



# 植物内源ABA水平的动态调控机制

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**摘要** ABA具有调节植物生长发育和对环境胁迫做出快速反应的重要功能, 植物内源ABA水平受到ABA合成、代谢及转运等途径的复杂调控。该文综述了近年来植物ABA从头合成、羟基化代谢、可逆糖基化代谢及ABA转运等领域的最新研究进展, 重点讨论ABA合成与代谢基因的表达调控机制, 并展望了今后的研究方向。

**关键词** 脱落酸, ABA合成, ABA代谢, ABA转运

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植物激素脱落酸(abscisic acid, ABA)能调节种子成熟、休眠与萌发、气孔运动及叶片衰老等重要生理过程, 并介导植物对环境胁迫的快速反应。植物特定组织中内源ABA水平受ABA从头合成、羟基化代谢、糖基化失活和去糖基活化以及ABA长距离转运等的动态调控(魏开发等, 2012; 伍静辉等, 2018; Ma et al., 2018) (图1A)。近20年来, 植物ABA合成、代谢和信号转导研究取得了重要进展, 但ABA合成与代谢基因的启动和表达调控机制的研究却相对滞后。本文依据近年来植物内源ABA水平的动态调控机制的相关研究, 综述了植物ABA从头合成、羟基化与糖基化代谢以及ABA转运等领域的最新研究成果, 着重讨论ABA合成与代谢基因的表达调控机制(图1B), 并展望了今后的研究方向, 旨在为植物抗逆研究提供理论参考。

## 1 植物ABA从头合成的调控机制

### 1.1 ABA合成酶基因表达谱及突变体表型

高等植物ABA从头(*de novo*)合成的第1步是玉米黄质(zeaxanthin)被玉米黄质环氧酶(zeaxanthin epoxidase, ZEP)催化形成环氧玉米黄质(antheraxanthin), 继而环氧化为紫黄质(violaxanthin), 紫黄质异构化为9'-顺式-紫黄质(9'-*cis*-violaxanthin), 或被新黄质合成

酶(neoxanthin synthase, ABA4)催化为反式-新黄质(*trans*-neoxanthin), 进而异构化为9'-顺式-新黄质(9'-*cis*-neoxanthin) (Nambara and Marion-Poll, 2005)。自1996年以来相继从烟草(*Nicotiana glauca*) (NpABA2)、拟南芥(*Arabidopsis thaliana*) (AtABA1/LOS6)、水稻(*Oryza sativa*) (OsABA1)、番茄(*Solanum lycopersicum*) (SlHPP3)和长豇豆(*Vigna unguiculata*) (VuABA1)中克隆了ZEP基因, 不同物种的ZEP功能缺失突变体都表现为内源ABA含量降低、种子不休眠、植株呈萎蔫状及干旱不能诱导ABA合成等特征(Endo et al., 2014)。拟南芥*aba1*突变体株型矮小, 叶片形状和内部结构畸形; 而ABA1过表达植株的抗盐和抗旱性增强, 在光照条件下气孔开度小于野生型, 说明ABA具有调节植物生长发育和抗逆性的重要功能(Barrero et al., 2005; Park et al., 2008)。植物ABA4蛋白高度保守, 定位于叶绿体内囊体膜。拟南芥*aba4*突变体仅营养组织与野生型有差异, 脱水不能诱导合成ABA, 推测ABA4参与脱水胁迫下的ABA合成(North et al., 2007)。

ABA从头合成的限速步骤是叶绿体类囊体膜和基质的9'-顺式-环氧类胡萝卜素双加氧酶(9'-*cis*-epoxycarotenoid-dioxygenase, NCED)将9'-顺式-紫黄质和9'-顺式-新黄质氧化切割为黄质醛(xanthoxin)。Tan等(1997)在玉米胎生突变体*vp14*中克隆到VP14基因, 并发现叶片萎蔫对VP14基因的诱导与ABA增加一致。

