植物生理学报 *Plant Physiology Journal* 2024, 60 (2): 271–283
doi: 10.13592/j.cnki.ppj.300193

综　述 Reviews

NAC转录因子调控植物生长发育和胁迫应答的研究进展

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摘要: 由于植物具有固着生长的特性, 其在生长发育过程中往往面临多种来自环境的不利影响。因此, 植物必须通过不同的调节机制以维持生长发育和应对胁迫的危害。NAC(NAM/ATAF/CUC)是植物中重要的转录因子家族之一, 由高度保守的N端和相对多变的C端组成, 可以影响植物花器官发育、开花时间、叶片衰老、果实成熟、细胞次生壁形成和根系发育等过程, 并参与植物对多种生物胁迫和非生物胁迫的响应过程。本文概述了植物中NAC家族成员在生长发育和胁迫应答过程中发挥的功能, 为深入解析NAC转录因子的分子调控机制及其应用提供理论依据。

关键词: NAC转录因子; 生长发育; 胁迫应答; 分子调控

Research advances on NAC transcription factors regulating plant development and stress responses

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Abstract: Due to the sessile characteristics, plants often face various adverse environmental factors during growth and development. Thus, they have evolved different regulatory mechanisms to maintain growth, development, and to overcome the effects of stresses. NAC (NAM/ATAF/CUC) is one of the important transcription factor families in plants, consisting of a highly conserved N-terminus and a relatively variable C-terminus. NACs regulate the flower organ development, flowering time, leaf senescence, fruit ripening, secondary cell wall formation, root development, and are also involved in plant responses to various biotic and abiotic stresses. This review summarizes the functions of NAC family members in growth, development and stress responses of plants, to provide a theoretical basis for further dissection of the molecular mechanisms and applications of NAC transcription factors.

Key words: NAC transcription factors; growth and development; stress response; molecular regulation

植物在生长发育的各个阶段均会受到各种胁迫的影响, 且花期和种子成熟阶段遭受胁迫会严重影响作物产量。转录因子在调控植物生长发育和胁迫应答方面具有关键作用, 不同转录因子家族在植物抵御生物和非生物胁迫过程中均具有重

收稿　2023-04-18　　**修定**　2023-10-12
资助　国家自然科学基金(32272055和31972963)和江苏省“青蓝工程”项目。

要作用(Ng等2018)。NAC (NAM/ATAF/CUC)家族的命名源于矮牵牛(*Petunia hybrida*)的NAM (no apical meristem)、拟南芥的ATAF1/2 (Arabidopsis transcription activator factor 1/2)和CUC2 (cup-shaped cotyledon 2), 可在植物不同发育阶段和不同组织中表达(Ooka等2003)。目前已在拟南芥(*Arabidopsis thaliana*; Nuruzzaman等2010)、水稻(*Oryza sativa*; Puranik等2012)、火龙果(*Hylocereus undatus*; Hu等2022)和猕猴桃(*Actinidia chinensis*; Li等2021)等物种中鉴定出大量NAC成员。本文针对植物NAC转录因子的结构特征, 其参与花器官发育、开花时间、叶片衰老、果实成熟、分生组织维持、侧生器官形成、细胞次生壁形成、根系发育和生物胁迫、非生物胁迫应答中发挥的功能进行了综述。

1 NAC转录因子家族的结构特征

NAC家族具有保守的N端NAC结构域和相对多变的C端TAR (transcriptional activation region)结构域(图1)。前者由5个相对保守的亚结构域组成(A、B、C、D和E), 根据其序列相似性可将该家族分为两类, I类包括14个亚类(TERN、ONAC022、SENU5、NAP、AtNAC3、ATAF、OsNAC3、NAC2、ANAC011、TIP、OsNAC8、OsNAC7、NAC1、NAM), II类包括4个亚类(ANAC001、ONAC003、ONAC001、ANAC063)。TAR结构域具有转录激活功能, 同一亚族的TAR结构域具有保守基序(Ooka等2003)。同一亚族的NAC成员具有保守功能, 如拟南芥NAM亚家族成员CUC1/2/3均可促进茎尖分生组织的形成(Hibara等2006), 拟南芥NAC7亚家族的SND1/ANAC12和NST1/ANAC43均可促进细胞次生壁的形成(Ko等2007; Liu等2021)。此外, 同一亚族成员也存在功能分化, 如拟南芥ATAF成员ATAF1参与响应干旱、高盐和热胁迫(Alshareef等2022), 而ATAF2参与调控拟南芥的叶片衰老(Nagahage等2020)。

