

NAC转录因子在植物对生物和非生物胁迫响应中的功能

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摘要: NAC蛋白是植物中最大的转录因子家族之一, 在生长发育、衰老以及逆境应答等多个生物学过程中起重要作用。本文简要综述了NAC转录因子在植物对生物和非生物胁迫反应应答中的功能及其机制。

关键词: NAC; 转录因子; 结构; 生物逆境; 非生物逆境

生活在自然界中的植物, 无时无刻不受到生物和非生物的胁迫。在适应环境的过程中, 生物调节大量基因的协同表达, 其中就包括转录因子。转录因子通过激活和抑制防卫基因的表达起作用。根据DNA结合区域的不同, 植物转录因子(transcription factor, TF)可划分成很多家族(Schwechheimer等1998)。如在拟南芥中, 大约有2 500个基因属于转录因子(Pérez-Rodríguez等2010), 分属于37个不同家族。其中, NAC (NAM、ATAF1,2和CUC2)类转录因子就是植物所特有的最大转录因子家族之一, 且在多种植物中被鉴定和研究, 如拟南芥、水稻、小麦、葡萄、毛白杨、大豆和烟草(Nuruzzaman等2010; Le等2011; Rushton等2008)。现已证实, NAC转录因子参与了多个途径, 包括次生壁的形成(Zhong等2010)、细胞分裂(Kim等2006)、生长发育(Olsen等2005; Mao等2007; Chen等2015)、衰老(Yang等2011; Liang等2014)以及生物和非生物逆境反应(Christianson等2010; Nakashima等2007)等过程。NAC转录因子广泛参与植物生长发育的许多方面, 如顶端分生组织的产生、细胞分裂、开花、侧根发育、分蘖及分蘖角度、衰老等(Takada等2001; Vroemen等2003; Mitsuda等2005; Zhong等2006; Yang等2011; Zhang和Gan 2012; Chen等2015)。此外, 大量的转录因子参与了逆境反应, 20%~25%的NAC基因参与至少一种或者一种以上逆境反应(Nuruzzaman等2010)。本文简要综述了NAC转录因子的结构特征、分类以及在生物和非生物逆境中的功能及其相关研究进展。

1 NAC转录因子家族的结构特征及分类

NAC转录因子有典型和非典型两种结构。典型的NAC转录因子N端含151~159个氨基酸残基, 且高度保守; C端转录调控区的模体在亚组内保守性较高, 但在不同亚组间差异很大, 在生化上可以

激活或抑制转录的功能。部分NAC蛋白在其转录调控区也具有蛋白结合能力(Kjaersgaard等2011)。还有一类NAC蛋白含 α -螺旋的跨膜基序NTLs, 可以锚定于细胞膜或者内质网上, 拟南芥中有18个NTLs, 水稻中则只有5个NTLs (Kim等2010)。非典型NAC转录因子可以是单独的或者两个串联的结构域(Jensen等2010)。除去典型的NAC结构域外, suppressor of gamma response 1 (SOG1)在N端NAC结构域还有一段延伸区域, vascular plant one-zinc finger (VOZ)蛋白还含有一个保守的能结合DNA的锌指结构, 但NAC结构域位于C端而调控区(TR结构域)则位于N端(Mitsuda等2004)。

NAC结合结构域(NAC binding domain)又可以根据结合DNA的能力, 分为A~E五个亚结构域, 其中, 亚结构域A可能与转录因子功能二聚体形成有关, B和E可能与NAC基因的功能多样性有关, C和D结合DNA (Duval等2002; Ooka等2003)。

在28 469条水稻和28 581条拟南芥cDNA序列中, 分别鉴定到75个和105个NAC转录因子, 并根据氨基酸序列特征将其分成I和II两组, 其中组I又分成14个亚组, 组II分为4个亚组(Ooka等2003)。Fang等(2008)采用系统序列分析方法研究了水稻140个*OsNAC*或类似*OsNAC*转录因子基因, 并将水稻NAC转录因子家族分为5类(I~V)。其中, 54个水稻*OsNAC*基因归属于I类, 并分成5个亚类, 已报道的与发育相关的*OsNAC*转录因子归属于I-2、I-3、I-4亚类; 也有54个水稻*OsNAC*基因成员归属于II类, 其进化树比I类更复杂, 且多数基因的功能还没有报道; 14个*OsNAC*基因归属于III类, 已报导的如

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SNAC1、*OsNAC6*等胁迫相关的NAC转录因子基因归属于此类; IV类包含14个*OsNAC*基因; V类包含2个基因。

