

New Insights into the Effects of Heat Stress on Plant Growth and Development - A Review

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ABSTRACT

Heat stress, a large consequence of global warming and climate change, is a serious threat to plant survival, agricultural productivity, and global food security. As one of the most important abiotic stresses, heat stress negatively impacts crop growth and development, yield, and quality. Global temperatures are expected to increase by 1.8 to 4.0 °C by the end of the 21st century, making it important to understand how plants respond to elevated temperatures. A proper understanding of how heat stress affects plant structure, physiology, and underlying molecular and biochemical processes, as well as the mechanisms involved in plant adaptation, is necessary for the development of effective mitigation and management strategies. To increase plant tolerance to heat stress, several methods have been used, including improved agronomic practices and crop improvement through conventional and modern breeding. This review summarizes current knowledge regarding the impacts of heat stress on plant morphological traits and physiological functions, molecular and biochemical pathways, and focuses on the integrated view of key adaptive mechanisms that allow plants to withstand high-temperature stress.

Keywords- adaptation, biochemical, heat stress, molecular, plant physiology, and morphology.

I. INTRODUCTION

Climate change, as the most important implication of changes in weather patterns, temperature, and rainfall, has a profound impact on plant growth and development, crop yield, and quality [1]. Each plant species has a certain range of minimum and maximum temperatures at different stages of development, and temperatures outside this optimal range limit growth and development [2]. Heat stress, one of the most critical outcomes of climate change and a major abiotic stress, has a negative impact on all stages of plant growth from germination to harvest. By disrupting important metabolic processes, heat stress severely compromises crop productivity and is a serious threat to global food security [3].

The heat stress inhibits the growth, development, and yield of plants all over the world through its influence on morphological, physiological, phenological, biochemical, and molecular processes. This stress leads to protein denaturation and accumulation of membrane systems, thereby inactivating enzymes that reduce plant productivity, especially seed productivity in legumes [4]. In addition, heat stress affects important physiological and metabolic functions such as germination, respiration, and photosynthesis, and disrupts hormonal balance; therefore, its effects adversely impact plant health and yield formation [5]. Also, heat stress interferes with plant water balance and other physiological processes, leading

to decreases in nutrient uptake, root biomass, and chlorophyll content, membrane permeability, and eventually, plant biomass and yield [6].

The heat stress has diverse impacts on plant growth and development in diverse crops. High temperature has a potent effect on morphological and anatomical structure, physiological and biochemical activities, reducing fruit production and quality in fruit crops [7]. During the reproductive stage, heat stress causes disturbance of development in terms of decreasing pollen viability, shortening the grain-filling stage, and modifying starch synthesis, which leads to a threat to grain composition and yield stability [8]. In tomato, the stages of flower development of floral organs (especially anthers) are more sensitive to high temperatures than female floral parts. Exposure to heat stress in these stages leads to morphological changes in flowers and to poor fruit setting, resulting in high yield losses [9].

Similarly, the potato should be grown and developed under 15 to 20 °C and beyond 24 °C, yields are lower because of the change in morphology as well as physiological activity of the plant [10]. The effect of heat stress in soybeans is to reduce the seed germination, photosynthetic efficiency, and transpiration and to elevate the vulnerability of pathogenic infection, which leads to reduced yield and economic returns [11]. It has been established that high temperatures are a major inhibitor of primary shoot and secondary root growth in ginseng [12]. Heat stress in *Arabidopsis thaliana* has had an adverse effect, especially on reproductive processes, which causes extreme decreases in the size of plants and other growth parameters [13].

The review summarizes the existing studies on the impact of high-temperature stress on plant growth and development with a specific focus on plant morphology, physiology, and metabolomic responses. It is crucial to know how heat stress can impact the performance of plants, especially at critical developmental stages, to reduce the maximum heat-related injury and enhance the tolerance of plants to heat in a warming global climate.

II. IMPACT OF HEAT STRESS ON THE MORPHOLOGY AND ANATOMY OF PLANTS

Plant morphology is very sensitive to heat stress, which eventually limits the yield of plants as well as their productivity [4]. The heat stress influences negatively the plant morphology at all its growth and development stages, but the severity of its impact depends on the developmental stage. As an example, when the seeds are germinating, increased temperature may cause abnormal growth and development or even end growth and development, which is based on the intensity of the stress and the species of the plant [5]. Heat stress on fruit crops causes a compromise in the morphology and anatomy of fruits, which decreases the amount and quality of fruits [14].

