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Gyanendra Kumar Rai *Editors*

Thermotolerance in Crop Plants

 Springer

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Preface

Global climate change has now become reality rather than myth, as evident from the decrease in the production and productivity of agriculturally important crops. The major challenges before us are—how to feed the burgeoning population and how to protect them from the menace of malnutrition. Abiotic stress has severely affected the quantity and quality of the grains. Out of all the abiotic stresses, heat stress has been considered as most damaging for the crop plants. Even an increase of 1 °C in temperature has been reported to reduce the crop yield by ~4%. We have very limited information about various factors responsible for modulating the tolerance level of the plant. Genetic, physiological, biochemical, and molecular approaches are considered as a prerequisite for countering the effect of stress in plants. This book entitled *Thermotolerance in Crop Plants* covers different aspects of stress tolerance in crop plants starting from the severity of the problem on quantity and quality of yield under present threat of global climate change to other mechanistic dimensions like—physiochemical and molecular mechanism underlying thermotolerance, signaling mechanism under heat stress, role of heat shock proteins (HSPs) in modulating the thermotolerance, different approaches used in the past to develop heat stress-tolerant crop plants, list of developed thermotolerant agriculturally important crop plants, redox homeostasis under heat stress, effect of exogenous application of phytohormones on tolerance level of the plant, carbon partition and distribution under heat stress, omics approaches for the development of climate smart-crop, etc. This insightful book gives lucid information about various mechanisms underlying heat stress tolerance in plants and approaches to modulate the thermotolerance with future possibilities of developing climate smart crop. This book will be useful for the life science students (MSc and PhD), researchers working

in the area of manipulating abiotic stress tolerance in crop plants, scientists, professors, etc.

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The original version of this book has been revised: the affiliation of the third editor Dr. Gyanendra Kumar Rai has been updated. A correction to this book can be found at https://doi.org/10.1007/978-981-19-3800-9_15

Contents

1	Heat Stress in Wheat: Adaptation Strategies	1
	P. Shashikumara, Rahul Gajghate, Narayan Bhatt Devate, Harikrishna, H. M. Mamrutha, K. Gopalareddy, and G. P. Singh	
2	Molecular Markers Mediated Heat Stress Tolerance in Crop Plants	23
	Md. Shamim, Mahesh Kumar, and Deepti Srivastava	
3	Physiology of Crop Yield Under Heat Stress	45
	Prakshi Aneja, Aditi Dwivedi, and Aashish Ranjan	
4	Physiological Traits for Improving Heat Stress Tolerance in Plants	81
	Sourabh Karwa, Akshay Sakhare, Chandrapal Vishwakarma, Sunder Singh Arya, Madan Pal, and Sudhir Kumar	
5	Understanding the Mechanism of High-Temperature Stress Effect and Tolerance in Wheat	105
	Ranjan Das, Soibam Helena Devi, Sangita Das, Merentoshi Mollier, and Sujata Pachoni	
6	Reactive Oxygen Species: Friend or Foe	129
	Gyanendra Kumar Rai, Muntazir Mushtaq, Basharat A. Bhat, Ranjeet Ranjan Kumar, Monika Singh, and Pradeep Kumar Rai	
7	CDPKs Based Signalling Network: Protecting the Wheat from Heat	163
	Ranjeet Ranjan Kumar, Sindhu Sareen, Jasdeep C. Padaria, Bhupinder Singh, and Shelly Praveen	
8	Heat Shock Proteins: Catalytic Chaperones Involved in Modulating Thermotolerance in Plants	181
	Anil Dahuja, Suneha Goswami, Ranjeet Ranjan Kumar, Vinutha T, and Shelly Praveen	

9	Starch Metabolism under Heat Stress	195
	Suneha Goswami, Ranjeet Ranjan Kumar, Suman Bakshi, and Shelly Praveen	
10	Heat Stress and Grain Quality	211
	Sneh Narwal, Sonia Sheoran, Dinesh Kumar, Antim Kundu, and Ajeet Singh	
11	OMICS Tools and Techniques for Study of Defense Mechanism in Plants	237
	Dwijesh Chandra Mishra, Sayanti Guha Majumdar, Neeraj Budhlakoti, Anuj Kumar, and Krishna Kumar Chaturvedi	
12	Induced Mutagenesis for High-Temperature Tolerance in Crop Plants	251
	Suman Bakshi, Sanjay J. Jambhulkar, Ranjeet Ranjan Kumar, Pradeep Bhati, and Uttam Kumar	
13	CRISPR/Cas-Based Genome Editing to Enhance Heat Stress Tolerance in Crop Plants	281
	Gopika Mote, Pravin Jadhav, Sayali Magar, Pranita Thakur, Mangesh Moharil, and Rajkumar Biradar	
14	Genomics-Enabled Breeding for Heat and Drought Stress Tolerance in Crop Plants	299
	Ved Prakash Rai and Manish Kumar Vishwakarma	
	Correction to: Thermotolerance in Crop Plants	C1
	Ranjeet Ranjan Kumar, Shelly Praveen, and Gyanendra Kumar Rai	

