Chapter 9
Role of Heat Shock Proteins (HSPs) and Heat Stress Tolerance in Crop Plants

Zeba Khan and Durre Shahwar

Abstract Environmental stresses can alter the physiological mechanisms of plants by dysfunctioning proteins which is a major consequence of less crop productivity. Heat stress (high temperature (HT)) is one of the major abiotic stresses that causes damage to the plant tissues. Such stress limits the crop production by altering developmental growth, metabolism and productivity. Better crop yield and sustainable food quality in HT become the potent agricultural goal in this ongoing climate change era. In the molecular level, the plant's survival strategy in HT condition is to change the expression of gene during transcription/translation process resulting in the generation of heat shock proteins (HSPs). Sometimes it alters the level of heat shock factors (HSFs) that control the expression of heat shock and non-heat shock gene. These HSPs are ubiquitous and are produced in all organisms from prokaryotes to eukaryotes under stress condition and are highly conserved and constitutively function as molecular chaperons, which multipurpose function. Apart from the heat stress, HSPs are known to be expressed during other stressful conditions such as during tissue damage, inflammation, hypoxia, UV light, cold stress, water stress, etc. HSPs have been classified in plants on the basis of approximate molecular weight and their intracellular localization. Plants growing under HT stress can perceive HT stimulus and transmit the signal causing effect in terms of physio-biochemical and gene regulatory responses. Under HT, oxidative stress is generated as a result of the production of reactive oxygen species (ROS) which alters the synthesis of macromolecules and nucleic acids. Thus, HSPs play an important role in maintaining cell membrane integrity, ROS scavenging and production of antioxidants, osmolytes. In this chapter, we are discussing physiological and biochemical responses to heat stress and the adopted molecular approaches for the mitigation strategy of the plant under HT.

Keywords Chaperons · Heat shock proteins · ROS · Stress tolerance · Crop productivity

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Z. Khan (✉) · D. Shahwar
Department of Botany, Aligarh Muslim University, Aligarh, Uttar Pradesh, India

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Abbreviations

HS	Heat stress
HSF	Heat shock factor
HSPs	Heat shock transcription factors
HSPs	Heat shock proteins
HT	High temperature
QTL	Quantitative trace loci
ROS	Reactive oxygen species
TFs	Transcription factors

1 Introduction

One of the stresses exerted by the environment on the plant is heat stress which produces certain heat shock proteins (HSPs). In today's scenario, increase in the mean temperature due to global warming is raising serious concerns in the agriculture around the world causing an estimated annual loss of crop yield up to billions of dollars (Mittler et al. 2012). Heat shocks cause severe damage to the crop by altering protein synthesis, inactivating major enzymes and membrane damage. High temperature limits the plant growth and induces oxidative stress, culminating into yield loss and nutrient quality.

Heat stress causes improper folding of polypeptide chains of non-native proteins leading to unfavourable protein aggregations resulting in dysfunctioning of proteins (Moriwaki et al. 1999). Plants have developed molecular chaperons for stabilizing protein by assembling multi-protein complexes, folding or unfolding of proteins, control of cell cycle and signalling, transport of proteins into respective compartments at the subcellular level to protect it against stress or apoptosis (Lindquist and Craig 1988).

HSPs, heat shock transcription factor (HSF) and chaperons are necessary for balance and restoration of protein structure and sustain the condition of the plant under high-temperature stress (Boston et al. 1996). Lethal doses of high temperature induce heat shock response which protects the organism from cellular damage and enables the renewal of normal cellular and physiological activities allowing a higher level of thermotolerance in plants (Schöffl et al. 1998). Heat shock response is also associated with many environmental stresses. High temperature or heat stress can cause excessive generation of ROS and oxidative damage (Hasanuzzaman et al. 2012a, b, c, 2013a; Asthir 2015). The plant enables to tolerate heat stress under high-temperature condition by making some changes in the plant body such as plants accumulate different metabolites like antioxidants, osmoprotectants and HSPs by altering their metabolism in various ways (Bokszczanin and Fragkostefanakis 2013; Hasanuzzaman et al. 2013c). Heat stress also causes alterations at molecular level where genes are involved in the expression of factor such as osmoprotectants (glycine betaine, GB; proline, Pro; trehalose, Tre; etc.), phytohormones (gibberellic acids, GA; abscisic acid, ABA; brassinosteroids, BR; jasmonic acids, JA; salicylic acid, SA; etc.), detoxifying enzymes, signalling molecules (e.g. nitric oxide, NO), transporters, regulatory proteins, free radical scavengers, polyamines (spermidine, Spd; putrescine, Put; and spermine, Spm) and protectants in trace elements (silicon, Si; selenium, Se; etc.). These factors involved in signalling cascades and transcriptional control process have been found effective to counter effect of HT stress (Wang et al. 2004; Krasensky and Jonak 2012; Semenov and Halford 2009; Hasanuzzaman et al. 2010, 2012b, c, 2013a, b; Waraich et al. 2012; Barnabás et al. 2008). HSPs or molecular chaperons are an important class of protein which plays an important role in stress signal transduction for protection and repair protein damage and maintains plant homeostasis (Boston et al. 1996).

