植物ABI4转录因子的研究进展

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摘要: Abscisic acid-insensitive 4 (ABI4)属于APETALA2/ethylene responsive factor (AP2/ERF)类转录因子, 它是在研究ABA信号转导途径中被发现和鉴定的。近年来, ABI4被认为是一种具有多种调节功能的转录因子, 它参与了植物种子萌发和幼苗形态建成、质体/线粒体反向信号传递、脂类合成和分解、糖信号和ABA应答等诸多重要的生物学事件。本文综述了ABI4转录因子的结构特征、转录调控模式、基因表达调控和参与的信号转导功能等的最新研究进展。

关键词: 植物; ABI4; 转录因子; 信号转导

转录因子abscisic acid-insensitive 4 (ABI4)首先在松属裸子植物中被发现, 而在藓属和卷柏属植物中仅发现了ABI4-like蛋白的存在。由于ABI4-like蛋白中缺少8个氨基酸的ABI4特征序列LRP元件(LRPLLPRP), 而被子植物的ABI4蛋白均含有LRP元件, 因此推测高等被子植物中的ABI4结构可能是从物种自然进化和选择过程逐渐演化而来(Mizoi等2012)。*abi4* (*abscisic acid-insensitive 4*)最初是通过正向遗传学筛选到的一系列ABA不敏感突变体而获此命名, 除此之外还发现了*abi1*、*abi2*、*abi3*和*abi5*突变体。Finkelstein等(1994)通过γ射线照射拟南芥种子的方法筛选到了一个ABA不敏感突变体, 并命名它为*abi4*。在一定ABA浓度条件下, 野生型拟南芥种子无法萌发, 而*abi4*突变体的萌发则不受影响, 这说明*abi4*的突变基因参与ABA抑制的拟南芥种子萌发。目前已经知道上述五个突变等位基因的功能, ABI1和ABI2均编码PP2C蛋白磷酸酶, ABI3、ABI4和ABI5则编码不同类别的转录因子。

1 ABI4的结构特征和功能元件分析

Finkelstein等(1998)在拟南芥中成功精细定位了*abi4*突变基因(At2g40220)。研究结果表明ABI4编码一个转录因子, 它包含一段与APETALA2 (AP2) DNA结合结构域高度同源的序列。在拟南芥基因组中至少存在147个包含APETALA2/ethylene responsive factor (AP2/ERF)结构域的蛋白。这些蛋白可被分为5大类: AP2亚家族、RAV亚家族、CBF/DREB亚家族、ERF亚家族和一个特异蛋白AL079349 (Sakuma等2002)。ABI4属于CBF/DREB亚家族。CBF/DREB亚家族所有成员仅包含1个AP2/ERF结构域, 该结构域的第14和19位氨基酸分别为缬氨酸和谷氨酸, 而ERF亚家族则为丙氨酸和天冬氨酸。蛋白同源序列比对的结果显示, 位于近N端60~70个氨基酸残基构成的AP2/ERF结构域在各物种中非常保守。该AP2/ERF结构域包含1个α螺旋和3个β折叠, 其中前2个β折叠所形成的高级结构负责ABI4与特异DNA序列的识别和结合(Lindner等2010; Nakano等2006; 杜磊等2013)。近年来研究发现, ABI4蛋白不仅含有高度保守的AP2/ERF结合域, 而且存在其他的保守功能元件, 例如: CMIV-1/AP2相关元件、LRP特异元件和PEST序列元件等。其中, CMIV-1/AP2相关元件位于AP2结构域前端, 包含15个氨基酸残基(RKCK-AGKGGPDNKFR)的细胞核定位信号序列(nuclear localization signal, NLS); LRP特异元件包含8个氨基酸残基(LRPLLPRP); 而PEST元件则富含脯氨酸、谷氨酸、丝氨酸和苏氨酸的PEST序列(图1)。

近年来, 已有学者对构成拟南芥ABI4的所有保守功能元件进行了系统性分析。核酸在线预测分析工具(www.sbc.su.se/~maccallr/nucpred/)显示: 在拟南芥ABI4的AP2/ERF元件前侧近N端的CMIV-1/AP2相关元件包含NLS, 而在LRP和PEST元件中均未发现NLS的存在。Gregorio等(2014)通过原生质体瞬时表达系统来研究ABI4各组分元件在ABI4定位和功能中的作用, 他们构建了一系列

