

园艺植物热激转录因子研究进展

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摘要: 当植物遭受环境胁迫时, 热激转录因子(Heat stress transcription factors, Hsfs)作为重要的调节因子, 广泛参与多种生物和非生物胁迫响应, 在植物耐高温胁迫和其他生命活动发挥重要作用。相比于动物, 植物中的Hsfs家族成员数量众多、功能多样、调控机制更加复杂。目前植物Hsfs的研究主要集中于模式植物和部分大田作物, 且研究对象多数为A族成员, 有关园艺植物中热激转录因子的研究起步较晚。笔者详细介绍了植物热激转录因子的家族成员和蛋白结构, 重点阐述了模式植物和园艺植物中Hsfs在应答温度(高温、低温), 干旱以及高盐等胁迫中的研究进展, 并探讨和展望了植物热激转录因子未来可能的研究热点, 以期为进一步阐明园艺植物热激转录因子的功能和分子机制提供依据和参考。

关键词: 园艺植物; 热激转录因子; 非生物胁迫; 功能

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Research progress of heat stress transcription factors (Hsfs) in horticultural plants

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Abstract: Under natural conditions, plants are constantly subjected to various stresses. In particular, abiotic stress is one of the primary causes for crop loss worldwide, which greatly reduces crop productivity. In order to improve crop yield, it is urgent to elucidate the potential molecular mechanism of plant stress to abiotic stress. With the global warming, high temperature stress has become an important abiotic stress affecting plant growth and crop yield. When plants are subjected to heat stress, a series of responses will be triggered, thus leading to the rapid accumulation of heat shock protein. They play critical important roles in the process of plant resistance. Genes regulated the expression of heat shock proteins are called plant heat shock transcription factor (*Hsf*). As one of crucial regulators in regulation network, plant heat shock transcription factor, could bind to HSE cis-acting elements in promoters of stress-inducible genes and respond to multiple biotic and abiotic stresses. *Hsfs* are classified into three classes in plants, including *HsfA*, *HsfB*, and *HsfC*, respectively. Similar to all non-plant *Hsfs*, the HR-A/B region of class B is compact, however, members of class A 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. *HsfAs* has attracted a lot of attention, but few on class B (*HsfBs*) and class C (*HsfCs*). The

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identification of the *Hsfs* family were previously reported only in a few model plant species such as *Arabidopsis*, tomato, and rice. In recent years, the availability of the ever-increasing number of complete plant genomes and EST sequences, lead to the identification of a large numbers of *Hsfs* families from more than 20 plant species at the genome-wide scale. For instance, there are 21 *Hsf* encoding genes in *Arabidopsis*, 26 in tomato, 25 in pepper, 25 in apple, and 19 in grapevine. Similar to many other species, plant Hsf proteins share a well-conserved modular structure, and consist of five parts, including N-terminal DNA-binding domain (DBD), oligomerization domain (OD or HR-A/B region), nuclear localization signal (NLS), nuclear export signal (NES) and acidic C-terminal domain (CTD), respectively. Plant *Hsfs* are core regulators in regulation of heat-stress (HS), low temperature, salt, and drought. Therefore, it is necessary to clarify the function of Hsfs that participate in various abiotic stresses. 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. *HsfAs* play critical roles in regulating the expression of *Hsp* genes in heat stress. At present, the functional investigation of *Hsfs* under HS condition was mainly concentrated in *HsfsA1*, *HsfsA2* and *HsfsB*. *HsfsA1* is a main regulator of heat shock response and cannot be replaced by other *Hsfs*. The function and structure of *HsfA2* are similar to those of *HsfA1*, playing a key component of plant cell heat shock signal transduction. In contrast to *HsfAs*, *HsfBs* have no transcriptional activity due to lack of the activator domain. These indicate striking species-specific deviation in the functional diversification of some members of the *Hsfs* family. In this review, genome-wide expression profiling of plant *Hsfs* genes under heat stresses has been investigated extensively in various horticultural plants. The expression of *Hsfs* in apple, citrus, eggplant and strawberry were either regulated or down-regulated by HS. Furthermore, *Hsfs* play an important role under different abiotic stress conditions. Talking about the study on *Hsfs*, high temperature stress is still an important factor, and the response mechanism of *Hsfs* to other stresses is relatively less, especially to low temperature stress and biological stress. In previous studies, some heat shock proteins involved in low temperature stress response were identified by our research group. The data showed that a large number of *Hsps* are involved in cold response, including 6 down-regulated genes and 4 up-regulated genes. This paper summarized the structural characteristics, classification and the function of plant heat shock transcription factors in response to various stress conditions, including high temperature stress, drought stress, high salt stress and other stresses. In addition, the development and application prospects of plant heat shock transcription factors in future research hotspots were discussed, aiming to provide the basis and reference for elucidating the function and molecular mechanism of *Hsfs* in plants. A combination of advanced high throughput technologies will provide the critical information to elucidate the whole complexity of *Hsfs* in abiotic stress responses and different signaling pathways.

