International Journal of Environment and Climate Change

Volume 14, Issue 6, Page 322-331, 2024; Article no.IJECC.118258
ISSN: 2581-8627
(Past name: British Journal of Environment & Climate Change, Past ISSN: 2231–4784)

Adaptation and Mitigation of High Temperature Stress in Tomato

Ammu Alphonsa John [a++*] and Roy Stephen [a#]

[a] *Department of Plant Physiology, College of Agriculture, Vellayani, Trivandrum, India.*

Authors' contributions

This work was carried out in collaboration between both authors. Both authors read and approved the final manuscript.

Article Information

DOI: https://doi.org/10.9734/ijecc/2024/v14i64231

Open Peer Review History:
This journal follows the Advanced Open Peer Review policy. Identity of the Reviewers, Editor(s) and additional Reviewers, peer review comments, different versions of the manuscript, comments of the editors, etc are available here: https://www.sdiarticle5.com/review-history/118258

Review Article

Received: 13/04/2024
Accepted: 16/06/2024
Published: 18/06/2024

ABSTRACT

Tomato (*Solanum lycopersicum* L.) holds considerable economic significance as a vegetable crop globally, ranking second in both cultivated area and production worldwide. Optimal growth conditions for tomatoes typically fall within the temperature range of 25°C - 30°C during the day and around 20°C at night. However, deviations from these thresholds can lead to irreversible damage to plant growth and development. To counteract the adverse effects of high temperatures, tomato plants employ various adaptive mechanisms involving physiological, morphological, anatomical, and biochemical changes. Efforts to enhance thermotolerance in tomatoes encompass a range of strategies, including agronomic practices, the application of growth regulators and fertilizers to induce acclimation responses, breeding programs aimed at developing heat-resistant cultivars, and genetic modification. Various other methods are also employed to mitigate the impacts of high-temperature stress on plants, such as pretreating seeds with low concentrations of inorganic salts, applying osmoprotectants and signaling molecules through foliar sprays, and subjecting plants to preconditioning measures. These approaches facilitate stress avoidance and foster the development of inherent mechanisms for high-temperature tolerance in plants.

Keywords: High temperature; tomato; mitigation; heat stress.

[++] *Ph. D Scholar;*
[#] *Professor;*
**Corresponding author: E-mail: ammualphons@gmail.com;*

Cite as: *John, Ammu Alphonsa, and Roy Stephen. 2024. "Adaptation and Mitigation of High Temperature Stress in Tomato". International Journal of Environment and Climate Change 14 (6):322-31. https://doi.org/10.9734/ijecc/2024/v14i64231.*

1. INTRODUCTION

Adverse environmental conditions such as escalating ambient temperatures, water scarcity, and salinity are anticipated consequences of the overarching phenomenon known as global climate change, posing significant threats to agriculture. Among these, heat stress emerges as a primary adverse weather factor associated with climate change, exerting detrimental effects on crop productivity. According to the IPCC's 2012 report, the global mean surface air temperature saw a 0.5°C rise during the 20th century, with projections indicating further increases ranging from 1.5°C - 4.5°C by the end of the 21st century [1,2,3].

Heat stress can be delineated as the elevation of temperatures beyond a critical threshold for a duration significant enough to induce irreversible damage to the growth as well as development of plants. The ramifications of high temperatures on plants encompass a spectrum of adverse effects, including the inhibition of seed germination, stunted plant growth, aberrant development, diminished crop quality, perturbations in photosynthesis, phenological shifts, reduced dry matter production, heightened water loss, oxidative stress, and ultimately, diminished yields. This underscores the urgency of developing robust strategies to mitigate the impacts of heat stress on agricultural systems, safeguarding global food security amidst changing climatic conditions.

2. TOMATO AND HIGH TEMPERATURE

Around the world, tomatoes are regarded as a significant and profitable agricultural vegetable crop. The Solanaceae family, which includes the tomato, also includes many other well-known crops, including the potato, eggplant, and pepper. One of the most heat-sensitive vegetable crops with significant economic and commercial value is the tomato. Tomatoes grow best at temperatures between 25°C - 30°C at the time of the day and 20°C at night [4]. A few degrees beyond this threshold can have detrimental effects that are rather substantial, such as diminished fruit set, aberrant development, flower abscission, and a decline in pollen quality [5]. Because of this, the importance of tomatoes as a crop globally, the predicted rise in temperatures in the near future, research on tomato heat stress response, the mitigation of adverse impacts of tomato heat stress, and the need to maximize yield, all contribute to the need for improved tomato production.

3. MITIGATION AND ADAPTATION STRATEGIES

Plants use built-in high-temperature tolerance and stress avoidance strategies to adapt to high temperatures. A popular technique to lessen the impact of high temperatures on seeds is to treat them beforehand with small amounts of inorganic salts. Apart from that, preconditioning plants and applying osmoprotectants and signaling molecules topically work [6]. Plants modify their physiological, morphological, anatomical, and biochemical processes in response to high temperatures. Strategies to mitigate yield reduction due to climate change include replacing sensitive genotypes with heat-tolerant cultivars, adjusting sowing times, and using growth regulators. Improving tomato thermotolerance can involve modifying agronomic practices, acclimating plants through growth regulators and fertilizers, and employing genetic modification.

