

The Research Progress of Heat Shock Transcription Factors in Plants

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Abstract

High temperature is often predicted to reduce crop yield and grain quality recently. Heat shock transcription factors (Hsfs) play a central regulatory role in alleviating the harm caused by high temperature on plant. Hsfs exist in all eukaryotes. According to the different characteristics of structure, Hsfs are divided into 3 classes, A, B and C. Class A and B genes are heat responsible, but Class C genes have no response to heat stress. Class As are reported to play a central regulation role in heat protection through regulating HSPs. But the biological roles of Class Bs are not well known, Class C, not known. Hsfs are reported to regulate not only in the process of heat tolerance but also drought, salt, oxidation, heavy metal and osmotic stress tolerance. A series of genes encoding heat shock proteins, molecular chaperone, active oxygen scavenging enzymes and other functional proteins can be transactivated by Hsfs. And the transactivation relies on the binding of the DNA binding domain and heat shock element (HSE) in the promoter regions of the down-stream genes. In this paper, the classification, biological function, down-stream genes and regulation mechanism of Hsfs are introduced, for the purpose of providing theoretical guidance to plant heat and other adverse stress research.

Keywords

High Temperature, Heat Shock Transcription Factors, Classification, Heat Shock Proteins, Regulation Mechanism

植物热激转录因子研究进展

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摘要

近年来高温天气带来的作物减产现象频现, 热激转录因子家族*Hsfs*在缓解高温对植物的伤害中发挥重要的作用。*Hsfs*基因广泛存在于所有真核生物中, 根据结构特点, *Hsfs*被分为A、B、C三大家族, 目前对*HsfA*家族功能研究较多, 对*HsfB*家族研究较少, 对*HsfC*家族的研究未见报道。根据以往研究, *Hsfs*不仅参与植物抵御高温胁迫的调控过程, 还参与植物抗旱、抗盐、抗氧化、抗重金属和抗高渗透胁迫过程。大部分*Hsfs*家族成员是通过调控一系列热激蛋白, 分子伴侣, 活性氧清除酶和其他功能蛋白基因发挥抗逆作用的。*Hsfs*通过与下游基因启动子区域HSEs元件结合而调控下游基因的表达。本文综合了近几年的国内外研究报道, 详细介绍了*Hsfs*家族的分类、功能、下游基因种类、调控机理等, 以期能为植物抗高温和其他逆境胁迫研究提供理论指导。

关键词

高温, 热激转录因子, 分类, 热激蛋白, 调控机制

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1. 引言

随着全球气候变暖, 高温胁迫带来的作物减产现象频现[1] [2]。特别是开花和灌浆期的高温胁迫, 是导致谷类作物减产的主要原因之一[1] [2]。高温胁迫对植物的直接伤害是蛋白质分子变性、生物膜结构破坏、自由基和活性氧化物累积、体内生理生化代谢紊乱[3]。植物体内存在着以 *Chf/Dreb*、*bZIP*、*Myb/Myc*、*Wrky*、*Nac* 和 *Hsf* 等转录因子家族为核心的应对逆境胁迫的一系列信号感知传导基因网络调控系统, 其中, 热激转录因子家族 *Hsfs* 在缓解高温对植物的伤害中发挥重要作用[4]。

2. 热激转录因子的种类

Hsfs 基因存在于所有的真核生物中, 酵母和动物体内只有少数 *Hsfs* 基因, 而植物体内存在着大量的 *Hsfs* 基因[3]。到目前为止, 至少分离鉴定了 21 个拟南芥 *Hsfs* [5]、16 个番茄 *Hsfs* [6]、28 个大麦 *Hsfs* [7]、25 个水稻 *Hsfs* [8] [9]、34 个大豆 *Hsfs* [10]、40 个棉花 *Hsfs* [11]和 56 个小麦 *Hsfs* [12]。所有的 *Hsfs* 都具有一个高度保守的 DNA 结合结构域(DBD)和两个疏水氨基酸重复片段 HR-A 区和 HR-B 区[3] [13]。根据它们的蛋白质结构, *Hsfs* 被分为 A、B 和 C 亚家族(图 1)。*HsfA* 亚家族在 HR-A 和 HR-B 之间有一段长的氨基酸链插入, 在 C 末端含有一段富含芳香族 - 疏水 - 酸性氨基酸尾巴(AHA), *HsfB* 亚家族在 HR-A 和 HR-B 之间没有插入序列, 而 *HsfC* 亚家族成员在 HR-A 和 HR-B 之间的插入序列很短[3] [13]。近年来在单子叶植物中发现了一类特殊 *HsfC* 亚家族成员, 被划分为 *HsfC2* 亚家族[3] [13], *HsfC2* 亚家族在 HR-A 和 HR-B 之间有很短的插入序列, 在 C 末端有一个 AHA 相似的尾巴。

