小分子热激蛋白参与植物抗逆性方面的研究进展

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摘要 小分子热激蛋白(sHSPs)是植物面临逆境胁迫时,被激活且表达增强的一类蛋白,属于热激蛋白的一个亚家族。sHSPs 作为分子伴侣,在植物抵抗高温热害、低温冷害以及种子发育中具有重要的作用。综述了 sHSPs 的分类、特点和功能,重点讲述了其参与植物抗逆性方面的研究进展,对目前研究中存在的问题进行了讨论,并对今后的研究方向进行了展望。

关键词 小分子热激蛋白;抗逆性;功能
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Advances of Small Heat Shock Proteins Participating in Plant Resistance

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Abstract sHSPs,a subfamily of heat shock proteins,are activated and highly expressed when plants exposed to adverse stresses.As a molecular chaperone,sHSPs play crucial roles in the resistance of heat,cold and seed development.The classification,characteristics and function were reviewed,especially the role in plant resistance.And related problems in the current study were discussed and the future research fields were prospected.

Key words Small heat shock proteins;Stress resistance;Function

非生物胁迫因子,如干旱、盐渍化、高低温以及化学污染物等,会引起植物细胞破坏和次生代谢物的产生[1]。高温会影响植物的代谢系统,特别是细胞膜的稳定性和生理过程,如光合作用、蒸腾作用等,而植物通过增强分子伴侣的转录和信号转导,释放活性氧(ROS),合成抗氧化物质,积累渗透调节物质[2]。由于高温胁迫而产生的热激蛋白(heat shock proteins,HSPs)[3],又被称为"逆境诱导的蛋白"或"逆境蛋白"[4-6],几乎存在于所有的生物体内,且高度保守[6],正常条件下的含量较低(低于蛋白总量的 5%),但在外界环境不利条件刺激时,会大量合成(约占蛋白总量的 15%)[7]。其中,小分子热激蛋白(sHSPs)属于热激蛋白的一个亚家族,其作为分子伴侣,在植物抵抗高温热害、低温冷害以及种子发育中具有重要的作用。笔者综述了 sHSPs 的特点、分类和生物功能,对其参与植物抗逆性方面的研究进展进行了重点描述,对目前研究中存在的问题进行了讨论,并对今后的研究方向进行了展望。

1 热激蛋白的特点

据报道,意大利科学家 Ritossa 将果蝇放在高温环境下研究其基因和蛋白质变化时,首先发现了热激蛋白[8]。随后,在几乎所有的生物中均发现了热激蛋白[9],且其羧基端有一个被称为"heat-shock"的结构域[10]。热激蛋白的分子量为 10~200 kD,在热胁迫时,作为分子伴侣参与信号的传导[11]。植物热激蛋白根据分子量大小,可以分为 HSP60、HSP70、HSP90、HSP100 和小分子 HSP 家族(sHSPs)[11-13]。不同植物中的热激蛋白的数目差异较大[14],例如,在拟南芥中有 13 个 HSP20、8 个 HSP70、7 个 HSP90、8 个 HSP100 以及 21 个热激蛋白转录因子(Hsfs)[15],但是在番茄中有 15 个 Hsfs[16]。

小分子热激蛋白(sHSPs)的分子量为 12~43 kD,且大部分蛋白的 C 端都包含 1 个 80~100 个氨基酸序列的 α-晶体蛋白(ACD)结构域[17-18]。高等植物中含有 20 种以上的 sHSPs[19]。sHSPs 在正常的生长条件下是检测不到的,但逆境条件能激活其表达[20-22]。热激蛋白的特点一般包括保守性,反应短时性,影响因素多样性,交叉耐受性以及种类多样性[23]。一般情况下,生物胁迫和非生物胁迫均可以诱导小分子热激蛋白的表达,其中高温胁迫是最主要的因素[24]。有研究表明,正常条件下,sHSPs 的含量很低,但是高温胁迫时,在短时间内含量急剧增加,且种类比其他热激蛋白多[7,25]。

