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Physiological and Agronomic Responses of Tomato (*Solanum lycopersicum*) Under Heat Stress: Implications for Climate Resilience and Yield Performance

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ABSTRACT: Climate change-induced heat stress poses a significant threat to agricultural productivity, particularly in heat-sensitive crops like tomato (*Solanum lycopersicum*). This study evaluates the phenotypic and agronomic responses of tomato plants to varying heat stress conditions, specifically focusing on key physiological traits such as photosynthetic efficiency, chlorophyll content, membrane stability, and pollen viability. The research further explores the impact of heat stress on fruit set, plant height, stem diameter, leaf number, days to flowering, and fruit yield. Tomato plants exposed to elevated temperatures exhibited a decline in photosynthetic efficiency, chlorophyll content, and membrane stability, while pollen viability and fruit set were adversely affected under high heat conditions. Agronomic traits such as plant height, stem diameter, and fruit yield were also significantly reduced under heat stress. The study highlights the variability in stress tolerance among genotypes, indicating potential avenues for selecting heat-tolerant cultivars. The findings underscore the importance of developing strategies to mitigate the impacts of heat stress on tomato production, thereby contributing to food security and climate resilience in future agricultural systems.

Keywords: Tomato (*Solanum lycopersicum*), Heat stress tolerance, Photosynthetic efficiency, Chlorophyll content, Membrane stability index.

INTRODUCTION

Tomato (*Solanum lycopersicum* L.) is one of the most important vegetable crops cultivated globally, valued for its economic significance, nutritional benefits, and versatile use in the food industry (Kumar *et al*., 2021). It is a rich source of essential vitamins, minerals, antioxidants, and phytochemicals, contributing to improved human health. However, tomato production is highly sensitive to environmental stresses, particularly high-temperature stress, which has become a major challenge in the face of global climate change (Vijayakumar *et al*., 2020). Rising temperatures have led to substantial reductions in tomato yield and fruit quality, threatening food security and economic stability, especially in regions experiencing extreme heat events (Kaushal *et al.*, 2016).

High-temperature stress during critical growth stages, such as flowering and fruit development, adversely affects tomato plants by disrupting various physiological, biochemical, and reproductive processes (Luo *et al*., 2023; Lee *et al*., 2024). Heat stress impairs photosynthetic efficiency, reduces chlorophyll content, and increases membrane damage, ultimately limiting the plant's ability to maintain growth and yield (Fahad *et al*., 2017). It also reduces pollen viability, hinders fruit set, and negatively impacts overall fruit yield and quality (Mehmood *et al.*, 2025). The ability of tomato genotypes to maintain these traits under high temperatures is essential for their heat stress tolerance and agronomic performance (Shaheen *et al*., 2016).

To address this issue, there is a need to identify and characterize heat-tolerant tomato genotypes with desirable agronomic and physiological traits. Variations among genotypes in their responses to heat stress offer opportunities to screen and select heat-tolerant lines for future breeding programs. Key traits such as membrane stability index (MSI), photosynthetic efficiency, chlorophyll content, pollen viability, and fruit set percentage serve as important indicators of heat tolerance and can help identify heat-resilient genotypes.

The present study aims to evaluate the physiological, reproductive, and agronomic responses of diverse tomato genotypes under high-temperature stress conditions. The objectives of the study are to assess physiological traits such as leaf temperature, photosynthetic efficiency, chlorophyll content, and membrane stability index; determine reproductive traits, including pollen viability and fruit set percentage and evaluate agronomic traits such as plant height, stem diameter, number of leaves, and total fruit yield.

This research will provide critical insights into the mechanisms of heat stress tolerance in tomato and identify potential genotypes with superior performance under high-temperature conditions. The findings of this study will serve as a foundation for breeding programs focused on the development of heat-tolerant tomato cultivars, thereby contributing to sustainable tomato production under changing climatic conditions.