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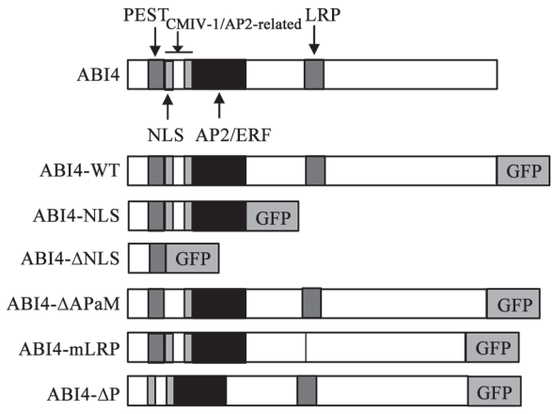

图1 ABI4包含的功能元件

Fig.1 Functional motif of ABI4

参考Gregorio等(2014)文献, 有所修改。

包含表达ABI4功能元件和绿色荧光蛋白(green fluorescent protein, GFP)融合蛋白的载体(图1): *ABI4-WT* (含有ABI4完整的开放阅读框)、*ABI4-NLS* (N端117个氨基酸序列, 仅包含NLS和AP2元件)、*ABI4-ΔNLS* (仅包含NLS序列上游39个氨基酸序列, 缺失NLS和AP2元件)、*ABI4-ΔAPaM* (缺失15个氨基酸序列的CMIV-1/AP2相关元件)、*ABI4-mLRP* (缺失LRP元件)、*ABI4-ΔP* (仅缺失PEST元件)。GFP融合蛋白的原生质体定位实验结果显示: ABI4-mLRP蛋白定位在细胞核, 这说明LRP元件与ABI4蛋白定位无关。缺失NLS元件或CMIV-1/AP2相关元件(*ABI4-ΔNLS*和*ABI4-ΔAPaM*) GFP融合蛋白能同时定位于细胞质和细胞核, 而ABI4-NLS则定位于细胞核, 这表明NLS和CMIV-1/AP2相关元件参与ABI4蛋白的细胞核定位。其次, 当ABI4蛋白缺失PEST或CMIV-1/AP2相关元件后, ABI4-ΔAPaM和ABI4-ΔP融合蛋白相对含量相较于ABI4-WT显著升高, 而缺失LRP元件则无明显影响, 这表明PEST和CMIV-1/AP2相关元件参与维持了ABI4蛋白结构稳定性(Rice等2000; Gregorio等2014)。

Gregorio等(2014)还利用荧光素(*luciferase*, *LUC*)构建报告基因载体*pABI4-CE1:LUC*, 通过监测LUC的荧光强度来衡量ABI4各功能元件对ABI4蛋白稳定性的影响。利用原生质体瞬时表达系统共转*pABI4-CE1:LUC*和*p35S:ABI4*后, 完整的ABI4-WT蛋白通过特异性识别*pABI4-CE1:LUC*载体上的CE1基序来转录激活报告基因*LUC*的表达(Bossi等2009), 因此能检测到强烈的LUC荧光。如果ABI4蛋白缺失LRP (共转*pABI4-CE1:LUC*和*p35S:ABI4-mLRP*)或CMIV-1/AP2 (共转*pABI4-CE1:LUC*和*p35S:ABI4-ΔAPaM*)相关元件, ABI4-ΔAPaM或ABI4-mLRP的LUC荧光强度显著下降; 而缺失PEST元件的LUC活性则略高于ABI4-WT, 这些结果表明LRP和AP2相关元件在维持ABI4蛋白稳定性中具有重要作用。此外, 在对照中(单转*pABI4-CE1:LUC*)也能检测到稍许*LUC*表达, 我们猜测这可能是由于原生质体中本身就存在一定量的ABI4蛋白导致产生微弱的自激活现象, 也不排除这可能是实验的背景本底值。

