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# 植物 NAC 转录因子的结构及功能研究进展

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**摘要:**NAC(NAM、ATAF1/2、CUC1/2)转录因子是植物特有的一类转录因子家族,在植物生长发育、生物及非生物胁迫反应中具有重要的调控作用。NAC 蛋白的 N 端均存在 1 个高度保守的 NAC 结构域,而 C 端是变化的转录调控区。通过总结前人的研究进展,综述 NAC 转录因子在植物分生组织和器官边界的形成、根的生长、植物细胞次生壁的生长、植物衰老、激素调控和胁迫反应等过程中的重要调控作用,指出今后 NAC 转录因子的研究方向。

**关键词:**植物;NAC 转录因子;生长发育;胁迫;NAC 生理功能

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植物在生长发育过程中极易受到逆境胁迫的影响。胁迫主要包括干旱、高盐、低温、高温等非生物胁迫和虫害、病原菌侵入等生物胁迫,这些胁迫通常会影响植物的正常生长发育。在长期的进化过程中,植物产生了一系列生理生化机制来适应、抵御或消除胁迫的影响。其中,基因表达调控是调节植物逆境胁迫最常见的一种方式。植物细胞感知逆境胁迫信号后,会通过某些信号途径将信号传递给胁迫应答的转录因子(transcription factor,简称 TF),转录因子可以通过其 DNA 结合结构域(DNA binding domain,简称 DBD)和靶基因上游启动子区域的特异 DNA 序列模体(顺式作用元件)结合,从而调控靶基因在植物的不同组织、不同细胞或不同环境条件下的特异表达,从而激活植物抗逆反应,降低胁迫对植物造成的伤害<sup>[1-3]</sup>。由于转录因子在植物生长发育和应对胁迫等过程中具有重要的调控作用,因此对转录因子的研究一直是功能基因组研究的重要内容。近几十年来,世界各国科研人员通过基因组测序和功能分析,相继从不同植物中克隆到了大量的转录因子<sup>[4]</sup>,希望通过研究它们的功能,来揭示植物的抗逆机制。

NAC 转录因子是植物特有的一类转录因子家

族,命名取自于矮牵牛(*Petunia hybrida*)的 NAM(*no apical meristem*)基因、拟南芥(*Arabidopsis thaliana*)的 ATAF1/2 基因,以及 CUC2(*cup-shaped cotyledon*)基因的首字母。1996 年,Souer 等研究人员从矮牵牛中克隆出第 1 个 NAC 转录因子家族成员 NAM,它影响矮牵牛顶端分生组织的形成与分化<sup>[5]</sup>。随后,NAC 转录因子相继在拟南芥、水稻、葡萄、小麦、大豆、木薯、番茄、黄瓜等物种中被发现(表 1),是植物中最大的转录因子家族之一。很多研究表明,NAC 转录因子不仅参与了植物根、茎、叶、花的生长发育、果实成熟、激素调控,还参与了生物及非生物胁迫等生理生化反应过程的调控<sup>[6-7]</sup>。

## 1 NAC 转录因子的结构

NAC 转录因子最显著的结构特点是在蛋白质的 N 端存在 1 个高度保守的 NAC 结构域(约 150 ~ 160 个氨基酸),而 C 端是变化的转录调控区(transcriptional activation region,简称 TAR)(图 1)。NAC 结构域是 NAC 转录因子的结合域,可以分为 5 个亚结构域(A ~ E),其中亚结构域 C 和 D 高度保守且含有核定位信号,可能与 DNA 的结合有关,而亚结构域 B 和 E 则变化多样,可能会赋予 NAC 不同的功能<sup>[9]</sup>。有研究表明,亚结构域 E 能参与调控植物发育时期或组织特异性,并能够协同亚结构域 D 与 DNA 结合<sup>[49]</sup>。亚结构域 A 在不同的物种中也高度保守,可能与 NAC 蛋白形成二聚体有关<sup>[50]</sup>。NAC 蛋白的 C 端具有高度的多样性,但会频繁出现一些简单氨基酸的重复排列,例如 Thr(苏氨酸)、