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Schwartz等(1997)证明重组的VP14蛋白可切割9'-顺式-紫黄质形成黄质醛,推测VP14具有NCED功能。目前,已证明植物NCED蛋白是一个多基因家族,先后从水稻(*OsNCED1-5*)、拟南芥(*AtNCED2/3/5/6/9*)、四季豆(*Phaseolus vulgaris*) (*PvNCED1*)、鳄梨(*Persea americana*) (*PaNCED1/3*)以及菟丝子(*Cuscuta reflexa*) (*CrNCED1/2*)中克隆到NCED基因(Endo et al., 2014)。水稻*OsNCED1*在叶片中表达量最高,*OsNCED2*主要在种子中表达,*OsNCED5*参与水稻籽粒灌浆期ABA的合成,*OsNCED3*转基因拟南芥ABA含量增加,叶片形态发生改变(Zhu et al., 2009)。拟南芥基因组有9个VP14同源序列(*AtNCED1-9*),其中*AtNCED2/3/5/6/9*编码蛋白具有NCED酶活性,*AtNCED2/3*在植物根和叶中表达量较高。干旱迅速诱导*AtNCED3*基因表达并促进ABA合成,*AtNCED3*过表达株系的内源ABA水平较高、叶片蒸腾速率较低、抗旱性较强,且ABA响应基因的转录本增加(任慧波等, 2007; Hao et al., 2009)。种子成熟晚期*AtNCED5/6/9*表达显著增强,*AtNCED6*在胚乳中表达,*AtNCED5/9*在胚乳和胚中表达。*nced6/nced9*双突变体种子内源ABA含量和休眠程度显著降低,说明*AtNCED6/9*主要调控种子休眠(Tan et al., 2003; Lefebvre et al., 2006)。*nced3/nced5*双突变体内源ABA含量减少、营养器官变小且植株抗旱性降低,说明*AtNCED3/5*参与植物生长发育和胁迫响应(Frey et al., 2012)。

ABA合成最后2步是胞质溶胶中的黄质醛被短链脱氢酶/还原酶(short chain dehydrogenase/reductase-like, SDR1)还原为ABA醛(ABA aldehyde),继而被ABA醛氧化酶(ABA-aldehyde oxidase, AAO)和钼辅因子硫化酶(molybdenum cofactor sulfuryase, MoCo)转化为活性ABA。拟南芥仅有1个*AtABA/SDR1* (*abscisic acid 2*)基因,在所有器官中组成型表达,且不受ABA、盐和甘露醇诱导。*aba2*突变体内源ABA含量减少、种子不休眠、植株呈萎蔫状且主根变短,外源ABA可恢复其主根根长;而*AtABA2*过表达株系的表型与之相反(Lin et al., 2007)。拟南芥有4个AAO基因(*AtAAO1-4*),*AtAAO1*和*AtAAO4*分别在干种子和发育中的角果大量表达;*AtAAO3*是种子和失水叶片中ABA合成关键酶,*aao3*突变体植株呈萎蔫状、种子休眠程度略有降低(Seo et al., 2004)。番茄*sitiens*突变体不能将ABA醛转化为活性ABA,导致内源ABA缺

失而呈萎蔫状,*AtAAO3*异位表达能恢复番茄*sitiens*表型(Harrison et al., 2011)。豌豆(*Pisum sativum*)中有3个*PsAO*基因,重组*PsAO3*蛋白显示AAO酶活性,干旱使豌豆叶和根的*PsAO3*基因表达量增加(Zdunek-Zastocka and Sobczak, 2013)。拟南芥*AtLOS5/ABA3*、番茄*SiFLACCA*和烟草*NpABA1/CKP1*基因编码MoCo酶,可将ABA醛转化为ABA(Endo et al., 2014)。*AtLOS5/ABA3*在所有器官中均表达,受干旱、盐和ABA诱导,*los5*突变体内源ABA含量减少、叶片蒸腾速率增加,抗冷、抗盐及抗旱性减弱,但*AtLOS5*过表达可提高转基因棉花(*Gossypium hirsutum*)的内源ABA水平和抗旱性(Xiong et al., 2001; Yue et al., 2012)。

## 1.2 ABA合成酶基因的表达调控

近年来,植物ABA合成酶基因的表达调控研究取得了重要进展。参与*AtABA1*、*AtNCED2/3/5/6/9*、*AhNCED1*、*AtAAO3*和*AtABA3*基因表达调控的相关转录因子与调节蛋白见图1B。