2 NAC转录因子调控植物生长发育

2.1 NAC调控花器官发育和开花时间

NAC家族成员在调控花药、心皮、萼片、雄蕊发育以及开花时间等方面均发挥重要作用(图2)。拟南芥*cuc1*、*cuc2*、*cuc1 cuc2*突变体的心皮分化异常、萼片和雄蕊愈合、胚珠发育异常等现象, 过表达*CUC1*或*CUC2*可促进拟南芥心皮边缘分生组织形成(Kamiuchi等2014)。番茄(*Solanum lycopersicum*)中miR164的靶基因*SlNAM2*在花瓣和花萼的边界表达, miR164可促进萼片和花瓣融合, 而过表达靶位点突变的*mSlNAM2*可恢复该融合表型(Hendelman等2013)。郁金香(*Tulipa gesneriana*)的TgNAP (NAC-like, activated by apetala3/pistillata)蛋白可激活水杨酸合成基因*TgICS1* (*isochorismate synthase 1*)和*TgPAL1* (*phenylalanine ammonialyase 1*)转录, 抑制过氧化物酶编码基因*POD12* (*peroxidase 12*)和*POD17*表达, 从而降低植株对活性氧(reactive oxygen species, ROS)的清除能力。通过病毒诱导的基因沉默(virus-induced gene silencing, VIGS)技术抑制*TgNAP*可延缓外源水杨酸和H_2O_2诱导的郁金香花瓣衰老; 而过表达*TgNAP*可促进拟南芥的花瓣衰老(Meng等2022a)。在拟南芥中异源表达甘蔗(*Saccharum officinarum*) *ScNAC23*可提高植株对赤霉素的敏感性, 促进开花基因*AtLFY* (*leafy*)和叶片衰老基因*AtSAG12* (*senescnece-associated gene 12*)等上调表达, 从而加速拟南芥抽苔、开花和叶片衰老(Fang等2021)。过表达小麦(*Triticum turgidum*)的*TtNTL3A* (*NAC with transmembrane motif 1-like 3A*)可促进拟南芥早花, 提高植株对盐和干旱胁迫的耐性(Saidi等2022)。Pei等(2013)鉴定了

图1 NAC转录因子的结构特征

Fig. 1 Structural characteristics of NAC transcription factors

图2 NAC转录因子在植物生长发育中的调控作用

Fig. 2 Regulatory role of NAC transcription factors during plant growth and development

实箭头和虚箭头分别代表促进和抑制生长发育; At: 拟南芥; Fa: 草莓; Fv: 野草莓; Gh: 棉花; Gm: 大豆; Vvi: 葡萄; Os: 水稻; Rh: 玫瑰; Sc: 甘蔗; Sl: 番茄; Tt: 小麦。

调控玫瑰(*Rosa hybrida*)细胞生长的乙烯响应基因, 其中*RhNAC- 100*可负调控拟南芥花瓣细胞的生长, 导致花瓣减小; 而烟草脆裂病毒(tobacco rattle virus, TRV)诱导*RhNAC100*沉默可导致玫瑰花瓣变大。RhNAC100通过与纤维素合成酶编码基因*RhCesA2* (*cellulose synthase 2*)、水通道蛋白编码基因*RhPIP1;1* (*plasma membrane intrinsic protein 1;1*) 和*RhPIP2;1*的启动子结合, 从而调控花瓣下表皮细胞的生长。

2.2 NAC参与调控植物叶片衰老过程

叶片衰老是植物受多种外界环境和内源信号影响产生的现象。NAC家族成员在植物叶片衰老过程中发挥着重要的调控作用(图2)。拟南芥*AtNAP*的突变可延迟叶片衰老, 在突变体中回补*AtNAP*或水稻同源基因均可恢复其表型(Guo和Gan 2006)。拟南芥*ANAC017*/*082*/*090*突变会加速叶片衰老, 且水杨酸响应基因*PR1* (*pathogenesis-related protein 1*)、*EDS5* (*enhanced disease susceptibility 5*)和ROS胁迫响应基因*DUF239* (*domain of unknown function 239*)等均上调表达(Kim等2018)。拟南芥*ANAC017*可能通过调控靶基因*ANAC016*表达, 加速自噬等衰老相关过程, 促进叶片衰老和细胞死亡(Broda等2021)。过表达拟南芥*ATAF2*会诱导叶片衰老调节因子*ORE1* (*oresara 1*)等表达, 加速叶片衰老; 而*ataf2*突变体可延迟黑暗诱导的叶片衰老过程, 且叶片衰老相关基因在突变体中下调表达(Nagahage等2020)。过表达拟南芥*ANAC087*可导致莲座叶和分枝数增加, 加速叶片衰老(Vargas-Hernandez等2022)。

烟草(*Nicotiana tabacum*)的*NtNAC080*与*AtNAP*同源, 过表达该基因会导致拟南芥叶片提前衰老(Li等2018)。白菜型油菜(*Brassica rapa*)的BrNAC029可通过与叶绿素分解代谢基因*BrPAO* (*pheophorbide a oxygenase*)和*BrSGR2* (*staygreen 2*)、细胞分裂素氧化酶编码基因*BrCKX1* (*cytokinin oxidase 1*)和衰老基因*BrSAG113*的启动子结合, 促进叶绿素和内源细胞分裂素降解; 过表达*BrNAC029*会加速烟草和拟南芥叶片衰老(Li等2023)。在豇豆(*Vigna unguiculata*)中, 过表达*VuNAC1*/*2*可使叶面积增大, 茎加粗, 根瘤增大, 根系变密, 开花时间

