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Multifaceted Responses to Heat Stress in Plants: A Review of the Morpho-physiological, Biochemical and Anatomical Changes

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Authors' contributions

This work was carried out in collaboration among all authors. All authors read and approved the final manuscript.

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Review Article

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ABSTRACT

Heat stress, a significant abiotic factor, adversely affects plant growth and productivity by disrupting various physiological and biochemical processes. Plants, being immobile, respond to environmental changes through alterations in gene expression, metabolism, and growth dynamics. Elevated temperatures, exceeding the threshold for heat tolerance, negatively influence critical

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functions such as photosynthesis, respiration, water balance, and membrane stability. Root development is particularly sensitive to heat stress, resulting in reduced root mass and impaired water and nutrient uptake. Photosynthetic capacity diminishes due to decreased chlorophyll content and impaired photochemical reactions, leading to reduced biomass and yield. Heat stress impacts plant water status by disturbing hydraulic conductivity and increasing membrane permeability, leading to dehydration and a decline in water potential. This stress reduces membrane stability, resulting in electrolyte leakage and cellular damage. It also induces the production of reactive oxygen species (ROS), which requires the activation of antioxidant enzymes to minimize oxidative stress. Also, to maintain osmotic balance and enhance stress tolerance, plants accumulate osmolytes such as proline. Additionally, anatomical adaptations in leaves, stems, and roots, such as changes in stomatal density, xylem vessel size, and gas exchange patterns, highlight the plant's strategies to cope with heat stress. Understanding these varied responses is crucial for developing strategies to enhance crop resilience in the face of increasing global temperatures and climate change.

Keywords: Heat stress; roots; photosynthesis; membrane; ROS; xylem vessels.

1. INTRODUCTION

Plants being immobile gets significantly affected by various abiotic environmental factors leading to a variety of responses, including alterations in biological processes such as gene expression and cell metabolism, as well as impacting overall growth and development [1]. These abiotic stress factors comprise of extreme temperature variations, drought, flooding, salinity, metal exposure, and nutrient deficiencies [2]. Each of these stresses causes different types of responses in plants [3]. Since the beginning of 21st century, a noticeable rise in ambient temperatures has been recorded, with projections indicating a continued upward trend as a result of climate change [4]. An elevation in temperature that surpasses the threshold level by even one degree is classified as heat stress [5]. Each degree centigrade increases in average growing season temperature reduces crop yield by 17% [6]. Heat stress affects plant growth throughout all developmental stages, with the threshold for heat tolerance varying considerably at different growth phases. This stress negatively influences several physiological processes, including photosynthesis, respiration, water balance, and membrane stability [7]. Growth inhibition due to excessive heat occurs from its thermal impact on various physiological and developmental processes [8]. A noticeable hindrance in plant growth, initiated by a specific daily mean temperature, is termed as the threshold temperature, which varies depending on the plant species and the genotypes within each species [9]. A rise in temperature lead to dehydration of cells, resulting in diminished cell size and reduction in growth [10]. Thus, heat stress emerges as a critical abiotic factor that disrupts plant growth and development by impairing physiological and biochemical processes, ultimately posing a significant threat to global agricultural productivity and food security. A detailed outline showing effects of heat stress on various physiological and biochemical parameters is shown in Fig. 1.

2. IMPACT OF HEAT STRESS ON ROOT ARCHITECTURE AND FUNCTION

In general, root growth tends to be more sensitive to heat stress as compared to shoot growth due to the fact that roots typically have a lower optimal temperature for growth. As a result, a reduction in root mass may lead to a reduction in shoot mass [11]. Heat stress impacts root growth in plants by limiting root elongation, reducing biomass allocation, altering root architecture, and impairing water and nutrient absorption. It disrupts cellular homeostasis, damages root meristematic tissues, and affects hormone signalling pathways critical for root development [12]. A rise in temperature would restrict root development and modify the architecture of the root system, ultimately diminishing the of root: shoot ratio. Numerous studies have verified that heat stress has a detrimental effect on both root architecture and root mass and these alterations in root structure also adversely impact the absorption of water and nutrients by the plants [13-15]. Under heat stress, water loss is exacerbated due to increased transpiration, while reduced root elongation and impaired membrane stability limit the plant's ability to absorb water effectively [16]. The decreased functionality of nutrient uptake proteins and the inhibition of carbohydrate transport from shoots to roots further hinder

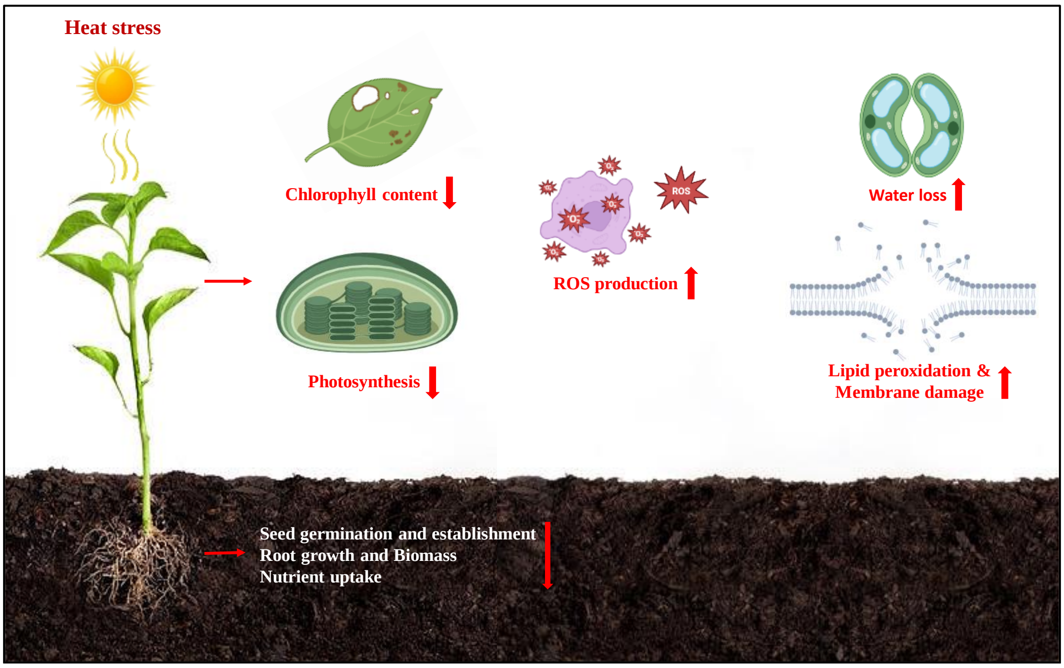

Fig. 1. Effects of heat stress on various physio-biochemical aspects of plants

nutrient absorption and assimilation [17]. Also, heat stress damages root meristematic cells and disrupts ion homeostasis, reducing the uptake of essential nutrients like nitrogen, potassium, and phosphorus. These physiological and biochemical disruptions culminate in diminished fresh and dry weight of plants and hamper overall plant growth, including shoot development [18].

