, acidity, total phenols, and vitamin C in tolerant genotypes, with concurrent decreases in pH, electrical conductivity, flavonoids, lycopene, and β-carotene (Vijayakumar et al., 2021). These quality shifts indicate that heat does not uniformly degrade composition; instead, it tends to re-balance primary and secondary metabolites, sometimes improving acidity- or vitamin-related traits while reducing carotenoid-based color and nutritional value.

The effect of temperature on fruit quality also depends on developmental stage, humidity, and the specific metabolite considered. Increasing fruit temperature from 21°C-26°C reduced total carotene without affecting lycopene, whereas a further rise from 27°C-32°C reduced ascorbate, lycopene, and precursor contents but increased rutin, caffeic acid derivatives, and glucosides, showing that antioxidant pathways are highly temperature-sensitive. Under combined high temperature and high relative humidity, enzyme activities linked to sucrose breakdown and organic acid metabolism shifted in ways that reduced soluble sugar, vitamin C, total sugar, and the sugar/acid ratio, while increasing titratable acidity; notably, 32°C with 70% relative humidity was identified as the best condition for maintaining fruit quality during the reproductive period under high-temperature stress (Zheng et al., 2022).

6 Physiological and Molecular Mechanisms of Temperature Regulation Effects

6.1 Hormonal regulation under temperature stress

Temperature stress in tomato triggers broad hormonal reprogramming rather than a single-pathway response. Across heat-stress studies, hormone-associated genes are repeatedly among the temperature-responsive transcripts, and genotype-dependent thermotolerance is linked in part to differential regulation of auxin- and ethylene-related genes (Hu et al., 2020). Brassinosteroid signaling appears to be one important branch of this response, because BR treatment in tomato increases RBOH1 expression and apoplastic H_2O_2, while silencing RBOH1 compromises heat tolerance (Li et al., 2021).

Hormonal regulation also integrates developmental temperature responses and cross-stress protection. Day-night temperature difference regulates stem elongation through changes in gibberellin and IAA biosynthesis, with negative DIF suppressing both hormone levels and elongation-related gene expression (Ohtaka et al., 2020). Under extreme temperatures, strigolactones act upstream of ABA-dependent protection, since heat and cold induce strigolactone biosynthesis genes, and ABA deficiency abolishes strigolactone-induced transcription of HSP70, CBF1, and antioxidant-related genes (Chi et al., 2021).

6.2 Heat and cold stress response pathways

The core heat stress response in tomato is organized around HSF-HSP networks that preserve protein homeostasis and cellular survival. Hsfs control transcriptional reprogramming at high temperature and activate canonical HSR genes, especially heat shock proteins, which function as molecular chaperones to prevent protein misfolding and aggregation. Within tomato, HsfA1 has a uniquely central role, because plants with HsfA1 cosuppression become extremely heat-sensitive and fail to induce normal synthesis of chaperones and other Hsfs under elevated temperature.

Cold and heat pathways also intersect with ROS and kinase signaling, but the specific regulators differ by stress type. In heat-stressed tomato, SlMAPK3 acts as a negative regulator of thermotolerance, since knockout mutants show less wilting and membrane damage, lower ROS, and higher antioxidant enzyme activity together with

increased HSF and HSP expression. Under chilling, tomato appears to use more than the classical CBF route alone: SlGRAS4 promotes chilling tolerance by directly activating many cold-response targets and SlCBF promoters, while functioning as a distinct regulon that operates independently of the ICE1-CBF pathway (Liu et al., 2020).

6.3 Molecular regulation of temperature-responsive genes

Temperature-responsive gene regulation in tomato combines conserved stress modules with substantial genotype- and tissue-specific variation. In seedlings, most heat stress transcription factors and HSP genes respond similarly across genotypes, but hormone- and RNA-related regulators such as HsfA6b show differential expression associated with thermotolerance (Hu et al., 2020). In reproductive tissues, heat-stressed microspores upregulate small HSPs, HSP70, HSP90, HSFA2, and HSFA3, while tolerant microspores show higher basal expression of several protective genes before stress, consistent with a primed thermotolerance state (Frank et al., 2009).