3. 热激转录因子的功能

Hsfs 家族成员在植物抵御高温胁迫和其他逆境过程中发挥重要作用[6] [14] [15]。作为水稻, 大豆, 番茄和拟南芥中的主要 *Hsfs* 成员, 超表达 *HsfA1* 显著提高它们的抗热性[14] [15]。超表达 *HsfA2* 基因显著

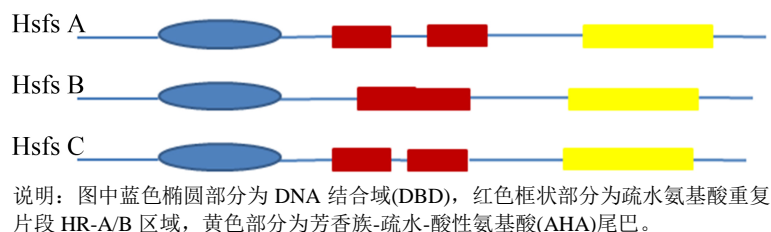


Figure 1. The classification of the Heat Shock Factors family

图 1. 热激转录因子家族的分类

提高拟南芥的抗强光、抗盐、抗超氧化、抗高渗透胁迫的能力[16] [17] [18]。转基因拟南芥超表达水稻 *HsfA2e* ($p < 0.01$)的抗盐性显著提高[19]而转基因拟南芥超表达番茄 *HsfA3* ($p < 0.01$)的盐敏感性显著提高[20]。水稻或者小麦中超表达 *HsfA4a* 显著提高它们抗重金属元素镉的能力和抗氧化能力[21]。大部分 *HsfB* 亚家族成员的表达量在高温胁迫下显著升高, 除此之外, *HsfB* 亚家族成员被认为与生物胁迫的抗性调控有关, 因为降低 *HsfB1* 和 *HsfB2b* 表达量引起植物真菌抗性基因表达量的增高[22] [23] [24]。同一转录因子在不同的植物中的功能也会有差异[25]。例如, *HsfB1* 在番茄中被证明是一个协同激活因子, 与 *HsfA* 家族成员一同参与热胁迫的调控[26], 而在拟南芥中, *HsfB1* 被证明是 *HsfA2* 和 *HsfA7* 的抑制因子[27]。目前, *HsfC* 亚家族基因的功能研究却很少被报道, 特别是单子叶植物特有的 *HsfC2* 亚家族基因的功能尚未见报道。

4. 热激转录因子的下游基因

大部分 *Hsfs* 家族成员是通过调控一系列热激蛋白, 分子伴侣, 活性氧清除酶和其他功能蛋白基因发挥抗逆作用的, 如 *HsfA1*、*A2*、*A3*、*A4*、*A6* 和 *A9* 等亚家族成员[12] [25]。转基因植物超表达这些 *Hsfs* 基因呈现出很强的抗热性, 一系列的热激蛋白和高温保护有关的基因在转基因植株中的表达量增高, 敲除这些 *Hsfs* 基因使植株对高温的敏感性提高[6] [12] [23] [28] [29]。转 *HsfA1a* 基因番茄通过上调 *Hsp17* 等基因的表达显著提高抗热性[6], 通过上调 *ATGs* 基因(*autophagy-related*, 自噬相关基因)的表达显著提高其抗旱性[30]。拟南芥中超表达百合 *HsfA1* 基因能上调 *Hsp17.6*、*18.2*、*22*、*70*、*90.1*、*101* 等一系列热激蛋白基因, 热激转录因子 *HsfA2*、*A7a*、*A7b* 基因, 转录因子 *Dreb* 及甜菜碱合成酶基因 *Galsyn* 的表达量[31]。拟南芥 *HsfA2* 是调控超氧化物清除酶系的关键转录因子, 能激活胞质抗坏血酸过氧化物酶 (*ascorbate peroxidase*, *APX*) *APX1* 和 *APX2* 的表达[18] [32]。也有少数 *Hsfs* 基因被证明是抑制热激蛋白的表达, *HsfA5* 是 *HsfsA4* 激活因子的特异抑制因子, 它不直接调控热激蛋白的表达, 而是通过形成 *HsfA4/A5* 复合体使 *HsfA4* 不能发挥作用, 从而间接抑制热激蛋白基因的表达[33]。*HsfA1d* 和 *HsfA1e* 是 *HsfA2* 的抑制因子, 超表达 *HsfA1d* 或者 *HsfA1e* 都会抑制 *HsfA2* 下游基因的表达[33]。Xue 等从小麦基因组中鉴定了 56 条 *Hsfs* 基因, 其中 *HsfA2b* 和 *HsfA4e* 能转录激活热激蛋白 *Hsp17* 和 *Hsp90* 基因[12], *HsfA6f* 能转录激活一系列强烈响应热胁迫和干旱胁迫的基因表达, 如热激蛋白基因 *Hsp16.8*, *Hsp17*, *Hsp17.3*, *Hsp90*, 高尔基体抗凋亡蛋白基因 *TaGAAP* (*Golgi anti-apoptotic protein*), 分子伴侣 *TaRof* 和二磷酸核酮糖羧化酶活化酶基因 *TaRCAL* (*Rubisco activase large isoform*)等[29]。

