Chapter 3
Heat Shock Proteins and Abiotic Stress Tolerance in Plants

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Abstract Abiotic stresses restrict plant growth and development, and reduce harvest index of many crop species worldwide. Maintenance of native conformation of proteins and reducing the accumulation of non-native proteins are imperative for survival under stress conditions as such stresses frequently lead to protein aggregation causing metabolic dysfunction. Heat shock proteins (HSP) play a key role in conferring abiotic stress tolerance. Plants protect themselves from numerous stresses by inducing HSP, besides some stress-responsive proteins, suggesting analogous response mechanisms. A close association between the HSP and ROS also co-exists, indicating that plants have evolved to gain a higher degree of regulation over ROS toxicity and can use ROS as elicitor to induce HSP for better adaptations through activating an array of molecules. Therefore, unraveling the mechanisms of plant response against various stress and the role of HSP in acquired stress tolerance is utmost important to delineate their specific function as a part of stress-responsive module. The HSP have been well characterized in different crop species, albeit the knowledge about their correlation with genome sequence information as well as their functional plasticity is limited.

Keywords Abiotic Stress · Chaperones · Co-chaperones · Heat shock factor · Heat shock protein · Protein folding · Stress tolerance

Abbreviations

ACD	α-crystalline C-terminal domains
HLS	High light stress
HMS	Heavy metal stress
HOP	Hsp70-Hsp90 organizing protein

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A. A. A. Asea, P. Kaur (eds.), *Regulation of Heat Shock Protein Responses*, Heat
Shock Proteins 13, https://doi.org/10.1007/978-3-319-74715-6_3

HSE	Heat shock element
HSF	Heat shock factor
HSP	Heat shock protein
HTS	High temperature stress
LTS	Low temperature stress
NMD	Nonsense-mediated mRNA degradation
PCD	Programmed cell death
PTM	Post-translational modification
ROS	Reactive oxygen species
sHSP	Small heat shock protein
UPS	Ubiquitin proteasome system

3.1 Introduction

Plants are sessile, and are continuously exposed to environmental stresses, both biotic and abiotic. Abiotic stresses alone or most often their combinatorial effect/s leads huge yield loss worldwide, as they cause severe threat to plant's survival (Mittler 2006). However, plants have evolved a variety of mechanisms to acclimatize to changing environmental conditions. They undergo drastic adjustments and alterations in physiological as well as molecular programs with efficient molecular machineries to perceive and overcome such stresses (Ahuja et al. 2010). Plants induce different stress-responsive biomolecules as a part of their tolerance mechanisms. One of the most important such biomolecules is the molecular chaperones, which act in reducing cells from the adverse effects of stress. Heat shock proteins (HSP) are one of the significant classes of molecular chaperones, which act in response to various stresses viz., extreme temperature, dehydration, salinity, oxidative, heavy metals, high intensity irradiations and wounding, among others (Swindell et al. 2007; Al-Whaibi 2011; Xu et al. 2011). The roles of HSP are apparently more in response to high temperature stress (HTS) when compared with other stresses. The heat shock response and the HSP are predicted to be evolutionary conserved. There is an intimate association between expressions of HSP with that of resistance to HTS, but in-depth mechanism through which HSP work to increase thermotolerance is yet to be fully understood (Singh et al. 2016). In general, regulation of protein folding and unfolding, in conjunction with their subcellular localization and eventually the degradation of unfolded and denatured proteins is the principal function of HSP (Singh et al. 2016). Several studies revealed the assorted functions of HSP and/or their homologues through their constitutive or temporal expression under the tight regulation of cell cycle, cell growth and development. These studies further suggested the role of HSP in plant growth and development particularly in embryogenesis, seed and fruit development (Siddique et al. 2008; Al-Whaibi 2011; Koo et al. 2015). The role of HSP has also been predicted in tuber development (Lehesranta et al. 2006; Agrawal et al. 2008; Agrawal et al. 2013), and nutrient acquisition during tuberization (Shekhar et al. 2016).

Several HSP have been identified and characterized in organisms across the species (Bharti and Nover 2002). Presence of conserved heat-shock domain (~70 amino acids) at carboxylic terminal is the main distinctive feature of all HSP (Helm et al. 1993), while little homology is observed in the amino-terminal regions (Chen and Vierling 1991; Vierling 1991). It has, therefore, been hypothesized that the heat-shock domain favors the accumulation of low molecular weight aggregates (sHSP), and their diversity in amino termini might be responsible for either precise substrate specificities or separate functions (Helm et al. 1993). Altogether, HSP in a range of 10–200 kDa molecular weights are distinguished as chaperones, which play a key role in stress-responsive signal transduction (Schöffl et al. 1999). It has been increasingly evident that HSP act in association with heat stress transcription factors (HSFs). The HSFs, in plant, are considered to be one of the vital components of signal transduction cascade mediating the expression and regulation of genes implicated in several abiotic stress responses (Guo et al. 2016). The increased expression of HSP under the control of HSFs is thought to play a significant role in thermotolerance (Kotak et al. 2007). The coordinated role/s of HSP and HSFs in the development of tolerance against various abiotic stresses is depicted in Fig. 3.1.

Our existing knowledge about the role of HSP and HSFs has been recapitulated in several recent reports (Baniwal et al. 2004; Wang et al. 2004; Nakamoto and Vigh 2007; Guo et al. 2016). Previous attempts to enhance thermotolerance via ectopic expression of a solitary HSP or HSF gene exhibited limited impact owing to the intricacy and genetic complexity of the HTS response (Vinocur and Altman 2005; Fragkostefanakis et al. 2015). Genome-wide expression analysis as well as the comparative proteomics in Arabidopsis subjected to HTS, or the mutants with impaired thermotolerance significantly extended our understanding of HTS responses (Larkindale et al. 2005; Echevarría-Zomeño et al. 2016). Comparative expression data analyses revealed a similar transcript accumulation pattern in different plant species subjected to HTS. Interestingly, ~ 2% of the genome has been predicted to be affected by HTS. (Rizhsky et al. 2004; Rensink et al. 2005; Lim et al. 2006).