2 Classification of Heat Shock Proteins (HSPs)

HSPs are a family of proteins that are produced by cells under the stressful condition in almost all organisms. HSPs are ubiquitous, obtained in both prokaryotic and eukaryotic cells. It plays an essential role in cell functions because of its high level of conservation. They have been extensively studied by the researchers on the basis of cellular localization, regulation and functions (Hightower 1991; Benjamin and McMillan 1998). Italian scientist (Ritossa 1962) described the gene expression in chromosome of *Drosophila melanogaster* following exposure to heat shock. It was the beginning of discovery of heat shock proteins, but nowadays heat shock proteins are considered to be induced by different kinds of stresses such as low temperature, UV light, wound healing or other abiotic stresses (Vierling 1991; Boston et al. 1996). It has been shown that during the cell growth and development, HSPs are responsible for folding of protein, assembly, translocation and degradation (Lindquist and Craig 1988; Wang et al. 2004). Whitley et al. (1999) reported that some HSPs accomplish chaperon functions under stress conditions within the cell, due to which they are also known to be HSPs because of their aggregation when denatured by high temperature. There are five major families of HSPs in plants and animals conservatively recognized as molecular chaperons.

The molecular size of HSP families ranges from 10 to more than 100 kDa, located in various cellular compartments. The HSPs were grouped into five families (Kregel 2002) on the basis of their molecular weight such as HSP100, HSP90, HSP70, HSP60 and small HSP (sHSP) (Wang et al. 2004; Kotak et al. 2007; Gupta et al. 2010; Al-Whaibi 2011) (Fig. 9.1, Table 9.1). Some of these HSPs are mainly found in cytoplasm and are expressed in response to biotic and abiotic stresses (Vierling 1991; Boston et al. 1996). Moreover, these HSPs are also found in several cytoplasmic organelles such as endoplasmic reticulum, mitochondria, chloroplasts and the nucleus which plays a dynamic role in protein homeostasis (Vierling 1991; Boston et al. 1996).

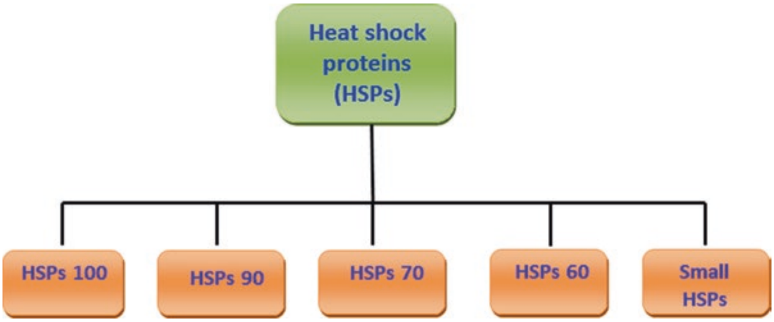

Fig. 9.1 Classification of heat shock proteins (HSPs)

Table 9.1 Sites and functions of HSP families (Kregel 2002)

HSP family/ classification	Cellular location/site	Function/role
HSP 20 (sHSPs)	Cytosol, endoplasmic reticulum, mitochondria, chloroplast	Preventing aggregation, co-chaperons
HSP 27 (sHSPs)	Cytosol, nucleus	Microfilament, antiapoptotic, stabilization
HSP 60	Mitochondria	Prevents aggregation of denatured proteins, refolds proteins, proapoptotic
HSP 70 family		Antiapoptotic
HSP 72 (HSP 70)	Nucleus, cytosol	Cytoprotection, protein folding
HSP 73 (Hsc 70)	Nucleus, cytosol	Molecular chaperons
HSP 75 (mHSP 70)	Mitochondria	Molecular chaperons
HSP 78 (GRP78)	Endoplasmic reticulum (ER)	Molecular chaperons, cytoprotection
HSP 90	Cytosol, nucleus, endoplasmic reticulum (ER)	Translocation of protein, regulation of steroid hormone receptors
HSP100/104	Cytosol	Folding of protein

2.1 HSP100

Heat shock protein with the molecular weight of 100 to 104 is categorized into HSP 100 family present in both prokaryotes and eukaryotes and located in the cytoplasm with HSP 40, HSP 70 and HSP 90. The bacterial HSP 100 proteins are known to be considered as Clp proteins which are made up of two-subunit protease system (Squires and Squires 1992). The larger subunit ClpA functions as chaperon, whereas smaller subunit ClpP is protease. HSP100 are categorized into two major classes of protein: class 1 protein containing two ATP-binding sites and class 2 proteins containing only one ATP-binding site (Schirmer et al. 1996; Miernyk 1999). Under heat stress condition, HSP 100 proteins reactivate the aggregated proteins by resolubilization of nonfunctional protein and also help to break irreversible polypeptides (Bosl et al. 2006; Kim et al. 2007; Gupta et al. 2010). A member of this family is essential for high-temperature tolerance but not for germination and growth in plants (Queitsch et al. 2000; Hong and Vierling 2001; Lin et al. 2014). The yeast homolog HSP 104 is necessary for induced thermotolerance in yeast. HSP 100 of yeast have deletion which can be complemented with the wild type of plant HSP 100 homologs from several crops like *Arabidopsis*, wheat, soybean, tobacco, etc. so it can be concluded that roles of plant HSP 100 proteins and yeast are conserved in thermotolerance (Lee et al. 1994). Wells et al. (1998) and Ling et al. (2000) suggested that plant HSP 101 not only plays an important role in HT but also has been also involved as RNA-binding protein for mediating translational enhancement of TMV (tobacco mosaic virus) RNA and ferredoxin mRNA (Ling et al. 2000). According to Lee et al. (2006), HSP 100 family is also involved in housekeeping functions, necessary for development of chloroplast. It seems that this class also participates in facilitating the normal situation after severe stress in organism (Gurley 2000).