2 小分子热激蛋白的分类

sHSPs 具有丰富的功能和遗传多样性[26],在生物体应对生物或非生物胁迫中,能够维持天然蛋白的稳定性,并在保护膜结构等方面发挥重要的作用。小分子热激蛋白在高等植物中极为丰富,且为核基因编码,分布在细胞的各个部位[27]。根据蛋白的亚细胞定位和氨基酸序列的同源性可以将植物的 sHSPs 分为 5 个大的亚家族:①定位在细胞质或细胞核的 CⅠ、CⅡ、CⅢ、CⅣ、CⅤ、CⅥ和 CⅦ亚家族;②定位于线粒体的 MⅠ和 MⅡ亚家族;③定位于质体的 P 亚家族;④定位于内质网的 ER 亚家族;⑤定位于过氧化物酶体的 Po 亚家族[28-29]。

不同植物中,小分子热激蛋白的种类和数目也各异,这可能与植物的种类以及生活习性有关。在拟南芥中有 19 个 *sHSPs* 基因,其中定位在细胞质/细胞核中的 *sHSPs* 有 13 个,定位在内质网中和过氧化物酶体中的 *sHSP* 各 1 个,定位在

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线粒体和叶绿体中的 *sHSPs* 各 2 个[21]。在水稻中鉴定出了 23 个 *sHSPs* 基因,分布在不同细胞器中的 *sHSPs* 个数也不尽相同[30]。其他作物中,大豆中有 51 个 *sHSPs* 基因[31],大白菜[32]和小麦中[33]各自至少有 27 个 *sHSPs* 基因,番茄中至少有 42 个 *sHSPs* 基因[34],辣椒的至少有 35 个 *sHSPs* 基因[35]。虽然不同作物的 *sHSPs* 数目差异较大,但是相同点是定位于细胞质/细胞核中的 *sHSPs* 所占比例较大。

3 小分子热激蛋白的功能

任何蛋白的功能都是由其构造和三维结构的折叠方式所决定的[36]。热激蛋白(HSPs)能够保护细胞免受伤害,帮助蛋白质折叠[25]。sHSPs 发挥其分子伴侣的作用,形成的聚合体能够与体内受胁迫后产生的损伤蛋白相结合以防止它们聚集;在 ATP 存在的条件下与 HSP100 或 HSP70 相互作用,帮助受损蛋白重新折叠,恢复其生物功能[17-18]。

3.1 分子伴侣,防止蛋白降解 作为分子伴侣,在所有的动植物中,sHSPs 能调控蛋白质的折叠、积累及其定位和降解[37-40]。在依赖 ATP 酶的条件下,能够识别并结合到未展开的蛋白质,从而抑制蛋白质的聚集,这样可以保护细胞不受高温伤害,且能够修补被损伤的蛋白质[41]。豌豆的 sHSP18.1 能够结合到未展开的蛋白质,并与其他热激蛋白如 HSP70 或 HSP100 作用,形成复合体,以维持蛋白的正常结构和功能[42]。

3.2 参与种子发育 有研究表明,sHSPs 在玉米种子发育过程中大量表达,例如 HSP60 和 HSP70 热激蛋白[43]。另外,贮藏的种子暴露于过热的环境中,会产生一系列的细胞代谢反应,一些正常的蛋白质合成会减少,但小分子热激蛋白的含量会显著升高[44-45]。过表达 *AtHSP*22.0 基因后,拟南芥种子耐受衣霉素胁迫的能力明显提高,种子萌发率明显高于野生型[46]。细胞质 CI 型小热激蛋白(sHSP)在种子的胚胎形成以及成熟过程中表达量均会升高[47]。另外,小分子热激蛋白可以减轻番茄种子萌芽对光照的依赖性[48]。Ca^{2+}-CaM 在热激信号转导中通过激活热激转录因子的 DNA 结合活性来实现[49]。研究表明,热激后,拟南芥 *AtCaM*3 基因的表达水平明显升高,说明该基因可能参与了热激信号转导[50]。

3.3 参与植物抗逆性 sHSPs 在植物面临生物胁迫和非生物胁迫时发挥着重要的作用,且抗胁迫能力具有多样性[6]。但目前研究较多的是 sHSPs 在植物面临高温、低温和盐渍化等非生物胁迫下起的作用(表 1)。