3.2 Hsp as Chaperones

The HSP have long been anticipated to function as molecular chaperones, which actively participate in protein quality control to maintain cellular homeostasis in stressed as well as in unstressed conditions. Besides their function as molecular chaperones, detail information as to how some HSP and sHSP contribute to stress tolerance in plants from HTS in particular and other stresses in general. Are still unclear. Several molecular chaperones are identified as stress-associated proteins, most of which are originally categorized as HSP (Wang et al. 2004). In plants, five major classes of HSP have been catalogued based on their estimated molecular weight, amino acid sequence and functions; (I) Hsp100, (II) Hsp90, (III) Hsp70, (IV) Hsp60, and (V) sHSP. Some other proteins have also been identified having

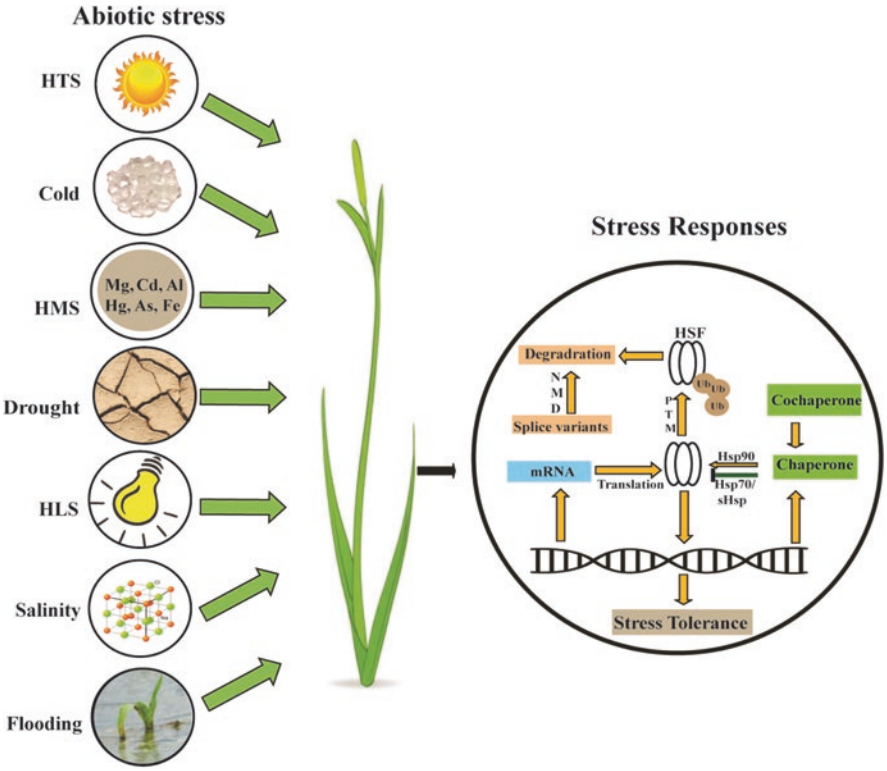

Fig. 3.1 Abiotic stress responses in plants and molecular adaptation. Abiotic stress elicits myriad of responses in plants that include the induction of various stress-responsive biomolecules. Increased expression of heat shock transcription factors (HSFs) bind to promoter regions of stress-responsive genes, eventually leading to the expression of stress-inducible HSFs, chaperones, co-chaperones and downstream HTS-responsive genes. The network of HTS-inducible HSFs is tightly regulated by the chaperone and their co-chaperones. The regulation of HSF-chaperone/co-chaperone complex is orchestrated by post-translational modification (PTM) and also, by chaperone-mediated ubiquitination and degradation by the ubiquitin proteasome system (UPS). The HSP also regulate the activities of HSFs by the association or disassociation with HSF complex, besides alternative splicing and nonsense-mediated mRNA degradation (NMD). HTS, high temperature stress; HMS, heavy metal stress; HLS, high light stress

chaperone-like functions, for examples, calnexin/calreticulin and protein disulfide isomerase since they help in protein folding (Wang et al. 2004; Al-Whaibi 2011). The HSP are localized in cytoplasm as well as in organelles, for instances, nucleus, chloroplasts, mitochondria and ER (Vierling 1991; Waters et al. 1996; Boston et al. 1996).

3.2.1 Hsp100

These chaperones are the members of the large AAA ATPase superfamily, which are implicated in multivariate stress responses. The reactivation of aggregated proteins is one of the exclusive functions of this class through re-solubilization of protein aggregates. Additionally, they help irreversibly damaged proteins to undergo degradation pathway (Wang et al. 2004; Al-Whaibi 2011). Some members of this class also play a key role in maintaining the housekeeping functions and chloroplast biogenesis Lee et al. 2007). Furthermore, these HSP contribute in expediting the post-stress normal conditions (Gurley 2000). To evade the aggregation of proteins, Hsp100 works cooperatively with Hsp70. The aggregated proteins are solubilized by the Hsp100 family proteins, which with the help of Hsp70 system could be subsequently refolded in the earlier conformations. Chaperones of Hsp100 family, in plants, are often constitutively expressed similar to several other HSP/chaperones. Their expression is induced by various environmental stresses, and is tightly regulated for developmental and metabolic cues (Queitsch et al. 2000; Keeler et al. 2000; Adam et al. 2001; Adam and Clarke 2002).

3.2.2 Hsp90

Similar to Hsp100, the chaperones of Hsp90 also work in association with Hsp70, and constitute a major part of chaperone complexes. While the major role of Hsp90 is protein folding, it also acts as the key component in signal-transduction networks, cell-cycle control, protein trafficking and in the regulation of glucocorticoid receptor activity (Pratt and Toft 2003; Pratt et al. 2004). Furthermore, the role of Hsp90 has long been acknowledged in phyto-pathogen resistance (Hubert et al. 2003; Liu et al. 2004; Thao et al. 2007). A study by Yamada et al. (2007) suggested its role in regulation of HSF in the absence and presence of HTS (Yamada et al. 2007). Expression of Hsp90 is developmentally regulated and shows differential expression in response to different abiotic stresses (Wang et al. 2004). Organelle-specific Hsp90 have been isolated and characterized from different plant species, which showed 63–71% homology at amino acid level with that of yeast and animal. In Arabidopsis, seven Hsp90 family proteins has been annotated with cytosolic subfamily AtHsp90–1 to AtHsp90–4, whereas plastid, mitochondria and ER comprising AtHsp90–5, AtHsp90–6 and AtHsp90–7, respectively (Krishna and Gloor 2001).