2.2 HSP90

HSP90 is found both in prokaryotic and eukaryotic cells, and it is most abundant in the cytoplasm and endoplasmic reticulum and induced under heat stress. It possesses ATP-binding domain at N-terminal, substrate-interacting middle domain and dimerization domain at C-terminal (Jackson 2013). HSP90 assists in proper folding of proteins and also plays an important role in protein trafficking, protein degradation, signal transduction and cell cycle control (Efeoglu 2009). Being important for proper functioning of many signalling pathways, HSP90 plays an important role in regulation of cellular response to environmental and other external stimuli, on exposure to stress by redirecting cellular metabolism in such a way so as to endure tolerance (Wang et al. 2004). HSP90 genes have been isolated from different plants such as *Arabidopsis* tomato (Koning et al. 1992), maize (Marrs et al. 1993) and *Brassica napus* (Krishna et al. 1995) and *thaliana* (Krishna and Gloor 2001). HSP 90 is subdivided into HSP 90α and HSP90 β. HSP 90 cohered with protein kinases, intermediate filaments, steroid receptors, actin microfilaments and microtubules in a specific manner. This class of HSPs plays another key role to regulate the glucocorticoid receptor (GR) activity (Pratt et al. 2004). Matsumiya et al. (2009) and Gupta et al. (2010) recorded that HSP90 connects with different intracellular proteins such as tubulin, calmodulin, kinases, actin and receptor proteins under physiological conditions. It has been reported that HSP 90 is key for normal growth and development in *Arabidopsis* and *Nicotiana benthamiana* (Liu et al. 2004; Sangster and Queitsch 2005; Sangster et al. 2007). Cytoplasmic HSP90 is also considered accountable for resistance against pathogen by reacting with resistance protein (R) which is signal receptor of the pathogen. Liu et al. (2004) studied reaction between HSP90 and resistance protein in *A. thaliana* and tobacco species, viz. *Nicotiana tabacum* and *N. benthamiana*. HSP90-silenced *N. benthamiana* plants exhibited growth and phenotypic alterations such as chlorotic leaves, change in flowering time and morphology.

2.3 HSP70

HSP 70 family is highly conserved classes of HSPs and present in the cytosol. Apart from being induced by high temperature and other stresses, constitutively expressed HSP70 has also important functions under no stress (Efeoğlu 2009). It has a GRP78 family which helps protein folding and refolding and enables to block protein degradation in ER. HSP 70 aids in transmembrane transport of newly synthesized protein by stabilizing them in partially folded state and removes denatured proteins and also prohibits their aggregation (Su and Li 2008). HSP 70 contains two domains of which one is of a ~45 kDa amino terminal ATP-binding domain and another one is a ~25 kDa carboxyl terminal substrate-binding domain. HSP70 functions both co- and post-translationally in higher eukaryotes. Rouch et al. (2004) reported that HSP70 and small HSPs work as molecular chaperon exhibiting coherent role in protecting plant cell from high-temperature stress.

According to Zhang et al. (2008), HSP70 and small HSP17.6 play an important role in the development of cross-adaptation to temperature stress induced by heat acclimation (HA) or cold acclimation (CA) pretreatment in grape plants. HSP70 binds to protein precursor for transfer via membranes of cell organelles such as chloroplast (Jackson-Constan et al. 2001; Soll 2002). HSP70 B is the type of HSP70 protein situated in the matrix of chloroplasts and helps in reconstruction and photoprotection of photosystem II during photoinhibition (Schroda et al. 1999). Su and Li (2008) studied that presence of HSP70 is essential in the stroma of chloroplast for the differentiation of germinating seeds during heat tolerance. HSP70 also plays an important role during biotic stress responses. Heat shock cognate 70 (HSC70) chaperon present in cytoplasm and nucleus is highly homologous to HSP70 and regulates immune responses along with SGT1 in case of *Arabidopsis thaliana*. HSP70 also plays an important function in microbial pathogenesis. Boevink and Oparka (2005) and Hafren et al. (2010) reported that HSP 70 controls the reproduction and movement of virus which induces infection. Chen et al. (2008) studied that *N. benthamiana* is infected by *Potato virus* X, *Tobacco mosaic virus* and *Watermelon mosaic virus* enhanced by cytoplasmic HSP70.

2.4 HSP60

HSP60 is located in mitochondria with mitochondrial protein import and macromolecular assembly. HSP 60 is also referred to as P60 lymphocyte protein, mitochondrial matrix protein P1 and HSPD1. In some literature it is also called as chaperonins as they are important in helping plastid protein such as rubisco (Wang et al. 2004) and assist in attaining functional configuration of imported proteins to the chloroplast

(Jackson-Constan et al. 2001). HSP60 chaperonins assist the proper folding of imported proteins, also protect from aggregation and misfolding and promote correct refolding and assembly of unfolded polypeptides in mitochondrial matrix produced under stress. Wang et al. (2004) reported that HSP 60 is generally facilitating plastid proteins such as Rubisco. HSP60 has been involved in stress response as well. The upregulation of HSP60 during stress allows regulation of cellular processes occurring in the cell. Many researchers have shown that HSP60 and other HSPs are necessary for survival of cells under toxic or stressful conditions (Rossi et al. 2002).

