The Plant Heat Stress Transcription Factors (HSFs): Structure, Regulation, and Function in Response to Abiotic Stresses

Meng Guo 1, Jin-Hong Liu 1, Xiao Ma 1, De-Xu Luo 2, Zhen-Hui Gong 1* and Ming-Hui Lu 1*

1 Department of Vegetable Science, College of Horticulture, Northwest A&F University, Yangling, China, 2 Vegetable Research and Development Centre, Huaiyin Institute of Agricultural Sciences in Jiangsu Xuhuai Region, Huai’an, China

Abiotic stresses such as high temperature, salinity, and drought adversely affect the survival, growth, and reproduction of plants. Plants respond to such unfavorable changes through developmental, physiological, and biochemical ways, and these responses require expression of stress-responsive genes, which are regulated by a network of transcription factors (TFs), including heat stress transcription factors (HSFs). HSFs play a crucial role in plants response to several abiotic stresses by regulating the expression of stress-responsive genes, such as heat shock proteins (Hsps). In this review, we describe the conserved structure of plant HSFs, the identification of HSF gene families from various plant species, their expression profiling under abiotic stress conditions, regulation at different levels and function in abiotic stresses. Despite plant HSFs share highly conserved structure, their remarkable diversification across plants reflects their numerous functions as well as their integration into the complex stress signaling and response networks, which can be employed in crop improvement strategies via biotechnological intervention.

Keywords: plant, heat stress, transcription factors, heat shock proteins, abiotic stress, transcriptional regulation

INTRODUCTION

Plants as sessile organisms are routinely confronted by a variety of abiotic or biotic stresses, such as water deficiency, high salt, extreme temperatures, chemical pollutants, oxidative stress, nematodes, herbivores, and pathogens (Al-Whaibi, 2011). Especially, abiotic stress is the primary cause of crop loss worldwide, reducing crop productivity by an estimated 50% annually (Wang et al., 2004). Unlike animals, plants could not change their sites to escape from the unfavorable stresses, but have attained certain adaptations to these rapidly changing stresses during evolution, such as the dominance of sporophyte that encloses the sensitive gametophyte, the presence of leaf epidermis with stomata for gas exchange, the formation of stress resistant dormant organs, and the presence of conducting tissues in long-lived and big plants for long-distance nutrient and water transport (Baniwal et al., 2004; Al-Whaibi, 2011). A network of interconnected cellular stress response systems is a prerequisite for plant survival and productivity (Scharf et al., 2012), and their understanding is important for developing new methods to enhance plant stress tolerance.

A complex stress response network and a wide array of mechanisms for adapting to plants’ changing environments at the physiological, biochemical, and molecular levels increase
the tolerance to the stresses (Bartels and Sunkar, 2005; Zhou et al., 2009; Nakashima et al., 2012). The phytohormone abscisic acid (ABA) produced under abiotic stress conditions, induces leaf stomata closure and triggers the activation of many stress-related genes, thus playing a key role in responses to abiotic stress factors (Lata and Prasad, 2011). With the molecular techniques such as microarray analysis and large-scale transcriptome analysis, a large array of abiotic stress responsive genes has been identified in plants (Fowler and Thomashow, 2002; Nakashima et al., 2009). These genes not only play a role in the protection of the cells from stress by the production of important enzymes and metabolic proteins (functional proteins) but also in regulating signal transduction and gene expression in the stress response (regulatory proteins; Lata and Prasad, 2011; Nakashima et al., 2012). Among the regulatory proteins, transcription factors (TFs) play a crucial role in the conversion of stress signal perception to stress-responsive gene expression by interacting with cis-acting elements present in the promoter region of various target stress-responsive genes in the signal transduction processes, thus activating signaling cascade whole network of genes that act together in enhancing plant tolerance to the harsh environmental conditions (Akhtar et al., 2012). In plant genomes, ~7% of the coding sequences are assigned to TFs and many of these often belong to large gene families compared with animals and yeasts, such as the heat stress transcription factors (HSFs) family (Baniwal et al., 2004; Udvardi et al., 2007).

Plant HSFs are the terminal components of a signal transduction chain mediating the expression of genes responsive to various abiotic stresses (Nover et al., 2001). Many studies have reported on the central roles of HSFs in various abiotic stresses, including heat stress (HS) (Scharf et al., 2012), however, most analyses of HSFs function in stress responses examine individual stresses, not a combination of abiotic stress factors. In natural conditions, plants are routinely subjected to a combination of different abiotic stresses, such as the combination of drought, heat, and salinity stresses (Sewelam et al., 2014). The response of plants to a combination of different abiotic stresses cannot be directly extrapolated from the response of plants to each of the different stresses applied individually, therefore it is crucial to characterize the acclimation responses of plants to a combination of abiotic stresses and identify multiple stress responsive genes (Mittler, 2006; Colmenero-Flores and Rosales, 2014). Comprehensive characterization of multifunctional HSFs will provide the basis for investigating their functions in plant abiotic stress responses. In this review, the focus will be on the recent progress of the roles of HSFs in abiotic stress responses, with an emphasis on HS. In addition, recent advances in characterization of HSFs regulation will be also discussed.