提前, 荚果产量增加, 粒重增大, 植株提前衰老; 而抑制*VuNAC1/2*表达会导致植株生长和开花延迟(Srivastava等2023)。黑麦草(*Lolium perenne*)的LpNAL可与叶绿素分解代谢基因*LpSGR*和*LpNYC1* (*nonyellowing coloring 1*)的启动子结合, 抑制叶片衰老(Yu等2022)。白毛杨(*Populus tomentosa*)中NAC成员PtRD26 (responsive to desiccation 26)的可变剪接变体PtRD26IR通过抑制其他衰老相关的*NAC*基因(如*PtNAC039/055/076/086/109*)的表达, 从而调控叶片衰老过程(Wang等2021a)。异源表达葡萄(*Vitis vinifera*)的*DRL1* (*responsive to desiccation like 1*)可抑制脱落酸生物合成和调控相关基因(*NCED1/5*、*ZEP1*、*ABA2/4*等)的表达, 降低植株对脱落酸的敏感性, 延缓烟草的叶片衰老(Zhu等2019)。柳枝稷(*Panicum virgatum*)的PvNAP1/2可靶向激活叶绿素分解代谢基因, 促进叶绿素降解和叶片衰老; CCCH类锌指蛋白PvSSG (strong stay-green)可与PvNAP1/2互作, 抑制其对下游靶基因的激活作用, 从而抑制叶片衰老(Xie等2022)。番茄的SlNAP2通过与*NOR* (*non-ripening*)的启动子结合激活其表达, *NOR*可以正调控叶片衰老相关基因的表达, 促进拟南芥和番茄的叶片衰老(Ma等2019)。

2.3 NAC参与调控植物果实成熟

果实成熟过程涉及各种外观和风味(如颜色、质地、香味)的变化, 以及呼吸作用、细胞壁合成与降解、叶绿素降解、类胡萝卜素生物合成、不同营养物质间转化等生理生化过程。NAC家族可以参与调控果实结构、颜色、风味、种子发育、果实衰老等过程, 从而影响果实的成熟(图2)。如番茄*SlNOR*、猕猴桃*AdNAC6/7*、和枇杷(*Eriobotrya japonica*) *EjNAC1*等可以影响果实的结构; 苹果(*Malus domestica*) *MdNAC9/42/52*、番木瓜(*Carica papaya*) *CpNAC1/2*、桃(*Prunus persica*) *PpNAC1/19*、草莓(*Fragaria* × *ananassa*) *FaNAC035*和金桔(*Fortunella crassifolia*) *FcrNAC22*等可影响果实颜色; 香蕉(*Musa acuminata*) *MaNAC67-like*、西瓜(*Citrullus lanatus*) *ClNAC68*、柑橘(*Citrus reticulata*) *CitNAC62*、柿子(*Diospyros kaki*) *DkNAC13/16*和草莓*FaNAC035*等可影响果实风味; 番茄*SlNOR-like1*、西瓜*ClNAC68*、拟南芥*AtNAM*和*AtNAC2*、水稻*ONAC127/ 129*、葡萄*VvNAC26*等可影响种子发育; 荔枝(*Litchi chinensis*) *LcNAC1/13*和拟南芥*AtNAP*、*AtNAM*、*AtNAC2*可以影响果实衰老(Liu等2022)。草莓的*FaNAC35/FaRIF* (*ripening inducing factor*)在果实成熟过程中高表达, *FaRIF*干扰植株的果实变软、色素和糖分积累减慢, 抑制了果实成熟(Martin-Pizarro等2021)。葡萄的VviNAC60通过上调*VviSGR1*诱导叶绿素降解, VviNAC60-VviNAC03复合体通过上调*VviMYBA1*诱导花青素积累。在葡萄中过表达*VviNAC60*导致植株生长迟缓, 叶片提前衰老; 该基因可以回补番茄*nor*突变体果实成熟延迟的表型(D’inca等2023)。此外, 植物果实成熟受乙烯、赤霉素、脱落酸等激素调控。番茄*SlNAC1/6*和*SlNAM1*、苹果*MdNAC1/2*、拟南芥*AtJUB1* (*jungbrunnen 1*)、番木瓜*CpNAC3*和*CpNACS4*、香蕉*MaNAC1/2/42*、桃*PpNAP1/4/6*、猕猴桃*AdNAC2/3/6/7*、甜瓜(*Cucumis melo*) *CmNAC-NOR*等基因均可通过乙烯途径影响果实成熟。拟南芥*AtJUB1*等基因还可通过赤霉素途径影响果实成熟。桃*PpNAP1/4/6*、草莓*FaNAC35*、柑橘*CrNAC036*等基因可通过脱落酸途径影响果实成熟(Liu等2022)。

