植物生理学报 *Plant Physiology Journal* 2019, 55 (7): 915–924 doi: 10.13592/j.cnki.ppj.2019.0107

植物NAC转录因子的生物学功能

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摘要: 在长期进化过程中, 植物体内形成精密的调控机制来抵御环境胁迫, 转录因子在转录水平调控胁迫相关基因的表达进而参与调控植物的抗逆反应。NAC (NAM、ATAF1/2、CUC2)是植物特有的最大的转录因子家族之一, 具有独特的结构特征, 由保守的N端结构域和多变的C端转录激活域组成。很多物种的NAC转录因子已经被发现并进行了功能鉴定。一般而言, 同源进化关系上属于同一家族的NAC转录因子具有相似的生物学功能。近年来, 对NAC转录因子生物学功能的研究不断深入, 表明NAC转录因子可以通过植物激素信号通路广泛调控植物的生长发育, 如器官边界的建成、次生壁和根的生长、衰老过程等植物生命历程, 并响应多种非生物和生物胁迫。本文综述了植物NAC转录因子参与生长发育、响应胁迫等生物学过程的研究进展, 为深入探讨其调控机理及更好地将*NAC*基因应用于农业生产提供参考。

关键词: NAC; 生物学功能; 调控; 综述

植物在复杂环境中能够调节体内新陈代谢和生长发育进程, 这些生命进程经常受到转录因子的调控。已经证明bZIP、NAC、MYB、WRKY等转录因子家族在植物生长发育和逆境响应中发挥重要作用(Golldack等2011)。NAC转录因子是植物特有的最大转录因子家族之一, NAC是由NAM (no apical meristem)、ATAF1/2 (*Arabidopsis* transcription activation factor)、CUC2 (cup-shaped cotyledon)的首字母缩写而成(Souer等1996)。随着植物完整基因组和表达序列标签(expressed sequence tag, EST)的不断增多, 已在拟南芥(*Arabidopsis thaliana*) (Souer等1996)、水稻(*Oryza sativa*) (Nuruzzaman等2010)、小麦(*Triticum aestivum*) (Borrill等2017)、大豆(*Glycine max*) (Le等2011)、棉花(*Gossypium* spp.) (Sun等2018)和苜蓿(*Medicago truncatula*) (Ling等2017)等许多物种中发现了大量的*NAC*基因。研究表明NAC转录因子广泛参与植物生长发育和响应逆境胁迫。本文从NAC转录因子的结构及参与的生长发育过程和抗逆反应几个方面进行综述。

1 NAC转录因子的结构特征

NAC转录因子具有独特的结构特征, 由保守的N端蛋白结构域(protein binding domain, PBD)和多变的C端转录激活域(transcription regulatory region, TRR)组成。N端结构域由A、B、C、D、E五个亚域组成, 这些结构与核定位及下游靶基因DNA序列的识别和结合密切相关。C端具有转录激活或转录抑制作用(Olsen等2005)。Ooka等(2003)在C端多变区发现了13个不同的相对保守区域, 这些区域分属于不同的亚族, C端序列的多变与NAC蛋白功能的多样化有紧密联系。尽管C端序列多变, 但富含酸性氨基酸、脯氨酸、丝氨酸、苏氨酸等简单重复区域是转录激活所必需的(Olsen等2005)。大部分NAC转录因子定位于细胞核, 有些NAC转录因子C端含有跨膜元件, 锚定在细胞质膜或内质网上, 称为NAC膜结合的转录因子(NAC membrane-bound transcription factors, NAC MTFs) (Seo等2008)。

NAC转录因子的启动子上含有多个响应激素信号通路和逆境胁迫的元件, 如*OsNAC19*启动子中发现了脱落酸(abscisic acid, ABA)响应元件(ABA response element, ABRE)、茉莉酸甲酯(methyl jasmonate, MeJA)响应元件(MeJA response element, JARE)、水杨酸(salicylic acid, SA)响应元件(SA response, TCA)、逆境胁迫顺式作用元件(defence- and stress-response, TC富集重复序列)、高温响应元件(heat stress response element, HSE)、低温响应元件(low temperature response, LTR) (Satheesh等

收稿 2019-03-04 修定 2019-06-18

资助 国家自然科学基金(31760071和31160186)和新疆维吾尔自治区自然科学基金(2015211C274)。

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2014), 表明NAC转录因子参与调控植物的逆境胁迫反应。

2 NAC转录因子的生物学功能

*NAC*基因广泛参与植物的生长发育和逆境胁迫响应。研究发现属于同一亚家族的*NAC*基因具有相似功能(Jin等2017), 如NAM亚家族成员拟南芥的CUC1和CUC2以及矮牵牛(*Petunia* spp.)的NAM, 均参与器官边界建成和分生组织的形成(Souer等1996; Aida等1999); ATAF1、ATAF2、BnNACs、HvNAC6和StNAC同属ATAF亚家族, 在生物和非生物胁迫反应中发挥功能(Jensen等2008; Hegedus等2003)。本文利用已经报道的具有生物学功能的部分代表性NAC转录因子的氨基酸序列制作了进化树图谱(图1)。所选基因的主要功能如表1~3所示, 表明同源关系较近的NAC转录因子具有相似的生物学功能。

2.1 参与植物的生长发育

NAC转录因子调控植物生长发育的整个生命进程(表1), 如植物次生壁和木质部的形成、根的生长、植物的衰老。

2.1.1 参与植物次生壁和木质部形成

植物次生壁和木质部的形成是植物重要的生命现象, 是植物木材能源形成的基础。NAC转录因子之间相互作用调控植物次生壁的形成。

拟南芥VND6/7 (vascular-related NAC domain protein6/7)在初级根微管的形成和原生及后生木质部微管的发育过程中起作用(Yamaguchi等2010)。拟南芥*SND1* (secondary wall-associated NAC domain protein1)和它的同源基因*NST1* (NAC secondary wall thickening-promoting factor1)能够正向调控纤维次生壁的形成(Zhong等2010), 在拟南芥中发现*MYB46*是SND1的靶基因, SND1能够激活*MYB46*基因的表达, 诱发次生壁相关基因的高度上调表达, 促进纤维素、木聚糖、木质素和细胞中次生壁的沉积(Zhong等2007; Zhong等2011)。黄瓜(*Cucumis sativus*)基因组中已发现12个NAC转录因子在野生型的刺及毛状体中的表达量显著高于其他组织部位; 赤霉素(gibberellin, GA)、生长素(auxin, IAA)、MeJA、乙烯利四种植物激素处理促进了黄瓜表面刺及毛状体的形成且密度显著增加, 12个NAC转录因子的表达也呈现上升趋势, 这暗示黄瓜的NAC通过不同的植物激素途径参与黄瓜毛状体和刺的形成及密度的发育(Liu等2018)。