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表 1 已发表的不同植物中 NAC 转录因子的数量

物种	拉丁文	数量(个)	参考文献
拟南芥	<i>Arabidopsis thaliana</i>	117	[8-9]
水稻	<i>Oryza sativa</i>	151	[8-10]
白杨	<i>Populus trichocarpa</i>	163	[11]
大豆	<i>Glycine max</i>	152	[12]
苹果	<i>Malus domestica</i>	180	[13]
马铃薯	<i>Solanum tuberosum</i>	110	[14]
雷蒙德氏棉	<i>Gossypium raimondii</i>	149	[15-16]
陆地棉	<i>G. hirsutum</i>	283	[16]
海岛棉	<i>G. barbadense</i>	267	[16]
小米	<i>Setaria italica</i>	147	[17]
葡萄	<i>Vitis vinifera</i>	74	[18]
木豆	<i>Cajanus cajan</i>	88	[19]
白菜	<i>Brassica rapa</i>	204	[20]
玉米	<i>Zea mays</i>	152	[21]
香蕉	<i>Musa acuminata</i>	167	[22]
鹰嘴豆	<i>Cicer arietinum</i>	71	[23]
木薯	<i>Manihot esculenta</i>	96	[24]
蒺藜苜蓿	<i>Medicago truncatula</i>	97	[25]
番茄	<i>Solanum lycopersicum</i>	104	[26]
麻风树	<i>Jatropha curcas</i>	100	[27]
二穗短柄草	<i>Brachypodium distachyon</i>	101	[28]
梅花	<i>Prunus mume</i>	113	[29]
乌拉尔图小麦	<i>Triticum urartu</i>	87	[30]
普通小麦	<i>T. aestivum</i>	488	[31]
硬粒小麦	<i>T. turgidum</i>	168	[32]
茶树	<i>Camellia sinensis</i>	45	[33]
萝卜	<i>Raphanus sativus</i>	172	[34]
甜瓜	<i>Cucumis melo</i>	82	[35]
川桑	<i>Morus notabilis</i>	79	[36]
苦荞麦	<i>Fagopyrum tataricum</i>	80	[37]
烟草	<i>Nicotiana tabacum</i>	154	[38]
大豆	<i>Glycine max</i>	139	[39]
黄瓜	<i>Cucumis sativus</i>	91	[40-41]
芝麻	<i>Sesamum indicum</i>	87	[42]
藜麦	<i>Chenopodium quinoa</i>	90	[43]
辣椒	<i>Capsicum annuum</i>	104	[44]
野草莓	<i>Fragaria vesca</i>	112	[45]
白梨	<i>Pyrus bretschneideri</i>	183	[46]
垂枝桦	<i>Betula pendula</i>	114	[47]
菠萝	<i>Ananas comosus</i>	73	[48]

Ser(丝氨酸)、Pro(脯氨酸)、Glu(谷氨酸)或者酸性氨基酸残基等,这是植物转录激活结构域的典型特征。这些简单氨基酸的重复排列在 NAC 同一亚家族是保守的,在不同的亚家族之间却有明显的差

异。一些特殊的 NAC 蛋白在 C 端会有一段跨膜区(transmembrane motifs,简称 TMs),这种 C 端具有跨膜特性的 NAC 转录因子(NAC with transmembrane motif 1,简称 NTM1)一般被称为 NTL(NTM1-like)蛋白,必须从膜上被释放并转运到核中才能行使调控功能<sup>[51-52]</sup>。有些 NAC 转录因子只有 NAC 结构域,缺少转录调控区;更有的 NAC 结构域在 C 端,转录调控区在 N 端,中间含有一个保守的锌指结构。

通过 X 射线观察拟南芥 ANAC019 的 NAC 结构域的晶体结构,发现它是以数个螺旋元件包围一个螺旋状的结构,并和  $\beta$ -折叠组成一种未知的结构<sup>[50]</sup>,而且 NAC 结构域可通过盐桥等作用形成一侧带正电荷的蛋白二聚体<sup>[50,53]</sup>,这可能是它们结合 DNA 的基本形式。

