·综 述·

Zn^{2+}依赖型组蛋白去乙酰化酶在植物非生物胁迫响应中的作用及机制

魏明[#]，赵萌[#]，吴欣蕊，伍国强[*]

兰州理工大学 生命科学与工程学院，甘肃 兰州 730050

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摘 要：Zn^{2+}依赖型组蛋白去乙酰化酶(Zn^{2+}-dependent histone deacetylases, HDAs)是一类与酵母还原性钾依赖型 3 (reduced potassium dependency 3, RPD3)高度同源的去乙酰化酶蛋白家族。HDAs 通过去除组蛋白和非组蛋白赖氨酸残基上的乙酰基而广泛调控染色体稳定、基因转录和蛋白质活性。在植物中，HDAs 介导的去乙酰化修饰在植物生长发育和非生物胁迫响应中发挥重要作用。本文综述了植物 HDAs 的发现、结构与分类、去乙酰化机制，重点总结了该蛋白家族在植物非生物胁迫中的调控作用，并对未来研究方向进行展望，为 HDAs 介导的表观遗传学研究提供了理论支持。

关键词：Zn^{2+}依赖型组蛋白去乙酰化酶；表观遗传；去乙酰化；非生物胁迫

Functions and mechanisms of Zn^{2+}-dependent histone deacetylase in plant responses to abiotic stress

WEI Ming[#], ZHAO Meng[#], WU Xinrui, WU Guoqiang[*]

School of Life Science and Engineering, Lanzhou University of Technology, Lanzhou 730050, Gansu, China

Abstract: The HDAs (a subfamily of histone deacetylases), a class of Zn^{2+}-dependent histone deacetylases, are highly homologous to the reduced potassium dependency 3 (RPD3) in yeast.

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[#]These authors contributed equally to this work.

*Corresponding author. E-mail: gqwu@lut.edu.cn

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HDAs extensively regulate chromosome stability, gene transcription, and protein activity by catalyzing the removal of acetyl group from histone and non-histone lysine residues. HDA-mediated deacetylation is essential for plant growth, development, and responses to abiotic stress. We review the research progress in HDAs regarding the discovery, structures, classification, deacetylation process, and roles in regulating plant responses to abiotic stress. Furthermore, this paper prospects the future research on HDAs, aiming to provide theoretical support for the research on epigenetic regulation mediated by HDAs.

Keywords: Zn^{2+}-dependent histone deacetylases; epigenetics; deacetylation; abiotic stress

在真核生物中，核小体是染色质的基本组成单位，由 146 bp DNA 缠绕于组蛋白八聚体而形成保守的核蛋白复合体[1-2]。组蛋白八聚体由 4 种核心组蛋白 H2A、H2B、H3 和 H4 各 2 分子组成，其中 H3、H4 位于核心颗粒中央，H2A、H2B 位于两侧[3]。H3、H4 等组蛋白 N 端氨基酸特别是赖氨酸(lysine, Lys)残基伸出核小体核心区域，易被各种化学基团共价修饰[4-5]。组蛋白修饰类型主要包括(去)甲基化、(去)磷酸化、(去)乙酰化和(去)泛素化等[6]。组蛋白修饰导致组蛋白与其包裹 DNA 的亲和性发生改变，进而影响染色质结构与基因的转录、复制及修复过程[7-9]。研究表明，组蛋白修饰在动植物生长发育、胁迫响应、代谢与疾病发生等过程中发挥重要作用[10-12]。

作为表观遗传的重要类型，乙酰化和去乙酰化修饰分别由组蛋白乙酰基转移酶(histone acetyltransferases, HATs)和组蛋白去乙酰化酶(histone deacetylases, HDACs)动态调控，两者可逆催化组蛋白 N 端 Lys 残基的乙酰化反应，以改变核小体结构和染色质状态[6,13]。HATs 使得组蛋白与 DNA 的亲和性减弱，促进染色质结构疏松及增强基因转录活性，而 HDACs 作用相反，会导致基因转录下调或沉默[14-16]。根据 HDACs 去乙酰化酶结构域在酵母中的同源性及酶活性辅助因子的不同，HDACs 可进一步分为 3 个亚家族，即 HDAs、NAD 依赖型去乙酰化酶(NAD-dependent sirtuins, SRTs)和去乙酰化酶 2 (histone deacetylase 2, HD2)[9,17]。HDAs 是与酵母 RPD3s 结构域同源的 Zn^{2+}依赖型去乙酰化酶类，也是目前 HDACs 中研究最为广泛的一类蛋白[18]。SRTs 与酵母沉默信息调节蛋白 2 (yeast silent information regulator 2, SIR2)同源，其结构与 HDAs 有显著区别，辅助因子为尼古丁腺嘌呤二核苷酸(nicotine adenine dinucleotide, NAD)[19]。在酵母及动物中均未发现 HD2s 的同源蛋白，表明其是植物特有的一类去乙酰化酶[20]。

HDAs 在真核生物中广泛分布，是 HDACs 中最大的一个亚家族，由 10 余个成员组成，各成员同源性高且具有保守的去乙酰化酶活性功能域。在植物中，HDAs 通过对组蛋白或非组蛋白中 Lys 的去乙酰化作用而广泛调控植物非生物胁迫，成为表观遗传学研究领域的热点之一[21]。鉴于此，本文总结了植物 HDAs 的发现、结构与分类、去乙酰化机制，重点对 HDAs 调控植物非生物胁迫的研究成果加以综述，并对该家族未来研究进行展望，以期为农作物抗逆性遗传改良提供基因资源和理论依据。

1 HDAs 的鉴定、结构与分类

1.1 HDAs 的鉴定

Brosch 等[22]首次在玉米(*Zea mays*)萌动胚中分离和纯化出 HDA1 蛋白，随后 Rossi 等[23]克隆

了该基因并通过互补酿酒酵母(*Saccharomyces cerevisiae*) RPD3 缺陷菌株的实验验证了 ZmHDA1 的功能。如表 1 所示，研究人员相继在拟南芥(*Arabidopsis thaliana*)[24]、水稻(*Oryzae sativa*)[25]、葡萄(*Vitis vinifera*)[26]、番茄(*Solanum lycopersicum*)[27]、荔枝(*Litchi chinensis*)[28]和大豆(*Glycine max*)[29]等植物中发现或克隆到 HDAs 基因。小麦(*Triticum aestivum*) HDAs 基因家族成员数最多，为 37 个[37]；而红麻(*Hibiscus cannabinus*)最少，仅有 5 个成员[30]；在模式植物拟南芥[24]、水稻[25]、玉米(*Zea mays*)[32]中各鉴定到 12、14 和 12 个成员。此外，表 1 中所列单子叶与双子叶 HDAs 家族成员的平均数量分别是 16 个与 12 个，这说明不同类型植物 HDAs 成员数量存在一定差异，这可能与物种进化中基因重复有关。