2.1.2 参与植物根的生长

生长素信号调控植物根的生长, 拟南芥*NAC1*基因作为miR164的靶基因, 其表达受到miR164的负调控, NAC1可以转导生长素信号, 促进侧根的形成(Guo等2005)。渗透胁迫下, 过表达*Stu*-mi164基因的马铃薯(*Solanum tuberosum*)通过生长素信号通路负调控其靶基因*NAC*, 导致其渗透势降低, 侧根数减少, 根长不变(Zhang等2018); 玉米(*Zea mays*) *ZmNAC1*也受到miR164的负调控, 在拟南芥中过表达*ZmNAC1*引起侧根数增多(Li等2012)。

2.1.3 参与植物衰老

植物衰老受到内源激素乙烯(ethylene, ET)的调控, NAC转录因子通过乙烯信号途径参与植物果实成熟和器官衰老过程, *BFN1* (bifunctional nuclease1)是植物衰老相关基因, ORE1 (ANAC092)能够激活下游基因*BFN1*的表达, 促进植物的衰老(Matallana-Ramirez等2013)。ORE1、miR164和EIN2形成的三叉调控通路(trifurcate feed-forward pathway)在植物衰老和细胞死亡中具有重要作用(图2) (Kim等2009)。*ORE1*的上调表达依赖于叶片衰老过程诱发*EIN2* (ethylene insensitive 2)的表达, 在早期衰老过程中miR164负调控*ORE1*的表达, 但在衰老后期由于EIN2负调控miR164的表达, 从而导致*ORE1*上调表达, 进而促进*NAC1*的表达, 引起蛋白质的泛素化导致细胞程序性死亡或者衰老(Kim等2009)。

拟南芥中ATAF1的活性受到ABA和H_2O_2的调控, ATAF1正调控叶绿素发育和维持的基因*GLK1* (golden2-like1)和衰老相关基因*ORE1* (*NAC092*)的表达, 作为叶片衰老的正调控因子发挥作用(Garapati等2015)。衰老过程伴随营养元素的重新分配和再活化, 减缓叶片的衰老对提高植物的光合作用十分有利, Zhao等(2015)发现TaNAC-S可负调控叶片衰老, 增加小麦的氮浓度, 不仅提高了小麦产量, 还增加了谷类蛋白的含量。野生型小麦NAM-B1和OsNAC5都可加速衰老, 促进叶中营养到生长粮食