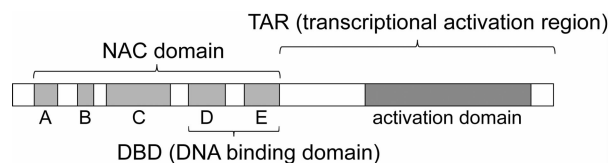


图1 NAC 蛋白的基本结构

## 2 NAC 转录因子的生理功能

NAC 转录因子因其在结构上有一定的共性和特性,其家族成员在功能上也有一定的共同点和多样性。但在植物不同部位、生长的不同时期,特定的 NAC 转录因子发挥的作用也不尽相同。总体来说,NAC 转录因子对植物生长调控主要表现在如下几个方面。

### 2.1 参与植物分生组织和器官边界的形成

矮牵牛 *NAM* 基因主要在分生组织和器官原基边界的细胞内表达,*nam* 突变体缺少茎顶端分生组织(shoot apical meristem,简称 SAM),器官发育异常,导致幼苗大部分死亡,少部分存活下来的植株在成苗期花器官也会出现发育异常,说明 *NAM* 基因可能在分生组织器官原基的形成中起着一定的作用<sup>[5]</sup>。拟南芥 *AtNAM* 在胚胎 SAM 的整个区域均大量表达,暗示着参与 *AtNAM* 也参与 SAM 的形成<sup>[54]</sup>。CUC 蛋白与矮牵牛 *NAM* 蛋白属于同一亚家族,拟南芥 *cuc1cuc2* 双基因突变体中子叶、萼片和雄蕊融合,难以形成 SAM,而单基因的突变体却没有明显的表型,说明它们参与植物顶端分生组织的形成,且存在功能的冗余<sup>[55]</sup>。进一步研究发现,*CUC1* 在拟南芥胚的顶端分生组织和花器官原基的边界处表达,处于 *STM*(*SHOOT MERISTEMLESS*)基因的上

游,可以激活很多 SAM 相关基因的表达,超量表达 *CUC1* 可以激活芽尖组织周缘细胞,诱导子叶不定芽的形成<sup>[56-57]</sup>。有趣的是,*CUC1* 也可以通过一种不依赖 *STM* 的途径促进 SAM 的形成,该途径受到 *ASI* (*ASYMMETRIC1*) 和 *AS2* 基因的负调控<sup>[58]</sup>。此外,*CUC1* 可以正调控 *LIGHT - DEPENDENT SHORT HYPOCOTYLS 4* (*LSH4*) 及其同源基因 *LSH3* 的表达,而在茎尖超量表达 *LSH4* 会抑制植物营养生长阶段叶片的生长,以及生殖生长阶段花中额外的芽或芽器官的形成<sup>[59]</sup>。*CUC3* 基因主要在花器官原基边界表达,其表达量会被 *CUC1* 和 *CUC2* 所促进,超表达 *CUC3* 能促进胚后期的茎分生组织和器官边界的形成<sup>[60-61]</sup>。玉米 *ZmNAM1/2* 和 *ZmCUC3* 在胚芽鞘与叶原基的边界处大量表达,参与茎尖分生组织的形成<sup>[62]</sup>。由此可见,植物 NAM 亚族基因在分生组织和器官边界的形成中起着关键的作用。