Key words: Horticultural plant; Heat stress transcription factor; Abiotic stress; Function

随着全球气候变暖,热胁迫对植物的影响日益加剧。当遭受热胁迫时,植物体内会产生一系列应激反应,从而引起植物体内迅速累积热激蛋白(Heat shock proteins, Hsps)^[1]。热激蛋白普遍存在于整个生物界,常作为分子伴侣在细胞反应中促使其他蛋白进行折叠、分配、运输和降解,以维持细胞的存活,在植物抗逆过程中起到非常重要的作用^[2-3]。调

节热激蛋白表达的基因被称为植物热激转录因子,其主要通过特异性识别并结合热激蛋白基因启动子区的热激元件(Heat shock element, HSE),调控热激蛋白基因的转录和表达^[1,4]。

植物体内的热激转录因子最早是从番茄(*Solanum lycopersicum*)中克隆获得^[5],相继在一些动物中也克隆了热激转录因子基因。与动物相比,植物热

激转录因子在结构、数量等方面更加复杂^[6]。笔者针对热激转录因子的家族类别、蛋白结构域、以及其在非生物逆境中的功能等方面的研究进展进行了概述。

1 Hsfs 基因家族类别

Hsfs 由多基因家族编码,根据其蛋白质结构的差异,可分成 A、B、C 三类^[7]。目前有关 A 类 Hsfs 研究较多, B 类和 C 类 Hsfs 的报道相对较少。Hsfs 基因首次在酵母中^[8]克隆分离,随后在果蝇^[9]和哺乳动物^[10-11]中也相继被报道。与脊椎动物(4 条)、果蝇(1 条)、秀丽隐杆线虫(1 条)和酵母(1 条)^[12-13]中的 Hsfs 成员相比,植物 Hsfs 家族

包含了大量的成员。早期有关 Hsfs 基因仅在一些模式植物如拟南芥(*Arabidopsis thaliana*)、番茄、玉米(*Zea mais*)等中被报道^[6,14],如拟南芥中有 21 条 Hsfs,番茄中有 26 条,玉米中有 30 条。随着多种植物基因组测序的完成,已在多种植物中发现数量不等的 Hsfs 基因家族成员,包括苹果(*Malus domestica*)^[15]、茶树(*Camellia sinensis*)^[16]、华东葡萄(*Vitis pseudoreticulata*)^[17]、中国白梨(*Pyrus bretschneideri*)^[18]、桃(*Prunus persica*)^[18]、辣椒(*Capsicum annuum* L.)^[19]和胡萝卜(*Daucus carota*)^[20]等园艺植物以及大豆(*Glycine max*)^[6]、棉花(*Gossypium hirsutum*)^[21]、小麦(*Triticum aestivum*)^[22]等作物(表 1)。

表 1 近年报道的植物热激转录因子

Table 1 The HSF family in plant species reported mainly in recent years

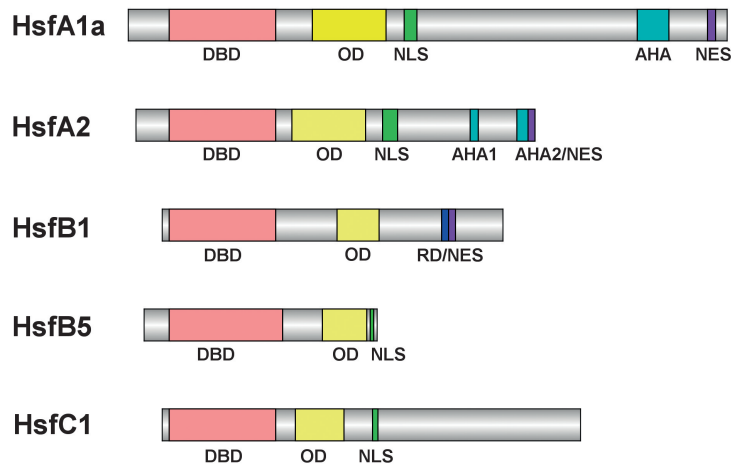
物种 Species	Hsfs			总数 In total	文献来源 References
	A 类 Class A	B 类 Class B	C 类 Class C		
拟南芥 <i>Arabidopsis thaliana</i>	15	5	1	21	[6]
番茄 <i>Solanum lycopersicum</i>	17	8	1	26	[6]
玉米 <i>Zea mais</i>	16	9	5	30	[6]
辣椒 <i>Capsicum annuum</i> L.	17	7	1	25	[19]
苹果 <i>Malus domestica</i>	16	7	2	25	[15]
茶 <i>Camellia sinensis</i>	9	6	1	16	[16]
大白菜 <i>Brassica rapa pekinensis</i>	19	9	2	30	[23]
胡萝卜 <i>Daucus carota</i>	27	7	1	35	[20]
草莓 <i>Fragaria vesca</i>	11	5	1	17	[24]
中国白梨 <i>Pyrus bretschneideri</i>	19	8	2	29	[18]
梅花 <i>Prunus mume</i>	11	5	1	17	[18]
桃 <i>Prunus persica</i>	10	6	1	17	[18]
西洋梨 <i>Pyrus communis</i>	22	9	2	33	[18]
华东葡萄 <i>Vitis pseudoreticulata</i>	11	7	1	19	[17]
柑橘 <i>Citrus reticulata</i>	11	6	1	18	[25]
水稻 <i>Oryza sativa</i>	13	8	4	25	[6]
小麦 <i>Triticum aestivum</i>	33	11	12	56	[22]
大豆 <i>Glycine max</i>	28	22	2	52	[6]
棉花 <i>Gossypium hirsutum</i>	22	15	3	40	[21]