3.2.3 Hsp70

The Hsp70 chaperones function in association with co-chaperones, for example, DnaJ/Hsp40 and GrpE etc., which prevent aggregation of misfolded proteins and facilitate refolding of non-native proteins under stressed as well as unstressed conditions (Sung et al. 2001; Su and Li 2008). They play a distinct role in protein import and translocation, particularly in the chloroplast and mitochondria. The Hsp70 act as the major components of driving irreparable proteins to lysosomal or proteasomal degradation pathway thereby preventing unfolded protein response (UPR) (Kaufman 1999; Huang et al. 1999). Constitutive expression of several members of Hsp70 family has been reported and often referred to as 70-kDa heat-shock cognate (Hsc70), while rest of the members usually express during the stressful conditions. Moreover, some of them are associated to regulating the biological function of folded regulatory proteins, which presumably act as negative repressors of HSF-mediated transcription. There exists a large number of Hsp70 family chaperones in plants, for instance, 18 Hsp70 in Arabidopsis genome of which 14 are represented by DnaK and 4 are represented by Hsp110/SSE subfamily (Wang et al. 2004). Available data suggest their role in transcriptional regulation of heat-shock genes by preventing transcriptional activation by their HSFs. Interaction of Hsp70 with HSF inhibits trimerization and thereby binding of HSF to heat-shock elements (Kim and Schöffl 2002). Additionally, Hsp70 acts as a key module of guidance complex import i.e. translocon, which co-operatively binds to protein precursor and drives into target organelles (Jackson-Constan et al. 2001; Soll 2002). It is apparent that Hsp70B in the stroma of chloroplasts contribute throughout and/or after the photoinhibition to the photo-protection and/or restoring the function of photosystem II. Further, stromal Hsp70 is needed for the differentiation of germinating seeds and tolerance against HTS (Schroda et al. 1999; Su and Li 2008).

3.2.4 Hsp60

The members of Hsp60 family are also known as chaperonins, which evolutionarily shows homology with GroEL from E. coli. This class of molecular chaperones are ubiquitously found in prokaryotes, but in eukaryotes they are predominantly found in mitochondria and plastids. These proteins are crucial for assisting the Rubisco and other plastid proteins (Hartl 1996; Wang et al. 2004). An earlier study indicated the role of Hsp60 in folding and aggregation of many chloroplast and mitochondrial resident proteins (Lubben et al. 1989). The chaperonins act as post-transcriptional regulator of many proteins as their cooperative binding helps to prevent aggregation of the target proteins (Parsell and Lindquist 1993). Information pertaining to the plant chaperonins are restricted and it seems that the stromal chaperones (Hsp70 and Hsp60) are associated in managing functional conformation of those proteins, which have chloroplast-mediated import signal (Jackson-Constan et al. 2001).

3.3 sHSP Family

The sHSP family chaperones are omnipresent and evolutionally conserved having molecular weight ranging from 12–42 kDa. Since the molecular weight of most of the sHSP are in the range of 15–22 kDa, they are also named as Hsp20. The sHSP are different with respect to the other HSP as they encompass extremely conserved 80–100 long amino acid sequences known as α-crystalline C-terminal domains (ACD). The sHSP function in an ATP-independent manner and bind co-operatively to the non-native protein substrates. This protein complex subsequently interacts further with other chaperones such as ClpB and Hsp70/Hsp40 for reactivation of the denatured proteins. Similar to other classes, sHSP also play crucial role in cellular protection via avoiding stress-induced protein aggregation (Muthusamy et al. 2017). In addition, sHSP are the decisive components for different developmental processes in plants (Siddique et al. 2008; Al-Whaibi 2011; Koo et al. 2015). Considering sequence similarity, cellular location and functions, sHSP constitute a more diverse family when compared with the other HSP/chaperones. Recent studies indicate that all sHSP are encoded by nuclear genomes. The sHSP are reported to be localized to the cytoplasm, nucleus, mitochondria, chloroplast, ER and peroxisome (Waters 2013). The defensive role of sHSP against a wide range of biotic and abiotic stresses has been increasingly evident in different crop species including rice (Sarkar et al. 2009), wheat (Muthusamy et al. 2017), tomato (Yu et al. 2016), soybean (Lopes-Caitar et al. 2013), maize (Hu et al. 2010), barley (Reddy et al. 2014) and pepper (Guo et al. 2015). Studies related to the roles of HSP in several crops in different abiotic stresses is enlisted in Table 3.1.

3.4 Role of Hsp in Abiotic Stress

3.4.1 High Temperature Stress

The escalating earth temperature has far-reaching effects and any increase in the optimum temperature imparts negative impact on plant growth and productivity. Over the past decade, the omics studies revealed several HSP to be differentially regulated under HTS. Several previous investigations suggested the role of Hsp70 in various crops (Hu et al. 2009; Rollins et al. 2013; Zhang et al. 2014a, b; Singh et al. 2016; Zhang et al. 2017). Its role/s in protein translation, translocation, folding and preventing protein aggregates have been well explored. The members of Hsp70 has been classified into three categories: cytosolic, mitochondrial (mtHsp70) and chloroplastic Hsp70 (cpHsp70) (Yu et al. 2015). While cytosolic Hsp70 is the key regulator of HTS-mediated response (Jungkunz et al. 2011), the role of cpHsp70 has been found in chloroplast development (Sung et al. 2001, Kim and An 2013). The member of Hsp70 and Hsp90 are often found to be upregulated in response to HTS (Majoul et al. 2004; Hu et al. 2009; Li et al. 2013). Previous investigation showed

Table 3.1 Studies on the roles of HSP in different crops

Type of HSP	Stress type	Organism	Reference
Hsp70	Heat stress	Rice, wheat, foxtail millet, *Chrysanthemum*, barley	Hu et al. (2009), Zhang et al. (2017), Singh et al. (2016), Zhang et al. (2014), and Rollins et al. (2013)
Hsp90	Heat stress	Wheat, alfalfa, soybean	Majoul et al. (2004), Li et al. (2013), and Xu et al. (2013)
Hsp100 and 101	Heat stress	Rice, maize, *Brassica*	Singla et al. (1998), Lee et al. (2007), Young et al. (2001), and Young et al. (2004)
Hsp60	Heat stress	Grasses	Xu et al. (2011)
Hsp17.8 and Hsp 17.2	Heat stress	*Rosa chinensis* *Camellia sinensis*	Wang et al. (2017), Jiang et al. (2009)
Hsp17.6	Heat stress	*Brassica napus*	Young et al. (2004)
Hsp17.7	Cold stress	Peach	Zhang et al. (2011)
Hsp17.5	Cold stress	Chestnut	Soto et al. (1999)
Hsp17.4 and 17.6	Cold stress	Tomato	Sanchez-Bel et al. (2012)
Hsp26	Cold stress	Tomato, sweet pepper	Sanchez-Bel et al. (2012), Guo et al. (2007)
Hsp70	Cold stress	Wheat, barley, maize, pea, tobacco and Arabidopsis	Vítámvás et al. (2012), Kosová et al. (2013), Kollipara et al. (2002), Dumont et al. (2011), Jin et al. (2011), and Bae et al. (2003)
Hsp90	Cold stress	Wheat, tobacco, maize, sunflower and Arabidopsis	Jin et al. (2011), Kollipara et al. (2002), Balbuena et al. (2011), and Reddy et al. (1998)
Hsp21, 25, 95 and 75	Cold stress	Rice	(Hahn and Walbot 1989)
Tom 111 and tom 66	Cold stress	Tomato	Sabehat et al. (1998)
Hsp18.1, 18.2 and 22	Cold stress	Grapefruits	Rozenzvieg et al. (2004)
sHSP1	Cold stress	Plum	Sun et al. (2010)
Hsp94, 89, 75, 60, 58, 37 and 21	Dehydration stress	*Gossypium hirsutum*	Burke et al. (1985)
Hsp70	Dehydration stress	*Zea mays, Cicer arietinum, Aphanothece, Oryza sativa*	Benešová et al. (2012), Jaiswal et al. (2013), Subba et al. (2013a, b), Bhushan et al. (2011), Choudhary et al. (2009), Pandey et al. (2008), Sugino et al. (1999)
Hsp26	Dehydration stress	*Zea mays*	Benešová et al. (2012)
Hsp70 and binding protein (BiP)	Dehydration stress	*Nicotiana tabacum*	Alvim et al. (2001), Ono et al. (2001)