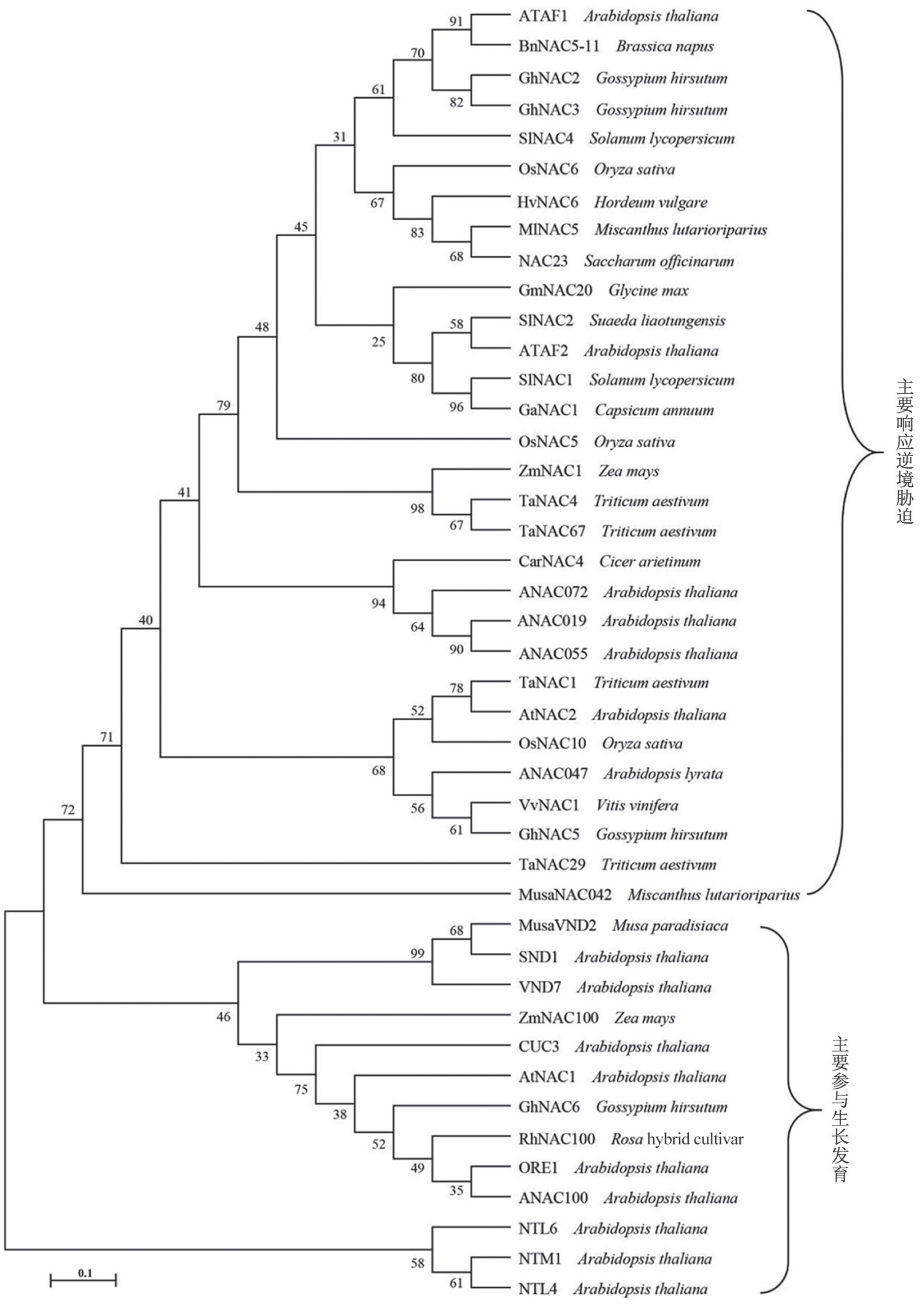

图1 NAC转录因子的系统进化树

Fig.1 Phylogenetic tree of plant NAC transcription factors

表1 NAC转录因子参与植物生长发育

Table 1 NAC transcription factors involved in plant growth development

植物生长和发育阶段	基因	物种	参考文献
器官边界建成和顶端分生组织	*CUC1/2*、*NAM*	拟南芥	Aida 1999
细胞分裂和次生壁及木质部形成	*GhXND1*	棉花	Li等2014
种子萌发、种子大小	*NTL6/8*	拟南芥	Kim等2008
	ONAC020/23/26	水稻	Mathew等2016
根生长	*TaNAC1*	小麦	Wang等2015
	GmNAC20	大豆	Hao等2011
	ZmNAC1	玉米	Li等2012
花器官形成	*NTL8*、*LOV1*	拟南芥	Yoo等2007
果实成熟	*ATAF1*	拟南芥	Garapati等2015
	MaNAC1/2	香蕉	Shan等2012
植物衰老和细胞死亡	*NLT4*	拟南芥	Delessert等2005
	PvNAC1/2	柳枝稷	Yang等2015a
	VvNAC1	葡萄	Le Hénanff等2013
胚胎发育	*PaNAC03*	云杉	Dalman等2017

表2 NAC转录因子响应非生物胁迫

Table 2 NAC transcription factors responsive to abiotic stress

转化的物种	目的基因	响应的胁迫和激素	提高的抗性	参考文献
拟南芥	*ANAC019/055/072* (拟南芥)	盐、旱、ABA	旱	Tran等2004
	TaNAC67 (小麦)	旱、冷、ABA	旱、冻	Mao等2014
	MlNAC5 (芒草)	旱、盐、冷、ABA等	干旱和冷	Yang等2015b
	ONAC063 (水稻)	高盐、氧化、渗透	高温、盐、渗透	Yokotani等2009
	CiNAC3/4 (中央锦鸡儿)	盐、温度、渗透、ABA	盐	Han等2015
	ThNAC13 (柽柳)	盐、渗透	盐、渗透	Wang等2017
	SNAC3 (水稻)	旱、盐、高温、ABA	高温、旱、氧化	Fang等2015
	OsNAC10、*ONAC022* (水稻)	盐、旱、ABA	盐、旱、低温	Jeong等2010; Hong等2016
烟草	*TaNAC2a* (小麦)	旱、盐、冷、ABA	旱	Tang等2012
	SlNAC35 (番茄)	旱、盐	盐、旱	Wang等2016
小麦	*TaNAC69* (小麦)	旱、盐、冷	盐、旱	Xue等2011
	SNAC1 (水稻)	旱、盐、冷、ABA	旱、盐	Saad等2013
番茄	*SlNAC1* (番茄)	冷、盐、激素等	冷	Ma等2013
香蕉	*MaNAC042* (香蕉)	旱、盐	盐、旱	Tak等2016
棉花	*SNAC1* (水稻)	旱、盐、冷、ABA	盐、旱	Liu等2014
菊花	*DgNAC1* (菊花)	旱	旱	Zhao等2018

的再活化, 进而提高粮食的蛋白及微量元素锌和铁的含量(Liang等2014)。

2.2 在植物非生物胁迫反应中的调控作用

NAC转录因子在植物应对环境胁迫刺激的复杂信号网络中具有重要作用, 成为潜在提高植物逆境胁迫的候选基因。转录组分析已得到大量参与非生物胁迫的NAC转录因子(表2)。NAC转录因子抵抗非生物胁迫, 主要是通过激活胁迫相关基因的表达, 引起代谢产物的积累, 从而提高植物对非生物胁迫的抗性(Nakashima等2012)。

2.2.1 调控干旱和盐胁迫

干旱和盐胁迫是影响植物生长发育的主要不利因素, NAC转录因子通过激活响应干旱胁迫的下游基因, 来提高干旱耐受性。ERD1 (early responsive to dehydration stress1)和AREB1 (abscisic acid-responsive element binding protein1)在植物的非生