2 Hsfs 结构特征

Hsfs 蛋白具有高度保守的结构,主要包括五个部分(图 1),分别是 N 端 DNA 结合结构域(DNA-binding domain, DBD)、寡聚域(Oligomerization domain, OD 或 HR-A/B)、核定位信号域(Nuclear localization signal, NLS)、核输出信号(Nuclear export signal, NES)与酸性 C 端转录激活结构域(C-terminal

domain, CTD)^[6-7,26]。

DBD 区域高度保守,其内部结合域疏水中心存在一个高度保守的螺旋-转角-螺旋(H2-T-H3)的疏水结构,其功能与 HSE 的保守基序(5'-nGAAnnTTCnnGAAn-3')的识别以及结合相关^[27]。此外,HR-A/B 区域可通过一段碱性氨基酸与 DBD 区域相连^[28]。该区域在空间上形成 coiled-coil 的结构(helical coiled-coil structure),可以使热激转录因



DBD. DNA 结合域;OD. 寡聚域;NLS. 细胞核定位信号;NES. 细胞核输出信号;AHA. 激活结构;RD. 转录抑制结构。

DBD. DNA binding domain; OD. Oligomerization domain; NLS. Nuclear localization signal; NES. Nuclear export signal; AHA. Activator motifs; RD. Repressor domain.

图1 热激转录因子蛋白结构域^[6]

Fig. 1 Protein domains of HSFs^[6]

子形成同源三聚体,这与热激蛋白的合成密切相关^[29]。通过在HR-A和HR-B之间插入的氨基酸残基数目的不同,可将热激转录因子划分为三类,分别是插入21个氨基酸的A类,插入7个氨基酸的C类以及没有氨基酸插入的B类^[7,30]。

NLS由一簇单组分或双组分碱性氨基酸残基组成,可引导Hsfs进入细胞核^[31]。而NES则仅存在于某些植物中,并富含亮氨酸,能够帮助Hsfs从细胞核输出到细胞质,并与NLS具有协同作用,共同维持细胞的平衡^[32-33]。

在热激转录因子蛋白结构域中,酸性C端转录激活结构域变异较大,该结构域仅存在于A类热激转录因子中,并通过一些由芳香族氨基酸残基(色氨

酸、苯丙氨酸、酪氨酸)、大的疏水性氨基酸残基(亮氨酸、异亮氨酸、缬氨酸)和酸性氨基酸(谷氨酸、天冬氨酸)组成的AHA短肽基序发挥转录激活功能^[34]。

3 植物热激转录因子Hsfs在非生物胁迫中的功能

在自然环境下,植物常常受到各种胁迫的影响,尤其是非生物胁迫^[6,35]。研究植物对非生物胁迫响应的分子机制对提高农作物的产量具有重要意义。植物Hsfs基因是热胁迫响应中重要的核心调节因子^[14],参与响应多种非生物胁迫,如高温、低温、盐、干旱等,因此阐明其功能对于Hsfs基因参与各种非生物胁迫是十分必要的^[6](表2)。

表2 近年来主要报道的热激转录因子及其功能

Table 2 The heat stress transcription factors and function reported mainly in recent years

物种 Species	转录因子 TFs	功能 Function	文献来源 References
拟南芥 <i>Arabidopsis thaliana</i>	<i>AtHsfA1a/b/c/d</i>	正调控热应激反应 Positively regulate heat stress response	[36]
	<i>AtHsfA2</i>	正调控热应激反应 Positively regulate heat stress response	[37]
	<i>AtHsfB</i>	负调控热应激反应 Negatively regulate heat stress response	[38]
	<i>AtHsfA6a/3</i>	响应干旱胁迫 Response to drought stress	[39-40]
番茄 <i>Solanum lycopersicum</i>	<i>SlHsfA1a</i>	正调控热应激反应 Positively regulate heat stress response	[41]
	<i>SlHsfA2</i>	响应热胁迫 Response to heat stress	[41]
	<i>SlHsfA3</i>	正调控热应激反应 Positively regulate heat stress response	[42]

表2(续) Table 2(continued)

