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Heat Stress Responses in Plants: Unraveling the Thermal Sensory Machinery and Protective Strategies

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Abstract: *Repeated super high temperature events increasingly threaten global crop production and natural ecosystems. Spatial clustering of extreme heat in the dry season leads to chronic heat stress that disrupts iron metabolic pathways and fundamental plant physiological processes, from photosynthetic carbon assimilation to cellular membrane stability; such stress takes a toll on yield. Here, we propose a detailed review on the mechanisms of plant responses to high temperature stresses, including thermal sensing perception and associated acclimation response. Conceptually, thermal stress is characterized by changes in plasma membrane fluidity, leading to transient Ca^{2+} fluxes and the generation of reactive oxygen species (ROS). The events associated with those signaling platforms activate several cascade signal transduction networks, mainly consisting of mitogen-activated protein kinases (MAPKs) and calcium-dependent protein kinases (CDPKs), finally resulting in activation of heat shock factors (HSFs). Thus, plants activate the expression of molecular chaperones, specifically heat shock proteins (HSPs), in order to avoid protein denaturation and allow for correct folding. Simultaneously, a potent antioxidant system composed of both enzymatic (e.g., superoxide dismutase) and non-enzymatic metabolites is activated to counteract an overwhelming oxidative injury. Moreover, metabolic reprogramming establishes a reserve of compatible solutes that upholds osmolarity and membrane stability. Especially, for Indian agriculture, where staple crops like Triticum aestivum are under higher threat to terminal heat stress, this knowledge of the genetic and biochemical pathways becomes very important. This analysis underscores the vital need of molecular breeding strategies in conjunction with advanced biotechnological interventions to create thermotolerant cultivars raising a challenge towards global food security against the incessant advance of climate change*

Keywords: Thermotolerance, Heat Shock Proteins, Oxidative Stress, Signal Transduction, Photosynthesis

I. INTRODUCTION

Due to global climate change ambient temperature rises drastically which exposes agricultural ecosystems and natural flora to environmental stress, heat shock or elevated atmospheric temperatures. Heat stress, a temporary or permanent rise in temperature above the threshold optimum for plant growth, is one of the most formidable challenges to global food security. Just high temperature in some countries, like India with agriculture economy on the very top of the economy, such tremendously increased temperature anomalies will dramatically influence to be highly threatening for crops productivity at large scale like *Triticum aestivum* (wheat), *Oryza sativa* (rice). The disruption of physiological and biochemical processes is multi level and involves the heart of plant survival as well as reproductive success under heat stress. Due to their sessile nature, plants have no physical way of escaping thermal extremes and, therefore, they have evolved highly complex and elaborate temperature sensing mechanisms that are integrated with sophisticated signalling pathways allowing them to mount defensive responses. Understanding the underlying thermal mechano-sensory machinery and subsequent protective strategies is potentially instrumental for breeding climate resilient varieties that can maintain yield under suboptimal thermoperiods. The cellular effects of supra-optimal temperatures are immediate,

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for the kinetic energy will disrupt membrane fluidity and destabilise protein structures. At this stage, the disruption of physical structure activates a series of signal transduction pathways, triggered mainly by calcium ions (Ca^{2+}) and reactive oxygen species (ROS) as well as complex lipid signaling networks. All these main sensors convert the physical stimulus heat to molecular signals then it transmits via cellular pathways activating these HSFs or dormant transcription factors. At an elevated temperature, HSFs accumulate in the nucleus and bind to heat shock elements located within the promoter regions of heat-responsive genes. This genomic reprogramming leads to a systemic production of heat shock proteins (HSPs) which act as molecular chaperones, preventing protein aggregation, aiding in the refolding of denatured proteins, and degrading irreparably damaged cellular components. In addition, high temperature stress alone can greatly reduce photosynthetic efficiency via impairment in the oxygen-evolving complex of PSII and reduced RuBisCO affinity to CO_2. Plants use a powerful enzymatic and non-enzymatic antioxidant defense system to counteract the oxidative burst that occurs following electron transport chain leakage. Enzymes, such as superoxide dismutase (SOD), ascorbate peroxidase (APX), and catalase (CAT) cooperate with non-enzymatic metabolites including ascorbic acid and glutathione to clear damaging ROS mainly O_2^{2-} or H_2O_2. This chapter sheds light on the intricate multifactorial nature of heat stress responses in plants taking a critical view of the thermal sensors and trigger, signal transduction pathways, physiological abnormalities subsequently leading to protective global climate environments thriving mechanisms deployed by plant systems for attaining thermotolerance today. In addition, a recently published paper revealing the interactive crosstalk among these regulatory networks and phytohormone signaling (ABA-responsive genes) further elucidates their involvement in modulating adaptive metabolic adjustments.