已经知道, PEST序列元件参与蛋白质的泛素化及降解。例如, 酵母生长过程中会诱导产生包含PEST的果糖1,6二磷酸酶(fructose-1,6-bisphosphatase, FBPase)。FBPase蛋白在3种泛素结合酶(Ubc1、Ubc4和Ubc5)和26S蛋白酶体作用下迅速泛素化随后被降解(Schork等1995)。蛋白合成抑制剂放线菌酮使ABI4-WT蛋白表达量逐渐减少, 而添加26S蛋白酶体抑制剂MG132后则导致ABI4-WT蛋白表达量升高, 这已暗示着26S蛋白酶体在降解ABI4蛋白中的功能。进一步实验发现, 缺失PEST元件的ABI4-ΔP融合蛋白表达量则不受MG132的影响。同时发现, ABI4-WT蛋白在细胞中的半衰期为3 h, 而ABI4-ΔP蛋白则在6 h内保持稳定。这些结果进一步说明26S蛋白酶体通过识别PEST元件降解ABI4蛋白(Finkelstein等2011)。综合上述实验结果可以得知, 拟南芥ABI4蛋白的各个功能元件对于维持ABI4蛋白的亚细胞定位、蛋白稳定性和功能活性等方面分别具有不同的作用。

2 ABI4转录调控模式

ABI4能激活或抑制一系列下游基因的表达, 这些基因的功能主要包括胚后期发育、种子萌发和幼苗生长、ABA信号转导、脂类代谢和光合作用等(Nott等2006; Wind等2013; 洪岚等2011)。多数受ABI4诱导表达的靶标基因在启动子区域均含有ABI4的特征结合基序, 如S box [CACYKSCA] (Bossi等2009)。也有结果显示, 拟南芥80%受ABI4诱导的基因在启动子区域含有CACCG的CE1-like序列(Reeves等2011)。ABI4结合靶基因对基序特

异性的要求不高, ABI4能够与CE1-like序列结合, 驱动下游基因的表达(Finkelstein等1998; Niu等2002)。有趣的是, 由于*ABI4*自身启动子中也包含了CE1-like序列, ABI4能被自身转录激活(Bossi等2009)。同时凝胶阻滞实验显示, 某些不含*ABI4*特征性结合基序的基因依然表现出可以与*ABI4*结合的特点, 包括CCAC、G(A/C)CACGT(G/A)和GC(C/G)GCTT(T)序列(Shkolnik-Inbar等2013; Wind等2013)。ABI4还能通过与某些bZIP类转录因子的协同作用来调控下游基因表达(Brocard-Gifford等2003; Feng等2014)。

由于ABI4识别的DNA基序特异性要求不高, 因此如果该DNA基序恰好位于某个其他转录因子识别基序的内部或者附近, 那么ABI4则对该基因的转录产生竞争性抑制效应。例如, 捕光叶绿素结合蛋白(light-harvest chlorophyll a/b binding protein, LHCB)和1,5二磷酸核酮糖羧化酶小亚基(1,5-bisphosphate carboxylases small subunit)等与光合作用相关的基因启动子区域含有GCCACGTG或CACGTGGC基序(Zhang等2015)。该基序中恰好存在CE1-like序列和G-box序列重叠的现象, 因此G-box结合蛋白对该基序的激活调控受到ABI4的竞争性抑制(Acevedo-Hernández等2005)。转录组的数据也证实, *abi4*对光合作用相关基因的表达起负调控作用(Foyer等2007; Reeves等2011)。反之, 受ABI4激活基因的启动子区域则不存在上述重叠现象。由于受ABI4调控的光合作用有关的基因与质体反向信号密切相关, 本文在随后对ABI4介导的质体反向信号调控机制进行综述。

3 *ABI4*的表达调控

*ABI4*基因本身在拟南芥不同的生长时期和组织部位表达均存在差异(Shkolnik-Inbar和Bar-Zvi 2011)。ABI4参与高浓度糖抑制的种子萌发, 并在种子发育和幼苗早期生长过程中起重要作用。与之一致的是, *ABI4*基因在发育的种子中表达量较高, 亦在幼苗期的子叶、下胚轴和根部能检测到表达(Soderman等2000; Bossi等2009; Cui等2012)。ABI4在营养器官中表达水平较低, 但依然具有生理功能(Arenas-Huertero等2000; Kerchev等2011)。这是ABI4受到26S蛋白酶介导的转录后调控的结果(Finkelestein等2011; Gregorio等2014), 上文已对其机制做详尽阐述, 此处不再赘述。此外, 也有学者在花粉、叶片维管组织和韧皮部中检测到*ABI4*基因的表达(Soderman等2000; Shkolnik-Inbar和BarZvi 2010, 2011)。