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Heat Stress in Wheat: Adaptation Strategies

1

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Abstract

Globally wheat productivity is affected due to unfavorable effects of different biotic and abiotic stresses. Combating these stresses to minimize the yield losses in wheat crop is the major area of concern to ensure food security. Among the different abiotic stresses, increase in ambient temperature is one of the major threats to global wheat production. Wheat being second most important crop in the world accounts for 20% of global protein. Heat stress impairs physiological functions, hormonal productions and reduces photosynthetic efficiency, metabolic activities, and pollen viability resulting in loss in grain yield. To cope up with heat stress, wheat plant evolves various adaptive strategies which includes morphological, physiological, molecular, epigenetic, and biochemical. The current chapter presents inclusive information on importance of heat stress, its effect on various growth stages and the different strategies adapted by wheat crop to cope up with heat stress, which helps the wheat researchers in developing climate resilient wheat.

Keywords

Wheat · Abiotic stress · Heat stress · Adaptation strategies · Heat stress priming

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1.1 Introduction

Wheat (*Triticum* spp.) is the most widely cultivated rabi cereal and staple crop in many countries across the globe. As per FAO estimation, an additional 198 million tonnes of wheat are required by 2050 to meet the ever-growing future wheat demand (Sharma et al. 2015a, b). However, wheat growing areas are frequently exposed to unpredictable temperature fluctuations during critical crop growth stages, thereby affecting grain yield significantly. The temporal variation in temperature during wheat crop season has already been reported to affect the productivity in many parts of the globe (Fontana et al. 2015; Mueller et al. 2015). Low latitude wheat growing zones with around 100 million hectares of wheat area is more predominantly heat prone across the globe (Braun et al. 2010). A total of 30 different wheat crop models were tested by Asseng et al. (2014) with crop growing mean temperatures ranged 15 °C–32 °C, which includes the artificial heating. Their analysis suggests that the higher temperatures already affected wheat grain yield in majority wheat growing areas. During the period between 1981 and 2010, average yield reductions ranged 1–28% across 30 world sites for every 2 °C rise in temperature; this yield reduction increased and ranged 6–55% for every 4 °C rise in temperature. They also estimated that the global wheat production will be reduced by 6% for every rise in 1 °C. Higher yield variability due to higher temperature was observed in low latitudes as compared to high latitudes. Singh et al. (2011) reported yield reduction of 400 kg per hectare if the March–April month mean temperature rises even 1 °C in India. Elevated temperature during grain filling stage resulted in terminal heat stress and yield reduction in wheat. When the mean temperature reaches above 31 °C during grain filling stage, then the terminal heat stress occurs in wheat.

Heat stress is a complex phenomenon, which affects growth and development, impaired physiological functions (Mondal et al. 2013). The heat stress in wheat alters the hormonal productions (Krasensky and Jonak 2012), photosynthetic efficiency (Ashraf and Harris 2013), metabolic activities (Farooq et al. 2011), and plant water relations (Hasanuzzaman et al. 2013), pollen tube development and pollen mortality (Oshino et al. 2011). Heat stress also causes the enhanced production of reactive oxygen species (Wang et al. 2011) and ethylene (Hays et al. 2007). Increasing temperature will have impact on sustaining global wheat production and in turn food security, particularly during the period of climate change (Tripathi et al. 2016). Elevated temperature affects seed germination resulting in poor plant stand, decreased photosynthesis, membrane instability, senescence, reduced pollen viability and finally less grains with reduced grain size (Asseng et al. 2011). The severity of such effects greatly depends on the cultivars and phenological stages. Heat stress during flowering causes pollen and anther sterility leading to reduced grain number, while high temperature coincides with grain filling stage, which leads to reduced grain weight and in turn reduced yield (Mondal et al. 2013). Temperature stress due to change in the climate pattern necessitates to determine the heat stress effects and possible ways of improvement for sustainable wheat production under heat stress prone environments.

Adoption of climate smart practices is necessary to control the damages caused by the elevated temperatures during crop growth. Adaptation strategies towards climate change are needed to minimize the crop damages (Niles et al. 2015). Plants have different adaptive mechanisms under heat stress including avoidance, escape, and tolerance. Development of heat-tolerant wheat cultivars by the utilization of diverse genetic sources is the most sustainable and eco-friendly strategy to mitigate the heat stress effects (Ortiz et al. 2008). Choice of cultivars and adjustments in sowing dates are two important adoptive measures under heat prone environments (Deryng et al. 2014). Other adaptation strategies include antioxidants defense (Caverzan et al. 2016) and osmo-protectants (Kaushal et al. 2016) along with several molecular adaptation mechanisms and management practices like surface cooling by irrigation (Lobell et al. 2008).

Thorough understanding of the genetic, molecular, physiological, and biochemical mechanisms through genomic, transcriptomic, proteomics, and metabolomics analysis would help in the mitigation of heat stress in wheat. Identification of major heat responsive proteins and genes is important to integrate them in crop breeding programs. Functional validation of major heat responsive genes/proteins will also pave the way for the development of heat-tolerant varieties in wheat breeding programs. Thus, the present chapter focuses on compiling the information on significant effect of heat stress on different growth stages of wheat and the strategies adapted for overcoming the stress effect.

