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Photosystem II Performance and Heat Stress Tolerance in Tomato (*Solanum lycopersicum* L.): Insights from Chlorophyll Fluorescence and Electron Transport Analysis

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ABSTRACT: Heat stress is a critical environmental factor affecting crop productivity by impairing photosynthetic efficiency. This study evaluated the impact of high-temperature stress on Photosystem II (PSII) functionality in 24 tomato (*Solanum lycopersicum*) genotypes using chlorophyll fluorescence parameters, including maximum quantum efficiency (Fv/Fm), effective quantum yield of PSII photochemistry (Y(II)), regulated non-photochemical quenching (Y(NPQ)), non-regulated energy dissipation (Y(NO)), and electron transport rate (ETR). Measurements were conducted at three developmental stages: early (ES), mid (MS), and final (FS). Under control conditions, Fv/Fm values ranged from 0.593 to 0.76 (ES), 0.654 to 0.887 (MS), and 0.533 to 0.694 (FS), with a significant decline under heat stress across all genotypes. Similarly, Y(II) and ETR decreased under stress, indicating reduced photochemical efficiency and electron transport activity. In contrast, Y(NO) increased, suggesting enhanced non-regulated energy dissipation, while Y(NPQ) exhibited genotype-specific variations in photoprotective energy dissipation. Genotypes SG3, SG4, SG6, SG10, SG17, SG18, and SG24 demonstrated relatively higher PSII efficiency and ETR under stress, suggesting superior heat tolerance. Conversely, SG1, SG11, SG19, and SG21 exhibited the most pronounced reductions, indicating susceptibility. Correlation analysis revealed strong positive relationships between Fv/Fm, Y(II), and ETR, while Y(NO) showed a negative association with these parameters, highlighting its detrimental effect on PSII efficiency. Principal component analysis (PCA) confirmed a shift in trait associations under stress, emphasizing increased reliance on photoprotective mechanisms. Overall, this study underscores the variability in PSII functionality among tomato genotypes under heat stress, identifying promising candidates for breeding programs aimed at enhancing thermotolerance and improving crop resilience in high-temperature environments.

Keywords: Photosystem II, Heat Stress, Tomato, Electron Transport Chain, Chlorophyll

INTRODUCTION

Heat stress is a critical abiotic factor that significantly impacts plant growth, development, and productivity (Calanca, 2016). Tomato (*Solanum lycopersicum* L.), an economically and nutritionally important crop, is highly susceptible to elevated temperatures, which can impair physiological and biochemical processes, ultimately reducing yield and fruit quality (Dasgan *et al.,* 2021). Among the various physiological mechanisms affected by heat stress, the photosynthetic apparatus, particularly Photosystem II (PSII), plays a pivotal role in determining plant resilience (Muhammad *et al.,* 2021).

PSII is a crucial component of the photosynthetic electron transport chain, responsible for the initial photochemical reactions that drive photosynthesis (Roach and Krieger-Liszkay 2014). Heat stress can disrupt PSII function by causing damage to the D1 protein, increasing photoinhibition, and reducing photosynthetic efficiency (Allakhverdiev *et al*., 2008). As a result, assessing PSII efficiency under high-temperature conditions can provide valuable insights into the mechanisms underlying heat tolerance in tomato and aid in selecting resilient genotypes for breeding programs.

Chlorophyll fluorescence analysis has emerged as a reliable, non-invasive tool for evaluating PSII function under stress conditions (Guidi and Calatayud 2014). Key fluorescence parameters such as the maximum quantum efficiency of PSII photochemistry (Fv/Fm), effective quantum yield (Y(II)), regulated energy dissipation (Y(NPQ)), non-regulated energy dissipation (Y(NO)), and electron transport rate (ETR) provide comprehensive information on photochemical efficiency and the plant's ability to manage excess light energy (Perera-Castro and Flexas 2023).

This study aims to evaluate the PSII performance of diverse tomato genotypes under heat stress by analyzing chlorophyll fluorescence parameters. The findings will enhance our understanding of genotype-specific variations in PSII efficiency and contribute to identifying physiological markers for heat tolerance. This research will provide valuable insights for breeding heat-resilient tomato cultivars, thereby improving agricultural sustainability and productivity under changing climatic conditions.

MATERIALS AND METHODS

A. Plant Material and Growth Conditions

A diverse set of tomato (*Solanum lycopersicum* L.) genotypes was selected to evaluate Photosystem II (PSII) performance under heat stress conditions. Seeds were obtained from a well-characterized germplasm collection. The seeds were sown in seed trays containing a standard potting mix composed of peat moss, perlite, and vermiculite in a 3:1:1 ratio. Following germination, seedlings were transplanted into pots (10 cm diameter) filled with the same potting mixture and maintained under controlled greenhouse conditions at 25 ± 2°C, with a 16-hour photoperiod and relative humidity of 60-70%.

