

Strategies to Boost Heat Tolerance in Tomato: Adapting to Rising Temperatures

Rupsha Bhowmick, Anirneeta De*

School of Agriculture, Swami Vivekananda University,
Telinipara, Barrackpore, North 24 Parganas, West Bengal
700121, India

* Corresponding author: anirneetad@svu.ac.in

Abstract

Tomato (*Solanum lycopersicum*) is one of the most important vegetable crops worldwide, ranking second in both cultivation area and production. Tomatoes grow best at temperatures between 25–30°C during the day and around 20°C at night. However, higher temperatures can seriously damage their growth and development. To survive heat stress, tomatoes adapt by making various changes in their physiology, structure, and biochemistry. Improving their tolerance to high temperatures can be achieved through different methods. These include better farming practices, using growth regulators and fertilizers, breeding heat-resistant varieties, and genetic modification. Simple strategies like treating seeds with low doses of inorganic salts before sowing, spraying plants with osmoprotectants or signaling molecules, and preconditioning plants can also help reduce the harmful effects of heat stress. These methods help tomatoes avoid stress and develop natural mechanisms to tolerate high temperatures.

Keywords Tomato, Thermotolerance, Stress Mitigation Strategies.

Introduction

Tomato (*Solanum lycopersicum* L.), a member of the Solanaceae family, is one of the most important horticultural crops grown worldwide, valued for its nutritional, economic, and industrial significance. It ranks second among vegetable crops globally in terms of both cultivated area and production volume, surpassed only by potato (FAO, 2023). The fruit is a rich source of vitamins A and C, lycopene—a powerful antioxidant—and minerals, making it a staple in both fresh consumption and processed forms such as sauces, pastes, and juices (Rai et al., 2020). Its adaptability to diverse agro-climatic zones and relatively short growth cycle make it a preferred choice for both subsistence and commercial agriculture.

Globally, tomatoes are cultivated on over 5 million hectares, with annual production exceeding 182 million tonnes. Leading producers include China, India, the United States, Turkey, and Egypt (FAOSTAT, 2023). However, despite its wide adaptability, tomato is highly sensitive to climatic stress, especially elevated temperatures. Its narrow optimal temperature range—25–30°C during the day and 18–20°C at night—means that deviations, particularly prolonged heat episodes, can lead to significant reductions in plant vigor, reproductive development, and fruit yield (Sato et al., 2000; Wahid et al., 2007).

Recent climate models predict a global average temperature increase of 1.5–2°C by the mid-21st century under most greenhouse gas emission scenarios, with more frequent and intense heatwaves projected in many parts of the world (IPCC, 2021). For heat-sensitive crops like tomato, such climatic anomalies are increasingly becoming critical production bottlenecks. High temperatures negatively influence a wide range of physiological and biochemical processes, including membrane stability, pollen viability, photosynthesis, enzymatic activity, and water relations, thereby compromising both yield and quality (Bita & Gerats, 2013; Firon et al., 2006).

Particularly during the reproductive phase, heat stress can lead to abnormal floral development, poor pollen germination,

reduced fruit set, and fruit abnormalities like blossom end rot (Camejo et al., 2005; Sato et al., 2006). These effects are further exacerbated under concurrent abiotic stresses such as drought or salinity, which often co-occur with high temperatures in arid and semi-arid regions (Hasanuzzaman et al., 2013).

Addressing heat stress in tomato has thus emerged as a high priority for sustainable horticultural production under climate change. Researchers and growers are increasingly focusing on integrated thermotolerance strategies encompassing improved agronomic management (e.g., microclimate modification, irrigation scheduling), exogenous application of protectants (e.g., growth regulators, osmoprotectants), development of heat-resilient cultivars through classical breeding, and cutting-edge genomic tools such as marker-assisted selection, transgenic approaches, and genome editing (Zhang et al., 2022; Pan et al., 2021).

This review provides a comprehensive synthesis of the physiological and molecular impacts of heat stress in tomato, and explores various mitigation strategies—both traditional and modern—that can enhance thermotolerance and ensure stable yields in a warming world.

Physiological and Biochemical Impacts of Heat Stress in Tomato

Heat stress, typically defined as temperatures exceeding the optimal range for tomato growth (25–30°C during the day and 18–20°C at night), can severely impair plant development and productivity. Tomatoes are especially vulnerable during their reproductive stages, but all growth phases—from germination to fruit maturation—are susceptible to high-temperature stress (Sato et al., 2000; Wahid et al., 2007). The detrimental effects of heat stress are multifaceted, affecting a wide range of physiological, cellular, and molecular processes.

