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# Plant Responses to Heat Stress and Thermotolerance

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## ABSTRACT

With increasing challenges posed by climate change, it is predicted that warming, drought, floods and storm events will become even more frequent and severe and will further reduce crop yields, especially in the tropics and subtropics. Temperatures above the normal optimum cause heat stress (HS) at different levels in all living organisms. Heat stress disturbs cellular homeostasis and causes denaturation and dysfunction in numerous proteins, leading to severe retardation in growth, development and even death. In plants, the major sites of heat stress injury are the oxygen-evolving complex (OEC) along with linked biochemical reactions in photosystem II (PSII). Perception of heat stress by plants usually triggers sensors at the plasma membrane and causes a transient opening of $Ca^{2+}$ channels, possibly via modulation of membrane fluidity. Heat stress differentially influences the constancy of various proteins, membranes, RNA species and cytoskeleton structures and alters the efficiency of enzymatic reactions in the cell for which the major physiological processes obstacle and creates metabolic imbalance. The physio-morphological description under heat stress reveals reduced rate of germination percentage, plant emergence, abnormal seedlings, poor seedling vigor, reduced radical and plumule growth of germinated seedlings, which are the major impacts caused by heat stress documented in a variety of cultivated plant species. Heat spell at reproductive developmental stages declines flower production or flowers may not produce fruit or seed. In fact, the overproduction of reactive oxygen species (ROS) causing wide-ranging cellular damage and inhibition of physiological functions in plants. Nevertheless, stress positively leads to induce $Ca^{2+}$ influx and cytoskeletal restructuring, ensuing in the upregulation of mitogen activated protein kinases (MAPK) and calcium dependent protein kinase (CDPK). Signaling of these cascades at nuclear level that leads to the production of antioxidants and compatible osmolytes for cell water balance and osmotic adjustment. The sensing of high temperature and induction of signaling cascades are vital adaptive ladder in managing with challengers of heat stress. Significantly, thermotolerance mechanism is largely connected to display of heat shock response and this is completed by reprogramming of gene expression; thereby allowing plants to manage with heat stress. For that reason, greater emphasis on heat stress management is obligatory for heat tolerance features.

**Keywords:** Heat stress, Thermotolerance, Signaling, Tolerance

## INTRODUCTION

Heat stress is a major abiotic stress that influences plant morphology, physiology, reproduction and productivity worldwide. Plant growth and development inhabits repetitive biochemical reactions that are susceptible to temperature. Heat stress, singly or in combination with drought, is a common constraint during anthesis and grain filling stages in many cereal crops of temperate regions. Even a short period of heat stress can cause significant decrease in floral buds and flowers abortion though great variations in sensitivity within and among plant species and variety exist. The escalating drastic impacts of heat stress (HS) are putting global food production as well as nutritional security at high risk. The physiological and molecular responses to HS are vital to research areas. Molecular techniques are being adopted for producing heat tolerant crop plants. With a view to successfully produce heat stress tolerant crop varieties under the condition of global climate change, there is acute need of knowledge and investigations about heat stress

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tolerance mechanisms at physiological, biochemical and molecular levels. Plants continuously struggle to modify their metabolic process in many ways in response to heat stress, specifically by generating key solutes that leads to establish proteins and osmotic adjustment and re-establish the redox balance of cell and homeostasis by modifying the antioxidant system. There is an immense need to systematically assess wild species and accessions tolerating extreme degrees of higher temperatures. In that regard, searching for novel donors with high heat tolerance or escape mechanisms is of key importance.

Increased food demand with crops growing under sub-optimal conditions. Consequently, it is genuine to mention that during crop growth and development, temperature plays an important role in dry matter partitioning, transpiration [1,2] photosynthetic activity, respiration [3,4] and root and plant development [5].

In this article, the impacts of heat stress and tolerance at certain growth and developmental levels of plants and approaches that are used to improve heat stress tolerance in crop plants have been reviewed briefly, whereas detailing molecular advances made in heat stress research in the last several years are beyond the scope of this review article.

## HEAT STRESS RESPONSES

High temperature stress is a major environmental stress that influences physiology of plants and limits plant growth, metabolism and productivity worldwide. Heat stress differentially influences the constancy of various proteins, membranes, RNA species and cytoskeleton structures and alters the efficiency of enzymatic reactions in the cell for which the major physiological processes obstacle and creates metabolic imbalance [6-9]. The ideal conditions for plant growth and development generally occur within a different range of temperature [10] with low or high temperature (HT) reducing growth and developmental rates [11,12]. Similarly, heat stress has far-reaching effects on plant reproductive organ, seed weight and number of seeds. The increase in temperatures to crop-specific thresholds (for wheat 10-21°C) enhance the rate of grain filling by enhancing cell-division rates in the tissue of endosperm and increasing rates of metabolism [13]. Dry matter partitioning, which is the product of the movement of photosynthetic assimilate from source-sink organs, is enhanced between 10-30°C in winter-season cereals [14]. The devastating decrease in growth and development, harvest index (HI) and seed yield were found for various crops. The decline of grain number resulted from the impact of heat stress on meiosis followed by transfer of pollen during anthesis; growth of ovaries during pre-anthesis periods.