The plant organs vary in terms of their heat stress sensitivity, with roots being the most sensitive. Root mass and action tend to be reduced by heat stress [6]. Studies of morphological traits in plants indicate that the sensitivity of root traits and functions to elevated temperatures is higher than that of other growth parameters, such as germination rate, stem length, and total biomass [15]. In potatoes, the ambient temperature greater than 25 °C leads to excessive shoot elongation, increased lateral branching, and smaller leaves, and at the same time inhibits tuber and stolon development [10]. In maize, heat stress reduces leaf area, delays flowering, and reduces plant height, thereby affecting the structure and function of chloroplasts [16]. Similarly, in soybeans, extended exposure to high temperatures delays seed germination, reduces seed vigour, and reduces grain size, milling quality, and dry matter accumulation [11].

In addition to being observed at the organ level, heat stress is known to affect plants at the cellular and subcellular levels. There are also structural changes in principal cellular organelles, such as changes in chloroplast shape, alterations in stromal lamellae, changes in vacuole size, and changes in photosystem II integrity, which all impair plant growth and productivity [9]. In addition to this, heat stress changes cell wall arrangement and biogenesis, retards stem elongation, and extensively suppresses genes related to cell wall development, which once again restrains plant development at elevated temperatures [12].

III. IMPACT OF HEAT STRESS ON THE PLANT PHYSIOLOGY

Heat stress is one of the most significant abiotic stress factors that has a negative impact on a large spectrum of physiological processes in plants, such as photosynthesis, respiration, water relations, and reproductive development [5]. Heat stress alters the plant growth rates, reproduction, and fitness by interfering with these processes, posing a threat to the stability of the ecosystem and crop productivity in a global rise in temperature [17]. Among the primary physiological consequences of heat stress are a decrease in photosynthetic capacity, which is largely linked to a decrease in chlorophyll content and malfunctioning of photochemical reactions, leading to lower biomass accumulation and yield. Heat stress also has serious impacts on plant water status. High temperatures interfere with hydraulic conductivity, enhance membrane permeability and decrease water potential, which results in dehydration and physiological imbalance [6]. Moreover, higher temperatures that are beyond the tolerance of a plant have negative effects on respiration and further weaken energy

metabolism. The effect of heat stress is that it affects the development of reproductive structures through the formation of structural abnormalities, decreasing photosynthetic efficiency, and retards growth by inhibiting seed growth. An increase in temperature during the period of seed filling interferes with biochemical activities, leading to low seed size and yield. Heat stress can significantly lower crop productivity, especially at stages, namely microsporogenesis and anthesis [2].

Heat stress has a serious negative effect on the rate of photosynthesis and the efficiency of photosystem II (Fv/Fm) in plant species, but the stomatal conductance and transpiration responses differ across species [15]. Also, heat stress reduces net carbon fixation, membrane stability, and water balance [18]. Any injury in the structure of chloroplasts increases the rate of leaf senescence and decreases biomass accretion [19]. The reproductive processes are particularly susceptible, as heat stress reduces pollen fertility and negatively affects fruit and seed development, and the level of damage varies by species and stress intensity [20].

At the biochemical level, high temperatures and associated oxidative stress result in the damage of proteins and photosynthetic pigments, especially of photosystem II. The enzymes are vital, including RuBisCO, which denatures and decreases the catalytic capacity, raising the formation of reactive oxygen species (ROS), including superoxide radicals and hydrogen peroxide. Such alterations not only drain light energy of conversion to chemical energy and fixation of carbon, but also favor the oxidative damage of cellular structures, especially chloroplasts and photosynthetic pigments [21].

High temperatures, such as 45 °C, are extremely high for embryonic cells and may have a negative impact on germination and seed development. At these reproductive periods, e.g. flowering and grain filling, optimum temperatures are 12-22 °C and any 1 °C increase in average temperature may result in high yield losses [22].