2.4 NAC参与植物分生组织的维持

叶片由茎尖分生组织(shoot apical meristem, SAM)两侧的叶原基发育而来。拟南芥*CUC1*可以维持细胞的未分化状态, 促进SAM的形成。拟南芥*AtCUC2/3*突变会不同程度的抑制腋分生组织形成和叶、茎等器官的边界分化(Hibara等2006)。过表达*AtCUC3*也可增加叶片锯齿, 突变体*cuc3*的叶表型与之相反; AtCUC2/3是叶齿形成所必需的调控因子, 二者分别在早期叶齿形成、晚期叶齿形成和维持中发挥作用(Hasson等2011)。水稻*OsCUC1/3*单突变体的分生组织和器官边界异常, 雄蕊减少, 器官融合(如叶片、花丝); 且双突变体的发育缺陷更严重。OsCUC1通过与叶片卷曲蛋白CLD1 (curled leaf and dwarf 1)互作调控叶片的形态(Wang等2021b)。水稻*osnam*突变体的叶片融合, 穗小且分枝减少, 花器官形态异常; 且*osnam oscuc3*双突变体的叶片愈合更严重, *OsNAM*和*OsCUC3*在调控器官边界分化中存在功能冗余(Chang等2021)。棉花(*Gossypium hirsutum*)的GhCUC2与GhBRC1 (branched 1)相互作用, 通过脱落酸信号通路负调控植物分枝。过表达miR164靶位点突变的*GhCUC2m*导致棉花分枝变短, 异源表达*GhCUC2m*导致拟南芥分枝数减少(Zhan等2021)。拟南芥CUC2/3通过与*DA1*启动子结合、激活其表达, 促进其底物UBP15 (ubiquitin-specific protease 15)降解, 从而正调控腋生分生组织的发生、影响株型(Li等2020)。综上, NAC成员在维持植物分生组织活性、叶原基等发育过程中具有重要的调控作用(图2)。

2.5 NAC调控植物细胞次生壁形成

植物细胞次生壁在花药和角果开裂、维持机械支撑、促进水分运输、抵御病原菌入侵等方面发挥重要作用。NAC成员也参与调控植物次生壁的形成过程(图2)。拟南芥*SND1* (*secondary wall-associated NAC domain 1*)在茎的束间纤维和木纤维中特异表达, 抑制*SND1*表达会延缓纤维的次生壁增厚。过表达*SND1*可使纤维素合成*CesA7*、木聚糖合成*FRA8* (*fragile fiber 8*)和木质素合成*CCoAOMT* (*caffeoyl CoA O-methyltransferase*)等基因表达上调, 导致叶表皮和叶肉细胞、花和茎细胞的次生壁异常增厚(Zhong等2006)。拟南芥*ANAC012*可抑制木纤维的次生壁发育, 增加木质部导管的细胞壁厚度, 降低花序轴和根中细胞壁的纤维素含量(Ko等2007)。拟南芥*nst1* (*NAC secondary wall thickening promoting factor 1*)突变会抑制脱落酸合成, 降低细胞次生壁的厚度和木质化程度(Liu等2021)。过表达野草莓(*F. vesca*)的*FvNST1b*会导致拟南芥极端矮化, 花药、雄蕊、叶片的细胞次生壁增厚, 且次生壁合成相关基因均上调表达(Dang等2022)。在烟草叶片中分别过表达棉花*SND1*和*NST1/2*亚族的*GhNAC140*/*28*/*70*/*120*会导致次生壁增厚(Fang等2020)。

2.6 NAC参与调控植物根系发育

根系是植物吸收水分和养分的重要器官。拟南芥ANAC087/046在根冠中表达, 可参与调控细胞程序性死亡。ANAC087通过促进核酸酶编码基因*BFN1* (*bifunctional nucelase 1*)表达, 调节侧根根冠的染色质降解(Huysmans等2018)。水稻*OsNAC2*主要在主根根尖、冠根和侧根原基中表达; *OsNAC2*干扰植株的主根长度和冠根数量增加, 生长素合成相关基因*OsIPT3* (*isopentenyl transferase 3*)、*OsLOGL3*等表达量下调, 而*OsCKX4*和*OsCKX5*的表达上调(Mao等2020)。拟南芥NAC056主要在根系和下胚轴中表达, 可靶向结合并诱导硝酸盐同化基因*NIA1* (*nitrate reductase 1*)表达, 提高根系对硝酸盐胁迫的耐受能力, 促进侧根的起始(Xu等2022)。拟南芥*NAC075*突变可降低主根对低水平NO_3^-的敏感性; 低NO_3^-条件可激活CBL互作蛋白激酶1 (CBL-interacting protein kinase 1, CIPK1), 进而使NAC075磷酸化, 抑制NAC075从根中柱向内皮层转移, 进而调控下游靶基因*WRKY53*的表达, 抑制根系的生长(Xiao等2022)。水稻*OsNAC016*受磷酸饥饿响应蛋白OsPHR1/4 (phosphate starvation response protein 1/4)调控; 在缺磷条件下, *OsNAC016*过表达株系的磷含量低于野生型, 根生长受到抑制; 而*osnac016*突变体对低磷胁迫的敏感性降低, 表明*OsNAC016*通过负调节水稻磷饥饿反应抑制根系发育(Sun等2023)。大豆(*Glycine max*)的*GmNAC109*可促进拟南芥侧根的形成, 提高植株对干旱和盐胁迫的耐受性(Yang等2019; 图2)。