2 NAC转录因子在对非生物逆境响应中的作用

影响植物生长发育的非生物逆境包括干旱、

盐害和极端温度等。植物在受到非生物逆境胁迫时, 会形成一套与之相适应的抵抗机制。研究发现, NAC转录因子参与了植物对非生物逆境胁迫的抗性反应(表1), 通过依赖脱落酸(abscisic acid, ABA)或者不依赖ABA途径直接或者间接调控逆境应答

表1 已知非生物胁迫相关NAC基因及其功能

Table 1 The list of NAC genes related to abiotic stress and their functions

基因	方法	转基因的寄主	来源的生物	改变的性质	参考文献
<i>ANAC019</i>	过量表达	拟南芥	拟南芥	提高抗旱性	Trans等2004
<i>ANAC055</i>	过量表达	拟南芥	拟南芥	提高抗旱性	Trans等2004
<i>ANAC072/RD26</i>	过量表达/ 敲除突变体	拟南芥	拟南芥	正调控对干旱的抗性	Trans等2004; Fujita等2004
<i>ANAC096</i>	过量表达	拟南芥	拟南芥	提高对干旱和渗透的耐性	Xu等2013
<i>ATAF1</i>	过量表达/ 敲除突变体	拟南芥	拟南芥	改变对干旱的抗性	Lu等2007; Wu等2009
<i>AtNAC2</i>	过量表达	拟南芥	拟南芥	提高耐盐性	He等2005
<i>NAC019</i>	过量表达	拟南芥	拟南芥	提高耐热性	Guan等2014
<i>AtNAP</i>	过量表达/T-DNA 插入突变体	拟南芥	拟南芥	负调节对盐害的抗性	Seok等2016
<i>NAC72</i>	敲除突变体	拟南芥	拟南芥	负调控干旱抗性	Wu等2016
<i>NAC016</i>	过量表达/敲 除突变体	拟南芥	拟南芥	负调控干旱抗性	Sakurab等2015
<i>SNAC1</i>	过量表达	水稻	水稻	提高对干旱和盐害的耐性	Hu等2006
<i>SNAC2</i>	过量表达	水稻	水稻	提高对干旱、冷害和盐害的耐性	Hu等2008
<i>OsNAC4</i>	过量表达	水稻	水稻	提高对干旱和盐害的耐性	Kaneda等2009
<i>OsNAC5</i>	过量表达	水稻	水稻	提高对干旱、冷害和盐害的耐性	Takasaki等2010
<i>OsNAC6</i>	过量表达	水稻	水稻	提高对干旱、冷害和盐害的耐性	Ohnishi等2005; Nakashima等2007; Lee等2017a
<i>OsNAC9</i>	过量表达	水稻	水稻	提高对干旱和盐害的耐性	Redillas等2012
<i>OsNAC10</i>	过量表达	水稻	水稻	提高抗旱性	Jeong等2010
<i>OsNAC022</i>	过量表达	水稻	水稻	提高对干旱和盐害的耐性	Hong等2016
<i>OsNAC45</i>	过量表达	水稻	水稻	提高对干旱和盐害的耐性	Zheng等2009
<i>ONAC095</i>	抑制突变体	水稻	水稻	提高抗旱性, 降低冷害耐性	Huang等2016
<i>ONAC106</i>	过量表达	水稻	水稻	提高对盐害的耐性	Sakuraba等2015
<i>OsNAP</i>	过量表达	水稻	水稻	提高对干旱、冷害和盐害的耐性	Chen等2014
<i>ATAF1</i>	过量表达	水稻	拟南芥	提高耐盐性	Liu等2016
<i>SNAC1</i>	过量表达	棉花/小麦	水稻	提高对干旱和盐害耐性	Liu等2014; Saad等2013
<i>ONAC063</i>	过量表达	拟南芥	水稻	提高耐盐性	Yokotani等2009
<i>SISRNI</i>	VIGS	番茄	番茄	提高对氧化胁迫和干旱的耐性	Liu等2014
<i>SINAC1</i>	过量表达	番茄	番茄	提高耐冷性	Ma等2013
<i>SINAC4</i>	RNAi	番茄	番茄	增加对盐害和干旱的敏感性	Zhu等2014
<i>SINAM1</i>	过量表达	烟草	番茄	提高耐冷性	Li等2016
<i>SINAC53</i>	过量表达	烟草	番茄	提高对干旱和盐害耐性	Wang等2016
<i>TaNAC69</i>	过量表达	小麦	小麦	提高抗旱性	Xue等2011
<i>TaNAC29</i>	过量表达	拟南芥	小麦	提高对干旱和盐害耐性	Huang等2015; Xu等2015
<i>TaNAC47</i>	过量表达	拟南芥	小麦	提高对干旱、盐害和冷害的耐性	Zhang等2016
<i>TaNAC67</i>	过量表达	拟南芥	小麦	提高对干旱、盐害和冷害的耐性	Mao等2014
<i>TaNAC2</i>	过量表达	拟南芥	小麦	提高对干旱、盐害和冷害的耐性	Mao等2012