1.2 HDAs 结构与分类

以拟南芥 HDAs 保守结构域为例，典型的 HDAs 一般由 N 端组蛋白去乙酰化酶结构域(hist_deacety, HD)和 C 端未知功能的延伸组成(图 1)[41]。HD 基本功能是去除组蛋白 Lys 残基 ε-氨基上的乙酰基，以恢复 Lys 的正电荷属性[9]。X 射线晶体结构分析表明，植物 HDAs 的 HD 三维空间结构类似于精氨酸(arginine, Arg)酶，由 α/β 构成水解酶核心结构域，其中 α 螺旋和平行的 β 折叠构成酶活性口袋，其内部的酪氨酸(tyrosine, Tyr)、组氨酸(histidine, His)及天冬氨酸(aspartic acid, Asp)组成 Zn^{2+}结合域[42-43]。以拟南芥 AtHDA6 为例，利用 SWISS-MODEL 同源建模在线工具(https://swissmodel.expasy.org/)预测该蛋白 HD 结构域的三维结构，发现其与 Arg 水解酶的空间结构相似度较高，由 11 股 α 螺旋和 6 股平行的 β 折叠组成，β1–6 及 α1/2/6/7/8/9/10/11 构成酶活性口袋，其他 α 螺旋则位于口袋外侧(图 2)；对组蛋白去乙酰化酶晶体分析还表明，单个 Tyr 及串联的 His 二联体(His-His)是酰胺键水解活性所必需的，而 Asp-His 及与另一环中的 Asp 残基(Asp-His- Asp)是 Zn^{2+}结合的关键氨基酸[18]。

表 1 不同物种 HDAs 基因

Table 1 The HDAs genes in different plant species

Species	Gene number	Subgroup I	Subgroup II	Subgroup III	Subgroup Unclassified	Class	References
Arabidopsis thaliana	12	6	3	1	2	Dicotyledon	[24]
Oryzae sativa	14	8	2	1	3	Monocotyledon	[25]
Vitis vinifera	9	/	/	/	/	Monocotyledon	[26]
Solanum lycopersicum	10	4	4	1	1	Dicotyledon	[27]
Litchi chinensis	9	/	/	/	/	Dicotyledon	[28]
Glycine max	18	11	5	1	1	Dicotyledon	[29]
Hibiscus cannabinus	5	/	/	/	/	Dicotyledon	[30]
Gossypium hirsutum	18	8	4	2	4	Dicotyledon	[31]
Zea mays	12	6	5	1	/	Monocotyledon	[32]
Dendrobium officinale	10	/	/	/	/	Monocotyledon	[33]
Camellia sinensis	8	4	3	1		Dicotyledon	[34]
Brassica rapa	16	/	/	/	/	Dicotyledon	[35]
Cannabis sativa	10	2	2	1	5	Dicotyledon	[36]
Triticum aestivum	37	/	/	/	/	Monocotyledon	[37]
Sorghum bicolor	12	6	4	2	/	Monocotyledon	[38]
Fagopyrum tataricum	9	/	/	/	/	Dicotyledon	[39]
Salvia miltiorrhiza	12	/	/	/	/	Dicotyledon	[40]

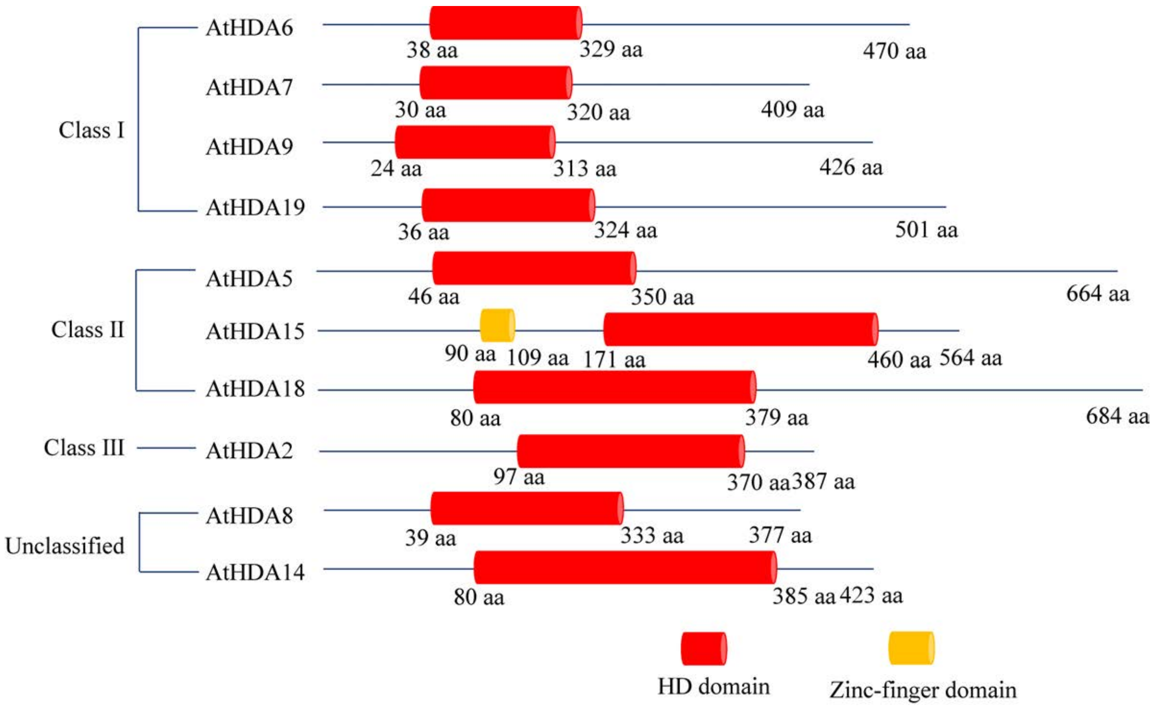

图 1　拟南芥 HDAs 家族蛋白结构域　不同颜色的柱体代表不同的结构域，数字代表各结构域的相对位置。

Figure 1　Domains of HDAs from *Arabidopsis thaliana*. The columns of different colors represent different domains, the numbers represent the relative position of the domains.

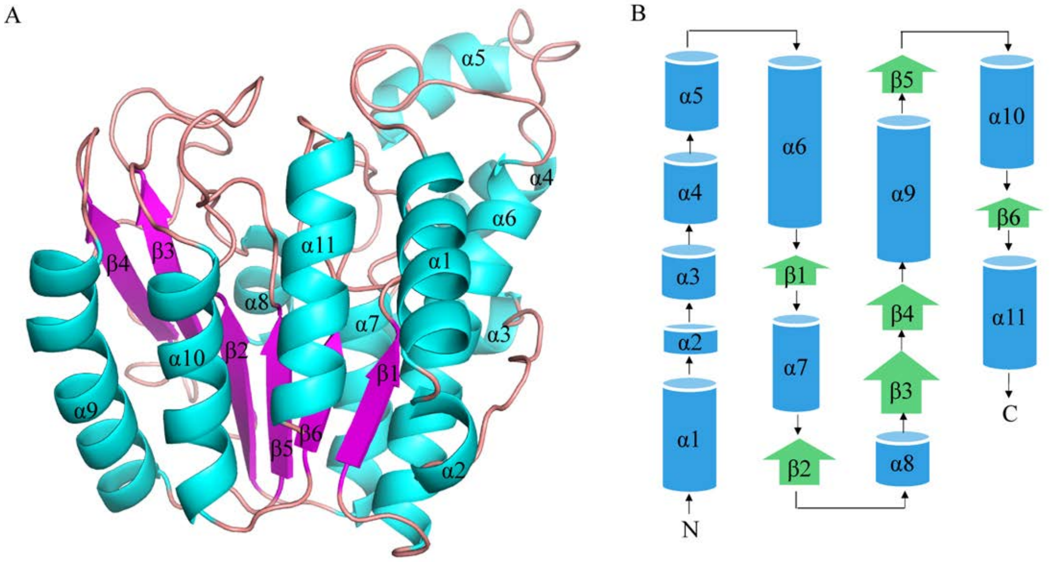

图 2　拟南芥 AtHDA6 蛋白 HD 结构域三维空间结构分析　A：拟南芥 AtHDA6 蛋白 HD 结构域三维空间结构；B：AtHDA6 蛋白 HD 结构域二维拓扑图。

Figure 2　Three-dimensional spatial structure analysis of HD domain of *Arabidopsis* AtHDA6 protein. A: Three-dimensional spatial structure of HD domain of AtHDA6; B: Two-dimensional topological map of HD domain of AtHDA6 protein.