● Reproductive Abnormalities and Reduced Fruit Set

High temperatures during the flowering and pollination stages are particularly damaging. Floral organ development is disrupted, resulting in shortened styles, malformed anthers, and poorly developed ovules. Pollen viability

and germination rates drop significantly under heat stress, leading to reduced fertilization efficiency and fruit set (Firon et al., 2006; Pressman et al., 2002). In tomato, exposure to temperatures above 32°C during anthesis can lead to pollen sterility due to carbohydrate deficiency and abnormal tapetum degeneration, ultimately compromising yield (Zinn et al., 2010).

● **Inhibition of Photosynthesis**

Photosynthesis is one of the most heat-sensitive physiological processes in tomato. Elevated temperatures impair photosystem II (PSII) activity, degrade chlorophyll pigments, and increase photorespiration, leading to reduced carbon fixation and energy assimilation (Camejo et al., 2005). Enzymes involved in the Calvin cycle, such as Rubisco, become unstable at high temperatures, further lowering photosynthetic efficiency. Heat-stressed tomato plants also exhibit a decline in stomatal conductance, which limits CO₂ uptake and exacerbates the inhibition of photosynthesis (Mathur et al., 2014).

● **Membrane Damage and Electrolyte Leakage**

Heat stress alters the lipid composition and fluidity of cellular membranes, particularly the thylakoid membranes of chloroplasts and the plasma membrane. These structural changes increase membrane permeability, leading to electrolyte leakage, protein denaturation, and impaired cellular compartmentalization (Wahid et al., 2007). The loss of membrane integrity is often used as a diagnostic indicator of heat-induced cellular injury in physiological screening assays (Savicka & Škute, 2010).

● **Accumulation of Reactive Oxygen Species (ROS)**

One of the primary biochemical responses to heat stress is the overproduction of reactive oxygen species (ROS) such as superoxide radicals (O₂^{•−}), hydrogen peroxide (H₂O₂), and hydroxyl radicals (•OH). Although ROS are normal byproducts of metabolism, their excessive accumulation under stress leads to oxidative damage to proteins, lipids, and nucleic acids (Mittler, 2002). Lipid peroxidation, in particular,

damages cellular membranes and contributes to cell death if ROS are not efficiently detoxified.

• **Protective Responses: Heat Shock Proteins and Antioxidants**

To mitigate the damaging effects of high temperatures, tomato plants activate a range of defense mechanisms. These include:

- Heat shock proteins (HSPs): Molecular chaperones such as HSP70 and HSP101 stabilize unfolded proteins, prevent aggregation, and assist in protein refolding during and after heat stress (Kotak et al., 2007).
- Antioxidant enzymes: Key enzymatic antioxidants – such as superoxide dismutase (SOD), catalase (CAT), and ascorbate peroxidase (APX) – scavenge ROS and protect cells from oxidative stress (Hasanuzzaman et al., 2013).
- Compatible solutes and osmoprotectants: Compounds like proline, glycine betaine, and trehalose accumulate in tomato tissues under stress, functioning as osmolytes, stabilizers of proteins and membranes, and ROS quenchers (Ashraf & Foolad, 2007; Bitá & Gerats, 2013).

These biochemical adaptations collectively contribute to the acquired thermotolerance of the plant, enabling it to survive transient periods of elevated temperatures.

Agronomic Strategies for Enhancing Heat Tolerance

Agronomic management practices play a pivotal role in mitigating the adverse effects of heat stress on tomato production. These strategies are particularly important for smallholder farmers in tropical and subtropical regions who may not have access to advanced genetic or biotechnological solutions. Effective field-level interventions can help optimize plant microclimate, improve resource use efficiency, and maintain physiological stability during periods of high temperature (Kumar et al., 2012; Jagadish et al., 2016). The following are key agronomic approaches employed to enhance heat tolerance in tomato cultivation:

- **Adjusting Sowing Dates and Irrigation Management**

One of the simplest yet most effective methods for avoiding heat-induced reproductive failure is to adjust the sowing calendar such that the sensitive flowering and fruiting stages do not coincide with peak summer temperatures. This practice is particularly useful in regions with well-defined hot seasons. For instance, shifting sowing to avoid temperatures above 32–35°C during anthesis has been shown to significantly improve fruit set and yield in tomato (Sato et al., 2006).

In parallel, precise irrigation scheduling helps mitigate heat stress by sustaining transpiration and maintaining cellular hydration. During heatwaves, frequent, shallow irrigation can lower canopy temperature through evaporative cooling and reduce oxidative stress by supporting the antioxidant defense system (Prasad et al., 2008). Drip irrigation systems, combined with mulching, further enhance water-use efficiency and prevent thermal fluctuations in the root zone (Kumar et al., 2012).