Recent genomic studies show that these responses are organized into complex regulatory networks rather than isolated genes. In tomato flower buds, co-expression analysis under heat identified novel HSR-related transcription factors such as SlWRKY75, SlMYB117, and SlNAM, and experimentally validated HSF-regulated targets including SlGrpE, SlERDJ3A, SlTIL, and SlPOM1 (Li et al., 2023). Genetic mapping and transcriptomics further indicate that heat tolerance is polygenic, with major QTL regions enriched for plant hormone signaling, MAPK signaling, sugar metabolism, and fatty acid metabolism, and with tolerant genotypes showing more gene upregulation than sensitive genotypes under heat stress.

7 Case Study: Effects of Temperature Regulation Strategies on Greenhouse Tomato Production

7.1 Experimental background and temperature management treatments

Recent greenhouse case studies have tested temperature regulation through both structural control and targeted thermal treatments rather than by relying on ambient protection alone. In commercial and research settings, treatments included multi-point canopy monitoring to detect spatial thermal gradients, geothermal pipe heating with water temperatures of 25°C, 35°C, and 45°C against an unheated control, and comparisons between regulated greenhouse environments and more variable open-field conditions (Ouyang et al., 2022; Šalagovič et al., 2024). These designs reflect a common experimental logic: quantify how precisely managed air or root-zone temperature modifies crop performance relative to uncontrolled or weakly controlled systems.

Other studies used dynamic or stage-specific strategies that more closely resemble practical greenhouse decision-making. A low pre-night temperature integration strategy imposed 9.4°C, 11.3°C, 13.3°C, and 15.1°C pulses for the first 3 h of the night while keeping the same 24-h mean temperature, whereas root-zone regulation trials combined daytime air temperatures of 20°C, 25°C, 30°C, and 35°C with root-zone settings of 15°C, 20°C, 25°C, and 30°C to identify efficient combinations for early growth (Ju et al., 2023). Additional greenhouse studies also evaluated heat mitigation through micro-spray plus drip irrigation, and precision control through sensor placement near the ground, canopy, and roof, showing that temperature management treatments increasingly integrate climate control with real-time monitoring and automated adjustment (Figure 2) (Xue et al., 2023; Zhang et al., 2024).

7.2 Effects of temperature regulation on growth and physiological responses

Temperature regulation consistently altered vegetative growth and physiological activity in greenhouse tomatoes. Soil warming significantly affected plant height, leaf area index, assimilation rate, leaf temperature, chlorophyll, and dry matter accumulation, and across two years the strongest treatment ranked T3 > T2 > T1 > control for most growth and physiological indicators (Ouyang et al., 2022). Root-zone regulation produced similarly clear effects during early growth, with 20°C-25°C root-zone settings generally supporting favorable crop growth rate and relative growth rate across several air temperature regimes (Ju et al., 2023).

Heat mitigation strategies also improved physiological resilience when greenhouse temperatures became excessive. Under high-temperature greenhouse conditions, micro-spray reduced average daily air temperature by about 0.76°C-0.8°C and leaf temperature by 4.6°C-4.9°C, while increasing photosynthetic rate, PSII efficiency,

and stomatal conductance relative to drip irrigation alone (Xue et al., 2023). At the same time, genotype-focused greenhouse screening showed that high temperature depressed photosynthesis, chlorophyll, proline balance, and vegetative traits such as plant height and shoot and root fresh weight, confirming that the value of temperature regulation depends partly on cultivar heat tolerance (Rajametov et al., 2021).