表1 (续)

基因	方法	转基因的寄主	来源的生物	改变的性质	参考文献
<i>TaNAC2a</i>	过量表达	烟草	小麦	提高抗旱性	Tang等2012
<i>TaNAC2L</i>	过量表达	拟南芥	小麦	提高耐热性	Guo等2015
<i>GmNAC20</i>	过量表达	拟南芥	大豆	提高对盐害和冷害的耐性	Hao等2011
<i>GmNAC11</i>	过量表达	拟南芥	大豆	提高耐盐性	Hao等2011
<i>NAC67</i>	过量表达	水稻	小米	提高对干旱和盐害耐性	Rahman等2016
<i>EcNAC1</i>	过量表达	烟草	小米	提高对氧化和干旱的耐性	Ramegowda等2012
<i>BnNAC2/BnNAC5</i>	过量表达	拟南芥	油菜	提高耐盐性	Zhong等2012
<i>BnNAC485</i>	过量表达	油菜/拟南芥	油菜	提高对渗透和干旱的耐性	Ying等2014
<i>GmNAC2</i>	过量表达	棉花/拟南芥	棉花	提高抗旱性	Gunapati等2016
<i>GbNAC1</i>	过量表达/VIGS	拟南芥/棉花	棉花	正调控对干旱和盐害的耐性	Wang等2016
<i>ZmNAC55</i>	过量表达	拟南芥	玉米	提高抗旱性	Mao等2016
<i>ZmSNAC1</i>	过量表达	拟南芥	玉米	提高抗旱性	Lu等2012
<i>AhNAC3</i>	过量表达	烟草	花生	提高抗旱性	Liu等2013
<i>AhNAC2</i>	过量表达	拟南芥	花生	提高对干旱和盐害的耐性	Liu等2011
<i>NAC26</i>	过量表达	拟南芥	葡萄	提高抗旱性	Fang等2016
<i>VvNAC1</i>	过量表达	拟南芥	葡萄	提高对渗透、盐害和冷害的抗性	Le Hénanff等2013
<i>PtrANC72</i>	过量表达	拟南芥	枸橘	降低抗旱性	Wu等2016
<i>CarNAC4</i>	过量表达	拟南芥	鹰嘴豆	提高耐盐性	Yu等2016
<i>MuNAC4</i>	过量表达	落花生	马豆	提高抗旱性	Pandurangaiah等2014
<i>AaNAC1</i>	过量表达	青蒿/拟南芥	青蒿	提高抗旱性	Lv等2016
<i>DgNAC1</i>	过量表达	烟草	菊花	提高耐盐性	Liu等2011
<i>NAC (HM237304)</i>	过量表达	拟南芥	苜蓿	提高抗旱性	Wang 2013
<i>MINAC5</i>	过量表达	拟南芥	芒草	提高对干旱和冷害耐性	Yang等2015
<i>MINAC9</i>	过量表达	拟南芥	芒草	提高对干旱和冷害耐性	Zhao等2016
<i>CiNAC3</i>	过量表达	拟南芥	锦鸡儿	提高耐盐性	Han等2015
<i>CiNAC4</i>	过量表达	拟南芥	锦鸡儿	提高耐盐性	Han等2015
<i>RhNAC3</i>	VIGS/过量表达	玫瑰/拟南芥	玫瑰	改变抗旱性	Jiang等2014
<i>PeNAC1</i>	过量表达	拟南芥	胡杨	提高耐盐性	Wang等2013
<i>SINAC1</i>	过量表达	拟南芥	碱蓬	提高对干旱、盐害和冷害的耐性	Li等2014

基因的表达。过量表达拟南芥*ANAC019*、*ANAC055*和*ANAC072/RD26*三个基因,能显著提高植株的抗旱能力,通过与*ERD1*基因的启动子CATGTG核心区域结合,调控*ERD1*及其下游基因的表达,从而参与抗旱胁迫反应(Trans等2004)。过量表达*ANAC072/RD26*的转基因植株对ABA高度敏感,且ABA应答基因和非生物胁迫相关基因上调表达,内源ABA含量高于野生型;而*anac072/rd26*突变体对ABA不敏感,ABA应答基因的表达受到抑制,内源ABA低于野生型,表明*ANAC072/RD26*基因通过依赖ABA抗逆信号途径正向调控抗旱胁迫反应(Fujita等2004)。过量表达*OsNAC6*,改变了根的结构(包括增加根的数量和直径)和烟草胺的合成,从而提高水稻对干旱的抗性(Lee等2017a)。根特异性过量表达*OsNAC10*的水稻植株在繁殖阶段对干旱的抗性提高(Jeong等2010)。*ANAC096*通过与bZIP类型