1.2 Effect of Heat Stress on Wheat Crop

The wheat crop under field may encounter either with sudden or slow increase in temperature and they have negative influence on various growth stages of wheat (McClung and Davis 2010; Grant et al. 2011). The high temperature effect on wheat crop depends on duration and extent of heat stress and also on pheno stage of the crop (Ruelland and Zachowski 2010). Some of the major effect of heat stress on various growth stages and on quality of wheat grains are discussed below.

1.2.1 Effect of Heat Stress on Vegetative Phase

The primary effect of heat stress is the impairment of seed germination and poor crop stand establishment (Johkan et al. 2011; Hossain et al. 2013). High temperature of around 45 °C severely degenerates mitochondria, changes the protein expression profiles, reduces ATP accumulation, and oxygen uptake in imbibing wheat embryos, resulting in loss of seed quality relating to seed mass, vigor, and germination which later reduces crop stands (Balla et al. 2012; Hampton et al. 2013). Warm environment produces lower biomass compared to plants grown under optimum or low temperature. Day and night temperature around 30 and 25 °C, respectively, has severe effects on leaf development and productive tiller formation in wheat. It is reported that high temperatures are generally involved in regulation of leaf

appearance rates and leaf-elongation rates along with decreasing leaf-elongation duration (Rahman et al. 2009). The plant height is significantly reduced which adds for reduced biomass under high temperature. Though vegetative stages are affected by heat stress, many a times cooler temperatures at reproductive period will make up its loss (Mamrutha et al. 2020).

Photosynthesis is the primary traits influenced by heat stress and mainly affects rubisco, rubisco activase activity, functioning of photosystems and thylakoid membrane (Iwai et al. 2010; Mathur et al. 2014). The availability of high O₂ concentration promotes photorespiration under high temperature. The change in solubility of O₂ and CO₂ gases was observed under heat stress condition causing increase in flag leaf photorespiration in wheat (Almeselmani et al. 2012). Extended duration of heat stress results in gradual senescence while intensive heat stress for short period of time leads to protein denaturation and aggregation, causing death of the plant (Pandey et al. 2019). High temperature (>34 °C) accelerates the leaf senescence due to reduction in biosynthesis of chlorophyll (Hasanuzzaman et al. 2013). It affects the water relation and content in the plant, cell dehydration is observed under heat stress due to reduction in osmotic potential (Ahmad et al. 2010).

1.2.2 Effect of Heat Stress on Reproductive Phase

The incidence of reproductive stage heat stress has been found to be more detrimental in wheat production (Nawaz et al. 2013; Mamrutha et al. 2020). One degree rise in average temperature during reproductive phase can cause severe yield loss in wheat (Bennett et al. 2012; Yu et al. 2014). The optimum temperature for flowering and grain filling ranges from 12 °C to 22 °C (Sharma et al. 2019). Anthesis stage is considered very crucial with respect to heat stress because the induction of heat stress just before and at this stage showed significant increase in floral abortion and lower number of seeds (Gupta et al. 2013; Asthir and Bhatia 2014; Sharma et al. 2016). Both micro-sporogenesis and mega-sporogenesis are affected under heat stress, resulting in lower seed-set. Early stage of gametogenesis is harmed when heat stress occurs during meiosis (Saini et al. 1983; Kaur and Behl 2010). The grain development phenomenon depends upon the grain filling rate and duration which is highly sensitive to heat stress (Gourdji et al. 2013; Lobell and Gourdji 2012). 1–2 °C rise in temperature lowers seed weight due to decrease in grain filling duration, thus resulting in production of smaller seed size (Sharma et al. 2019). Short-term heat stress during grain filling may result in grain yield loss up to 23%. In heat stress, grain number is decreased causing reduction in harvest index (Mason et al. 2010).

1.2.3 Effect of Heat Stress on Grain Quality Traits

Heat stress associated decrease in assimilate production and remobilization result in reduced grain quality (Lizana and Calderini 2013). Starch is the major constituents of wheat and is made up of amylose and amylopectin. Amylose content is key

parameter to mark starch quality. Starch characteristics are affected by variation in amylose content and high temperature is associated with increase in amylose content and amylose:amylopectin ratio (Sharma et al. 2015a, b). ADP-Glucose Pyrophosphorylase (AGPase) and starch synthase are key enzymes involved in starch biosynthesis, at high temperature, there is decrease in starch content in grain up to one-third of total endosperm starch, which is caused due to decrease in efficiency of these two enzymes (Liu et al. 2011). Under heat stress, there is increase in total soluble sugar and protein (Asthir and Bhatia 2014) content with increase in essential amino acids fractions, leaf nitrogen content, and sedimentation index as kernel size is smaller (Iqbal et al. 2017). It is observed that heat stress during grain filling can significantly alleviate protein concentration while lowering the functionality of protein and this augment seems to be higher when high temperatures are imposed in early stages of grain filling (Corbellini et al. 1997; Vijayalakshmi et al. 2010). Comparison of milled grains from control and high temperature treated plants revealed alterations in peaks assigned to polysaccharides and proteins (Corbellini et al. 1998; Castro et al. 2007; Daniel and Triboi 2001).