3.1 Agronomic Practices

Temperature stress reduction for agricultural plants may be efficiently achieved via the use of sustainable agronomic and resource management methods.

3.1.1 Priming

Priming induces enhancement of stress tolerance to major abiotic stresses. Plant tolerance against stress is supposedly enhanced by some compounds obtained from plants. A natural plant-derived compound eugenol, may protect tomato plants from the TYLCV (Tomato Yellow Leaf Curl Virus) and enhance traits associated with thermotolerance, such as higher average fresh weight and survival rates. Salicylic acid (SA) levels and the expression of a few downstream genes appear to be increased by eugenol and anise oil. It has been discovered that eugenol and anise oil may function as priming agents, raising the SA content to mediate the thermotolerance of tomato plants. Under heat stress, SA can affect the thermotolerance of agricultural plants [7].

3.1.2 Heat hardening of seed

To safeguard plants from high-temperature stress, a variety of mechanisms can be employed. One such mechanism is seed hardening, a method that enhances seed physiology. Pre-sowing treatments, such as soaking the seeds in water, an osmotic solution, or growth regulators, can help accomplish seed hardening. Furthermore, raising the temperature of the seeds above the highest point at which they may develop will also help to harden the seeds. These treatments stop radicles from poking through the seed coat, allowing the seeds to begin the initial phases of germination. In comparison to non-hardened plants, plants that are planted from hardened seeds in the field have a better start. Because they are in a highly developed stage, toughened plants may be able to withstand harsh environmental pressures like high temperatures more readily. Better results were obtained by pre-sowing tomato seeds that had been heat-hardened for one or two hours at 50 or 60 degrees Celsius. This may have been caused by the seeds germination process, which in turn provided the tomato seedlings a better start and continued growth [8].

3.1.3 PGPR

The use of helpful microorganisms in agricultural techniques is essential for maintaining increasing crop yield in the face of various abiotic stressors. Certain microorganisms associating with plants have been shown to accentuate stress tolerance in plants, PGPR (Plant growth-promoting rhizobacteria) or PGPB (plant growth-promoting bacteria), mychorrizhal fungi are some of them [9]. PGPR contributes to the growth of plants by two main mechanisms: the production of plant growth regulators and improved availability of nutrients are examples of direct mechanisms; the other types of mechanisms include the suppression of pathogens through antibiosis, ISR (induced systemic resistance), and lytic enzyme synthesis [10]. Plant growth is enhanced by PGPR through enhanced nutrient absorption, specifically in the case of phosphorus. The synthesis of phytohormones such as siderophores, indole-3-acetic acid, gibberellic acid, abscisic acid, and cytokinins is important in this respect. Antioxidants produced by PGPR promote the buildup of abscisic acid (ABA) and inhibit the production of ROS (Reactive Oxygen Species). Plants can get energy and nitrogen from bacteria that produce ACC [11]. Plants under abiotic stress conditions are more effective when injected with ACC-deaminase-producing bacteria because this produces longer roots and helps the plants absorb more water [12]. Under both normal as well as heat-stressed situations, *Bacillus cereus* enhances the activities that promote plant development and exhibits the activities of 1-aminocyclopropane-1-carboxylate (ACC)-deaminase and exopolysaccharide [13]. It might thus be an effective strategy for enhancing tomato crop development in heat-stressed environments. In order to demonstrate this, [13] looked at how plant biomass responded to the *Bacillus cereus* inoculation in two different tomato varieties: Sweetie and Riogrande. Heat stress decreased Riogrande and Sweetie's shoot length relative to the untreated control, whereas “bacterial inoculation under normal settings (T1) enhanced both kinds' shoot lengths compared to the uninoculated control (C) under the normal conditions. In contrast to the uninoculated heat stress treatment (T2), bacterial inoculation under heat stress circumstances (T3) increased the shoot length for Riogrande and Sweetie. In comparison to the untreated control, bacterial inoculation also lengthened the roots of both kinds under normal circumstances. Similar to T2 (without bacteria under heat stress), T3 (bacterial inoculation under heat stress) increased root length”. *Bacillus cereus* (T1) up-regulated the accumulation of dry & fresh biomass in Sweetie & Riogrande in comparison to T2. Additionally, the study [13] noted that as compared to the untreated control, the treated plants, Riogrande and Sweetie, had more leaf surface area. In comparison to uninoculated treatments, bacterial inoculation enhanced the number of flowers and fruits in both kinds under both normal and heat stress conditions.

3.1.4 Biofertilizer

An environmentally acceptable and alternative method of increasing agricultural crop productivity and mitigating the negative impacts of high temperatures is to employ PGPB and humic compounds [14]. Plant development is stimulated by HA (Humic Acid), a heterogeneous combination of several chemicals that occurs under both abiotic and biotic stress situations. Another strategy to combat abiotic stress is through the application of PGPB. These bacteria can improve biofilm formation and reduce levels of abscisic acid (ABA) and heat shock proteins (HSP), thereby increasing plant tolerance to heat stress. In tomato plants that have been grown in both normal as well as heat-stressed environments, the combination application of SA1 and HA can increase biomass and chlorophyll fluorescence [15]. While heat stress causes a drop in SA (Salicylic Acid) content and an increase in ABA levels, applying SA1 and HA together causes an increase in SA levels and a decrease in ABA levels. Moreover, plants treated with SA1 and HA had greater amounts of superoxide dismutase, ascorbate peroxidase, and lower glutathione, according to observation [15]. Co-application of SA1, as well as HA, enhances amino acid content, although heat stress considerably reduces it. Under situations of heat stress, this therapy also leads to considerably greater absorption of potassium, phosphorus, and iron. Furthermore, heat stress-responsive transcription factors and higher-affinity potassium transporters are increased in SA1+HA-treated plants [15].