B. Heat Stress Treatment

At the four-true-leaf stage, plants were subjected to heat stress in a growth chamber. The temperature was gradually increased to 40 ± 2°C during the daytime, while nighttime temperatures were maintained at 30 ± 2°C. Control plants were maintained at 25 ± 2°C. The heat stress treatment was applied for seven days. Plants were regularly watered to maintain uniform soil moisture levels, and no additional fertilizers were applied to prevent confounding effects.

C. Measurement of Photosystem II Efficiency

PSII performance was assessed using a pulse-amplitude modulated (PAM) fluorometer (PAM Junior, Heinz Walz GmbH, Germany). Measurements were taken from the fully expanded third leaf from the top of each plant under dark-adapted and light-adapted conditions. The following parameters were recorded:

a. Maximum Quantum Efficiency of PSII (Fv/Fm): After 30 minutes of dark adaptation, the minimal fluorescence yield (Fo) and maximal fluorescence yield (Fm) were determined, and Fv/Fm was calculated as: This parameter represents the maximum efficiency at which light energy is converted into chemical energy by PSII.

b. Effective Quantum Yield of PSII Photochemistry (Y(II)): Measured under actinic light conditions as: where Fs is the steady-state fluorescence and Fm' is the maximal fluorescence yield under light-adapted conditions.

c. Quantum Yield of Regulated Energy Dissipation (Y(NPQ)): Representing the fraction of light energy dissipated as regulated thermal dissipation, calculated as:

d. Quantum Yield of Non-regulated Energy Dissipation (Y(NO)): Representing passive energy dissipation, calculated as:

e. Electron Transport Rate (ETR): Estimated using the formula: where PPFD represents the photosynthetic photon flux density (in µmol photons m^{-2} s^{-1}), 0.5 accounts for the fraction of excitation energy distributed to PSII, and 0.84 represents the assumed leaf absorptance.

D. Correlation and Principal Component Analysis

Pearson's correlation coefficients were calculated to evaluate interrelationships among PSII parameters. Principal component analysis (PCA) was performed to identify major sources of variation among genotypes in response to heat stress. Data were standardized before PCA to ensure equal weighting of all parameters. PCA was conducted using R software (R Core Team, 2023) with the prcomp function in the stats package, and biplots were generated using the ggbiplot package.

E. Statistical Analysis

Experiments were conducted using a completely randomized design (CRD) with three biological replicates per genotype. Data were analyzed using one-way analysis of variance (ANOVA) followed by Tukey's HSD test ($p < 0.05$) to determine significant differences between control and heat-stressed plants. Statistical analyses were performed using SPSS (IBM SPSS Statistics v.26) and R software.

RESULTS AND DISCUSSION

A. Photochemical quantum yield of PS II (Fv/Fm)

The study on the impact of heat stress on Photosystem II in tomato genotypes, measured using the Fv/Fm parameter, revealed considerable variation across 24 genotypes under both control and stress conditions. Under control conditions, the Fv/Fm values for the early stage (ES) ranged from 0.593 (SG21) to 0.76 (SG3), while under stress, these values decreased, ranging from 0.587 (SG21) to 0.744 (SG3). For the mid-stage (MS), Fv/Fm values under control conditions were higher, ranging from 0.654 (SG23) to 0.887 (SG3), but under stress, these values declined, ranging from 0.616 (SG21) to 0.865 (SG3). Similarly, for the final stage (FS), Fv/Fm values under control ranged from 0.533 (SG19) to 0.694 (SG24), while under stress, the range decreased to 0.482 (SG19) to 0.671 (SG24).

Overall, the results indicate that heat stress adversely affected Fv/Fm values across all stages and genotypes, suggesting impaired efficiency of Photosystem II under high-temperature conditions. Genotypes such as SG3 and SG24 maintained relatively higher Fv/Fm values under stress, indicating better tolerance to heat stress. Conversely, genotypes like SG19 and SG21 exhibited substantial reductions in Fv/Fm values under stress, highlighting their susceptibility. These findings underscore the variability in photosynthetic performance among tomato genotypes under heat stress and identify potential candidates for breeding programs aimed at improving heat stress tolerance.

The reduction in Fv/Fm values under heat stress reflects the adverse effects of high temperatures on the efficiency of Photosystem II (PSII) in tomato genotypes. PSII is highly sensitive to thermal stress, and decreased Fv/Fm ratios under stress indicate photoinhibition (Jiang *et al*., 2021), reduced quantum yield of PSII, and damage to the photosynthetic apparatus (Li *et al*., 2023). The decline observed across all genotypes highlights the universal susceptibility of photosynthesis to heat stress, but the extent of the reduction varies, showcasing genotypic differences in resilience.