另一方面, ABI4的表达和功能发挥受到一系列外界环境因子和激素的影响。种子和幼苗期中的ABI4表达丰度受高浓度葡萄糖(6%)、高盐和ABA的强烈诱导(Shkolnik-Inbar和BarZviv 2008)。有趣的是, *abi4*突变体较野生型更耐高盐胁迫(Quesada等2000), 这可能是由于ABI4负调控Na^+专一性转运蛋白HKT1;1导致的(Shkolnik-Inbar等2013)。除了受外界环境因子的调节, *ABI4*基因的表达还受到多种激素的共同调节。例如, 拟南芥根部*ABI4*的表达被ABA和细胞分裂素(cytokinin, CTK)诱导, 但受生长素(auxin)抑制; 水杨酸(salicylic acid, SA)和茉莉酸(jasmonic acid, JA)均能诱导幼苗期*ABI4*的表达(Kong等2013)。ABI4还参与SA和JA诱导的ABI5的表达, ABI4在SA和JA诱导三酰甘油积累的过程中存在交叉对话。ABI4也能与包括ABI5在内的一类bZIP转录因子协同调控下游靶标基因的表达(Reeves等2011)。此外, 转录因子WRKY18/40/60三者通过互作与ABI4启动子区域W-box结合负调控ABI4转录, 从而调控ABA信号转导(Liu等2012)。

4 ABI4在信号转导中的作用

ABI4在植物生长发育信号转导途径中具有非常重要的作用(León等2013; Wind等2013; 胡鹏伟等2013)。先前的报道集中阐明了ABI4是ABA和糖信号途径中的关键调控因子, 它调节众多应答ABA/糖信号的下游基因表达, 并参与种子成熟与休眠、种子萌发和幼苗形态建成(Finkelstein等2002; Brocard-Gifford等2003)。最近一系列的研究表明, ABI4参与调节植物质体/线粒体逆向信号通路、脂质降解代谢、侧根发生、氧化还原稳态维持等(Nott等2006; Foyer等2012; Gregorio等2014; Penfield等2006; Shkolnik-Inbar和Bar-Zvi 2010)。

4.1 ABI4参与糖应答信号通路

糖是生物体的能量来源, 亦组成细胞结构的基本单位。植物体感知外界高浓度糖后能负向反馈调节光合作用相关基因的表达, 激活糖合成淀粉的信号通路, 降低光合作用产物含量(Smeekens

和Hellmann 2014)。此外, 外界高浓度糖会导致拟南芥产生明显的生长抑制, 如种子萌发速度减缓、叶绿体发育停滞和子叶无法绿化等(Dekkers等2004)。拟南芥*abi4*突变体具有对葡萄糖和果糖不敏感表型(Huijser等2000; Arenas-Huertero等2000)。糖信号对ABI4的诱导存在时间效应, 7%葡萄糖溶液仅能诱导ABI4表达持续6 d (2 d龄拟南芥; Arroyo等2003)。葡萄糖很可能通过维持ABI4蛋白的稳定性来调控对种子萌发和幼苗生长的抑制效应(Finkelestein等2011)。有意思的是, 在葡萄糖超敏感的突变体*dog1* (delay of germination1)和*SCARECROW*中ABI4表达受明显的诱导, 这说明ABI4在调控葡萄糖引起的幼苗形态建成中具有重要作用(Teng等2008; Cui等2012)。