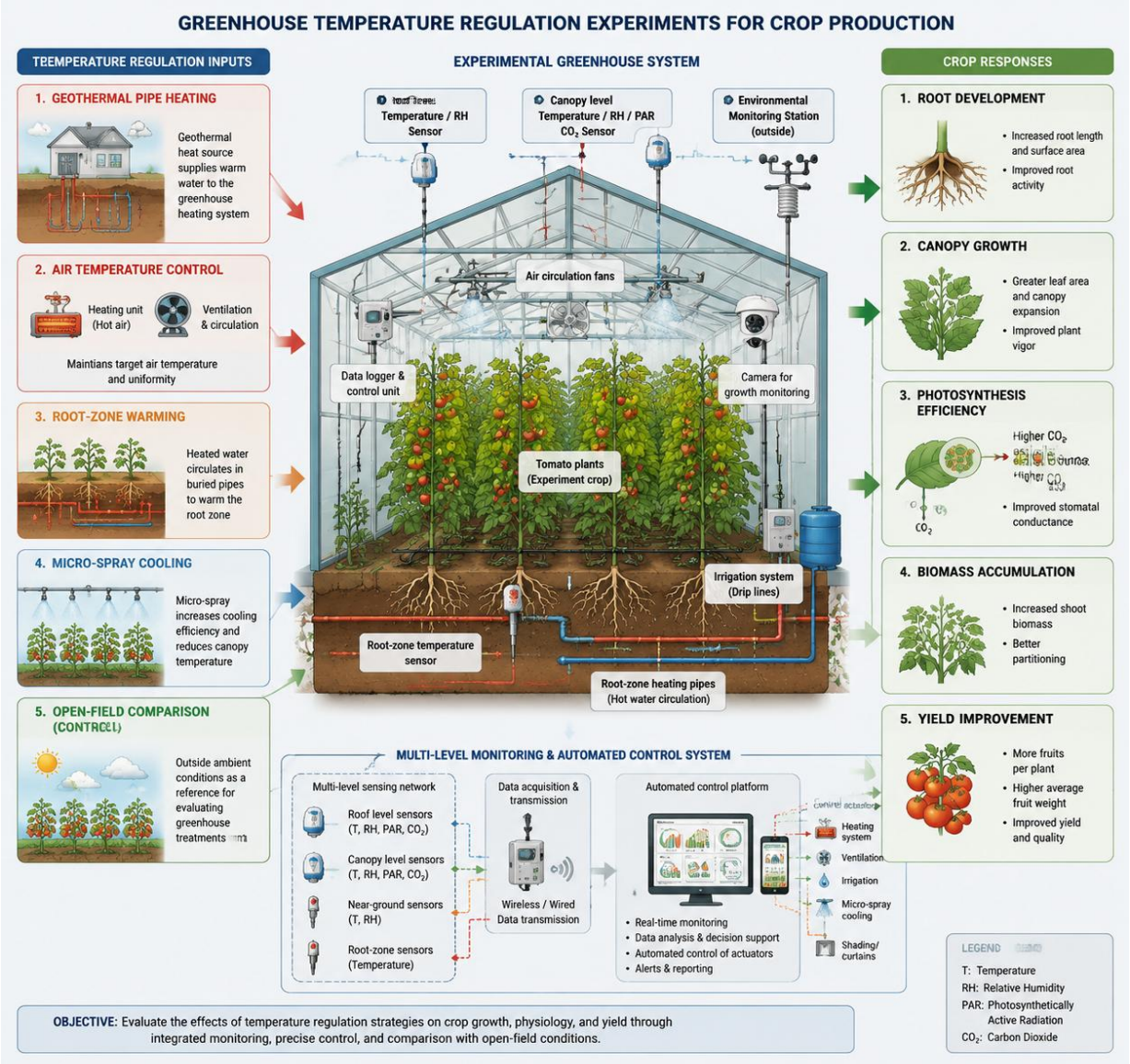

Figure 2 Experimental framework for evaluating greenhouse temperature regulation strategies and their effects on crop growth performance

7.3 Effects on yield performance and economic benefits

The yield effects of greenhouse temperature regulation were substantial, but they depended on how effectively the strategy stabilized the crop microclimate. In a greenhouse versus open-field comparison, weekly temperature variation was only about ±1.0°C in the greenhouse versus ±10.2°C in the open field, and the more stable greenhouse environment produced higher yields while reducing the risk of total crop loss (Efeta et al., 2025). In another greenhouse study, passive solar protection increased marketable tomato yield by 1.8-fold over open-field production, although adding shade delayed flowering and reduced marketable yield by 48%, showing that not every cooling-oriented intervention improves productivity (Angmo et al., 2021).

More intensive regulation strategies also translated into measurable yield and economic gains. Geothermal soil warming increased yield by about 18.2%-18.6% and water productivity by 32.6%-33.5%, with optimal soil temperatures estimated at 26.1°C in spring/summer and 20.6°C in autumn/winter (Ouyang et al., 2022). Economic

case evidence from overwinter tomato production in North China further showed that soft-shell solar greenhouses raised average daily temperature by 10°C-15°C, reduced low-temperature stress duration by 25%, and improved net returns when combined with variety optimization and scenario-based sales, indicating that greenhouse temperature regulation can generate both biological and commercial benefits when paired with cultivar and market strategy (Liu et al., 2025).