已有研究表明,植物多个转录因子家族参与ABA合成酶基因的转录调控,其中MYB、AP2/ERF、WRKY、NAC、bHLH和NGA等家族的转录因子促进ABA合成基因转录,而NFX和HD-ZIP等转录因子抑制ABA合成基因的表达。例如,拟南芥*AtMYB96*通过结合*AtNCED2/6*启动子促进ABA合成和种子休眠(Lee et al., 2015)。*AP2/ERF* (APETALA2/ethylene-responsive factor)家族的*AtORA47* (octadecanoid-responsive AP2/ERF-domain transcription factor 47)结合*AtNCED3/9*启动子的O-box元件,促进损伤时ABA合成与信号转导(Chen et al., 2016);而*AtDREB2C* (dehydration-responsive element binding factor)通过结合*AtNCED9*启动子的DRE元件激活高温胁迫下种子的ABA合成(Je et al., 2014)。拟南芥*AtWRKY57*结合*AtNCED3*启动子,促进干旱诱导的ABA合成、提高植物的耐旱性(Jiang et al., 2012)。*NAC*转录因子中的*AtATAF1*结合*AtNCED3*启动子,促进ABA合成(Jensen et al., 2013)。*AtNAP* (NAC-like, activated by AP3/PI)结合*AtAAO3*启动子,促进衰老叶片ABA合成与叶绿素降解(Yang et al., 2014)。与*AtNAP*同源的谷子(*Setaria italica*) *SiNAC1*促进ABA合成,是叶片衰老的正调节因子(Ren et al., 2018)。*AtbHLH68*过表达株系的抗旱性增强、植株侧