2.5 Small HSPs (sHSPs)

sHSPs are class of heat shock proteins which are ubiquitously produced both in prokaryotic and eukaryotic cells in response to heat stress, having size ranging from 15 to 42 kDa. In *A. thaliana*, 13 sHSPs are classified into 6 classes on the basis of intracellular localization and sequence relatedness, an additional 6 open reading frame encoding proteins which are distantly related to plastidial class of sHsps (Scharf et al. 2001). The C-terminal region of these proteins has a common alpha-crystallin domain containing 80–100 amino acid residues (Seo et al. 2006). It also has an NH2-terminal end which is quite divergent and belongs to different classes. Gupta et al. (2010) reported that small HSPs also work as chaperons like other HSPs, preventing undesirable interaction of protein, and facilitate refolding of denatured proteins. sHSPs also involve in protecting by hampering the thermal aggregation of protein (van Montfort et al. 2001). Unlike other HSPs, the activity of small HSPs is independent of ATP (Miernyk 1999). According to Kotak et al. (2007) and Liberek et al. (2008), HSP20 is the type of sHSPs which sustained denatured proteins in a folding state and enables ATP-dependent disaggregation through the HSP70/90 chaperon system. sHSPs are also known for viral infection similar to HSP70/HSP40 (Verchot 2012). Several researchers reported that it also plays an important role in plant disease resistance. For example, HSPs 20 is the member of small HSPs, which associate with I-2 and provide resistance to *Fusarium oxysporum* (Simons et al. 1998) by the accumulation of I-2 (Verchot 2012). Another HSP20 from *N. tabacum* (NtsHSP) is known to be involved in resistance against biotic stress, for example, disease resistance in plants (Maimbo et al. 2007). Mogk et al. (2003) reported that sHSP 18.1 from *Pisum sativum* and sHSP 16.6 from *Synechocystis*, isolated under lab condition, bind to unfolded proteins and further enable refolding of proteins by HSP70/HSP100 complexes. sHSPs play an important role in thermotolerance as well as other biotic and abiotic stresses which occur as a result of genetic changes produced in the absence of any environmental stress at specific developmental stages such as germination, pollen development embryogenesis and fruit maturation in the expression of sHSPs in transgenic plants (Harndahl et al. 1999; Sun et al. 2001, 2002).

3 Role of HSPs in Encountering High-Temperature Stress

High-temperature stress induces expression of defence genes which normally do not express under normal condition (Morimoto 1993). Gupta et al. (2010) reviewed that gene expression and synthesis of proteins inside the cells are triggered by stress. However, a factor that causes stress firstly blocks cell metabolism including DNA replication, transcription, mRNA export and translation, until cells start to recover (Biamonti and Caceres 2009).

Expression/transcription of HSP genes is regulated by regulatory proteins known as heat stress transcription factors (HSFs) which are present in an inactive form inside the cell cytoplasm (Nover and Baniwal 2006). HSFs contribute in all phases of heat stress response including maintenance and recovery. According to Baniwal et al. (2004) and Hu et al. (2009), HSFs are also known as transcriptional activators for heat shock response. There are 15 known HSFs in *Arabidopsis thaliana* (Nover et al. 2001), whereas in tomato >21 HSFs are known to play an important role in heat stress response (Scharf et al. 1998). Out of 21 only 2 of these HSFs such as HSF A2 and HSF B1 are heat inducible, but their expressions are controlled by HsfA1which is known to be a master regulator of the HSR (Mishra et al. 2002).

HsfA2 is a dominant HSF during high-temperature stress because it is recognized as 'work horse' of the stress response. When plant feels high-temperature stress, the inactive HSFs located in the cytosol are detached from HSP and activated and polymerized into triplets/trimers. After this phenomenon, these trimers' HSF gets phosphorylated in the cytoplasm and transported into the nucleus where they stick to the heat shock element located in the promoter region on the HSP gene. After transcription and translation of mRNA, level of HSPs in the cytoplasm increases (Usman et al. 2014) (Fig. 9.2). Role of HSPs under heat stress in different crop plants has been enlisted in Table 9.2.

4 HSPs/Chaperons Induced Heat Stress Response Mechanism in Plants

Heat stress induces protein denaturation which is a constant direct or indirect consequence of not only heat stress but any physical stress, as stresses are defined as factors impeding normal cellular functions carried out by proteins. Among the HSP/chaperon 'client proteins', many of them are primary metabolism enzymes and signal transduction proteins which play essential roles in the folding of proteins and in turn proper functioning of cells under stress. Plants respond to unfavourable changes through developmental, physiological and biochemical ways, and these responses require the expression of stress-responsive genes, which are regulated by a network of transcription factors (TFs), called as heat stress transcription factors (HSFs), that form an active trimeric complex, move to the site of the target genes and rapidly initiate transcription, recruited under stress conditions such as cold, osmotic,