## 2.2 调控根的发育

拟南芥 *NAC1* 基因受生长素 (auxin) 的诱导,主要在根尖和侧根生长原基表达,超量表达 *NAC1* 能促进侧根发育,而反义表达 *NAC1* 能抑制 *TIR1* (transport inhibitor responsive protein 1) 诱导的侧根发育,而生长素应答因子 *AIR3* (*auxin - induced in rootcultures 3*) 和 *DBP* (*DNA - binding protein*) 基因表达也受到 *NAC1* 的诱导,说明 *NAC1* 可以介导生长素信号以促进侧根的形成<sup>[63]</sup>。进一步研究表明,拟南芥 *SINAT5* 蛋白能促进 E3 泛素复合体与 *NAC1* 的连接,进而降低 *NAC1* 蛋白水平,减弱生长素信号,从而限制侧根的发育和伸长<sup>[64]</sup>。*OsNAC2* 也可以通过整合生长素和细胞分裂素 (cytokinin) 信号途径来调控根的发育<sup>[65]</sup>。*ANAC092/AtNAC2/ORE1* 基因也在根中特异表达,参与侧根的形成与发育<sup>[66]</sup>。进一步研究表明,*ANAC092* 可以结合 *ARF8* (*AUXIN RESPONSE FACTOR 8*) 和 *PIN4* (*PIN - FORMED 4*) 的启动子,通过控制生长素信号途径来负调控根的发育<sup>[67]</sup>。*TaRNAC1* 是小麦根中特异表达的 NAC 转录因子,在根中超量表达 *TaRNAC1* 的转基因小麦根长、生物量和干旱抗性明显增加<sup>[68]</sup>。在拟南芥中超量表达一些来自于其他物种的 NAC 基因,也能促进侧根的形成,如 *BnNAC14*<sup>[69]</sup>、*GmANC20*<sup>[70]</sup>、*GmNAC109*<sup>[71]</sup>、*CiNAC3* 和 *CiNAC4*<sup>[72]</sup> 基因等。

## 2.3 调节植物细胞次生壁的生长

一些 NAC 转录因子会调节细胞次生壁的生长。在拟南芥中,*nst1nst2* 双突变体均表现出花药内皮层

缺乏次生壁,花药异常开裂,表明 *NST1* (*NAC SECONDARY WALL THICKENING PROMOTING FACTOR1*) 和 *NST2* 参与花粉花药次生壁的形成,而且存在功能的冗余<sup>[73]</sup>。在拟南芥 *nst - 1nst - 3* 双敲除转基因植株中,除维管导管以外,维管束间纤维与木质部次生壁的加厚被完全抑制,表明 *NST1* 和 *NST3* 也参与调控木质组织中次生壁的正常形成<sup>[74]</sup>,它们之间也存在部分功能的冗余<sup>[75]</sup>。苜蓿 *MtNST1* 是拟南芥 *NST1/2/3* 的同源基因,*MtNST1* 的 Tnt1 逆转座子插入突变体出现花粉囊无法裂开,维管素纤维不再木质化<sup>[76]</sup>。拟南芥 *SND1* (*SECONDARY WALL - ASSOCIATED NAC DOMAIN PROTEIN1*) 在茎秆维管束间纤维和木质纤维中特异表达,异位超量表达 *SND1* 基因,会使非厚壁的正常细胞大量沉积次级细胞壁而成为厚壁细胞,表明 *SND1* 与纤维次级壁的厚度有关<sup>[77]</sup>。敲除 *SND1* 基因不能明显抑制次级纤维壁的加厚,而 *snd1nst1* 双突变体抑制的表型非常明显,细胞中纤维素、木聚糖、木质素等成分含量明显降低,说明 *SND1* 和 *NST1* 共同参与调控纤维素次生壁的生长<sup>[78]</sup>。拟南芥 *VND6* (*vascular - related NAC Domain 6*) 和 *VND7* 分别在主根的后生木质部和原生木质部中表达,超量表达 *VND6*、*VND7* 均能导致根的后生木质部细胞或原生木质部细胞发育异常,而抑制 *VND6*、*VND7* 的表达则会抑制后生木质部或原生木质部的发育,同时 *VND7* 能恢复 *snd1nst1* 双突变体抑制次级纤维壁加厚的表型,说明它们在调控拟南芥根原生木质部导管的分化中起着关键作用<sup>[79]</sup>。进一步研究表明,*SND1* 及其同源蛋白 *NST1*、*NST2*、*VND6* 和 *VND7* 通过调控下游基因 MYB 类蛋白因子 (如 MYB46、MYB58、MYB63 等) 的表达,最终激活次生壁的纤维素、木聚糖和木质素合成的相关基因 (如 *LAC4* 等),促进不同类型细胞次生壁的生物合成<sup>[80-83]</sup>。此外,一些 *SND1* 的同源基因 (如 *PtVNSs/PtrWNDs* 等) 能够恢复 *NST1* 和 *NST3* 双突变引起的维管束间纤维细胞次生壁的缺陷,它们的超量表达会引起杨树叶片和拟南芥幼苗的次生壁增厚<sup>[84-85]</sup>。水稻 *OsSWNs* 和玉米 *ZmSWNs* 也能互补拟南芥 *snd1nst1* 双突变体在次生细胞壁加厚方面缺陷的表型<sup>[86]</sup>。这些结果表明,在植物界中与 *SND1* 同源的 NAC 转录因子调控次生壁的生物合成机制可能是普遍存在的。