MATERIAL AND METHODS

A. Plant Material and Experimental Design

A diverse set of tomato (*Solanum lycopersicum* L.) genotypes, comprising standard checks, were evaluated under high-temperature stress to assess their physiological, and agronomic responses. The experiment was conducted in a controlled environment at a research facility, where temperatures were regulated to simulate high-temperature stress conditions (38/28°C, day/night) alongside optimal temperature control (30/20°C, day/night). Seeds were sown in nursery trays, and healthy seedlings at the four-leaf stage were transplanted into pots filled with a 3:1:1 mixture of loamy soil, sand, and farmyard manure. Each genotype was replicated three times in a randomized complete block design (RCBD). Plants were irrigated regularly, and appropriate nutrient management practices were followed throughout the experiment.

B. Heat Stress Treatment

After 30 days of transplanting, the plants were subjected to high-temperature stress for 15 days during the flowering stage, as this stage is most sensitive to heat stress. Temperature and relative humidity were monitored continuously in the controlled chambers using data loggers to ensure consistency. Control plants were maintained under optimal conditions.

C. Physiological Traits

Leaf Temperature. Leaf temperature was measured at midday (12:00 PM) using a non-contact infrared thermometer (Model: Fluke 62 Max). Measurements were taken from three leaves per plant (fully expanded, mature leaves), and the average was recorded.

Photosynthetic Efficiency. Photosynthetic efficiency was determined using chlorophyll fluorescence analysis (Fv/Fm) with a portable pulse-modulated fluorometer (Hansatech Instruments). Measurements were taken after 30 minutes of dark adaptation to assess the maximum quantum efficiency of PSII.

Chlorophyll Content. Chlorophyll content was estimated non-destructively using a SPAD-502 chlorophyll meter (Konica Minolta). Three readings were taken from fully expanded leaves per plant, and the average SPAD value was recorded.

Membrane Stability Index (MSI). Membrane stability was assessed following the method of Blum and Ebercon (1981). Leaf discs (0.5 g) were collected from fully expanded leaves and washed with deionized water. The samples were incubated in 10 ml of distilled water at 40°C (T1) for 30 minutes and then at 100°C (T2) for 10 minutes. The electrical conductivity (EC) of the solutions was measured before and after heating using a conductivity meter.

D. Reproductive Traits

Pollen Viability. Pollen viability was evaluated using Alexander's stain. Fresh pollen samples were collected and stained, after which viable (stained) and non-viable (unstained) pollen grains were counted under a light microscope. The percentage of viable pollen was calculated for each genotype.

Fruit Set Percentage. Fruit set was determined by recording the number of flowers and the number of fruits per plant.

E. Agronomic Traits

Plant Height and Stem Diameter. Plant height (cm) was measured from the base of the stem to the tip of the main shoot using a measuring scale. Stem diameter (mm) was measured at the base of the plant using a digital Vernier caliper.

Number of Leaves. The number of fully expanded leaves per plant was recorded at the end of the treatment period.

Fruit Yield. Total fruit yield per plant was recorded by weighing mature fruits harvested from each plant. The average yield per genotype was calculated and expressed in tons per hectare (t/ha).

F. Statistical Analysis

All data were subjected to statistical analysis using analysis of variance (ANOVA) to identify significant differences among genotypes under heat stress and control conditions. Means were compared using Duncan's multiple range test (DMRT) at a significance level of $p < 0.05$. Statistical analyses were performed using SPSS software (version 26.0).

RESULTS

Phenotypic Variation in Tomato Genotypes under Evaluation

A total of 65 tomato genotypes (T1 to T65) were evaluated for six key phenotypic traits: leaf temperature (°C), photosynthetic efficiency (%), chlorophyll content (SPAD), membrane stability (%), pollen viability (%), and fruit set (%). Significant variation was observed among the genotypes for all measured traits, indicating differential responses to environmental conditions.