1.3 Heat Stress Adaptation Strategies

1.3.1 Morphological Adaptation Strategies

Abiotic stresses, such as drought, heat, cold, salinity, and heavy metals are severely affecting the plant growth, development, and yield of the crop (Raghavendra et al. 2020; Jain et al. 2014). Meanwhile, plants try to adapt to such adverse conditions through modifying their morphological structure to sustain in the existing environment (Hossain et al. 2016; Sah et al. 2016).

The plant will show morphological modification to overcome combined effects of heat and drought stress. The rapid ground cover will withhold evaporation of water from the soil under plant canopy. This increases water availability to maintain evapotranspiration, keeps cooler plant canopy under heat stress (Cossani and Reynolds 2012; Khan and Kabir 2014). Early emergence of seedlings and early ground cover are important adaptive traits used for selection of earliness in wheat germplasm (Mondal et al. 2017). Leaf rolling and leaf thickening through changes in lipid composition are important survival mechanisms under prevailing heat stress (Nawaz et al. 2013). The presence of leaf hairs and waxy covering on leaf and stem surface avoids heat stress. These leaf modifications lead to reduced exposure to solar radiations, smaller leaf boundary evacuate heat to ambient more rapidly and increases transpiration leaf cooling of the plant under heat stress condition (Hasanuzzaman et al. 2013). Flag leaf area and awn length are also effective traits correlated with grain yield under heat stress conditions (Munjal and Suresh 2020). The early maturing varieties can escape terminal heat stress situations with minimum yield loss under heat stress. For late sown conditions days to heading, days to maturity, plant height, number of effective tillers per plant, and biological yield are important yield attributing parameters which need to be considered in wheat.

1.3.2 Physiological Adaptations

Under high temperature condition, plants show tendency to reduce cell size, closure of stomata, and increased trichomes density in leaves (Anon et al. 2004). Cell membrane is highly susceptible and affected by increasing temperature. The thermotolerant wheat genotype maintains cell membrane stability, avoiding the leakage of electrolytes thereby protecting membrane from disintegration due to high temperature (Blum and Ebercon 1981). Estimation of osmotic potential of the cell gives the idea on cell membrane stability. The scavenging reactive oxygen species which are produced due to oxidative stress are important activities to avoid cell membrane breakdown. The tolerant plant will have good deep root system and enhanced transpiration ability to keep cooler plant canopy under heat stress. Through use of infrared gun, we can estimate canopy temperature (CT) and cooler canopy genotypes are considered to be the heat-tolerant lines (Hütsch et al. 2019). Higher temperature indirectly induces drought stress. Plant will adopt with changing in root parameters to absorb more water from the deep layers of soil. Cooler canopy indicates higher water use efficiency and nutrient use efficiency with stable yield (Singh et al. 2017). Transpiration is inevitable process and crucial for plants for water and nutrient uptake, photosynthesis and maintaining canopy temperature. The rise in temperature causes decrease in stomatal conductivity thereby halting transpiration process. Tolerant lines maintain higher stomatal conductance compared to susceptible genotypes so that they maintain required transpiration rate and water balance (Pooja and Munjal 2019). High throughput, non-destructive instruments like infrared gun, green seeker, porometer, and chlorophyll meter can be used for evaluation of wheat genotypes under heat and drought condition. Canopy temperature is negatively correlated with transpiration and grain yield (Manu et al. 2020; Shashikumara et al. 2020). Normalized difference vegetation index (NDVI) recorded using green seeker measures greenness of plant canopy and thus chlorophyll content, this can be estimated at different growth stages of crop (Harikrishna et al. 2016). Similarly, chlorophyll meter is used to estimate chlorophyll content thus genotypes having higher NDVI and chlorophyll content index under heat stress will have more chlorophyll content resulting in higher photosynthetic efficiency (Puttamadanayaka et al. 2020). Many studies have reported QTLs for physiological traits like NDVI, chlorophyll reading, and CT under heat and drought stress in wheat (Sunil et al. 2020; Puttamadanayaka et al. 2020).