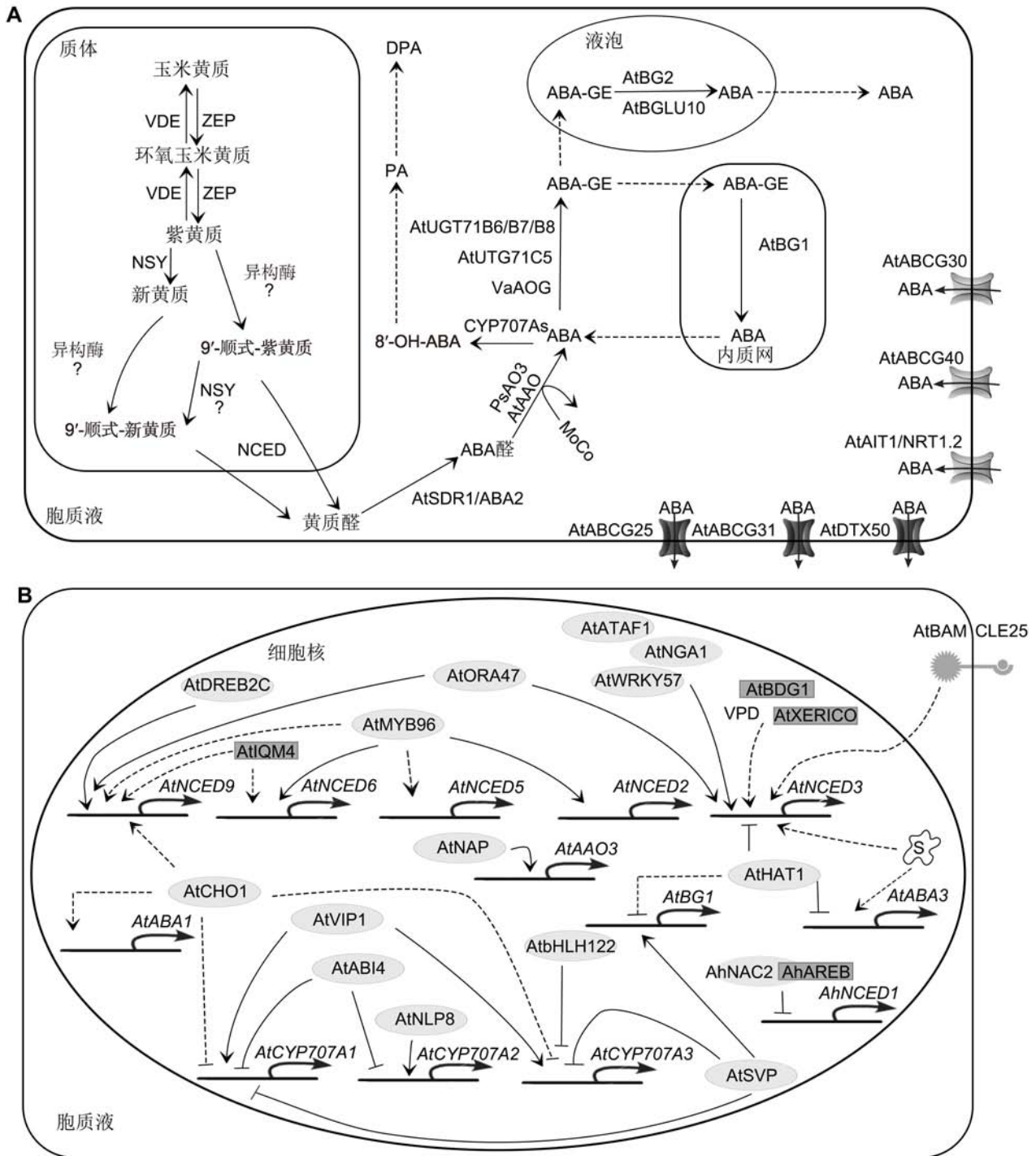


图1 植物ABA合成、代谢和转运途径及ABA合成与代谢基因的表达调控

(A) ABA合成、代谢和转运途径; (B) ABA合成与代谢基因的表达调控。椭圆表示转录因子, 矩形表示调节蛋白。

**Figure 1** The ABA biosynthesis, catabolism and transportation pathway and the expression regulation of the ABA biosynthetic and catabolic genes in plant

(A) The ABA biosynthesis, catabolism and transportation pathway; (B) The expression regulation of the ABA biosynthetic and catabolic genes. The ellipses represent transcription factors, the rectangles represent regulatory proteins.

根减少,推测 *AtbHLH68* 通过ABA依赖途径调节ABA代谢和/或信号(Le Hir et al., 2017)。NGAs (NGA TH-As) 家族转录因子 *AtNGA1* 结合 *AtNCED3* 启动子的NBE (NGA-binding element) 顺式元件,通过激活 *AtNCED3* 转录促进干旱诱导的ABA合成(Sato et al., 2018)。拟南芥 *AtNFXL2* (nuclear transcription factor X-box binding protein-like 2) 抑制内源ABA合成和信号, *atnfxl2* 缺失突变体气孔导度降低,耐旱性增强; *AtNFXL2* 同工型 *AtNFXL2-78* 直接抑制 *SHINE* (*SHINE1/SHN1*, *SHN2*, *SHN3*) 基因和 *BDG1* (*BODYGUARD1*) 基因转录, *SHINE* 与表皮蜡质合成相关, *BDG1* 调控表皮角质层发育,二者同时促进胁迫环境下植物ABA的合成(Lisso et al., 2011, 2012)。除正反馈调节外,ABA合成还存在负反馈调节,如花生(*Arachis hypogaea*) AhNAC2和AhAREB1蛋白复合体介导ABA合成的负反馈调节,外源ABA促进AhNAC2和AhAREB1结合到 *AhNCED1* 启动子,进而抑制 *AhNCED1* 转录,其中AhAREB1是主要负调节因子(Liu et al., 2016)。HD-ZIP II 转录因子 *AtHAT1* (homeodomain-leucine zipper protein 1) 结合 *AtABA3* 和 *AtNCED3* 的启动子,抑制ABA合成和信号(Tan et al., 2018)。

植物LSM (like-Sm protein) 和XERICO (greek for 'drought tolerant') 蛋白分别在mRNA代谢和蛋白水平调控内源ABA水平。LSMs是真核生物中高度保守的蛋白家族,参与RNA代谢(如剪切、脱帽和降解)。拟南芥 *sad1* (*supersensitive to ABA and drought*) 突变体对干旱和外源ABA敏感性增强, *sad1* 植物缺失ABA合成的正反馈调节和干旱诱导的ABA合成,图位克隆确定 *SAD1* 基因编码LSM5蛋白(Xiong et al., 2001)。转录组分析表明, *SAD1/LSM5* 蛋白可动态调控拟南芥转录组前体mRNA剪切效率和剪切位点的识别,表明 *SAD1/LSM5* 可能通过调控胁迫基因的表达而介导植物胁迫反应(Cui et al., 2014)。LSM1-7复合体通过促进mRNA脱帽和随后的5'-3'降解参与精确的mRNA流转(turnover)和P-bodies形成。当拟南芥暴露在冷和高盐环境时,LSM1-7复合体通过差异化调控 *AtNCED3* 和 *AtNCED5* mRNA流转而调节内源ABA水平(Perea-Resa et al., 2016)。拟南芥XERICO蛋白C端含RING-H2锌指基序, *XERICO* 表达上调能显著提高细胞ABA水平并增强植物的抗旱性,已知很

多RING-H2蛋白具有E3泛素连接酶功能,而酵母双杂交实验显示, *AtUBC8* (E2 ubiquitin-conjugating enzyme) 和 *AtTLP9* (ASK1-interacting F-box protein) 是XERICO潜在的互作蛋白,推测XERICO在蛋白水平调节细胞ABA水平(Ko et al., 2006)。