3. HEAT STRESS-INDUCED ALTERATIONS IN PHOTOSYNTHETIC CAPACITY AND EFFICIENCY

Photosynthesis, a crucial process in green plants [19], becomes particularly vulnerable during stressful conditions, especially affecting the photochemical reactions occurring in the thylakoid membranes within the chloroplast stroma [20]. Elevated temperatures impact the photosynthetic process by altering the rate of chemical reactions and changing the structural organization. High temperatures can denature or deactivate critical enzymes involved in the Calvin cycle, such as Rubisco, reducing the efficiency of carbon fixation [21]. Additionally, elevated temperatures impair the thylakoid membrane's structure, where the light-dependent reactions of photosynthesis occur. This leads to a reduction in the photosynthetic electron transport chain's efficiency, ultimately decreasing the production of ATP and NADPH required for carbon assimilation [22] (Fig. 2). High temperatures can cause both reversible and irreversible changes in the physiochemical properties and functional structure of the thylakoid membrane [23]. In plants, exposure to climatic stress typically leads to a decrease in chlorophyll concentrations and a reduction in the photochemical reactions of thylakoid proteins. This decrease in chlorophyll pigments directly impacts the photosynthetic activity of crops [24]. Heat stress can destabilize the thylakoid membrane structure, causing disorganization of these protein complexes, which are crucial for capturing light energy and facilitating electron transfer during photosynthesis [25].

Temperature fluctuations have been reported to significantly influence photosynthesis in crops, primarily due to the diminished presence of chlorophyll [24]. This indicates that changes in temperature can directly affect the plant's ability to photosynthesize efficiently, which is crucial for its growth and development [19]. The chlorophyll levels in plants depend on a delicate equilibrium between synthesis and degradation. When subjected to heat stress, this equilibrium is disrupted, resulting in reduced chlorophyll concentration in the plants [21]. Heat stress induces leaf senescence by disrupting chloroplasts and causing damage to chlorophyll through both direct and indirect mechanisms, including photo-oxidation. These processes

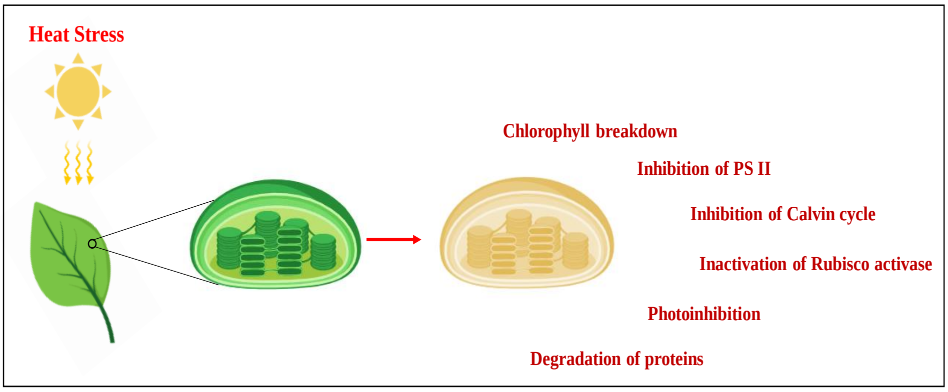

Fig. 2. Representation of the effects of heat stress on chloroplast structure and function

significantly inhibit the photosynthetic capacity of the plant, leading to a reduction in biomass and seed yield [26]. Heat stress reduces photosynthetic capacity by impairing photosystems, degrading chlorophyll, and disrupting enzymatic processes in the Calvin cycle. This leads to reduced energy production and carbon fixation, causing visible effects on leaves, such as chlorosis, wilting, and a decline in growth [27].

4. IMPACT OF HEAT STRESS ON PLANT WATER STATUS AND HYDRATION DYNAMICS

The plant water status is often regarded as the most critical variable under changing ambient temperatures [28]. Under heat stress, hydraulic conductivity tends to increase, leading to enhanced aquaporin activity [29]. This makes the membrane more permeable, facilitating greater water flow through its pores [30]. However, this heightened membrane permeability can have adverse effects, such as dehydration of flowers and grains [31]. This dehydration occurs because the increased permeability disrupts the gradient that drives water flow into flowers or grains, especially under heat stress conditions [32]. Typically, during the daytime, increased transpiration rates and higher stomatal conductance lead to water deficiency in plants, resulting in reductions in water potential. This water deficit can perturb various physiological processes within the plant [33]. An increase in leaf temperature leads to a decrease in water potential and relative water content in leaves, ultimately resulting in reduced photosynthetic productivity [34]. In field conditions, the crucial physiological indicator is leaf water potential, which is affected by both soil water status and the demand for evaporation. Water loss occurs more frequently during daylight hours compared to nighttime because higher stomatal conductance followed by increased transpiration lowers the water potential [35]. Thus, heat stress negatively impacts plant water status by increasing transpiration rates and reducing water uptake which leads to cellular dehydration and disruption of metabolic activities in tissues [8].

5. IMPACT OF HEAT STRESS ON MEMBRANE STABILITY AND ELECTROLYTE LEAKAGE

Among all components of a plant cell, plasma membranes are considered the most heat-sensitive, as they are primary sites for injury [36]. When plants experience heat injury, the membranes of sensitive plants undergo a phase transition from a solid-gel structure to a more flexible liquid-crystalline structure [18]. This transition can occur due to the denaturation of proteins or an increase in unsaturated fatty acids, resulting in increased fluidity of the membrane [37]. Under stress conditions, the extent of injury can be assessed by measuring the loss of membrane integrity, which is reflected in the leakage of organic and inorganic ions from the cell [38]. Electrolytic leakage, a measure of membrane stability, is influenced by various factors including plant or tissue age, sampling organ, developmental stage, growing season, and plant species [39]. Membrane stability is typically higher in mature tissues compared to younger ones, and different plant species exhibit varying resistance, with some, like desert or heat-tolerant species, showing better tolerance to heat-induced membrane damage [40]. The membrane stability index (MSI) is regarded as a crucial tool for assessing the heat tolerance potential of a specific genotype [41]. This is because membrane damage tends to escalate with higher stress levels, making MSI an effective indicator of heat tolerance in plants [42]. Heat-induced electrolyte leakage and reduced membrane stability index and RWC has been reported in various crops including cowpea [43], barley [44], sorghum [45], potato and cotton [46], mustard [47], soybean [48], rice [27,31], tomato [49] , mungbean [50], and wheat [51].