的转录因子ABRE结合因子和ABRE结合蛋白(ABF/AREB)互作,提高拟南芥对干旱和渗透的抗性,使其在干旱和渗透逆境下得以存活,即*ANAC096*和*ABF2*及*ABF4*直接互作,激活植物对干旱和渗透逆境反应中ABA诱导的基因的表达(Xu等2013)。*ONAC106*过量表达的水稻植株抗盐性增强,这是通过调节盐害信号途径中的关键基因如*OsNAC5*、*OsDREB2A*、*OsLEA3*和*OsbZIP23*的表达来实现的(Sakuraba等2015)。过量表达*ATAF1*的水稻植株对盐害的抗性和对ABA的敏感性显著提高,是通过提高逆境相关基因如*OsLEA3*、*OsSalTI*和*OsPMI*的表达(Liu等2016)。过量表达拟南芥ABA相关基因*VIN2*可以提高植株的抗盐能力,*VIN2*通过与*COR*和*RD*基因启动子结合从而发挥其在逆境胁迫中的调控作用(Yang等2011)。过量表达*ONAC063*的拟南芥植株对盐害和渗透逆境的抗性提高,是由

于上调表达包括淀粉酶基因*AMY1*在内的盐诱导基因(Yokotani等2009)。*AtNAC2*提高拟南芥对盐害的抗性,对盐害的反应需要乙烯(ethylene)途径和生长素信号途径的参与,但是不需要ABA信号途径(He等2005)。过量表达*NAC019*的拟南芥植株对热的抗性提高,通过与*RCF2*的互作(Guan等2014)。拟南芥NAC转录因子*JUNGBRUNNEN1 (ANAC042)*呈现出热相关的表达模式,其过量表达植株对热逆境的抗性增强(Shahnejat-Bushehri等2012)。

当然,对于大多数的NAC基因而言,只是参与了对一个非生物逆境抗性的调节。乙烯途径的抑制和ABA/JA途径的激活导致植物逆境抗性的增强(Gunapati等2016)。但是,更多的研究表明,拟南芥和水稻中部分NAC转录因子同时参与了对多个逆境反应的调控。在水稻中,至少有5个NAC基因同时正调控抗旱和抗盐胁迫反应,并受ABA的调控。过量表达*SNAC1*基因提高了水稻对干旱的耐受性,甚至在田间干旱条件下还能提高结实率,研究发现,*SNAC1*定位于气孔保卫细胞中,通过促进气孔关闭,减少水分丧失来提高抗旱能力;过量表达*SNAC1*的转基因水稻耐盐性也增强,是因为与气孔运动、渗透调节、细胞膜稳定性、脱毒等胁迫相关基因的表达提高(Hu等2006)。最新研究表明,甚至*SNAC1*的下游基因*OsSRO1C*和*OsPPI8*也在水稻抗旱方面发挥重要作用(You等2013; 2014a, b)。另外,*SNAC1*在其他作物中的过量表达也表现出类似的现象,如在棉花中过量表达提高其对干旱和盐害的抗性,是通过降低蒸腾作用来实现的(Liu等2014);过量表达的小麦与野生型相比,叶中含更多的水分和叶绿素,根部的鲜重和干重都增加,通过调节逆境相关基因的表达增加了对盐害和干旱的抗性(Saad等2013)。过量表达*OsNAC9*、*OsNAC4*、*ONAC045*和*ONAC022*的转基因水稻植株通过增强如*OsLEA3*、*OsPM1*、*OsDREB*和*PP2C*等胁迫相关基因的表达,来提高对干旱和高盐的耐受性(Redillas等2012; Kaneda等2009; Zheng等2009; Hong等2016)。在干旱条件下,过量表达*OsNAC10*基因还能使水稻的产量增加25%~42% (Jeong等2010)。甚至部分NAC基因如*SNAC2*、*OsNAC5*、*OsNAC6*、*OsNAC10*和*OsNAP*过量表达能提高植物对干旱、冷害和盐害的抗性,通过调控逆境反