3 NAC转录因子调控植物对非生物胁迫的响应

3.1 NAC参与调控干旱胁迫应答

植物为了适应土壤中的水分梯度, 会通过改变根系生长和结构、关闭气孔等方式来提高生存能力。现有研究报道NAC可参与调控植物对干旱胁迫的应答过程, 影响植物的耐旱性(图3)。拟南芥NTL6主要在质膜中表达, 非生物胁迫和外源脱落酸处理可诱导NTL6蛋白降解。过表达*NTL6*可提高拟南芥的耐旱性, 而*NTL6*抑制表达材料反之(Kim等2012)。拟南芥ANAC096通过与bZIP类转录因子ABF2 (ABRE binding factor 2)和ABF4相互作用, 共同激活*RD29A*转录; *ANAC096*突变可增强*abf2 abf4*双突变体对脱落酸的耐受性和对渗透胁迫的敏感性(Xu等2013)。甘薯(*Ipomoea batatas*) IbNAC3可与拟南芥ANAC011/072/083/100和NAP互作, 干扰拟南芥NAC成员间的互作, 提高植株对盐和渗透胁迫的耐性(Meng等2022b)。过表达*ONAC066*和*SNAC1*可降低水稻的失水速率, 提高

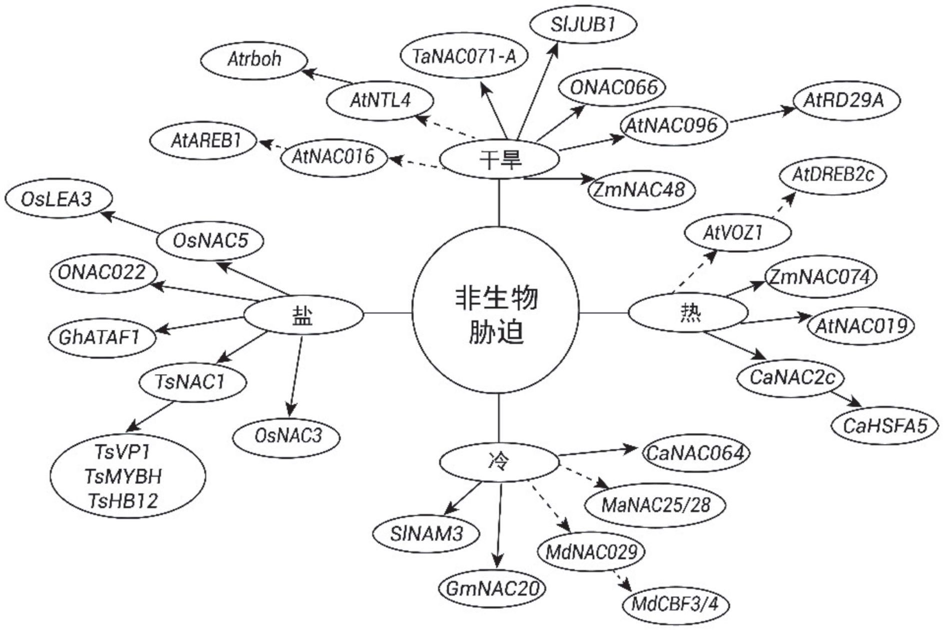

图3 NAC转录因子在植物响应非生物胁迫中的作用

Fig. 3 Role of NAC transcription factors response to abiotic stresses in plant

实箭头和虚箭头分别代表增强和降低植物对非生物胁迫的耐受性; At: 拟南芥; Ca: 辣椒; Gh: 棉花; Gm: 大豆; Ma: 香蕉; Md: 苹果; Os: 水稻; Sl: 番茄; Ts: 小盐芥; Ta: 小麦; Zm: 玉米。

植株的耐旱性及对脱落酸的敏感性(Hu等2006; Yuan等2019)。番茄*SlNAC6*过表达植株生长缓慢, 对聚乙二醇胁迫的耐性增强, 失水速率和氧化损伤程度降低, 且内源脱落酸含量增加, 脱落酸信号转导相关基因的转录水平增加(Jian等2021)。拟南芥AtJUB1可与番茄的*SlDREB1* (*dehydration-responsive element-binding factor 1*)、*SlDREB2*和*SlDELLA*启动子结合, 正调控番茄的耐旱性; 抑制番茄*SlJUB1*基因表达可降低植株的耐旱性, 而过表达反之(Thirumalaikumar等2018)。异源表达黑小麦(*Triticosecale wittmack*)的*TwNAC01*可促进拟南芥根长, 降低叶片失水速率; 降低*TwNAC01*表达可抑制黑小麦的主根长度、延缓根系发育; 且干旱胁迫条件下, *TwNAC01*抑制表达植株叶片的MDA和H_2O_2含量高于野生型, 而相对含水量、气孔导度等均低于野生型(Wang等2022)。在小麦中, 与耐旱性连锁的*TaNAC071-A*启动子包含108 bp的插入突变, 该插入位点包含2个MYB (v-myb avian myeloblastosis viral oncogene homolog)顺式调控元件, 可直接与TaMYBL1结合, 从而调控*TaNAC071-A*的表达水平和植株的耐旱性。过表达*TaNAC071-A*可提高小麦的水分利用效率和胁迫响应基因的表达水平, 显著提高植株的耐旱性(Mao等2022)。小麦*TaRNAC1* (*root-expressed NAC transcription factor 1*)可以增加根长和生物量, 提高植株的耐旱性和产量(Chen等2018)。玉米(*Zea mays*)的*ZmNAC48*可提高拟南芥的耐旱性。该基因的天然反义转录本*cis*-NATZmNAC48对*ZmNAC48*具有负调控作用, 过表达该反义转录本会影响玉米气孔关闭, 降低玉米的耐旱性(Mao等2021)。