*abi4*是通过遗传筛选ABA不敏感突变体得到的(Finkelstein 1994)。进一步的遗传精细定位鉴定发现, 一系列糖应答不敏感突变体均是由于*ABI4*等位基因发生突变导致, 例如*sun6*、*sis5*、*isi3*和*gin6*等(Huijser等2000; Arenas-Huertero等2012)。通过正向和反向遗传学手段, 已有研究集中阐述了ABI4介导的糖信号通路和幼苗形态建成受阻的分子机制。ABI4通过结合糖应答基因启动子区域CE1-like基序元件来调控基因表达, 如淀粉合成途径中的ADP-葡萄糖焦磷酸化酶大亚基*ApL3*和淀粉分支酶*SBE2.2* (Bossi等2009)。Rook等(2001)后续利用糖诱导基因*ApL3*的启动子区域作为遗传筛选标记筛选到蔗糖不敏感突变体*isi* (*impaired sucrose induction)*。最近, Li等(2014)通过拟南芥Col和C24生态型杂交的F2群体鉴定到了一个糖信号感知数量性状基因座(*GSQ11*), 该基因编码一个NAC家族转录因子ANAC060。ABI4转录因子结合启动子正向调控*GSQ11/ANAC060*转录, 葡萄糖信号通过ABA信号通路来调控*GSQ11/ANAC060*的基因表达。*anac060*突变体对ABA和高浓度葡萄糖不敏感, 葡萄糖诱导的ABA含量上升和*ABI4*表达也在*anac060*中被削弱。这说明*ANAC060*突变对*ABI4*产生负反馈调节, 从而导致对葡萄糖不敏感。

4.2 ABI4参与种子休眠和萌发

种子休眠是植物重要的适应特性之一。植物内源激素ABA和赤霉素GA共同调控种子休眠和萌发, 它们之间存在拮抗效应。ABA含量在种子休眠阶段较高, 而在种子发芽前期ABA含量会迅速降低。研究表明, *abi4*存在早萌现象, 而ABI4过表达株系(*OE-ABI4*)则出现萌发滞后的现象(Shu等2013)。未经低温层积处理的*abi4*干燥种子中ABA含量显著低于野生型, 而GA含量高于野生型, 这是由于一系列ABA和GA合成基因表达发生改变引起的。拟南芥*CYP707A*基因家族编码脱落酸羟化酶, 其中*CYP707A1*和*CYP707A2*是ABA代谢过程中的关键酶, 在种子萌发过程中该酶使ABA羟基化导致种子产生早萌的现象。ABI4通过结合基因启动子区域来竞争性抑制*CYP707A1*和*CYP707A2*基因的表达。有趣的是, *abi4*亦能挽救*cyp707a1*和*cyp707a2*突变体种子萌发延迟的现象。这些结果说明ABI4通过ABA和GA代谢来调节拟南芥种子休眠和萌发。

ABI4的表达量随着种子的萌发和幼苗形态建成而逐步降低(Shkolnik-Inbar和Bar-Zvi 2011)。与之相应的是, 过量表达ABI4能加剧ABA引起的拟南芥种子萌发受抑(Finkelestein等2011)。ABI4与ABI3和ABI5在调控ABA应答及其抑制的种子萌发过程中存在协同互作现象(Söderman等2000)。ABI4调控的种子萌发和幼苗形态建成还需要其他因子的参与, 如RAV1、MYB96和ABH1等。其中, RAV1 (Related to ABI3/VP1)是一种包含AP2和B3两种DNA结合结构域的转录因子, 它对ABA抑制的种子萌发和早期幼苗发育信号途径起负调控作用, *rav1*突变体对ABA抑制的种子萌发和幼苗形态建成超敏感, 而*RAV1*过表达植株则对ABA不敏感。RAV1通过与ABI3/4/5的启动子结合来抑制它们的表达, 进而控制对ABA的应答(Feng等2014)。MYB96是一种响应脱落酸R2R3型MYB转录因子(Seo等2009)。*myb96*突变体种子的萌发对ABA不敏感, 而*MYB96*过表达植株则对ABA超敏感(Lee等2015)。MYB96能直接结合*ABI4*启动子区域正向调控ABI4表达, 从而影响ABA抑制的种子萌发。*ABH1*编码CBC蛋白大亚基(CAP binding complex), 它负责mRNA的5'帽子结构结合并参与RNA聚合酶II的转录和pri-miRNA的成熟加工。有趣的是, *abh1*突变体种子萌发对ABA超敏感的表型能被*ABI4*突变所逆转(Daszkowska-Golec等2013)。同时, *ABH1*突变引起的*MYB33*和*MYB101*表达上调亦