3.3.1 耐热性。高温胁迫下,植物的生长缓慢,光合效率下降,叶绿体的小分子热激蛋白(CPsHSP)作为细胞质体中含量最丰富的热激蛋白[19,26],在植物遇到热胁迫时,它对参与光合作用的细胞器有保护作用[51],因为 CPsHSP 的生成可以减轻光系统Ⅱ(PSⅡ)的光抑制[52],且同种植物的不同基因型中,耐热性的强弱与 CPsHSP 的表达水平有关[53]。另外,CPsHSP 在植物遇到高温胁迫时可以保护叶绿体膜,与膜结合,并稳定细胞的膜结构[54-55]。研究者通过转基因试验也验证了 CPsHSP 在热胁迫中的作用。高温胁迫时,在烟草中过量表达 CPsHSPs 可以增加光系统Ⅱ的稳定性[56]。番茄的 CPsHSPs 只有在高温胁迫下(47 ℃)才会对 PSⅡ起到保护作用,但是在常温下(25 ℃)没有此作用[57]。

表 1 sHSPs 参与植物抗逆性的部分基因

Table 1 Some genes of sHSPs participating in plant resistance

抗性 Resistance	植物 Plant	基因 Gene	文献 Literature
耐热 Heat tolerance	番茄	*CPsHSPs*	[57]
	水稻	*sHSP*17.7	[58]
	水稻	*OsHSP*18.0	[61]
	辣椒	*CaHSP*26	[67]
	拟南芥	*AtHSP*22.0	[69]
	花生	*sHSP*	[71]
	牡丹	*sHSP*	[72]
耐冷 Cold tolerance	番茄	*sHSP*	[79]
	桑树	*sHSP*	[77]
	绿豆	*sHSP*	[78]
抗旱 Drought resistance	拟南芥	*AtHSP*17.6A	[80]
	拟南芥	*HSP*17.4	[83]
耐盐 Salt tolerance	紫花苜蓿	*MsHSP*17.7	[84]
耐重金属镉 Cadmium tolerance	水稻	*OsMSR*3	[40]

小分子热激蛋白在水稻中的过表达能够显著提高转基因植物的耐热性。研究表明,在水稻中过表达小分子热激蛋白基因 *sHSP*17.7 可以增强转基因植物的耐热性和对 B 类紫外线的抗性[58],另外还发现该基因在水稻的抗旱中也起到重要作用[59]。水稻 *OsHSP*18.6 的转基因植物的耐热性和抵抗其他非生物胁迫的能力明显提高[60]。RNAi 干扰水稻 *OsHSP*18.0 降低了植物对细菌的抗性,以及耐热性和耐盐性[61]。过表达线粒体的热激蛋白基因可以明显抑制植物的细胞程序性死亡 PCD 反应[62]。小分子热激蛋白之间可以发生相互作用,如水稻 HSP17.7 可以与 HSP16.9A 互作,从而形成复合体参与植物的耐热反应[63]。

线粒体的 sHSPs 在植物耐热性方面发挥了重要的作用,其可以保护光系统Ⅱ蛋白质复合物不受损伤,保证细胞正常的电子传递、ATP 合成,使得植物在高温胁迫下保持正常生长[64]。研究表明,番茄线粒体 HSP22 蛋白的积累可以提高其细胞的抗氧化胁迫能力和适应性[65]。研究者将辣椒的小热激蛋白基因 *CaHSP*24 进行了分子克隆和逆境表达分析,发现该基因在非生物胁迫下的表达量明显上升,说明该基因参与了植物的逆境响应[66]。另外,将辣椒的 *CaHSP*26 基因在拟南芥中异位过表达,可以增强转基因植物耐热能力[67]。内质网小分子热激蛋白在高温下的表达量会显著升高,例如番茄的 *LeHSP*21.3 和拟南芥的 *AtHSP*22.0 对高温有一定的抵御作用[68-69]。在烟草中过表达甜椒细胞质小分子热激蛋白基因 *CaHSP*26 可以显著提高转基因植物的耐热能力[70]。花生的小热激蛋白基因(*sHSP*)的诱导表达可以增强其在高温下的生理性适应能力[71]。有研究者结合高温胁迫下的牡丹的转录组测序,确定了小热激蛋白参与牡丹对高温的抵抗能力[72]。