Stay green is the key trait associated with heat tolerance in wheat. Majorly, the exposure to heat stress during anthesis stage and grain filling stage reduces pollen viability, seed set, starch and protein accumulation (Barnab'as et al. 2008; Zahedi and Jenner 2003). Under such circumstances, heat-tolerant wheat genotypes have increased availability of stem water-soluble carbohydrates for the developing grains. This increases grain filling producing higher number of grains per spike than heat susceptible lines. The delayed senescence, i.e., stay greenness, is important key indicator of adaptation to heat stress, which is an indicative of higher leaf chlorophyll contents at anthesis stage (Fokar et al. 1998). The stay-green genotype is able to maintain better grain filling under higher temperatures. This modification allows

wheat genotypes to have high photosynthetic rate, reduced canopy temperature, and remobilization of assimilates to grain developing under heat stress (Rehman et al. 2021). Genotypes showing delayed senescence remain greener during later stages of crop growth and can divert photosynthesis to developing grains maintaining stable yield under terminal heat stress (Thomas and Ougham 2014). There is significant variability available in wheat for stay greenness, hence this trait can be exploited to develop heat-tolerant genotypes. Accumulation of osmolytes such as sugars and sugar alcohols (polyols), proline, tertiary and quaternary ammonium compounds, and tertiary sulfonium compounds under various abiotic stresses including heat stress is a key adaptive mechanism in plants. For example, accumulation of glycine-betaine and prolines will buffer redox potential of cells under heat and other abiotic stresses (Sakamoto and Murata 2002). Similarly, other osmolytes like c-4-aminobutyric acid (GABA) accumulates in the stressed tissue, which triggers various timely physiological responses in plants for adaptation to stress conditions (Kinnersley and Turano 2000). Overall wheat heat-tolerant genotype will show physiological adaptation through increasing transpiration, efficient photosynthesis during post anthesis stages, and higher stem reserve mobilization.

1.3.3 Molecular Adaptation Strategies

Plants exposed to heat stress, initially it causes plasma membrane disruption, ionic effects, and osmotic changes. This initiates a downstream signaling and transcriptional cascade that activate stress-responsive mechanism for repair damaged membranes and proteins for reestablishment of cellular homeostasis. Rise in temperature beyond critical limit causes changes in the plasma membrane fluidity which in turn leads to formation of phosphatidic acid (PA) and phosphatidylinositol 4, 5-bisphosphate (PIP2) and triggers Ca^{2+} influx and cytoskeletal reorganization resulting in the activation of some mitogen-activated protein kinases (MAPK) and calcium-dependent protein kinases (CDPK). These molecules play role as signal for G-protein-coupled receptors and these molecules activate secondary messenger proteins which travel over nuclear membrane of cells and activate genes associated with heat tolerance (Mishkind et al. 2009; Singh Kuldeep et al. 2012). The heat stress causes dissociation of chaperons from heat shock transcription factors (HSFs) and then these factors will bind to heat response elements (HREs). Now these HREs activate heat response genes (HRGs) (Zhu 2016). In general, under normal condition chaperon BIP bound by a common transcription factor bZIP28, and prevents movement of bZIP28 into nucleus. When cell exposed to heat stress, it causes destabilization in the interaction between bZIP28 and BIP, which leads to dissociation of molecules. Then bZIP28 moves to nucleus and activates various genes related to heat tolerance (Abhinandan et al. 2018). HSP 70 and HSP 90 are present in low amount and bound to transcription factor (TF), HsfA1 under normal condition. The rise in temperature causes production of ROS in the plant cell, which destabilizes interaction between HSP 70 and HSP 90 with *TF HsfA1*, which is free until now will enter the nucleus and activates heat shock protein coding genes (Ohama et al. 2017).

Induction of HSPs is a mechanism of acquiring heat tolerance as they play chaperone-like activity and also involved in signal transduction, gene activation, maintaining cellular redox state and in protecting photosynthetic electron transport (Nollen and Morimoto 2002). The transcriptome analysis of heat susceptible (Chinese Spring) and tolerant wheat (TAM107) genotypes identified putative heat stress-responsive genes encoding HSFs, HSP, transcription factors, and proteins involved in phytohormones biosynthesis/signaling, calcium and sugar signal pathways, RNA metabolism, ribosomal proteins, and primary and secondary metabolisms (Qin et al. 2008). The expression level of HSP90 and HSP101 under heat stress was observed in heat-tolerant genotype C306 (Vishwakarma et al. 2018; Almeselmani et al. 2012). Chauhan et al. (2011) identified many genes such as HSPs, transporters, lipid transfer protein, L-myo-inositol-1-phosphate synthase, protein modifiers, calcium binding proteins, signaling molecules, helicase-like protein, membrane binding proteins, alanine amino transferase, activator of HSP90, peptidyl prolyl isomerase, stress-induced protein Sti-1, and heat shock factor, which were highly inducible by high temperature and remained stable at both temperature regimes. *TaHsfA6f*, a member of the A6 subclass of heat shock transcription factors, which is upregulated during heat stress, regulates TaGAAP, TaHSP, and TaRof1 genes in wheat and has a positive impact on thermotolerance (Xue et al. 2015).

1.3.4 Biochemical Adaptation Strategies

The adaptive responses that plants have developed to reduce heat-induced damage to cells at biochemical level is to cease the efficiency of ribulose-1,5-bisphosphate (RuBP) carboxylase/oxygenase (Rubisco) in the Calvin–Benson–Bassham cycle (Weis 1981; Degen et al. 2021). The render inactive is mainly because of an ineffectual Rubisco activity regulation by the molecular chaperone called as Rubisco activase (Rca) (Crafts-Brandner and Salvucci 2000; Salvucci et al. 2001) as its regulation is sensitive to temperature (Salvucci et al. 2001; Carmo-Silva and Salvucci 2011, Carmo-Silva et al. 2012). Degen et al. (2021) studied the activity of three isoforms of Rca (Rca1 β , Rca2 β , and Rca2 α) in wheat, which differ in their thermostability. The transcript of Rca1 β is increased by 40-fold in 4 h at higher temperature and again comes to its natural level in controlled temperature after 4 h. The rapid change in the Rca isoform abundance at higher temperature improved the knowledge of the regulation and insight mechanism into the carbon assimilation to improve wheat productivity.