(continued)

Table 3.1 (continued)

Type of HSP	Stress type	Organism	Reference
Hsp90, Hsp20, CPN60, DnaJ	Dehydration stress	*Oryza sativa, Cicer arietinum*	Bhushan et al. (2011), Pandey et al. (2010)
Hsp19, chaperonin 21 precursor	Dehydration stress	*Cicer arietinum*	Subba et al. (2013a, b)
Hsp24.1	Dehydration stress	*Oryza sativa*	Agrawal et al. (2016)
Hsp17.7	Dehydration stress	*Oryza sativa*	Sato and Yokoya (2008), Sun et al. (2001)
Hsp17.5	Dehydration stress	Barley	Reddy et al. (2014)
Hsp70	Heavy metal	*Lycopersicon,* poplar, *Lotus corniculatus, Arabidopsis* and soybean	Neumann et al. (1994), Navascués et al. (2012), Yang et al. (2015), Sarry et al. (2006), Duressa et al. (2011)
Hsp90	Heavy metal (Cadmium)	*Oryza sativa*	Ogawa et al. (2009)
Hsp26	Heavy metal (Cadmium)	Soybean	Czarnecka et al. (1988)
Hsp17.7	Heavy metal (lead and arsenic)	Carrot	Lee et al. (2011)
Hsp 20,22,23.1	Heavy metal	Poplar	Yang et al. (2015)
Hsp90.3	Heavy metal	Arabidopsis	Song et al. (2012)
Hsp90	Salt stress	Soybean, Arabidopsis, *Glycine max*	Pi et al. (2016), Song et al. (2009a, b), and Xu et al. (2013)
Hsp70	Salt stress	Tomato, rice	Manaa et al. (2011), Hoang et al. (2015)
Hsp110	Salt stress	*Oryza sativa*	Singla et al. (1997)
Hsp100/ clpB2,B4 & D2	Salt stress	Wheat	Muthusamy et al. (2017)
Hsp100/clpB1	Salt stress	*Oryza sativa*	Mishra et al. (2016)
Hsp16.9	Salt stress	*Oryza sativa*	Jung et al. (2014)
Hsp16.45	Salt stress	*Lilum davidii*	Mu et al. (2013)
Hsp 17.8	Salt stress	*Rosa chinensis*	Jiang et al. (2009)
Hsp101,80 and 70	Light stress	*Arabidopsis thaliana, Chlamydomonas*	Rossel et al. (2002), Giacomelli et al. (2006)
Hsp70	Flood stress	Maize, soybean, rice, Arabidopsis	Chen et al. (2014a, b), Komatsu et al. (2013), Qi et al. (2011), and Banti et al. (2010)
Cpn60	Flood stress	Soybean	Komatsu et al. (2011)
Hsp 101	Flood stress	*Arabidopsis thaliana*	Banti et al. (2010)

(continued)

Table 3.1 (continued)

Type of HSP	Stress type	Organism	Reference
Hsp23.6	Flood stress	*Solanum lycopersicum*	Hüther et al. (2017)
Hsp90, 90.2, 90.5, 90.7	Oxidative stress	*Arabidopsis thaliana*	Song et al. (2009a, b), Nishizawa-Yokoi et al. (2010)
ClpB-cyt, ClpC2 and ClpD1	Oxidative stress	*Oryza sativa*	Singh et al. (2010)
Hsp70	Oxidative stress	*Oryza sativa*	Chankova et al. (2014)
Hsp17.6	Oxidative stress	*Arabidopsis thaliana*	Scarpeci et al. (2008)
Hsp18.6, Hsp16.9B and Hsp23.7	Combined stress	*Oryza sativa*	Zou et al. (2012), Wang et al. (2015), and Jung et al. (2014)
Hsp17.6A	Combined stress	*Arabidopsis thaliana*	Sun et al. (2001)
Hsp90	Combined stress	Soybean	Xu et al. (2013)
Hsp17.5	Combined stress	*Nelumbo nucifera*	Zhou et al. (2012)

maximum induction of OsHsp90.1, all forms of GmHsp90 (A, B & C) and AtHsp90 under HTS (Hu et al. 2009; Prasad et al. 2010; Xu et al. 2013). Hsp90.2 inhibits the expression of HSF under unstressed condition, while HSFs are induced under HTS via inhibition of Hsp90.2 (Yamada et al. 2007). A number of Hsp100 (Hsp 97, 100, 101, 103, 108, 110, 114 and 118) were found to be upregulated in response to HTS (Singla et al. 1998; Young et al. 2001; Lee et al. 2007). Of the Hsp100 members, Hsp101 was found to be very critical for thermotolerance (Queitsch et al. 2000). The Hsp100 class not only responds to HTS, but also helps in organelle development such as chloroplast and mitochondria (Pyatrikas et al. 2014; Merret et al. 2017). Inhibition of Hsp101 in Arabidopsis showed reduced growth under extreme high temperature and constitutive expression of Hsp100 could provide better adaptation (Queitsch et al. 2000; Nieto-Sotelo et al. 2002). Increased transcript accumulation of Hsp17.6 and Hsp101 were observed in reproductive organs of Brassica under HTS. Similar observation was also observed in maize (Dupuis and Dumas 1990; Young et al. 2004). Since reproductive stages are more thermosensitive than the vegetative stage of plants, the HSP are induced in various reproductive stages under the HTS (Duck and Folk 1994; Sung et al. 2001). Conversely, constitutive overexpression of AtHsp90.3 compromised tolerance to HTS in Arabidopsis via delayed expression of HSFs and some HSP (Xu et al. 2010).

Hsp60 behaves very similar to Hsp70 as it shares some functions such as protein folding. The organellar Hsp60 is structurally very different from bacterial Hsp60 (Hartl 1996; Wang et al. 2004). Chloroplastic Hsp60 is crucial for assembling the Rubisco enzyme in native conformation and showed constitutive expression under normal condition, but little upregulation is observed in response to HTS (Xu et al.