- **Mulching and Shade Netting**

Mulching, whether organic (e.g., straw, crop residues) or synthetic (e.g., plastic film), has been widely adopted to regulate soil microclimate. It conserves soil moisture, suppresses weeds, and most importantly, moderates diurnal soil temperature variations. Studies have shown that mulched plots can exhibit soil temperature reductions of 2–5°C compared to unmulched controls during hot seasons, directly improving plant growth and yield (Borah et al., 2019).

Shade netting, using materials that filter sunlight and reduce radiation load on the plant canopy, is another effective strategy. Nets with 30–50% shading capacity lower ambient temperature, reduce photoinhibition, and enhance leaf water status. Ali et al. (2020) reported that tomatoes grown under shade nets exhibited better pollen viability, higher chlorophyll content, and increased fruit yield compared to open-field conditions during heat stress periods. Additionally, shade structures can protect against wind and reduce evapotranspiration losses.

- **Nutrient Management**

Optimal nutrient management enhances the physiological resilience of tomato plants under high-temperature conditions. Potassium (K) plays a crucial role in stomatal regulation, osmotic adjustment, and enzyme activation, all of which are essential during heat stress. Calcium (Ca) stabilizes cell membranes and is involved in signal transduction pathways that trigger stress responses. Magnesium (Mg) is vital for chlorophyll synthesis and ATP production (Cakmak, 2005; Farooq et al., 2017).

Moreover, foliar application of micronutrients such as zinc (Zn), boron (B), and silicon (Si) has been shown to enhance antioxidant enzyme activity and membrane stability under heat conditions. Silicon, in particular, reduces transpiration losses, improves water-use efficiency, and strengthens cell walls, thereby increasing plant tolerance to both heat and drought stress (Gong et al., 2005; Soundararajan et al., 2014).

Combining nutrient management with organic amendments like compost or biochar can further improve soil structure, increase water-holding capacity, and buffer temperature stress, especially in sandy or degraded soils commonly found in arid zones.

Use of Growth Regulators and Chemical Priming

The exogenous application of plant growth regulators (PGRs), osmoprotectants, and chemical elicitors offers a promising and cost-effective strategy to enhance thermotolerance in tomato plants. These compounds help regulate physiological responses, activate stress-related gene expression, and improve the antioxidant defense system, thereby mitigating the adverse impacts of high temperatures (Hasanuzzaman et al., 2013; Wang et al., 2021).

- **Plant Growth Regulators (PGRs)**

PGRs such as salicylic acid (SA), abscisic acid (ABA), jasmonic acid (JA), and ethylene (ET) are critical in mediating plant responses to abiotic stress, including heat. These molecules participate in signaling cascades that regulate gene expression and metabolic processes involved in heat stress response.

- SA plays a central role in enhancing heat tolerance by modulating the expression of heat shock proteins (HSPs), increasing antioxidant enzyme activities (such as superoxide dismutase and catalase), and stabilizing membranes (Horváth et al., 2007). SA treatment has been shown to reduce lipid peroxidation and electrolyte leakage in tomato under heat stress.

- ABA regulates stomatal closure to minimize water loss and induces stress-related genes, improving plant water relations and cellular osmotic balance during high temperatures (Zhang et al., 2006).

- JA has been implicated in enhancing antioxidant metabolism and maintaining photosynthetic capacity under thermal stress (Kumar et al., 2020).

Combined or sequential application of these regulators may produce synergistic effects on thermotolerance pathways.

● **Osmoprotectants and Antioxidants**

Osmoprotectants are low molecular weight compounds that accumulate in response to abiotic stresses. They play crucial roles in osmoregulation, membrane stabilization, and ROS detoxification.

- Proline and glycine betaine are two well-characterized osmolytes that stabilize proteins and cellular structures during heat stress. Their exogenous application improves membrane integrity and chlorophyll content in tomato leaves exposed to high temperatures (Ashraf & Foolad, 2007).

- Trehalose, a non-reducing disaccharide, enhances stress tolerance by stabilizing protein structures and protecting organelles from denaturation (Liu et al., 2013).

- Ascorbic acid (vitamin C) and tocopherol (vitamin E) function as non-enzymatic antioxidants that scavenge ROS and reinforce cellular redox homeostasis during heat episodes (Hasanuzzaman et al., 2013).

Foliar spraying with these compounds before or during heatwaves can improve survival and recovery of tomato plants.

● **Seed Priming with Inorganic Salts**

Seed priming with low concentrations of inorganic salts such as sodium chloride (NaCl), calcium chloride (CaCl₂), and potassium nitrate (KNO₃) is an emerging method to induce pre-adaptive responses in plants.