表3 NAC转录因子响应生物胁迫

Table 3 NAC transcription factors responsive to biotic stress

物种	基因	靶基因	功能	研究方法	参考文献
拟南芥	*ATAF1*	*PR-1*、*PR-5*、*PDF1.2*	负调控灰霉菌/丁香假单胞菌	过表达/基因敲除	Wang等2009
	ATAF2	*PR1*、*PR2*、*PR4*、*PR5*、*PDF1.1*、*PDF1.2*	负调控尖胞镰刀菌, 抑制病程蛋白的表达	过表达/基因敲除	Delessert等2005
	ANAC019/055	*VSP1*、*LOX2*	负调控灰霉菌	过表达/双突变	Bu等2008
小麦	*TaNAC*	*PR1*、*PR2*、*PDF1.2*	负调控条锈病、丁香假单胞菌	VIGS/过表达	Wang等2015
大麦	*HvNAC6*	*HvPR-1b*、*HvPrx8*、*HvOxOa*	正调控白粉病	过表达/基因沉默	Jensen等2007
水稻	*OsNAC111*	*PR2*、*PR8*	抵抗稻瘟病	过表达	Yokotani等2014
	ONAC122/131	*OsLOX*、*OsPR1a*、*OsWRKY45*	抵抗稻瘟病	基因沉默	Sun等2013
	OsNAC4	*OsHSP90*、*IREN*	引起病原体的超敏反应	过表达	Taga等2009
番茄	*SlNAC1*	*WRKY*、*TGA*、*MYB*、*NAC*	增加番茄卷叶病毒(TLCV) DNA的积累	瞬时	Selth等2005
	SlNAC35	*PR1a*、*NPR1*、*PR2*、*PR5*	提高细菌性病原体抗性	过表达	Wang等2016
棉花	*GhATAF1*	*GhJAZ1*、*GhPDF1.2*、*GhPR1/3*、*GhWRKY70*	负调控真菌/灰霉病原体	过表达	He等2016

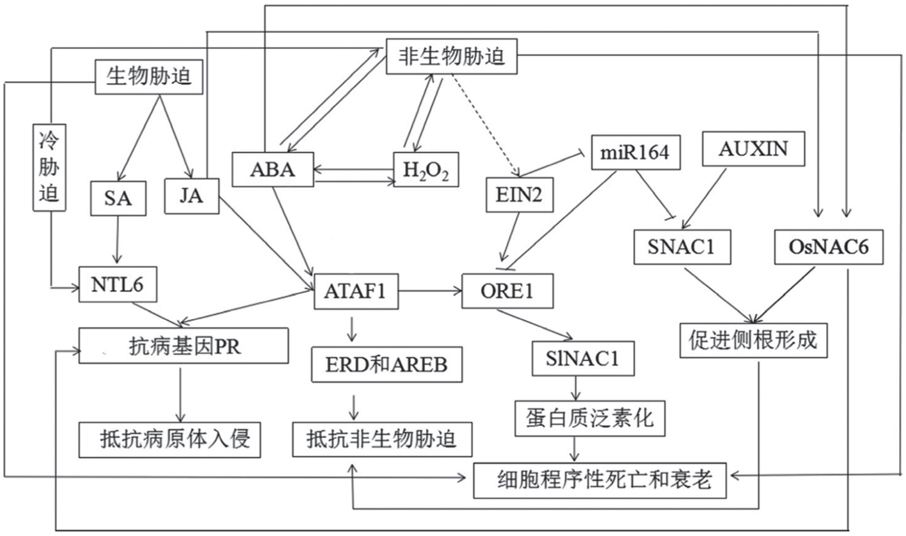

图2 NAC转录因子共同参与植物的生长发育和逆境胁迫响应

Fig.2 NAC transcription factors involved in plant growth development and stress response

ABA: 脱落酸; AREB: abscisic acid-responsive element binding protein; EIN2: ethylen insensitive2; ERD: early responsive to dehydration stress; JA: 茉莉酸; NTL: NTM-like; PR: 病程相关蛋白; SA: 水杨酸。

物胁迫防御中非常重要。拟南芥ANAC019/055/072能与*ERD1*启动子结合激活*ERD1*基因表达, 从而增加拟南芥的抗旱性(Tran等2004)。拟南芥NAC016能够与*NAP* (NAC-like, activated by AP3/PI)启动子上的NAC016BM (binding motif)结合促进其表达, NAC016、NAP可以分别与*AREB1*启动子上的NAC016BM1和NAPBM1结合抑制AREB1的表达, 降低对干旱的耐受性, 故推测NAC016、NAP、AREB1形成交叉调控通路响应干旱胁迫(Sakuraba等2015)。

植物根的生长能够很好地适应干旱和盐胁迫环境, 番茄(*S. lycopersicum*) *SlNAC35*通过ABA依赖的途径调控生长素信号通路中的*ARF1*、*ARF2*、*ARF8* (auxin response factors)的表达促进根的生长

和发育, 从而提高抗旱耐盐性(Wang等2016); 水稻过表达*ONAC022*显著导致气孔关闭, 失水降低, 但光合作用没有显著减少, 从而提高了水稻营养期的耐盐性和生殖期水稻的结籽率和抗旱性(Hong等2016), *OsNAC5*通过增大水稻根中木质部和通气组织细胞的大小增加根的直径, 提高水稻的耐旱性(Jeong等2013); 大麦(*Hordeum vulgare*)中过表达*HvNAC1*后, 干旱胁迫下能增加气孔阻力, 维持较高的光合作用, 提高抗旱性, 此外, 还能通过增加大麦的分蘖数、谷粒数、粒重等提高大麦的产量(Al Abdallat等2014)。

2.2.2 响应其他非生物胁迫

NAC转录因子还响应极端温度、氧化胁迫等非生物胁迫, *JUB1/ANAC042* (jungbrunnen1)响应热胁迫, 与热休克因子(heat shock factor, HSFA2)和热休克蛋白(heat shock protein32, HSA32)的功能类似, 能够提高植物的耐热性(Shahnejat-Bushehri等2012)。CBF (C-repeat binding factor)是冷信号中ICE1 (inducer of C-repeat binding factor expression1)的下游组件, 香蕉(*Musa acuminata*)中*MaNAC1*是MaICE1的靶基因, MaNAC1可与MaCBF结合, MaNAC1可通过ICE1-CBF信号通路提高香蕉的抗冷性(Shan等2014)。苹果(*Malus pumila*)中, MdNAC029通过与*MdCBF1*和*MdCBF4*启动子结合直接抑制其表达, 以CBF依赖性方式负调控植物耐寒性(An等2018)。氧化胁迫能够引发MRR (mitochondrial retrograde regulation), ANAC013通过与线粒体功能障碍基序(mitochondrial dysfunction motif, MDM)顺式调节元件的直接相互作用介导MRR诱导的线粒体功能障碍刺激(mitochondrial dysfunction stimulon, MDS)基因表达, 增加拟南芥的氧化应激耐受性(De Clercq等2013)。