2010). The mutation in cpHsp60 leads to the improper development of chloroplast (Wang et al. 2004). While mtHsp60 remains inactive during normal condition, induced expression is observed only in elevated temperature, presumably protect the mitochondria (Xu et al. 2010).

Several earlier studies, based on the proteomic analysis under HTS, showed differential expression of different types of sHSP (Hsp18.1, 17.9, 17.4, 22.3, 26 and 16.9) (Majoul et al. 2004; Lin et al. 2005; Lin et al. 2010; Liao et al. 2014; Kumar et al. 2017a, b). Expression of several sHSP (16.9, 17.7, 18, 18.9, 23.5 and 26.6) were shown to be upregulated in thermotolerant cultivar, while downregulated in sensitive cultivar (Chandel et al. 2013; Mishra et al. 2017). This clearly indicates that the expression of sHSP are cultivar-specific. Genome-wide analysis of sHsp 15, 25, 26 and 27 of foxtail millet substantiated these results as they were highly upregulated during HTS (Singh et al. 2016). Additionally, sHsp16.9 and variants of Hsp17 were reported to be elevated in various crops in response to HTS (Süle et al. 2004; Zhang et al. 2013). Overexpression of chloroplastic chaperone DnaJ/Hsp40 also showed increased tolerance in response to HTS by promoting synhesis of antioxidants and reduced accumulation of ROS (Wang et al. 2017). Similarly, heterologous expression of Hsp17.8 and Hsp17.2 displayed improved adaptation under HTS in Rosa chinensis and Camellia sinensis, respectively (Talamè et al. 2007). The increase in exposure of hydrophobic sites of dodecameric complex of NtHsp18.3 under HTS suggest fact that HTS induces the conformational change in 3-D so that it can protect other cellular proteins (Maimbo et al. 2007). The overexpression of sHsp17.7 in rice and carrot exhibited improved thermotolerance (Malik et al. 1999; Murakami et al. 2004). Similar to these reports, overexpression of Hsp21.4 showed upregulation of Hsp101 and Hsp70, suggesting the positive effect of sHSP in alleviating the damage caused by HTS in P. forrestii (Zhang et al. 2014a, b). Interaction studies of sHSP indicate that the sHSP may aggregate through ACD and form heteromeric complex, and promote stress adaptation (Chen et al. 2014a, b).

3.4.2 Cold Stress

Low temperature or cold stress, a major factor of abiotic stresses, decreases the rate of uptake of water and nutrients, leading to cell desiccation and starvation. Cold stress can be divided into two subgroups, chilling stress (temperature less than 20 °C) and freezing stress (temperature less than 0 °C). To acclimatize to low temperature stress (LTS), plant induces the synthesis of variety of new proteins and also provide protection to existing proteins. Induction of HSP is the crucial part of cold acclimation. The members of Hsp70 are highly induced in various crops viz., wheat (Vítámvás et al. 2012; Kosová et al. 2013), rice (Lee et al. 2009), barley (Hlaváčková et al. 2013), maize (Kollipara et al. 2002), pea (Dumont et al. 2011), besides model plants tobacco (Jin et al. 2011) and Arabidopsis (Bae et al. 2003) in response to LTS.

The expression of Hsp90 under LTS is dependent on the developmental stages and crop species. Expression of Hsp90was shown to be downregulated under LTS in wheat (Vítámvás et al. 2012), while upregulated in tobacco (Jin et al. 2011), maize (Kollipara et al. 2002), rape seed (Reddy et al. 1998) and sunflower (Balbuena et al. 2011). The expression of few HSP such as Hsp95 and Hsp75 are highly induced in response to LTS in rice (Hahn and Walbot 1989). The stability of Rubisco is also maintained in LTS via induced expression of Hsp60 and Hsp21 (Rinalducci et al. 2011; Kosová et al. 2013). However, expression of Hsp60 and Hsp21 was shown to be downregulated in sunflower (Balbuena et al. 2011). Importantly, the sHSP not only protect the protein structure and folding, but also maintain the membrane fluidity and electrolyte leakage, thereby contributing to cold tolerance. There have been several investigations on LTS-responsive sHSP in tomato (Sanchez-Bel et al. 2012), chestnuts (Soto et al. 1999), rice (Hahn and Walbot 1989) and plum (Sun et al. 2010). Many sHSP were shown to be expressed in LTS only when subjected to pre-heat treatments. Two sHSP, tom66 and tom111 in tomato, exhibiting limited or no expression under LTS were found to be induced when subjected to pre-heat treatment followed by low temperature (Sabehat et al. 1998). This phenomenon is not restricted to tomato, but exists in different crops such as sweet pepper (Guo et al. 2007), peach (Zhang et al. 2011) and grapefruits (Rozenzvieg et al. 2004). It seems that when plants are subjected to low temperature after pre-heat treatment, the induction of sHSP is higher as compared to high molecular weight HSP, indicating the recruitment of diverse HSP to generate cold tolerance (Zhang et al. 2011).

3.4.3 Dehydration Stress

During dehydration, the cellular machinery adjusts itself to maintain water potential, which leads to improved antioxidant activity that reduces the production of reactive oxygen species (ROS) and prevents oxidative damage. Under such stress, many HSP which are mainly present in the cytoplasm, are involved in transferring the cellular signals to the nucleus that dictate the cell fate decision (Breiman 2014). HTS is generally accompanied by dehydration, but these aspects are rarely studied. One such investigation in cotton involved comparison of transcript abundance of HSP, which revealed steady state level in non-irrigated plants, but were not detected in irrigated plants (Burke et al. 1985). In a similar attempt, synthesis of HSP in dehydration- and heat-sensitive, and dehydration- and heat-resistant lines of maize, was examined under two environmental stress treatments, dehydration and high temperature, and independently at high temperature (Ristic et al. 1991). In both the lines, the pattern of synthesis of HSP was similar for high as well as low molecular weight proteins, indicating intraspecific differences in the synthesis of HSP. Pareek et al. (1998) reported different levels of these proteins in several dehydration-responsive wild species of rice. In yet another study, Benešová et al. (2012) showed induced expression of Hsp26 and Hsp70 isoforms in maize exposed to dehydration. Induction of HSP was found to be more in dehydration-tolerant than dehydration-sensitive cultivar. Similarly, expression of Hsp70 was shown to be downregulated in early stages in dehydration-tolerant chickpea cultivar as against dehydration-sensitive one, which showed high abundance in initial stage and reduced expression in later stages. This indicates that Hsp70 expression is dependent on genotypes as well as growth stages (Jaiswal et al. 2013). There have been numerous studies demonstrating improved tolerance to environmental stress including dehydration, albeit the underlying mechanism is not fully understood (Sugino et al. 1999; Alvim et al. 2001; Ono et al. 2001). Subba et al. (2013a, b) observed similar trend in the case of sHSP; the expression was higher in dehydration-tolerant, while lower in dehydration-sensitive chickpea cultivar. The expression of sHSP was also found to be genotype-specific in various other crops, for instance, poplar (Bonhomme et al. 2009) and Kentucky bluegrass (Xu and Huang 2010). The proteomic landscape of the extracellular matrix unraveled that Hsp90, Hsp70, GroEL Hsp20, peptidyl-prolyl cis-trans isomerase and chaperonin 60 are upregulated in response to dehydration (Pandey et al. 2010; Bhushan et al. 2011). Similarly, dehydration-responsive nuclear proteome displays upregulation of Hsp70, co-chaperone DnaJ, Grp chaperonin 60β and several sHSP (Pandey et al. 2008; Choudhary et al. 2009). It is evident that the status of HSP are modified covalently through the phosphorylation of residues under dehydration. In addition, phosphorylation of chaperonin 21 precursor and Hsp19 activate the defense pathway in response to dehydration (Subba et al. 2013a, b). A complex response of chaperone was also observed in which isoforms of stress-induced protein (sti1) showed differential dehydration-responsive expression (Agrawal et al. 2016). Cruz de carvalho et al. (2014) demonstrated distinct dehydration response in bryophytes and showed association of many HSP with dehydration adaptation (Cruz de carvalho et al. 2014).