According to a recent study [15], under normal growth circumstances, tomato plants' shoot length, fresh weight, and dry weight were considerably increased when humic acid (HA), isolate SA1, and their combination application (SA1+HA) were applied. Comparing the fresh and dried weight of the roots to the control, similar increases were seen. In comparison to plants treated with either SA1 or HA alone, as well as the heat-stressed control plants, the combination SA1+HA treatment dramatically decreased the negative impacts of heat stress on tomato plants. These plants also had much greater growth qualities. In particular, SA1+HA-treated plants showed a notable regeneration of fresh weight (1.5-fold) and dry weight (single-fold) during heat stress. When compared to the heat-stressed control plants, the plants treated by using SA1+HA also depicted a considerable increase in chlorophyll fluorescence. Consequently, co-applying SA1+HA to tomato plants is beneficial in reducing heat-stress-related damage and has the potential to be marketed as a biofertilizer. This method increases plant resilience and production under harsh environmental circumstances by using the synergistic effects of HA and SA1 [15,16].

3.2 Biochemical Strategies

Exogenous application of protectants such as osmoprotectants like spermidine, phytohormones like Brassinosteroid, Jasmonic acid, and Salicylic acid, signaling molecules like flavonols and melatonin, trace elements such as silicon, etc., have shown a beneficial effect on tomato grown under heat stress as these protectants have growth-promoting and antioxidant capacity

3.2.1 Phytohormones

3.2.1.1 Brassinosteroid (BRs)

A class of steroid phytohormones known as BRs have been crucial for photosynthesis, plant development & growth, and resistance to both biotic and abiotic stressors. A unique opportunity to increase agricultural yields by BR biosynthesis, conversion, or perception modulation exists since it can alter plant metabolism and shield plants from abiotic stressors [17]. As a result, BRs have been thought of as hormones that have a significant impact on agricultural productivity. There is evidence that BRs can activate the genes responsible for encoding structural and regulatory proteins, including heat shock proteins (HSPs) and antioxidants. According to recent research [18], exogenous treatment of 24-epibrassinolide (EBR) can increase apoplastic H2O2 buildup, boost activation of MPK1/2, and promote tolerance to oxidative as well as heat stress in tomatoes. It can also increase transcript levels of RBOH1, MPK1, and MPK2. The investigation of Nie et al. [18] investigated 24-epibrassinolide's (EBR) ability to withstand thermal shock. For ten hours, plants that had been pre-treated with 0, 0.01, 0.1, and 1mm EBR were subjected to heat stress at 42°C and 200±20mmol m^-2 s^-1 of light intensity. Under typical circumstances, Pn rose by 24.8% and 33.3% with the administration of 0.01 and 0.1mm EBR, correspondingly, but Fv/Fm did not substantially change between the two EBR concentrations administered (Fig. 1) [18].

3.2.1.2 Salicylic acid (SA)

During the HR (Hypersensitive Response) and SAR (Systemic Acquired Resistance), salicylic acid (SA) is an essential component of signaling pathways. Heat shock transcription factor trimers are stabilized by SA, which facilitates their binding to heat shock element promoters in heat shock-related genes. SA can induce long-term thermotolerance by upregulating the expression levels of HSP70 and HSF, which helps mitigate heat stress damage [19]. Additionally, SA increases the maximum quantum yield of photosystem II in *Solanum lycopersicum* [20].

3.2.1.3 Jasmonic acid (JA)

During hot seasons, cultivated tomato plants are susceptible to exhibiting stigma exertion due to prevalent high temperatures, which hampers pollination and induces failure of fruit collection. In cultivated tomatoes, high temperature-induced stigma exsertion is caused by more severely decreased stamens than pistils, in contrast to the stigma exsertion seen in wild tomato plants. Pistil and stamen lengths are further determined by the unique interactions of pectin, sugar, expansion, and cyclin at high temperatures, which lead to cell wall remodeling, differentially localized cell division, and selective cell enlargement. Moreover, exogenous JA may successfully restore tomato stigma exsertion in place of auxin via regulating the JA/COI1 signaling pathway. Auxin and jasmonate (JA) both regulate cell proliferation and enlargement in stamens and pistils [21]. To confirm the involvement of auxin (IAA) and JA in the development of stigma-exsertion in high-temperature environments, [21] investigated the exogenous application of varying concentrations of IAA and JA solutions to the flower buds of 'Micro-Tom' plants at intervals of two days until six days following the temperature shift. Rather than auxin, they discovered that exogenous injection of JA may counteract stigma exsertion brought on by high-temperature treatment. Exogenous JA or MeJA (methyl jasmonate) spray prevented the length decrease of pistils and stamens produced by the high temperature, which in turn reduced the rate of stigma exsertion in a dose-dependent manner. After JA was applied, the shortened stamens and pistils lengths caused by the high temperature were precisely restored by 10-5 M JA and, to a lesser extent, by 10-4 M JA. However, no discernible effects were seen on the stamens and pistils lengths by 10-6 M JA (Fig.2). More notably, for either 10^{-5} M JA or 10^{-4} M JA, the stigma exsertion rates of HT-treated plants were drastically reduced from 72% to 27% and 22%, respectively. The severity of the stamen and pistil development high-temperature damage even was significantly reduced by the application of 10^{-5} M or 10^{-4} M MeJA [21].