5. 热激转录因子对下游基因的调控机理

正常条件的下, *Hsfs* 转录因子以无活性的单体状态存在于细胞质中, 当植物遭受高温或其他逆境胁迫时, *Hsfs* 通过疏水的 HR-A 和 HR-B 区相互结合形成活性 *Hsfs* 三体, 活性三体通过保守的 DBD 结构域准确的识别并结合于下游基因启动子的 HSEs 元件, 激活热激蛋白 *Hsp* (*Heat shock proteins*)基因、分子伴侣基因或其他下游基因的转录表达[25]。*Hsp* 及辅助分子伴侣能够帮助失活的蛋白质重新组装成有活性的高级结构, 维护正常的细胞功能[3] [25] (图 2)。

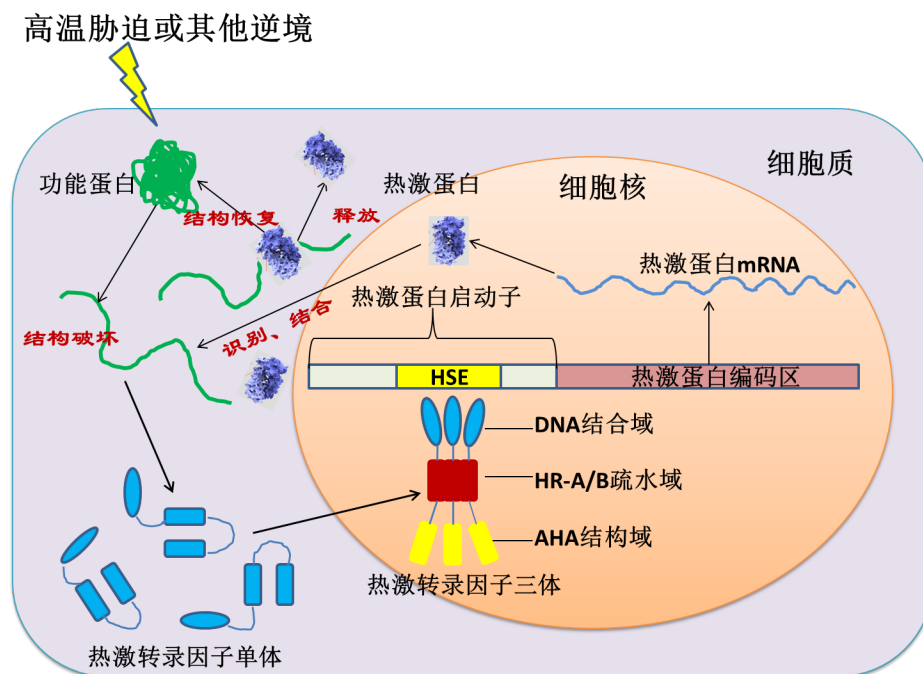


Figure 2. The mechanism of heat shock factors involved in high temperature and other abiotic stress tolerance

图 2. 热激转录因子调控植物抵御高温胁迫及其他逆境胁迫的机理

Hsfs 通过结合下游基因的启动子中的热激元件 HSEs 而调控目标基因的表达[34]。*Hsfs* 下游基因的启动子中的 HSEs 具有一致的序列, 最初被定义为至少三个重复单位的 5'-nGAAn-3' [34]。在高等真核生物中, 启动子中具有 5'-AGAAAnnTTCT-3' 序列, 下游基因才能被 *Hsfs* 转录激活[5]。在小麦中, 通过 DNA 结合实验, 发现 *TaHsfA2b*、*TaHsfA4e*、*TaHsfA6f* 能结合 5'-GAA/Cnn(CTC)/(TTC)/(TTT)nnGAA-3' 序列[12] [29], 转录激活实验(Transactivation Assay)结果表明, *TaHsfA2b*、*TaHsfA4e*、*TaHsfA6f* 对下游基因的激活依赖于 HSEs 的存在, 如果下游基因启动子中删除或者将 5'-GAA/Cnn(CTC)/(TTC)/(TTT)nnGAA-3' 突变成其他序列, *TaHsfA2b*、*TaHsfA4e*、*TaHsfA6f* 则不能转录激活下游基因[12] [29]。

6. 展望

随着高温天气和热胁迫灾害的频现, 热激转录因子的研究日益成为研究热点。更多的有重要功能的热激转录因子家族成员被挖掘。另外, 研究内容日益拓宽, 从最开始对胁迫的响应到抗逆性状研究, 以及抗逆性机制的研究, 研究深度不断加大。目前研究不仅关注与热激因子的抗热性研究, 也关注热激转录因子的多调控网络研究, 特别是热激因子的抗旱抗热联合调控研究。随着研究的深入, 植物抗高温、干热风等非生物逆境胁迫伤害的机理将进一步被揭示。

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