STRUCTURE AND CLASSIFICATION OF PLANT HSFs

Typically, plant HSF proteins share a well conserved modular structure (Figure 1). The N-terminal DNA binding domain (DBD) is characterized by a central helix-turn-helix motif that specifically binds to the heat stress elements (HSEs) in the target promoters, and subsequently activates the transcription of stress-inducible genes (Baniwal et al., 2004; Sakurai and Enoki, 2010; Scharf et al., 2012). The oligomerization domain (OD) with a bipartite heptad pattern of hydrophobic amino acid residues (HR-A/B region) is connected to the DBD by a flexible linker (Baniwal et al., 2004). Based on the length of the flexible linker region between DBD and HR-A/B regions and the number of amino acid residues inserted into the HR-A/B regions, plant HSFs are classified into three classes, HSPA, B, and C (Nover et al., 2001; Kotak et al., 2004). The HR-A/B regions of HSFs are compact and similar to all non-plant HSFs, however, members of class HSPA and C have an extended HR-A/B region due to an insertion of 21 (HSFAs) and 7 (HSFCs) amino acid residues between the HR-A and HR-B parts, respectively (Nover et al., 1996; Scharf et al., 2012). The C-terminal activation domains of plant HSFs are characterized by short peptide motifs (AHA motifs), which are crucial for the activator function in many cases (Döbring et al., 2000). The AHA motifs formed of aromatic, large hydrophobic, and acidic amino acid residues, are HSFa-specific motifs but not found in class HSBF or C (Döbring et al., 2000; Kotak et al., 2004). In addition, nuclear localization signal (NLS) and nuclear export signal (NES) of HSFs function in the assembly of a nuclear import complex built of the target protein and the receptor-mediated export in complex with the NES receptor exportin-α, respectively (Görlich and Kutay, 1999; Heerklotz et al., 2001; Baniwal et al., 2004). Notably, members of class HSBF (except HSBF5) comprise a characteristic tetrapeptide–LFGV—in the C-terminal domain, functioning as repressor domain (RD; Czarnecka-Verner et al., 2000; Ikeda and Ohme-Takagi, 2009; Frągkostefanakis et al., 2015).

IDENTIFICATION OF PLANT HSF FAMILIES

Compared with few HSF members in vertebrates (4), Drosophila (1), Caenorhabditis elegans (1), and yeast (one HSF plus three HSF-related proteins; Nover et al., 1996; Nakai, 1999), plant HSF families comprise a large number of HSF members derived from a complex plant-specific superfamily and are present in a wide range of species. In the previous reports, the identification of the HSF family in plants was performed only in few model species such as Arabidopsis, tomato, and rice (Baniwal et al., 2004; Scharf et al., 2012). In recent years, based on the availability of an ever-increasing number of complete plant genomes and EST sequences, a large numbers of HSF families from more than 20 plant species have been identified at genome-wide scale. As shown in Table 1, there are 21 HSF encoding genes in Arabidopsis (Scharf et al., 2012), 24 in tomato (Scharf et al., 2012; Frągkostefanakis et al., 2015), 25 in pepper (Guo et al., 2015), 52 in soybean (Scharf et al., 2012), at least 56 in wheat (Xue et al., 2014), and so on. Compared with the HSF families of soybean, carrot (35 members) and cotton (40 members), the families of Arabidopsis and tomato are considered small. Currently, maximum of HSF genes were identified in wheat and soybean among monocots and eudicots, respectively. The multiplicity of
### TABLE 1 | The HSF family in plant species.