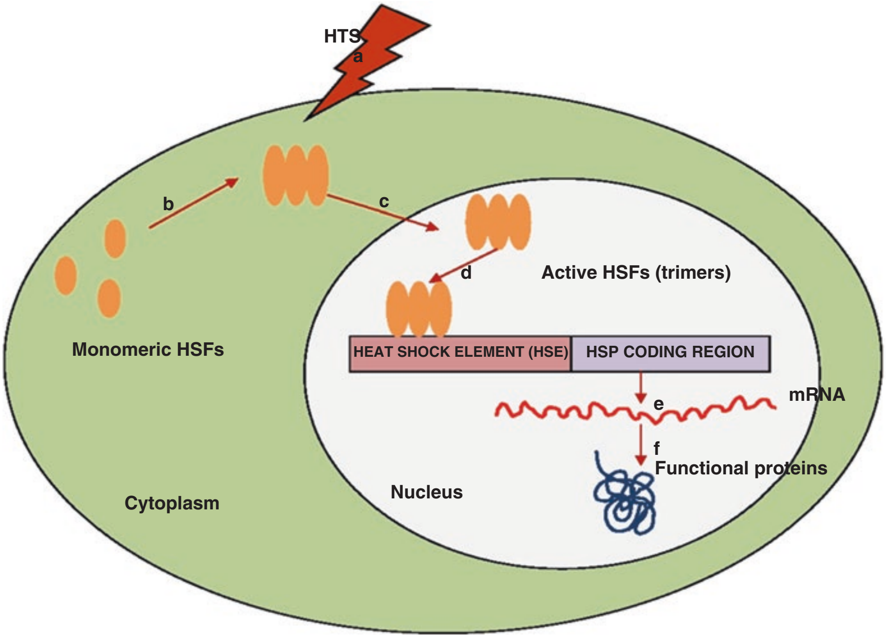

Fig. 9.2 Illustrative diagram exhibiting the molecular mechanism of heat shock proteins (HSPs)

Table 9.2 Role of HSPs in different crops

Types of HSP	Stress types	Organisms	References
HSP70	Heat stress	Rice, wheat, foxtail, millet, *Chrysanthemum*, barley	Hu et al. (2009), Rollins et al. (2013), Singh et al. (2016), Zhang et al. (2017)
HSP90	Heat stress	Wheat, alfalfa, soybean	Li et al. (2013), Xu et al. (2013)
HSP100 and HSP101	Heat stress	Rice, maize, *Brassica*	Young et al. (2004)
HSP60	Heat stress	Grasses	Xu et al. (2011)
HSP17.8 and HSP17.2	Heat stress	*Rosa chinensis*, *Camellia sinensis*	Jiang et al. (2009), Wang et al. (2017)
HSP17.6	Heat stress	*Brassica napus*	Young et al. (2004)

drought, salt, UV, high light, oxidative stress and pathogen infection (Swindell et al. 2007). These HSFs are present in the cytoplasm as single and free because there is no binding activity with DNA in the absence of stress, however when stress starts, the factors aggregate in triplet and accumulate in the nucleus. Inducers of molecular chaperons, or heat shock transcription factors are grouped into three classes A, B and C, according to the structural differences in their triplets aggregation, as plant HsfA such as HsfA1 and HsfA2 in *Lycopersicon esculentum*, plant Hsf B such as Hsf B1 in *L. esculentum* and plant Hsf C (Tripp et al. 2009). $HSFA_2$ has been found to be the dominant HSF in tomato and *Arabidopsis* on the basis of its high activator potential for transcription of HSP genes and its strong accumulation under long-term heat stress or repeated cycles of heat stress and recovery (Mishra et al. 2002). HSFA2 and A1 form heterodimers resulting in synergistic transcriptional activation of HS genes after HSFA2 are accumulated in the nucleus of cells (Chan-Schaminet et al. 2009). Studies in the tomato showed that HsfA1a is the master regulator that is responsible for the induced stress gene expression including the synthesis of both HsfB1 and HsfA2 (Asthir 2015). Studies on B and C class heat shock transcription factors are meagre in plants and are considered inhibitory as they lack the activator motif AHA (aromatic, hydrophobic, acidic) that is necessary for the transcriptional activity of class A HSFs (Jacob et al. 2017). Each HSF has its role in the regulatory network in plants. However, all cooperate in regulating many functions and different stages of response to periodical heat stress (triggering, maintenance and recovery).

5 Heat Stress Tolerance in Crops

In the natural environment, plants are usually exposed to the combined effect of temperature and light. But excess exposure of plants to a temperature above the range of optimal can cause disturbance to the overall life cycle of the plant.

5.1 Effect of Heat Stress on Germination and Plant Growth

Heat stress acts as a prime factor in altering the rate of plant development. Each species has a specific tolerance temperature range from the boundaries of observable growth. Reduced germination percentage, plant emergence, growth inhibition, abnormal seedlings, poor seedling vigour and reduced radical and stunted seedlings are major impacts caused by heat stress recognized in a variety of cultivated plant species (Kumar et al. 2011). High temperatures may also show visual stress symptoms like discolouration of fruits and leaves, scorching of the twigs and leaves senescence (Vollenweider and Gunthardt-Goerg 2005). It has been studied that the increase in temperature to optimum thresholds stimulates biochemical mechanisms, affecting the rate of development and declining the lengths of growing seasons which could have consequently an adverse impact on yield (Cleland et al. 2007). Studies in maize showed elevated temperature beyond 37 °C impaired protein synthesis in embryo leading inhibition in germination and complete halt of coleoptile growth at 45 °C (Riley 1981; Akman 2009). According to Sung et al. (2001), HSP70s may be needed in two important aspects of protein metabolism during germination. First, as a result of seed desiccation during HT, proteins that are unfolded or misfolded could be susceptible to aggregation during seed imbibition (i.e. rehydration of proteins), and presence of these HSP70 chaperons in every compartment of the cells soon after rehydration is necessary to minimize the toxic effects of protein aggregation. Second, the initiation of active synthesis and translocation of proteins must be protected for the proper functioning of metabolic activities during germination.