3.2.1.4 Gibberellic acid

GA3, also known as gibberellic acid, is a plant hormone that affects various plant processes like plant height, leaf expansion, dry matter accumulation, tissue differentiation, cell division, net absorption rate, blooming, photosynthesis, and transpiration rate [22]. Additionally, GA3 is a diterpenoid molecule that has been demonstrated to contribute significantly to stress resistance in various crops by influencing physiology, morphology, and enzymatic activities [23,24]. GA3 plays a vital role in activating enzymes that scavenge reactive oxygen species

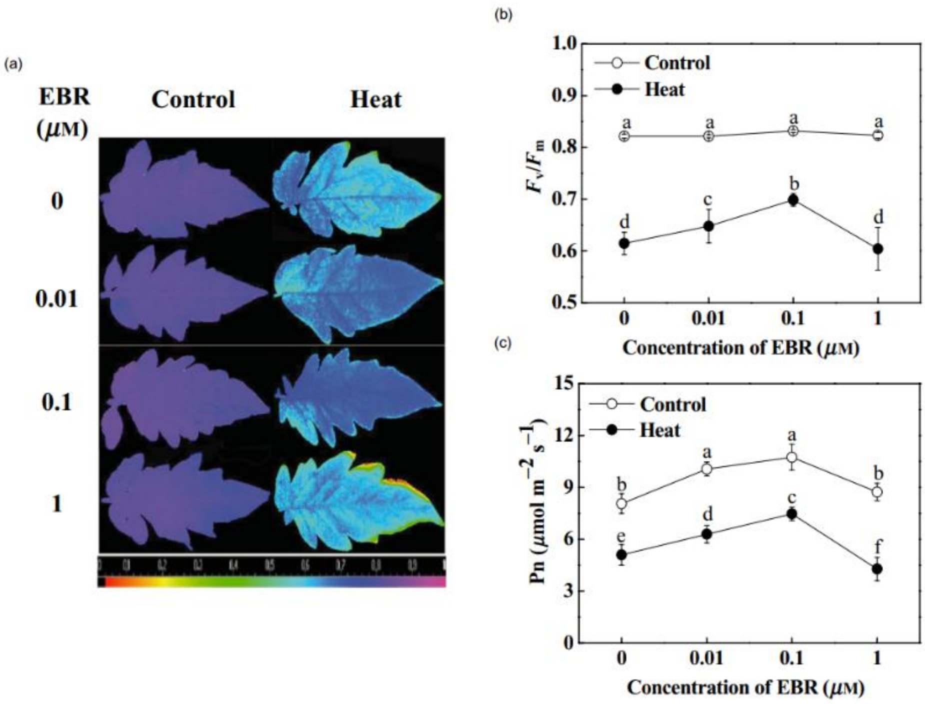

Fig. 1. Effect of EBR on photosynthetic rate (Pn) and chlorophyll fluorescence [18]

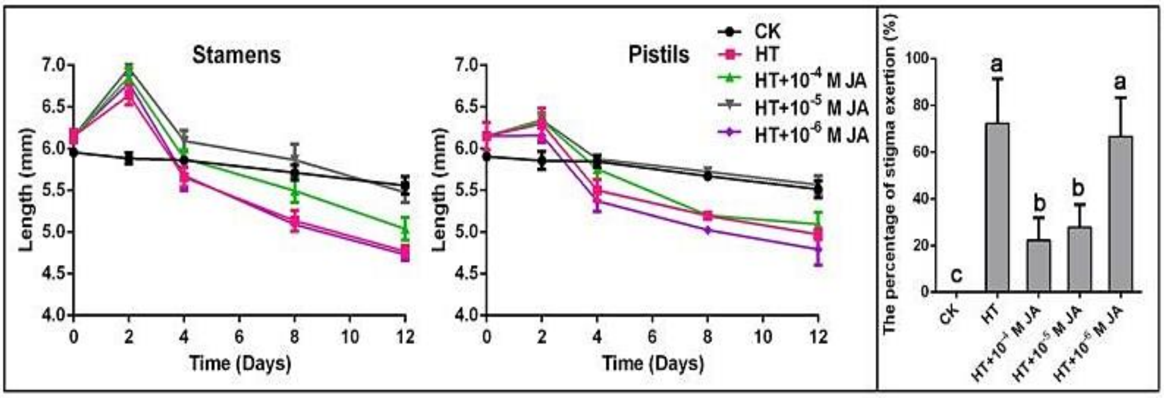

Fig. 2. Response of stigma and pistil under high temperature to MeJA application [21]

(ROS), thereby enhancing the antioxidant defense against abiotic stress [25]. Guo et al. [26] examined the physiology and growth of two tomato varieties ('Ahmar' and 'Roma') in two growth chambers set at 25 and 45 °C following the application of exogenous gibberellic acid (GA3). After 45 days of planting, tomato plants were treated with GA3 at concentrations of 25, 50, 75, and 100 mg L−1, while untreated plants were used as a control. It was found that, in both temperature conditions, 'Roma' plants showed the highest shoot and root biomass when they received 75 mg L−1 GA3, followed by 50 mg L−1 GA3. They concluded that, when tomato plants are subjected to heat stress, applying GA3 through foliar spray could potentially mitigate the detrimental effects and enhance the plant's physiological responses and growth.