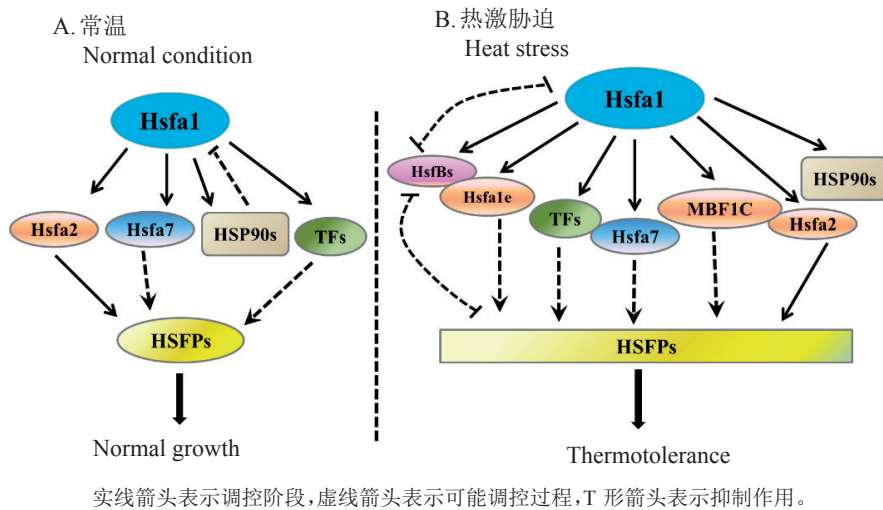
物种 Species	转录因子 TFs	功能 Function	文献来源 References
	<i>SlHsfB1</i>	响应热胁迫 Response to heat stress	[6]
玉米 <i>Zea mays</i>	<i>ZmHsfA2</i>	正调控热应激反应 Positively regulate heat stress response	[43-44]
水稻 <i>Oryza sativa</i>	<i>OsHsfA2e</i>	正调控热应激反应 Positively regulate heat stress response	[45]
	<i>OsHsfB2b</i>	负调控干旱胁迫 Negatively regulate drought stress response	[46]
	<i>OsHsfA2s/A4s/A7/A9</i>	响应盐胁迫 Response to salt stress	[47]
	<i>OsHsfA2a/B4b/C2a</i>	响应氧化胁迫 Response to oxidative stress	[48]
	<i>OsHsfA3/A4d/A7/A9/C1/C2b</i>	响应低温胁迫 Response to low temperature stress	[47]
百合 <i>Lilium brownii</i>	<i>LbHsfA2</i>	正调控热应激反应 Positively regulate heat stress response	[49]
小麦 <i>Triticum aestivum</i>	<i>TaHsfA6</i>	正调控热应激反应 Positively regulate heat stress response	[22]
	<i>TaHsf3</i>	正调控低温胁迫 Positively regulate low temperature stress	[50]
苹果 <i>Malus domestica</i>	<i>MdHsfA2a/A2b/A3b/A3c</i>	正调控热应激反应 Positively regulate heat stress response	[15]
柑橘 <i>Citrus reticulata</i>	<i>CcHsfs</i>	正调控热应激反应 Positively regulate heat stress response	[25]
辣椒 <i>Capsicum annuum</i> L.	<i>CaHsfA2/A3/A6c/B1/B5</i>	正调控热应激反应 Positively regulate heat stress response	[19]
	<i>CaHsfA1b/A3/A9/A9d/C1</i>	正调控盐胁迫 Positively regulate salt stress	[19]
茄子 <i>Solanum melongema</i> L.	<i>SmHsfA3/A6a/A6b</i>	响应热胁迫 Response to heat stress	[51]
	<i>SmHsfB1</i>	响应热胁迫 Response to heat stress	[51]
草莓 <i>Fragaria vesca</i>	<i>FvHsfA1d/A2a/A3a</i>	正调控热应激反应 Positively regulate heat stress response	[24]
	<i>FvHsfB1a</i>	正调控热应激反应 Positively regulate heat stress response	[24]
	<i>FvHsfA3a/A4a/B1a/C1a</i>	响应干旱胁迫 Response to drought stress	[24]
	<i>FvHsfA2a/A3/A5/A9a/B1</i>	响应盐胁迫 Response to salt stress	[24]
	<i>FvHsfA3a/A4a/A9a</i>	响应低温胁迫 Response to low temperature stress	[24]
胡萝卜 <i>Daucus carota</i>	<i>DcHsf09/16</i>	响应干旱胁迫 Response to drought stress	[20]
	<i>DcHsf01/10/16</i>	响应盐胁迫 Response to salt stress	[20]
	<i>DcHsf16</i>	正调控低温胁迫 Positively regulate low temperature stress	[20]
大白菜 <i>Brassica rapa pekinensis</i>	<i>BraHsf001/043</i>	响应盐胁迫 Response to salt stress	[23]
	<i>BraHsf001/039/043</i>	响应低温胁迫 Response to low temperature stress	[23]
菠菜 <i>Spinacia oleracea</i> L.	<i>SoHsfA1/B1</i>	正调控干旱胁迫 Positively regulate drought stress response	[52]
华东葡萄 <i>Vitis pseudoreticulata</i>	<i>VaHsfA2a/A6a/B3a/C1a</i>	响应低温胁迫 Response to low temperature stress	[17]