Increasing evidence suggest that there is a strong correlation between accumulation of sHSP and stress tolerance in plant The sHSP, usually undetectable under normal physiological conditions, are induced upon stress treatment (Low et al. 2000). Overexpression of sHsp17.7 in transgenic rice displayed increased dehydration tolerance (Sato and Yokoya 2008). The function of sHsp17.7 has been demonstrated during osmotic stress, when proteins are prone to be denatured upon dehydration (Sun et al. 2001). A recent genome-wide sequence survey in barley led to the identification of several sHSP and HSFs putatively involved in dehydration response (Reddy et al. 2014).

3.4.4 Metallic Stress

Metals are crucial for plant growth and development in the optimum concentration, but when the concentration increases in the natural environment causes heavy metal stress (HMS). It is evident that Hsp70 is activated when exposed to cadmium and aluminum stress in Arabidopsis (Sarry et al. 2006), tomato (Neumann et al. 1994), poplar (Yang et al. 2015), bird's-foot trefoil (Navascués et al. 2012) and soybean (Duressa et al. 2011). The time-dependent gene expression analyses revealed high abundance of Hsp80 and Hsp17.9 in rice when exposed to cadmium stress (Ogawa et al. 2009). Hsp90 was previously shown to be differentially regulated in poplar (Ogawa et al. 2009) and bird's-foot trefoil (Yang et al. 2015) under HMS. Czarnecka et al. (1988) showed that cadmium could partially inhibit the intron processing by favoring the expression of Hsp26 in soybean (Czarnecka et al. 1988). Constitutive expression of AtHsp90.3 has been shown to impair tolerance to Cd-stress causing lower germination potential and shorter root length possibly via reducing the activities of antioxidative enzymes (Song et al. 2012). Expression of Hsp17.7 was found to be increased in carrot under lead and arsenic stress (Lee and Ahn 2013). The HMS-responsive proteomic analysis of poplar revealed induction of diverse sHSP, for instances, sHsp20, 22 and 23.1 (Yang et al. 2015).

3.4.5 Salt Stress

More than 20% of the cultivated land worldwide are affected by salinity stress, which has been increasing in every successive year posing serious threats to agriculture. The proteomic landscape of soybean showed differential expression of Hsp70-Hsp90 organizing protein (HOP), Hsp90, chaperonin 20, chloroplastic Hsp70 and chaperonin 60 under hypersalinity (Pi et al. 2016). Overexpression of Hsp90.2, 90.5 and 90.7 in Arabidopsis showed tolerance towards hypersalinity (Song et al. 2009a, b; Xu et al. 2013). Salinity-induced high expression of Hsp70 was evident in both sensitive and tolerant genotypes of soyabean, though the abundance was higher in the sensitive genotypes (Manaa et al. 2011). Transgenic plants expressing Hsp70 were shown to modulate the programmed cell death (PCD) under hypersalinity wherein Hsp70 acts as anti-apoptotic protein (Hoang et al. 2015). Higher induction of Hsp110 was also observed in rice when exposed to hypersalinity (Singla et al. 1997). Additionally, ClpB/Hsp100 B2, B3 and ClpD2 are predicted to function as molecular chaperone, and their expressions are highly increased under salt stress (Muthusamy et al. 2016). Overexpression of ClpD1 and sHSP has also been shown to cause better adaptation to salt stress (Jiang et al. 2009; Mu et al. 2013; Jung et al. 2014; Mishra et al. 2016). A previous study on mitochondrial electron transport in maize indicated a strong association between accumulation of sHSP and tolerance to hypersalinity (Hamilton and Heckathorn 2001).

3.4.6 Light Stress

Light is an essential component for plant to carry out photosynthesis, but excessive light damages the photosynthetic apparatus and affects plant growth and development. Plant uses several mechanisms to overcome the photooxidative damage, the most common being the HSP, which are highly induced by high light stress (HLS). Rossel et al. (2002) demonstrated that Arabidopsis seedlings, upon exposed to HLS, activates HSP-chaperone pathway and induces the expression of different forms of HSP and sHSP. The increased expression of HSP and co-chaperones reduces the photooxidative damage and helps protein folding (Rossel et al. 2002). The upregulation of chloroplastic Hsp70 reaffirms the role of HSP in protection of photosystem

II during photoinhibition (Giacomelli et al. 2006). Kropat et al. (1997) reported the similar observation, the HLS-induced overaccumulation of the nuclear Hsp70, in Chlamydomonas.

Photoperiodism plays an important role in chloroplast development. In a recent report, Wang et al. (2016) showed that high abundance of HSP-associated proteins such as FKBP19, FKBP16–1, FKBP16–4 and CYP20–3 in dark-adapted chloroplast, which help in proper folding of the unfolded proteins (Wang et al. 2016). It has previously been observed that the exposure of marine ecosystem, particularly seagrasses to HLS induces the synthesis of new HSP (Hsp70, Sti and ClpB1) and chaperonin 60 (Kumar et al. 2017a, b). The HLS-induced posttranslational regulation of mitochondrial sHsp23 has also been observed in the cell suspension of Chenopodium rubrum (Korotaeva et al. 2001).