Our knowledge about plant thermal sensing machinery

How plants sense the first increase in temperature is central to plant stress biology. Plants are immobile organisms, constantly subject to ambient temperature change without the option of relocation to more favorable environments. That puts the burden on them to develop a very complex thermal sensory system that is sensitive enough to pick up faint temperature variations and convert these physical sensations into strong biochemical signals. This sensory system is a integrated multi-dimensional network of membrane dynamics, secondary signaling and genomic reprogramming to maintain cell viability when exposed to thermal extremes. At the core of this thinking is acute alteration of plasma membrane lipids which later leads to rapid calcium-ion entry and acts as immediate signals for downstream signalling cascades (Bita & Gerats, 2013; Hasanuzzaman *et al*., 2013).

The major sensor of these temperature changes is in the cellular membrane. The lipid bilayer displays a precise compromise between fluidity and rigidity under optimal physiological conditions, which is essential for the function of membrane proteins. Nevertheless, supraoptimum heat increases the kinetic energy and hyperfluidizes the lipid matrix. This physical perturbation serves as an initial thermodetector, causing the activation of membrane-delimited calcium channels. Consequently, a fast and temporary influx of calcium ions from the apoplast and intracellular stores into the cytosol occurs. This unique calcium pulse acts as a fundamental unit of information, which is interpreted by specific Ca^{2+} sensor proteins, including calmodulin and calcium-dependent protein kinases that carry the signal onward to downstream effectors. Concurrently, hydrogen peroxide is quickly produced in the presence of an apoplastic enzyme: the plasma membrane NADPH oxidase RbohD that together with calcium transients regulates heat stress gene expression and increases general thermo-tolerance (Hayes *et al*., 2020).

The generation of reactive oxygen species complements these calcium-mediated signaling. Whereas it has been traditionally accepted that forms of reactive oxygen species (ROS) are commonly just harmful byproducts of metabolic activity, they act as important secondary messengers in the early stages of heat stress. A burst of superoxide radicals and hydrogen peroxide is generated when thermal stress disrupts electron transport chains in chloroplasts and mitochondria. Under tightly regulated levels, these molecules act as essential signaling moieties that traverse membranes to impact the redox state of particular cysteine residues on regulatory proteins. This ROS signal functions in close association with the signal to trigger intricate signal transduction pathways, especially of the Mitogen-Activated Protein Kinase cascade. These pathways ultimately converge to modulate the activity of heat-shock transcription factors, thus enabling the rapid expression of chaperones and genes related to thermotolerance (Saidi *et al*., 2010). Additional membrane-associated lipids, particularly phosphoinositides and phosphatidic acid, regulate this response by

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promoting structural lipid flipping and stabilizing the plasma membrane through the actions of phospholipases and translocases (Niu & Xiang, 2018).

These different signals-membrane fluidity, calcium flux and ROS signaling-all merge to activate transcriptional regulators like Heat Shock Factors. Activated HSFs then translocate to the nucleus, where they bind to highly conserved heat shock elements located in the promoter regions of heat-inducible genes. There goes massive transcription and translation of heat shock proteins, responsible molecular chaperones to prevent protein aggregation and help folding, this genomic reprogramming. This coordinates a standardized defensive reaction that is crucial for plant survival. Additionally to these transcriptional mechanisms, increasing data indicate that certain cytosolic calmodulin-binding domain-containing plasma membrane-localized channels act as precise molecular thermometers either regulating these early signaling cascades (Bokszczanin, 2013).

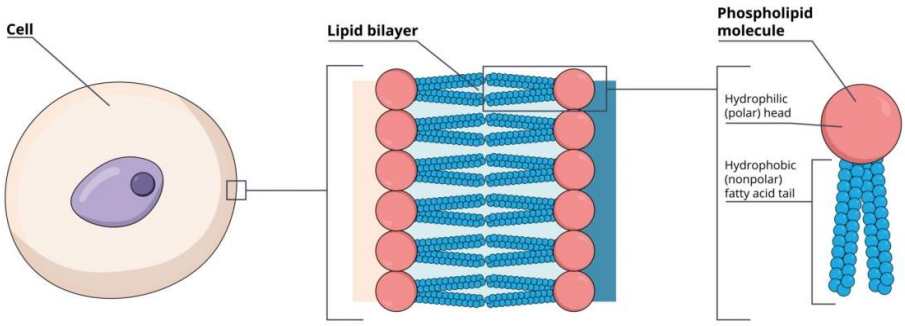
Nitric oxide has also been identified as an upstream modulator of these calcium-dependent pathways, which helps link the plant's diverse biochemical responses to thermal stress (Sun & Guo 2016).