Genotypes such as SG3 and SG24, which maintained relatively higher Fv/Fm values under heat stress, demonstrate better photoprotective mechanisms and efficient repair of PSII components. These genotypes likely possess enhanced thermal stability of the D1 protein in PSII, robust antioxidant defense systems, and efficient energy dissipation mechanisms to mitigate stress-induced damage. These attributes make them promising candidates for breeding programs aimed at improving heat tolerance in tomatoes.

In contrast, genotypes such as SG19 and SG21, which exhibited significant reductions in Fv/Fm values, are likely more susceptible to photoinhibition and oxidative damage under heat stress. Their performance indicates limited capacity to cope with excess excitation energy, leading to impaired photosynthetic efficiency and potential declines in growth and yield (He *et al*., 2018).

The stage-specific variation in Fv/Fm values suggests that heat stress impacts PSII differently across the plant's developmental stages (Shanker *et al*., 2022). Higher sensitivity during the final stage (FS) could be attributed to cumulative stress effects or reduced repair capacity of PSII. This stage-dependent response underscores the need to evaluate heat tolerance at multiple growth stages to comprehensively assess genotypic performance.

The significant variability in Fv/Fm values under stress among genotypes suggests that PSII efficiency can serve as a reliable physiological marker for screening and selecting heat-tolerant tomato genotypes. By identifying genotypes with stable Fv/Fm values under stress, breeding programs can target the integration of superior photosynthetic traits into new cultivars (Arya *et al.*, 2024).

B. Effective photochemical quantum Y(II)

The study examined the impact of heat stress on Photosystem II functionality in tomato genotypes, focusing on quantum yield of PSII photochemistry (Y(II)) across 24 genotypes under control and stress conditions. The data revealed significant variability in Y(II) values among genotypes at different developmental stages, including early stage (ES), mid-stage (MS), and final stage (FS).

Under control conditions, Y(II) values at the ES ranged from 0.427 (SG1) to 0.526 (SG18), with the highest values observed in SG18 and SG10. Under stress conditions, Y(II) values at the ES showed a reduction across all genotypes, ranging from 0.372 (SG11) to 0.510 (SG17). At the MS, Y(II) values under control conditions ranged from 0.442 (SG11) to 0.570 (SG4). Under stress, the range was lower, spanning from 0.384 (SG11) to 0.564 (SG4), indicating significant genotype-specific differences in the ability to maintain Y(II) under heat stress. At the FS, control values ranged from 0.347 (SG1) to 0.431 (SG18), while under stress, values ranged from 0.289 (SG1) to 0.402 (SG4).

Genotypes SG4, SG17, and SG10 exhibited comparatively higher Y(II) values under stress, suggesting a better ability to sustain photosynthetic efficiency under high-temperature conditions. Conversely, genotypes such as SG1 and SG11 showed the most pronounced reductions in Y(II), indicating greater susceptibility to heat stress. The decline in Y(II) values across all genotypes under stress highlights the negative impact of heat stress on PSII functionality, with differential responses observed among genotypes. These findings provide valuable insights for selecting heat-tolerant genotypes for breeding programs aimed at improving photosynthetic performance and resilience in tomato under heat stress conditions.

The results of this study highlight the detrimental effects of heat stress on Photosystem II (PSII) functionality in tomato genotypes, as evidenced by the significant reductions in quantum yield of PSII photochemistry (Y(II)) under stress conditions. Heat stress, known to impair the efficiency of light energy conversion in plants, resulted in a decline in Y(II) across all genotypes, suggesting that elevated temperatures affect the integrity and functionality of PSII. This disruption in photosynthetic efficiency is likely to lead to reduced carbon assimilation, which can impact overall plant growth and yield.

The observed variability in Y(II) responses among tomato genotypes under heat stress points to genotype-specific differences in heat tolerance mechanisms. Genotypes such as SG4, SG17, and SG10 demonstrated comparatively higher Y(II) values under stress, indicating their better ability to sustain photosynthetic efficiency despite the heat-induced damage. This resilience may be attributed to several factors, including enhanced thermal stability of PSII components, efficient repair mechanisms, and an improved ability to dissipate excess light energy through non-photochemical quenching (NPQ). These genotypes could serve as promising candidates for breeding programs aimed at improving heat tolerance in tomato.

In contrast, genotypes such as SG1 and SG11 exhibited more pronounced reductions in Y(II) under heat stress, indicating that these genotypes are more vulnerable to heat-induced damage. The reduced Y(II) in these genotypes suggests a greater susceptibility to photoinhibition and a decreased capacity for repair of PSII under stress conditions. These genotypes may be less effective at coping with heat stress, possibly due to limited ability to maintain electron transport and repair photodamaged PSII complexes. Understanding the molecular and biochemical mechanisms behind this sensitivity could provide valuable insights for enhancing heat tolerance in susceptible genotypes.