2.3 在植物生物胁迫反应中的调控作用

SA、茉莉酸(jasmonic acid, JA)/ET和脱落酸(abscisic acid, ABA)信号途径是植物响应病原体入侵的植物激素信号通路, NAC转录因子可以通过不同的方式参与这些途径, 调控植物受到的生物胁迫过程(表3)。MYC2 (myelocytomatosis2)和ERF1 (ethylene response factor1)是JA/ET信号通路的成分, *AtWRKY70*受到SA诱导并且正调控该信号通路中的基因, 但JA信号抑制*AtWRKY70*的表达且负调控该信号通路中的基因(Wang等2015)。病程相关蛋白(pathogenesis related protein, PR)的积累对植物抵御病原体的入侵非常重要。有些NAC转录因子激活*PR*基因的表达, 从而在入侵位点诱发超敏反应和细胞死亡(Jensen等2008; Yokotani等2014)。相反, 有些*NAC*基因通过抑制*PR*基因的表达负调控病原抗性(Wang等2015)。

过表达小麦*TaNAC1*的拟南芥在病原体感染时*MYC2*和*ERF1*的表达改变, 而AtWRKY70受到抑制, 进一步导致SA诱导的*PR*基因的表达降低, 表明*TaNAC1*通过JA/ET信号通路增加了拟南芥对丁香假单胞菌(*Pseudomonas syringae*)的敏感性(Wang等2015)。MaNAC5与MaWRKY1和MaWRKY2一起调控病程相关基因的表达, 在SA和MeJA诱导的抗病信号通路中响应病原体入侵(Shan等2016)。*ANAC019/055*是AtMYC2的下游基因, AtMYC2能激活JA诱导响应损伤的基因*VSP1* (vegetative storage protein1)和*LOX2* (lipoxygenase2)的表达, 负调控PR的表达, *ANAC019/055*的表达依赖于AtMYC2, 过表达*ANAC019/055*增加了拟南芥对灰霉菌(*Botrytis cinerea*)的敏感性(Bu等2008)。

2.4 同时参与调控植物生长发育和逆境胁迫应答

逆境影响植物的生长发育。反过来, 植物也可以通过调节生长发育与逆境胁迫相关的一系列信号级联通路来抵抗逆境胁迫, 植物激素在这个交叉网络的调控中具有重要作用, NAC转录因子就参与到整个调控网络之中(图2) (Garapati等2015; Zhou等2017)。

ABA、SA和JA等植物激素调控植物的抗逆反应和植物根的生长发育。ATAF1通过植物激素信号通路参与植物衰老和逆境胁迫应答(图2), *ATAF1*的表达受ABA的诱导, 同时ATAF1结合到ABA合成基因*NCED3*启动子的特定序列元件上, 调节ABA合成, 响应植物的逆境胁迫(Jesen等2013); 此外, ATAF1通过抑制ABA合成的关键基因*AAO3*的表达负调控ABA的合成间接提高JA/ET信号通路中防御基因*PDF1.2a*、*PDF1.2b*、*PDF1.1*的表达, 增强对白粉病的抗性(Jesen等2008; Lu等2007; Wu等2010)。植物衰老中, H_2O_2诱导*ATAF1*的表达, ATAF1通过抑制*GLK1* (golden2-like1)降低叶绿素含量, 激活*ORE1*基因表达, 加速植物的衰老过程(Garapati等2015)。与之相反, NAC042/JUB1作为中心调控子, 参与细胞体内H_2O_2的平衡, 通过H_2O_2负调控植物衰老, 能够降低细胞内的H_2O_2的含量, 通过DREB2A提高转基因植株热耐受性, 延缓植株衰老(Wu等2012)。

综上所述, NAC转录因子通过植物激素信号形成交叉通路参与植物的生长发育和逆境胁迫响应, 在植物的多个方面起到重要的调控作用。

3 展望

NAC转录因子具有重要的生物学功能, 尤其是具有抗性、促生长、增产量的功能基因对作物的育种具有巨大的应用前景。目前已经发现很多物种的NAC转录因子, 但是还有很多家族成员需要挖掘和功能鉴定, 并且NAC转录因子在植物生长发育过程和抗逆的信号网络调控机制并不完善, 未来还有大量的工作要做。可以从以下几个方面展开研究: (1)利用已有的*NAC*基因数据, 通过进化树分析预测不同物种NAC可能的生物学功能, 并对其进行功能鉴定; (2) NAC转录因子的调控网络复杂, 涉及很多因子间的相互作用, 研究它们之间的信号作用对阐明NAC转录因子在植物生命进程中的调控机理很重要; (3)对极端抗逆植物NAC转录因子的功能挖掘更有助于揭示植物的抗性机理。

参考文献(References)

Aida M, Ishida T, Tasaka M (1999). Shoot apical meristem and cotyledon formation during *Arabidopsis* embryogenesis: interaction among the *CUP-SHAPED COTYLEDON* and *SHOOT MERISTEMLESS* genes. Development, 126 (8): 1563–1570

Al Abdallat AM, Ayad JY, Abu Elenein JM, et al (2014). Overexpression of the transcription factor *HvSNAC1* improves drought tolerance in barley (*Hordeum vulgare* L.). Mol Breeding, 33 (2): 401–414

An JP, Li R, Qu FJ, et al (2018). An apple NAC transcription factor negatively regulates cold tolerance via CBF-dependent pathway. J Plant Physiol, 221: 74–80

Borrill P, Harrington SA, Uauy C (2017). Genome-wide sequence and expression analysis of the NAC transcription factor family in polyploid wheat. G3-Genes Genom Genet, 7 (9): 3019–3029

Bu Q, Jiang H, Li CB, et al (2008). Role of the *Arabidopsis thaliana* NAC transcription factors ANAC019 and ANAC055 in regulating jasmonic acid-signaled defense responses. Cell Res, 18 (7): 756–767

Dalman K, Wind JJ, Nemesio-Gorriz M, et al (2017). Overexpression of *PaNAC03*, a stress induced NAC gene family transcription factor in Norway spruce leads to reduced flavonol biosynthesis and aberrant embryo development. BMC Plant Biol, 17: 6