应中下游靶标基因的表达来实现(Song等2011; Ohnishi等2005; Nakashima等2007; Takasaki等2010; Hu等2008; Jeong等2010; Chen等2014)。然而,一些NAC基因在不同的非生物逆境条件下,表现出不同的调节作用,如*ONAC095*的抑制突变体对干旱的抗性增强,而对冷害的抗性降低(Huang等2016)。甚至,过量表达有些NAC基因会产生一些负面效应,如植株矮化、开花延迟、结实率降低等。这些不利表型可通过利用如*OsNAC6*、*RCc3*的逆境诱导型启动子来克服(Nakashima等2007; Jeong等2010)。

除了上述的对植物的逆境反应有正向调控作用的NAC转录因子外,有的NAC基因负向调节植物对逆境的耐性。拟南芥中,*AtNAP*的T-DNA插入突变体对盐害抗性增强,而过量表达*AtNAP*的拟南芥植株对盐害的抗性减弱,表明*AtNAP*是耐盐反应的负调节子,通过对*AREB1*的转录抑制来实现(Seok等2017)。*NAC072*在*ABF3*介导的ABA响应的基因调节中有双重作用(Li等2016)。水稻中,以miR164为靶标的NAC基因是干旱抗性的负调节子,通过调节干旱相关基因的表达来实现(Fang等2014)。*nac72*拟南芥突变体对干旱的抗性增强,可能是部分通过调控腐胺相关的活性氧动态平衡的调节(Wu等2016)。拟南芥突变体*nac016*表现出较强的干旱抗性,而*NAC016*过表达的株系表现出较弱的干旱抗性,表明*ANC016*通过抑制*AREB1*的转录负调节植物对干旱的耐性(Sakuraba等2015)。拟南芥突变体*ataf1*抗旱能力增强,且*COR47*、*ERD10*、*KINI*、*RD22*等抗旱相关基因表达增强(Lu等2007);但Wu等(2009)发现,过量表达*ATAF1*的拟南芥植株抗旱性增强,*ADH1*、*RD29A*和*COR47*这些抗旱相关基因的表达量上升。这个相悖的结果,需要进一步的验证。

3 NAC转录因子在抗病响应中的作用

植物在整个生命周期中,除了受到各种非生物逆境的胁迫,还会受到细菌、真菌和病毒等病原物的侵害。植物在长期的进化过程中,形成了一系列复杂而又精细的抗病机制。在植物体中主要有3条抗病信号途径:依赖于水杨酸(salicylic acid, SA)、茉莉酸(jasmonic acid, JA)和乙烯的信号途径。通过这3条的抗病信号途径来激活防卫反应

基因的表达,从而激活植物的抗病防卫反应。NAC转录因子在调控植物对不同类型病原菌的抗病反应中都起到重要作用,通过调控相关基因的表达,正向或负向调节植物对病原菌的抗病反应。

过量表达*ANAC019*和*ANAC055*的拟南芥植株对灰霉菌(*Botrytis cinerea*)的抗性降低,JA诱导的防卫基因*VSP1*和*LOX2*的表达增强;而*anac019/anac055*双突变体则提高拟南芥对灰霉病的抗性,*VSP1*和*LOX2*的表达降低,表明*ANAC019*和*ANAC055*可能参与了JA介导的防卫反应,并转录调控JA诱导的防卫基因*VSP1*和*LOX2*的表达(Bu等2008)。过量表达膜结合NAC转录因子*NTL6*的拟南芥植株对*Pseudomonas syringae* pv. *tomato* DC3000 (*Pst* DC3000)的抗性提高,通过调节*PR*基因的表达来实现(Seo等2010)。*ATAF1*基因的表达受灰霉菌侵染或JA处理的诱导。在拟南芥中,过量表达*ATAF1*会导致对灰霉病抗性降低,一些病程相关(pathogenesis-related, PR)蛋白的基因表达量降低(Wu等2009; Wang等2009b),而利用嵌合抑制子技术抑制内源*ATAF1*蛋白活性导致对灰霉菌、*Pst* DC3000和*Aternaria brassicicola*的抗性增加,通过调节*PR*基因的表达来实现(Wang等2009b)。*ATAF2*基因与*ATAF1*高度同源,其表达受JA和SA诱导,过量表达*ATAF2*导致*PR1*、*PDF1.2*等防卫基因表达水平下降,且对枯萎病菌的敏感性增加;与之相对应,缺失突变体中这些防卫基因表达水平增强,枯萎病抗性增强(Delessert等2005)。然而,*ATAF2*可正向调控对烟草花叶病毒(*Tobacco mosaic virus*, TMV)的抗性,过量表达*ATAF2*能减弱TMV侵染后病毒的积累,防卫反应基因*PR1*、*PR2*和*PDF1.2*表达量升高(Wang等2009a)。