Through combining physical membrane sensing with fast chemical signaling, plants can adjust their physiological responses and reduce the impacts of high temperatures. This complex machinery highlights the evolutionary spirit of plant systems, by changing from a simple perception of the environment to its second-order consequence: regulation of an extended thermotolerance. Deciphering this interaction between the earlier sensitivity to heat and downstream mechanisms of cellular protection, which is critical for understanding how to engineer heat-tolerant crop types in a warming climate, will remain an important area of active research. Additionally, the accumulation of class-specific organic solutes that assists in maintaining the integrity of membranes and stability of proteins (i.e., compatible osmolytes and secondary metabolites) complements these temporary signaling cascades to restore homeostasis (Guihur *et al*., 2022).

Membrane Fluidity And Calcium Ion Transduction

The cell membrane is the main sensor of temperature changes in plants. Lipid bilayer has a careful equilibrium of fluidity and rigidity in ideal situations. When heat is present, the kinetic energy of the lipid molecules increases to such an extent that it hyper-fluidizes the otherwise had lipid matrix. This structural change opens up the gate of cyclic nucleotide-gated channels and other calcium-permeable transporters, resulting in an instant influx into the cytosol (Liu *et al*., 2015; Pinto *et al*., 2015).

Figure 1: Cellular Membrane Lipid Bilayer Structural Architecture



This brief intracellular build-up of cytosolic calcium is enough to lead downstream signaling pathways since electrophysiological assays show saturation in < 10 minutes in Baird *et al*., 2021). In addition, the physical state of the lipid bilayer acts as a barrier mediating function with these channels being activated at lower membrane lipid saturation levels (Sharma *et al*., 2023). As described above modulators alter the fatty acid composition, and plants acclimated to it upregulate this process over long time, reprogramming the viscosity of the bilayer in order to shift its thermal activation

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point (increasing/ decreasing PT sensor vesicles threshold) (Lenzoni & Knight 2018). In addition to these homeostatic changes, cytoskeletal reorganization effectively provides a structural scaffold that connects membrane-bound sensors with the intracellular machinery which enables localized and specific control of signaling molecules under thermal stress (Awasthi *et al*., 2015).

Figure 2: Heat Stress Symptoms On Damaged Plant Leaves

This hyper-fluidity opens the calcium channels within membranes. Consequently, a fast and fluctuating entry of Ca^{2+} ions from the apoplast and intracellular organelles (such as vacuole and endoplasmic reticulum) into the cytosol is rapidly evoked. Calcium sensors like calmodulin (CaM), and calcium-dependent protein kinases (CDPKs) decode this Ca^{2+} signature. This contributes to conformational changes by binding Ca^{2+}, which leads to the phosphorylation of downstream target proteins that transduce the heat stress signal into the nucleus. Calcium signallings achieve orchestration through interactions of calcium-binding proteins (CBPs) that serve as basic decoders, such as calcineurin B-like proteins, which mediate environmental physical stimuli and nuclear transcriptional condensates (Ahmad *et al*., 2021; Yang *et al*., 2023).

Table 1: Physiological Consequences Of Heat Stress In Various Crop Plants

Crop Species	Scientific Name	Primary Physiological Response	Yield Penalty Impact
Wheat	*Triticum aestivum*	Accelerated senescence, grain shriveling	Severe reduction in harvest index
Rice	*Oryza sativa*	Spikelet sterility during anthesis phase	Massive loss of viable grains
Tomato	*Solanum lycopersicum*	Impaired pollen tube elongation	Reduced fruit set and size
Maize	*Zea mays*	Tassel blasting and silk desiccation	Disrupted fertilization, kernel abortion
Soybean	*Glycine max*	Premature pod abscission and drop	Significant decrease in pod count
Cotton	*Gossypium hirsutum*	Boll shedding and fiber weakening	Lowered lint yield and quality
Chickpea	*Cicer arietinum*	Stunted vegetative growth, floral abortion	Diminished seed weight and count

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Oxygen Reactive Species As Primary Messengers

Reactive oxygen species (ROS), which are recognised chiefly for their damaging effect on cells, play an essential role as secondary messengers during the early phases of heat stress. Superoxide radicals (O^{2-}) and hydrogen peroxide (H_2O_2) are produced by disruption of electron transport chains in chloroplasts and mitochondria. These molecules together with calcium signaling activate respiratory burst oxidase homolog D, which enhances the oxidative burst and systemic signal transduction (Sajid *et al*., 2018).