The regulation of heat-shock responses in inflorescence is largely uncharacterized [15,16] as male and female organs are most sensitive to extreme temperature, especially ≥ 30°C [17]. Besides these, heat stress damages both male and female gametophytes and as a consequence, there is decreased pollen viability, reduced pollen germination, pollen tube growth inhibition, stigma receptivity reduction and reduced ovule function, declined fertilization, limited embryogenesis, poor ovule viability, enhanced ovule abortion and a decrease in yield.

## PHYSIOLOGICAL RESPONSES

The physio-morphological characteristics under heat stress reduced germination percentage, plant emergence, abnormal seedlings, poor seedling vigor, reduced radical and plumule growth of geminated seedlings are major impacts caused by heat stress recognized in a variety of cultivated plant species [18-20]. Damage to leaf-tip and margins, rolling and drying of leaves and necrosis were observed in sugarcane due to heat stress [21]. Major alterations occur in chloroplasts like altered structural organization of thylakoids, loss of grana stacking and swelling of grana under heat stress [22,23]. Further, all through reproduction, a short period of heat stress can cause significant decrease in floral buds and flowers abortion although great variations in sensitivity within and among plant species and variety exists [24]. Even heat spell at reproductive developmental stages plant may produces no flowers or flowers may not produce fruit or seed [25,26].

### Membrane damage

Heat stress severely affects the structure and functions of the membrane, thereby increasing membranes fluidity due to denaturation of proteins and increased level of unsaturated fatty acids, causing a transition from solid gel to flexible crystalline liquid structure [27]. An electrolyte leakage value acts as a pointer of membrane injury that reflects stress-induced alterations. This has been used to evaluate the thermostability of membranes under heat stress [28]. The increased permeability and leakage of ions out of the cell has been used as a measure of cell membrane stability and as a screen test for heat stress tolerance [29]. This happens due to overproduction of reactive oxygen species (ROS) causing extensive cellular damage and inhibition of physiological processes in plants. Although anti-oxidative mechanisms would be an immediate endogenic choice of the plants to counter ROS production, this mechanism can be impaired by heat stress causing a rise in ROS intracellular concentration and an increase in the damage. Diverse metabolic pathways are reliant upon enzymes, which are responsive to various degrees of high temperatures. The accumulation of surplus and damaging ROS are most commonly singlet oxygen ($^1O_2$), superoxide radical ($O_2$), hydrogen peroxide ($H_2O_2$) and hydroxyl radical (OH) which are responsible for oxidative stress [30]. The major sites of ROS generation are the reaction centers of PSI and PSII in chloroplasts though ROS are also generated in other organelles, viz., peroxisomes and mitochondria [31]. Researchers identified tolerant genotypes that are proved to be more productive under extreme field stress conditions. The thermostability of

the membrane has been successfully employed to evaluate HS tolerance in several crops worldwide.

**Photosynthesis**

Photosynthesis is a vital process and is often restricted by various abiotic stresses especially under the heat stress and high light conditions. The negative impact of heat stress on plant growth and crop yield were mainly caused by its negative impacts on the photosynthetic process, which are the most thermosensitive aspects of plant functions [32]. The relative water content (RWC), chlorophyll content and PSII activity decreased under high light and heat co-stresses [33]. It is found that photosystem II is thought to be more highly responsive to HS or high light than photosystem I [34]. The photosynthetic process is very sensitive under HS conditions and reduction in chlorophyll contents might be one of the main reasons for the decline in photosynthesis, as an enzyme chlorophyllase helps in conversion of chlorophyll into phytol and chlorophyllide [35]. Remarkably, the increase in temperature from 18-33°C raises the rates of maintenance respiration by greater than 80% [36]. Under elevated temperatures, the rate of respiration measurement could be an appropriate pointer for stimulation of plant response to heat stress, as the rate of respiration rises much more than the rate of photosynthesis initially decreases [10].

**Water relations**

Heat stress influences plant-water relations due to the faster depletion of water from the soil. This largely affects the temperature of soil and the overall transpiration [37]. Heat stress evidently directly and indirectly affects plant functions and leads to osmotic adjustments by impaired photosynthesis, enhanced respiration, a decline in leaf osmotic potentials and decreased sugar concentration level [38]. Water loss during daytime was more common under heat stress, as of increased transpiration than night time, causing stress in snap bean (*Phaseolus vulgaris* L.) [39]. Under severe heat stress, high stomatal conductance boosts transpirational heat dissipation intolerant genotypes of chickpea as long as soil water is available [40].