6. IMPACT OF HEAT STRESS ON YIELD ATTRIBUTES

Abiotic stress occurring later in the reproductive stage can lead to source limitation for seed yield by triggering leaf shedding and/or accelerating maturity [52]. However, yield compensation can occur through both increased branching and enhanced efficiency of pod retention [53]. Flowering represents the most sensitive stage to temperature stress damage, likely attributable to its vulnerability during pollen development, anthesis, and fertilization, ultimately resulting in reduced crop yield [39]. An increase in temperature have been noted to stimulate plant development while concurrently inducing flower abortion, leading to significant yield losses [54]. Temperatures exceeding 27°C led to a decrease in the number of siliquae on the main shoot and the number of seeds per siliqua, potentially attributed to increased floral sterility [55]. Similarly, floral sterility in canola was observed, along with the development of flowers into seedless parthenocarpic fruits and/or flower abortion under heat [56]. Terminal heat stress in mustard during the flowering and siliqua formation stages led to a significant decrease in the number of siliquae per plant, primarily due to increased instances of flower and siliqua abscission [57].

7. IMPACT OF HEAT STRESS ON OXIDATIVE STRESS AND ANTIOXIDANT ENZYME ACTIVITY

Heat stress has the potential to disrupt enzymes and metabolic pathways, leading to the buildup of harmful reactive oxygen species, including singlet oxygen ($^1O_2$), superoxide radical ($O_2^{\bullet-}$), hydrogen peroxide (H_2O_2), and hydroxyl radical ($OH^{\bullet}$), which are associated with oxidative stress [58]. While the reaction centres of photosystem I and photosystem II in chloroplasts are the primary sites of ROS production, these are also generated in peroxisomes and mitochondria [59]. Hydroxyl radicals have the ability to interact with various biomolecules including pigments, proteins, lipids, and DNA, affecting nearly all components of cells [60]. Similarly, singlet oxygen has the capability to directly oxidize proteins, polyunsaturated fatty acids, and DNA [61]. Under stress conditions, the generation of ROS surpasses the ability of the antioxidant system to neutralize them, leading to significant cellular harm and mortality [62]. In these instances, external protective agents and genetic modification of defensive genes can enhance the defense mechanism, a phenomenon also observed in oxidative damage caused by heat stress [63]. Plants have developed several mechanisms to tolerate heat stress, and one such mechanism involves reducing oxidative stress through the production of antioxidants and increasing total antioxidant capacity [64]. Superoxide dismutase (SOD) is typically regarded as the primary defense mechanism against oxidative stress [65]. This enzyme facilitates the conversion of $O_2^{\bullet-}$ into either molecular oxygen (O_2) or H_2O_2 [66]. H_2O_2 is further broken down by peroxidase (POX) and catalase (CAT). While both enzymes are involved in degrading H_2O_2, CAT primarily focuses on neutralizing the excess ROS during stressful conditions [67]. In contrast, POX plays a more nuanced role in finely modulating ROS signalling [60]. The plant's ability to combat oxidative stress is partially dependent on the induction of SOD activity, which in turn leads to the upregulation of other downstream antioxidative enzymes [68]. CAT and SOD are the most active enzymes in response to environmental stressful conditions [65] (Fig. 3).

8. IMPACT OF HEAT STRESS ON OSMOLYTE ACCUMULATION

Heat stress trigger significant modifications in plant biochemistry and metabolism [69]. In order to enhance plant resilience against abiotic stresses and uphold a high RWC, plants may accumulate various low molecular mass compounds known collectively as compatible solutes, including proline [70]. These solutes serve multiple protective roles within heat-stressed cells [71]. Proline, classified as a non-essential amino acid due to its ability to be synthesized by plants, possesses an imino group (–NH) instead of the typical amino group ($–NH_2$) [72]. It is known as one of the most extensively studied thermoprotectants observed in response to stress and serves as an osmolyte for osmotic adjustment [73]. Additionally, proline aids in stabilizing various structures, including proteins and membranes, within plant cells under

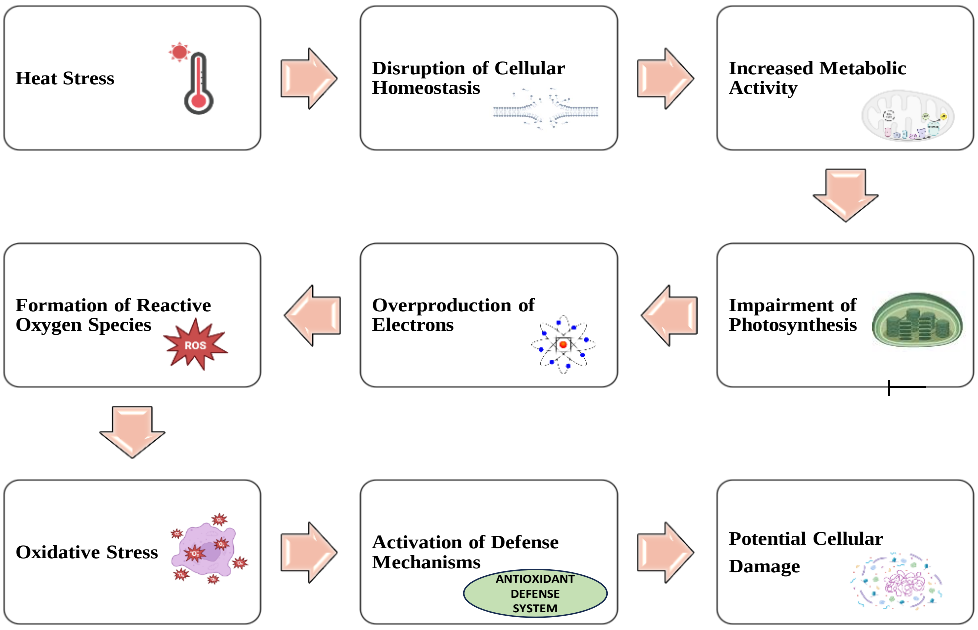

Fig. 3. Effects of heat stress on oxidative stress and antioxidant defense mechanism

stressful conditions across multiple crop species [74]. The most significant accumulation of proline happens in late sown crops, primarily due to an increase in γ-glutamyl kinase activity and a decline in proline oxidase activity [75]. This increase in proline levels under heat stress is linked to the regulation of cellular osmotic balance [63]. Additionally, the exogenous application of biostimulants can trigger physiological activities and activate osmotic adjustment compounds in plants, including proline, total soluble sugars, and amino acids [76]. Plants employ a rapid proline accumulation strategy as a means to mitigate water loss during adverse conditions, thereby aiding in the maintenance of cellular water equilibrium [77].