NAC 转录因子对植物次生壁生长有着双向作

用,既可能促进其生长,又可能抑制其生长。拟南芥 *ANAC012* 在开花茎和根的形成层区特异表达,超量表达 *ANAC012* 会显著抑制木纤维中次生壁的形成,但轻微地增加了木质部导管的细胞壁厚度<sup>[87]</sup>。拟南芥 *XND1* (*xylem NAC domain 1*) 在木质部中高度表达,超量表达 *XND1* 的转基因植株下胚轴原生木质部区域薄壁细胞的次生壁生长会受到明显的抑制,显示出极端矮化的表型<sup>[88]</sup>。

## 2.4 调控植物衰老

有研究表明,一些 NAC 转录因子能够间接或直接地加速或延缓植物衰老过程。*NAM-B1* 是野生二粒小麦的一个 NAC 转录因子,能正调控衰老,促进营养成分从营养器官向籽粒转移<sup>[89]</sup>。*AtNAP* (*NAC-like, activated by APETALA 3/PISTILLATA*) 是一个典型的叶片衰老相关基因,超量表达 *AtNAP* 的转基因植株明显早衰,*atnap* 突变体则表现出延缓叶片衰老的表型<sup>[90]</sup>。进一步研究发现,*AtNAP* 可以被脱落酸 (abscisic acid, 简称 ABA) 所诱导,可以和 *SAG113* (*SENESCENCE-ASSOCIATED GENE113*) 的启动子结合,形成一个 ABA-*AtNAP*-*SAG113* 蛋白调控链来控制叶片衰老时的气孔运动和失水速率,进而调控叶片衰老进程<sup>[91]</sup>。水稻中 *AtNAP* 的同源基因 *OsNAP* 可以互补 *atnap* 的表型,在调控水稻衰老发育过程中也发挥着重要作用<sup>[92-93]</sup>。此外,在金丝慈竹 (*Bambusa emeiensis* ‘*Viridiflavus*’) 中的同源基因 *BeNAC1* 也能互补 *atnap* 的表型,在拟南芥中超量表达 *BeNAC1* 也会产生不同的早衰表型<sup>[94]</sup>。超量表达甜瓜 *CmNAC60* 基因的拟南芥转基因植株叶片衰老也明显加速<sup>[95]</sup>。另一个同源基因 *GhNAP* 也能通过调节 ABA 介导的叶片衰老途径来调控棉花的产量和纤维质量<sup>[96]</sup>。拟南芥 *ANAC092/AtNAC2/ORE1*<sup>[97-98]</sup>、*ANAC032*<sup>[99]</sup> 等既能正调控依赖年龄的叶片衰老,也在盐胁迫诱导的叶片衰老过程中起着重要的作用。一些 NAC 转录因子可以直接结合在叶绿素降解途径相关基因的启动子上,通过调节叶绿素的代谢来调控叶片衰老进程,如 *OsNAP*<sup>[92]</sup>、*ANAC016*<sup>[100]</sup>、*BrNAC055*<sup>[101]</sup>、*SlNAP2*<sup>[102]</sup> 等。大多数调控叶片衰老的 NAC 转录因子都是以正调控的方式来调控叶片衰老,但也有少量的 NAC 转录因子是以负调控的方式进行调控的,如 *ONAC106*<sup>[103]</sup>、*DRLI*<sup>[104]</sup> 等。