| Species                        | HSFA1 | HSFA2 | HSFA3 | HSFA4 | HSFA5 | HSFA6 | HSFA7 | HSFA8 | HSFA9 | HSFB1 | HSFB2 | HSFB3 | HSFB4 | HSFB5 | HSFC1 | HSFC2 | In total | References                  |
|-------------------------------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|---------|-----------------------------|
| Arabidopsis thaliana          | 4     | 1     | 1     | 2     | 1     | 2     | 2     | 1     | 1     | 1     | 2     | 1     | 1     | 0     | 1     | 0       | 21 | Scharf et al., 2012 |
| Tomato (Solanum lycopersicum) | 4     | 1     | 1     | 3     | 1     | 2     | 1     | 1     | 1     | 1     | 2     | 2     | 2     | 1     | 1     | 0       | 24 | Scharf et al., 2012; Fragkostefanakis et al., 2015 |
| Castor bean (Ricinus communis)| 2     | 1     | 1     | 2     | 1     | 1     | 1     | 1     | 1     | 1     | 2     | 1     | 2     | 1     | 1     | 0       | 19 | Scharf et al., 2012 |
| Pepper (Capsicum annuum)      | 3     | 1     | 1     | 3     | 1     | 3     | 0     | 1     | 4     | 1     | 2     | 2     | 1     | 1     | 1     | 0       | 25 | Guo et al., 2015 |
| Apple (Malus domestica)       | 4     | 2     | 3     | 1     | 2     | 0     | 0     | 2     | 2     | 2     | 1     | 2     | 2     | 0     | 2     | 0       | 25 | Giorno et al., 2012 |
| Tea (Camellia sinensis)       | 2     | 0     | 1     | 2     | 2     | 1     | 0     | 1     | 0     | 1     | 4     | 0     | 1     | 0     | 1     | 0       | 16 | Liu et al., 2016 |
| Soybean (Glycine max)         | 5     | 3     | 4     | 4     | 2     | 3     | 3     | 2     | 2     | 4     | 6     | 2     | 8     | 2     | 2     | 0       | 52 | Scharf et al., 2012 |
| Cotton (Gossypium hirsutum)   | 6     | 1     | 1     | 3     | 2     | 2     | 2     | 3     | 3     | 4     | 1     | 5     | 2     | 3     | 0       | 40 | Wang et al., 2014 |
| Chinese cabbage (Brassica rapa pekinensis) | 8     | 1     | 1     | 1     | 1     | 4     | 2     | 1     | 0     | 2     | 3     | 2     | 2     | 0     | 2     | 0       | 30 | Huang et al., 2015a |
| Poplar (Populus trichocarpa)  | 3     | 1     | 1     | 3     | 2     | 2     | 2     | 2     | 1     | 1     | 3     | 2     | 4     | 2     | 1     | 0       | 27 | Scharf et al., 2012 |
| Carrot (Daucus carota)        | 2     | 4     | 4     | 8     | 1     | 0     | 5     | 0     | 3     | 2     | 2     | 1     | 2     | 0     | 1     | 0       | 35 | Huang et al., 2015b |
| Strawberry (Fragaria vesca)   | 2     | 1     | 1     | 2     | 1     | 1     | 1     | 1     | 1     | 1     | 2     | 1     | 1     | 0     | 1     | 0       | 17 | Hu et al., 2015 |
| Willow (Salix suchowensis)    | 3     | 1     | 1     | 3     | 1     | 2     | 2     | 2     | 1     | 1     | 2     | 1     | 4     | 2     | 1     | 0       | 27 | Zhang et al., 2015 |
| Chinese white pear (Pyrus bretschneideri) | 3     | 1     | 2     | 4     | 1     | 3     | 2     | 1     | 2     | 2     | 1     | 3     | 1     | 1     | 2     | 0       | 29 | Qiao et al., 2015 |
| Chinese plum (Prunus salicina) | 2     | 1     | 1     | 2     | 1     | 1     | 1     | 1     | 1     | 2     | 0     | 1     | 1     | 1     | 0     | 1       | 17 | Qiao et al., 2015 |
| Peach (Amygdalus persica)     | 2     | 1     | 1     | 2     | 0     | 1     | 1     | 1     | 1     | 1     | 2     | 1     | 1     | 1     | 1     | 0       | 17 | Qiao et al., 2015 |
| European pear (Pyrus communis) | 4     | 3     | 2     | 4     | 1     | 2     | 2     | 2     | 2     | 2     | 3     | 2     | 0     | 2     | 2     | 0       | 33 | Qiao et al., 2015 |
| Maize (Zea mays)              | 2     | 3     | 1     | 3     | 1     | 2     | 2     | 2     | 0     | 2     | 4     | 0     | 3     | 0     | 3     | 2       | 30 | Scharf et al., 2012 |
| Rice (Oryza sativa)           | 1     | 3     | 1     | 2     | 1     | 2     | 2     | 1     | 0     | 1     | 3     | 0     | 4     | 0     | 2     | 2       | 25 | Scharf et al., 2012 |
| Wheat (Triticum aestivum)     | 3     | 9     | 2     | 6     | 2     | 6     | 2     | 3     | 0     | 3     | 5     | 0     | 3     | 0     | 5     | 7       | 56 | Xue et al., 2014 |
| Millet (Sorghum bicolor)      | 1     | 3     | 1     | 2     | 1     | 2     | 1     | 0     | 1     | 3     | 0     | 3     | 0     | 2     | 2       | 24 | Scharf et al., 2012 |
| Brachypodium (Brachypodium distachyon) | 1     | 3     | 1     | 2     | 1     | 2     | 1     | 0     | 1     | 3     | 0     | 3     | 0     | 2     | 2       | 24 | Scharf et al., 2012 |
HSFs in plants may be related to the gene duplications and whole-genome duplications at different points of evolution, followed by extensive gene loss (Scharf et al., 2012).

Interestingly, among the 25 species listed in Table 1, including 20 eudicots and 5 monocots, members of subclass HSFA9, B3, and B5 were confined to the eudicots but not to the monocots, which emerged presumably after the split of monocots and eudicots. In addition, a variable number of the monocot-specific type HSFC2 genes (2–7 genes) are found in all 5 monocots, not in eudicots, attributing to gene duplications on the monocot lineage. Higher number of class HSFC genes are identified in monocots, such as in wheat, maximum of 5 and 7 genes are assigned into subclass HSFC1 and C2, respectively, which is the most marked difference between monocots and eudicots (Scharf et al., 2012). The large size of the plant HSFs family inevitably complicates the unraveling of their function under stress conditions.