De Clercq I, Vermeirssen V, Van Aken O, et al (2013). The membrane-bound NAC transcription factor ANAC013 functions in mitochondrial retrograde regulation of the oxidative stress response in *Arabidopsis*. Plant Cell, 25 (9): 3472–3490

Delessert C, Kazan K, Wilson IW, et al (2005). The transcription factor ATAF2 represses the expression of pathogenesis-related genes in *Arabidopsis*. Plant J, 43 (5): 745–757

Fang Y, Liao K, Du H, et al (2015). A stress-responsive NAC transcription factor SNAC3 confers heat and drought tolerance through modulation of reactive oxygen species in rice. J Exp Bot, 66 (21): 6803–6817

Garapati P, Xue GP, Munné-Bosch S, et al (2015). Transcription factor ATAF1 in *Arabidopsis* promotes senescence by direct regulation of key chloroplast maintenance and senescence transcriptional cascades. Plant Physiol, 168 (3): 1122–1139

Golldack D, Lüking I, Yang O (2011). Plant tolerance to drought and salinity: stress regulating transcription factors and their functional significance in the cellular transcriptional network. Plant Cell Rep, 30 (8): 1383–1391

Guo HS, Xie Q, Fei JF, et al (2005). MicroRNA directs mRNA cleavage of the transcription factor *NAC1* to downregulate auxin signals for *Arabidopsis* lateral root development. Plant Cell, 17 (5): 1376–1386

Han X, Feng Z, Xing D, et al (2015). Two NAC transcription factors from *Caragana intermedia* altered salt tolerance of the transgenic *Arabidopsis*. BMC Plant Biol, 15: 208

Hao YJ, Wei W, Song QX, et al (2011). Soybean NAC transcription factors promote abiotic stress tolerance and lateral root formation in transgenic plants. Plant J, 68 (2): 302–313

He X, Zhu L, Xu L, et al (2016). GhATAF1, a NAC transcription factor, confers abiotic and biotic stress responses by regulating phytohormonal signaling networks. Plant Cell Rep, 35 (10): 2167–2179

Hegedus D, Yu M, Baldwin D, et al (2003). Molecular characterization of *Brassica napus* NAC domain transcriptional activators induced in response to biotic and abiotic stress. Plant Mol Biol, 53 (3): 383–397

Hong Y, Zhang H, Huang L, et al (2016). Overexpression of a stress-responsive NAC transcription factor gene

ONAC022 improves drought and salt tolerance in rice. Front Plant Sci, 7: 4

Jensen MK, Hagedorn PH, de Torres-Zabala M, et al (2008). Transcriptional regulation by an NAC (NAM–ATAF1,2–CUC2) transcription factor attenuates ABA signalling for efficient basal defence towards *Blumeria graminis* f. sp. *hordei* in *Arabidopsis*. Plant J, 56 (6): 867–880

Jensen MK, Lindemose S, de Masi F, et al (2013). ATAF1 transcription factor directly regulates abscisic acid biosynthetic gene *NCED3* in *Arabidopsis thaliana*. FEBS Open Bio, 3: 321–327

Jensen MK, Rung JH, Gregersen PL, et al (2007). The *Hv*NAC6 transcription factor: a positive regulator of penetration resistance in barley and *Arabidopsis*. Plant Mol Biol, 65 (1–2): 137–150

Jeong JS, Kim YS, Baek KH, et al (2010). Root-specific expression of *OsNAC10* improves drought tolerance and grain yield in rice under field drought conditions. Plant Physiol, 153: 185–197

Jeong JS, Kim YS, Redillas MCFR, et al (2013). *OsNAC5* overexpression enlarges root diameter in rice plants leading to enhanced drought tolerance and increased grain yield in the field. Plant Biotechnol J, 11: 101–114

Jin X, Ren J, Nevo E, et al (2017). Divergent evolutionary patterns of NAC transcription factors are associated with diversification and gene duplications in angiosperm. Front Plant Sci, 8: 1156–1171

Kim JH, Woo HR, Kim J, et al (2009). Trifurcate feed-forward regulation of age-dependent cell death involving *miR164* in *Arabidopsis*. Science, 323 (5917): 1053–1057

Kim SG, Lee AK, Yoon HK, et al (2008). A membrane-bound NAC transcription factor NTL8 regulates gibberellic acid-mediated salt signaling in *Arabidopsis* seed germination. Plant J, 55: 77–88

Le DT, Nishiyama R, Watanabe Y, et al (2011). Genome-wide survey and expression analysis of the plant-specific NAC transcription factor family in soybean during development and dehydration stress. DNA Res, 18 (4): 263–276

Le Hénanff G, Profizi C, Courteaux B, et al (2013). Grapevine NAC1 transcription factor as a convergent node in developmental processes, abiotic stresses, and necrotrophic/biotrophic pathogen tolerance. J Exp Bot, 64 (16): 4877–4893

Li J, Guo G, Guo W, et al (2012). miRNA164-directed cleavage of *ZmNAC1* confers lateral root development in maize (*Zea mays* L.). BMC Plant Biol, 12: 220–234

Li W, Huang GQ, Zhou W, et al (2014). A cotton (*Gossypium hirsutum*) gene encoding a NAC transcription factor is involved in negative regulation of plant xylem development. Plant Physiol Bioch, 83: 134–141

Liang C, Wang Y, Zhu Y, et al (2014). OsNAP connects abscisic acid and leaf senescence by fine-tuning abscisic acid biosynthesis and directly targeting senescence-associated genes in rice. Proc Natl Acad Sci USA, 111 (27): 10013–10018

Ling L, Song L, Wang Y, et al (2017). Genome-wide analysis and expression patterns of the NAC transcription factor family in *Medicago truncatula*. Physiol Mol Biol Plants, 23 (2): 343–356

Liu G, Li X, Jin S, et al (2014). Overexpression of rice NAC gene *SNAC1* improves drought and salt tolerance by enhancing root development and reducing transpiration rate in transgenic cotton. PLoS ONE, 9: e86895