- Priming triggers early metabolic activation, promotes uniform germination, and improves seedling vigor under stress conditions.

- In tomatoes, Anwar et al. (2011) demonstrated that salt-primed seeds produced seedlings with higher antioxidant activity, better membrane stability, and improved tolerance to heat shock.

Priming also alters gene expression patterns to “precondition” the plant’s stress-response machinery.

● **Breeding Heat-Tolerant Tomato Varieties**

Conventional plant breeding has made meaningful progress in identifying and integrating traits associated with heat tolerance into elite tomato cultivars. Key thermotolerance traits include:

- High pollen viability and stigma receptivity at elevated temperatures

- Maintenance of fruit set and yield under stress

- Enhanced chlorophyll retention and photosynthetic efficiency

- Early flowering and reduced thermal sensitivity during reproductive stages (Peet et al., 1998)

Wild tomato species such as *Solanum pennellii*, *S. habrochaites*, and *S. peruvianum* have been recognized as important reservoirs of thermotolerance genes. These species exhibit better photosynthetic performance, higher antioxidant capacity, and reproductive resilience under heat stress (Reddy et al., 2014).

Modern breeding approaches employ marker-assisted selection (MAS) and quantitative trait locus (QTL) mapping to accelerate the incorporation of heat tolerance traits.

- QTLs like qHT2.1 and qHT5.1 have been associated with reproductive-stage heat tolerance and fruit yield stability (Xu et al., 2017).

- Introgression lines developed from wild relatives enable the dissection of complex traits and identification of new alleles for breeding heat-resilient varieties (Foolad, 2007).

Despite these advances, breeding for heat tolerance remains challenging due to the polygenic nature of the trait and strong genotype $\times$ environment interactions.

Genetic Engineering and Genomic Approaches

Biotechnological tools have enabled precise manipulation of genes and pathways involved in heat tolerance, offering new frontiers for tomato improvement.

- **Heat Shock Proteins and Transcription Factors**

Heat shock proteins (HSPs) and heat shock transcription factors (HSFs) are pivotal for thermotolerance.

- Overexpression of HSP101 and HSP70 in transgenic tomatoes enhances protein folding capacity, reduces aggregation of denatured proteins, and promotes stress recovery (Kotak et al., 2007).

- HSFA1 and HSFA2, master regulators of the heat stress response, activate the expression of downstream HSP genes and antioxidant enzymes, improving survival under prolonged heat exposure (Fragkostefanakis et al., 2016).

These genetic interventions have shown promise in both lab and field environments.

- **CRISPR/Cas9 and Genome Editing**

CRISPR/Cas9 offers precise and efficient gene editing capabilities to enhance heat tolerance without introducing foreign DNA.

- Recent studies have used CRISPR to knock out SIMPK3, a negative regulator of thermotolerance, resulting

in improved heat stress performance in edited tomato lines (Pan et al., 2021).

- Editing of transcription factors, hormonal pathways, and heat-sensitive promoters holds potential for tailoring tomato responses to specific environmental conditions.

Genome-edited varieties can also circumvent some of the regulatory barriers associated with transgenic crops.

• **Transcriptomic and Metabolomic Profiling**

Omics technologies have revolutionized our understanding of the tomato heat stress response:

- Transcriptomics identifies differentially expressed genes (DEGs) associated with stress perception, signal transduction, and protective responses (Wang et al., 2019).
- Metabolomics reveals dynamic changes in sugars, amino acids, and secondary metabolites under heat stress, offering insights into adaptive metabolic reprogramming (Sánchez-Bel et al., 2015).

Integration of multi-omics datasets facilitates the discovery of novel candidate genes, biomarkers, and regulatory networks for precision breeding.

Conclusion and Future Directions

With the growing threat of global warming, ensuring heat resilience in tomato is imperative for food and nutritional security. Tomato's narrow optimal temperature range and sensitivity during reproductive stages make it particularly vulnerable to elevated temperatures.

A multidisciplinary approach is essential to address this challenge. Future strategies must combine:

- Agro-technological solutions such as optimized planting schedules, irrigation, and shading
- Chemical priming and exogenous applications for rapid field deployment
- Conventional and molecular breeding using wild relatives and QTL mapping

- Genomic tools including CRISPR/Cas9 and transcriptomic profiling to target heat-responsive genes

Collaboration between geneticists, agronomists, molecular biologists, and farmers will be crucial to translating laboratory discoveries into heat-resilient tomato cultivars suitable for diverse environments. Long-term resilience will also require investments in digital breeding platforms, phenomics, and policy support to accelerate the development and deployment of climate-smart varieties.

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