3.2.2 Signalling molecule

3.2.2.1 Melatonin

All living things, including animals & plants, contain the naturally occurring low-molecular weight multiregulatory chemical known as melatonin (N-acetyl-5-methoxytryptamine). It has a multifaceted biological role as a plant master regulator and defender in a variety of variable environmental situations, including high temperatures, salt, heavy metals, drought, oxidative stress, and UV radiation. Melatonin also accelerates the germination of seeds, affects the architecture of roots and plants, improves the fertility of development, improves leaf senescence, controls the metabolism of nitrogen, and alters physiological procedures by inducing differential gene expression. The most essential function of melatonin is the detoxification of ROS by producing free radical scavengers [27]. Additionally, melatonin regulates polyamines and nitric oxide (NO)production, as well as mitigating the oxidative damage that tomato seedlings sustain from heat stress. According to research Jahan et al. [28], as compared to untreated heat-stressed plants, the administration of 100 µM melatonin significantly reduced the membrane damage index and MDA concentration, indicating that it is a very efficient method of mitigating the severe effects of heat stress. While SOD activity decreased considerably to 1.89 times lower than the control due to heat stress, which impacts antioxidant functions, SOD activity improved greatly and was 1.29 times greater in plants treated with melatonin than in heat-stressed seedlings that were not treated.

3.2.3 Trace element (Silicon)

The second most common element in the crust of the Earth is silicon (Si), which is well known to be good for plant development and yield. Si increases a plant's ability to withstand a wide range of biotic and abiotic stressors, like drought as well as salt stress, high temperatures, nutrient deficiencies, aluminum toxicity, and insect and disease resistance [29]. Si activates several reaction pathways during stress, thereby stimulating antioxidants, improving mineral absorption and organic acid anion exudation, producing phenolic compounds, and regulating hormone development. Si treatment for tomato seedlings increases the resilience and function of tomato plants under heat stress and develops stress resistance via modifying oxidative stress, heat shock proteins (HSP), endogenous phytohormones, and the corresponding mRNA gene expression patterns. Si treatment lowers heat-mediated oxidative stress and raises the photosynthetic pigment concentration in the plant by triggering the antioxidant defense system [30].

The exogenous administration of silicon in tomato plants was examined in a research [30]. Under both normal as well as heat stress circumstances, the administration of Si boosted growth metrics such as shoot biomass, stem diameter, and shoot length. Si treatment greatly enhanced root shape and lengthened roots whereas heat stress decreased biomass and root length. Under both circumstances, the weights of the roots and new roots similarly increased. When Si was applied, the concentration of carotenoid, chlorophyll a, and chlorophyll b increased significantly, but in heat-stressed Si-deficient plants, these were reduced (Fig. 3). Additionally, Si treatment reduced ROS-induced lipid peroxidation and improved relative water content (RWC) compared to untreated plants.

3.2.4 Osmoprotectants

Osmoprotectants, or compatible solutes, stabilize cellular membranes and proteins while maintaining osmotic potential during stress. Among these, polyamines are critical, including aliphatic polyamines like spermidine (Spd), putrescine (Put), and spermine (Spm), which have been included in several physiological procedures such as development, plant growth, fruit growth, flowering, stress response, senescence, and fruit ripening [31]. Polyamines act as antioxidants under adverse environmental conditions [32]. Exogenously applied polyamines reduce hydrogen peroxide (H2O2) levels and malondialdehyde content, increasing antioxidant levels. High temperatures inhibit ethylene synthesis, proteoglycan accumulation, and lycopene synthesis, ultimately affecting fruit ripening. The number of genes involved in signal transduction is dramatically increased when exogenous Spd is pre-treated under high-temperature settings. Significant modulation is seen in response to Spd therapy in genes linked to hormone pathways, oxidation-reduction, polyamine production, regulatory factors, and ethylene. Thus, during tomato fruit ripening, Spd can reduce the damaging effects of heat stress [33].