Phytohormones play an important role in coordinating the response to heat stress in wheat crop and act as naturally occurring heat dissipating barrier in plant by maintaining antioxidants level (Ahmed et al. 2016). Phytohormones such as abscisic acid (ABA), salicylic acid (SA), and cytokinins have vital role and crucial function in the response of HS to plant (Mittler et al. 2012; Peleg and Blumwald 2011; Xia et al. 2015; Zhou et al. 2014). ABA hormone plays a major role in root to shoot stress signaling (Kudoyarova et al. 2011), stomatal closure and prevents leaf expansion. Artificial application of ABA enhances the filling rate and sink capacity in grain by adjusting endogenous hormone molecule to stimulate endosperm cell

division and aggregation of photosynthate products (Yang et al. 2014). Salicylic acid (SA) regulates important plant physiological processes including photosynthesis and proline metabolism under stress conditions, thereby providing protection to plant (Khan et al. 2013; Miura and Tada 2014).

SA is an important component of the signaling pathway that counters to hypersensitive response and systemic acquired resistance (Kawano et al. 1998). It helps to balance the heat shock transcription factors and encourage to stick up with the heat shock element along with the promoter of heat shock-related genes, thus controlling the signaling pathway in high temperature stress condition and advocating the growth of the plant (Wang and Li 2006). The role of cytokinin is no doubt so important to mitigate heat stress by changing grain cytokinin content under HS conditions. It is the general coordinator between the stay-green trait and senescence. Exogenous cytokinins increase grain yield of winter wheat cultivars by improving stay-green characteristics under heat stress (Yang et al. 2016). Banowitz et al. (1999) found the correlation with the cytokinin content and the reduction in grain filling and grain weight during HS.

The production of reactive oxygen species (ROS) in the cell organelle (PS I and PS II of chloroplasts, mitochondria, peroxisomes, and endoplasmic reticulum) causes oxidative damage during the initial stage of heat stress (Wahid et al. 2007; Liu and Huang 2000), if continues for the long time then proteolysis occurs in the cell membrane and triggers the cell death program (Qi et al. 2011; Mittler et al. 2011; Marutani et al. 2012; Suzuki et al. 2012). To overcome the production of ROS, the enzymatic and nonenzymatic defense mechanism exists in wheat. In the enzymatic defense mechanism, superoxide dismutase (SOD) has the property to convert superoxide radical (O_2^-) into hydrogen peroxide (H_2O_2) and singlet oxygen (O_2), which is evacuated by ascorbate peroxidase (APX) using ascorbate as substrate and catalase (CAT) by glutathione reductase to convert glutathione disulfide to the sulfhydryl from glutathione (Suzuki et al. 2011). The nonenzymatic defense system involves reduction in glutathione (scavengers of singlet oxygen, hydrogen peroxide and hydroxyl radical), tocopherols (scavengers of H_2O_2 ; upregulation of APX and GR), ascorbic acid (donate electron in various enzymatic and nonenzymatic reaction), and carotenoids (inhibit singlet oxygen formation) (Sharma et al. 2012; Kumar et al. 2013; Puthur 2016; Tiwari et al. 2018). Thus, to overcome the negative effect of ROS, the enrichment of antioxidant in cell is a better approach (Sharma and Dubey 2005). Reassurance against oxidative stress is a major key to determine the endurance of a crop under HS. To get more information about the expression aggregation and development pathway of antioxidants under heat stress condition will help to plan and make a significant step in the development of heat-tolerant lines.

1.3.5 Epigenetic Mechanism for Stress Response and Adaptation

Environmental stresses such as heat, drought, salinity, and freezing are the main abiotic stress threat to wheat. The recent study confirms that the plants engage with

sophisticated epigenetic mechanisms to overcome the loss and damage by the environmental stresses (Kong et al. 2020). Among abiotic stress epigenetic regulation to HS responses has attracted increasing interest in researchers. Epigenetics is defined as the change in gene expression without alteration in the DNA sequences, which is crucial for the plant to environmental stresses (McCormick 2018; Zhao et al. 2021). The regulatory mechanism of epigenetics in response to HS (also other abiotic stress) involves DNA methylation, modification in histone chromatin remodeling, lncRNAs, sRNAs, change in the gene expression pattern and/or epigenetic memory of plants under HS (Liu et al. 2015; Ueda and Seki 2020).