8 Conclusions and Future Perspectives

Temperature exerts a pervasive influence on tomato performance because developmental, physiological, and reproductive processes respond differently to thermal conditions across the crop cycle. Tomato is sensitive to temperatures below 12°C and above 32°C, and high temperature particularly decreases fruit yield while also altering multiple physiological traits and fruit quality attributes. Reviews of sub-optimal and supra-optimal conditions further show that cooler conditions can slow leaf and truss initiation, increase leaf thickness, reduce relative growth rate, and impair pollen quality, whereas warmer conditions can accelerate early development yet compromise later vegetative growth, fruit set, and seasonal yield stability. The overall yield outcome reflects the integration of many distinct temperature-sensitive processes rather than a single limiting trait. High temperature negatively affects both vegetative growth and reproductive development, leading to losses in fruit set, yield, and quality, while genotype-dependent differences in pollen viability, photosynthesis, and fruit-setting ability explain why some cultivars perform better under stress than others. Experimental and field-based evidence also indicates that elevated temperature can reduce fruit number, fruit weight, and marketable quality, although moderate chilling in some systems can induce acclimation and preserve yield, highlighting that the effect of temperature regulation depends on stress intensity, duration, and developmental stage.

Future research in temperature-controlled tomato production should move beyond describing stress injury and focus on predictive, trait-based, and mechanistic strategies for intervention. High-throughput phenotyping, including thermal infrared, hyperspectral, and chlorophyll fluorescence imaging, now offers non-destructive ways to detect heat-response traits, while GWAS and integrated genomics can identify markers for targeted breeding of thermotolerant cultivars. At the same time, molecular research increasingly supports the use of candidate genes related to flowering, pollen development, fruit set, heat shock responses, and epigenetic regulation as practical targets for breeding under recurrent heat stress. A second priority is to connect crop genetics with greenhouse engineering and climate-control technologies at commercial scale. Survey evidence from 326 ha of high-tech hydroponic greenhouses exposed to extreme summer heat showed that even advanced systems suffered yield loss and rising water, fertilizer, and electricity use, indicating that current climate-control capacity is often insufficient under future warming. Research should therefore test combinations of improved cooling, renewable-energy integration, season shifting, and heat-resilient varieties, while also evaluating emerging interventions such as prime editing, which increased tomato yield by 33% under heat stress without fruit-quality penalties through heat-responsive regulation of source-sink relations.

The implications for sustainable tomato production are both agronomic and systemic. Climate warming is projected to reduce processing tomato production in major producing regions by about 6% by 2050, with some leading areas facing additional water constraints, which implies that climate resilience will depend not only on plant tolerance but also on regional shifts in production systems and resource availability. In greenhouse systems, adaptation will require integrated approaches that combine structural innovations, precision irrigation, decision-support tools, and climate-resilient cultivars, because elevated temperature increasingly acts together with high radiation, water shortage, and vapor pressure deficits rather than in isolation. Sustainable and climate-resilient tomato production will therefore depend on combining biological resilience with technological and management innovation. Multidisciplinary strategies that unite breeding, genetic engineering, physiological knowledge, agronomic adjustment, precision monitoring, and beneficial microorganisms are increasingly viewed as essential for maintaining yield and food security under climate change. For tomato specifically, advanced ventilation, shading, renewable-energy-supported climate buffering, and cultivar selection for reproductive heat tolerance appear especially important because stable temperature and humidity are central to fruit set, lycopene formation, and marketable yield preservation in warmer production environments.

References

Alsamir M., Mahmood T., Trethowan R., and Ahmad N., 2020, An overview of heat stress in tomato (*Solanum lycopersicum* L.), Saudi Journal of Biological Sciences, 28(3): 1654-1663.
https://doi.org/10.1016/j.sjbs.2020.11.088

Angmo P., Phuntsog N., Namgail D., Chaurasia O., and Stobdan T., 2021, Effect of shading and high temperature amplitude in greenhouse on growth, photosynthesis, yield and phenolic contents of tomato (*Lycopersicum esculentum* Mill.), Physiology and Molecular Biology of Plants, 27(7): 1539-1546.
https://doi.org/10.1007/s12298-021-01032-z

Ayankojo I.T., and Morgan K., 2020, Increasing air temperatures and its effects on growth and productivity of tomato in South Florida, Plants, 9(9): 1245.
https://doi.org/10.3390/plants9091245