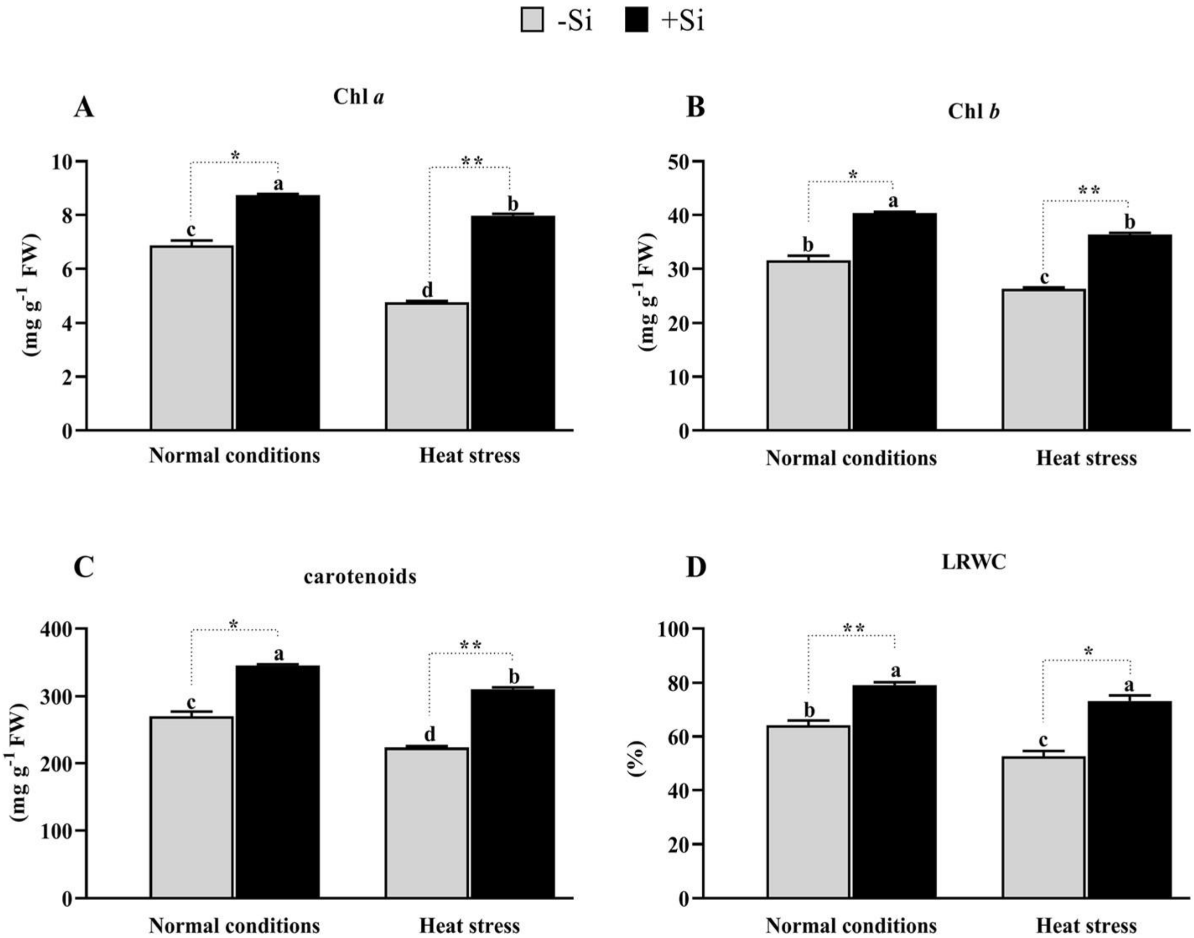

Fig. 3. Pigment concentration in silicon-treated and untreated tomato plants [30]

3.3 Biotechnological Innovative Strategies

Through genetic selection, tomato's ability to withstand heat might be considerably increased. To choose appropriate breeding techniques and parental lines that take into account the degree and severity of gene behavior of heat resistance traits and sub-traits in a breeding program, it is crucial to comprehend the type and magnitude of gene actions. Researchers found that the germplasm under consideration regulates heat tolerance traits through additive, domination, and epistatic gene impacts, with one of these effects predominating. Ahmad et al. [34] observed that primarily additive gene effects dominated the pollen fertility and fruit set inheritance. Likewise, they discovered that the inheritance of fruit collection, fruit quantity per vine, fruit weight, brix, and number of flowers per cluster has been significantly influenced by additive gene effects. They reported total dominance in the inheritance of fruit sets and significant heterosis in the weight of the fruits under heat stress.

Important elements that mediate heat tolerance are tomato heat-stress transcription factors (Hsfs), which function as either activators or repressors. When temperatures rise, tomato HsfA2 builds up and improves the male reproductive tissues' ability to withstand extreme heat stress. The heat tolerance pathway is repressed by HsfB1, on the other hand, transgenic tomato plants with enhanced HsfB1 repression have higher heat tolerance. To increase tomato heat tolerance, these genes may be candidates for site-directed mutation. Using a larger number of re-sequenced accessions, one can select intriguing lines bearing favorable alleles to be examined under heat stress once a candidate gene has been cloned and a favorable allele has been identified. It is anticipated that an integrated method incorporating gene editing, genetic alteration, and plant breeding will have an impact on food crop productivity. The breakdown of the genetic architecture and genes governing heat tolerance leads to a rise in heat tolerance mechanisms; the possibility of targeted mutation on these genes would give helpful tools for quick monitoring of the emergence of heat-tolerant varieties. Furthermore, essential elements that either function as activators or repressors in modulating heat tolerance are tomato heat stress transcription factors (Hsfs). Thus, to increase tomato heat tolerance, these genes may be candidates for site-directed mutation [35].