The decline in Y(II) values observed across all genotypes under heat stress is consistent with the general understanding that high temperatures can induce oxidative stress, leading to damage in the photosynthetic apparatus. This damage is often exacerbated by prolonged exposure to elevated temperatures, which may impair the plant's ability to cope with heat stress, particularly during critical developmental stages such as flowering and fruit set. Furthermore, the significant reduction in Y(II) across all stages (early, mid, and final) suggests that heat stress has a cumulative effect on photosynthetic performance, potentially limiting the overall growth and productivity of tomato plants.

The genotype-specific differences observed in this study underscore the importance of selecting heat-tolerant varieties for future breeding efforts. By focusing on genotypes with higher Y(II) values under heat stress, it may be possible to develop tomato varieties that are better equipped to withstand elevated temperatures, thereby improving their yield stability under increasingly variable climatic conditions. These findings provide a foundation for further research into the physiological and molecular bases of heat tolerance in tomato, with the potential for enhancing climate resilience in this important crop.

C. Quantum yield of non-light induced non-photochemical fluorescence quenching Y(NPQ)

The study evaluated the impact of heat stress on Photosystem II by analysing the quantum yieldfor regulated non-photochemical quenching (Y(NPQ)) across 24 tomato genotypes under control and stress conditions at three developmental stages: early stage (ES), mid-stage (MS), and final stage (FS). The data demonstrated significant variability in Y(NPQ) values among genotypes, reflecting differential responses to heat stress.

Under control conditions, Y(NPQ) values at the ES ranged from -0.064 (SG17) to 0.072 (SG14). Under stress, a reduction in Y(NPQ) was observed in most genotypes, with values ranging from -0.074 (SG17) to 0.062 (SG14). At the MS, Y(NPQ) under control ranged from -0.051 (SG21) to 0.075 (SG14), while stress conditions resulted in values ranging from -0.058 (SG21) to 0.065 (SG14). At the FS, control values ranged from -0.074 (SG17) to 0.070 (SG14), whereas stress conditions ranged from -0.078 (SG17) to 0.061 (SG14).

Genotypes SG6, SG14, and SG7 consistently maintained positive Y(NPQ) values under both control and stress conditions, indicating better photoprotective mechanisms through regulated non-photochemical quenching under heat stress. In contrast, genotypes such as SG17 and SG21 exhibited highly negative Y(NPQ) values, suggesting poor regulation of excess energy dissipation and heightened susceptibility to photoinhibition.

The observed reduction in Y(NPQ) under stress conditions highlights the negative impact of heat stress on the photoprotective capacity of Photosystem II in tomato genotypes. Genotypes exhibiting stable or positive Y(NPQ) values under stress conditions are potential candidates for breeding programs aimed at improving thermotolerance in tomato.

This study highlights the impact of heat stress on the photoprotective capacity of Photosystem II in tomato genotypes, specifically focusing on the quantum yield for regulated non-photochemical quenching (Y(NPQ)). The observed variability in Y(NPQ) values among the genotypes reflects differential abilities to manage excess light energy under heat stress, a crucial aspect of photosynthetic efficiency and plant thermotolerance (Estrada *et al.,* 2015).

Under heat stress, the general reduction in Y(NPQ) across most genotypes suggests a compromised ability to dissipate excess absorbed light energy via non-photochemical mechanisms, which are vital in protecting the photosynthetic apparatus from photodamage. Photoinhibition, a consequence of this stress, occurs when excess energy overwhelms the photosynthetic system, leading to the accumulation of reactive oxygen species (ROS) and damage to Photosystem II (Singh and Thakur 2018). The decline in Y(NPQ) across all stages further indicates that heat stress affects the plant's ability to regulate this energy dissipation over time, leading to a gradual deterioration of photosynthetic efficiency (Falcioni *et al.,* 2024).

Genotypes such as SG6, SG14, and SG7 demonstrated relatively stable or positive Y(NPQ) values under both control and heat stress conditions. This suggests that these genotypes possess more robust photoprotective mechanisms, likely involving efficient regulation of excess energy dissipation, which allows them to better manage heat-induced stress. The ability to maintain positive Y(NPQ) values under stress conditions reflects their capacity to protect the photosynthetic apparatus from damage, thereby enhancing their overall heat tolerance. These genotypes could serve as valuable candidates for breeding programs focused on improving heat resilience in tomato plants.

On the other hand, genotypes like SG17 and SG21 exhibited highly negative Y(NPQ) values, indicating a poor ability to regulate excess energy dissipation. Such genotypes are more susceptible to photoinhibition under heat stress, which may impair their photosynthetic capacity and limit their growth and productivity. The inability to maintain effective energy regulation during periods of heat stress could lead to increased oxidative stress, cell damage, and a significant reduction in plant performance.