此外, 还存在一些正调控植物对干旱敏感性的NAC成员。拟南芥*ATAF1*受干旱胁迫和脱落酸诱导表达, *ataf1*突变体的耐旱性增强, 且干旱胁迫响应的标记基因*COR47/RD17*、*ERD10* (*early responsive to dehydration 10*)、*KIN1*等上调表达(Lu等2007)。拟南芥NTL4通过结合ROS生物合成酶编码基因*Atrboh* (*burst oxidase homolog*)启动子, 促进ROS的产生, 负调控拟南芥的耐旱性(Lee等

2012)。在干旱胁迫下, 拟南芥NAC016直接与脱落酸响应元件结合蛋白*AREB1* (abscisic acid-responsive element binding protein 1)的启动子结合, 抑制其表达, 降低植株的耐旱性(Sakuraba等2015)。水稻*ONAC095*过表达材料对干旱胁迫的耐受性与野生型无明显差异; 而该基因的抑制表达材料在干旱条件下的失水速率降低, 脯氨酸和可溶性糖含量增加, 干旱响应基因的表达量上调, 植株的耐旱性增强(Huang等2016)。

3.2 NAC参与调控盐胁迫应答

盐胁迫是影响植物生长发育的主要非生物胁迫之一, 植物可通过调节渗透耐受性、组织耐受性和离子排斥降低盐胁迫的影响。研究发现*NAC*基因可参与调控植物对盐胁迫的应答过程(图3)。在盐胁迫下, 拟南芥*anac040*突变体种子的萌发率高于野生型(Song等2022b)。水稻*OsNAC3*突变可引起幼苗中Na^+积累, 增强植株的盐敏感性, 降低其对脱落酸的敏感性(Zhang等2021a)。过表达*ONAC022*可缓解盐胁迫时水稻根和幼苗中Na^+积累, 提高植株耐盐性(Hong等2016)。过表达*OsNAC5*和*SNAC1*均可提高水稻的耐盐性; 且OsNAC5可与胚胎发育调控基因*OsLEA3* (*late embryogenesis abundant 3*)的启动子结合(Hu等2006; Takasaki等2010)。过表达*OsNAC6*可提高盐胁迫条件下水稻的存活率, 且植株的生长速度和产量与对照无明显差异(Nakashima等2007)。小盐芥(*Thellungiella salsuginea*)的TsNAC1可与离子运输正调控因子*TsVP1* (*vacuolar H^+-ppase 1*)、*MYBH* (*MYB hypocotyl elongation-related*)和*HB12* (*homeobox 12*)的启动子结合, 正调控其表达。在小盐芥和拟南芥中过表达*TsNAC1*可提高植株对干旱、冷和盐胁迫的耐受性, 延缓植株的生长(Liu等2018a)。棉花的*GhATAF1*可以提高脱落酸应答基因*GhABI4*、维持Na^+/K^+平衡的转运基因*GhHKT1*和其他胁迫响应基因的表达水平, 从而提高棉花的耐盐性(He等2016)。

3.3 NAC参与调控冷胁迫应答

冷胁迫包括低温(<15°C)和冻害(<0°C), 二者均会在一定程度上降低植物的生产力。*NAC*基因也可参与调控植物对冷胁迫的应答过程(图3)。异源表达大豆*GmNAC20*可提高水稻在冷胁迫下的相对含水量、叶绿素和脯氨酸含量, 提高抗氧化酶活性, 降低MDA含量和离子渗漏率, 从而提高植株的耐冷性(Yarra和Wei 2021)。在冷胁迫下, 番茄*SlNAM3*过表达植株的PSII原初光能转化效率较野生型高, 且相对离子渗漏率更低, 植株的萎蔫程度低于野生型; miR164a-SlNAM3模块可通过诱导乙烯产生, 提高番茄的耐冷性(Dong等2022)。异源过表达火龙果的*HuNAC20/25*可降低低温胁迫下拟南芥的离子渗漏率、MDA、H_2O_2和O_2^-含量, 且冷响应基因*AtRD29A*、*AtCOR15A* (*cold-regulated 15A*)等上调表达, 从而提高拟南芥对冷胁迫的耐受性(Hu等2022)。辣椒(*Capsicum annuum*)的CaNAC064可与低温诱导的单蛋白酶互作, 从而正调控辣椒的耐冷性(Hou等2020)。此外, 在水稻中过表达*OsSNAC2*, 在拟南芥中过表达葡萄的*VvNAC17*、小麦的*TaNAC2*、大豆的*GmNAC20*也可提高植株的耐冷性(Hao等2011; Hu等2008; Ju等2020; Mao等2012)。香蕉的*MaNAC25/28*通过正调控磷脂降解基因的表达, 促进磷脂酸产生, 从而负调控果实的耐寒性(Song等2022a)。苹果MdNAC029可以与*MdCBF3/4*的启动子结合抑制其表达, 过表达*MdNAC029*可降低苹果愈伤组织和拟南芥的耐寒性(An等2018)。