Bertin N., 2004, Analysis of the tomato fruit growth response to temperature and plant fruit load in relation to cell division, cell expansion and DNA endoreduplication, Annals of Botany, 95(3): 439-447.
https://doi.org/10.1093/aob/mci042

Bristow S., Hernandez-Espinoza L.H., Bonarota M.S., and Barrios-Masias F., 2021, Tomato rootstocks mediate plant-water relations and leaf nutrient profiles of a common scion under suboptimal soil temperatures, Frontiers in Plant Science, 11: 618488.
https://doi.org/10.3389/fpls.2020.618488

Chi C., Xu X.C., Wang M., Zhang H., Fang P., Zhou J., Xia X., Shi K., Zhou Y., and Yu J., 2021, Strigolactones positively regulate abscisic acid-dependent heat and cold tolerance in tomato, Horticulture Research, 8: 228.
https://doi.org/10.1038/s41438-021-00668-y

Dasgan H., Dere S., Akhoundnejad Y., and Arpacı B., 2021, Effects of high-temperature stress during plant cultivation on tomato (*Solanum lycopersicum* L.) fruit nutrient content, Acta Horticulturae, 2021(1): 7994417.

Efeta B., D'arc U.J., Claude S.J., Pancras N., and Jonathan M., 2025, The influence of temperature difference on crop physiological process: Systematic growth analysis of *Solanum lycopersicum* (tomatoes) in both greenhouse and open field, East African Journal of Agriculture and Biotechnology, 8(2): 3973.
https://doi.org/10.37284/eajab.8.2.3973

Elazazi E., Ziems L., Mahmood T., Eltanger N., Al-Qahtani M., Shahsil N., Al-Kuwari A., Metwally M., Trethowan R., and Dong C., 2024, Genotypic selection using quantitative trait loci for better productivity under high temperature stress in tomato (*Solanum lycopersicum* L.), Horticulturae, 10(8): 874.
https://doi.org/10.3390/horticulturae10080874

Fortunato S., Lasorella C., Dipierro N., Vita F., and De Pinto M.C., 2023, Redox signaling in plant heat stress response, Antioxidants, 12(3): 605.
https://doi.org/10.3390/antiox12030605

Frank G., Pressman E., Ophir R., Althan L., Shaked R., Freedman M., Shen S., and Firon N., 2009, Transcriptional profiling of maturing tomato (*Solanum lycopersicum* L.) microspores reveals the involvement of heat shock proteins, ROS scavengers, hormones, and sugars in the heat stress response, Journal of Experimental Botany, 60(13): 3891-3908.
https://doi.org/10.1093/jxb/erp234

Gao H., and Wu F., 2024, Physiological and transcriptomic analysis of tomato in response to sub-optimal temperature stress, Plant Signaling and Behavior, 19(1): 2332018.
https://doi.org/10.1080/15592324.2024.2332018

Graci S., and Barone A., 2024, Tomato plant response to heat stress: a focus on candidate genes for yield-related traits, Frontiers in Plant Science, 14: 1245661.
https://doi.org/10.3389/fpls.2023.1245661

Hasanuzzaman M., Bhuyan M., Zulfiqar F., Raza A., Mohsin S., Mahmud J., Fujita M., and Fotopoulos V., 2020, Reactive oxygen species and antioxidant defense in plants under abiotic stress: Revisiting the crucial role of a universal defense regulator, Antioxidants, 9(8): 681.
https://doi.org/10.3390/antiox9080681

Hu Y., Fragkostefanakis S., Schleiff E., and Simm S., 2020, Transcriptional basis for differential thermosensitivity of seedlings of various tomato genotypes, Genes, 11(6): 655.
https://doi.org/10.3390/genes11060655

Ju S.H., Lee B., Kim E.J., Go Y., Park J., and Na H., 2023, Effects of the air temperature and root zone temperature in greenhouses on the early growth of tomatoes, Korean Journal of Horticultural Science and Technology, 41(4): 390-402.
https://doi.org/10.7235/hort.20230036

Khan Q., Wang Y., Xia G., Yang H., Luo Z., and Zhang Y., 2024, Deleterious effects of heat stress on the tomato, its innate responses, and potential preventive strategies in the realm of emerging technologies, Metabolites, 14(5): 283.
https://doi.org/10.3390/metabo14050283

Labouriau L.G., and Osborn J., 1984, Temperature dependence of the germination of tomato seeds, Journal of Thermal Biology, 9(4): 285-294.
https://doi.org/10.1016/0306-4565(84)90010-X