The results emphasize the importance of Y(NPQ) as a potential marker for identifying genotypes with superior heat tolerance. In addition to other physiological parameters, Y(NPQ) can provide insights into the photoprotective mechanisms that are essential for mitigating the negative impacts of heat stress on photosynthesis. The genotypes that demonstrate stable or positive Y(NPQ) values under stress could be incorporated into breeding programs aimed at developing heat-tolerant tomato varieties. By improving the thermotolerance of tomato through better regulation of non-photochemical quenching, it may be possible to enhance productivity and stability under fluctuating temperature conditions, thereby ensuring sustainable tomato production in the face of climate change.

Overall, this study underscores the crucial role of Y(NPQ) in assessing heat stress tolerance in tomato and provides a basis for future breeding strategies aimed at improving heat resilience in this important crop.

D. Quantum yield of light induced non photochemical fluorescence quenching Y (NO)

The impact of heat stress on Photosystem II was assessed in 24 tomato genotypes by analysing the quantum yield of non-regulated energy dissipation (Y(NO)) under control and stress conditions across three developmental stages: early stage (ES), mid-stage (MS), and final stage (FS). The results revealed significant differences in Y(NO) among genotypes, highlighting their differential responses to heat stress.

Under control conditions, Y(NO) at the ES ranged from 0.432 (SG14) to 0.614 (SG1), while stress conditions increased Y(NO) values, ranging from 0.489 (SG14) to 0.648 (SG1). At the MS, Y(NO) ranged from 0.384 (SG6) to 0.576 (SG1) under control conditions and increased under stress, ranging from 0.407 (SG6) to 0.618 (SG1). Similarly, at the FS, Y(NO) under control conditions ranged from 0.528 (SG14) to 0.703 (SG1), while stress conditions elevated these values, ranging from 0.543 (SG14) to 0.767 (SG1).

The majority of genotypes exhibited an increase in Y(NO) under stress conditions, indicating a reduction in the efficiency of Photosystem II and an increased proportion of absorbed light being dissipated as heat or fluorescence. Genotypes SG1, SG13, and SG21 demonstrated the highest Y(NO) under both control and stress conditions, suggesting a lower capacity for photochemical energy conversion under heat stress. Conversely, genotypes SG6 and SG14 exhibited relatively low Y(NO) values, indicating better maintenance of Photosystem II efficiency and a lower propensity for photoinhibition under heat stress.

Overall, the results highlight the detrimental effect of heat stress on Photosystem II efficiency in tomato genotypes, as indicated by the increased Y(NO) values. Genotypes with relatively lower Y(NO) under stress conditions, such as SG6 and SG14, may possess enhanced photoprotective mechanisms and are potential candidates for breeding programs aimed at improving heat stress tolerance.

This study evaluated the impact of heat stress on Photosystem II functionality in tomato genotypes, specifically focusing on the quantum yield of non-regulated energy dissipation (Y(NO)) as a measure of the inefficiency in energy utilization under heat stress conditions. The observed variability in Y(NO) values across genotypes under control and stress conditions emphasizes the differential responses of tomato genotypes to heat stress and highlights the importance of energy dissipation mechanisms in maintaining photosynthetic efficiency during adverse conditions (Pan *et al.*, 2018).

Under heat stress, the majority of genotypes exhibited an increase in Y(NO), suggesting a reduction in the efficiency of Photosystem II. This increase reflects a shift in the balance between photochemical energy conversion and the non-regulated dissipation of excess absorbed light energy. In particular, elevated Y(NO) values indicate that more energy is being dissipated as heat or fluorescence, a sign that the photosynthetic apparatus is overwhelmed by excess light (Tikkanen *et al.*, 2012). The greater the increase in Y(NO), the more significant the photoinhibition, which can impair overall plant growth and yield. This highlights the detrimental effects of heat stress on photosynthetic efficiency and its potential to limit productivity.

Genotypes such as SG1, SG13, and SG21 exhibited consistently high Y(NO) values under both control and stress conditions, indicating a lower capacity for photochemical energy conversion. These genotypes may have a reduced ability to efficiently convert absorbed light into chemical energy under stress, which could result in a greater proportion of energy being dissipated as heat. Such genotypes are more susceptible to heat-induced photoinhibition, leading to reduced photosynthetic performance under elevated temperatures.

In contrast, genotypes SG6 and SG14 maintained relatively lower Y(NO) values, suggesting that they were more efficient in maintaining Photosystem II functionality under heat stress. These genotypes may possess better photoprotective mechanisms that help mitigate the impact of excess light energy, such as enhanced non-photochemical quenching or more efficient repair mechanisms for photodamaged components of the photosynthetic machinery. These traits are likely to contribute to better heat tolerance, as they reduce the susceptibility of the plants to photoinhibition and oxidative damage.