为探究植物 HDAs 基因家族的系统发育和进化关系，以拟南芥 AtHDAs 的 HD 结构域的氨基酸序列为查询序列，在 NCBI (https://www.ncbi.nlm.nih.gov/)及各物种数据库中共检索到拟南芥、玉米、小麦、水稻、菠菜、番茄和藜麦(*Chenopodium quinoa*)这 7 种植物共 98 条 HDAs 蛋白的氨基酸序列。为进一步分析 HDAs 的保守性和进化关系，运用 MEGA 11.0 软件对上述序列进行多重比对，并基于邻接(neighbor-joining, NJ)法，以检验参数 bootstrap 重复 1 000 次创建系统发育树。结果表明，HDAs 分为 I、II和 III 三个亚簇，其中 I 簇、II簇分别有 44 个和 41 个成员，III 簇成员最少，除小麦外各物种仅含 1 个成员。在拟南芥中，12 个 AtHDAs 中有 6 个成员(AtHDA6/7/9/10/17/19)被聚类到 I 簇，5 个成员(AtHDA5/8/14/15/18)被聚类到 II 簇，仅 AtHDA2 被聚类到 III 簇。AtHDA6/9/19 是植物 HDAs 中被广泛研究的 3 个成员，其均被聚类到 I 簇，而与它们系统发育关系接近的是番茄 SlHDA3/4/1 (图 3)。根据 HDAs 系统发育和进化关系推测，上述 HDAs 在植物生长发育或胁迫响应中可能发挥调控作用，然而包括拟南芥在内的位于 II 簇的绝大多数 HDAs 的功能仍需要进一步探索。

2 HDAs 介导的去乙酰化调控机制

2.1 HDAs 催化蛋白质的去乙酰化反应

HDAs 的 HD 功能域(313−330 aa)的作用是去除组蛋白 N 端乙酰化 Lys (acetylated lysine, Kac)中的乙酰基团，以恢复 Lys 本身的正电荷属性，促进组蛋白与带负电荷 DNA 的静电吸引力，最终使得染色质凝聚成更加紧密的结构[9]。这种固缩染色质阻碍了转录因子或 RNA 聚合酶与基因组启动子序列的特异性结合，致使该区域基因转录下调或沉默[15-17] (图 4)。已有研究结果表明，HDAs 除定位于细胞核外还起作用于细胞质，或穿梭于核质间，这提示该家族蛋白还可能参与非组蛋白的去乙酰化或与其他蛋白相互作用共同调控靶蛋白的活性[45]。如定位在胞质的水稻 OsHDA714 能特异地去除核糖体蛋白 Lys 上的乙酰基，从而调控蛋白质的翻译效率[46]。而 OsHDA716 与碱性亮氨酸拉链蛋白 46 (basic leucine zipper 46, bZIP46)、OsHDA703 与油菜素抗性蛋白 1 (brassinazole-resistant 1, BZR1)，以及 AtHDA6 与油菜素内酯不敏感 2 (brassinosteriod insensitive 2, BIN2)等能相互作用，引起相关蛋白活性改变并显著调控低温胁迫等过程[47-49]。HDAs 介导的去乙酰化修饰多发生在 H3、H4 组蛋白 N 端 Lys 残基，其中 H3K9/14/18/23/27ac、H4K5/8/12/16/20ac 是主要的修饰位点[50-54]。组蛋白去乙酰化反应中，首先 Zn^{2+}与 Asp-His 及与另一环中的 Asp 残基结合(Asp-His-Asp)；一旦 Lys N 端 ε-氨基上的乙酰基底物(N^{ε}-Kac)进入 HDAs 活性口袋，1 分子水(H_2O)便快速攻击 Kac 中的酰胺键(−CO-NH−)，并形成由 Tyr 稳定的四面体中间复合物(图 5A、5B)。上述步骤由口袋内的 2 对 His-Asp 催化，其中 1 对催化质子(H)交换，另一对参与过渡态的稳定。最后，在质子化 His-Asp 的辅助下，形成 Lys 和乙酸分子(图 5C)。总之，HDAs 在 Zn^{2+}协助下利用水分子中的羟基(−OH)攻击 N^{ε}-Kac 的酰胺键(−CO-NH−)，再通过其他活性氨基酸稳定过渡态和快速发生质子转移，最终使得组蛋白的 N^{ε}-Kac 脱去乙酰基(acetyl, Ac)[18]。

2.2 乙酰化修饰的调控

研究表明，由于乙酰辅酶 A (acetyl-CoA)是乙酰基的供体，因而组蛋白的乙酰化过程受胞内乙酰 CoA 浓度的影响[55-57]。如水稻 ATP-柠檬酸裂解酶(ATP-citrate lyase, ACL)突变引起