Lee K., Rajametov S., Jeong H., Cho M., Lee O., Kim S.G., Yang E., and Chae W., 2022, Comprehensive understanding of selecting traits for heat tolerance during vegetative and reproductive growth stages in tomato, Agronomy, 12(4): 834.
https://doi.org/10.3390/agronomy12040834

Li H., Liu Y., Li Y., Yang Q., Yang T., Zhou Z., Li Y., Zhang N., Lyu Y., Zhu Y., and Lin T., 2023, Heat shock transcription factors regulate thermotolerance gene networks in tomato (*Solanum lycopersicum*) flower buds, Horticultural Plant Journal, 11(1): 199-210.
https://doi.org/10.1016/j.hpj.2023.06.004

Li N.Y., Euring D., Cha J., Lin Z., Lu M., Huang L.J., and Kim W.Y., 2021, Plant hormone-mediated regulation of heat tolerance in response to global climate change, Frontiers in Plant Science, 11: 627969.
https://doi.org/10.3389/fpls.2020.627969

Liu H., Zhao H., Liu S., Tian Y., Li W., Wang B., Hu X., Sun D., Wang T., Wu S., Wang F., Zhu N., Tao Y., and Lei X., 2025, When tomatoes hit the winter: A counterattack to overwinter production in soft-shell solar greenhouses in North China, Horticulturae, 11(4): 436.
https://doi.org/10.3390/horticulturae11040436

Liu T., Ye X., Li M., Li J., Qi H., and Hu X., 2020, H_2O_2 and NO are involved in trehalose-regulated oxidative stress tolerance in cold-stressed tomato plants, Environmental and Experimental Botany, 171: 103961.
https://doi.org/10.1016/j.envexpbot.2019.103961

Liu Y., Shi Y., Zhu N., Zhong S., Bouzayen M., and Li Z.G., 2020, SlGRAS4 mediates a novel regulatory pathway promoting chilling tolerance in tomato, Plant Biotechnology Journal, 18(7): 1620-1633.
https://doi.org/10.1111/pbi.13328

Lu X., Wu J., Shi Q., Sun S., Cheng Y., Zhou G., Li R., Wang H., Van Der Knaap E., and Cui X., 2025, A feedback loop at the THERMOSENSITIVE PARTHENOCARPY 4 locus controls tomato fruit set under heat stress, Nature Communications, 16(1): 4184.
https://doi.org/10.1038/s41467-025-59522-7

Luo J., Yang Z., Zhang F., and Li C., 2023, Effect of nitrogen application on enhancing high-temperature stress tolerance of tomato plants during the flowering and fruiting stage, Frontiers in Plant Science, 14: 1172078.
https://doi.org/10.3389/fpls.2023.1172078

Miao Y., Ren J.R., Zhang Y.Z., Chen X.C., Qi M.Q., Li T.L., Zhang G.Z., and Liu Y.L., 2023, Effect of low root-zone temperature on photosynthesis, root structure and mineral element absorption of tomato seedlings, Scientia Horticulturae, 315: 111956.
https://doi.org/10.1016/j.scienta.2023.111956

Miller G., Beery A., Singh P., Wang F., Zelingher R., Motenko E., and Lieberman-Lazarovich M., 2021, Contrasting processing tomato cultivars unlink yield and pollen viability under heat stress, AoB Plants, 13(4): plab046.
https://doi.org/10.1093/aobpla/plab046

Ohtaka K., Yoshida A., Kakei Y., Fukui K., Kojima M., Takebayashi Y., Yano K., Imanishi S., and Sakakibara H., 2020, Difference between day and night temperatures affects stem elongation in tomato (*Solanum lycopersicum*) seedlings via regulation of gibberellin and auxin synthesis, Frontiers in Plant Science, 11: 577235.
https://doi.org/10.3389/fpls.2020.577235

Ouyang Z., Tian J., Yan X., and Shen H., 2022, Photosynthesis, yield and fruit quality of tomatoes and soil microorganisms in response to soil temperature in the greenhouse, Irrigation and Drainage, 71(3): 604-618.
https://doi.org/10.1002/ird.2678

Rajametov S., Yang E., Jeong H., Cho M., Chae S., and Paudel N., 2021, Heat treatment in two tomato cultivars: A study of the effect on physiological and growth recovery, Horticulturae, 7(5): 119.
https://doi.org/10.3390/horticulturae7050119