The increase in Y(NO) across most genotypes under heat stress underscores the negative impact of elevated temperatures on the efficiency of Photosystem II. However, the genotypes with relatively lower Y(NO) values, such as SG6 and SG14, may represent valuable genetic resources for breeding programs aimed at improving heat stress tolerance. These genotypes could potentially serve as a basis for developing tomato varieties with enhanced capacity for photosynthesis and better performance under heat stress conditions, which are expected to become more frequent due to climate change.

Overall, this study emphasizes the utility of Y(NO) as a useful parameter for assessing heat tolerance in tomato plants. Genotypes exhibiting lower Y(NO) values under heat stress are likely to exhibit better overall photosynthetic efficiency and thermotolerance. Such genotypes could be targeted in breeding programs focused on developing tomato cultivars with improved heat stress resilience, thus ensuring better yields and productivity under changing environmental conditions.

E. Electron transport rate (ETR)

The electron transport rate (ETR), an indicator of the efficiency of Photosystem II under control and heat stress conditions, was analysed across 24 tomato genotypes at three developmental stages: early stage (ES), mid-stage (MS), and final stage (FS). The results reveal a decline in ETR under stress conditions across all genotypes, demonstrating the negative impact of heat stress on photosynthetic efficiency.

Under control conditions, ETR at the ES ranged from 34.0746 (SG1) to 41.9748 (SG18). At the MS, values ranged from 35.299 (SG11) to 45.515 (SG4), and at the FS, ETR ranged from 27.696 (SG1) to 34.372 (SG18). Genotypes SG4, SG6, SG18, and SG10 exhibited the highest ETR values, indicating robust electron transport activity under optimal conditions.

Under heat stress, ETR decreased across all developmental stages. At the ES, values ranged from 29.647 (SG11) to 40.658 (SG17), indicating a reduction in electron transport efficiency. At the MS, ETR ranged from 30.632 (SG11) to 44.996 (SG4), with genotype SG4 maintaining relatively high ETR. At the FS, ETR was lowest for SG1 (23.029) and highest for SG4 (32.081).

A notable reduction in ETR under stress was observed in all genotypes. The most pronounced decrease was recorded in SG1 (6.09%), whereas SG17 retained a high ETR (1.26% reduction). Genotype SG4 maintained the highest ETR (44.996), while SG11 recorded the lowest (30.632), indicating that some genotypes demonstrate better adaptability to stress at this stage. Heat stress resulted in the most significant ETR reduction at FS. SG1 and SG11 exhibited the lowest ETR, while SG4 showed the least reduction among genotypes.

Genotypes SG4, SG6, SG10, and SG18 consistently exhibited higher ETR under both control and stress conditions, suggesting their relative tolerance to heat stress. Conversely, genotypes SG1, SG11, and SG15 showed substantial declines in ETR, indicating greater susceptibility. The findings indicate that heat stress significantly impairs ETR across all tomato genotypes and developmental stages, with variations in the extent of the decline among genotypes. Genotypes SG4, SG6, SG10, and SG18 demonstrated superior performance in maintaining ETR under heat stress, suggesting their potential suitability for breeding programs aimed at enhancing heat tolerance.

The study evaluated the impact of heat stress on the electron transport rate (ETR) in Photosystem II across 24 tomato genotypes, offering insights into the genotypic variation in photosynthetic efficiency under high-temperature conditions. ETR serves as a key parameter for assessing the capacity of plants to maintain electron flow through Photosystem II during photosynthesis (Calzadilla *et al.*, 2022). The observed decline in ETR under stress conditions underscores the detrimental effects of heat stress on the functionality of the photosynthetic apparatus in tomato genotypes.

Heat stress impairs the electron transport chain by disrupting the thylakoid membrane structure, reducing the efficiency of energy transfer between photosystems, and promoting photoinhibition (Ivanov *et al.,* 2017). The observed reduction in ETR across all genotypes highlights these stress-induced damages. Genotypes with the most significant ETR reductions are likely to experience compromised photosynthetic performance, lower carbon assimilation, and reduced growth and yield potential under high temperatures.

Notably, genotypes SG4, SG6, SG10, and SG18 demonstrated consistently higher ETR values under both control and stress conditions, indicating robust photosynthetic machinery and better adaptability to heat stress (Zahra *et al.,* 2023). This suggests that these genotypes may possess enhanced mechanisms for maintaining thylakoid integrity, dissipating excess energy, or repairing damaged components of the photosynthetic apparatus. Such traits make these genotypes promising candidates for breeding programs aimed at improving thermotolerance.