Liu X, Wang T, Bartholomew E, et al (2018). Comprehensive analysis of NAC transcription factors and their expression during fruit spine development in cucumber (*Cucumis sativus* L.). Hortic Res, 5: 31

Lu PL, Chen NZ, An R, et al (2007). A novel drought-inducible gene, *ATAF1*, encodes a NAC family protein that negatively regulates the expression of stress-responsive genes in *Arabidopsis*. Plant Mol Biol, 63 (2): 289–305

Ma NN, Zuo YQ, Liang XQ, et al (2013). The multiple stress-responsive transcription factor *SlNAC1* improves the chilling tolerance of tomato. Physiol Plantarum, 149 (4): 474–486

Mao X, Chen S, Li A, et al (2014). Novel NAC transcription factor TaNAC67 confers enhanced multi-abiotic stress tolerances in *Arabidopsis*. PLoS ONE, 9: e84359

Matallana-Ramirez LP, Rauf M, Farage-Barhom S, et al (2013). NAC transcription factor ORE1 and senescence-induced *BIFUNCTIONAL NUCLEASE1* (*BFN1*) constitute a regulatory cascade in *Arabidopsis*. Mol Plant, 6 (5): 1438–1452

Mathew IE, Das S, Mahto A, et al (2016). Three rice NAC transcription factors heteromerize and are associated with seed size. Front Plant Sci, 7: 1638

Nakashima K, Takasaki H, Mizoi J, et al (2012). NAC transcription factors in plant abiotic stress responses. BBA-Gene Regul Mech, 1819: 97–103

Nuruzzaman M, Manimekalai R, Sharoni AM, et al (2010). Genome-wide analysis of NAC transcription factor family in rice. Gene, 465 (1–2): 30–44

Olsen AN, Ernst HA, Lo Leggio L, et al (2005). NAC transcription factors: structurally distinct, functionally diverse. Trends Plant Sci, 10: 79–87

Ooka H, Satoh K, Doi K (2003). Comprehensive analysis of NAC family genes in *Oryza sativa* and *Arabidopsis thaliana*. DNA Res, 10: 239–247

Saad ASI, Li X, Li HP, et al (2013). A rice stress-responsive *NAC* gene enhances tolerance of transgenic wheat to drought and salt stresses. Plant Sci, 203–204: 33–40

Sakuraba Y, Kim YS, Han SH, et al (2015). The *Arabidopsis* transcription factor NAC016 promotes drought stress responses by repressing *AREB1* transcription through a trifurcate feed-forward regulatory loop involving NAP. Plant Cell, 27 (6): 1771–1787

Satheesh V, Jagannadham PTK, Chidambaranathan P, et al (2014). NAC transcription factor genes: genome-wide identification, phylogenetic, motif and *cis*-regulatory element analysis in pigeonpea (*Cajanus cajan* (L.) Millsp.). Mol Biol Rep, 41 (12): 7763–7773

Selth LA, Dogra SC, Rasheed MS, et al (2005). A NAC domain protein interacts with *Tomato leaf curl virus* replication accessory protein and enhances viral replication. Plant Cell, 17: 311–325

Seo PJ, Kim SG, Park CM (2008). Membrane-bound transcription factors in plants. Trends Plant Sci, 13: 550–556

Shahnejat-Bushehri S, Mueller-Roeber B, Balazadeh S (2012). *Arabidopsis* NAC transcription factor JUNGBRUNNEN1 affects thermomemory-associated genes and enhances heat stress tolerance in primed and unprimed conditions. Plant Signal Behav, 7 (12): 1518–1521

Shan W, Chen JY, Kuang JF, et al (2016). Banana fruit NAC transcription factor MaNAC5 cooperates with MaWRKYs to enhance the expression of pathogenesis related genes against *Colletotrichum musae*. Mol Plant Pathol, 17 (3): 330–338

Shan W, Kuang JF, Chen L, et al (2012). Molecular characterization of banana NAC transcription factors and their interactions with ethylene signalling component EIL during fruit ripening. J Exp Bot, 63 (14): 5171–5187

Shan W, Kuang JF, Lu WJ, et al (2014). Banana fruit NAC transcription factor MaNAC1 is a direct target of MaICE1 and involved in cold stress through interacting with MaCBF1. Plant Cell Environ, 37 (9): 2116–2127

Souer E, van Houwelingen A, Kloos D (1996). The *No Apical Meristem* gene of petunia is required for pattern formation in embryos and flowers and is expressed at meristem and primordia boundaries. Cell, 85: 159–170

Sun H, Hu M, Li J, et al (2018). Comprehensive analysis of NAC transcription factors uncovers their roles during fiber development and stress response in cotton. BMC Plant Biol, 18: 150–165

Sun L, Zhang H, Li D, et al (2013). Functions of rice NAC transcriptional factors, ONAC122 and ONAC131, in defense responses against *Magnaporthe grisea*. Plant Mol Biol, 81 (1–2): 41–56

Taga Y, Takai R, Kaneda T, et al (2009). Role of OsHSP90 and IREN, Ca^{2+} dependent nuclease, in plant hypersensitive cell death induced by transcription factor OsNAC4. Plant Signal Behav, 4 (8): 740–742

Tak H, Negi S, Ganapathi TR (2016). Banana *NAC* transcription factor *MusaNAC042* is positively associated with drought and salinity tolerance. Protoplasma, 254: 803–816

Tang YM, Liu MY, Gao SQ, et al (2012). Molecular characterization of novel *TaNAC* genes in wheat and overexpression of *TaNAC2a* confers drought tolerance in tobacco. Physiol Plantarum, 144: 210–224

Tran LSP, Nakashima K, Sakuma Y, et al (2004). Isolation and functional analysis of *Arabidopsis* stress-inducible NAC transcription factors that bind to a drought-responsive *cis*-element in the *early responsive to dehydration stress 1* promoter. Plant Cell, 16 (9): 2481–2498