4. CONCLUSION

Historically, instances of extraordinarily high temperatures leading to destructive consequences have been recorded, typically arising once in a century. However, projections indicate an alarming trend of increasing occurrences of such unexpected heat spikes in the future. Consequently, it is imperative to proactively devise strategies for detection and management, including the identification and collection of heat-tolerant genotypes, as well as the breeding of cultivars capable of withstanding such challenging conditions. By undertaking these measures, it becomes feasible to avert potential losses in agricultural production. Hence, there exists an urgent imperative to delve into the physiological and genetic mechanisms underlying heat tolerance and to embark on the development of heat-tolerant tomato varieties. Such endeavors are crucial not only for enhancing the quality, quantity, and stability of tomato production but also for ensuring resilience across diverse environmental conditions. Expanding research on CEA (controlled environmental agriculture) systems, such as greenhouses and vertical farming, where temperature and other environmental conditions can be tightly controlled to optimize tomato growth and yield is helpful. Integrate remote sensing technologies and precision agriculture tools to monitor plant health and environmental conditions in real-time also enable timely interventions to mitigate heat stress effects. Developing climate adaptation policing and conducting research on effective policies and frameworks that support farmers in adapting to high temperature stress, like subsidies for heat-tolerant seeds, investment in infrastructure, and education programs on best practices etc. will help to overcome the problem. So future research must focus on a multi-faceted approach, integrating genetic, agronomic, and technological innovations.

DISCLAIMER (ARTIFICIAL INTELLIGENCE)

We hereby declare that NO generative AI technologies such as Large Language Models (ChatGPT, COPILOT, etc) and text-to-image generators have been used during writing or editing of manuscripts.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

REFERENCES

1. Arunima AS, Manju RV, Viji MM, Roy S, Sarada S, Beena R. Role of Nutrients and Biofertilizers for Improved Tolerance of Tomato under Elevated Co2 Induced High Temperature Stress. J. Exp. Agric. Int. 2023;45(12):9-15.
Available:https://journaljeai.com/index.php/JEAI/article/view/2260
[Accessed on: 2024 May 28];
2. Nandhitha GK, Vanitha K, Chandrasekhar CN. Screening of Rice (*Oryza sativa* L.) Genotypes for High Temperature Stress under Temperature Induction Response. Int. J. Plant Soil Sci. [Internet]. 2022 Sep. 22;34(23):141-7.
Available:https://journalijpss.com/index.php/IJPSS/article/view/2018
[Accessed on: 2024 May 28]
3. Qu AL, Ding YF, Jiang Q, Zhu C. Molecular mechanisms of the plant heat stress response. Biochemical and biophysical research communications. 2013;432(2):203-7.
4. Shamshiri RR, Jones JW, Thorp KR, Ahmad D, Man HC, Taheri S. Review of optimum temperature, humidity, and vapour pressure deficit for microclimate evaluation and control in greenhouse cultivation of tomato: A review. Intl. Agrophys. 2018;32:287-302.
5. Hazra P, Ansary SH, Dutta AK, Balacheva E, Atanassova B. Breeding tomato tolerant to high temperature stress. Acta Hortic. 2009;830:241-248
6. Wahid A, Gelani S, Ashraf M, Foolad MR. Heat tolerance in plants: an overview. Environ. Exp. Bot. 2007;61:199-203.
7. Tsai WA, Weng SH, Chen MC, Lin JS, Tsai WS. Priming of plant resistance to heat stress and tomato yellow leaf curl thailand virus with plant-derived materials. Front. Plant Sci. 2019;10:906
8. Ibrahim SK, El-Muqadam LA. Enhancing thermotolerance of tomato plants (*Lycopersicon esculentum* mill) by heat hardening of seeds. Bull. Natl. Res. Cent. 2019;43:126.
9. Agrahari RK, Singh P, Koyama H, Panda SK. Plant-microbe Interactions for Sustainable Agriculture in the Post-genomic Era. Curr Genomics. 2020;21(3): 168-178.
10. Glick BR. Plant growth-promoting bacteria: Mechanisms and applications. *Scientifica (Cairo)*. 2012; 2012:963401.
11. Glick BR, Penrose DM, Li J. A model for the lowering of plant ethylene concentrations by plant growth promoting bacteria. J. Theor. Biol. 1998;190:63-68
12. Zahir ZA, Ghani U, Naveed M, Nadeem SM, Asghar HN. Comparative effectiveness of Pseudomonas and Serratia sp. Containing ACC-deaminase for improving growth and yield of wheat (*Triticum aestivum* L.) under salt-stressed conditions. Arch. Microbiol. 2009;191:415–424.
13. MukhtarT, Rehman S, Smith D, Sultan T, Seleiman MF, Alsadon AA, et al. Mitigation of Heat Stress in *Solanum lycopersicum* L. by ACC-deaminase and Exopolysaccharide Producing *Bacillus cereus*: Effects on Biochemical Profiling. Sustainability. 2020;12:2159.
14. Canellas LP, Olivares FL. Physiological responses to humic substances as plant growth promoter. Chem. Biol. Technol. Agric. 2014;1:3.
15. Khan MA, Asaf S, Khan AL, Jan R, Kang SM, Kim KM. Extending thermotolerance to tomato seedlings by inoculation with SA1 isolate of *Bacillus cereus* and comparison with exogenous humic acid application. PLoS ONE. 2020;15(4).
16. Bhupenchandra I, Chongtham SK, Devi EL, et al. Role of biostimulants in mitigating the effects of climate change on crop performance. Front. Plant Sci. 2022;13: 967665.
17. Xia XJ, Huang LF, Zhou YH, Mao WH, Shi K, Wu JX. Brassinosteroids promote photosynthesis and growth by enhancing activation of Rubisco and expression of photosynthetic genes in *Cucumis sativus*. Planta. 2009a;230:1185–1196.
18. Nie WF, Wang MM, Xia XJ, Zhou YH, Shi K, Chen Z et al. Silencing of tomato RBOH1 and MPK2 abolishes brassinosteroid- induced H2O2 generation and stress tolerance. Plant Cell Environ. 2013;36(4):789-803.
19. Snyman M, Cronje MJ. Modulation of heat shock factors accompanies salicylic acid-mediated potentiation of Hsp70 in tomato seedlings. J. Exp. Bot. 2008;59:2125-32.
20. Mohammad SJ, Yu W, Sheng S, Min Z, Zheng C, Jianqiang W, Jin S, Shirong G. Exogenous salicylic acid increases the heat tolerance in Tomato (*Solanum lycopersicum* L) by enhancing photosynthesis efficiency and improving antioxidant defense system through