Conversely, genotypes SG1, SG11, and SG15 exhibited significant declines in ETR under stress, reflecting their susceptibility to heat stress. These genotypes are likely less capable of mitigating the effects of excess light energy or repairing stress-induced damage to Photosystem II, leading to reduced photosynthetic efficiency and greater photoinhibition.

The variations in ETR among genotypes and across developmental stages further illustrate the complex interplay between genotype, developmental stage, and environmental stress in determining photosynthetic performance. Genotype SG4, which consistently maintained the highest ETR across all stages under stress, demonstrates strong potential as a resilient candidate for improving heat stress tolerance in tomato breeding programs.

F. Correlation

The correlation analysis revealed significant relationships among various photosynthetic traits under stress conditions. Fv/Fm and Y(II) showed a strong positive correlation ($r = 0.99$) across all stages, indicating that the efficiency of Photosystem II (PSII) closely aligns with its actual quantum yield. Similarly, the Electron Transport Rate (ETR) exhibited a near-perfect correlation ($r \approx 1.0$) with Y(II), emphasizing its role as a critical indicator of PSII activity. In contrast, Y(NO), representing non-regulated energy dissipation, showed a strong negative correlation with both Fv/Fm ($r = -0.97$) and Y(II) ($r = -0.95$), highlighting its detrimental effect on PSII efficiency and electron transport. The regulated energy dissipation parameter, Y(NPQ), showed weaker correlations with Fv/Fm and Y(II), suggesting a limited direct influence under these conditions. Stage-specific variations in correlation strengths were observed, indicating that the impact of stress on photosynthetic performance may vary across developmental stages. These results underscore the importance of minimizing non-regulated energy dissipation (Y(NO)) to enhance PSII efficiency and electron transport rates under stress, thereby improving the photosynthetic performance of tomato genotypes.

G. Principal component analysis

The Principal Component Analysis (PCA) under normal and stressed conditions provided insights into the relationships between photosynthetic traits.

Under normal conditions (A), Component 1 explained 55% of the total variance, while Component 2 contributed an additional 28%. Traits such as Y(NPQ)-T, Y(NPQ)-A, Fv/Fm-T, Fv/Fm-G, and ETR-T were clustered together along the positive axis of Component 1, indicating a strong positive association among them. Conversely, Y(NO)-A and Y(NO)-G were positioned on the negative side of both components, suggesting a negative relationship with PSII efficiency and regulated energy dissipation parameters. These results highlight the coordination of energy dissipation, electron transport, and PSII efficiency under optimal conditions.

Under stressed conditions (B), the variance explained by Component 1 decreased to 46.1%, while Component 2 accounted for 27.3%. Y(II)-T, ETR-T, and ETR-A were strongly grouped along the positive axis of Component 1, showing their close relationship under stress. Traits such as Fv/Fm-A and Fv/Fm-G shifted closer to Y(NPQ)-A, suggesting a more significant role for regulated energy dissipation in maintaining PSII efficiency under stress. Y(NO)-A and Y(NO)-G remained negatively associated with most other traits, reflecting their detrimental impact under stress conditions.

Overall, the PCA revealed that while energy dissipation and electron transport remain tightly linked under both conditions, stress induces a shift in trait relationships, emphasizing the increased reliance on regulated energy dissipation mechanisms to sustain photosynthetic performance.

CONCLUSIONS

These findings underscore the importance of PSII efficiency and energy dissipation balance in determining heat tolerance in tomato. The identification of tolerant genotypes provides a valuable resource for breeding programs aimed at developing climate-resilient cultivars capable of maintaining productivity under rising global temperatures.

FUTURE SCOPE

This study establishes key photosynthetic traits (Fv/Fm, Y(II), Y(NPQ), Y(NO), and ETR) as reliable markers of tomato heat stress tolerance. Future work should integrate these traits with molecular, biochemical, and metabolomic studies to uncover thermotolerance mechanisms. Promising genotypes identified here can be utilized in breeding programs supported by QTL mapping, GWAS, and genomic selection. Stage-specific and field-based evaluations, including combined stress scenarios, will strengthen trait validation. Overall, integrating physiological screening with precision phenotyping will accelerate the development of climate-resilient tomato cultivars.

REFERENCES

Allakhverdiev, S. I., Kreslavski, V. D., Klimov, V. V., Los, D. A., Carpentier, R. & Mohanty, P. (2008). Heat stress: an overview of molecular responses in photosynthesis. *Photosynthesis Research*, *98*(1), 541-550.

Arya, S., Sahoo, R. N., Sehgal, V. K., Bandyopadhyay, K., Rejith, R. G., Chinnusamy, V., ... & Manjaiah, K. M. (2024). High-throughput chlorophyll fluorescence image-based phenotyping for water deficit stress tolerance in wheat. *Plant Physiology Reports*, 1-16.