Wang F, Lin R, Feng J, et al (2015). TaNAC1 acts as a negative regulator of stripe rust resistance in wheat, enhances susceptibility to *Pseudomonas syringae*, and promotes lateral root development in transgenic *Arabidopsis thaliana*. Front Plant Sci, 6: 108–125

Wang G, Zhang S, Ma X, et al (2016). A stress-associated NAC transcription factor (SlNAC35) from tomato plays a positive role in biotic and abiotic stresses. Physiol Plantarum, 158 (1): 45–64

Wang L, Li Z, Lu M, et al (2017). ThNAC13, a NAC transcription factor from *Tamarix hispida*, confers salt and osmotic stress tolerance to transgenic *Tamarix* and *Arabidopsis*. Front Plant Sci, 8: 635

Wang XE, Basnayake BMVS, Zhang H, et al (2009). The *Arabidopsis* ATAF1, a NAC transcription factor, is a negative regulator of defense responses against necrotrophic fungal and bacterial pathogens. MPMI, 22 (10): 1227–1238

Wu A, Allu AD, Garapati P, et al (2012). *JUNGBRUNNEN1*, a reactive oxygen species–responsive NAC transcription factor, regulates longevity in *Arabidopsis*. Plant Cell, 24 (2): 482–506

Wu Y, Deng Z, Lai J, et al (2010). Dual function of *Arabidopsis ATAF1* in abiotic and biotic stress responses. Cell Res, 19 (11): 1279–1290

Xue GP, Way HM, Richardson T, et al (2011). Overexpression of *TaNAC69* leads to enhanced transcript levels of stress up-regulated genes and dehydration tolerance in bread wheat. Mol Plant, 4 (4): 697–712

Yamaguchi M, Kubo M, Fukuda H, et al (2010). VASCULAR-RELATED NAC-DOMAIN7 is involved in the differentiation of all types of xylem vessels in *Arabidopsis* roots and shoots. Plant J, 55 (4): 652–664

Yang J, Worley E, Torres-Jerez I, et al (2015a). *PvNAC1* and *PvNAC2* are associated with leaf senescence and nitrogen use efficiency in switchgrass. Bioenerg Res, 8: 868–880

Yang X, Wang X, Ji L, et al (2015b). Overexpression of a *Miscanthus lutarioriparius* NAC gene *MlNAC5* confers enhanced drought and cold tolerance in *Arabidopsis*. Plant

Cell Rep, 34 (6): 943–958

Yokotani N, Ichikawa T, Kondou Y, et al (2009). Tolerance to various environmental stresses conferred by the salt-responsive rice gene *ONAC063* in transgenic *Arabidopsis*. Planta, 229 (5): 1065–1075

Yokotani N, Tsuchida-Mayama T, Ichikawa H, et al (2014). OsNAC111, a blast disease-responsive transcription factor in rice, positively regulates the expression of defense-related genes. MPMI, 27 (10): 1027–1034

Yoo SY, Kim Y, Kim SY, et al (2007). Control of flowering time and cold response by a NAC-domain protein in *Arabidopsis*. PLoS ONE, 7: e642

Zhang L, Yao L, Zhang N, et al (2018). Lateral root development in potato is mediated by Stu-mi164 regulation of NAC transcription factor. Front Plant Sci, 9: 383–392

Zhao D, Derkx AP, Liu DC, et al (2015). Overexpression of a NAC transcription factor delays leaf senescence and increases grain nitrogen concentration in wheat. Plant Biol, 17 (4): 904–913

Zhao Q, Zhong M, He L, et al (2018). Overexpression of a chrysanthemum transcription factor gene *DgNAC1* improves drought tolerance in chrysanthemum. Plant Cell Tiss Org Cult, 135: 119–132

Zhong R, Lee C, McCarthy RL, et al (2011). Transcriptional activation of secondary wall biosynthesis by rice and maize NAC and MYB transcription factors. Plant Cell Physiol, 52 (10): 1856–1871

Zhong R, Lee C, Ye ZH (2010). Functional characterization of poplar wood-associated NAC domain transcription factors. Plant Physiol, 152 (4): 1044–1055

Zhong R, Richardson EA, Ye ZH (2007). The MYB46 transcription factor is a direct target of *SND1* and regulates secondary wall biosynthesis in *Arabidopsis*. Plant Cell, 19 (9): 2776–2792

Zhou HH, Huang H, Xu BL, et al (2017). Biological function of NAC transcription factors in plant abiotic and biotic stress responses. Plant Physiol J, 53 (8): 1372–1382 (in Chinese with English abstract) [周鸿慧, 黄红, 徐彬磊等 (2017). NAC转录因子在植物对生物和非生物胁迫响应中的功能. 植物生理学报, 53 (8): 1372–1382]

Biological functions of plant NAC transcription factors

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Abstract: In the long-term evolution process, plants have formed complicated regulatory mechanism to resist environmental stress. Transcription factors regulate the expression of stress-related genes at the transcriptional level and participate in the regulation of plant stress resistance. NAC (NAM, ATAF1/2 and CUC2) is one of the plant-specific and largest families of transcription factors with unique structural characteristics. NAC consists of conservative N-terminal DNA-binding domain and variable C-terminal transcriptional activation domain. NAC transcription factors have been found and identified in many species. In general, NAC transcription factors belonging to the same family in homologous evolutionary relationships have similar biological function. In recent years, the research on the biological functions of NAC transcription factors has been deepening. It has been shown that NAC transcription factors can regulate plant growth and development through plant hormone signaling pathways, such as the formation of organ boundaries, secondary wall and root growth, plant senescence, and so on, as well as their response to a variety of abiotic and biotic stresses. In this paper, the biological functions of plant NAC transcription factors involved in growth and development, and response to biotic and abiotic stresses were summarized, which would lay the foundation for further study of its regulation mechanism and provide broad application prospects for agricultural production.

Key words: NAC; biological function; regulation; review

Received 2019-03-04 Accepted 2019-06-18

This work was supported by the National Natural Science Foundation of China (31760071 and 31160186), and the Natural Science Foundation of Xinjiang Uygur Autonomous Region (2015211C274).

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