scavenging of reactive oxygen species. Scientia Horticulturae. 2019;247: 421-429.
21. Pan C, Yang D, Zhao X, Jiao C, Yan Y, Wang Q, et al. Tomato stigma exsertion induced by high temperature is associated with the jasmonate signaling pathway: tomato stigma esxertion, heat stress, jasmonate. Plant Cell Environ. 2019;42: 1205-1221.
22. Fahad S, Hussain S, Bano A, Saud S, Hassan S, Shan D, et al. Potential role of phytohormones and plant growth-promoting rhizobacteria in abiotic stresses: Consequences for changing environment. Environ. Sci. Pollut. Res. 2015;22:4907–4921.
23. Uzal O, Yasar F. Effects of GA3 hormone treatments on ion uptake and growth of pepper plants under cadmium stress. Appl. Ecol. Environ. Res. 2017;**15**:1347–1357.
24. Ji P, Tang X, Jiang Y, Tong Y, Gao P, Han W. Potential of gibberellic acid 3 (GA3) for enhancing the phytoremediation efficiency of *Solanum nigrum* L. Bull. Environ. Contam. Toxicol. 2015;95:810–814.
25. Javed T, Ali MM, Shabbir R, Anwar R, Afzal I, Mauro RP. Alleviation of copper-induced stress in pea (*Pisum sativum* L.) through foliar application of gibberellic acid. Biology (Basel) 2021;10:120.
26. Guo T, Gull S, Ali MM, Yousef AF, Ercisli S, Kalaji HM, et al. Heat stress mitigation in tomato (*Solanum lycopersicum* L.) through foliar application of gibberellic acid. Sci Rep. 2022;12(1):11324.
27. Shi H, Tan DX, Reiter RJ, Ye T, Yang F, Chan Z. Melatonin induces class A1 heat-shock factors (HSFA 1s) and their possible involvement of thermotolerance in Arabidopsis. J Pineal Res. 2015;58(3): 335–342.
28. Jahan MS, Shu S, Wang Y, Chen Z, He M, Tao M, et al. Melatonin alleviates heat-induced damage of tomato seedlings by balancing redox homeostasis and modulating polyamine and nitric oxide biosynthesis. BMC plant biol. 2019;19(1): 414.
29. Richmond KE, Sussman M. Got silicon? The non-essential beneficial plant nutrient. Curr Opin Plant Biol. 2003;6:268–272.
30. Khan A, Khan AL, Imran M. Silicon-induced thermotolerance in *Solanum lycopersicum* L. via activation of antioxidant system, heat shock proteins, and endogenous phytohormones. BMC Plant Biol. 2020;20(248).
31. Shao J, Huang K, Batool M, Idrees F, Afzal R, Haroon M, et al. Versatile roles of polyamines in improving abiotic stress tolerance of plants. Front Plant Sci. 2022; 13:1003155.
32. Kakkar RK, Sawhney VK. Polyamine research in plants—A changing perspective. Physiol. Plant. 2002;116(3): 281-292.
33. Cheng L, Sun R, Wang F, Peng Z, Kon F. Spermidine affects the transcriptome responses to high temperature stress in ripening tomato fruit. J. Zhejiang Univ. Sci. 2012;283–297.
34. Ahmad R, Iqbal MS, Ibrar D, Mahmood T, Naveed MS, Naeem MK. A review on heat stress response in different genotypes of tomato crop (*Solanum lycopersicum* L.). Intl. J. Modern Agric. 2013;2:64-71.
35. Ayenan MAT, Danquah A, Hanson P, Ampomah-Dwamena C, Sodedji FAK, Asante IK. Accelerating Breeding for Heat Tolerance in Tomato (*Solanum lycopersicum* L.): An Integrated Approach. *Agro.* 2019:9:720

Peer-review history:
The peer review history for this paper can be accessed here:
https://www.sdiarticle5.com/review-history/118258