Calanca, P. P. (2016). Effects of abiotic stress in crop production. In *Quantification of climate variability, adaptation and mitigation for agricultural sustainability* (pp. 165-180). Cham: Springer International Publishing.

Calzadilla, P. I., Carvalho, F. E. L., Gomez, R., Neto, M. L. & Signorelli, S. (2022). Assessing photosynthesis in plant systems: A cornerstone to aid in the selection of resistant and productive crops. *Environmental and Experimental Botany*, *201*, 104950.

Dasgan, H. Y., Dere, S., Akhoundnejad, Y. & Arpaci, B. B. (2021). Effects of high-temperature stress during plant cultivation on tomato (*Solanum lycopersicum* L.) fruit nutrient content. *Journal of Food Quality*, *2021*(1), 7994417.

Estrada, F., Escobar, A., Romero-Bravo, S., González-Talice, J., Poblete-Echeverría, C., Caligari, P. D. & Lobos, G. A. (2015). Fluorescence phenotyping in blueberry breeding for genotype selection under drought conditions, with or without heat stress. *Scientia Horticulturae*, *181*, 147-161.

Falcioni, R., Chicati, M. L., de Oliveira, R. B., Antunes, W. C., Hasanuzzaman, M., Demattê, J. A. & Nanni, M. R. (2024). Decreased Photosynthetic Efficiency in *Nicotiana tabacum* L. under Transient Heat Stress. *Plants*, *13*(3), 395.

Guidi, L. & Calatayud, A. (2014). Non-invasive tools to estimate stress-induced changes in photosynthetic performance in plants inhabiting Mediterranean areas. *Environmental and Experimental Botany*, *103*, 42-52.

He, L., Yu, L., Li, B., Du, N. & Guo, S. (2018). The effect of exogenous calcium on cucumber fruit quality, photosynthesis, chlorophyll fluorescence, and fast chlorophyll fluorescence during the fruiting period under hypoxic stress. *BMC Plant Biology*, *18*, 1-10.

Ivanov, A. G., Velitchkova, M. Y., Allakhverdiev, S. I. & Huner, N. P. (2017). Heat stress-induced effects of photosystem I: an overview of structural and functional responses. *Photosynthesis Research*, *133*, 17-30.

Jiang, Y., Feng, X., Wang, H., Chen, Y. & Sun, Y. (2021). Heat-induced down-regulation of photosystem II protects photosystem I in honeysuckle (*Lonicera japonica*). *Journal of Plant Research*, *134*, 1311-1321.

Li, Z., Ji, W., Hong, E., Fan, Z., Lin, B., Xia, X. & Zhu, X. (2023). Study on heat resistance of peony using photosynthetic indexes and rapid fluorescence kinetics. *Horticulturae*, *9*(1), 100.

Muhammad, I., Shalmani, A., Ali, M., Yang, Q. H., Ahmad, H. & Li, F. B. (2021). Mechanisms regulating the dynamics of photosynthesis under abiotic stresses. *Frontiers in Plant Science*, *11*, 615942.

Pan, C., Ahammed, G. J., Li, X. & Shi, K. (2018). Elevated CO_2 improves photosynthesis under high temperature by attenuating the functional limitations to energy fluxes, electron transport and redox homeostasis in tomato leaves. *Frontiers in Plant Science*, *9*, 1739.

Perera-Castro, A. V. & Flexas, J. (2023). The ratio of electron transport to assimilation (ETR/AN): underutilized but essential for assessing both equipment's proper performance and plant status. *Planta*, *257*(2), 29.

Roach, T. & Krieger-Liszkay, A. (2014). Regulation of photosynthetic electron transport and photoinhibition. *Current Protein and Peptide Science*, *15*(4), 351-362.

Shanker, A. K., Amirineni, S., Bhanu, D., Yadav, S. K., Jyothilakshmi, N., Vanaja, M. & Singh, V. K. (2022). High-resolution dissection of photosystem II electron transport reveals differential response to water deficit and heat stress in isolation and combination in pearl millet [*Pennisetum glaucum* (L.) R. Br.]. *Frontiers in Plant Science*, *13*, 892676.

Singh, J. & Thakur, J. K. (2018). Photosynthesis and abiotic stress in plants. *Biotic and Abiotic Stress Tolerance in Plants*, 27-46.

Tikkanen, M., Grieco, M., Nurmi, M., Rantala, M., Suorsa, M. & Aro, E. M. (2012). Regulation of the photosynthetic apparatus under fluctuating growth

light. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *367*(1608), 3486-3493.
Zahra, N., Hafeez, M. B., Ghaffar, A., Kausar, A., Al Zeidi, M., Siddique, K. H. & Farooq, M. (2023). Plant photosynthesis under heat stress: Effects and management. *Environmental and Experimental Botany*, *206*, 105178.

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