### EXPRESSION ANALYSIS OF PLANT HSF GENES

The role of plant HSFs in abiotic stresses, especially in HS, has been recently brought to light (Fragkostefanakis et al., 2015). Although mRNA levels cannot be used to draw immediate conclusions about protein levels, they can point out directions of further investigations (Scharf et al., 2012). Genome-wide expression profiling of plant HSF genes under different abiotic stresses has been investigated extensively in various species. Most plant HSFs are regulated by HS, including up- and down-regulation. Upon HS, the transcript levels of HSFA2 and A6 members became the dominant HSFs in wheat, suggesting an important regulatory role during HS (Xue et al., 2014). Among 23 rice OsHSF genes, 16 OsHSFs were up-regulated by two-folds (log2 value) in response to HS, including 8 genes up-regulated by two-folds only during early heat shock (HS for 10 min) and 8 genes up-regulated at both short (HS for 10 min) and prolong (HS for 30 min) HS treatment, however, OsHSFC1a was noted to be down-regulated by the early HS treatment (Mittal et al., 2009), similarly, many HSF genes from different plant species, such as GhHSF3, 18, 24, 32, 37, and 40 from cotton (Wang et al., 2014), ZmHSF-06, -10, -14, -20, and -21 from maize (Lin et al., 2011), MdHSFA9b and B4a/b from apple (Giorno et al., 2012) showed down-regulation under HS treatment. The expression of Arabidopsis HSFA2 was not detectable in control cell cultures but was detected strongly after HS treatment (Nover et al., 2001), and the similar situation also emerged in the expression profiles of pepper CaHSFA2 (Guo et al., 2015), maize ZmHSF-01 and ZmHSF-04 (HSFA2 group; Lin et al., 2011), apple MdHSFA2a and A2b (Giorno et al., 2012), and tomato SHSFA2 (Mishra et al., 2002). The HS-dependent translocation of HSFA2 in Arabidopsis (Evrand et al., 2013) and tomato (Chan-Schaminet et al., 2009) and redox-dependent translocation of AtHSFA8 (Giesguth et al., 2015) from the cytosol to nucleus may play central roles in plant HS and oxidative stress responses. In addition, many other abiotic stresses like cold, salinity and drought, and phytohormones such as jasmonic acid (JA), abscisic acid (ABA), salicylic acid (SA), and ethylene (Et) also have been shown to regulate the expression of plant HSF genes (Hu et al., 2015; Huang et al., 2015b; Zhang et al., 2015). The different abiotic stresses and phytohormone signaling pathways are assumed to interact and share some common elements that formed as potential “node” for crosstalk (Akhtar et al., 2012). These plant HSF genes may act as cross-point or node connecting several pathways and simultaneously regulate abiotic and phytohormone signaling pathways.

Plant HSF genes are not only induced by stress response but also by development, cell differentiation, and proliferation. For example, expression of Arabidopsis AtHSFA2 gene increases during the process of callus formation and growth from root explants (Che et al., 2002). In addition, HSFA2 is more highly induced in tomato anther than in the other flower tissues, and further induced under both short and prolonged HS conditions, which is similar to its expression in leaves (Giorno et al., 2012).

![FIGURE 1 | Basic structure of HSFs. The block diagrams represent five tomato HSFs with their conserved functional domains. The conserved domains are identified by Heatster (http://www.cibiv.at/services/hsf/). DBD, DNA binding domain; OD, oligomerization domain (HR-A/B region); NLS, nuclear localization signal; NES, nuclear export signal; AHA, activator motifs; RD, tetrapeptide motif–LFGV–as core of repressor domain. (Adapted from Scharf et al., 2012).](image)
In rice, the expression of OsHSFA2a gene is highly stimulated by HS particularly in root and shoot tissues as well as during panicle and seed development, while OsHSFA7 and A9 show developing seed-specific expression, in a similar pattern with those of HSF9 in sunflower and Arabidopsis (Chauhan et al., 2011; Scharf et al., 2012). These studies elaborate the border of conditions that are known to induce plant HSFs expression.

**REGULATION OF PLANT HSF GENES**

The studies on regulation of plant HSFs mainly focus on four levels including transcriptional, post-transcriptional, translational, and post-translation level (Fragkostefanakis et al., 2015). Transcription is the first step at which activity of a gene can be regulated by binding of specific TFs to the cis-acting elements located on the regulatory region of its promoter (Figure 2). The Arabidopsis AtHSFA1d and A1e binding to the HSE cluster in the 5'-flanking region of AtHSFA2 gene is involved in high light (HL)-inducible HSFA2 expression, activating AtHSFA2 transcription (Nishiizawa-Yokoi et al., 2011). Under HS, the Arabidopsis dehydration-responsive element (DRE)-binding protein 2A (DREB2A gene) directly regulates AtHSFA3 transcription via binding the two DRE core elements in the AtHSFA3 promoter (Yoshida et al., 2008). As AtHSFA9 is exclusively expressed in late stages of seed development among the Arabidopsis family of 21 HSFs, a TF may be involved in the regulation of AtHSFA9 expression during seed development. Kotak et al. (2007) reported that ABSCISIC ACID–INSENSITIVE3 (ABI3) gene could activate the AtHSFA9 promoter based on an RY/Sph motif (8-bp sequence, CATGCATG) as putative seed-related regulatory element in the AtHSFA9 promoter provided an essential binding site for ABI3. Interestingly, unlike Arabidopsis AtHSFA1d and A1e, AtHSFB1 and B2b are transcriptional repressors and negatively regulate the expression of HS-inducible HSFs including not only AtHSFA2 and A7a but also themselves (Ikeda et al., 2011).