3.3.2 耐冷性与抗旱性。低温环境会诱导一些蛋白的表达,

包括脱水蛋白[73]、热稳定蛋白[74]和热激蛋白[75]等,这些蛋白可以在一定程度上减缓低温给植物造成的伤害。低温可以诱导番茄叶片中线粒体小热激蛋白的表达[68]。过表达叶绿体小分子热激蛋白可以增强番茄植物的耐冷性[76]。研究报道,内质网小热激蛋白的积累可以增强桑树对于寒冷季节的低温驯化能力[77]。绿豆苗经过热激后产生的热激蛋白可以在一定程度上增强植物对低温的抗性[78]。与此类似,有研究者将经过热激的番茄放到低温环境中,发现经过热激处理的番茄较对照的耐低温能力增强[79]。关于 sHSP 提高植物耐冷性的原因,一方面可能是因为其可以提高细胞膜的流动性,另一方面可以与细胞膜结合相互作用,从而保护膜系统的完整性,增强植物的耐冷能力[55]。

研究表明,拟南芥中过表达 *AtHSP*17.6*A* 可以增强植物的耐盐和抗旱能力[80]。也有研究表明,在拟南芥中异位过表达百合的小分子热激蛋白基因 *LimHSP*16.45,通过阻止不可逆蛋白的聚集和清除细胞内的活性氧等途径,提高转基因植物对逆境胁迫的抵抗能力[81]。植物在缺水逆境条件下,会破坏细胞质膜分子排列,改变膜的透性,影响其正常代谢过程;研究表明植物在抵抗高温和抗旱的机制上会存在一定的交叉性[82]。研究表明,干旱敏感突变株的小分子热激蛋白基因 *HSP*17.4 表达量很低,热诱导后 *HSP*17.4 大量表达,并提高了拟南芥的抗旱性,表明小热激蛋白 HSP17.4 在干旱胁迫下同样可以通过保护细胞组分,使植物维持生长发育[83]。

3.3.3 其他。有研究表明,紫花苜蓿的小热激蛋白基因(*MsHSP*17.7)在高温、高盐、氧化胁迫以及干旱环境中均可以被诱导表达,且 *MsHSP*17.7 过表达转基因植物可以显著提高植物对高盐胁迫的抗性能力,表明该基因在植物抵抗盐渍化胁迫方面具有重要的作用[84]。研究者在番茄中分离了内质网小热激蛋白基因(*ERsHSP*),过表达该基因的转基因植物的抗衣霉素能力较对照显著增强,说明该基因可以在一定程度上减轻外界给内质网带来的胁迫压力[85]。通过将水稻的 *OsMSR*3 基因(小热激蛋白的家族 I 成员之一)在拟南芥中异位表达,可以增强其对镉(Cd)的抵抗性[40]。

4　存在问题与展望

近年来,不同的非生物胁迫因素严重影响了植物的生长与发育。增强植物本身的抗逆能力以及选育优良的抗逆品种是提高抗胁迫性的主要途径。植物对高温以及其他逆境胁迫响应也是一个多基因控制的复杂的生物过程,许多研究已证明小热激蛋白能够在植物面临逆境胁迫时激活表达,通过分子伴侣功能保护正常的蛋白免被降解,维持植物生长与发育。虽然 sHSPs 在许多植物中已经被报道,但大部分是围绕过表达量的变化来改变植物抗逆性方面,sHSPs 如何提高植物的抗性,具体通过什么信号途径尚不清楚。

因此,今后关于小分子热激蛋白的研究方向主要集中在以下方面:①挖掘与鉴定新的小分子热激蛋白基因,丰富 sHSPs 家族;②筛选与 sHSPs 互作的蛋白,深入研究其机制;③鉴定小分子热激蛋白转录因子的靶蛋白,了解其在植物抗逆性方面的遗传网络;④分析定位在细胞不同位置的 sHSPs 蛋白的进化和分子关系,为植物的耐热性分子辅助育种提供理论指导。

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