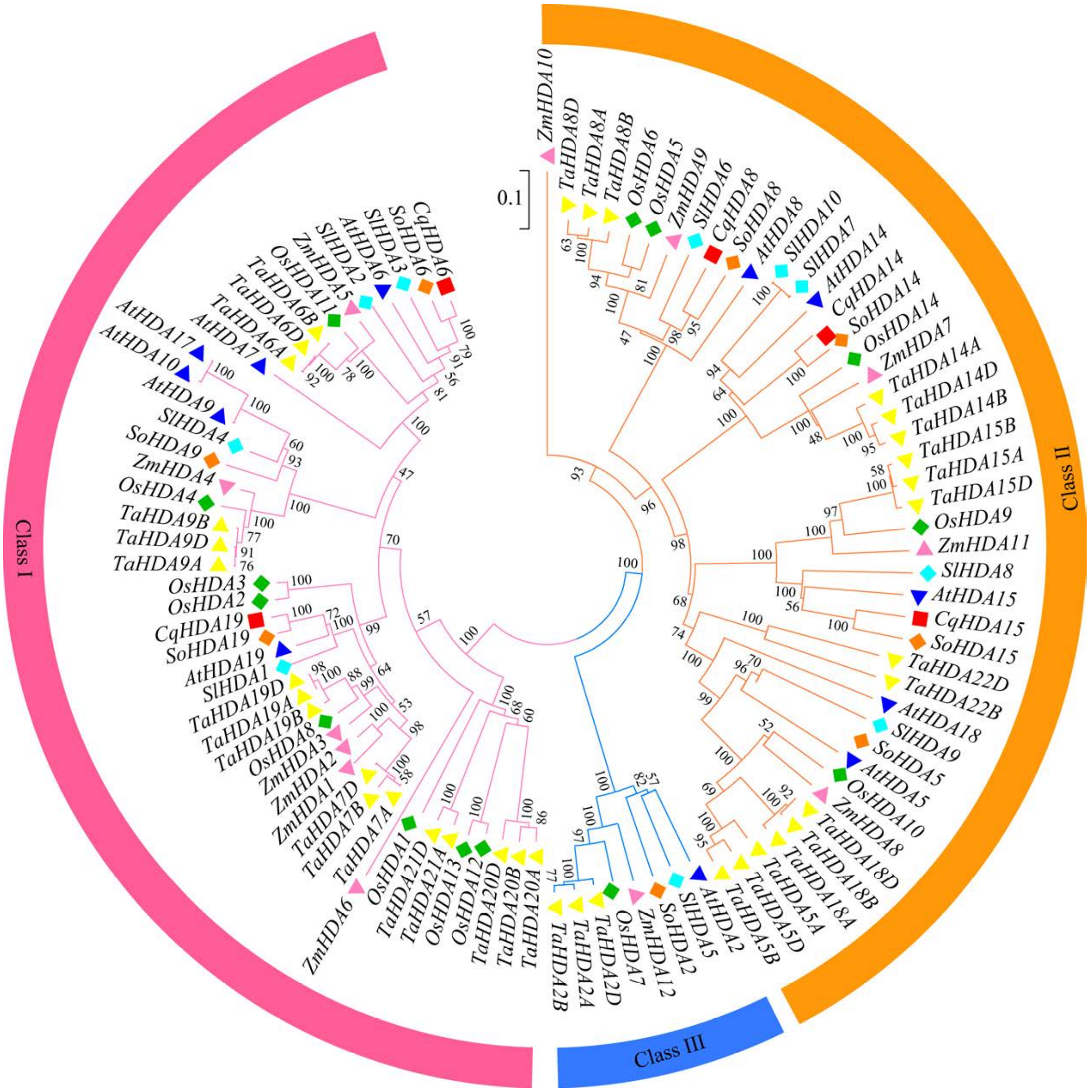

图 3　不同植物 HDAs 基因家族的系统进化分析　采用 MEGA 11.0 软件进行序列多重比较和系统进化树构建[44]。蓝色三角形表示拟南芥，粉色三角形表示玉米，黄色三角形表示小麦，绿色菱形表示水稻，橙色菱形表示菠菜，蓝色菱形表示番茄，红色正方形表示藜麦。上述 98 条序列的基因登录号以附表形式提交至国家微生物数据中心，登录号为 NMDCX0001705。

Figure 3　Evolutionary analysis of HDAs gene family in different plants. MEGA 11.0 software was used for multiple sequence comparisons and phylogenetic tree construction[44]. The blue triangle represents *Arabidopsis thaliana*, pink triangle represents *Zea mays*, the yellow triangle represents *Triticum aestivum*, green diamond represents *Oryzae sativa*, the orange diamond represents *Spinacia oleracea*, the blue diamond represents *Solanum lycopersicum*, and the red square represents *Chenopodium quinoa*. The accession numbers of the above 98 sequences were registered in National Microbial Data Center (NMDC), as shown in the attached table. The registration number is NMDCX0001705.

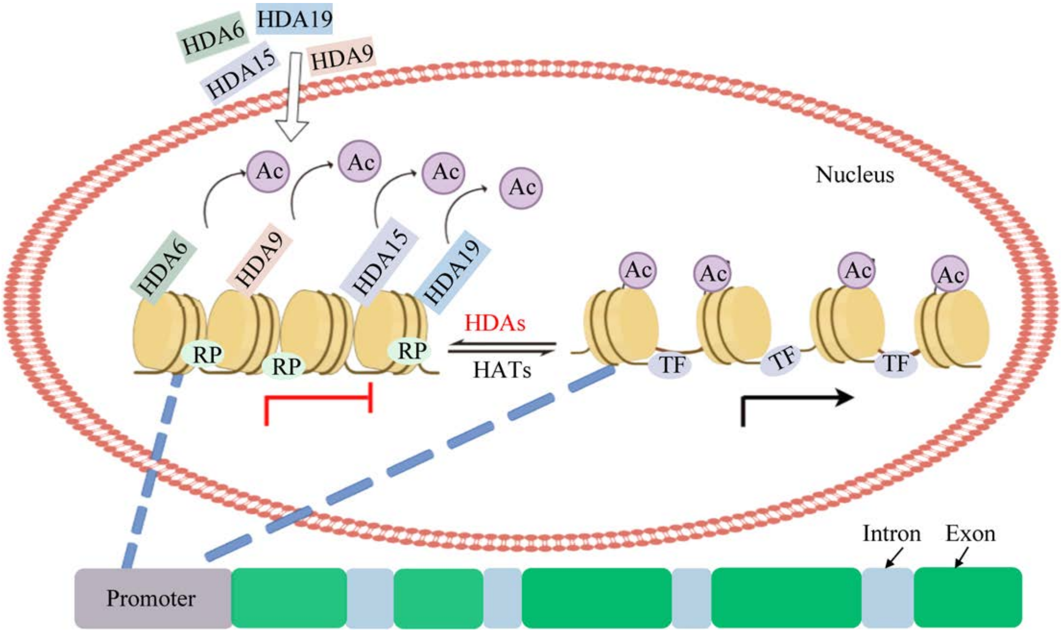

图 4　组蛋白去乙酰化抑制基因表达的分子作用　HDAs，如 HDA6/9/15/19 等被招募到靶基因启动子区，去除该区域核小体上 Kac 中的乙酰基，引起染色质固缩并阻碍了转录因子与启动子序列的结合，导致靶基因转录下调或沉默。

Figure 4　The molecular role of histone deacetylation on gene expression. HDAs, such as HDA6/9/15/19, are recruited to gene promoters and then remove the acetyl group (Ac) of the Kac in the nucleosome. This causes chromatin condensation and prevents transcription factors (TFs) from binding to the promoter, resulting in transcriptional downregulation or silencing of target genes.

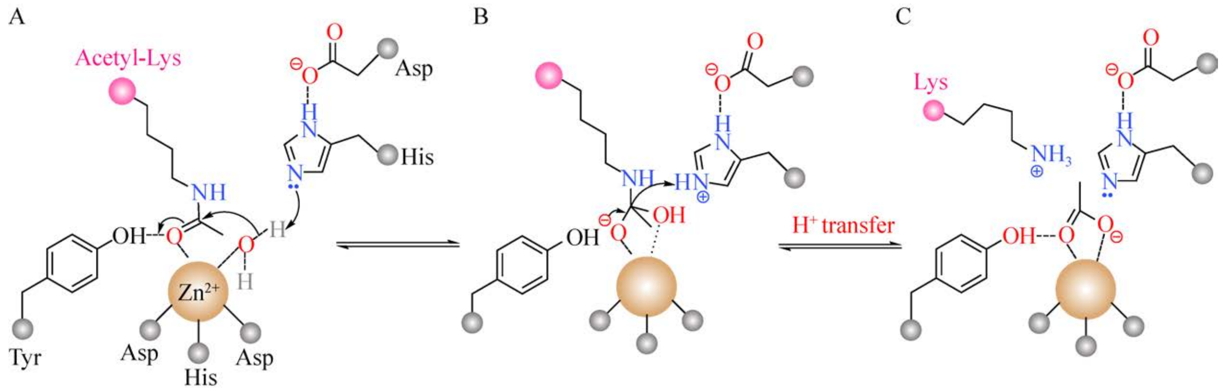

图 5　HDAs 催化蛋白质去乙酰化的反应机制　A：Zn^{2+}结合；B：过渡态稳定；C：质子转移与产物生成。HDAs 催化过程主要包括以上 3 个阶段，其中最后一步的 2 个质子分别来自 His-Asp 二联体和乙酸分子[18]。

Figure 5　The mechanism of protein deacetylation catalyzed by HDAs. A: Zn^{2+} binding; B: Transition state stabilization; C: Proton transfer and product formation. The catalytic process of HDAs mainly includes the above three stages, in the final step, two protons are transferred from the His-Asp dipeptide and the acetic acid molecule, respectively[18].