## 2.5 参与激素调控

很多 NAC 转录因子的表达量受到 ABA 的诱

导,参与 ABA 的生物合成,或者介导 ABA 的信号转导途径。如拟南芥 *ATAF1* 可以直接调节 ABA 合成基因 *NCED3* 的表达,来调控 ABA 的生物合成<sup>[105]</sup>。拟南芥 *VNI2* (*VND-INTERACTING2*) 是一个 NAC 转录因子,其表达量受 ABA 诱导,可以结合 *RD* (*RESPONSIVE TO DEHYDRATION*) 和 *COR* (*COLD-REGULATED*) 基因的启动子,通过调控 *RD* 和 *COR* 基因的表达量来介导盐胁迫和叶片衰老途径<sup>[106]</sup>。在拟南芥中超量表达 *ANAC072/RD26* 能提高 ABA 诱导相关基因和胁迫诱导相关基因的表达量,对 ABA 的敏感性增强,且增强了采后果实的抗逆性,而在 *ANAC072/RD26* 受到抑制的植株中这些基因的表达量同样受到抑制,对 ABA 不敏感,表明 *ANAC072/RD26* 在胁迫应答和 ABA 信号转导途径中起着重要作用<sup>[107]</sup>。水稻 *SNAC2* (*stress-responsive NAC 2*) 基因也受到 ABA 的诱导表达,它的超量表达植株表现出耐冷和抗盐的表型,并对 ABA 敏感<sup>[108]</sup>。此外,*OsNAP* 也可以通过介导 ABA 的信号转导途径来增强水稻的抗逆性,在 *OsNAP* 的超量表达转基因植株中,很多胁迫相关基因和胁迫相关转录因子的表达量明显上升<sup>[109]</sup>。由此可见,介导 ABA 的信号转导途径的 NAC 转录因子多数与逆境信号传导途径有关。

NAC 转录因子是茉莉酸 (jasmonic acid, 简称 JA) 信号的调控因子。超量表达 *ANAC072/RD26* 的转基因植株也增强了对茉莉酸甲酯 (methyl jasmonate, 简称 MeJA) 的敏感性,因此 *ANAC072/RD26* 可能同时介导 ABA 和 MeJA 的信号转导途径<sup>[107]</sup>。拟南芥 *ATAF1* 是 ABA 信号通路的一个负调控因子,但也能诱导 JA 途径相关防御信号基因的表达<sup>[110]</sup>。*OsNAP* 也可能通过 MeJA 信号传导途径正调控水稻叶片衰老途径<sup>[93]</sup>。NAC 转录因子 *RIM1* 是水稻矮缩病毒繁殖的宿主因子,*rim1* 突变体植株表现出根生长受抑制,编码 JA 生物合成相关基因的表达量明显上升,而且在 JA 处理下突变体植株和野生型植株一致,没有内源 JA 的积累,说明 *RIM1* 是 JA 信号的负调控因子<sup>[111]</sup>。

NAC 也可以参与生长素、细胞分裂素、乙烯和赤霉素 (gibberellins, 简称 GA) 等的信号转导途径<sup>[65-66,112]</sup>。拟南芥 *NAC1* 基因受生长素诱导并且介导生长素信号以促进侧根生长发育<sup>[63]</sup>。拟南芥 *AtNAC2* 受高盐诱导,这种诱导在乙烯超量突变体 *etol-1* 中被增强,在乙烯不敏感突变体 *etr1-1*、

*ein2-1* 和生长素敏感突变体 *tir1-1* 中受到抑制,而在 ABA 敏感突变体 *abi2-1*、*abi3-1* 和 *abi4-1* 中没有显著变化,说明 *AtNAC2* 的盐胁迫响应参与了乙烯和生长素信号途径,与 ABA 信号途径无关<sup>[66]</sup>。在拟南芥中,*NTL8* (*NTM 1-like 8*) 的表达受高盐诱导和 GA 的抑制,*NTL8* 可以经过不依赖 ABA 的 GA 途径介导拟南芥种子萌发过程中盐的调节<sup>[113]</sup>。

## 2.6 参与胁迫反应

植物在生长发育过程中极易受干旱、低温、高温、高盐等非生物胁迫和虫害、病原菌等生物胁迫的影响,植物细胞会产生对这些外界胁迫的感知,并通过多种复杂的信号传导途径将其传递给控制胁迫应答的转录因子,从而激活植物抗逆反应,降低逆境对植物造成的损害。*NAC* 转录因子在这些过程中扮演着重要的角色。