3.1 热激转录因子参与热胁迫响应

热胁迫响应是指在正常蛋白质合成受阻的同时产生热激蛋白的一种细胞生理活动。热激转录因子可以对 HSP 产生的过程进行调控。当植株受到热胁迫时,植物自身的 Hsfs 通过与 HSE 顺式作用元件特异性结合,同时募集其他转录因子结合在热激蛋白基因上,形成转录复合体,引发热激蛋白基因转录并累积 HSP^[12]。

A 类热激转录因子是热胁迫中的主要调节因子,可作为高温诱导基因表达的主要调控者,其功能研究最多。高温胁迫下,*HsfA1* 能够调控多种类型的基因表达(图 2),如热激蛋白类的 *HSP70*、

HSP101、*HsfA2*/*HsfA3*/*HsfB1* 等^[53]。拟南芥有 4 个 *AtHsfA1* 基因 (*AtHsfA1a/b/c/d*),其中 *AtHsfA1a* 和 *AtHsfA1b* 在热响应早期阶段能调控相关基因的表达,可减轻高温对植物造成的损害,另外当 4 个基因被同时敲除时,突变体植株对高温表现出敏感性^[36]。番茄中共有 26 个热激转录因子基因,目前有关番茄热激转录因子的功能研究主要聚焦在 *SIHsfA1a*、*SIHsfA2* 与 *SIHsfB1* 上,其中 *SIHsfA1a* 是热激响应的主要调节因子,且不能被其他 *SIHsfs* 代替^[41]。番茄中过量表达 *SIHsfA1a* 可以增加转基因株系体内 *SIHsfA2*、*SIHsfB1*、*SIHsp17C1* 和 *SIHsp104* 的表达,从而提高植株的耐热性;当 *SIHsfA1* 受到抑制时,植



Response stage of regulation are shown by solid arrows, possible progress of regulation by dotted arrows, and inhibitory is shown by T-arrow.

图2 HsfA1 在常温和热激条件下转录调节模式^[53]

Fig. 2 Models for transcriptional cascades regulated by HsfA1 proteins under normal condition and heat-stress conditions^[53]

株呈现出热敏感的状态^[41]。

HsfA2 在结构域功能上均与 HsfA1 较为相似,是植物细胞热激信号转导的关键组分,属于热激信号转导中 HsfA1 下游的响应因子。研究表明,HsfA2 与 HsfA1 蛋白互作,形成异源寡聚超级激活因子复合体,这种特异的结合使得 HsfA2 在细胞核中积累后能够协同激活热胁迫响应基因^[54]。研究发现,当番茄受到热胁迫时,细胞内会积累大量的 SIHsfsA2,表明 SIHsfA2 参与了热胁迫响应^[55]。玉米 *ZmHsfA2* 在拟南芥中过量表达,可以提高拟南芥的基础耐热性和持续耐热性^[43-44]。拟南芥 37 °C 热激处理后置于室温恢复后,*athsfA2* 突变体呈现出较为敏感的表型,说明 *AtHsfA2* 可以增强拟南芥的耐热性^[37]。此外,水稻 (*Oryza sativa*) *OsHsfA2e* 和百合 (*Lilium brownii*) *LbHsfA2* 在拟南芥中过量表达后同

样可以增强耐热性^[45,49]。

除了 HsfA1 和 HsfA2,植物体内其他 A 类 Hsfs 也参与了调控植物高温胁迫应答的反应。研究表明,*HsfA3* 作为 *DREB2A* 和 *DREB2C* 的下游基因,参与植物众多的非生物胁迫反应^[56-57]。研究人员发现番茄中 *SIHsfA3* 的表达受高温诱导,番茄 *SIHsfA3* 在拟南芥中过量表达,可提高转基因拟南芥的耐热性^[42]。小麦中过表达 *TaHsfA6* 后植株耐热性增强,同时热激蛋白、肌醇半乳糖苷合酶和谷胱甘肽-S-转移酶(GST)表达量显著提高^[22]。

与 A 类 Hsfs 结构域有所不同,B 类 Hsfs 由于缺少激活域导致其没有转录活性^[24,30,58]。B 类热激转录因子 C-末端的 BRD (B3 repression domain) 结构域可抑制正常条件下耐热基因的转录表达^[59],表明其在植物耐热性防御方面发挥重要的作用。HsfB1

可辅助HsfA1在热激响应中起调控作用^[58]。番茄中*SlHsfB1*可与A类*SlHsfA1a*、*SlHsfA2*形成三聚体,进而调控植物热胁迫响应相关基因的表达^[6]。然而,拟南芥*AtHsfB*族基因在热胁迫反应中多是负调控因子,在常温条件下,拟南芥*hsfb1hsfb2b*双突变体植株热诱导相关基因表达量增加,持续高温环境中,*hsfb1hsfb2b*双突变体耐热性较野生型植株略有提高^[38]。