Alternative splicing is a widespread process in eukaryotes that generates two or more different transcripts from the same precursor mRNA molecule by using different splice sites (Guerra et al., 2015). The complex post-transcriptional regulation of HSFs involves alternative splicing during different biological processes (Fragkostefanakis et al., 2015). Alternative splicing induced by HS is observed for AtHSFA2, A4c, A7b, B1, and B2b in Arabidopsis. Arabidopsis AtHSFA2 derives from splicing of the conserved intron in the DDB, and a new heat stress-induced splice variant, AtHSFA2-III encodes a small truncated AtHSFA2 isoform (S-AtHSFA2), which can bind to the TATA box-proximal clusters of HSE in the AtHSFA2 promoter to activate its own transcription, attributing to exon skipping in the intron of the DDB encoding region (Sugio et al., 2009; Liu et al., 2013). The exon skipping pattern of Physcomitrella patens PpHSFA1-1 is similar to that of AtHSFA2, which reveals that heat regulation for alternative splicing evolved early during land colonization of green plants (Chang et al., 2014). The alternative splicing induced by HS is also observed for rice OsHSFA2d, which encodes two main splice variant proteins, OsHSFA2dI localized to the nucleus and OsHSFA2dII localized to the nucleus and cytoplasm, respectively. The transcriptionally inactive spliced form of OsHSFA2d, OsHSFA2dIII, is the dominant under normal conditions; however, once the plant suffered from HS, OsHSFA2d is alternatively spliced into the transcriptionally active form, OsHSFA2dII, which participates in the HS response and the unfolded protein response by regulating expression of OsBiP1 (Cheng et al., 2015). Medicago sativa MsHSF1 is composed of four exons and three introns in the primary transcript and generates five splice transcript isoforms, including one spliced transcript MsHSF1b encoding an HSF1 protein that can specifically bind to the HSEs in vitro and four low-abundant spliced transcripts carrying the premature termination codon (He et al., 2007). These results suggest that the regulation of plant HSFs at post-transcriptional level is diversified.

Recently investigation suggests that the regulation of plant HSFs at translational level is mainly controlled by upstream micro open reading frames (uORFs) in their 5' untranslated regions (Figure 2; Jorgensen and Dorantes-Acosta, 2012; von Arnim et al., 2014; Fragkostefanakis et al., 2015). However, the information on uORFs of plant HSFs is mainly restricted to Arabidopsis. Zhu et al. (2012) reported that 7 members out of 21 Arabidopsis HSFs have at least one uORF, including AtHSFA1d, A1e, A2, A4a, B1, B2b, and C1, but only for the uORFs of AtHSFB1 and B2b there have been provided experimental evidence. The translation of AtHSFB1 is regulated by uORF2 but not by uORF1, whereas, neither uORFs of AtHSFB2b are involved in regulation of the main ORF translation. The UORF2 represses the translation of AtHSFB1 under normal condition, but the repression is deregulated under HS. The Arabidopsis HSF-like transcription factor TBF1, a major molecular switch for plant growth-to-defense transition, also contains two uORFs in the 5' untranslated region. Unlike AtHSFB1, both uORFs of TBF1 have inhibitory effects on TBF1 translation, with the effect of uORF2 epistatic to that of uORF1. Both uORFs contain four phenylalanine (Phe) residues, and Phe starvation is shown to alleviate translational repression by the uORFs. Once plants are suffered from pathogen challenge, the uncharged tRNA^Phe will temporary increase and the eukaryotic initiation factor 2α (eIF2α) phosphorylation will be triggered, which may facilitate ribosome reattachment to the TBF1 translation start codon downstream of uORFs and release the inhibitory effects of uORFs to initiate TBF1 translation (Jorgensen and Dorantes-Acosta, 2012; Pajerowska-Mukhtar et al., 2012). In general, not only abiotic but also biotic stresses are involved in the translational regulation of plant HSFs controlled by uORFs. However, the mechanism of plant HSFs translational control via uORFs is still scarce and needs further investigation.

Plant HSFs also undergo intensive post-translational regulation included phosphorylation, ubiquitination, and Small Ubiquitin-like MODifier (SUMO)-mediated degradation, oligomerization, and interaction with other non-HSF proteins (Figure 2; Scharf et al., 2012; Song et al., 2012). In Arabidopsis, the mitogen-activated protein kinase MAPK6 specifically targets the AtHSFA2, phosphorylates it on T249 and changes its intracellular localization under HS conditions (Evrrard et al., 2013); AtHSFA4A interacts with the MAP kinases.
MPK3 and MPK6 and is phosphorylated in vitro on three distinct sites, and Ser-309 being the major phosphorylation site (Pérez-Salamó et al., 2014). Nishizawa-Yokoi et al. (2010) reported that AtHSFA2 was regulated by the accumulation of polyubiquitinated proteins generated by the inhibition of 26S proteasome and AtHsp90. AtSUMO1 physically interacts with AtHSFA2 at the main SUMOylation site Lys315, leading to the repression of its transcriptional activity and ultimately disrupting the acquired thermotolerance pattern in Arabidopsis (Cohen-Peer et al., 2010). In addition, Arabidopsis FK506-binding proteins (FKBPs), ROF1 (FKBP62), and ROF2 (FKBP65) (Meiri and Breiman, 2009; Meiri et al., 2010), HSF binding protein (AtHSBP; Satyal et al., 1998), and tomato Hsp17.4-II (Port et al., 2004) also act as negative regulators for HSFA2 transcriptional activity. Unfortunately, few active regulation factors involved in HSF regulation are found to date.