乙酰 CoA 浓度降低，进而造成乙酰化反应产物 H3K14ac、H4K5ac 水平明显下降[58]。其次，HDAs 活性亦受到翻译后磷酸化、泛素化和亚硝基化等的修饰。拟南芥 AtHDA9 被磷酸化可以防止 26S 蛋白酶体对其进行降解，AtHDA6、AtHDA15 被磷酸化后其核定位与酶活性受到不同程度的影响[59-61]。AtHDA19 蛋白 4 个半胱氨酸(cysteine, Cys)上的巯基(−S)被亚硝基化(S-nitrosylation)后引起该蛋白向核内不断富集并显著增强了植物对氧化胁迫的耐受性[62]。此外，气体分子一氧化氮(nitric oxide, NO)能显著增强组蛋白的乙酰化水平，这提示 S-亚硝基化对 HDAs 的催化活性具有抑制作用[63-64]。

HDAs 与其他蛋白相互作用形成去乙酰化酶复合体是组蛋白去乙酰化的重要调控途径。最早被鉴定的是与酵母 RPD3s 同源的 SWI 非依赖性 3 (SWI-independent 3, SIN3)复合体，包括组蛋白去乙酰化酶 HDA6/19、转录共抑制因子 SIN3 类 1–6 (SIN3-like 1–6, SNL1–6)、组蛋白去乙酰化酶复合体 1 (histone deacetylation complex 1, HDC1)和 IRA1 多拷贝抑制子 1 (multi-copy suppressor of IRA1, MSI1)等，其中 HDA6/19 为复合体核心，SNL1–6 为支架蛋白，其他为 SIN3 相关蛋白，如组蛋白或 DNA 的结合蛋白等[65-66]。SNLs、HDC1、MSI1 等蛋白的突变不同程度影响 HDA6/19 等对 H3K9/14 的去乙酰化修饰，并显著调控植物生长、开花、激素信号和胁迫响应等过程[67-68]。除了 SIN3 型复合体外，利用亲和纯化质谱分析(affinity purification coupled MS, AP-MS)还在拟南芥中鉴定到 SANT (SWI3, ADA2, N-CoR and TFIIIB)、ESANT (ELM2-SANT)和 ARID (AT rich interactive domain)这 3 类植物特异的去乙酰化酶复合体[69]。SIN3、SANT、ESANT 和 ARID 均是重要的组蛋白或 DNA 结合蛋白家族，作用是将 HDAs 锚定于特定组蛋白位点，因而这些蛋白的活性会显著影响组蛋白的去乙酰化修饰。如 AtHDA9 与含 SANT 结构域的 PWR (Powerdress)、WD40 重复蛋白 HOS15 (high expression of osmotically responsive genes 15)三者相互作用形成 HDA9-PWR-HOS15 的 SANT 型复合体，而当这些蛋白突变或活性下降会显著影响基因组 H3Kac 去乙酰化的正常进行[70-71]。此外，拟南芥中 WRKY 转录因子 53 (WRKY transcription factor 53, WRKY53)与 AtHDA9、小分子泛素连接酶 SIZ1 (SUMO E3 ligase SAP and MIZ1 domain-containing ligase 1)与 HDA6 也能相互作用，进而负调控 HDA6/9 的酶催化活性[72-73]。综上所述，组蛋白(去)乙酰化受底物水平、翻译后修饰和去乙酰化酶复合体活性等多方面的影响。

3 HDAs 在植物非生物胁迫响应中的作用

非生物胁迫如盐碱、干旱、高低温等严重抑制农作物生长发育和产量形成，极大制约了农业和生态环境的可持续发展[74-76]。植物在长期适应和进化过程中，形成了独特的逆境适应机制。研究表明，HDAs 通过表观遗传修饰或与其他蛋白质相互作用在植物非生物胁迫响应中发挥重要调控作用[77-79] (图 6)。

3.1 HDAs 调控植物干旱胁迫响应

干旱是限制全球作物生产最主要的非生物胁迫之一，植物因失水引起气孔关闭、酶活性下降与细胞器受损，严重影响植物代谢和生长发育[80-81]。如表 2 所示，多个 AtHDAs[82-88]、*OsHDA704*[53,89]、谷子(*Setaria italica*) *SiHDA9*[90] 等基因广泛参与植物干旱胁迫响应过程。在拟南芥中，*AtHDA6* 突变体 *axe1-5*/*sil1* 能提高丙酮酸脱羧酶 1 (pyruvate decarboxylase 1, PDC1)

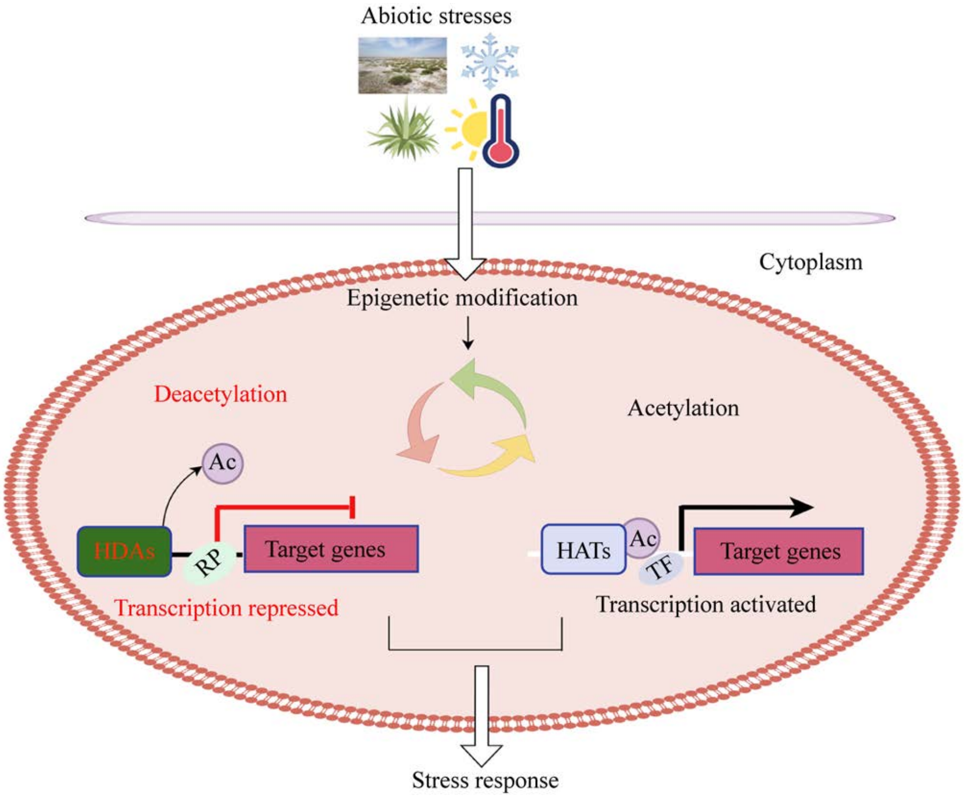

图 6　HDAs 调控植物非生物胁迫的表观遗传机制　非生物胁迫下，HDAs 与多种抑制蛋白形成去乙酰化酶复合体，结合到胁迫响应基因启动子区域，通过去乙酰化机制抑制靶基因转录，进而调控植物非生物胁迫响应过程。TF：转录因子；RP：抑制蛋白；Ac：乙酰基；HATs：组蛋白乙酰转移酶。

Figure 6　Epigenetic mechanism of HDAs on plant abiotic stress responses. Under abiotic stress, HDAs can form a deacetylase complex with repressed proteins (RP), which binds to the promoter region of stress response genes. Subsequently, the transcriptional activity of target genes is inhibited by histone deacetylation, regulating the response to abiotic stresses. TF: Transcription factor; RP: Repressed protein; Ac: Acetyl group; HATs: Histone acetyltransferases.