3.4 NAC参与调控热胁迫应答

随着全球气候变暖, 高温胁迫已成为影响植物生长发育的重要因素。*NAC*基因也可参与调控植物对热胁迫的应答过程(图3)。拟南芥*NTL4*可促进热胁迫下植株中H_2O_2积累, 加速热应激诱导的细胞死亡; 而*ntl4*突变体中H_2O_2水平显著降低(Lee等2014)。拟南芥的NAC019可与蛋白磷酸酶RCF2 (regulator of CBF gene expression 2)互作, 使NAC019去磷酸化; 与野生型相比, *nac019*突变体对热应激更敏感, 而*NAC019*过表达材料的耐热性增强(Guan等2014)。拟南芥NAC家族的VOZ1 (vascular plant one-zinc-finger 1)可抑制DREB2C的AP2 (apetala 2)结合域与DRE结合, 抑制*DREB2C*表达; 且*voz1 voz2*双突植株的耐热性增强(Song等2018)。拟南芥*ATAF1*受热刺激诱导表达, 热胁迫后*ataf1*突变体的存活率和鲜重均高于野生型(Alshareef等2022)。水稻*SNAC3*可降低热胁迫下H_2O_2和MDA含量、离

子渗漏率, 该基因可能通过调节ROS稳态提高水稻的抗逆性(Fang等2015)。水稻ONAC127和ONAC129主要在果皮中表达, 二者在稻米灌浆过程中可形成异源二聚体; 热胁迫可加剧*ONAC127*和*ONAC129*敲除和过表达植株灌浆不完全和籽粒萎缩的表型(Ren等2021)。玉米*ZmNAC074*编码一个膜结合转录因子, 可通过调节多种胁迫代谢产物(如ROS、MDA、可溶性蛋白)积累, 提高拟南芥的耐热性(Xi等2022)。在热胁迫下, 辣椒CaNAC2c可通过激活热休克因子*CaHSFA5* (*heat shock factor A5*)的转录、阻断H_2O_2积累, 提高植株对热胁迫的耐受性(Cai等2021)。

4 NAC转录因子在植物生物胁迫应答中的功能研究

植物通过激活ROS信号、植物激素信号、氧化还原状态改变等相关分子调控网络, 以防御病原体(细菌、真菌和病毒)入侵和缓解病原因子引起的危害。NAC可广泛参与不同植物对生物胁迫的免疫应答过程(图4)。拟南芥*NAC4*过表达植株在受到细菌侵染后, 会诱导细胞程序性死亡以阻止细菌入侵植物体(Lee等2017)。水稻*ONAC066*通过参与脱落酸信号途径, 促进可溶性糖和氨基酸的积累, 提高水稻对稻瘟病和白叶枯病的抗性(Liu等2018b)。过表达*ATAF2*/*ANAC081*会提高拟南芥对尖孢镰刀菌的敏感性, 显著抑制烟草花叶病毒的积累。烟草花叶病毒复制酶蛋白可以通过其解旋酶结构域与ATAF2互作, 促进在病毒感染时ATAF2降解, 从而促进病毒积累(Zhai等2020)。渐狭叶烟草(*N. attenuata*)的*NaNAC29*与拟南芥*NAP*基因高度同源, NaNAC29通过提高防御素蛋白编码基因*NaDLP1*(*defensin-like protein 1*)的表达水平, 促进叶片衰老, 从而参与植株对链格孢菌的防御反应(Ma等2021)。

研究发现水稻、小麦、大麦(*Hordeum vulgare*)、玉米、马铃薯(*Solanum tuberosum*)和番茄中均存在*NAC*基因通过ROS、水杨酸、脱落酸、乙烯和茉莉酸途径, 调控植株对不同病害的应答

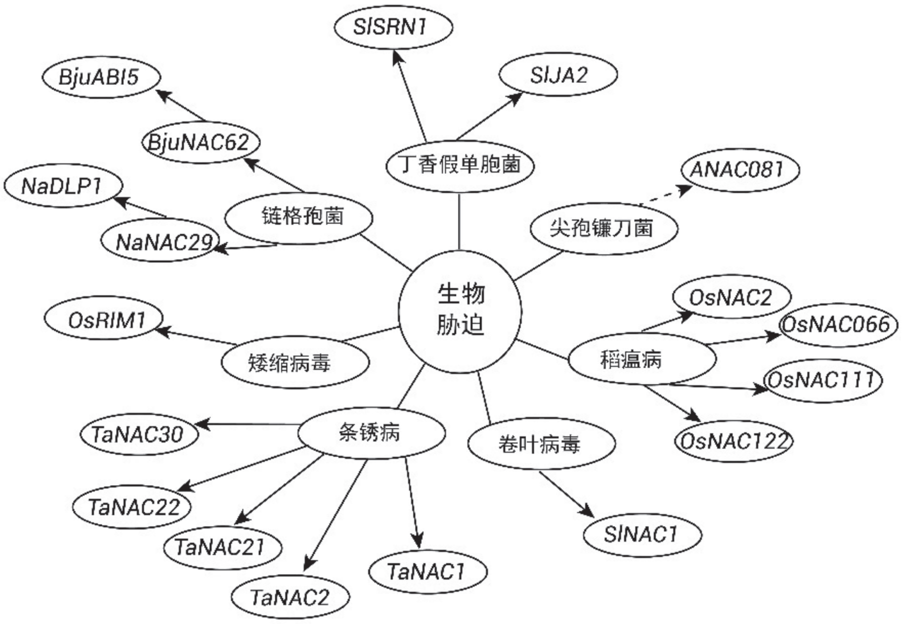

图4 NAC转录因子在植物响应生物胁迫中的作用

Fig. 4 Role of NAC transcription factors response to biotic stresses in plant

实箭头和虚箭头分别代表增强和降低植物对生物胁迫的耐受性; At: 拟南芥; Bju: 芥菜; Na: 渐狭叶烟草; Os: 水稻; Sl: 番茄; Ta: 小麦。