Heat stress can also interfere with nutrient uptake, transport, and assimilation, and lower crop quality, especially in terms of nutritional value and phytochemical abundance necessary for human health [23]. Heat stress in maize affects respiration, stomatal conductance, transpiration rate, chlorophyll fluorescence, and chlorophyll content, resulting in decreased yield [24]. High temperatures in tomatoes cause slowing or complete inhibition of germination, disruption of water relations and membrane stability, and changes in metabolite profiles [25]. In the same way, high temperatures adversely affect chlorophyll content, osmotic potential, seed oil storage, flowering, seed production, and fertility in Indian mustard, thereby decreasing yield potential [26]. High temperatures above 25 °C in potatoes disrupt nutrient distribution, inhibit vegetative growth, and delay the initiation and growth of tubers [10].

IV. EFFECT OF HEAT STRESS ON PLANT MOLECULAR AND BIOCHEMICAL PROCESSES

The plant's molecular and biochemical processes are also affected by heat stress, along with other vital traits. Changes in biochemical behavior, in turn, adversely affect plant growth and development, resulting in decreased pollen viability, reduced grain-filling period, and reduced starch synthesis in the endosperm [8].

During growth and development under heat stress, plants show increased expression of heat shock proteins (HSPs) and other stress-related proteins, and the production of reactive oxygen species (ROS) is one of the main plant responses to heat stress [5]. High temperature may disrupt water relations and membrane stability in plants and regulate hormone and primary and secondary metabolite levels. The regulation of ROS accumulation and antioxidant activity is species- and stress-intensity-dependent, and increases and decreases have been reported [15].

Heat stress leads to decreased membrane stability, electrolyte leakage, cellular damage, and, by increasing oxidative stress, it damages cellular functions. In response, plants increase the osmotic balance and overall stress tolerance via activation of antioxidant enzymes and accumulation of osmolytes such as proline [6]. Furthermore, heat stress causes protein denaturation and membrane lipid fluidity, leading to an overproduction of ROS and inhibiting the performance of the soybean photosynthetic apparatus [11].

Heat stress negatively impacts plant growth and development by disrupting cellular and metabolic processes. Plants react to this stress by thermomorphogenesis and regulatory networks and adapt to the adverse conditions induced by global warming through balancing of growth and defense, a process essential to maintain plant functioning [27]. At the cellular level, temperature has the potential to modify the plant epigenome, metabolome, proteome, and transcriptional patterns [28]. Because plant growth and development require many enzymatic reactions, most of which are sensitive to temperature variations, a temperature rise will denature proteins and prevent cell division and elongation [29, 30].

Key damages associated with heat stress are protein denaturation, enzyme inactivation, increased fluidity of membrane lipids, reduced protein synthesis/degradation, and membrane integrity is interrupted, which ultimately can lead to chronic cell damage or death at high temperatures [9]. Furthermore, heat stress also changes the allocation of carbohydrates so that dry matter is directed towards stems instead of roots, stolons, and tubers, resulting in fewer tubers formed and lower overall yield. Under these conditions, there is a response of genes encoding glucose/sucrose enzymes and transporters to temperature fluctuations, which results in changes in carbohydrate allocation and disturbance of starch formation in tubers [10].

V. PLANT ADAPTATION MECHANISM TO HEAT STRESS

Plants have various strategies to deal with heat stress to keep membrane stability, scavenging reactive oxygen species (ROS), generating antioxidants and accumulating compatible solutes [25]. Heat stress alters the expression of many genes, proteins, and transcription factors, thereby altering the signaling pathways involved in stress tolerance. In the initial stage of heat stress, plants have mechanisms to regulate immunity and nutrient management to reduce stress damage [31]. To counteract the disturbances in biochemical and physiological processes induced by stress, tolerance mechanisms that involve proteins, ion transporters, osmoprotectants, antioxidants and components of the signaling cascades and transcriptional regulation are activated [32]. Perception and response to heat stress is a complex process involving the activation of multiple regulatory and signaling pathways to ultimately result in metabolic adjustments to ensure cell survival [33].

At the cellular and molecular levels, heat stress induces the biosynthesis of heat shock proteins (HSPs), which play a critical role in protein folding and protection against denaturation, while normal cellular protein synthesis is temporarily repressed [29]. Heat stress also stimulates the antioxidant systems and ROS-scavenging mechanisms to reduce oxidative damage [30]. In maize, heat stress causes the endoplasmic reticulum (ER)-localized unfolded protein response (UPR) that results in the activation of transcription factors that control stress-responsive genes. The hormone signaling and alternative RNA splicing are also stimulated, which contribute to thermotolerance [34]. In addition, plants have evolved complex gene networks by regulatory proteins, functional proteins and non-coding RNAs that coordinate protein and RNA stability, signal transduction, metabolite transport and antioxidant defenses under high temperature conditions [35].