和乙醛脱氢酶 2 (acetaldehyade dehydrogenase 2, ALDH2)编码区 H4ac 的水平，由此增强了这些基因的转录并促进乙酸产物的合成，而乙酸又通过调控冠状素不敏感 1 (coronatine insensitive 1, COI1)介导的茉莉酸 (jasmonic acid, JA)信号增强了该突变植株的抗旱性[82]。*Athda9-1/2* 突变体无论是种子萌发还是幼苗根的生长都表现出对聚乙二醇(polyethylene glycol, PEG)模拟干旱胁迫的耐受性[83]。染色质免疫沉淀法(chromatin immunoprecipitation assay, ChIP)分析显示，拟南芥 AtHDA9 通过降低胁迫响应基因脂质转移蛋白 4 (lipid transfer protein 4, LIP4)、AP2.6 相关蛋白(related to AP2.6, RAP2.6)、转录因子 MYB29 等启动子区域 H3K9ac 水平负调控上述抗逆基因的转录，从而抑制植物的耐旱性[83]。然而，*Athda9-1* 和 *Athda9-2* 对 ABA 诱导的气孔关闭不敏感，却对生理性干旱即缺水胁迫敏感，表明 AtHDA9 也正向调控拟南芥生理性干旱[84]。进一步的研究表明，AtHDA9 与 ABA 不敏感 4 (ABA insensitive 4, ABI4)、PWR 形成复合体，通过对 H3ac 的去乙酰化修饰抑制 ABA 分解代谢基因细胞色素 707A1/2 (cytochrome

表 2 HDAs 在植物响应非生物胁迫中的作用

Table 2 The role of HDAs in plant response to abiotic stresses

HDAs	Target genes	Functions	Species	References
AtHDA6/9/19/15	*PDC1*, *ALDH2B7*, *COI1*, *LIP4*, *RAP2.6*, *MYB29*, *ABI4*, *PWR*, *CYP707A1/A2*, *RD29A/B*, *COR15A*, *MYB96*, *ROP6/10/11*	Involved in drought stress by regulating stress genes transcription and ABA or JA signaling	*Arabidopsis thaliana*	[82-88]
OsHDA704	*DST*, *ABIL2*, *WR2*, *ABI5*, *DSS1*	Positively regulate plant drought tolerance by inhibiting stomatal aperture and ABA-responsive genes transcription	*Oryzae sativa*	[53,89]
SiHDA9	*RAB18*, *RAP2.4*, *P5CS2*, *RD22*, *PIP1/4*	Negatively regulate plant drought tolerance by forming the repressing complex	*Setaria italica*	[90]
AtHDA6/9/15/19	*ABI1/2*, *KAT1/2*, *DREB2A*, *RD29A/B*, *WRKY53*, *ABI5*, *MAC3A/3B*	Involved in salt stress by regulating stress genes transcription and ABA signaling	*A. thaliana*	[64,83,91-98]
OsHDA710/706/704	*LEA3*, *ABI5*, *bZIP72*, *NHXI*, *PP2C49*, *DST*, *ABIL2*	Involved in salt stress by regulating stress genes transcription and ABA signaling	*O. sativa*	[99-100]
SlHDA5		positively regulates salt tolerance in plants but the molecular process is unclear	*Solanum lycopersicum*	[101]
AtHDA6/9/15	*HTT1*, *SAP10*, *SYT4*, *AT4G39360*, *AT2G23110*, *YUC8*, *PIF4*, *MED25*, *HOS1*, *YY1*, *HFR1*, *RD22/PIP1-4*	Involved in high-temperature stress by regulating the transcription of heat-induced genes	*A. thaliana*	[60,95,102-109]
AtHDA6		Positively regulate plant cold tolerance	*A. thaliana*	[110]
MdHDA6	*TCP15*, *ABI1*	Positively regulate plant cold tolerance by forming the repressing complex	*Malus domestica*	[111]
PvHDA6	*FLD*, *ELF3*	Regulate plant response to cold stress	*Phaseolus vulgaris*	[112]
DgHDA6	*DgCuZnSOD*, *DgCAT*, *DgP5CS*, *DgFAD*	The overexpression of DgHDA6 can improve cold tolerance in chrysanthemum by enhancing ROS scavenging capacity	*Chrysanthemum morifolium Ramat*	[113]
OsHDA716	*bZIP46*, *DREB1A*, *COLD1*	Negatively regulate plant cold tolerance by interacting with OsbZIP46 and inhibiting the expression of cold stress response genes	*O. sativa*	[47,114]

(待续)

(续表 2)

HDAs	Target genes	Functions	Species	References
MaHDA2	*MYB4*, *FAD3-1/3/4/7*	Positively regulate plant cold tolerance by interacting with MaMYB4 and inhibiting the expression of *MaFAD3-1/3/4/7* genes	*Musa acuminata*	[115]
AtHDA1/6/9/15	*SAG12*, *SEN4*, *PWR*, *WRKY53/57*, *NPX1*, *APG9*, *WHY1*, *NAC019*, *LARP1C*, *LOX2*	Involved in plant senescence by regulating senescence-associated genes transcription and JA signaling	*A. thaliana*	[116-120]
OsHDA701		Inhibits plant senescence but the molecular process is unclear	*O. sativa*	[121]

707A1/2, CYP707A1/2)的转录，因而通过增强ABA信号过程激活ABA响应基因(*RD29A*、*RD29B*、*COR15A*)的表达进而正向调控植物干旱胁迫[85]。干旱胁迫下，*Athda19-3*与*Athda19-5*突变体的存活率是野生型的2倍，且AtHDA19和组蛋白去乙酰化酶复合体HDC1存在相互作用，这提示AtHDA19也可能利用表观遗传机制负调控干旱胁迫[86-87]。利用双分子荧光互补(bimolecular fluorescence complementation, BiFC)和免疫共沉淀(co-immunoprecipitation, Co-IP)技术分析表明，AtHDA15与R2R3型转录因子MYB96相互作用协同抑制ABA负调控因子小G蛋白ROP6/10/11 (rho of plant 6/10/11)的表达，继而通过ABA信号正向调控干旱胁迫[88]。