能被*ABI4*突变所逆转, 这说明ABH1和ABI4在ABA信号中存在相互联系。

三酰甘油(triacylglycerol, TAG)是种子萌发过程中的重要能源物质。二脂酰甘油脂酰基转移酶(Diglyceride acyltransferase1, DGAT1)是TAG合成途径的限速酶。ABI4促进TAG合成。研究发现, ABA诱导的*DGAT1*表达和TAG含量的被*ABI4*突变抑制(Yang等2011), ABI4能与*DGAT1*启动子区域CE1-like元件结合来参与缺氮、ABA和高盐对TAG合成调控(Yang等2011; Kong等2013)。另一方面, ABI4通过抑制TAG降解参与ABA抑制的种子萌发(Penfield等2006)。

4.3 ABI4参与质体/线粒体反向信号通路

种子萌发后, 叶绿体的发育是幼苗形态建成的标志性事件。叶绿体细胞器含有3 000多个蛋白, 仅5%由叶绿体自身基因组编码, 剩余的则由核基因编码(nuclear encoded plastid proteins, NEPP)。叶绿体自身基因和NEPP这两类编码基因互相协调, 在叶绿体发育过程中具有重要作用(Nott等2006; Zhang等2015)。半自主性细胞器(叶绿体和线粒体)亦能通过反向信号通路向细胞核传递信号, 进而调节NEPP的表达。质体反向信号通路主要分为三种途径: 质体基因表达(plastid gene expression, PGE)通路、四吡咯化合物(tetrapyrrole)和质体蛋白输入(plastid protein import)。林可霉素(lincomycin)是叶绿体基因转录翻译的抑制剂(Sullivan和Gray 1999), 当lincomycin使叶绿体发育过程受阻时即产生质体反向信号, 细胞核编码的NEPP类基因表达下调(Nott等2006; Kleine等2009; Pogson等2008)。

GUN1 (genome uncoupled1)是质体PGE通路的重要功能蛋白, 它是pentatricopeptide repeat家族成员(Larkin 2014)。林可霉素几乎完全抑制了野生型NEPP基因*LHCB*的表达, 但*LHCB*的抑制在*gun1*突变体受严重削弱(Koussevitzky等2007; Sun等2011)。ABI4是GUN1介导的PGE通路调控质体反向信号的下游靶标。*abi4*突变体也具有对林可霉素不敏感的表型, 程度较*gun1*稍弱。过表达*ABI4*能回补林可霉素无法在*gun1*突变体中诱导*LHCB*的现象。有趣的是, ABI4介导的质体反向信号和糖信号可能存在交叉对话。高浓度葡萄糖几乎完全抑制了野生型中*LHCB*基因的表达, 这种抑制效应在*abi4*中被部分削弱, *gun1*突变体则完全不受影响。Sun等(2011)发现一个定位于拟南芥叶绿体外背膜上的植物同源结合域(plant homeodomain, PHD)转录因子PTM (At5g35210), 它参与了GUN1-ABI4介导的质体反向信号通路。质体反向信号驱动PTM蛋白N端水解, 产生的58 kDa蛋白定位于细胞核。一系列诱导产生质体反向信号的因素(如高光和林可霉素等)均能诱导PTM的表达。PTM通过结合ABI4启动子–288~–20区域来正向调控ABI4表达。进一步实验发现, PTM锚定ABI4启动子的过程受质体反向信号诱导的组蛋白甲基化驱动。ABI4对光合作用有关的核编码基因(如LHCB等)的表达则是通过直接竞争结合该类基因启动子区G-box引起的。

活性氧(reactive oxygen species, ROS)也参与ABI4介导的反向信号通路(León等2013)。线粒体呼吸链电子传递过程是植物ROS的主要来源之一。当线粒体呼吸链受抑时, 交替氧化酶(Alternative oxidase 1a, AOX1a)产生的ROS能传递线粒体反向信号(Popov 2003; Ng等2014)。ABI4通过与*AOX1a*启动子区域的CE1基序结合来抑制*AOX1A*表达(Giraud等2009)。Yao等(2015)鉴定了一个与根部分生组织细胞分裂有关的线粒体蛋白RRG (retarded root growth)。*RRG*突变抑制了ABA诱导的ROS的产生, ABA对*AOX1a*和*ABI4*的诱导能被*RRG*突变削弱, 这说明RRG蛋白参与了ABI4调控的线粒体活性氧反向信号。转录因子ZAT10/12调控细胞质抗坏血酸过氧化物酶cAPX来清除过量产生的ROS (Mitter等2009)。在强光照和除草剂等条件下, 拟南芥野生型*ZAT10/12*基因表达量迅速升高, 而这种诱导趋势在*gun1*和*abi4*突变体中被明显削弱(Koussevitzky等2007), 这暗示着ROS信号和GUN1-ABI4介导的质体反向信号存在某种联系。此外, ABI4也被证实参与了抗坏血酸维持的活性氧平衡。VTC1和VTC2是合成抗坏血酸途径中的关键酶。*vtc1*和*vtc2*突变体与*abi4*的转录表达谱中存在大量重叠调控基因。同时*abi4*的莲座叶抗坏血酸含量高于野生型, 这也说明了ABI4在抗坏血酸维持活性氧平衡中的功能(Kerchev等2011; Foyer等2012)。当ROS过量产生时, ABI4还能通过