The first low, controlled concentrations of H_2O_2 diffuses across membranes and subsequently oxidate certain cysteine residues on regulatory proteins as well as on transcription factors to change their activity. This ROS surge acts in concert with the Ca^{2+} signal to induce the MAPK cascade. This kinase signalling network is critical in regulating the activity of Heat Shock Factors (HSFs), connecting thermal sensing to genetic reprogramming. Moreover, these signaling networks facilitate the translocation of transcription factors into the nucleus to trigger thermotolerance-related genes (Finka & Goloubinoff, 2013).

Physiological And Biochemical Impacts Of Heat Stress

When temperature reaches the upper limit of adaptation, combined effects of hyper-fluids and oxidative bursts result in organelle shutdown, especially among energy generating organelles. These conditions are especially damaging to photosynthetic systems because superoxide radicals cause direct oxidative damage to thylakoid membranes, leading to decreased light-harvesting complex efficiency (Saeed *et al*., 2023).

Disruption Of Photosynthetic Electron Transport

Among the many physiological process that can be impacted by heat in plants, photosynthesis is considered to be among the most detailed (Atkin *et al*. 2005). Chloroplast is the location of photosynthesis and it is very sensitive to heat injury. In particular, elevated temperatures inhibit the activity of critical enzymes like Rubisco and Rubiscoactivase, while also destabilizing chloroplast and mitochondrial electron transport chains (Dard *et al*., 2023).

Figure 3: Chloroplast Structural Architecture Under Thermal Stress Dynamics

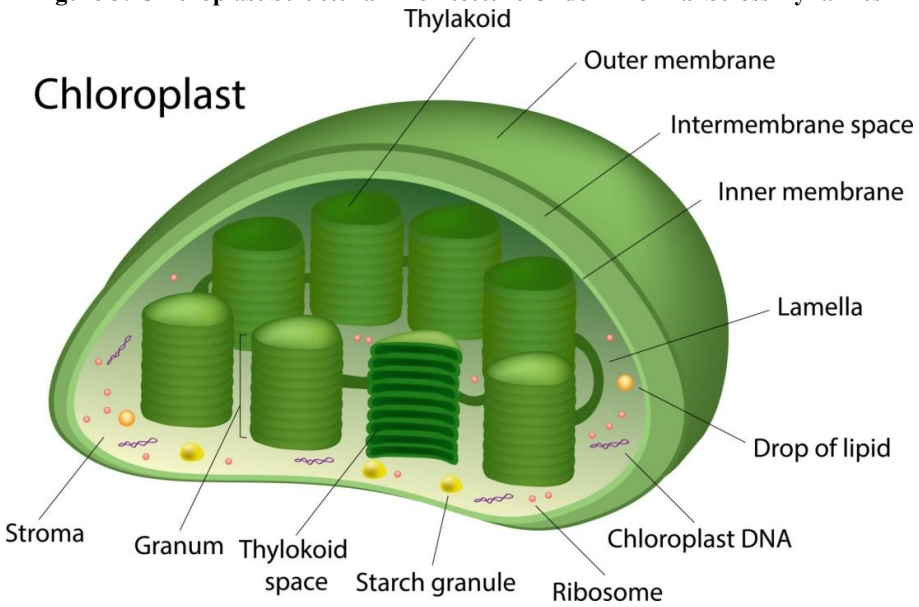

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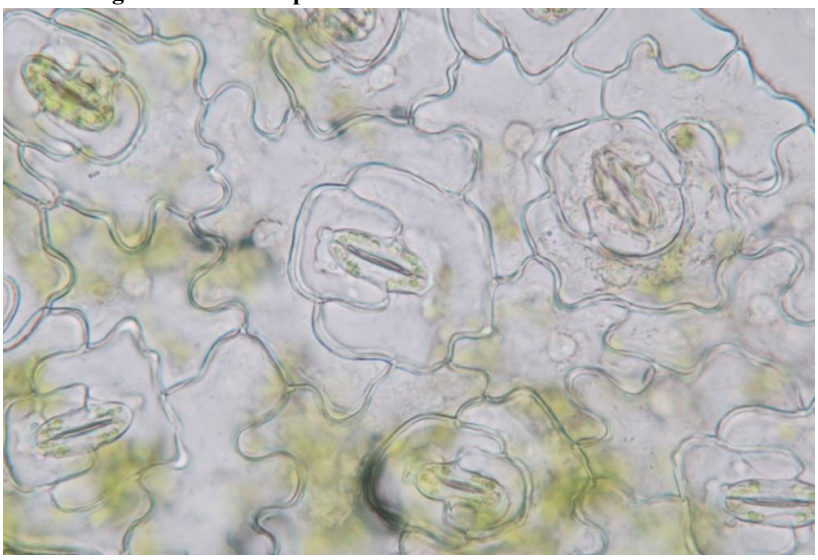
Figure 4: Microscopic View Of Plant Stomata Under Stress