Woody plants use some adaptive mechanisms to high-temperature stress by controlling the osmotic adjustment substances, the antioxidant enzyme activities, and transcriptional regulators. Their ability to sense heat stimuli and mount coordinated physiological, biochemical and genomic responses is crucial for survival under elevated temperatures [36]. Similarly, Indian mustard activates complex signaling pathways that result in cellular re-adjustments at the transcriptome, epigenome, proteome and metabolome levels in response to heat stress [26]. These responses are further supported by the activation of heat stress-responsive transcription factors that regulate thermotolerance-related gene expression [30]. Physiological and biochemical adjustments, signal transduction of heat, transcriptional regulation and synthesis of HSP contribute to plant heat stress tolerance [37].

Heat stress also causes excessive ROS generation, leading to membrane damage and enzymatic malfunction, ultimately suppressing plant growth and reducing maize grain yield [16]. Phytohormones, including indole acetic acid, gibberellic acid, abscisic acid, cytokinins, ethylene, salicylic acid, brassinosteroids, strigolactones and jasmonic acid, play a key role as endogenous signaling molecules coordinating physiological response, plant growth development and stress adaptation under heat stress [38]. Among these, a special mention has been made for salicylic acid in the regulation of developmental processes and induction of thermotolerance by complex chemical signaling interactions [39].

At the whole-plant level, heat stress induces morphological and anatomical adaptations in leaves, stems, and roots. These include changes in stomatal density, xylem vessel size and gas exchange characteristics, which together lead to an increased ability of the plant to cope with heat stress [6]. Furthermore, biotechnological approaches such as stress-related genes, proteomic and transcriptomic analyses, stay-green traits, and -omics-based approaches in transgenic plants are becoming increasingly recognized as promising approaches for developing climate-resilient chickpea cultivars [40].

VI. CONCLUSION AND FUTURE PERSPECTIVES

Climate change has emerged as a major environmental limitation on the growth, development, and productivity of plants through heat stress, which manifests at different levels of plant organization. Plants undergo adaptive modifications at the morphological and anatomical levels, including changes in leaf structure, stomatal density, vascular organization and root development to restrict water loss and enhance resource-use efficiency. Physiologically, heat stress interferes with photosynthesis, respiration, water relationships of plants, and hormonal balance, hence restraining growth and reproductive functions. Molecular and biochemical processes are also involved because the increase in temperature stimulates overproduction of reactive oxygen species, activation of antioxidant defense mechanisms, heat-shock proteins, gene expression, and complex signaling. A synchronized occurrence of these responses helps maintain cellular homeostasis and promote thermotolerance in plants. These processes are important to understand because of future breeding, biotechnology, and enhanced agronomic management of crops to develop heat-resilient crops as global temperatures continue to rise.

The future studies on heat stress tolerance should adopt concerted strategies by integrating traditional breeding and new biotechnological instruments to boost the ability of the plant to withstand increasing temperatures without compromising or reducing the yield. Further, more multi-layered mechanistic explanations of plants' responses to heat stress at the morphological, physiological, biochemical, and molecular scales are necessary to translate basic knowledge into real management and breeding practices. Molecular traits associated with heat stress responses are promising selection targets for breeding programs, supported by germplasm screening under field conditions and marker-assisted selection. Simultaneously, transgenic and genome-editing technologies, such as CRISPR-Cas9, as well as transcriptomic technologies,

such as RNA sequencing, will play an important role in deconstructing upstream regulatory networks that govern thermotolerance. The exogenous use of plant hormones and heat-protective compounds is also considered to be a complementary measure and is used to increase tolerance. The interdisciplinary and collaborative research is required to address some knowledge gaps, especially the effect of heat stress at different development phases of crops like rapeseed and Indian mustard. In general, developing sustainable and climate-resistant crop systems that will support future agricultural and nutritional demands entails a long-term, comprehensive and coordinated emphasis on genetics, physiology and crop control.

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Conflicts of Interest

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