9. IMPACT OF HEAT STRESS ON WATER LOSS AND GAS EXCHANGE DYNAMICS

An overall strategy for coping with heat stress involves minimizing cell size, expanding the diameter of xylem vessels, boosting stomatal density to enhance water transportation, and decreasing transpiration [78]. Stomata, which are small pores found in the epidermis of plants, are flanked by two guard cells that regulate the opening and closing of the pore to manage the exchange of carbon dioxide and water vapor on the leaf surface [79]. Typically, plants experiencing heat stress tend to have increased stomatal density and smaller stomata, aiming to enhance their efficiency in resisting heat [80]. Various studies demonstrate that elevated temperatures lead to an increase in stomatal density, which helps alleviate cell and tissue damage caused by heat stress. Additionally, there's a concurrent occurrence of stomatal opening under heat stress, indicating a dynamic regulatory mechanism to cope with elevated temperatures [81-83].

Stomata play a pivotal role in facilitating the exchange of gases between the atmosphere and the interior of the leaf [79]. Consequently, the behaviour of stomata is of utmost importance for the uptake of carbon dioxide to fulfil photosynthetic requirements, as well as for regulating leaf water loss, which directly influences processes such as evaporative cooling, nutrient uptake, and the overall water status of the plant [84]. This highlights the critical role that stomatal behaviour plays in the physiological processes essential for plant growth and survival [85-87]. In leaf stress physiology, a notable area where heat and drought present conflicting signals is in stomatal regulation [88]. Drought conditions prompt stomatal closure to minimize transpiration and preserve water, while heat induces stomatal opening to facilitate increased leaf cooling [89,90]. Transpiration is a key component of a plant's cooling system. Just like sweating in animals, transpiration helps dissipate heat from the plant's surface [91]. As water evaporates from the leaves, it absorbs heat energy, which cools the plant which is particularly important during hot weather when temperatures rise above the plant's ideal range [92].

Stomatal properties, including stomatal size, pore area, and stomatal density, play a crucial role in determining stomatal conductance (gs) in leaves [93]. Stomatal conductance reflects the leaf's capacity for exchanging water vapor with the atmosphere and is influenced by the number of stomata per unit leaf area and the size of the pore opening [84]. Consequently, changes in leaf morphology and functional responses to external weather conditions can affect stomatal conductance, consequently impacting photosynthesis and overall crop performance [94]. Higher stomatal conductance values at elevated temperatures are advantageous for plant performance because they alleviate diffusional limitations on CO_2 entering the leaf. This increase in intercellular CO_2 concentration helps mitigate the adverse effects of enhanced photorespiration under warmer leaf temperatures [95].

Moreover, higher stomatal conductance facilitates increased transpiration and evaporative cooling, thereby helping to maintain leaf temperature closer to the optimal level for photosynthesis (Topt), consequently reducing photorespiratory processes [96]. However, the elevated water loss resulting from higher gs can compromise the water status of the plant which, depending on the severity of water stress, may adversely affect plant performance and growth. Variations in stomatal anatomical features or regulation of stomatal pore width can impact gas exchange in various ways and may be influenced by genetic factors and growth conditions, including evaporative demand [97,98] and carbon dioxide levels [99,100].

10. IMPACT OF HEAT STRESS ON PLANT ANATOMICAL STRUCTURES

Heat stress leads to notable changes in the anatomy of leaves, stems, and roots [101-103]. In response to adverse environmental conditions, plants undergo diverse cellular and metabolic changes, potentially enhancing their survival capacity under stress [104]. Previous research has demonstrated that a rise in temperature lead to an increase in both outside-xylem hydraulic conductance and mesophyll conductance, thereby enhancing gas-phase conductance [105]. This augmentation in conductance can help maintain turgor pressure within guard cells and consequently result in higher transpiration rates [106]. A rise in hydraulic demand could lead to either larger channels, increased density of channels, or greater xylem size within the stem's cross-sectional area. This adaptive response allows them to enhance their capacity for transporting water, thereby better meeting the heightened demand for water caused by the elevated temperatures [107]. In seasonal climates, temperature is a crucial factor influencing the vascular development of woody plants [108]. An earlier increase in temperature can stimulate cambial activity, leading to an earlier onset of the growth season. In woody plants, elevated temperatures can either increase, or decrease the diameter of tracheid [109]. The response is species-specific. The increased diameter of xylem vessels or tracheid enhances the efficiency of water transport within the plant [110]. In herbaceous plants like potatoes, elevated temperatures may result in enlarged and deformed vessel cells, as well as improper phloem division. These alterations can have adverse effects on crop yields, as the enlargement of xylem negatively impacts the phloem by exerting mechanical pressure on its cells, leading to a reduction in sugar translocation [111]. Increase in the size of epidermal cells and the pith area was observed in mungbean genotype under heat stress [112]. Reduction in cell size serve to minimize excessive water loss, resulting in an increase in stomatal density and enlarged xylem vessels in plants experiencing heat stress [113].

11. CONCLUSION

Heat stress negatively affects various physiological, biochemical, and anatomical processes in plants, leading to detrimental impacts on growth, development, and yield. The disruption of root structure, photosynthetic efficiency, water status, membrane stability, and enzyme activity under elevated temperatures shows the complexity of plant responses to thermal stress. Additionally, heat-induced alterations in stomatal behaviour, gas exchange, and osmolyte accumulation further complicate the plant's ability to maintain optimal growth under such conditions. The adverse effects on yield attributes underscore the vulnerability of crops to rising temperatures, especially during critical reproductive stages. Understanding these mechanisms is crucial for developing strategies to enhance plant resilience, such as breeding heat-tolerant varieties or employing agronomic practices that mitigate the impact of heat stress. These insights contribute to addressing the broader challenge of sustaining agricultural productivity in the face of global climate change.