5.2 *Effect of Heat Stress on Yield*

Stress especially HS is the principal cause of reduced production of crops globally and in turn responsible for lowering the average yield of major crops by more than 50% (Mahajan and Tuteja 2005) by constraining grain filling. Heat stress can occur very abruptly and even short episodes of exposure to high temperature can cause a considerable decline in yield. The reasons behind the decreased yield under high temperature are impaired meiosis, pollen germination and pollen tube growth, reduced number of pollen grains, proembryo and unfertilized embryo (Cao et al. 2008). The reproductive phase is more sensitive to high temperature, as it interferes with anther dehiscence and gametophyte development, which resulted in a final yield reduction (Nadeem et al. 2018). High heat exposure during pod and seed set stages results in a substantial decrease in crop yield by a reduction in seed weight and effecting the economic production. Elevated temperature speeds up the rate of seed filling by reducing the duration of this stage ultimately affecting the yield potential (Kaushal et al. 2016). Many crop plants show early maturation, which is intimately linked with smaller yield losses under high temperatures, which may be attributed to the engagement of an escape mechanism (Adams et al. 2001). Heat stress negatively affects the nutritional quality of cereals and oilseeds as it substantially reduces the oil, starch and protein contents (Maestri et al. 2002). Studies on *Sorghum* show that high-temperature exposure (>36–38 °C) during flowering time for 10–15 days resulted in reduced pollen germination, failure of fertilization and flower abortion (Prasad et al. 2008; Singh et al. 2015). Similarly, it has been found that mean temperature beyond 34 °C enhances the rate of senescence in wheat resulting in a significant reduction in yield (Lobell and Gourdji 2012). In tomato (*Lycopersicum esculentum* Mill.), HS influences meiosis, fertilization and growth of fertilized embryo consequently resulting in a noticeable reduction in the yield (Camejo et al. 2005).

5.3 *Effect of Heat Stress on Plant Physiology*

The increase in temperature up to a certain level shows a positive response towards plant growth, photosynthesis, respiration and enzyme activity; after that these parameters tend to decline due to change in the cellular state, lipid composition, membrane fluidity and organelle properties of the plant (Hasanuzzaman et al. 2013d) (Fig. 9.3). Plants may experience different types of stress at different devel-

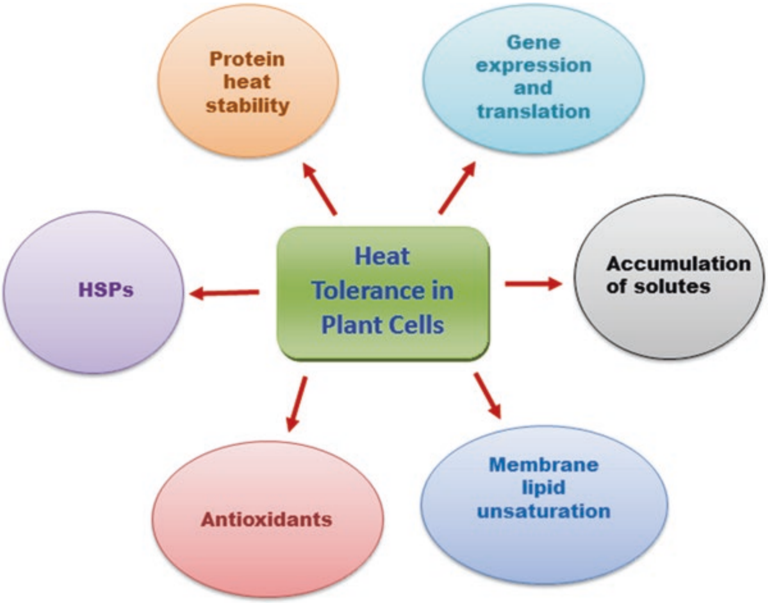

Fig. 9.3 Affecting factors for the cellular level of heat tolerance in crop plants

opmental stages, and their mechanisms of response to stress may vary in different tissues (Queitsch et al. 2000). High-temperature stress tends to reduce the relative water content of the crop and induces oxidative stress-mediated damage to the cell structures and associated proteins causing physiological drought.

5.3.1 Photosynthesis

High temperature, whether transitory or constant, affects plant growth and productivity by reducing photosynthesis. Photosynthesis is one of the most crucial heat-sensitive physiological processes in plants. Efficient photosynthesis involves photosynthetic pigments and photosystems, the electron transport system, CO_2 fixation pathways and glycolic metabolism. Damage to any of these components may reduce photosynthetic capacity (Ashraf and Harris 2013). Transitory or constant high-temperature stress reduces photosynthesis and limits plant growth and productivity (Wang et al. 2001); however moderate heat stress causes reversible-irreversible damage to the photosynthetic apparatus, resulting in greater inhibition of plant growth (Yan et al. 2011). Photosynthesis incorporates numerous components, including CO_2 reduction pathways, photosynthetic photosystems and the electron transport system, as its one of the most intricate physiological processes in plants (Ashraf and Harris 2013). High temperature alters leaf stomatal conductance and intercellular CO_2 concentration, resulting in the closure of stomata which might be another reason for impaired photosynthesis that affects the intercellular CO_2 (Greer and Weedon 2012). Ribulose-1,5-bisphosphate (RuBP) carboxylase/oxygenase (Rubisco) catalyses the first step in net photosynthetic CO_2 assimilation and photorespiratory carbon oxidation. The enzyme Rubisco is inefficient as a catalyst for the carboxylation of RuBP and is subject to competitive inhibition by O_2, inactivation by loss of carbamylation and dead-end inhibition by RuBP which make Rubisco rate limiting for photosynthesis. The decline in Rubisco activity results in a loss in photosynthesis. It is also suggested that high temperatures inactivate Rubisco activase (Salvucci and Crafts-Brandner 2004), which is essential for the activity of Rubisco. The repress of carboxylation processes by HT is likely a cause for the Rubisco decline that causes photosynthesis to plummet at higher temperatures. Under such conditions, inhibition of the repair of photodamaged PSII as a response to limitations in fixation of CO2 might accelerate photoinhibition.