**FUNCTION OF PLANT HSFs IN HS STRESS RESPONSE**

The major objective for agronomic research remains the enhancement of crop productivity under various abiotic stresses (Puranik et al., 2012). Among the major abiotic stresses, HS has an independent mode of action on the physiology and metabolism of plant cells, and has a negative effect on plant
growth and development, which may lead to catastrophic loss of crop productivity and result in widespread famine (Bita and Gerats, 2013). To deal with the threat posed by HS, unraveling the independent action and biological consequences is important. Based on the role of central regulators of the HS response (Banival et al., 2004), plant HSFs may be used for gene manipulation, contriving tolerance to HS in crops, while characterization of the functional plant HSFs under HS condition is the precondition.

Based on the previous studies, most current information on plant HSFs function under HS condition is derived from HSFA1 and A2 in tomato and Arabidopsis. HSFA1 subfamily is defined as a master regulator of HS responses. Tomato HSFA1a has a unique function as master regulator for acquired thermotolerance, and cannot be replaced by any other HSFs (Mishra et al., 2002). However, no comparable master regulator activity could be identified for any of the four AtHSFA1 (a, b, d, and e) with single or multiple mutants, and the role of master regulator for thermotolerance is shared among the four paralogs due to functional redundancy (Table 2; Liu et al., 2011; Scharf et al., 2012; Fragkostefanakis et al., 2015). Over-expression of soybeans GmHSFA1 can enhance the thermotolerance of transgenic soybeans possibly due to the activation under HS of downstream genes, such as GmHsp70, GmHsp22, and other GmHsps (Table 2; Zhu et al., 2006). Based on its overall sequence (at the protein level) similarity to HSFA1s from other plant species (especially the well-characterized LpHSFA1) and its constitutive expression pattern, GmHSFA1 may be the best candidate of master regulator in soybeans, which needs to be confirmed by an antisense silencing study. HSFA2 has been identified to be the dominant HSF in tomato and Arabidopsis based on its high activator potential for transcription of Hsp genes and the strong accumulation under conditions of long-term HS or repeated cycles of HS and recovery (Mishra et al., 2002; von Koskull-Döring et al., 2007). HSFA2 and A1 form heterodimers resulting in synergistic transcriptional activation of HS genes after HSFA2 is accumulated in the nucleus of cells (Chan-Schaminet et al., 2009). Localization of the tomato HSFA2 protein to the nucleus evidently required interaction with HSFA1, whereas Arabidopsis HSFA2 protein can localize to the nucleus without interacting with the HSFA1 protein (Scharf et al., 1998; Kotak et al., 2004). Over-expression of Arabidopsis HSFA2 in the HSFA1 quadruple knock-out (hsfA1a, b, d, and e) mutant improved the thermotolerance, suggesting that HSFA2 can be active and functional in the absence of HSFA1s in Arabidopsis, and it is tempting to speculate that interactions between HSFA2 and other HSFs may exist in the quadruple knock-out mutants (Liu and Charng, 2013; Fragkostefanakis et al., 2015). Enhanced thermotolerance has also been obtained by ectopic expression of rice HSFA2e and lily HSFA2 in Arabidopsis (Table 2; Yokotani et al., 2008; Xin et al., 2010). In addition to the effects of HSFA1 and A2 members on the thermotolerance level, several other HSF genes also function in the plant thermotolerance. For example, improved thermotolerance is observed in wheat plants over-expressing wheat TaHSFA6f, which relies on the concerted action of target genes, including TaHsps (TaHSP16.8, TaHSP17, TaHSP17.3, and TaHSP90.1-A1), TaRof1, galactinol synthase, and glutathione-S-transferase (GST; Xue et al., 2015); ectopic expression of tomato HSFA3 and wheat HSF3 in Arabidopsis also enhance its thermotolerance (Li et al., 2013; Zhang et al., 2013).

In contrast to HSFAs, HSFBs have no transcriptional activity on their own due to lack of an activator domain. The HS-induced tomato HSFB1 was suggested to be coactivator of HSFA1a by assembling into an enhanceosome-like complex resulting in the strong synergistic activation of reporter gene expression (Fragkostefanakis et al., 2015). The coactivator function of HSFB1 depends on the recruitment of the plant CREB binding protein (CBP) ortholog histone acetyl transferase HAC1 (von Koskull-Döring et al., 2007). Tomato HSFA1a, A2, and B1 form a triad of functionally interacting HSFs that is responsible for the transcriptional level of HS responsive genes during plant HS response and recovery (Perez et al., 2009; Scharf et al., 2012). However, HSFB1 from Arabidopsis was inactive as coactivator due to the essential histone-like motif GRGKMKMK with an invariant Lys residue (underlined) in tomato HSFB1 is replaced by GSRMTETK in Arabidopsis HSFB1 (Bharti et al., 2004). Interestingly, HSFB1 from Arabidopsis is characterized as a repressor of HS-inducible HSFs, such as HSFA2, A7a, B1, and B2b, however, the hsfb1, hsfb2b knockout mutant plants exhibit lower acquired thermotolerance than the wild type. This suggests that HSFB1 and HSFB2b may promote the activity of HSFA1 under HS conditions by repressing Hsps that interfere with the nuclear migration of HSFA1s, an activator of the early HS response (Ikeda et al., 2011). Over-expression of VpHSF1 (a member of class HSFB2 family) from Chinese Wild Vitis pseudoreticulata in tobacco demonstrated that VpHSF1 acted as a negative regulator in basal thermotolerance and a positive regulator in acquired thermotolerance (Peng et al., 2013). The above results indicate striking species-specific deviation in the functional diversification of some members of the HSF family (von Koskull-Döring et al., 2007).