DISCLAIMER (ARTIFICIAL INTELLIGENCE)

Author(s) hereby declares that NO generative AI technologies such as Large Language Models (ChatGPT, COPILOT, etc.) and text-to-image generators have been used during the writing or editing of this manuscript.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

REFERENCES

1. Zhang Y, Xu J, Li R, Ge Y, Li Y, Li R. Plants' response to abiotic stress: Mechanisms and strategies. International Journal of Molecular Sciences. 2023;24(13):10915.
2. Imran QM, Falak N, Hussain A, Mun BG, Yun BW. Abiotic stress in plants; stress perception to molecular response and role of biotechnological tools in stress resistance. Agronomy. 2021;11(8):1579.
3. Radha B, Sunitha NC, Sah RP, TP MA, Krishna GK, Umesh DK, Thomas S, Anilkumar C, Upadhyay S, Kumar A, Ch LN M. Physiological and molecular implications of multiple abiotic stresses on yield and quality of rice. Frontiers in Plant Science. 2023;13:996514.
4. Pandey GC, Mehta G, Sharma P, Sharma V. Terminal heat tolerance in wheat: An overview. Journal of Cereal Research. 2019;11(1).
5. Hasanuzzaman M, Nahar K, Alam MM, Roychowdhury R, Fujita M. Physiological, biochemical, and molecular mechanisms of heat stress tolerance in plants. International journal of molecular sciences. 2013;14(5):9643-84.
6. Lobel GH, Asner PK. Effect of high temperature on crop growth and yield. Prog. Agric. Eng. Sci. 2003;49:23-99.
7. Ahmad M, Imtiaz M, Shoib Nawaz M, Mubeen F, Imran A. What did we learn from current progress in heat stress tolerance in plants? Can microbes be a solution?. Frontiers in Plant Science. 2022;13:794782.
8. Fahad S, Bajwa AA, Nazir U, Anjum SA, Farooq A, Zohaib A, Sadia S, Nasim W, Adkins S, Saud S, Ihsan MZ. Crop production under drought and heat stress: plant responses and management options. Frontiers in plant science. 2017;8:1147.
9. Waqas MA, Wang X, Zafar SA, Noor MA, Hussain HA, Azher Nawaz M, Farooq M. Thermal stresses in maize: Effects and management strategies. Plants. 2021;10(2):293.
10. Parthasarathi T, Firdous S, David EM, Lesharadevi K, Djanaguiraman M. Effects of high temperature on crops. InAdvances in plant defense mechanisms; 2022. IntechOpen.
11. Mishra N, Jiang C, Chen L, Paul A, Chatterjee A, Shen G. Achieving abiotic stress tolerance in plants through antioxidative defense mechanisms. Frontiers in Plant Science. 2023;14:1110622.
12. Mishra S, Spaccarotella K, Gido J, Samanta I, Chowdhary G. Effects of heat stress on plant-nutrient relations: An update on nutrient uptake, transport, and assimilation. International Journal of Molecular Sciences. 2023;24(21):15670.
13. Wahid A, Gelani S, Ashraf M, Foolad MR. Heat tolerance in plants: an overview. Environmental and experimental botany. 2007;61(3):199-223.
14. Huang B, Rachmilevitch S, Xu J. Root carbon and protein metabolism associated with heat tolerance. Journal of experimental botany. 2012;63(9):3455-65.
15. Koevoets IT, Venema JH, Elzenga JT, Testerink C. Roots withstanding their environment: exploiting root system architecture responses to abiotic stress to improve crop tolerance. Frontiers in plant science. 2016;7:1335.
16. Giri A, Heckathorn S, Mishra S, Krause C. Heat stress decreases levels of nutrient-uptake and-assimilation proteins in tomato roots. Plants. 2017;6(1):6.
17. Huang D, Wu W, Abrams SR, Cutler AJ. The relationship of drought-related gene expression in Arabidopsis thaliana to hormonal and environmental factors. Journal of experimental Botany. 2008;59(11):2991-3007.
18. Nadeem M, Li J, Wang M, Shah L, Lu S, Wang X, Ma C. Unraveling field crops sensitivity to heat stress: Mechanisms, approaches, and future prospects. Agronomy. 2018;8(7):128.