相对而言,水稻中NAC转录因子在抗病方面的研究比较少,大多数的NAC在抗病中的功能未知。利用雀麦花叶病毒(*Brome mosaic virus*, BMV)介导的水稻病毒诱导的基因沉默(virus-induced gene silencing, VIGS)技术获得的*ONAC122*和*ONAC131*沉默植株,对水稻稻瘟病的抗性降低,且*PR*基因表达下调(Sun等2013),表明*ONAC122*和*ONAC131*正向调控对水稻稻瘟病的抗性。过量表达*OsNAC111*的水稻植株,通过诱导*PR*相关基因的表达,尤其是几丁质酶和 β -1,3-葡聚糖酶基因,对稻瘟病的抗性提高(Yokotani等2014)。*OsNAC6*的表达受稻瘟菌

处理的诱导,且过量表达*OsNAC6*的植株对稻瘟菌的抗性提高,它起到转录激活子的作用(Nakashima等2007)。*NAC*基因功能缺失突变体*rim1*突变体对矮缩病毒抗性增强,病毒数目显著减少。水稻NAC转录因子*RIM1*参与调控JA信号途径,且在*rim1*突变体中内源JA的含量增加,表明*RIM1*负调控JA信号途径(Yoshii等2010)。但是,*rim1*突变体对黄叶病毒和条纹叶枯病毒抗性没有变化。考虑到黄叶病毒和矮缩病毒都由叶蝉传播,并且水稻*RIM1*的表达量与黄叶病毒接种后病毒粒子数呈负相关,说明*RIM1*主要通过控制病毒繁殖达到抗病毒作用,而与传播途径无关(Yoshii等2010)。在水稻中过量表达*OsNAC4*会导致细胞死亡的加速,同时细胞膜完整性被破坏以及DNA片段化。在病菌侵染的情况下,对*OsNAC4*蛋白的亚细胞定位的研究发现其从细胞质聚集到细胞核,且这种转移依赖于蛋白的磷酸化(Kaneda等2009)。

除了水稻和拟南芥,部分NAC基因在抗病反应中的作用也在其他植物中进行了研究。利用VIGS技术获得的番茄*SISRNI*植株对灰霉菌和*Pst* DC3000的抗性降低,但对氧化胁迫和干旱的耐受性提高,同时积累更多的活性氧(reactive oxygen species, ROS),表明*SISRNI*正向调控对病原菌的抗性,负向调控对氧化胁迫和干旱的耐受性(Liu等2014)。*SINAC35*的表达受到细菌病原物和信号分子的诱导,过量表达*SINAC35*的转基因烟草植株对细菌病原物的抗性增强,ROS可能位于SA信号途径的上游(Wang等2016)。Jensen等(2007)利用基因沉默技术发现,大麦*HvNAC6*沉默降低了其对白粉病菌的抗性。用VIGS技术获得的*GbNAC1*沉默的棉花植株对黄萎病的抗性降低,而过量表达*GbNAC1*的拟南芥植株对黄萎病的抗性增强,表明*GbNAC1*正调控对黄萎病的抗性(Wang等2016)。过量表达*GhATAF1*的棉花植株对黄萎病菌和灰霉病菌的敏感性提高,通过抑制JA途径和激活SA途径来实现(He等2016)。小麦*TaNAC1*在拟南芥中的过量表达导致其对*Pst* DC3000的抗性减弱,是通过调节SA和JA信号途径,而用VIGS技术获得的小麦突变体增加了对条锈病的抗性(Wang等2015)。*TaNAC21/TaNAC22*沉默表达的小麦植株对条锈病的抗性增强,表明它们负调节了对条锈病的抗性(Feng等2014)。

葡萄*VvNAC1*在拟南芥中的过量表达,提高了对灰霉菌和卵菌的抗性,是通过调控防卫基因的表达(Le Hénanff等2013)。中国野生葡萄*VpNAC1*的表达受到白粉病菌和外源激素的诱导,过量表达*VpNAC1*的烟草植株提高了对白粉病菌和烟草黑胫病菌的抗性(Zhu等2012),这是通过调节*PR1*、*PR2*、*PR4*和*PR5*基因的表达来实现的。青蒿*AaNAC1*在青蒿和拟南芥中的过量表达提高了两者对灰霉菌的抗性,并使其体内青蒿素的含量增加(Lv等2016)。