**FUNCTION OF PLANT HSFs IN OTHER ABIOTIC STRESS RESPONSES**

Under natural conditions, plants frequently suffer from various abiotic stresses simultaneously; HS is compounded by additional abiotic stresses such as drought and salt stress (Bita and Gerats, 2013). The response of plant cells encountering a single stress condition can not reflect the real conditions in the field (Nishizawa et al., 2006). Gene manipulation of HSFs in plants is a significant approach to ameliorate the effects of combined HS and other abiotic stresses. Characterization of the functional HSFs involved in various abiotic stresses is necessary. The Arabidopsis HSFA1s are involved in response and tolerance to salt, osmotic, and oxidative stresses during seedling establishment (Liu et al., 2011). Especially, Arabidopsis HSFA1b controls a developmental component to drought tolerance and water productivity, however, the effect of HSFA1b over-expression on drought/dehydration tolerance does not involve changes in the expression of DREB2A or many otherABA- or dehydration-responsive genes (Bechtold et al., 2013). Given that
### TABLE 2 | Overview of plant HSF genotypes and corresponding stress responses.

| Genotype | Gene Source | Stress responses | References |
|----------|-------------|------------------|------------|
| **OVER-EXPRESSION** | | | |
| AtHSFA1 | Arabidopsis | Increased thermotolerance in transgenic Arabidopsis | Lee et al., 1995 |
| AtHSFA1b | Arabidopsis | Enhanced water productivity, resistance to drought in transgenic Arabidopsis | Bechtold et al., 2013 |
| AtHSFA2 | Arabidopsis | Increased thermotolerance, salt/osmotic stress tolerance, and enhanced callus growth of transgenic Arabidopsis | Ogawa et al., 2007 |
| AtHSFA2 | Arabidopsis | Increased tolerance to combined environmental stresses (high-light and heat-shock stresses) in transgenic Arabidopsis | Nishizawa et al., 2006 |
| AtHSFA2 | Arabidopsis | Enhanced anoxia tolerance in transgenic Arabidopsis | Banti et al., 2010 |
| AtHSF3 | Arabidopsis | Confirmed thermotolerance in transgenic Arabidopsis | Prändl et al., 1998 |
| AtHSFB1 | Arabidopsis | Repressed expression of HSF2a, HSF7a, HSFb2b, Hsp15.7CI under moderate heat conditions (28°C) in transgenic Arabidopsis | Ikeda et al., 2011 |
| AtHSFB2a | Arabidopsis | Reduced biomass production in the early phase of growth and damaged development of female gametophytes in transgenic Arabidopsis | Wunderlich et al., 2014 |
| LlHSFA1 | Lilium longiflorum | Interaction with LlHSFA2, enhanced thermotolerance in transgenic Arabidopsis | Gong et al., 2014 |
| LHSF2A | Lilium longiflorum | Improved thermotolerance in transgenic Arabidopsis | Xin et al., 2010 |
| OsHSFA2e | Oryza sativa | Enhanced thermotolerance and tolerance to high-salinity stress in transgenic Arabidopsis | Yokotani et al., 2008 |
| GmHSFA1 | Glycine max | Enhanced thermotolerance in transgenic soybean | Zhu et al., 2006 |
| BhHSF1 | Boea hygrometrica | Increased thermotolerance in transgenic Arabidopsis and tobaccos | Zhu et al., 2009 |
| VpHSF1 | Vitis pseudoreticulata | Reduced the basal thermotolerance, increased acquired thermotolerance, reduced the tolerance to osmotic stress in transgenic tobacco | Peng et al., 2013 |
| VvHSFA9 | Vitis vinifera | Positive modulation of seed germination and might negatively regulate flowering time of transgenic Arabidopsis | Li et al., 2015 |
| SiHSFA1 | Solanum lycopersicum | Master regulator of thermotolerance in transgenic tomato | Mishra et al., 2002 |
| SiHSFA3 | Solanum lycopersicum | Increased thermotolerance and salt hypersensitivity during seed germination in transgenic Arabidopsis | Li et al., 2013 |
| TaHSF3 | Triticum aestivum | Enhanced tolerance to extreme temperatures in transgenic Arabidopsis | Zhang et al., 2013 |
| TaHSFA4a | Triticum aestivum | Enhanced Cd tolerance by upregulating metallothionein gene expression in rice plants | Shim et al., 2009 |
| TaHSFA6f | Triticum aestivum | Improved thermotolerance in transgenic wheat | Xue et al., 2015 |
| CarHSFB2 | Cicer arietinum | Increased tolerance to drought and heat stress in transgenic Arabidopsis | Ma et al., 2016 |
| HaHSFA4a and A9 | Helianthus annuus | Synergistic functional effect on tolerance to severe dehydration and to drastic oxidative stress in transgenic tobacco | Personat et al., 2014 |
| **MUTANT** | | | |
| AtHSF1 and AtHSF3 | Arabidopsis | No obvious effects on the heat shock response in the individual mutant lines; double mutants were significantly impaired in HS gene expression | Lohmann et al., 2004 |
| AtHSFA2 | Arabidopsis | The expression of AtHSFA2 was strictly heat stress-dependent and this transcription factor represented a regulator of a subset of stress response genes (Hsp26.5, Hsp25.3, Hsp70b, APX2, RD29A, RD17, GolS1, IPS2, KSC1, ERD7, and ZAT10) in Arabidopsis | Schramm et al., 2006 |
| AtHSFA2 | Arabidopsis | AtHSFA2 knockout mutant showed an obvious phenotype, and was more sensitive to severe HS than the wild type after long but not short recovery periods. Acquired thermotolerance (AT) decayed faster in the absence of HSF2a, Hsa32 and class I small Hsp were less abundant in the mutant than in the wild type after long recovery. AtHSFA2 sustained the expression of Hsp genes and extended the duration of AT in Arabidopsis | Chang et al., 2007 |
| AtHSFA2 | Arabidopsis | Heat-dependent acclimation to anoxia was lost in an HSF2a knockout mutant | Banti et al., 2010 |
| AtHSFB2a | Arabidopsis | Knockdown of asHSPB2a correlated with an improved biomass production early in vegetative development but with an impaired development of female gametophytes | Wunderlich et al., 2014 |