19. Muhammad I, Shalmani A, Ali M, Yang QH, Ahmad H, Li FB. Mechanisms regulating the dynamics of photosynthesis under abiotic stresses. Frontiers in plant science. 2021;11:615942.
20. Jha Y. Regulation of photosynthesis under stress. InImproving Stress Resilience in Plants. Academic Press. 2024;35-48.
21. Hu S, Ding Y, Zhu C. Sensitivity and responses of chloroplasts to heat stress in plants. Frontiers in Plant Science. 2020;11:375.
22. Scafaro AP, Posch BC, Evans JR, Farquhar GD, Atkin OK. Rubisco deactivation and chloroplast electron transport rates co-limit photosynthesis above optimal leaf temperature in terrestrial plants. Nature Communications. 2023;14(1):2820.
23. Petrova N, Paunov M, Stoichev S, Todinova S, Taneva SG, Goltsev V, Krumova S. Thylakoid membrane reorganization, induced by growth light intensity, affects the plants susceptibility to drought stress. Photosynthetica. 2020;58:369-78.
24. Sherin G, Aswathi KR, Puthur JT. Photosynthetic functions in plants subjected to stresses are positively influenced by priming. Plant Stress. 2022;4:100079.
25. Bernfur K, Rutsdottir G, Emanuelsson C. The chloroplast-localized small heat shock protein Hsp21 associates with the thylakoid membranes in heat-stressed plants. Protein Science. 2017;26(9):1773-84.
26. Farooq M, Nadeem F, Gogoi N, Ullah A, Alghamdi SS, Nayyar H, Siddique KH. Heat stress in grain legumes during reproductive and grain-filling phases. Crop and Pasture Science. 2017;68(11):985-1005.
27. Wang Y, Lei B, Deng H, Liu X, Dong Y, Chen W, Lu X, Chen G, Zhang G, Tang W, Xiao Y. Exogenous Abscisic Acid Affects the Heat Tolerance of Rice Seedlings by Influencing the Accumulation of ROS. Antioxidants. 2023;12(7):1404.
28. Simbeye DS, Mkiramweni ME, Karaman B, Taskin S. Plant water stress monitoring and control system. Smart Agricultural Technology. 2023;3:100066.
29. Byrt CS, Zhang RY, Magrath I, Chan KX, De Rosa A, McGaughey S. Exploring aquaporin functions during changes in leaf water potential. Frontiers in Plant Science. 2023;14:1213454.
30. Kapilan R, Vaziri M, Zwiazek JJ. Regulation of aquaporins in plants under stress. Biological research. 2018;51:1-1.
31. Xu Y, Chu C, Yao S. The impact of high-temperature stress on rice: Challenges and solutions. The Crop Journal. 2021;9(5):963-76.
32. Gautam A, Pandey AK. Aquaporins responses under challenging environmental conditions and abiotic stress tolerance in plants. The Botanical Review. 2021;87(4):467-95.
33. Vesala T, Sevanto S, Grönholm T, Salmon Y, Nikinmaa E, Hari P, Hölttä T. Effect of leaf water potential on internal humidity and CO2 dissolution: reverse transpiration and improved water use efficiency under negative pressure. Frontiers in plant science. 2017;8:54.
34. Li Y, Song X, Li S, Salter WT, Barbour MM. The role of leaf water potential in the temperature response of mesophyll conductance. New phytologist. 2020;225(3):1193-205.
35. Dayer S, Herrera JC, Dai Z, Burlett R, Lamarque LJ, Delzon S, Bortolami G, Cochard H, Gambetta GA. Nighttime transpiration represents a negligible part of water loss and does not increase the risk of water stress in grapevine. Plant, Cell & Environment. 2021;44(2):387-98.
36. Cano-Ramirez DL, Carmona-Salazar L, Morales-Cedillo F, Ramírez-Salcedo J, Cahoon EB, Gavilanes-Ruíz M. Plasma membrane fluidity: an environment thermal detector in plants. Cells. 2021;10(10):2778.
37. Savchenko GE, Klyuchareva EA, Abramchik LM, Serdyuchenko EV. Effect of periodic heat shock on the inner membrane system of etioplasts. Russian journal of plant physiology. 2002;49:349-59.
38. Hatsugai N, Katagiri F. Quantification of plant cell death by electrolyte leakage assay. Bio-protocol. 2018;8(5):e2758-.
39. Liu H, Li Y, Peng T, Xue S. Transmembrane potential, an indicator in situ reporting cellular senescence and stress response in plant tissues. Plant Methods. 2023;19(1):27.
40. Niu Y, Xiang Y. An overview of biomembrane functions in plant responses to high-temperature stress. Frontiers in plant science. 2018;9:915.
41. Hongal DA, Raju D, Kumar S, Talukdar A, Das A, Kumari K, Dash PK, Chinnusamy V, Munshi AD, Behera TK, Dey SS. Elucidating the role of key physio-biochemical traits and molecular network conferring heat stress tolerance in cucumber. Frontiers in Plant Science. 2023;14:1128928.

42. Waqas MA, Wang X, Zafar SA, Noor MA, Hussain HA, Azher Nawaz M, Farooq M. Thermal stresses in maize: effects and management strategies. Plants. 2021;10(2):293.
43. Thiaw S, Hall AE. Comparison of selection for either leaf-electrolyte-leakage or pod set in enhancing heat tolerance and grain yield of cowpea. Field Crops Research. 2004;86(2-3):239-53.
44. Wahid A, Shabbir A. Induction of heat stress tolerance in barley seedlings by pre-sowing seed treatment with glycinebetaine. Plant Growth Regulation. 2005;46:133-41.
45. Takele A. Differential responses of electrolyte leakage and pigment compositions in maize and sorghum after exposure to and recovery from pre-and post-flowering dehydration. Agricultural Sciences in China. 2010;9(6):813-24.
46. Loka DA, Oosterhuis DM. Physiological and biochemical responses of two cotton (*Gossypium hirsutum* L.) cultivars differing in Thermotolerance to high night temperatures during Anthesis. Agriculture. 2020;10(9):407.
47. Rai H, Gupta RN, Sah SB, Dahiya OS. Seed characters based identification key for important varieties of Indian mustard (*Brassica juncea* L. Czern and Coss). Journal of Pharmacognosy and Phytochemistry. 2020;9(6):276-9.
48. Bian XH, Li W, Niu CF, Wei W, Hu Y, Han JQ, Lu X, Tao JJ, Jin M, Qin H, Zhou B. A class B heat shock factor selected for during soybean domestication contributes to salt tolerance by promoting flavonoid biosynthesis. New Phytologist. 2020;225(1):268-83.
49. Alsamir M, Mahmood T, Trethowan R, Ahmad N. An overview of heat stress in tomato (*Solanum lycopersicum* L.). Saudi journal of biological sciences. 2021;28(3):1654-63.
50. Priya M, Bhardwaj A, Jha UC, HanumanthaRao B, Prasad PV, Sharma KD, Siddique KH, Nayyar H. Investigating the influence of elevated temperature on nutritional and yield characteristics of mung bean (*Vigna radiata* L.) genotypes during seed filling in a controlled environment. Frontiers in Plant Science. 2023;14:1233954.
51. Aouz A, Khan I, Chattha MB, Ahmad S, Ali M, Ali I, Ali A, Alqahtani FM, Hashem M, Albishi TS, Qari SH. Silicon induces heat and salinity tolerance in wheat by increasing antioxidant activities, photosynthetic activity, nutrient homeostasis, and osmo-protectant synthesis. Plants. 2023;12(14):2606.
52. Krishnan P, Ramakrishnan B, Reddy KR, Reddy VR. High-temperature effects on rice growth, yield, and grain quality. Advances in agronomy. 2011;111:87-206.
53. Das R, Biswas S. Influence of abiotic stresses on seed production and quality. InSeed Biology Updates; 2022. IntechOpen.
54. Singh M, Rathore SS, Raja P. Physiological and stress studies of different rapeseed-mustard genotypes under terminal heat stress. International Journal of Genetic Engineering and Biotechnology. 2014;5(2):133-42.
55. Morrison MJ, Stewart DW. Heat stress during flowering in summer Brassica. Crop science. 2002;42(3):797-803.
56. Young LW, Wilen RW, Bonham-Smith PC. High temperature stress of Brassica napus during flowering reduces micro-and megagametophyte fertility, induces fruit abortion, and disrupts seed production. Journal of experimental botany. 2004;55(396):485-95.
57. Sinaki JM, Heravan EM, Rad AS, Noormohammadi GH, Zarei GH. The effects of water deficit during growth stages of canola (*Brassica napus* L.).
58. Sachdev S, Ansari SA, Ansari MI, Fujita M, Hasanuzzaman M. Abiotic stress and reactive oxygen species: Generation, signaling, and defense mechanisms. Antioxidants. 2021;10(2):277.
59. Foyer CH, Hanke G. ROS production and signalling in chloroplasts: cornerstones and evolving concepts. The Plant Journal. 2022;111(3):642-61.
60. Gupta S, Agarwal VP, Gupta NK. Efficacy of putrescine and benzyladenine on photosynthesis and productivity in relation to drought tolerance in wheat (*Triticum aestivum* L.). Physiology and Molecular Biology of Plants. 2012;18:331-6.
61. Kesawat MS, Satheesh N, Kherawat BS, Kumar A, Kim HU, Chung SM, Kumar M. Regulation of reactive oxygen species during salt stress in plants and their crosstalk with other signaling molecules—Current perspectives and future directions. Plants. 2023;12(4):864.
62. Jomova K, Raptova R, Alomar SY, Alwasel SH, Nepovimova E, Kuca K, Valko M. Reactive oxygen species, toxicity, oxidative stress, and antioxidants: Chronic diseases and aging. Archives of toxicology. 2023;97(10):2499-574.