Leaf Temperature and Photosynthetic Efficiency

Leaf temperature across genotypes ranged from 25°C to 30°C. Notably, genotypes such as T10, T13, T17, T20, and T64 recorded higher temperatures of 30°C, while genotypes like T4, T8, T22, T25, and T60 consistently exhibited lower leaf temperatures (25°C). Photosynthetic efficiency (PE) values varied from 75% to 90%, with genotypes T10, T22, and T27 displaying the highest PE values (90%). These genotypes could be indicative of superior photosynthetic performance under evaluation conditions. (Fig. 1).

Chlorophyll Content

Chlorophyll content, measured using SPAD values, revealed a broad range from 60 (T20, T40) to 100 (T13). Genotypes such as T13, T17, T46, and T54 displayed higher SPAD values (≥94), indicating higher chlorophyll retention and potential photosynthetic capacity (Fig. 1).

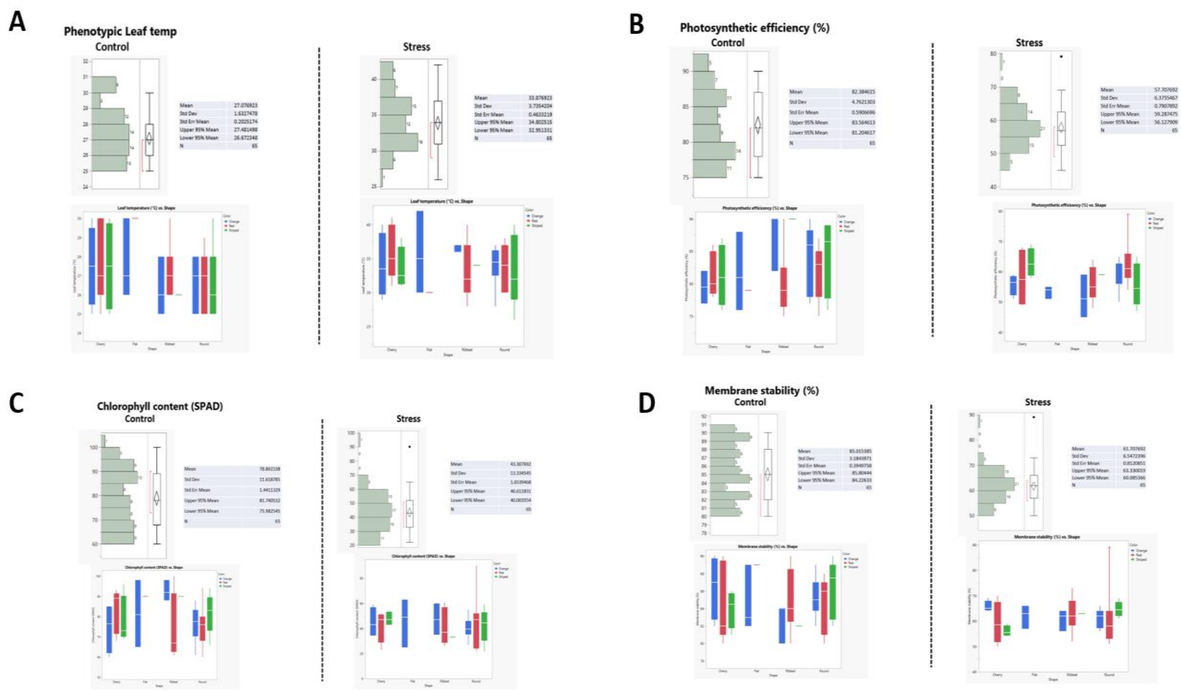

Fig. 1. Effect of heat stress on (A) phenotypic leaf temperature (B) Photosynthetic efficiency (C) Chlorophyll content (D) Membrane stability of tomato genotypes.

Membrane Stability

Membrane stability, a measure of cellular integrity, ranged between 60% and 96%. Genotypes T17 and T49 showed maximum membrane stability (96%), whereas genotypes like T11 and T20 recorded the lowest stability (61% and 60%, respectively). Membrane stability values exhibited a positive association with chlorophyll content, suggesting that higher cellular integrity supports chlorophyll retention under stress conditions (Fig. 1).