Above normal temperatures physically uncouple the thylakoid membranes, resulting in propagation of the oxygen-evolving complex (OEC) away from Photosystem II (PSII). It essentially stops the electron transport chain in its tracks. In addition, the activity of RuBisCO, the main carbon-fixing enzyme is highly inhibited. Rises in temperature similarly denature RuBisCOactivase, an enzyme that helps keep RuBisCO active and states rates of CO_2 assimilation plummet. At the same time, jasmonic acid-related pathways where Allene oxide synthase expression is inhibited lead to reduced plant productivity and stress resilience (Selinga *et al*., 2022). Simultaneously, grana stacking losses and chloroplast disorientation-associated proteins severely hinder photosynthetic efficiency, and ultimately exacerbate lipid peroxidation by-products (Chaudhary *et al*., 2020).

Table 2: Key Heat Shock Proteins And Their Specific Cellular Functions

Protein Family	Molecular Weight	Cellular Localization	Specific Protective Function
HSP100	~100 kDa	Cytosol, Chloroplast	Solubilizes aggregated protein complexes
HSP90	~90 kDa	Cytosol, Endoplasmic Reticulum	Regulates signal transduction receptor proteins
HSP70	~70 kDa	Cytosol, Nucleus, Mitochondria	Prevents aggregation, assists de novo folding
HSP60	~60 kDa	Mitochondria, Chloroplast	Facilitates folding of imported organellar proteins
sHSP	15-42 kDa	Cytosol, Chloroplast, Nucleus	Binds unfolded proteins acting as sponges
DNAJ	~40 kDa	Ubiquitous cellular distribution	Co-chaperones stimulating HSP70 ATPase activity
GrpE	~20 kDa	Mitochondria, Chloroplast	Nucleotide exchange factor for HSP70 systems

Disruption Of Cellular Respiration And Metabolism

Under heat stress, as photosynthesis begins to decline, dark respiration typically increases at first in the ongoing effort of the plant to make ATP for repair. Nonetheless, this high respiration rate quickly consumes carbohydrate stores, causing the cells to starve. Coupled to this naive metabolic state is the concurrent inactivation of mitochondrial complexes that affects oxidative phosphorylation efficiency and leads to a secondary energy crisis (Sehar *et al*., 2022).

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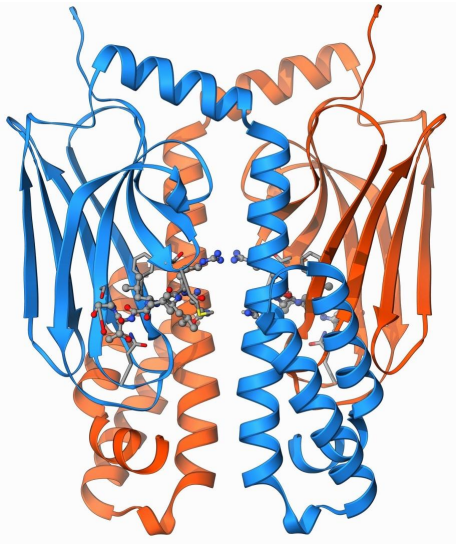
Plants close their stomata in order to reduce the excess loss of water through transpiration during high temperature episodes (that are generally associated with drought). This saves water (H_2O), but stops entry of CO_2, and leads to an intensifying photosynthetic crisis causing a pronounced metabolic imbalance. In addition, this decreased internal CO_2 concentration promotes oxygenation rather than carboxylation and thereby decreases overall quantum efficiency of electron transport (Haworth *et al*., 2018). In addition, continued exposure to these temperatures activates an oxidative burst which causes lipid peroxidation and extensive pigment bleaching that continue further the compromise of thylakoid membranes integrity (Zhang *et al*., 2023). In addition to these structural degradations, the degradation or impaired synthesis of key pigments including carotenoids and chlorophylls disrupts light-harvesting capabilities, which consequently impairs photochemical reactions (Rodrigues *et al*., 2023).

Figure 5: Molecular Structure Of Protective Heat Shock Proteins



Molecular Protective Strategies And Thermotolerance

Plants activate large-scale genetic and metabolic reconfigurations in response to supra-optimal temperatures related to the stabilization of structures, scavenging toxins and maintaining osmotic homeostasis. This defense is based primarily on the upregulation of heat shock proteins and heat shock factors, which act as molecular chaperones to prevent thermal denaturation of cellular proteins and enzymes (Chaudhary *et al*., 2022).

Heat shock proteins (HSPs) are a group of specialized molecules that serve vital functions in plant defense against biotic and abiotic stresses.