研究表明,高温胁迫下很多园艺植物中Hsfs的表达均受到不同程度的影响。苹果长时间暴露在自然高温环境下,大多数MdHsfs均被诱导表达,尤其是MdHsfA2a、MdHsfA2b、MdHsfA3b、MdHsfA3c在胁迫后表达量显著增加^[15]。从柑橘(*Citrus reticulata*)中分离鉴定的18条CcHsfs基因中,发现7条CcHsfs在40℃热胁迫下表达量显著提高^[25]。40℃处理辣椒耐热品系R9,除CaHsfB3a、CaHsfB3b和CaHsfC1外,大部分CaHsfs基因在热胁迫条件下均能上调表达,尤其CaHsfA2、A3、A6c、B1和B5的表达量较其他基因明显增加,是辣椒品系热胁迫的主要转录调控因子^[19]。值得注意的是,CaHsfB1、B2a、B2b、B4、B5在热胁迫下均上调表达,而CaHsfB3a、B3b在热敏感株系B6和耐热株系R9中却下调表达,表明B类型的热激转录因子在辣椒中扮演着不同的角色^[19]。另外,在黄瓜(*Cucumis sativus* L.)中研究也发现,黄瓜叶片中的热激转录因子在应对高温热激响应中表达水平存在显著的差异,其中有11个CsHsfs表达量显著提高,5个CsHsf表达量降低,4个CsHsf无明显差异,表明不同的CsHsfs在应对热激反应时发挥的作用有所不同^[60]。42℃处理下,茄子(*Solanum melongena* L.)的耐热品系和热敏品系中83%的SmHsfs均上调表达,其主要的转录因子SmHsfA3、SmHsfA6a、SmHsfA6b和SmHsfB1在耐热品系中的表达水平明显高于在热敏品系中的表达量,说明茄子SmHsfs参与了热胁迫响应过程^[51]。此外,42℃环境下,草莓(*Fragaria vesca*)中FvHsfA1d、FvHsfA2a、FvHsfA3a和FvHsfB1a等基因的表达量均呈现增加趋势^[24]。Wu等^[61]发现,百合中*LlHsfA3B*能形成3种剪接变体,其中的*LlHsfA3B-III*在热胁迫诱导下能够提高植株的耐热性,可减弱热胁迫反应带来的不利影响。

3.2 热激转录因子参与干旱胁迫

干旱可引发植物气孔关闭,导致光合和呼吸作

用减弱等,因此阐明Hsfs参与植物干旱胁迫是十分必要的。拟南芥中有很多*AtHsfs*成员受干旱诱导表达^[62]。如拟南芥中过表达*AtHsfA6a*可提高植株的抗旱性^[39]。此外,*AtHsf3*基因也被鉴定为干旱胁迫的信号基因^[40],*HsfA3*依赖于*DREB2A*转录因子发挥作用,而*DREB2A*的过表达可促进*Hsf3A*和其他相关基因的表达^[40、56]。Hu等^[24]对草莓进行干旱处理时发现,其叶片中FvHsfs成员在处理的不同阶段表达量不同,*FvHsfA3a*在干旱处理的前期和中期呈现上调表达,*FvHsfA4a*、*FvHsfB1a*和*FvHsfC1a*在干旱48h内上调表达,而在48h后先下调表达后上调表达。用PEG6000模拟干旱,白菜(*Brassica spp. pekinensis*)中大部分*BraHsfs*基因都为上调表达,但在‘Qingdao87-114’品系中*BraHsf001*下调表达^[23]。干旱胁迫下,胡萝卜‘Kurodagosun’中除了*DcHsf09*和*DcHsf16*,其他成员均呈下调表达,而在‘Junchuanhong’中*DcHsf10*、*DcHsf09*、和*DcHsf16*表达量显著增强^[20]。

研究显示,大多数Hsfs的A类成员在参与植株耐旱胁迫时,表达量都表现为增强,而HsfB2亚家族调控植物耐旱性时表现出多样性。过量表达水稻*OsHsfB2b*的转基因粳稻中丙二醛和电导率含量显著上升,而脯氨酸含量下降,其抗旱能力降低^[46]。在拟南芥中过表达鹰嘴豆(*Cicer arietinum* L.)*CarHsfB2*基因能够提高胁迫响应基因(*RD22*、*RD26*和*RD29A*)的转录水平,从而增强幼苗的耐旱性^[63]。此外,干旱条件下在拟南芥中过表达菠菜(*Spinacia oleracea* L.)*SoHsfA1*、*SoHsfB1*等基因,转基因拟南芥株系的萌发率明显高于野生型,同时用400 mmol·L⁻¹山梨醇模拟干旱胁迫后也能提高转基因拟南芥的耐旱性^[52]。由此可见,Hsfs是植物耐旱机制中的重要成员,然而,不同的Hsfs成员在调控植物耐旱性的表达模式有差异。