DNA Methylation

DNA Methylation is one of the main epigenetic mechanisms that controls and regulates the genome stability, growth and cures different stress in plant (Gahlaut et al. 2020). In DNA methylation process, the methyl group (CH₃) occupies the cytosine position of DNA to form 5-methylcytosine, to make CG, CHG, and CHH (H represents A, T, or C) (Cokus et al. 2008; Law and Jacobsen 2010) in which CG is the most abundant and widespread methylation site (Park et al. 2016). Several reports have been studied so far and confirm the involvement of DNA methylation in the regulation of genes implicated in the plant response to HS (Popova et al. 2013, Liu et al. 2015, 2017a, b). Cytosine-5 DNA methyltransferase (C5-MTases) gene family plays a crucial role in plant abiotic stress responses via DNA methylation. Fifty-two cytosine-5 DNA methyltransferases (C5-MTases) genes were identified through genome-wide identification and expression profiling of cytosine-5 DNA methyltransferases in wheat genome under heat and drought stress, the expression pattern of C5-MTase genes was differ, and it is specific for the developmental stage and particular tissue in plant (Gahlaut et al. 2020). In *Arabidopsis*, the histone acetyltransferase GENERAL CONTROL OF NONREPPRESSED PROTEIN5 (GCN5) has the main role to mitigate the irreversible effect due to HS by promoting H3K9 and H3K14 acetylation of heat shock factor A3 (HSFA3) and UV-HYPERSENSITIVE6 (UVH6). The same function result was confirmed by the Ni et al. (2018) in wheat, where the histone acetyltransferase TaGCN5 gene is upregulated under heat stress as in *Arabidopsis*.

Histone Modification

Histone is the basic structural unit of chromatin having a pair of copies of H2A, H2B, H3, and H4, encased in ≈ 147 bp DNA in the nucleosome. Methylation of DNA, histone acetylation and methylation intervene the plant HS response through activation or repression of gene expression. The histone methylation mostly takes place on the histone H3 lysine residue, viz., H3K4me3, H3K36me3, H3K79me3, H3K9me2, and H3K27me3, out of which H3K4me3 and H3K27me3 are more potent to conserve epigenetic marks for activation or repression of gene (Shi et al. 2004; Yaish et al. 2009; Thorstensen et al. 2011; Black et al. 2012; Yuan et al. 2013; Wang et al. 2020). The lysine-specific histone demethylase 1 (LSD1) is the main enzyme that specifically demethylates histone H3 lysine 4 (H3K4) me1/2 (Shi et al. 2004). In response to HS, plant will start the cascade process mediated through

epigenetic regulators viz., acetyltransferases, methyltransferases, deacetylases, and demethylases-mediated methylation and acetylation which are initiated by heat response-associated recruiters (e.g., TFs, lncRNAs) to specific histones in chromatin to regulate gene expression (Deng et al. 2018; Ueda and Seki 2020). Wang et al. (2016) studied the transgenerational memory of the plant where winding of histone demethylation and the global methylation of DNA are assured. The gene for LSD1, putative nucleic acid methyl transferases and binding proteins RNA methyltransferase, and ribosomal RNA FtsJ-like methyltransferase has showed greater level in the offspring of primed plants than in those of the non-primed plants under HS at post anthesis stage.

Chromatin Remodeling

Chromatin is a complex architecture of highly condensed and tightly coiled DNA and histone protein (Cedar and Bergman 2009). The condensed and tightly coiled chromatin (default state) restrains the access of RNA polymerase and other transcription factors to genes. To facilitate transcription, the tightly coiled structure of chromatin must be opened; this process is known as chromatin remodeling (Bannister and Kouzarides 2011). There are several chromatin remodelers available viz., SWI/SNF, ISWI, INO80, and CHD that responded chromatin on different organisms, under varied stresses, which leads to change in chromatin from transcriptionally inactive to a transcriptionally active state. The structure of chromatin at a given promoter is decisive to know the transcriptional readout (Bhadouriya et al. 2021).

Epigenetic Memory

To deal with the environmental stress plants elaborate their mechanism via epigenetic memory. If the memory of the stress is present only in the first stress-free generation, then it is called intergenerational memory, while if the memory is detected in a minimum of two stress-free generations, it is known as transgenerational memory (Tardieu et al. 2018; Bhadouriya et al. 2021). In transgenerational memory, the phenotypic traits possessed by the progeny are a result of environmental stress stimulus in an earlier generation but not in the parent or progeny (Bhadouriya et al. 2021). This transgenerational epigenetic memory can be maintained for at least three generations (Suter and Widmer 2013; Zhong et al. 2013). As these changes in the epigenome are stably inherited and passed to further generations, knowledge about these changes is crucial for stress management in plants (Bhadouriya et al. 2021).

1.4 Heat Stress Priming in Wheat

Plants adopt mechanism to withstand harsh environmental conditions. Priming is one among them where tolerance is developed in plant by prior exposure to the stress in early stage of life. Initial study on priming was concentrated to understand pathogen defense mechanism (Conrath et al. 2002). Priming enhances the tolerance

by prior exposure to sublethal stress to reprogramming and to activate the molecular machinery (Lämke and Bäurle 2017). Priming can be an excellent stress tolerance strategy in vast majority of stresses in many crops in less time to any variety if tolerant cultivar is not available.