One of the major features of the heat stress response is the precise and fast transcriptional and translational induction of Heat Shock Proteins (HSPs). These proteins have molecular chaperone-like functions. They impede the accumulation of denatured polypeptides and assist with the novel or damaged protein renaturation in efforts to maintain cellular homeostasis (Lamaoui *et al*., 2018).

Table 3: Enzymatic Antioxidants Combating Reactive Oxygen Species During Heat Stress

Antioxidant Enzyme	Cellular Compartment	Reactive Oxygen Target	Biochemical Output
Superoxide Dismutase	Chloroplast, Mitochondria	Superoxide radical (O^{2-})	Hydrogen peroxide (H_2O_2) and Oxygen
Catalase	Peroxisomes	Hydrogen peroxide (H_2O_2)	Water (H_2O) and Oxygen (O_2)
Ascorbate Peroxidase	Chloroplast, Cytosol	Hydrogen peroxide (H_2O_2)	Water utilizing ascorbate as donor
Glutathione Reductase	Chloroplast, Cytosol	Oxidized glutathione (GSSG)	Reduced glutathione (GSH) regeneration
Monodehydro	Cytosol, Peroxisomes	Monodehydroascorbate	Ascorbate regeneration using

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ascorbate		radical	NADH
Dehydro ascorbate	Chloroplast, Cytosol	Dehydroascorbate molecule	Ascorbate regeneration using GSH
Guaiacol Peroxidase	Cell Wall, Vacuole	Hydrogen peroxide (H_2O_2)	Lignin biosynthesis and defense signaling

If cellular proteins are not properly folded in their native 3D conformation due to kinetic thermal energy, hydrophobic residues are exposed and can cause protein aggregation which can be lethal. Given these exposed hydrophobic regions, HSPs bind to them and prevent aggregation in an ATP-dependent or independent manner. HSP70 and HSP90 families are molecular chaperones that actively refold denatured proteins, whereas small HSPs (sHSPs) are holdases, which bottleneck denatured proteins until larger cytoplasmic ATP-dependent chaperones can act on them. The expression of these protective systems is coordinated by the recognition of specific conserved cis elements found within HSP gene promoters by heat shock transcription factors that govern this regulatory process (Hu *et al*., 2020; Singh *et al*., 2023).

Enzymatic And Non-Enzymatic Antioxidant Defenses

Unregulated productions of ROS lead to lipid peroxidation, protein oxidation and nucleic acids damage. Plants activate a two-tiered antioxidant defense mechanism for thermotolerance. At the enzymatic level, Superoxide Dismutase (SOD) is the first line of defense, dismutating highly toxic O^{2-} into H_2O_2. Afterwards Mitigates Nosubstantial Inconvenience process H_2O_2 into non-harmful aspects (H_2O and O_2). The option of Ascorbate Peroxidase (APX) and Catalase (CAT) cleanse the detrimental substantial inconvenience to make it as harmless Substances 17. In addition to these enzymatic systems, nonenzymatic scavengers including secondary metabolites or accumulated compatible solutes add extra protection against cellular stress through their role in membrane stabilization and protection from reactive oxygen species (Bhardwaj *et al*., 2023).

Non-enzymes (correlation with the enzymatic pathway) - However, molecules like ascorbic acid (Vitamin C), glutathione, α-tocopherol (Vitamin E), and carotenoids directly neutralize free radicals in thylakoid membranes from photooxidative damage.

Accumulation of osmoprotectants and compatible solutes.

Cellular hydration is always compromised by heat stress. Plants also synthesize highly water-soluble organic compounds with low molecular weight, called compatible solutes or osmoprotectants. These metabolites such as proline (PRO), trehalose (TRE) and glycine betaine (GB) contribute to the cell turgor by accumulating within the cytosol, and stabilizing quaternary structures of proteins against thermal denaturation (He *et al*., 2018). Additionally, the other compatible solutes are good scavengers of hydroxyl radicals and resolve the cytosolic buffering capacity due to heat-induced changes in osmotic balance (Asthir, 2015). In addition to these osmoprotective functions, the contribution of reactive oxygen species to signalling in general has enabled heat shock transcription factors that regulate redox-related gene expression (Kilian *et al*., 2019) and play a role in enhancing systemic thermotolerance afterwards (Kerchev & Breusegem, 2021). This ensures a quick response to shifts in redox environment by utilizing heat shock factors to coordinate the counterbalancing need for ROS as signaling molecules with signaling coupled with oxidative injury potential (Driedonks *et al*., 2015; Fortunato, Lugo-Cervantes, & Fabbri, 2023).