3.4.7 Flooding Stress

Flooding is the major abiotic stress, which negatively affects plant growth and crop yield worldwide. Pathways involving various HSP, chaperones and co-chaperones are triggered by flooding stress-responsive. Largescale omics analyses in maize emphasized the role of Hsp70 in such stress (Chen et al. 2014a, b) via flooding stress-induced PCD through the maintenance of photosynthesis. Increased accumulation of Hsp70 in flooding-stressed soybean also indicated its pivotal role in flooding stress tolerance (Komatsu et al. 2013). These results were supported by the observation in rice protoplasts wherein ectopic expression of mtHsp70 led to inhibition of heat- and H_2O_2-induced PCD (Qi et al. 2011). Hypoxic or anoxic condition is the consequence of prolonged flooding stress. The transcript abundance of HSP were found to be upregulated under flooding stress in rice sensitive genotype, but few of them in the tolerant genotype. This indicated that even though HSP have a vital role against anoxia, these are not the principal components for the tolerance (Mertz-Henning et al. 2016). It unlikely that the HSP might act in association with other molecular signatures and help plants to endure the flooding stress. This is further substantiated by a proteometabolomic study of soybean under flooding stress wherein the acidic form of 60-kDa chaperonin was shown to be differentially regulated (Komatsu et al. 2011). It has been demonstrated that the expression of HsfA2 induces high abundance of Hsp70 and Hsp101, besides Sti1 and protect plants against anoxic condition (Banti et al. 2010; Hüther et al. 2017).

3.4.8 Overlapping and Secondary Stress

Plant response to environmental stress is controlled and regulated by a complex network of genes. Gene expression database of Arabidopsis, AtGenExpress, encompasses the consequences of multivariate abiotic stresses (Kilian et al. 2007). There exists a strong association of stress-responses and involvement of HTS and HSF, albeit the degree of interaction seems to be different suggesting a cross-talk among the networks. A recent global HTS-responsive gene expression profiling of rice suggested that HSP and their corresponding HSFs might be crucial in crosstalk of different stress signaling pathways (Hu et al. 2009). It is reasonable to deduce that the synchronized exposure to various abiotic stresses would simultaneously activate different stress-responsive pathways. Hence, there might be a synergistic and/or antagonistic impact on each other. The distinct pathways exclusively for the particular stress combinations might also be stimulated (Mittler 2006). Therefore, it is imperative to understand the role of HSP in relation to the combined stress responses. It has been increasingly evident that several HSP are responsive to multiple stresses (Al-Whaibi 2011), though there are instances wherein a particular stress-responsive HSP may not function in other stress or even differs crop-wise (Jin et al. 2011; Vítámvás et al. 2012). Investigations on combined stresses suggest increased expression of the genes encoding Hsp100, Hsp90, Hsp70 and sHSP. The combined as well as individual stress response include numerous commonly regulated genes. The expression of stress-responsive genes is fine tuned to combined stress condition, for instances, plants subjected to dehydration and HTS showed higher induction of HSP when compared individually to either dehydration or heat stressed plants (Rizhsky et al. 2002). Ectopic expression of OsHsp18.6 and OsHsp16.9B in rice were shown to have improved tolerance towards multiple stresses (Zou et al. 2012; Wang et al. 2015). Overexpression of OsHSP16.9B and OsHsp23.7 were also reported to induce increased tolerance to salt and dehydration (Zou et al. 2012). Similar outcome was observed by overexpression of Oshsp16.9 (Jung et al. 2014). In Arabidopsis, overexpression of AtHsp17.6A were shown to effect enhanced tolerance to hypersalinity and dehydration, whereas no effect was observed against HTS (Sun et al. 2001). Ectopic expression of GmHsp90 in Arabidopsis were shown to confer tolerance to HTS, hypersalinity and osmotic stress, albeit the response in hypersalinity was not as potent as HTS (Xu et al. 2013).

Osmotic and oxidative stresses are considered as secondary stress in plants. Song et al. (2009a, b) reported that suggested various types of Hsp90 in different compartments are essential for cellular homeostasis under such stress (Song et al. 2009a, b). Nishizawa-Yokoi et al. (2010) also reported that Hsp90 is responsible for induction of HsfA2 under oxidative stress (Nishizawa-Yokoi et al. 2010). Oxidative stress has previously been shown to induced the accumulation of ClpB-cyt/Hsp100, ClpC2 and ClpD1 in rice (Queitsch et al. 2000). Chankova et al. (2014) reported that Hsp70 functions as biomarker in oxidative stress tolerance. An earlier study reported in the involvement of cloroplastic sHSP in protection of photosynthetic electron transport from oxidative damage (Downs et al. 1999). Various forms of Hsp17 and Hsp16.4 were also found to be highly induced in moss (Ruibal et al. 2013), Arabidopsis (Scarpeci et al. 2008; Jiang et al. 2009) and carrot (Ahn and Song 2012). Furthermore, mitochondrial Hsp22 were found to be over-accumulated in response to oxidative stress in tomato (Banzet et al. 1998).

3.5 Hsp and Multistress Resistance: Connecting the Dots

Abiotic stress elicits multivarious responses in plants that encompass a sequence of physicochemical and molecular events. Multiple stress response mechanisms often function coordinately or synergistically to avoid cellular damage (Ahuja et al. 2010). While, the function of HSP in various abiotic stresses have been elucidated (Wang et al. 2004; Kotak et al. 2007; Al-Whaibi 2011), the precise mechanism is yet to be fully understood. The functions of HSP are not restricted to folding and maintenance of protein structures as some HSP and their co-chaperones have evidently been associated to signaling, besides protein targeting and degradation (Al-Whaibi 2011). Almost all the abiotic stresses cause to certain extent of oxidative stress, and there is a cross-talk between oxidative and abiotic stress signaling. The generation of H_2O_2 is a common phenomenon owing to the NADPH oxidase activity. The production of H_2O_2 has intimately been associated with the induction of stress-responsive genes in general and HTS-responsive genes in particular. This process is itself anticipated to be mediated by HSFs through direct sensing of H_2O_2 (Kotak et al. 2007). These facts suggest that the ROS production may influence *de novo* synthesis of HSP. Nonetheless, the information about the involvement of ROS in regulating abiotic stress-mediated HSP expression is still fragmentary (Kotak et al. 2007). Some of the HSP such as Hsp90 and Hsp70 class of chaperones and their co-chaperones interact with several components of signaling molecules viz., serine/threonine and/or tyrosine-kinase receptors, nuclear hormone receptors, and many more (Wang et al. 2004). Furthermore, existence of the redox status of thiol-containing molecules is key to the maintenance and balance of many crucial cellular functions. Some sHSP are implicated for the maintenance of the redox status per se in mammalian cells and likely to be playing a similar role in plants. The HSFs are involved not only for the basal tolerance against different abiotic stresses, but also initiate their acquisition. Several earlier reports addressed the possible role of Ca^{2+}/calmodulin-mediated signaling in abiotic stress-response. The HTS-induced cytosolic Ca^{2+} flux has been well documented, and an association through calmodulin (CaM) has been proposed. These altogether help HSFs and other transcription factors to bind to heat shock elements or their respective response elements to activate transcription of HSP (Kotak et al. 2007; Wang et al. 2004). A schematic representation of how HSP work in association with other elements in acquiring stress tolerance is presented in Fig. 3.2.