Ro S., Chea L., Ngoun S., Stewart Z., Roeurn S., Theam P., Lim S., Sor R., Kosal M., Roeun M., Dy K.S., and Prasad P., 2021, Response of tomato genotypes under different high temperatures in field and greenhouse conditions, Plants, 10(3): 449.
https://doi.org/10.3390/plants10030449

Šalagovič J., Vanhees D.J., Verboven P., Holsteens K., Verlinden B., Huysmans M., Van De Poel B., and Nicolaï B., 2024, Microclimate monitoring in commercial tomato (*Solanum lycopersicum* L.) greenhouse production and its effect on plant growth, yield and fruit quality, Frontiers in Horticulture, 3: 1425285.
https://doi.org/10.3389/fhort.2024.1425285

Talukder M.R., Ali N., Bappy H., Haque M., Abul M., Molla H., Alam M.Z., Mosharaf M.K., Limon S., and Quzzaman S.F.M.R., 2025, Fluctuation of ambient day-night temperature influences morphological traits, floral characters, fruit yield and quality of summer tomato genotypes grown in hydroponics, New Zealand Journal of Crop and Horticultural Science, 53(5): 2731-2754.
https://doi.org/10.1080/01140671.2025.2504209

Tindall J., Mills H., and Radcliffe D., 1990, The effect of root zone temperature on nutrient uptake of tomato, Journal of Plant Nutrition, 13(8): 939-956.
https://doi.org/10.1080/01904169009364127

Tokić M., Levanić L.D., Ludwig-Müller J., and Bauer N., 2023, Growth and molecular responses of tomato to prolonged and short-term heat exposure, International Journal of Molecular Sciences, 24(5): 4456.
https://doi.org/10.3390/ijms24054456

Van Ploeg D., and Heuvelink E., 2005, Influence of sub-optimal temperature on tomato growth and yield: A review, The Journal of Horticultural Science and Biotechnology, 80(6): 652-659.
https://doi.org/10.1080/14620316.2005.11511994

Vijayakumar A., Shaji S., Beena R., Sarada S., Rani S.T., Stephen R., Manju R., and Viji M., 2021, High temperature induced changes in quality and yield parameters of tomato (*Solanum lycopersicum* L.) and similarity coefficients among genotypes using SSR markers, Heliyon, 7(2): e05988.
https://doi.org/10.1016/j.heliyon.2021.e05988

Wang T., Chen Y., Wang C., Xia Z., Liu Z., Gao L., and Zhang W., 2024, SlNAC3 suppresses cold tolerance in tomatoes by enhancing ethylene biosynthesis, Plant, Cell and Environment, 47(8): 3132-3146.
https://doi.org/10.1111/pce.14933

Xue R., Zhang C., Yan H., Li J., Ren J., Akhlaq M., Hameed M.U., and Disasa K.N., 2023, Physiological response of tomato and cucumber plants to micro-spray in high-temperature environment: A scientific and effective means of alleviating crop heat stress, Agronomy, 13(11): 2798.
https://doi.org/10.3390/agronomy13112798

Yamaura H., Kanno K., Takano N., Isozaki M., and Iwasaki Y., 2021, Supra-optimal daily mean temperature stimulates plant growth and carbohydrate use in tomato, Scientia Horticulturae, 276: 109780.
https://doi.org/10.1016/j.scienta.2020.109780

Zepeda A.C., Vorage S., Van Mourik S., Heuvelink E., and Marcelis L.F.M., 2026, Too cold or too warm? Modelling seed set and fruit mass based on the effect of temperature on pollen quality, AoB Plants, 18(1): plag004.
https://doi.org/10.1093/aobpla/plag004

Zhang W., Zhong W., Liu Z., Du B., Li M., Huang M., Yu H., Chen B., and Tang Y., 2024, Precision regulation and forecasting of greenhouse tomato growth conditions using an improved GA-BP model, Sustainability, 16(10): 4161.
https://doi.org/10.3390/su16104161

Zheng Y., Yang Z., Wei T., and Zhao H., 2022, Response of tomato sugar and acid metabolism and fruit quality under different high temperature and relative humidity conditions, Phyton, 91(9): 2033-2054.
https://doi.org/10.32604/phyton.2022.019468

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