Mechanism of heat stress priming is relatively conserved well among many organisms (Mittler et al. 2012), exposure to sublethal heat stress induces reprogramming of cellular mechanism which led to thermotolerance in later stages of plant growth. Overall mechanism of priming and tolerance can be divided into three major steps as heat priming by exposure to sublethal heat stress, memory establishment, and adaptive response on second episode of lethal heat stress (Sanyal et al. 2018). Heat stress memory state induced by initial priming will be in activated state for several days by heat stress memory genes which enables relevant transcript to be expressed in high quantity to enhance the stability of proteins or enzymes upon occurrence of further heat stress (Chang et al. 2006, 2007; Nishizawa et al. 2006; Meiri and Breiman 2009; Lämke and Bäurle 2017).

Heat stress priming during early vegetative stage like stem elongation has positive impact on grain quality, yield, photosynthesis, etc. in wheat. However, phenological stage of crop during priming treatment influences the efficiency of priming (Fan et al. 2018). An early priming treatment at three and five leaf stage are not showing any significant difference over control (Mendanha et al. 2018), whereas priming at early booting stage has positive impact on tolerance (Fan et al. 2018) emphasizing importance of stage of crop during priming treatment. And it is true that priming response differs from cultivar to cultivar (Mendanha et al. 2018) and number of priming treatments. Multiple heat priming at seedling stage found to enhance antioxidant activity at later stage in winter wheat (Wang et al. 2014). There are many examples of transgenerational effect of heat priming, where progenies of heat primed parents performed well under heat stress and produced healthy phenotype and comparatively higher yield over control (Wang et al. 2016). This acquired thermotolerance in next generation plants may be a result of heritable epigenetic modification or signal transduction to trigger stress response factors in the progenies (Wang et al. 2016). Heat stress tolerance in the progenies of drought primed plant (Zhang et al. 2016) and increased nitrogen use efficiency of early-stage drought priming (Liu et al. 2017a, b) show interrelation among priming phenomenon of different abiotic stresses. Genome-wide expression analysis, transcriptome and proteome analysis revealed higher rate of photosynthesis, activity of antioxidants, lower cell membrane oxidative damage by the upregulation of genes responsible for heat stress response like HSPs, redox homeostasis, sensing, and signaling. However, metabolism-related genes were downregulated (Xin et al. 2016), which might have protective role by conserving energy and diverting it to plant survival. Heat priming acts as an adaptive mechanism to heat stress at cellular level and ensures the survival of plant under further heat stress condition. All the adaptive mechanisms discussed above along with their attributing traits are presented in Fig. 1.1.

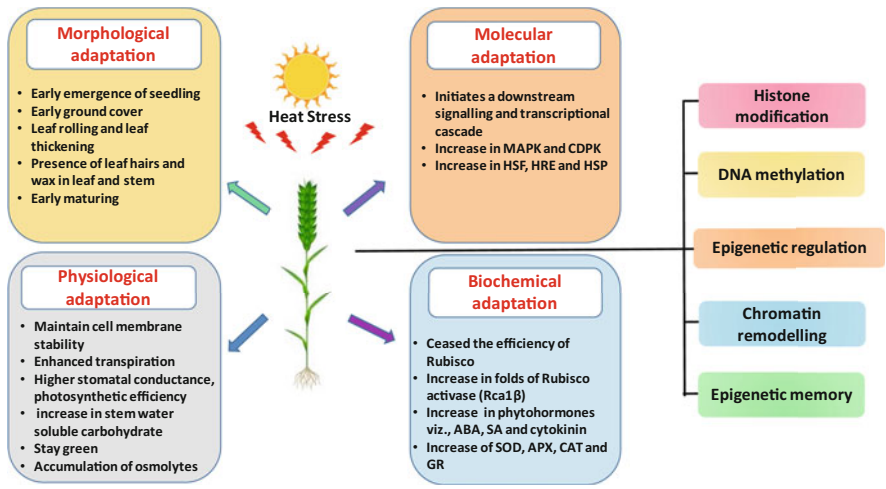


Fig. 1.1 Different heat stress adaptation mechanism in wheat

1.5 Summary

Wheat crop is challenged by heat stress affecting productivity in major wheat growing areas. In order to avoid effects of heat stress, plant adapted various strategies at morphological, physiological, molecular, epigenetic, and biochemical levels. Understanding about different mechanism by which wheat crop tolerate under heat stress situation will help us in selection and in improving the heat-tolerant varieties in wheat. Wheat being cold loving crop, the study on its response to heat stress is critical to have better insight into metabolisms, several pathways and cascades involved during the heat stress. Further, this knowledge will help us to screen the genotypes for heat tolerance and identifying number of genotypes having different desirable traits so that they can be recombined to develop tailor-made wheat with better heat tolerance. The various novel techniques like proteomics, genomics, and metabolomics can be applied to dissect genetics behind the heat stress response. This enables identification of molecular markers linked to heat stress tolerance genes facilitating the breeding for heat stress tolerance in wheat.

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