在水稻中，OsHDA704是与AtHDA15同源的HDA类去乙酰化酶，过量表达该蛋白引起水稻“抗旱耐盐”基因(drought and salt tolerance, *DST*)、ABI基因家族2 (ABA insensitive like 2, *ABIL2*)的表达量降低，使得植物叶片气孔开度降低、密度增加、植物失水减少，最终明显增强了转基因植株的抗旱性[89]。进一步研究发现，该转基因植株强的耐旱性还在于抗旱转录因子蜡质合成调节基因2 (wax synthesis regulatory 2, WR2)招募HDA704后共同调控干旱胁迫响应基因ABA不敏感5 (ABA insensitive 5, *ABI5*)、小粒矮秆基因1 (dwarf and small seed 1, *DSS1*)的H4K8ac水平，然后通过抑制*ABI5*、*DSS1*的表达正向调控水稻干旱胁迫[53]。谷子中SiHDA9与锌指同源结构域蛋白HAT3.1、SiHDA19形成的复合体可以降低ABA应答基因18 (responsive to ABA 18, *RAB18*)、AP2/ERF类转录因子2.4 (related to AP2.4, *RAP2.4*)、吡咯-5-羧酸合成酶2 (pyrroline-5-carboxylate synthetase 2, P5CS2)、脱水诱导基因22 (responsive to desiccation 22, *RD22*)、质膜固有蛋白1/4 (plasma membrane intrinsic protein 1/4, PIP1/4)的表达，进而负调控谷子耐旱性的响应[90]。以上结果充分表明，HDAs利用JA、ABA信号过程及通过抑制胁迫响应靶基因的转录等参与植物干旱胁迫响应。

3.2 HDAs调控植物盐胁迫响应

盐胁迫是制约全球作物生长和产量的主要环境因素，土壤高浓度盐离子对植物造成渗透胁迫、离子毒害和氧化损伤，致使作物减产甚至导致死亡[122]。*axe1-5*及干扰植株*CS24039*在种子萌发与幼苗生长中对盐胁迫的敏感性增加，且发现ABA和胁迫响应基因如*ABI1/2*、钾通道蛋白1/2 (potassium channel 1/2, *KAT1/2*)、脱水响应元件结合蛋白2A (dehydration-responsive element-binding protein 2A, *DREB2A*)、脱水响应基因29A/B (responsive to dehydration 29A/B, *RD29A/B*)的转录受到抑制，这说明AtHDA6通过ABA信号正调控植物耐盐性[91]。同时植物

特异的去乙酰化酶 AtHD2 的可变剪切体 HD2C 突变后的盐胁迫表型与 *axe1-5* 相似，并发现 HD2C 与 HDA6 相互作用参与 H3K9/14 乙酰化及 H3K9 的三甲基化反应[92]。与干旱胁迫类似，AtHDA9 通过去乙酰化机制抑制 *LIP4*、*RAP2.6*、*MYB2* 等基因的转录负调控植物的耐盐性[83,93]。AtHDA9 与 WRKY53 相互作用并互为各自活性的负调控因子，由此动态调控盐胁迫响应过程[72,94]。盐胁迫下，*AtHDA19-3* 与 *AtHDA19-5* 植株存活率超过 80%，而来自 II 类 HDAs 的四突变体 *AtHDA5/14/15/18* 却对盐胁迫超敏感，且在该四突变体中编辑 *HDA19* 后获得的五突变体又恢复了耐盐表型[95]。进一步探究 *AtHDA19* 在上述四突变体中的作用，盐胁迫诱导的转录组数据揭示，在 *AtHDA19* 与 *AtHDA5/14/15/18/19* 五突变体中共有 56.7%的盐胁迫响应基因具有相似的表达模式，且 ABA 合成及下游靶基因如 *ABI5* 的转录水平上升，表明 AtHDA19 与 AtHDA5/14/15/18 通过相互拮抗共同参与盐胁迫响应过程[96]。研究还发现，超高表达 *AtHDA15* 能诱导 ABA 合成基因 9-顺式环氧类胡萝卜素双加氧酶 3 (nine-*cis*-epoxycarotenoid dioxygenase 3, *NCED3*)表达，进而提高了植株内源 ABA 含量及通过该信号过程增强了植株的耐盐性[97]。另外，通过免疫纯化和基于质谱的蛋白质组分析揭示，盐胁迫下 AtHDA15 与剪接复合体 MAC (MOS4-associated complex)核心组分 MAC3A、MAC3B 相互作用，共同调控 ABA 响应基因的内含子可变剪切[98]。

水稻 *OsHDA710* 受到盐胁迫的诱导表达，敲除该基因后，盐胁迫和 ABA 响应基因如胚胎晚期富集蛋白 3 (late embryogenesis abundant group 3 protein, *LEA3*)、*ABI5*、*OsbZIP72* 和 Na^+/H^+逆向转运蛋白 1 (Na^+/H^+ exchanger 1, *NHX1*)启动区域 H3ac 升高，基因表达量增加，因此增强了植株的耐盐性[99]。相反地，OsHDA706 通过对 ABA 信号负调控基因蛋白磷酸酶 2C 49 (protein phosphatase 2C 49, *PP2C49*)中 H4K5ac、H4K8ac 进行去乙酰化修饰增强了 ABA 信号和水稻的耐盐性[100]。除干旱胁迫外，OsHDA704 也通过去乙酰化修饰抑制抗逆基因 *DST*、*ABIL2* 的表达，从而正向调控植物的耐盐性[89]。番茄 *SlHDA5-RNAi* 对盐胁迫较敏感，盐胁迫下干扰植株叶绿素迅速降解、叶片枯萎，表明 *SlHDA5* 也正向调控植物的耐盐性，然而其响应胁迫的分子机制目前仍不明晰[101]。总之，HDAs 广泛参与盐胁迫响应过程，但是否正向调控植株的耐盐性往往取决于 HDAs 下游靶基因的生物学作用。

3.3 HDAs 调控植物高低温胁迫响应

温度胁迫(高温和低温)对植物生长、发育和产量造成不可逆的影响[123]。由于全球气候变化，温度胁迫已经成为限制农作物生产的主要因素[124-125]。AtHDAs 家族基因如 *HDA6/9/15*[60,95,102-109]等在植物热胁迫响应中发挥十分重要的作用(表 2)。如 Popova 等[102]在研究 RNA 介导的 DNA 甲基化途径(RNA-directed DNA methylation, RdDM)调控热胁迫时发现，拟南芥 *AtHDA6* 缺失突变体对热胁迫超敏感；研究显示，SANT 复合体组分 SANT1/2/3/4 及 HDA6 的突变均能促使热诱导的 TAS1 基因 (heat-induced TAS1, *HTT1*)、胁迫相关蛋白基因 10 (stress-associated protein 10, *SAP10*)等的 H3Kac 水平升高及基因表达增强，然而 *SANT1/2/3/4* 植株耐热性增强，*HDA6* 突变体却对热胁迫十分敏感，这提示 AtHDA6 正向调控植株耐热性的分子机制并不依赖于 SANT 的活性[103]。高温胁迫下，HDA9 将 H2A.Z 组蛋白变体驱逐出生长素合成基因 8 (yucca 8, *YUC8*)