Organelle-localized low-molecular-weight HSPs have been identified to be produced at high temperatures, and their association with membranes upon heat stress was reported (Adamska and Kloppstech 1991), suggesting that HSPs play a key role in protecting photosynthetic electron transport, under high-light conditions. Dual role of LMW HSP21 in tomato has been described as protecting PSII from oxidative damage (Neta-Sharir et al. 2005). In vivo experiments have demonstrated that small HSPs could associate with thylakoids and protect O_2 evolution and OEC proteins of PSII against heat stress. The protein possesses the unique property to associate with thylakoid membranes during heat stress and support the stability of thylakoid membranes.

Heat stress induces changes in the structure of Chl-protein complexes, and the integrity of thylakoid membranes is also compromised due to destacking of thylakoid membrane (Gounaris et al. 1983), and thus inactivation of enzyme activity constitutes the early effects of thermal stress. These structural transformations are also reflected by the ion leakage from heat-stressed leaves (Inaba and Grandall 1988; Wahid and Shabbir 2005) and changes in energy distribution between the two photosystems (state transition mechanism) due to high-temperature stress in vivo (Mohanty et al. 2002). The heat-induced changes in the structure of Chl-protein complexes and the inactivation of enzyme activity constitute the early effects of thermal stress. Among the various components of the photosynthetic machinery, the oxygen-evolving complex of PSII is most sensitive to heat. This might be due to the loss of two out of four Mn ions from oxygen-evolving complex (Enami et al. 1994, 1998). The loss of photosynthetic activity is partly caused by the inactivation of the acceptor side of PSII and reduction of the rate of electron transport in the chloroplasts. The detrimental effects of heat on chlorophyll and the photosynthetic apparatus are also associated with the production of injurious reactive oxygen species (ROSs) (Camejo et al. 2006; Guo et al. 2007). High temperature modifies the activities of carbon metabolism enzymes, starch accumulation and sucrose synthesis, by down-regulating specific genes in carbohydrate metabolism (Ruan et al. 2010).

5.3.2 Water Loss

High temperature is generally associated with reduced water availability to the plants, and this water shortage results in the inhibition of the photosynthesis process, and the reserves become critical because respiration continues to demand substrates; as a result, the cellular activity is hampered and nutrient supply to the generative organs are diminished. Generally, plants try to stabilize their tissue water content irrespective of temperature when moisture is available in ample quantity; however, rise in temperature proves fatal under limited supply of water (Machado and Paulsen 2001). Wahid and Close (2007) observed a rapid reduction in leaf tissue water contents in sugarcane exposed to high temperature despite the fact that the ample quantity of water was available in the soil. This water loss is more during the day as compared to night because vital physiological activities like transpiration and photosynthesis also occur. Tsukaguchi et al. (2003) reported that under heat stress, water loss was more common during the daytime because of increased transpiration than night time, causing stress in snap bean (*Phaseolus vulgaris* L.). Sita et al. (2017) reported that heat stress affects plant-water relations due to the rapid loss of water from the soil, which affects soil temperature and transpiration. Heat stress also reduces the growth of the roots which limits the supply of water and nutrients to the above-ground parts of the plant (Wahid et al. 2007; Huang et al. 2012).

5.3.3 Oxidative Stress

A well-known consequence of elevated temperatures in plants is oxidative stress caused by a heat-induced imbalance of photosynthesis and respiration (Fitter and Hay 1987), which mediates damage to cell structures, including lipids, membranes, proteins and DNA. High-temperature stress causes multi-step injuries to the plasma membrane and produces activated oxygen species, where membrane lipids and pigments peroxidation compromise membrane permeability and function, resulting in cellular damage. ROS cause damage to a wide range of cellular components such as the photosynthetic apparatus and various other components, hindering thus metabolic activities and affecting plant growth and yield by limiting metabolic flux activities (Sairam and Tyagi 2004; Xu et al. 2006). Subsequently, ROS production contributes to the transduction of the heat signal and expression of heat shock genes (Königshofer et al. 2008).

To counteract the injurious effects of over-produced ROS under heat stress, plants have evolved complex antioxidative detoxification system which includes antioxidant enzymes such as superoxidase (SOD), catalase (CAT), guaiacol peroxidase (GPOX), glutathione reductase (GR), ascorbate peroxidase (APX), peroxidase (POX) and non-enzymatic antioxidants (Harsha et al. 2016); secondary metabolites such as phenolics including flavonoids, anthocyanins and steroids also play a significant role in combating abiotic stress responses associated with heat tolerance (Wahid 2007). These antioxidant enzymes either directly scavenge the ROS or protect plants indirectly by managing non-enzymatic defence (Anjum et al. 2011).

Rivero et al. (2001) observed accumulation of soluble phenolics in tomato followed by increased phenylalanine ammonia-lyase activity and decreased peroxidase and polyphenol oxidase activity, in response to heat stress and possible acclimation. It has also been observed that osmolyte production under high temperature is associated with protein stability and, in turn, stabilizes the structure of the membrane bilayer (Sung et al. 2003; Mirzaei et al. 2012). In response to ROS, increased content of malondialdehyde has been reported which is a pure indicator of drought-induced oxidative damage (Moller et al. 2007). For example, in pea, the lipid and protein peroxidation was increased four times under stress as compared to normal conditions (Moran et al. 1994).