3.3 热激转录因子参与盐胁迫

研究发现,拟南芥中部分Hsfs基因能够增强植株耐盐性,如*AtHsfA1*在盐胁迫下表达增强^[36]。小麦中的*TaHsf*(ID: Traes_5BL_FCB1625F3.1)较对照表达量也显著增强^[64]。水稻中多种A族成员均受盐胁迫诱导表达,如*OsHsfA2s*、*OsHsfA4s*、*OsHsfA7*、*OsHsfA9*等在胁迫后期表达量显著增加^[47]。此外,一些园艺植物Hsfs也参与盐胁迫响应。如用0.3 mol·L⁻¹ NaCl浇灌盆栽草莓,*FvHsfA3a*、*FvHsfA5a*、

FvHsfA9a 等基因表达量显著增强,有趣的是, *FvHsfA2a* 在盐胁迫前期上调表达,而 *FvHsfA3a*、*FvHsfA5a*、*FvHsfA9a* 和 *FvHsfB1* 在中期和后期表达增强^[24]。Ma 等^[23]于2014年发现用 $0.1 \text{ mol} \cdot \text{L}^{-1}$ NaCl 处理大白菜, *BraHsf001* 在‘Lubaisanhao’和‘Qingdao87-114’两个品系中表达模式不同,在前者中随着胁迫时间的延长, *BraHsf001* 表达量逐渐减弱,而在后者中却逐渐增强,此外在‘Lubaisanhao’品系中 *BraHsf043* 表达量逐渐减弱。用 $0.2 \text{ mol} \cdot \text{L}^{-1}$ 的 NaCl 处理胡萝卜, *DcHsf10*、*DcHsf01* 和 *DcHsf16* 在‘Junchuanhong’中表达增强,但在‘Kurodagosun’中除了 *DcHsf16* 外,其他基因的表达均呈现逐渐减弱的趋势^[20]。值得注意的是,盐胁迫下辣椒中的 *CaHsfA1b*、*CaHsfA3*、*CaHsfA9a*、*CaHsfA9d* 和 *CaHsfC1* 六个成员在根和茎中都呈上调表达,而 *CaHsfA1d*、*CaHsfA4b*、*CaHsfA8*、*CaHsfB2b* 和 *CaHsfB3a* 五个成员受盐胁迫诱导表达不明显^[19]。上述研究结果表明,不同 Hsfs 成员响应盐胁迫时其表达模式呈现多样性。

3.4 热激转录因子的其他作用

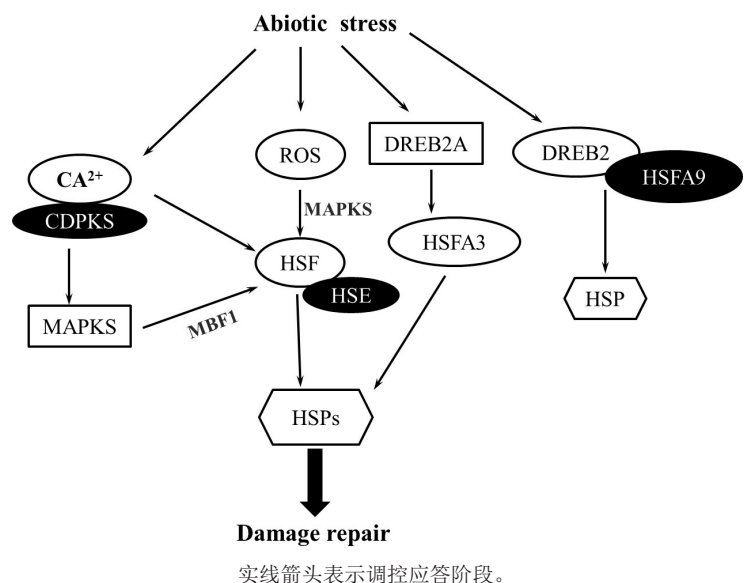
除了受高温、干旱以及盐胁迫外,植物还会遭受到其他非生物胁迫,如氧化胁迫、甲醛胁迫和冷害等。众多研究表明, Hsfs 同样在这些胁迫中对调控相关基因的表达起到重要的作用^[22, 65-66]。

氧胁迫可导致大量活性氧(Reactive oxygen species, ROS)的产生,如 H_2O_2 、超氧阴离子(O_2^-)等,从而对细胞造成损伤。氧化酶可以有效地清除植株细胞内产生的活性氧,因此,植株的抗逆性与氧化酶的活性密切相关。研究发现,用 $0.4 \text{ mmol} \cdot \text{L}^{-1}$ H_2O_2 处理拟南芥植株, *AtHsfA1a* 可激活 *HSP70* 的基因表达,修复受损细胞^[67]。番茄 *SlHsfs* 也能调控抗坏血酸过氧化酶 *APX1* 和 *APX2* 基因的表达^[68]。水稻中多个 *OsHsfs* 成员,如 *OsHsfA2a*、*OsHsfB4b* 和 *OsHsfC2a* 能够被 $0.01 \text{ mol} \cdot \text{L}^{-1}$ H_2O_2 激活,而这些成员在清除 ROS、减轻细胞损伤、抵抗氧化胁迫等方面发挥重要作用^[48]。