结合CBFA (CCAAT binding factor A)来控制四吡咯化合物HAP (heme activator protein)的形成, 进而调控质体反向信号通路中相关基因的表达(Zhang等2013)。以上结果表明ROS代谢在ABI4介导的反向信号通路中具有重要的作用。

4.4 ABI4参与侧根发生

研究表明, 在拟南芥根部成熟区检测到*ABI4*基因的表达。有趣的是, *ABI4*表达量影响侧根发生。*abi4*突变体的侧根密度和长度均高于野生型, 而其过表达后则减弱了侧根发生(Shkolnik-Inbar和Bar-Zvi 2010)。生长素的极性运输是调控植物侧根发生的关键因素, 这一过程由生长素运输载体PIN介导, ABI4通过调节生长素的极性运输来介导ABA和CTK抑制的拟南芥侧根发生。*ABI4*的表达受ABA和CTK的诱导, 但受生长素抑制。*abi4*突变体侧根发育不受ABA和CTK影响, 同时*PIN1*基因的表达亦对ABA和CTK不敏感, 而*ABI4*过表达株系的PIN1蛋白表达量明显降低。因此, ABA和CTK通过诱导*ABI4*基因的表达来抑制*PIN1*的表达, 从而影响生长素极性运输, 抑制侧根发生。

5 小结与展望

ABI4在植物生长发育和对逆境应答的过程中扮演了不可或缺的角色。它已逐渐被认为是具有多重功能的核心调节蛋白, 参与调控植物的萌发和幼苗形态建成、ABA应答、糖信号、质体/线粒体反向信号和光合作用等的信号传递。虽然近年来的研究使得我们对于ABI4的功能有了一定的认识, 但关于其作用的研究仍然不够全面, 如ABI4参与信号转导中一些至关重要的分子机制及与其他蛋白之间的互作关系等值得深入研究。已经知道, PTM传递GUN1介导的质体反向信号进入细胞核, 通过组蛋白甲基化修饰来调控ABI4的转录水平, 进而调节一系列NEPP基因表达(Sun等2011)。但是受抑制的*LHCB*基因的表达在*ptm/abi4*和*ptm/gun1*突变体中仅能部分被恢复, *ABI4*的表达在*ptm*突变体中仅被部分削弱, 这强烈暗示着GUN1-PTM-ABI4介导的质体反向信号还需要其他因子的参与。先前的研究表明, 一氧化氮、一氧化碳和硫化氢等气体信号分子均与ABA信号转导有关(Cao等2011; Castillo等2015; Jin等2013; Scuffi等2014; Wang等2015), 发掘并鉴定ABI4与上述分子之间的功能互作机制也将帮助我们更全面认识ABI4生物学功能。

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Research advances of transcription factor ABI4 in plants

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Abstract: Abscisic acid-insensitive 4 (ABI4) is a member of APETALA2/ethylene responsive factor (AP2/ERF) family, which was discovered and characterized to be an abscisic acid (ABA) signaling responsive transcription factor. Recent investigations illustrated that ABI4 is a multiple-faced regulatory factor in diverse cellular processes. These biological events include seed germination and seedling establishment, plastid and/or mitochondrial retrograde signaling, lipid metabolism, sugar signaling, and ABA responses etc. This paper summarized the latest research progress of ABI4 in terms of its structure characteristics, transcriptional regulation pattern, gene expression regulation, and signal transduction pathway.

Key words: plant; ABI4; transcription factor; signal transduction

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