63. Hasanuzzaman M, Bhuyan MB, Zulfiqar F, Raza A, Mohsin SM, Mahmud JA, Fujita M, Fotopoulos V. Reactive oxygen species and antioxidant defense in plants under abiotic stress: Revisiting the crucial role of a universal defense regulator. Antioxidants. 2020;9(8):681.
64. Lukić N, Kukavica B, Davidović-Plavšić B, Hasanagić D, Walter J. Plant stress memory is linked to high levels of anti-oxidative enzymes over several weeks. Environmental and Experimental Botany. 2020;178:104166.
65. Ighodaro OM, Akinloye OA. First line defence antioxidants-superoxide dismutase (SOD), catalase (CAT) and glutathione peroxidase (GPX): Their fundamental role in the entire antioxidant defence grid. Alexandria journal of medicine. 2018;54(4):287-93.
66. Mehta SK, Gowder SJ. Members of antioxidant machinery and their functions. Basic principles and clinical significance of oxidative stress. 2015;11:59-85.
67. Shu-Hsien H, Chih-Wen YU, Lin CH. Hydrogen peroxide functions as a stress signal in plants. Botanical Bulletin of Academia Sinica. 2005;46.
68. Abedi T, Pakniyat H. Antioxidant enzyme changes in response to drought stress in ten cultivars of oilseed rape (Brassica napus L.). Czech Journal of Genetics and Plant Breeding. 2010;46(1):27-34.
69. Dorado JF, Pinto G, Monteiro P, Chaves N, Alías JC, Rodrigo S, Camisón Á, Solla A. Heat stress and recovery effects on the physiology and biochemistry of *Castanea sativa* Mill. Frontiers in Forests and Global Change. 2023;5:1072661.
70. Spormann S, Nadais P, Sousa F, Pinto M, Martins M, Sousa B, Fidalgo F, Soares C. Accumulation of proline in plants under contaminated soils—are we on the same page?. Antioxidants. 2023;12(3):666.
71. Zulfiqar F, Akram NA, Ashraf M. Osmoprotection in plants under abiotic stresses: New insights into a classical phenomenon. Planta. 2020;251(1):3.
72. Kavi Kishor PB, Hima Kumari P, Sunita MS, Sreenivasulu N. Role of proline in cell wall synthesis and plant development and its implications in plant ontogeny. Frontiers in plant science. 2015;6:544.
73. Hayat S, Hayat Q, Alyemeni MN, Wani AS, Pichtel J, Ahmad A. Role of proline under changing environments: a review. Plant signaling & behavior. 2012;7(11):1456-66.
74. Hosseinifard M, Stefaniak S, Ghorbani Javid M, Soltani E, Wojtyla Ł, Garnczarska M. Contribution of exogenous proline to abiotic stresses tolerance in plants: a review. International Journal of Molecular Sciences. 2022;23(9):5186.
75. Khan AD, Ahmad M, Shah MK, Ahmed M. Performance of wheat genotypes for Morpho-Physiological traits using multivariate analysis under terminal heat stress. Pak. J. Bot. 2020;52(6):1981-8.
76. Islam MJ, Ryu BR, Azad MO, Rahman MH, Rana MS, Lim JD, Lim YS. Exogenous putrescine enhances salt tolerance and ginsenosides content in Korean ginseng (*Panax ginseng* Meyer) sprouts. Plants. 2021;10(7):1313.
77. Sihag P, Kumar U, Sagwal V, Kapoor P, Singh Y, Mehla S, Balyan P, Mir RR, Varshney RK, Singh KP, Dhankher OP. Effect of terminal heat stress on osmolyte accumulation and gene expression during grain filling in bread wheat (*Triticum aestivum* L.). The plant genome. 2024;17(1):e20307.
78. Bañon S, Fernandez JA, Franco JA, Torrecillas A, Alarcón JJ, Sánchez-Blanco MJ. Effects of water stress and night temperature preconditioning on water relations and morphological and anatomical changes of Lotus creticus plants. Scientia Horticulturae. 2004;101(3):333-42.
79. Harrison EL, Arce Cubas L, Gray JE, Hepworth C. The influence of stomatal morphology and distribution on photosynthetic gas exchange. The Plant Journal. 2020;101(4):768-79.
80. Gu K, Geng XM, Yue Y, Ozaki Y. Contribution of keeping more stable anatomical structure under high temperature to heat resistance of Rhododendron seedlings.
81. Shen J, Diao W, Zhang L, Acharya BR, Wang M, Zhao X, Chen D, Zhang W. Secreted peptide PIP1 induces stomatal closure by activation of guard cell anion channels in Arabidopsis. Frontiers in Plant Science. 2020;11:1029.
82. Taratima W, Chuanchumkan C, Maneerattanarungroj P, Trunjaruen A, Theerakulpisut P, Dongsansuk A. Effect of heat stress on some physiological and anatomical characteristics of rice (*Oryza sativa* L.) cv. KDML105 callus and seedling. Biology. 2022;11(11):1587.
83. Yang X, Han Y, Hao J, Qin X, Liu C, Fan S. Exogenous spermidine enhances the photosynthesis and ultrastructure of lettuce seedlings under high-temperature stress. Scientia Horticulturae. 2022;291:110570.