过程, 如水稻稻瘟病(*OsNAC2*/*122*/*111*等)、小麦白粉病(*TaNAC6s*)和赤霉病(*TaNAC6L-D*)、大麦白粉病(*HvNAC6*)、辣椒叶斑病(*HvSNAC1*)、玉米炭疽病(*ZmNAC41*/*15*/*111*等)、马铃薯青枯病(*StNACb4*和*StNAC43*)、番茄灰霉病(*SlNAC20*/*24*/*61*等) (Bian等2020)。水稻*RIM1* (*rice dwarf virus multiplication 1*)突变会增加植株对矮缩病毒的抗性(Yoshii等2009)。小麦*TaNAC1*/*2*/*21*/*22*/*30*等对条锈病具有负调控作用(Bian等2020)。小麦*TaNAC069*可被叶锈菌诱导上调表达, *TaNAC069*沉默植株对叶锈病的抗性显著降低(Zhang等2021b)。过表达小麦*TtNTL3A*可以提高拟南芥对禾谷镰孢菌的抗性, 并促进致病相关蛋白编码基因*AtPR-1*、*AtNPR1*(*non-expresser of PR-gene 1*)和植物防御蛋白编码基因*AtPDF1.2* (*plant defensin 1.2*)的表达。此外, *TtNTL3A*可能同时参与小麦对干旱和盐胁迫的响应(Saidi等2022)。番茄*SlSRN1* (*stress-related NAC1*)能增强植株对灰霉病和丁香假单胞菌的抗性(Liu等2014)。番茄NAC家族的*JA2* (*jasmonic acid 2*)可增强番茄对丁香假单胞菌的抗性; 而*JAL2* (*JA2-like*)负调控对丁香假单胞菌的抗性(Du等2014)。番茄卷叶病毒的复制增强子能诱导*SlNAC1*表达, 促进病毒DNA在感染细胞中积累(Selth等2005)。SlNAC20/24/47/61可能通过与*WRKY*和*MPK* (*mitogen-activated protein kinase*)启动子结合, 增加番茄对黄化曲叶病毒病的抗性(Huang等2017)。棉花的GhNAC100与茉莉酸相关基因*GhPR3*和*GhPDF1.2*启动子的CGTA-box结合并抑制其表达, 负调控植株对大丽轮枝菌的抗性(Hu等2020)。在芥菜(*B. juncea*)中过表达缺乏跨膜结构域的BjuNAC62ΔC可提高对芸薹生链格孢菌的抗性, 诱导*ABI5* (*ABA insensitive 5*)、*NCED3*和*AOS* (*allene oxide synthase*)表达(Mondal等2022)。

5 展望

NAC是植物的一个重要转录因子家族。近年来, 随着对该家族成员的深入研究, 已明确其在植物生长发育和胁迫应答方面均具有重要的调控作用。但目前对于NAC转录因子家族的研究仍存在一些不足, 未来可从以下方向深入探究NAC的分子调控机制, 为植物生长发育调控和抗逆性状改良等提供基础。(1)挖掘不同植物中miR164对*NAC*家族成员转录调控的分子机制, 丰富以NAC为核心的上游调控网络; (2)鉴于NAC转录因子家族成员数量众多, 其分子结构和功能存在差异, 需进一步研究不同成员之间的互作关系, 探究其在植物生长发育和胁迫响应中的协同调控作用; (3) NAC家族在植物生长发育和胁迫响应中的作用机制研究仍有待深入, 如NAC家族某个成员广泛参与多个生物学过程的分子机制解析; (4)挖掘NAC蛋白的下游靶基因, 并探究其调控生长发育和胁迫应答的分子机制, 将有利于解析NAC的生物学功能; (5)现有NAC家族调控胁迫应答的研究多集中于植物的营养生长阶段, 而关于生殖阶段的胁迫应答调控研究较少; (6) NAC家族在作物性状改良和育种中的应用研究有待深入, 如通过调控*NAC*基因的表达改善作物的耐旱性、耐盐性和抗病性等, 以及改善作物的产量和品质; (7)挖掘自然群体和诱变群体中*NAC*的优异等位变异, 并将其应用于作物品质、产量和抗逆性状育种改良; (8)利用基因编辑等技术实现*NAC*与其他抗逆基因的联合利用, 为作物抗逆育种提供新的策略和手段; (9)基于*NAC*基因的功能研究, 筛选发育调控和胁迫应答相关的启动子, 有助于重要基因的功能研究。综上, 深入解析NAC转录因子调控植物生长发育和胁迫应答的分子调控网络, 挖掘其上下游调控因子, 有助于作物品质、产量和抗逆性状改良。

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