Pollen Viability

Pollen viability among the evaluated genotypes ranged from 90% to 100%. Genotypes such as T15, T17, T22, and T27 consistently exhibited 100% pollen viability, indicating their potential for stable reproductive performance. In contrast, genotypes with lower viability (e.g., T28, T40, T47) exhibited values around 90% (Fig. 2).

Fruit Set

Fruit set percentage, a critical yield-associated trait, displayed variability between 80% and 92%. High fruit set values were observed in genotypes like T15, T17, T29, and T64 (≥91%), whereas T8, T11, and T55 recorded comparatively lower values (80%). Notably, genotypes with superior photosynthetic efficiency, membrane stability, and pollen viability generally showed higher fruit set percentages (Fig. 2).

Agronomic Performance Evaluation in Tomato Genotypes

A total of 65 tomato genotypes (T1 to T65) were evaluated for key agronomic traits: plant height (cm), stem diameter (mm), number of leaves, days to flowering, and fruit yield (t/h). Significant variation was observed among the genotypes, reflecting differences in growth, flowering behavior, and yield performance (Fig. 2).

Plant Height

Plant height ranged between 50 cm and 142 cm. The tallest genotypes were T3 (142 cm), T42 (142 cm), and T4 (134 cm), demonstrating superior vegetative growth. In contrast, T17 (57 cm), T23 (57 cm), and T18 (50 cm) displayed the lowest plant heights, indicative of their compact growth habit (Fig. 2).

Stem Diameter

Stem diameter values varied from 8 mm to 14 mm. Genotypes such as T2, T3, T6, T10, T39, and T43 exhibited the highest stem diameters (14 mm), suggesting robust stem development. Lower stem diameters (8 mm) were observed in genotypes like T9, T17, T23, T49, and T56 (Fig. 3).

Number of Leaves

The number of leaves per plant ranged from 8 to 16. Genotypes T10, T14, T18, T23, T39, and T42 consistently produced 16 leaves, indicative of their high vegetative growth potential. Conversely, genotypes T4, T8, T12, T17, and T49 recorded lower leaf numbers (8 leaves) (Fig. 3).

Days to Flowering

Days to flowering varied significantly among the genotypes, ranging from 52 days to 76 days. Early flowering was observed in genotypes T6 (52 days), T18, and T24 (55 days). In contrast, genotypes T12 (73 days), T22 (74 days), and T35 (76 days) exhibited delayed flowering (Fig. 3).