## PLANT TOLERANCE TO HEAT STRESS

High temperature effects on plant growth and development are reliant upon plant species. With an increasing climate change scenario, there is a better possibility of air temperatures exceeding the optimum range for many species. Exposure of plants to temperature extremes at the onset of the reproductive stage has a major impact on fruit or grain production across all species. Heat stress disturbs cellular homeostasis and causes denaturation and dysfunction in many proteins, leading to severe retardation in growth, development and even death. In plants, the major sites of heat stress injury are the oxygen-evolving complex (OEC) along with associated biochemical reactions in photosystem II (PSII). Ultimately, efficiency of electron transport is reduced or altered affecting electron flow from OEC towards the acceptor side of PSII. These alterations affect the generation of ATP and the regeneration of Rubisco for carbon fixation [41].

## AVOIDANCE AND TOLERANCE MECHANISM

Plants show various survival mechanisms under heat stress, which include long-term morphological and phenological adaptations and short-term acclimation or avoidance mechanisms such as transpirational cooling, alteration of leaf orientation or changing of membrane lipid compositions. Stomatal closure and water loss reduction, enhanced trachomatous and stomatal densities and bigger xylem vessels are the main heat-induced features in crop plants [42]. The capability of the plant to develop and grow to produce economic yield under heat stress is known as thermotolerance. Some important mechanisms including ion transporter, late embryogenesis abundant proteins (LEA), antioxidant defense, osmoprotectants and some factors linked with signaling cascade and transcriptional controls are fundamentally important to respond to heat stress [43]. It has been observed that several tissues in crop plants show differences in terms of developmental exposure, complexity and responses toward the prevailing stress types [44]. These mechanisms help to regenerate homeostasis and to protect and repair damaged membranes and proteins [45].

The osmotic or ionic effects, or changes in temperature or membrane fluidity are the initial stress signals, which activate stress-responsive mechanisms to re-establish homeostasis and protect and repair damaged proteins and membranes. Heat stress accelerates the kinetic energy and movement of molecules across membranes thereby loosening chemical bonds within molecules of biological membranes. This makes the lipid bilayer of biological membranes more fluid by either denaturation of proteins or an increase in unsaturated fatty acids [46]. The tertiary and quaternary structures of membrane proteins are also distorted by heat stress. Such distortions develop the permeability of membranes negatively and as a result there is increased loss of electrolytes. The enhanced solute leakage is an indication of decreased cell membrane thermostability (CMT). This indirect measure of heat-stress tolerance in diverse plant species of electrolyte leakage is influenced by plant/tissue age, sampling organ, developmental stage, growing season, amount of hardening and plant species. Heat tolerance in some species does not correlate with the degree of lipid saturation.

The more fluidity of lipid bilayer under stress leads to the initiation of $Ca^{2+}$ influx and cytoskeletal restructuring, consequential in the upregulation of mitogen activated protein kinases (MAPK) and calcium dependent protein kinase (CDPK). Signaling of cascades at nuclear level shows the way to the production of antioxidants and compatible osmolytes for cell water balance and osmotic adjustment. Further, the production of ROS in the organelles (e.g. chloroplast and mitochondria) is of great significance for

signaling as well as production of antioxidants [47]. The antioxidant defense mechanism is a part of heat-stress adaptation and its strength is correlated with acquisition of thermotolerance [48]. In short, sensing of high temperature and induction of signaling cascades are important adaptive steps in coping with challenges of heat stress.

## HEAT SHOCK PROTEINS

Thermotolerance mechanism is mainly related to display of heat shock response and completed by reprogramming of gene expression and thereby allowing plants to cope with the heat stress. During heat stress, the mRNAs encoding non-heat stress induced proteins are destabilized. Using Arabidopsis mutants, it was shown that, apart from heat shock proteins (HSP32 and HSP101), ABA, ROS and SA pathways are involved in the development and maintenance of acquired thermotolerance [49].

Under heat stress, most of the stress proteins are soluble in water and consequently contribute to stress tolerance most probably via hydration of cellular structures [50,51] elucidated the fact that during heat stress HSPs, ranging in molecular mass from about 10 to 200 kDa, have chaperone like functions and are involved in signal transduction. The tolerance conferred by HSPs results in improved physiological phenomena such as photosynthesis, assimilate partitioning, water and nutrient use efficiency and membrane stability [52-54]. Interestingly, in certain crop genotypes or species, such improvements make plant growth and development possible under heat stress.

## CONCLUSION

In view of foreseen global warming, greater emphasis on heat stress management is obligatory for heat tolerance features. In addition, knowledge relating to molecular basis and mechanism of tolerance that includes molecular cloning and characterization of genes is considered to pave the way for engineering plants that can withstand heat stress.

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