4 NAC基因表达及其蛋白活性的调控

4.1 MicroRNA对NAC基因表达调控

NAC转录因子的活性调控主要涉及转录和翻译水平。在转录水平上,主要是受到了microRNA的调控。microRNA是一类长度约22个核苷酸的非编码单链RNA分子,是一类重要的转录调控因子(Cuperus等2011)。它通过调控相应的靶标基因参与动植物内不同的生理和生化过程。研究发现,拟南芥*miR164*调控*NAC1*、*CUC1*等6个NAC转录因子(Rhoades等2002)。在拟南芥中,*NAC4*在*miR164*的调控下,促进病原物诱导的细胞死亡(Lee等2017b)。*miR164*可降低*NAC1*基因的表达量,当*NAC1*基因与*miR164*配对的碱基对发生突变后,*miR164*就不能降解*NAC1*;对*miR164*过量表达和缺失突变体中*NAC1* mRNA表达水平的研究发现,*NAC1* mRNA表达量与植株中*miR164*表达水平呈负相关,进一步证实*NAC1*基因受*miR164*直接调控(Guo等2005)。过量表达*miR164*表现出和*cuc1cuc2*双突变体类似的表型,这主要是由于*miR164*在转录水平降解了*CUC1*和*CUC2*的mRNA水平(Laufs等2004)。Fang等(2014)对水稻中*miR164*研究发现,有5个NAC转录因子直接受其调控(Li等2010),其中4个NAC转录因子(*OMTN2*、*OMTN3*、*OMTN4*、*OMTN6*)都负调控水稻对干旱的抗性。对水稻microRNA的基因组分析结果表明,microRNA调控NAC基因的表达,并参与了水稻叶片的衰老过程(Xu等2014)。Kaur等(2017)采用qRT-PCR分析,发现microRNAs和它们的NAC靶基因一起调控小麦对渗透压逆境的抗性。Xie等(2015)用第二代测序技术(next generation sequencing)揭示microRNAs通过调节NAC、MYB和MAPK等参与了棉花对干旱和盐害的反应。小麦中,*tae-miR164*的靶标基因*TaNAC21/22*负调控小麦对条锈病的抗性(Feng等2014)。

4.2 蛋白修饰对NAC活性的调控

磷酸化是转录因子翻译后修饰的一种重要形式,不仅调节转录因子的细胞定位,而且可以改变转录因子的活性。在无病原识别信号时,水稻OsNAC4均匀分布在细胞质和细胞核内;当病菌侵染时,OsNAC4蛋白在细胞质中迅速积累,并发生磷酸化修饰,随后经磷酸化修饰的OsNAC4蛋白进入细胞核内,调控细胞凋亡相关基因的表达,从而调控过敏反应(hypersensitive response, HR)(Kaneda等2009)。泛素介导的蛋白降解途径是翻译后调控NAC转录因子蛋白水平的另一个机制。在拟南芥中,含RING结构域的SINAT5具有泛素连接酶活性并可以将NAC1泛素化,导致NAC1蛋白降解,使其丧失生物学功能(Xie等2002)。SINAC1受到泛素蛋白酶体系统介导的降解的调控,因而SINAC1蛋白在蛋白酶体特异性抑制子MG132或者MG115存在的情况下是稳定的(Huang等2013)。小麦NAC转录因子TaNAC2L受到翻译后水平的调控,可能是通过蛋白酶体介导的途径降解(Guo等2015)。另外,NAC转录因子还能与其他蛋白发生互作,影响NAC转录因子活性,从而调控下游基因的转录表达。拟南芥ANAC019、ANAC055以及ANAC072/RD26等都能与锌指蛋白ZFHD1蛋白直接互作,激活下游基因的表达(Tran等2007)。

5 展望

综上所述,NAC转录因子参与了对生物和非生物逆境反应的调控。NAC家族是植物特有的一个庞大的成员众多且已明确在抗逆反应中起作用的只有少数几个NAC转录因子(表2),而大多数的转录因子尤其是水稻等农作物中的NAC转录因子在抗病过程中的功能需进一步研究,这可以通过过量表达相应的基因及构建功能丧失突变体等来实现。虽然已有越来越多的文献报道,NAC转录因子与其他蛋白相互作用(如依赖于钙的蛋白激酶、WRKY、MYB及ATDOF5.8等)(Vivek等2017; Shan等2016; Zeng等2016; He等2015),参与植物的逆境反应,但即使是这些功能已经知晓的NAC转录因子,对于它们的机制尚不明确。我们应更加深入的研究NAC转录因子的调控机制以及下游的靶标基因,这将有助于揭示其在抗病抗逆反应中的作用机制。