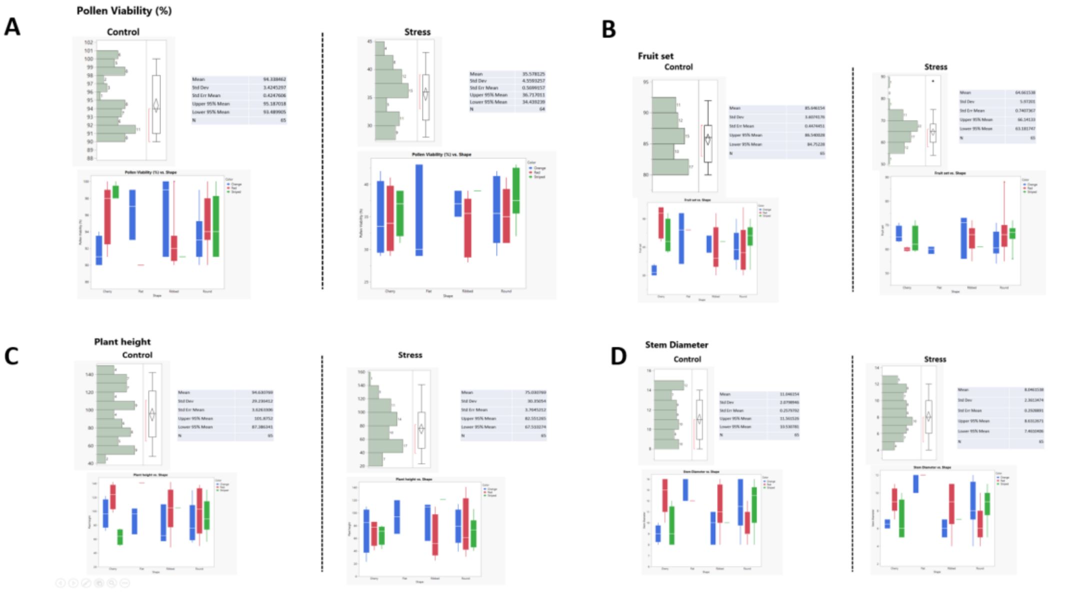

Fig. 2. Effect of heat stress on (A) Pollen viability (B) Fruit set (C) Plant height (D) Stem diameter of tomato genotypes.

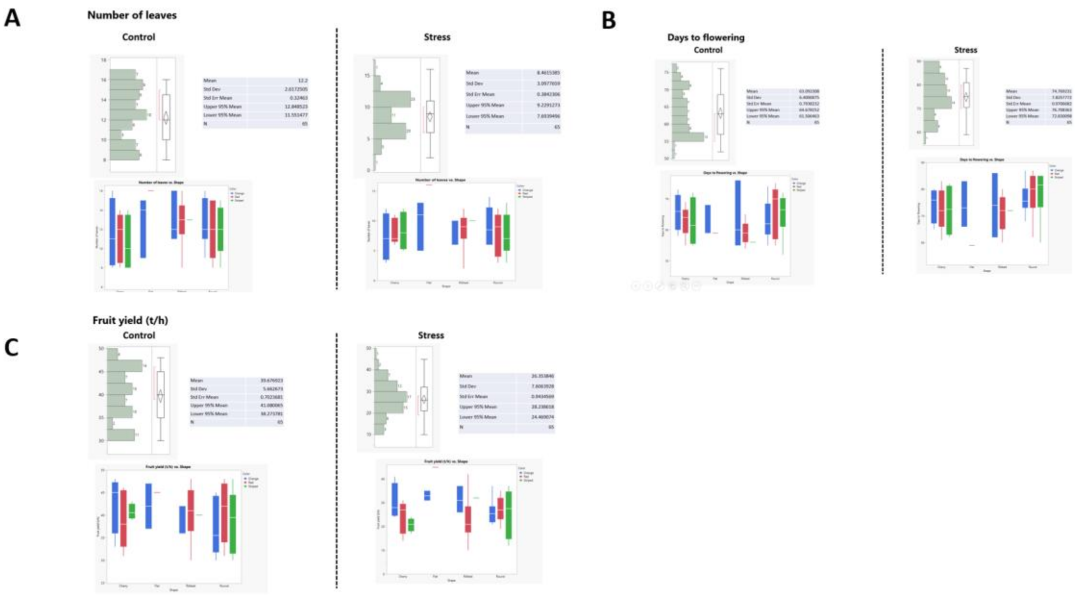

Fig. 3. Effect of heat stress on (A) Number of leaves (B) Days to flowering (C) Fruit yield (t/h).

Fruit Yield

Fruit yield, measured in tons per hectare (t/h), ranged from 30 t/h to 48 t/h. Genotypes T10, T11, T28, T36, and T50 achieved the highest yields (48 t/h), making them high-performing candidates. Lower yields (30 t/h) were observed in genotypes such as T9, T14, T19, T26, and T49 (Fig. 3).

Heat stress affected the physiological and agronomic traits

Under high-temperature stress conditions, significant reductions were observed across various phenotypic and agronomic traits, highlighting the adverse effects of elevated temperatures on tomato genotypes. Leaf Temperature increased notably under stress, with values ranging from 26°C to 42°C. The highest recorded leaf temperature (42°C) was associated with reduced chlorophyll content and fruit set, indicating heat-induced physiological limitations.