此外,甲醛胁迫作为非生物胁迫的一种,对生物的危害非常严重。张道君^[69]研究了转化拟南芥 *AtHsfA1d* 的烟草

与野生型烟草对 $4 \text{ mmol} \cdot \text{L}^{-1}$ 甲醛的吸收速率,以及在 $6 \text{ mmol} \cdot \text{L}^{-1}$ 甲醛的胁迫下烟草的鲜重和总蛋白含量的变化,证实了 *AtHsfA1d* 过表达烟草比野生型烟草具有更好的甲醛耐受性。

Hsfs 在植物抵御低温胁迫中同样发挥着重要作用。拟南芥中多数 *AtHsfs* 成员受低温诱导显著表达^[62]。水稻中 *OsHsfA3*、*OsHsfA4d*、*OsHsfA7* 和 *OsHsfA9* 等 A 族成员和 *OsHsfC1*、*OsHsfC2b* 等 C 族成员是感受低温环境的主要组分,在冷胁迫中起重要的作用^[47]。小麦 *TaHsf3* 转化拟南芥在 $4 \text{ }^\circ\text{C}$ 处理条件下,转基因株系存活率高于野生型,相对电导率低于野生型植株,表明 *TaHsf3* 参与低温胁迫反应正调控^[50]。此外,园艺作物草莓,在 $4 \text{ }^\circ\text{C}$ 处理条件下, *FvHsfA3a* 和 *FvHsfA4a* 在处理前期和中期表达量增加,后期逐渐减弱,而 *FvHsfA9a* 在处理 24 h 和 48 h 表达量最高^[24]。胡萝卜经 $4 \text{ }^\circ\text{C}$ 处理, *DcHsf01* 和 *DcHsf02* 在‘Kurodagosun’和‘Junchuanhong’两个品系中表达量降低,而 *DcHsf16* 表达量却增强^[20]。用 $4 \text{ }^\circ\text{C}$ 处理大白菜,‘Lubaisanhao’中 *BraHsf001* 表达减弱,而 *BraHsf039* 表达量增强,另外在‘Qingdao87-114’中, *BraHsf043* 表达量逐渐增加^[23]。经 $4 \text{ }^\circ\text{C}$ 处理的野生葡萄叶片, *VpHsfC1a* 呈上调表达,而 *VpHsfB3a* 却下调表达, *VaHsfA2a* 和 *VaHsfA6a* 在冷处理 8 h 时表达量最高^[17]。这些结果均表明 *Hsfs* 基因广泛参与不同的非生物胁迫,其调控模式具有多样性,参与的调控网络如图 3 所示。



Response stage of regulation are shown by solid arrows.

图3 热激转录因子在非生物胁迫下的调控模式^[26, 70-71]

Fig. 3 Regulation of HSF proteins under abiotic stress^[26, 70-71]

4 结论及展望

近年来,大量的植物热激转录因子被克隆与鉴定。由于植物基因组的复杂性,目前关于热激转录因子的研究主要集中于一些模式植物,如番茄、拟南芥等植物。随着现代分子生物学技术的不断进步,已从部分作物中克隆出了多个 *Hsfs*,纵观 *Hsfs* 近年来的研究进展,多集中于 A 类热激转录因子的功能,对 B、C 两类的研究相对缺乏,其生物学功能还有待进一步挖掘。

植物热激转录因子广泛参与多种非生物胁迫调控,如高温、干旱和高盐等,从而提高有效植物的抗逆性与高产量。在 *Hsfs* 参与调控各类逆境胁迫中的研究多以高温胁迫为主,对于 *Hsfs* 调控其他胁迫的响应机制仍然较少,尤其是低温胁迫和生物胁迫。笔者课题组前期通过山葡萄低温胁迫应答的高通量转录组测序分析,鉴定到一些热激蛋白参与低温胁迫响应表达,如 *Hsp17.4*、*Hsp17.6II*、*Hsp18.2*、*Hsp60*、*Hsp70* 和 *Hsp81-2* 六个热激蛋白在冷胁迫下呈下调表达,而 *Hsp18.2*、*Hsp20-like*、*Hsp21* 以及 *Hsp101* 热激蛋白呈上调表达^[72],推测可能由于山葡萄中的热激蛋白为适应冷胁迫而产生的进化趋异。此外,在番茄、拟南芥、水稻等研究中显示,不同 *Hsfs* 在逆境胁迫中通过参与不同胁迫响应的信号通路使其具有多样性和复杂性的表现。然而,在应对不同胁迫时,*Hsfs* 是如何感知信号并进行传导?如何精细定位以及其与互作蛋白靶向调控下游基因?这些问题目前尚未明晰,仍然是今后研究的的重点和难点。随着植物基因组学和蛋白组学的发展,深入解析 *Hsfs* 介导的复杂调控机制,对于提高园艺作物抗逆性与增加产量方面具有重要的意义。

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