3.6 Conclusions

The stress-response and the tolerance thereof are complex sequence of events, which are intimately interwoven in plants. Significant information is available about HSP and their roles in different stresses, their types and variety of functions. However, every class of HSP and their different members have precise task, yet their

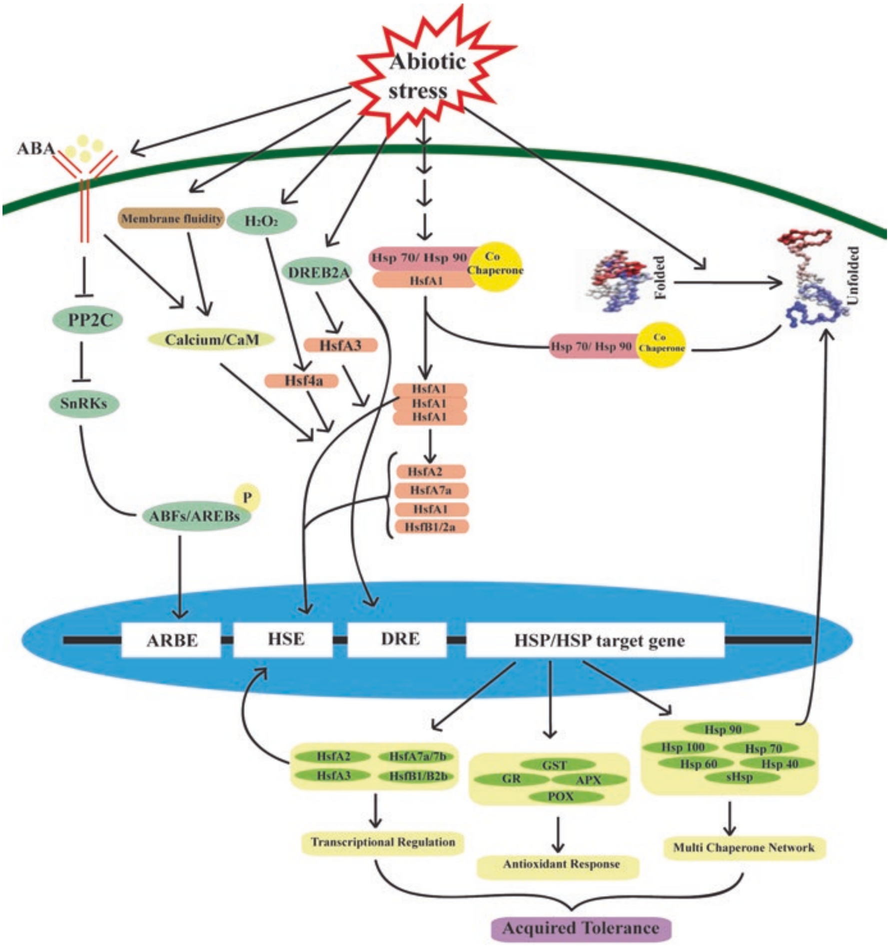

Fig. 3.2 Schematic representation of the involvement of HSP in defense pathway for acquired tolerance. Schematic diagram shows the role of HSP/chaperone and their interaction with other pathway proteins to circumvent the harsh environmental stress. The protein folding process is greatly affected during stress, which in turn results in propagation of misfolded proteins. To alleviate the misfolded protein response, a number of signaling pathways are activated in cellular milieu. The HSP and co-chaperones bind to misfolded protein facilitating the release of HsfA1, which further form trimer and translocate into the nucleus and binds to heat shock element (HSE) to activate the target genes. Major abiotic stresses activate the expression of DREBs, which eventually induces the upregulation of HsfA3. Furthermore, secondary stresses also increase intracellular H_2O_2 and trigger Hsf4a. Consequently, the fluidity of plasma membrane is disturbed which stimulates the cytosolic calcium and calmodulin, and results the upregulation of many HSFs. Abiotic stress especially, dehydration and hypersalinity increases the abundance of ABA and binds to ABA receptor, and inhibits the PP2C. Hence active SnRKs activates the ABF/AREBs and binds to ABRE of promotor region. The Hsfs and other regulatory proteins (DREB, ABFs etc.) bind to different cis-regulatory region and initiate the transcription of HSP, HSFs and antioxidant proteins. Accumulation of these biomolecules contribute to acquisition of stress tolerance in plants

synergy across different networks seems to be a fundamental aspect for the assimilated function. Under natural growth and developmental conditions or during the stress, the HSP/chaperone machinery decides the consequence of the non-native or denatured protein/s. The questions remain to be answered as to how a non-native or denatured protein is recognized by a particular chaperone, and how and when it is stabilized or protected from aggregation, or refolded in native conformations or destined for degradation? The current knowledge about the role of HSP as regulatory module as to how they sense the signal and eventually induce the transcriptional activation of other stress-responsive genes is limited. Almost all recent studies in plants and other organisms have been focused on the changes in the expression of HSP or HSFs and/or their co-chaperones. In most cases, the role of HSP under stress have been attributed on the basis of in vitro studies, primarily due to the lack of suitable mutants wherein the expression studies can be carried out. Therefore, future studies should be focused on generation of HSP-mutants in plants, their interaction with pathway proteins and so forth to elucidate the underlying mechanism of stress tolerance. Studies about the structural changes in different HSP and co-chaperones vis-à-vis to single or collective stress-response mechanisms in plants are particularly significant. It can be anticipated that active research pertaining to the cross-talk between HSP and co-chaperones with that of other stress response mechanisms will provide a new insight into stress tolerance. In fact, genome sequence information alone is inadequate about gene function, their regulation, and the molecular switch to acclimatize under stress conditions. Future efforts must focus on unravelling the molecular association amongst the HSP and different abiotic stresses which may provide avenue for developing resilient crops through genetic engineering or molecular breeding.

Acknowledgements This work was supported by the National Institute of Plant Genome Research (NIPGR). We kindly acknowledge the University Grant Commission (UGC), Govt. of India for providing predoctoral fellowship to D.M, Department of Biotechnology (DBT), Govt. of India for providing predoctoral fellowship to D.S., and DST-SERB for providing postdoctoral fellowship to S.S.

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