Photosynthetic Efficiency declined under stress, with values ranging from 45% to 79%. Genotype T65 maintained the highest photosynthetic efficiency at 79%, suggesting its superior ability to retain photosynthetic activity despite stress. Chlorophyll Content (SPAD values) decreased considerably under stress, varying between 22 SPAD and 90 SPAD. T65 exhibited the highest chlorophyll content (90 SPAD), demonstrating its resilience in retaining photosynthetic pigments.

Membrane Stability was significantly affected under stress, with values ranging from 50% to 89%. Genotype T65 maintained superior membrane stability at 89%, indicating its capacity to withstand cellular damage caused by high temperatures. Pollen Viability exhibited a sharp decline, ranging from 27% to 43% under stress. T34 retained relatively high pollen viability (42%), contributing to its capacity to produce fruit under adverse conditions.

Agronomic Traits such as plant height, stem diameter, and leaf number also showed significant reductions. Plant height ranged from 23 cm to 141 cm under stress, with T65 achieving the maximum plant height (141 cm). Stem diameter decreased, ranging from 2 mm to 16 mm, and T65 maintained a robust stem diameter of 12 mm. Leaf number declined to a range of 3 to 16 leaves under stress, with T65 producing the maximum number of leaves (16). Days to Flowering were delayed under stress, with flowering initiation occurring 5 to 15 days later compared to normal conditions, particularly in heat-sensitive genotypes. Fruit Yield, a critical parameter, exhibited substantial reductions under stress. Yields ranged from 10 t/h to 45 t/h, compared to higher yields under normal conditions. Genotype T65 recorded the highest yield (45 t/h), indicating its capacity to sustain productivity under heat stress. Overall, T65, T34, T28, and T37 emerged as the most heat-tolerant genotypes, showing superior performance across traits such as photosynthetic efficiency, chlorophyll content, membrane stability, and fruit yield under high-temperature stress.

A comprehensive comparative analysis of 65 tomato genotypes was conducted under normal and high-temperature stress conditions to evaluate their phenotypic and agronomic performance. The findings revealed significant reductions in most traits under stress, indicating the detrimental impact of elevated temperatures on plant physiology and productivity. Under stressed conditions, leaf temperature showed a substantial increase, ranging from 26°C to 42°C, while the range was more uniform under normal conditions. The highest leaf temperature recorded was 42°C, which was associated with reduced chlorophyll content and lower fruit set. Photosynthetic efficiency was also significantly affected, declining to a range of 45% to 79% under stress, whereas under normal conditions it varied between 48% and 77%. Among the genotypes, T65 demonstrated the highest photosynthetic efficiency (79%) under stress, suggesting its ability to maintain superior photosynthetic activity.

Chlorophyll content, as measured using SPAD values, reduced considerably under stress, with values ranging from 22 SPAD to 90 SPAD compared to 25 SPAD to 88 SPAD under normal conditions. Genotype T65 exhibited the highest chlorophyll content (90 SPAD), highlighting its resilience in retaining leaf pigments under stress. Similarly, membrane stability decreased significantly under stress, with values ranging from 50% to 89%, compared to 56% to 91% under normal conditions. Once again, T65 emerged as the most stable genotype, maintaining membrane stability at 89%. Pollen viability was particularly sensitive to high-temperature stress, declining to a range of 27% to 43%, compared to 30% to 50% under normal conditions. Genotype T34 retained relatively stable pollen viability (42%) under stress, which contributed to its ability to set fruit under adverse conditions.

Agronomic traits, including plant height, stem diameter, and leaf number, were all negatively impacted by high-temperature stress. Plant height reduced significantly, ranging from 23 cm to 141 cm under stress compared to 50 cm to 142 cm under normal conditions. T65 maintained maximum plant height (141 cm) despite the stress, indicating its robust growth. Stem diameter also declined slightly, with values ranging from 2 mm to 16 mm under stress, whereas normal conditions exhibited a range of 6 mm to 14 mm. T65 retained a sturdy stem diameter (12 mm) under stress. The number of leaves decreased under stress, with a range of 3 to 16 leaves, while under normal conditions, the range was between 8 and 16. T65 again demonstrated superior performance, producing the maximum number of leaves (16).