Thermal stress results in the generation of ROS and production of heat shock proteins. HSPs can function in protection as molecular chaperons to prevent but no reverse protein denaturation and aggregation, as membrane stabilizers and, possibly, as site-specific antioxidants. Under thermal stress the protein structure gets distorted; these HSPs fold the protein into shapes essential for their normal functioning. Different HSPs have been identified to be produced under heat stress. For example, HSP68, localized in mitochondrion, has been found to express under heat stress in cells of potato, maize, tomato, soybean and barley (Neumann et al.. 1993). According to Wahid et al. (2007), another HSP 101 localized in maize nucleus belongs to the Campylobacter invasion antigen B (CiaB) protein sub-family, whose members promote the renaturation of protein aggregates, and is essential for the induction of thermotolerance. Therefore, to counteract the negative effect of ROS, plants generate higher levels of the antioxidants (Sharma and Dubey 2005).

5.4 Effect of Heat Stress on the Molecular Response in Plants

High temperatures cause transcriptional repression of genes involved in cell growth, such as histones and DNA polymerases, and deregulation of DNA methylation and transposon activation (Sakata and Higashitani 2008; Pecinka et al. 2010; Smith and Workman 2012). At the molecular level, heat stress causes alterations in the expression of genes involved in direct protection HT (Aprile et al. 2009; Shinozaki and Yamaguchi-Shinozaki 2007). These include genes responsible for the expression of osmoprotectants, detoxifying enzymes, transporters and regulatory proteins (Semenov and Helford 2009; Moreno and Ollerana 2011). Protein thermostability is believed to be provided by chaperons, a specific class of proteins which assist in proper post-translational folding and in maintaining proteins in a functional state; heat stress results in misfolding of newly synthesized proteins and the denaturation of existing proteins. (Ellis 1990). Increased production of HSPs occurs when plants experience either abrupt or gradual increases in temperature resulting in heat stress (Nover et al. 2001).

Heat stress also leads to the transient activation of repetitive elements or silenced gene clusters close to the centromeric regions as well as the transient loss of epigenetic gene silencing (Lang-Mladek et al. 2010; Pecinka et al. 2010). Such gene silencing mechanisms are thought to be involved in transcriptional repression by hetero-chromatinization of repetitive DNA regions in plants (Khraiwesh et al. 2012). Heat stress is known to swiftly alter the pattern of gene expression, inducing the HSP complement and inhibiting expression of many genes expressed under normal temperature conditions (Yost and Lindquist 1988). Heat stress inhibits splicing, and it was hypothesized that HSP-encoding mRNAs can be processed properly due to the absence of introns in the corresponding genes. However, subsequently, it was shown that some HSP-encoding genes have introns and, under heat stress conditions, their mRNAs are correctly spliced nevertheless (Osteryoung et al. 1993; Visioli et al. 1997). It is also supposed that other proteins different from HSPs can contribute to heat tolerance including ubiquitin (Sun and Callis 1997), cytosolic Cu/Zn-SOD (Herouart and Inze 1994) and Mn-POD (Brown et al. 1993), whose expressions are stimulated upon heat stress. Wahid and Close (2007) identified three low-molecular-weight dehydrin proteins in sugarcane leaves with increased expression in response to heat stress; the functions of these proteins are apparently related to protein degradation pathway, minimizing the adverse effects of dehydration and oxidative stress at high temperature (Schoffl et al. 1999).

Modern breeding approaches involving a wide range of markers associated with the QTLs of high-temperature tolerance have been identified; however, their actual role in marker-assisted selection is very limited. A set of 4 QTLs in *Arabidopsis* and 11 QTLs in maize were identified which play an important role in thermotolerance (Frova and Sari-Gorla 1994). Mason et al. (2010) identified QTLs in wheat related to different traits involved in heat tolerance such as grain filling duration and leaf senescence.

6 Conclusions and Future Prospects

High temperature has become major abiotic stress across the world because it affects greatly plant growth, reproduction and productivity. Understanding the molecular mechanisms of plant response to heat stress is a prerequisite since plants show a wide range of responses to heat stresses. Increase in mean temperature of the earth culminates into global warming and release of greenhouse gases in the environment which affects the plant response depicted by a variety of alterations in the growth, physiology and morphology. Therefore plant response and adaptation to the increasing temperature need to be better understood for the important crop. Detailed research defining the mechanisms of thermotolerance and understanding the nature of heat shock signalling proteins and gene expression will be valuable for developing tolerant varieties. Temperature varies in different regions all around the world, and plants show adaptation to HT according to their developmental growth and their ability to adapt to variable climatic condition. Plants accumulate antioxidant, osmoprotectant, metabolites, HSPs and different metabolic pathways to hamper the heat stress.

Future research should be focused on developing HT-resistant varieties and high-temperature-tolerant transgenic crops. At the field level, heat stress effect can be decreased by managing cultural practices such as timing and methods of sowing, irrigation and selection of cultivars and species. Exogenous application of protectants such as osmoprotectants, phytohormones and mineral elements has shown beneficial effects on plant growing under HT, due to growth-promoting effect of these compounds, and also to develop such type of plants which synthesize these compounds may prove a promising technique in producing thermotolerance crop plant.

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