很多 *NAC* 基因的表达量直接受到非生物逆境的调控,如大豆中有超过 1/3 (58/152) 的 *NAC* 基因是潜在的胁迫响应基因<sup>[12]</sup>。在非生物胁迫中,绝大多数的报道集中在耐冷、耐旱和抗盐等方面。在水稻中超量表达内源基因 *SNAC1*<sup>[114]</sup>、*OsNAC6*<sup>[115]</sup>、*SNAC2*<sup>[108]</sup>、*ONAC045*<sup>[116]</sup>、*OsNAP*<sup>[109]</sup>、*ONAC106*<sup>[103]</sup>、*ONAC022*<sup>[117]</sup>、*OsNAC2*<sup>[118]</sup> 等,或外源基因 *ATAF1*<sup>[119]</sup>、*EcNAC67*<sup>[120]</sup> 等,均能一定程度地表现出耐冷、耐旱和抗盐的单一表型或者综合表型。在拟南芥中异源超表达不同物种来源的 *NAC* 成员也有类似的结果<sup>[71,121-127]</sup>。绝大部分 *NAC* 是正调控胁迫反应,但也有少部分 *NAC* 能负调控胁迫反应。如 *OsNAC95* 在水稻抗旱和耐冷胁迫反应中表现出相反的角色,它可以负调控抗旱胁迫,正调控耐冷胁迫<sup>[128]</sup>。拟南芥 *ANAC069* 能通过降低活性氧 (reactive oxygen species, 简称 ROS) 的清除能力和脯氨酸含量,来负调控高盐和渗透胁迫<sup>[129]</sup>。苹果 *MdNAC029*/*MdNAP* 以 C-repeat binding factor (CBF) 依赖的方式负调控植物的抗冷能力<sup>[130]</sup>。玉米 *ZmNAC071* 也通过负调控 ROS 清除能力来负调控 ABA 反应和渗透胁迫<sup>[131]</sup>。*NAC* 转录因子调控非生物胁迫反应绝大多数是通过 ABA 依赖的途径来进行的,也可以依赖其他激素的信号转导途径,如 JA<sup>[93,132-133]</sup>、GA/油菜素内酯 (brassinolide, 简称 BR)<sup>[134]</sup> 等。

一些报道表明,*NAC* 转录因子也参与生物胁迫。如水稻 *OsNAC6* 对抵抗稻瘟病有正调控作用<sup>[115]</sup>。*OsNAC19* 可能在 MeJA 信号途径中参与水

稻对稻瘟病菌的响应<sup>[135]</sup>。拟南芥中 *ATAF1*<sup>[136]</sup> 和 *ATAF2*<sup>[137]</sup> 分别对抗灰霉病和枯萎病有负调控作用。在大麦和拟南芥中超量表达 *ATAF1* 的同源基因 *HvNAC6* 可以增强耐渗透细胞对白粉病菌的抗性<sup>[138-139]</sup>,而超量表达 *ATAF1* 在棉花中的同源基因 *GhATAF1* 却增强了对灰葡萄孢菌的敏感性<sup>[132]</sup>。

## 3 展望

*NAC* 家族转录因子是植物特有的一类转录因子,广泛参与植物生长发育及胁迫反应。到目前为止,*NAC* 转录因子已经在几十种植物中被发现,但不同物种来源的 *NAC* 成员可能具有不同的生物学功能,如调控淀粉合成<sup>[140-141]</sup>、种子活力<sup>[142]</sup>、果实发育<sup>[143-144]</sup>、大豆抗毒素合成<sup>[145]</sup>、开花<sup>[146-147]</sup>、锌的转运<sup>[148]</sup> 等。因此,广泛研究 *NAC* 成员的功能不仅能揭示 *NAC* 蛋白的调控网络,而且通过控制 *NAC* 基因或 *NAC* 蛋白的表达,提高作物的抗逆性,进而提升产量。

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