Days to flowering were delayed under stress, with flowering onset occurring 5 to 15 days later than under normal conditions. This delay was more pronounced in heat-sensitive genotypes. Fruit yield, one of the most critical traits, showed substantial reductions under stress. Under normal conditions, yields ranged from 30 t/h to 48 t/h, but under stress, they declined to a range of 10 t/h to 45 t/h. T65 achieved the highest yield (45 t/h) under stress, demonstrating its ability to sustain productivity under high temperatures.

From the analysis, four genotypes emerged as stress-tolerant based on their superior performance across phenotypic and agronomic traits. T65 exhibited outstanding resilience, maintaining the highest photosynthetic efficiency, chlorophyll content, membrane stability, plant height, and fruit yield under stress. Genotype T34 displayed stable pollen viability and moderate yield, while T28 and T37 performed well in terms of leaf number, fruit set, and yield.

DISCUSSION

High-temperature stress is one of the most critical abiotic factors affecting plant growth, development, and productivity, particularly in thermosensitive crops like tomato (*Solanum lycopersicum*) (Alsamir *et al*., 2021). The present study highlights the significant impact of elevated temperatures on various physiological, biochemical, and agronomic traits in diverse tomato genotypes. The results indicate a clear decline in photosynthetic efficiency, chlorophyll content, membrane stability, pollen viability, and fruit yield, underscoring the detrimental effects of heat stress on the physiological and reproductive processes of tomato plants.

Under heat stress, leaf temperature increased significantly, which is a direct reflection of disrupted transpiration and impaired heat dissipation mechanisms. Genotypes that maintained relatively lower leaf temperatures, such as T34 and T37, demonstrated better physiological performance, suggesting their ability to regulate stomatal conductance effectively. Similar findings have been reported by previous studies, where leaf temperature is inversely related to heat tolerance, as efficient transpiration reduces heat accumulation (Ul Hassan *et al*., 2021).

Photosynthetic efficiency exhibited a sharp decline in most genotypes under stress, indicating a disruption in photosystem II (PSII) activity and overall photochemical processes (Sharma *et al*., 2020). Genotype T65 maintained the highest photosynthetic efficiency (79%), suggesting its superior capability to protect the photosynthetic machinery under elevated temperatures. The reduction in photosynthetic activity under stress has been widely attributed to thermal damage to chloroplast membranes and enzymes like Rubisco, leading to decreased carbon assimilation (Bhattacharya, 2022). Retention of photosynthetic efficiency under stress, as seen in T65, is a key indicator of heat tolerance.

A significant decline in chlorophyll content was observed under stress, as evidenced by reduced SPAD values across genotypes. Chlorophyll degradation is often accelerated by heat-induced oxidative stress, resulting in chlorophyll bleaching and impaired light absorption. Genotype T65 displayed the highest chlorophyll content (90 SPAD), indicating its resilience in maintaining photosynthetic pigments. This ability could be linked to enhanced antioxidant defense mechanisms that mitigate chlorophyll breakdown, as reported in previous studies on heat-stress tolerant genotypes (Raja *et al*., 2020). Membrane stability, which serves as a critical indicator of cellular integrity under stress, was severely affected in sensitive genotypes (Nijabat *et al*., 2020). High-temperature stress is known to increase lipid peroxidation, leading to membrane damage and electrolyte leakage. Genotype T65 exhibited the highest membrane stability (89%), suggesting enhanced membrane integrity and reduced oxidative damage. This finding aligns with earlier studies showing that heat-tolerant genotypes maintain higher membrane stability due to better osmotic adjustments and antioxidant protection (Liu *et al*., 2023).