(Continued)
CONCLUSION AND PERSPECTIVES

Understanding the molecular mechanisms of plants response to abiotic stresses such as heat, drought and salinity is a prerequisite for the manipulation of plants to improve stress tolerance and productivity. In response to these stresses, many genes are regulated mainly by TFs, and their gene products function in providing stress tolerance to plants (Lata and Prasad, 2011). One such class of the plant TFs is HSF that binds to HSE cis-acting elements in promoters of stress-inducible genes and plays central roles in the acquisition of plant tolerance against abiotic stresses. In this review, we have described the conserved structure of plant HSFs, the HSF gene families from various plant species based on the genome-wide identification, their expression profiling, different regulation levels and function in abiotic stresses. Plant HSF genes are important TFs that regulate the expression of various stress-responsive genes and play a key role in providing tolerance to multifarious abiotic stresses (Figure 3).

HSFs can be employed to engineer transgenic plants with higher tolerance to environmental stresses; however, many important questions should be addressed. The role of HSF genes in plants, especially in important agricultural crops needs a better...
understanding to minimize their negative effects in transgenic plants. For example, over-expressing VpHSF1 in tobacco not only increased the acquired thermotolerance but also reduced the basal thermotolerance and the tolerance to osmotic stress (Table 2; Peng et al., 2013); over-expression of tomato SlHSFA3 increased thermotolerance of transgenic Arabidopsis, but played a negative role in controlling seed germination under salt stress (Li et al., 2013). Because HSFs and chaperones play the broader role in cellular homeostasis, manipulation of HSFs may disrupt the homeostasis, leading to pleiotropic and undesired effects (Cabello et al., 2014; Frągkostefanakis et al., 2015). Although great progress has been achieved in the characterization of class HSFAs, the biological functions of HSFB and C members, and the HSFs active regulation factors remain to be clarified. Therefore, there is a dire need to understand the exact regulatory mechanisms of all the stress-responsive HSF genes. Most experiments on the role of HSFs in abiotic stress responses are limited to several model plants in laboratory conditions addressing individually abiotic stresses, which cannot represent precisely field conditions. As there is functional divergency between HSF orthologs in different plant species, it is necessary to adjust the research direction of HSFs function from few model plants to a broader variety of plant species, including the desired agricultural crops. In addition, marker-assisted selection can accelerate traditional crop breeding for stress tolerance traits, but decision of HSFs as candidate genes and developing proper functional markers has to be carefully decided due to the implication of HSFs in various developmental and stress response aspects (Frągkostefanakis et al., 2015).

In the future, a combination of advanced high throughput technologies, such as microarray, genomics, and proteomic approaches in various developmental stages and stress conditions will provide us with critical information to elucidate the whole complexity of HSFs integrated abiotic stress responses and different signaling pathways. Further studies are necessary to be focused on the functions of HSFs in agricultural crops under harsh field conditions, the dual (positive or negative) role of HSFs in different stress conditions and establishment of an HSF network in relation to the crosstalk between abiotic...
stress responses and plant growth, development and metabolism, which may provide practical and biotechnological approaches to improve the crop plants tolerance to extreme environment conditions.

 AUTHOR CONTRIBUTIONS

MG, ML, and ZG conceived and designed the paper; MG, JL, XM, and DL collected and analyzed the literature; MG wrote the paper.

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human and tobacco.

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