的核小体，从而促进了 *YUC8* 基因染色质开放，这使得光敏色素互作因子 4 (phytochrome interacting factor 4, PIF4)与 *YUC8* 启动子结合并激活了该基因的转录，这表明 HDA9 通过调控生长素的合成参与了植株热形态建成[104-105]。进一步发现，热胁迫下 HDA9 激活 *YUC8* 的转录还在于转录介体复合体亚基 25 (mediator complex subunit 25, MED25)与 PIF4、HDA9 的相互作用，这促使 HDA9 被招募到 *YUC8* 基因位点[106]。此外，热激促使蛋白磷酸酶 2AB′β (protein phosphatase 2AB′β, PP2AB′β)去磷酸化胞质的 HDA9，而热激后 HDA9 发生去磷酸化和借助高表达渗透响应基因 1 (high expression of osmotically responsive gene 1, *HOS1*)进入细胞核，最终在“阴阳蛋白 1” (yin-yang 1, YY1)协助下通过去乙酰化机制维持植株生长发育和热激响应间的平衡[60]。总之，HDA9 是热形态发生途径的重要组成部分[95]。*AtHDA15* 突变体 *hda15-1* 对热胁迫不敏感，且 HDA15 与远红光响应下胚轴伸长蛋白 1 (long hypocotyl in far red 1, HFR1)相互作用调控胁迫相关基因的表达，进而协同抑制温度响应基因的表达[107]。研究证实，植物特有的 *HD2B* 和 *HD2C* 也参与调控热胁迫过程。如 *hd2c-3* 对热胁迫具有较强抗性，但 *hd2b*/*hd2c* 双突变对热胁迫超敏感，HD2C 与染色质重塑复合物 SWI/SNF 相互作用共同调控热响应基因的表达，而 HD2B 和 HD2C 可通过 RdDM 途径中的一种核酸内切酶 4 (argonaute 4, AGO4)来维持热响应中 DNA 的甲基化[108-109]。

研究表明，HDAs 也能调控植物冷胁迫响应过程[47,110-115]。与对照相比，*axe1-5* 经冷处理后抗冻性下降，电解质渗透率增加和相关基因的转录发生改变[110]。与 AtHDA6 同源的苹果(*Malus domestica*) MdHDA6 与 TCP 类转录因子 15 (TCP family transcription factor 15, TCP15)相互拮抗，使得 HDA6 对 *ABI1* 基因组区域的组蛋白进行去乙酰化，进而抑制该基因表达并增强了苹果的耐寒性[111]。此外，冷胁迫诱导菜豆(*Phaseolus vulgaris*) *PvHDA6* 基因表达上调，过量表达菊花(*Chrysanthemum morifolium Ramat*) *DgHDA6* 能通过活性氧(reactive oxygen species, ROS)清除系统增强植株的耐寒性[112-113]。在水稻中，OsHDA716 负向调控植物冷胁迫，过表达该基因能显著抑制植物的耐寒性[47,114]。研究表明，OsHDA716 能与冷胁迫响应的正调控转录因子 bZIP46 相互作用并对其去乙酰化修饰而抑制了该基因表达，由此降低了 OsbZIP46 对 *DREB1A*、低温耐受性基因 1 (chilling tolerance divergence 1, *COLD1*)的转录激活，造成冷诱导的 Ca^{2+}内流降低并导致植物对冷胁迫超敏感[47,114]。香蕉(*Musa acuminata*) MaHDA2 与转录因子 MYB4 相互作用增强了 MYB4 对 ω-3 脂肪酸去饱和酶(ω-3 fatty acid desaturases, FADs)基因 *FAD3-1*/*3*/*4*/*7* 的转录抑制，使得香蕉果实中的不饱和脂肪酸含量大幅增加并显著提高了其耐冷性[115]。由此可见，HDAs 利用去乙酰化机制或与其他蛋白相互作用显著调控植物高低温胁迫。

4 HDAs 调控植物衰老过程

植物叶片衰老的显著特征是叶绿素降解和植物适应性地由营养吸收向营养再分配转变，这对植物光合作用、营养分配、胁迫响应和作物产量具有重要影响[126]。如表 2 所示，很多研究发现 HDAs 参与植物衰老过程。相比于野生型，*axe1-5* 及干扰植株(*HDA6–RNAi*)的叶片表现出滞绿的表型，另外还发现 H3 组蛋白乙酰化水平升高，然而衰老相关基因 12 (senescence-associated gene 12, *SAG12*)表达量下降，这提示

HDA6 负调控植物衰老可能不依赖于组蛋白去乙酰化[116]。AtHDA9 被发现在叶片衰老过程中起关键作用，其功能丧失突变体 *Athda9* 延缓了叶片衰老并增加了基因组 H3K27ac 水平；HDA9 与含 SANT 结构域蛋白 PWR、衰老调控转录因子 WRKY53 形成阻遏型复合体，通过去除 H3 的乙酰化标记抑制叶片衰老负调控基因 *WRKY57*、核蛋白 X1 (nuclear protein X1, *NPX1*)、自噬基因 9 (autophagy 9, *APG9*)的表达，从而加速了植物衰老过程[117]。据报道，AtHDA15 可被单链 DNA/RNA 结合蛋白 1 (whirly 1, WHY1)招募到衰老相关基因位点 *WRKY53*、*WRKY33* 等，通过降低这些基因启动子区域的 H3K9ac 水平抑制上述基因转录，最终显著减缓植物衰老[118]。有趣的是，HDA15 更加偏向通过降低 H3K9ac 水平来抑制 JA 信号途径 NAC 类转录因子 19 (NAC domain containing protein 19, NAC19)、LA 相关蛋白 1C (LA related protein 1C, LARP1C)、脂氧合酶 2 (lipoxygenase 2, LOX2)等的表达，从而延缓植物衰老[119]。另外，反义 *AtHDA1* 的转基因植物(antisense-AtHD1)增加了四乙酰化 H4 的水平，最终导致植物早衰及诱导产生发育异常的表型[120]。在水稻中，过量表达 *OsHDA710* 能上调光合作用、叶绿素生物合成相关基因的表达，同时也会下调程序性细胞死亡基因的表达，从而最终减缓了植物衰老[121]。以上结果表明，HDAs 可通过形成阻遏型复合体或抑制衰老相关基因表达显著调控植物衰老过程。

5 展望

HDAs 是一类与酵母 RPD3 高度同源的 Zn^{2+}依赖型组蛋白或非组蛋白去乙酰化酶。HDAs 主要通过形成 SIN3 等去乙酰化酶复合体而对组蛋白进行去乙酰化修饰，进而促使染色体固缩并导致靶基因转录下调或沉默。越来越多的研究表明，HDAs 在植物非生物胁迫如干旱、盐碱、高低温及植物衰老过程中发挥重要作用。目前对 HDAs 的研究主要集中在拟南芥、水稻等植物 HDA6/9/19 的去乙酰化机制和生物学调控作用，但其他大部分 HDAs 的结构及功能多样性亟待阐明。HDAs 介导的去乙酰化酶复合体组分鉴定及下游靶基因网络调节机制仍有待深入研究。此外，有关 HDAs 在其他植物特别是农作物中的组蛋白去乙酰化和生物学调控作用的研究也处于初步阶段。

未来组蛋白去乙酰化领域的研究可重点从以下方面着手：(1) 利用先进的组蛋白去乙酰化组学、双分子荧光互补(bimolecular fluorescence complementation, BiFC)、免疫共沉淀(co-immunoprecipitation, Co-IP)等技术鉴定 HDAs 介导的去乙酰化酶复合体组成及阐明作用机制；(2) 结合免疫共沉淀-测序(chromatin immunoprecipitation sequencing, ChIP-seq)方法挖掘 HDAs 催化的组蛋白去乙酰化位点及下游靶基因，揭示 HDAs 参与调控的分子网络和信号通路；(3) 采用过表达、基因编辑、敲除及 RNA 干扰等手段，进一步阐明 HDAs 在植物抗逆性中的分子基础，为农作物抗逆性遗传改良提供优异基因资源和理论基础。

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