Pollen viability and fruit set were significantly reduced under stress, which is consistent with previous findings linking heat stress to reproductive failure (Mesihovic *et al*., 2016). High temperatures disrupt pollen development, viability, and germination, ultimately reducing fruit set and yield (Pham *et al.,* 2020). Genotypes like T34 and T65 retained relatively higher pollen viability and fruit set, indicating their ability to maintain reproductive success under stress. The agronomic traits including plant height, stem diameter, and the number of leaves were severely affected under heat stress, as growth and development processes are highly sensitive to temperature fluctuations (Prasad *et al.,* 2018). Genotype T65 recorded the highest plant height (141 cm) and stem diameter, which might be attributed to its efficient resource allocation under stress. A similar observation was noted for the number of leaves, where T65 maintained higher vegetative growth compared to other genotypes.

The most critical impact of heat stress was observed on fruit yield, which decreased significantly across genotypes. Yield reductions were likely caused by a combination of reduced photosynthetic efficiency, impaired reproductive processes, and compromised membrane stability. However, genotype T65 exhibited the highest yield (45 t/h), demonstrating its ability to sustain productivity under stress. This superior performance can be linked to its capacity to maintain photosynthetic pigments, reproductive success, and cellular stability. Collectively, the results indicate that T65, followed by T34, T28, and T37, demonstrated strong resilience under high-temperature stress. These genotypes exhibited superior performance in traits such as photosynthetic efficiency, chlorophyll content, membrane stability, and fruit yield. The ability to maintain physiological and biochemical processes under stress highlights their potential as promising candidates for heat-stress breeding programs.

Overall, this study provides valuable insights into the physiological and agronomic responses of tomato genotypes under high-temperature stress. The findings emphasize the importance of identifying and incorporating heat-tolerant genotypes into breeding programs to ensure sustainable tomato production under changing climatic conditions. Future studies should focus on the molecular and genetic basis of heat tolerance, including the role of heat shock proteins, antioxidant systems, and hormonal regulation, to further enhance heat stress resilience in tomato.

CONCLUSIONS

The evaluation of 65 tomato genotypes under normal and high-temperature stress conditions revealed significant phenotypic and agronomic variability, highlighting the differential responses of genotypes to heat stress. Under stress, most genotypes exhibited elevated leaf temperature, reduced photosynthetic efficiency, decreased chlorophyll content, impaired membrane stability, lower pollen viability, delayed flowering, and reduced fruit yield. However, specific genotypes demonstrated resilience by maintaining physiological integrity and yield stability. Notably, T65 consistently outperformed others across multiple traits, including photosynthetic efficiency (79%), chlorophyll content (90 SPAD), membrane stability (89%), and fruit yield (45 t/h). Genotypes T34, T28, and T37 also displayed heat-tolerant characteristics, particularly in terms of pollen viability, leaf number, and fruit set. The strong association between physiological stability and reproductive success underscores the importance of integrated trait evaluation for identifying thermotolerant germplasm. These findings confirm that targeted screening of physiological and reproductive traits can effectively discriminate tolerant genotypes with potential for sustained productivity under climate stress.

FUTURE SCOPE

The identification of T65, T34, T28, and T37 as promising heat-tolerant genotypes provides a foundation for developing climate-resilient tomato cultivars. Future research should focus on validating these genotypes under diverse agro-climatic field conditions and across multiple growth stages to ensure stable performance. Advanced molecular approaches, including QTL mapping, GWAS, transcriptomics, and proteomics, could be employed to identify genes and regulatory networks linked to heat tolerance. Integrating physiological markers such as photosynthetic efficiency and membrane stability with molecular breeding tools will accelerate the development of resilient hybrids. Additionally, high-throughput phenotyping platforms, chlorophyll fluorescence imaging, and thermal imaging can enhance selection precision. Beyond breeding, exploring management practices such as optimized irrigation and foliar protectants may complement genetic tolerance. Collectively, these strategies will contribute to the development of robust tomato cultivars capable of maintaining yield and quality under rising global temperatures.

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