Molecules such as amino acids (proline), quaternary amines (glycine betaine) and soluble sugars (trehalose, sucrose etc.) don't interfere with normal cellular metabolism instead they lower the osmotic potential allowing the cell to hold water. Besides, they also behave like chemical chaperones that stabilize the hydration shell around important proteins and akes sure of bilayer structure stability. These compounds promote the saturation of membrane-associated lipids, stabilizing thylakoid membranes and preventing deterioration of critical photosynthetic reactions under extreme thermal fluctuations (Onaga & Wydra, 2016).

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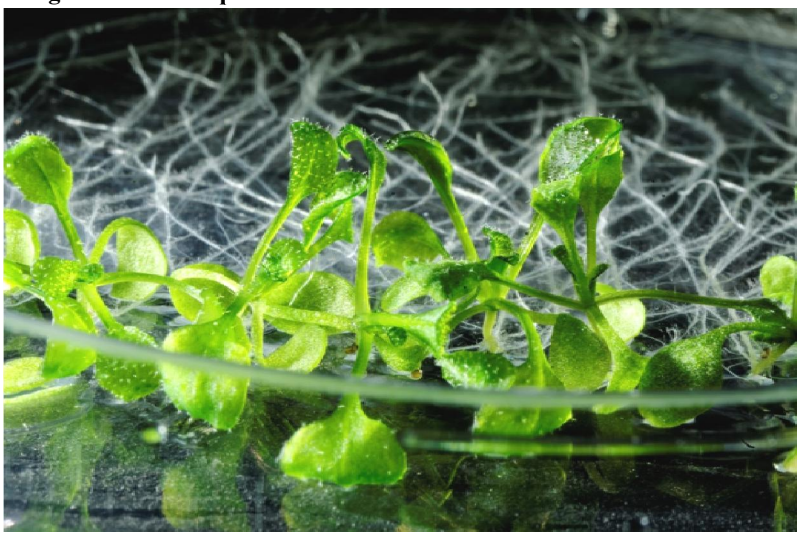
Figure 6: Arabidopsis Thaliana Plant under Thermal Stress Research



Agronomic Context And Climate Resilience In India

The vastness and diversity of the Indian subcontinent makes its agriculture sector particularly sensitive to changing paradigms of global warming. Heat waves occurring during key phenological stages pose an insurmountable risk to national food security. With a special focus on the reproductive growth stage, rapid changes in temperature considerably limit grain development and hence overall yield quality (Akbar, 2020).

Table 4: Major Signal Transduction Molecules Activated By High Temperature Stress

Signaling Molecule	Molecular Nature	Primary Activation Trigger	Downstream Cellular Effect
Calcium Ion (Ca^{2+})	Divalent Cation	Membrane fluidization	Activates CDPKs and Calmodulin sensors
Hydrogen Peroxide	Reactive Oxygen	Electron transport chain leak	Modulates MAPK cascades and transcription
Nitric Oxide (NO)	Reactive Nitrogen	Nitric oxide synthase activity	S-nitrosylation of regulatory proteins
Phosphatidic Acid	Lipid Messenger	Phospholipase D activation	Cytoskeletal rearrangement and MAPK activation
Calmodulin (CaM)	Calcium Sensor Protein	Binding of free Ca^{2+} ions	Regulates heat shock factor translocation
MAPK Cascades	Kinase Enzymes	ROS and Calcium signatures	Phosphorylates transcription factors in nucleus
Cyclic AMP (cAMP)	Cyclic Nucleotide	Adenylyl cyclase activation	Gene regulation and metabolic reprogramming

Sensibilization of Staple Crops To Terminal Heat

Major threat to *Triticum aestivum* (wheat) in the "breadbasket" of India, Indo-Gangetic plains, is known as "terminal heat stress" Sudden spikes in ambient temperature at the start of grain-filling stage (late February and March) precipitate senescence, too soon to ensure optimal yield from wheat crop. This process interferes with starch storage, resulting in the shortening of the grain-filling period and a considerable decrease in thousand-grain weight and overall crop harvest.

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Figure 7: Wheat Crop Yields Decimated By Severe Heat Stress

Figure 8: Tomato Plant Suffering From High Temperature Heat Stress

This limits the time available for starch accumulation in the endosperm, leading to shriveled grains and large yield penalties. In like manner, cultivation of *Solanum lycopersicum* (tomato) over different Indian states is disastrously affected. Extreme temperatures during flowering cause tomato pollen sterility, inhibiting pollen tube elongation, rampant floral abscission and significant decrease in fruit maturities. To overcome these challenges, contemporary