NAC水稻芯片的数据分析结果表明,多个NAC

表2 已知抗病相关NAC基因及其功能

Table 2 The list of NAC genes related to biotic stress and their functions

基因	方法	转基因的寄主	来源的生物	改变的性质	参考文献
<i>NTL6</i>	过量表达	拟南芥	拟南芥	提高对 <i>Pst</i> DC3000的抗性	Seo等2010
<i>ANAC019</i>	过量表达/ 敲除突变体	拟南芥	拟南芥	改变对灰霉菌的抗性	Bu等2008
<i>ANAC055</i>	过量表达/ 敲除突变体	拟南芥	拟南芥	改变对灰霉菌的抗性	Bu等2008
<i>ATAF1</i>	过量表达/ 嵌合抑制子	拟南芥	拟南芥	改变对灰霉菌、 <i>Pst</i> DC3000 和 <i>A. brassicicola</i> 的抗病性	Wu等2009; Wang等2009b
<i>ATAF2</i>	过量表达/ 敲除突变体	拟南芥	拟南芥	改变对对枯萎病菌和TMV的抗性	Delessert等2005; Wang等2009a
<i>ONAC122</i>	VIGS	水稻	水稻	降低对稻瘟病的抗性	Sun等2013
<i>ONAC131</i>	VIGS	水稻	水稻	降低对稻瘟病的抗性	Sun等2013
<i>OsNAC111</i>	过量表达	水稻	水稻	提高对稻瘟病的抗性	Yokotani等2014
<i>OsNAC6</i>	过量表达	水稻	水稻	提高对稻瘟病的抗性	Nakashima等2007
<i>RIMI</i>	缺失突变体	水稻	水稻	提高对矮缩病毒抗性	Yoshii等2010
<i>SISRNI</i>	VIGS	番茄	番茄	对灰霉菌和 <i>Pst</i> DC3000的抗性降低	Liu等2014
<i>SINAC35</i>	过量表达	烟草	番茄	提高对细菌病原物的抗性	Wang等2016
<i>HvNAC6</i>	VIGS	大麦	大麦	降低对白粉病菌的抗性	Jensen等2007
<i>HvNAC1</i>	过量表达	大麦	大麦	提高对柱隔孢菌叶斑病的抗性	McGrann等2015
<i>GbNAC1</i>	VIGS/过量表达	棉花/拟南芥	棉花	正调控对黄萎病的抗性	Wang等2016
<i>GhATAF1</i>	过量表达	棉花	棉花	提高对黄萎病菌和灰霉病菌的敏感性	He等2016
<i>TaNAC1</i>	过量表达/VIGS	小麦	拟南芥/小麦	对 <i>Pst</i> DC3000的抗性减弱/增加对条锈病的抗性	Wang等2015
<i>TaNAC21/</i> <i>TaNAC22</i>	VIGS	小麦	小麦	负调节对条锈病的抗性	Feng等2014
<i>VvNAC1</i>	过量表达	拟南芥	葡萄	提高对灰霉菌和卵菌的抗性	Le Hénanff等2013
<i>VpNAC1</i>	过量表达	拟南芥	中国野生葡萄	提高对白粉病菌和烟草黑胫病菌的抗性	Zhu等2012
<i>AaNAC1</i>	过量表达	拟南芥/青蒿	青蒿	提高对灰霉菌的抗性	Lv等2016

基因同时调节了多个反应(Sun等2015)。63个ONAC基因同时参与对不同的生物和非生物逆境的调控, 38个ONAC基因同时参与2个不同的非生物逆境, 65个ONAC基因同时参与2个不同的生物逆境, 表明这些同时参与不同反应的ONAC基因有多个生物学功能(Sun等2015)。这就要求我们去研究NAC转录因子功能的多效性。由于NAC转录因子存在普遍的功能冗余现象, 在研究NAC转录因子时, 可以用双突变体同时突变这些功能冗余的基因; 也可以采用嵌合抑制子(chimeric repressor)技术从蛋白的水平上去抑制内源转录因子的活性, 来克服功能冗余的现象。

大量的研究已经表明NAC转录因子在转基因育种中有很大的应用潜力。由于过量表达NAC基因的转基因植株对生物和非生物逆境的表型会发生一定程度的改变, 因此我们可以通过转基因技

术获得一些抗病、抗逆的转基因新材料。尤其是一些NAC转录因子功能有多效性, 可通过转入一个NAC转录因子而获得多个性状, 这在育种中极具优势。

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Biological function of NAC transcription factors in plant abiotic and biotic stress responses

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Abstract: NAC transcription factors are one of the largest families of transcriptional regulators in plants and have been shown to be involved in growth and development, senescence and stress response. This minireview summarizes the biological functions of NAC transcription factors in abiotic and biotic stress responses in plants.

Key words: NAC; transcription factor; structure; biotic stress; abiotic stress

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