84. Moore CE, Meacham-Hensold K, Lemonnier P, Slattery RA, Benjamin C, Bernacchi CJ, Lawson T, Cavanagh AP. The effect of increasing temperature on crop photosynthesis: from enzymes to ecosystems. Journal of experimental botany. 2021;72(8):2822-44.
85. Lawson T, Matthews J. Guard cell metabolism and stomatal function. Annual review of plant biology. 2020;71(1):273-302.
86. Lawson T, von Caemmerer S, Baroli I. Photosynthesis and stomatal behaviour. Progress in botany 72. 2011;265-304.
87. Matthews JS, Lawson T. Climate change and stomatal physiology. Annual plant reviews online. 2018;713-52.
88. Marchin RM, Backes D, Ossola A, Leishman MR, Tjoelker MG, Ellsworth DS. Extreme heat increases stomatal conductance and drought-induced mortality risk in vulnerable plant species. Global change biology. 2022;28(3):1133-46.
89. Arve LE, Torre S, Olsen JE, Tanino KK. Stomatal responses to drought stress and air humidity. InAbiotic stress in plants-Mechanisms and adaptations; 2011. IntechOpen.
90. Agurla S, Gahir S, Munemasa S, Murata Y, Raghavendra AS. Mechanism of stomatal closure in plants exposed to drought and cold stress. Survival strategies in extreme cold and desiccation: adaptation mechanisms and their applications. 2018;215-32.
91. Qingjuan Y, Wanyi S, Ziqi L. A microclimate model for plant transpiration effects. Urban Climate. 2022;45:101240.
92. Graamans L, van den Dobbelsteen A, Meinen E, Stanghellini C. Plant factories: Crop transpiration and energy balance. Agricultural Systems. 2017;153:138-47.
93. Allen MT, Pearcy RW. Stomatal behavior and photosynthetic performance under dynamic light regimes in a seasonally dry tropical rain forest. Oecologia. 2000;122:470-8.
94. Bertolino LT, Caine RS, Gray JE. Impact of stomatal density and morphology on water-use efficiency in a changing world. Frontiers in plant science. 2019;10:225.
95. Sadok W, Lopez JR, Smith KP. Transpiration increases under high-temperature stress: Potential mechanisms, trade-offs and prospects for crop resilience in a warming world. Plant, Cell & Environment. 2021;44(7):2102-16.
96. Urban J, Ingwers MW, McGuire MA, Teskey RO. Increase in leaf temperature opens stomata and decouples net photosynthesis from stomatal conductance in *Pinus taeda* and *Populus deltoides* x nigra. Journal of experimental botany. 2017;68(7):1757-67.
97. Aliniaeifard S, van Meeteren U. Natural variation in stomatal response to closing stimuli among Arabidopsis thaliana accessions after exposure to low VPD as a tool to recognize the mechanism of disturbed stomatal functioning. Journal of Experimental Botany. 2014;65(22):6529-42.
98. Giday H, Fanourakis D, Kjaer KH, Fomsgaard IS, Ottosen CO. Threshold response of stomatal closing ability to leaf abscisic acid concentration during growth. Journal of Experimental Botany. 2014; 65(15):4361-70.
99. Ainsworth EA, Rogers A. The response of photosynthesis and stomatal conductance to rising [CO2]: mechanisms and environmental interactions. Plant, cell & environment. 2007;30(3):258-70.
100. Berry JA, Beerling DJ, Franks PJ. Stomata: Key players in the earth system, past and present. Current opinion in plant biology. 2010;13(3):232-9.
101. Purnama PR, Purnama ER, Manuhara YS, Hariyanto S, Purnobasuki H. Effect of high temperature stress on changes in morphology, anatomy and chlorophyll content in tropical seagrass *Thalassia hemprichii*. AACL Bioflux. 2018;11(6):1825-33.
102. Shen HF, Zhao B, Xu JJ, Liang W, Huang WM, Li HH. Effects of heat stress on changes in physiology and anatomy in two cultivars of Rhododendron. South African Journal of Botany. 2017;112:338-45.
103. Bano C, Amist N, Singh NB. Morphological and anatomical modifications of plants for environmental stresses. Molecular plant abiotic stress: Biology and biotechnology. 2019;29-44.
104. Teixeira EI, Fischer G, Van Velthuizen H, Walter C, Ewert F. Global hot-spots of heat stress on agricultural crops due to climate change. Agricultural and Forest Meteorology. 2013;170:206-15.
105. Flexas J, Scoffoni C, Gago J, Sack L. Leaf mesophyll conductance and leaf hydraulic conductance: an introduction to their measurement and coordination. Journal of Experimental Botany. 2013;64(13):3965-81.
106. Buckley TN, John GP, Scoffoni C, Sack L. How does leaf anatomy influence water transport outside the xylem?. Plant Physiology. 2015;168(4):1616-35.

107. Medeiros JS, Ward JK. Increasing atmospheric [CO2] from glacial to future concentrations affects drought tolerance via impacts on leaves, xylem and their integrated function. New Phytologist. 2013;199(3):738-48.
108. Prislan P, Gričar J, de Luis M, Smith KT, Čufar K. Phenological variation in xylem and phloem formation in Fagus sylvatica from two contrasting sites. Agricultural and forest meteorology. 2013;180:142-51.
109. Begum S, Nakaba S, Yamagishi Y, Yamane K, Islam MA, Oribe Y, Ko JH, Jin HO, Funada R. A rapid decrease in temperature induces latewood formation in artificially reactivated cambium of conifer stems. Annals of botany. 2012;110(4):875-85.
110. Haworth M, Elliott-Kingston C, McElwain JC. Co-ordination of physiological and morphological responses of stomata to elevated [CO2] in vascular plants. Oecologia. 2013;171:71-82.
111. Paul S, Das MK, Baishya P, Ramteke A, Farooq M, Baroowa B, Sunkar R, Gogoi N. Effect of high temperature on yield associated parameters and vascular bundle development in five potato cultivars. Scientia Horticulturae. 2017;225:134-40.
112. Iqbal U, Hameed M, Ahmad F. Structural and functional traits underlying the capacity of Calotropis procera to face different stress conditions. Plant Physiology and Biochemistry. 2023;203:107992.
113. Chen WR, Zheng JS, Li YQ, Guo WD. Effects of high temperature on photosynthesis, chlorophyll fluorescence, chloroplast ultrastructure, and antioxidant activities in fingered citron. Russian Journal of Plant Physiology. 2012;59:732-40.

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