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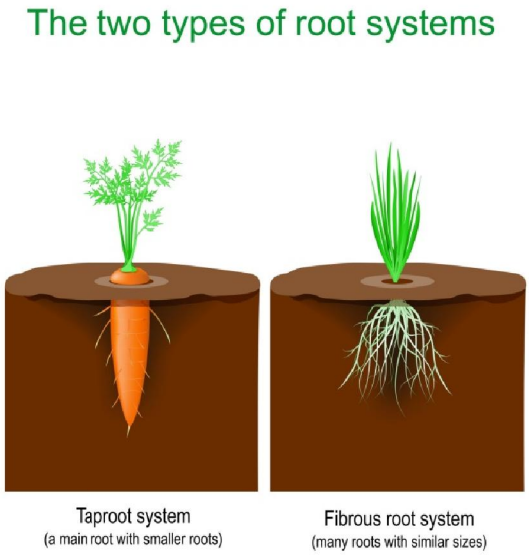
studies highlight marker-assisted breeding for developing climate-resilient cultivars and applying thermos-protectants to protect physiological functions during peak flowering (the stage identified as more susceptible to heat stress inhibition.

Biotechnological Approaches For Crop Improvement

Scientists are actively pursuing biotechnological and traditional breeding methods to develop thermotolerant cultivars ideal for maintaining agricultural production. Detailed molecular investigations have employed these QTLs in marker-assisted selection (MAS) to select superior heat tolerant genotypes such as Parbhani-51 and Lok-1 (K.M. *et al*. 2023).

Figure 9 Extreme Drought Heat On Crop Field (B)

Figure 10: Analyzing Plant Root System Architecture For Thermal Resilience



Current breeding programs make use of marker assisted selection (MAS) for the introgression of QTL regions linked with heat tolerance from wild relatives into elite breeding varieties. A wide range of genetic engineering approaches targeting the over-expression of certain transcription factors, including HSFs as well as genes controlling biosynthesis pathways for osmoprotectants such as trehalose and glycine betaine are successfully carried out. Additionally,

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increasing the activities of key starch biosynthesis enzymes such as soluble starch synthase (SSS) and starch branching enzymes (SBEs), is an important strategy for rectifying heat stress during grain filling period (Ullah *et al*., 2021).

Also, breeding deeper roots and better root architectural designs will permit the plants to access deeper soil moisture, which in turn will buffer the canopy from high thermal stress by continuing transpiration cooling. In addition to physiological adaptations, the utilization of biostimulants such as Ascophyllum nodosum extracts or exogenous proline and salicylic acid applications to enhance antioxidant defense systems seem promising for stabilising metabolic enzymes under extreme heat regimes (Carmody *et al*., 2020). These exogenous cues all promote heat shock proteins and antioxidant enzymes, which in sum preserve cellular integrity by eliminating reactive oxygen species that accumulate during thermal stress (Li *et al*., 2022).

Table 5: Agronomic Management Strategies To Mitigate Thermal Stress In Crops

Agronomic Strategy	Execution Method	Primary Protective Mechanism	Efficacy In Field Conditions
Surface Mulching	Application of crop residues	Reduces soil temperature and evaporation	Highly effective for shallow-rooted crops
Altered Sowing Dates	Advancing planting schedules	Escapes terminal heat during grain filling	Critical for wheat in Northern India
Shade Netting	Installing UV-stabilized nets	Reduces direct solar irradiance load	Economically viable for high-value horticulture
Micro-Irrigation	Drip and sprinkler systems	Lowers micro-climate canopy temperature	Excellent water-use efficiency and cooling
Foliar Osmoprotectants	Spraying salicylic acid or proline	Maintains cellular turgor and defense	Provides transient biochemical stress relief
Thermotolerant Cultivars	Planting improved genetics	Innate genetic capacity for heat survival	The most sustainable long-term solution
Soil Organic Amendments	Adding farmyard compost	Enhances soil moisture retention capacity	Improves overall rhizosphere thermal buffering

II. CONCLUSION

Heat stress remains one of the most serious threats to sustainable global agriculture and this highlights the need for an in-depth understanding of plant thermotolerance mechanisms. Plants employ a remarkably complex sensory machinery, activating fast signal transduction cascades via calcium ions and reactive oxygen species as this chapter describes. These major signals induce the activation of important transcription factors, leading to over-expression of molecular chaperones (mainly heat shock proteins), that preserve cellular homeostasis under extreme thermal conditions. In addition, effective antioxidant defense systems alleviate strong oxidative injury, and metabolic readjustments maintain key photosynthesis processes. These complex biochemical and molecular pathways must be exploited through late generation breeding programs to breed variety specifically with climate-resilient crops. In conclusion, decoding these defensive mechanisms can be a great asset to obtain food security in climate-vulnerable regions like India by sustaining crop productivity against the impending consequences of climate change.

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