最新研究显示,脱水胁迫时叶片VPD (vapour pressure deficit) 和根源CLE25肽触发ABA合成基因启动转录。大量证据表明,被子植物叶片VPD升高触发ABA合成,诱导气孔快速关闭,且证实叶片膨压降低仅需5分钟就能诱导 *AtNCED3* 转录、ABA合成增加,引起气孔关闭,但膨压感知受体候选蛋白 *AtAHK1* (*Arabidopsis* histidine kinase 1) 在此过程中未发挥关键作用(Sussmilch et al., 2017)。拟南芥CLE25肽 (*clavata3/embryo-surrounding region-related 25*) 通过维管束由根向叶传递水分亏缺信号,并联合叶片BAM (barely any meristem) 激酶受体调控ABA合成和叶片水分蒸腾;脱水胁迫促进根CLE25肽表达,根源CLE25肽被转运到叶促进ABA积累与气孔关闭;脱水胁迫不能诱导 *cle25* 突变体的 *AtNCED3* 表达,但外源CLE25肽可恢复突变体 *AtNCED3* 表达,证明CLE25-BAM是植物脱水胁迫中远距离信号转导的重要元件(Takahashi et al., 2018)。

此外,硫元素供应、角质层合成基因、钙调素信号蛋白也参与ABA生物合成的调控。叶绿体硫转运蛋白 *AtSULTR3;1* 功能缺失显著降低幼苗AAO酶活性和内源ABA水平,硫元素供应可提高 *AtNCED3* 和 *AtABA3* 转录水平;ABA促进 *AtSULTR3;1* 和其它硫代谢基因转录,表明硫在植物响应环境胁迫时发挥重要作用(Cao et al., 2014)。干旱使木质部汁液硫酸盐含量增加,进而促进保卫细胞 *AtNCED3* 表达和ABA合成,引起气孔关闭(Malcheska et al., 2017)。已知植物角质层作为物理屏障减少水分流失并介导ABA合成和信号转导,进而调控植物渗透胁迫反应。拟南芥 *ced1* (*9-cis-epoxycarotenoid dioxygenase defective 1*) 突变体对轻微渗透胁迫极为敏感, *CED1/BDG1* 基因促进ABA合成基因的表达(Wang et al., 2011b)。植物钙调素类似蛋白 *AtCML37* (calmodulin-like 37) 和 *AtCML42* 拮抗调控干旱胁迫诱导的ABA积累, *AtCML37* 为正调节因子,而 *AtCML42* 为负调节因子(Scholz et al., 2015)。我们也发现钙调素结合蛋白 *AtIQM4* 能促进种子ABA合成, *iqm4* 突变体种子ABA

含量降低, 角果 *AtNCED6/9* 表达量显著降低(Zhou et al., 2018)。

## 2 植物ABA羟基化代谢的表达调控

### 2.1 ABA代谢酶基因的表达谱及突变体表型

植物ABA在8'-羟化酶催化下生成8'-OH-ABA, 通过亲核反应生成PA (phaseic acid)或还原为DPA (dehydrophaseic acid)。不同物种8'-羟化酶家族成员的数量不尽相同: 拟南芥4个(*AtCYP707A1-4*), 水稻3个(*OsABA8ox1-3*), 大麦 (*Hordeum vulgare*) 2个(*HvABA8'OH1, 2*), 莴苣(*Lactuca sativa*) 4个(*LsABA8ox1-4*), 四季豆3个(*PvCYP707A1-3*), 玉米5个(*ABA8Ox1a/1b/2/3a/3b*) (Vallabhaneni and Wurtzel, 2010; Endo et al., 2014)。

拟南芥 *AtCYP707As* 转录本广泛存在于各种器官组织, 但表达量有所不同。例如, 花和角果中 *AtCYP707A1* 表达量最高, *AtCYP707A2* 和 *AtCYP707A3* 在叶、茎和根中表达较高, 但 *AtCYP707A4* 在所有组织中表达都较低, 种子吸胀增强 *AtCYP707A2* 的表达, 干旱抑制而复水促进所有 *AtCYP707As* 表达(Kushiro et al., 2004)。 *AtCYP707A1* 主要调节成熟中期种子ABA水平, 而 *AtCYP707A2* 调控成熟晚期至萌发阶段的ABA代谢(Okamoto et al., 2006)。 *AtCYP707A3* 是主要的干旱应答基因, 正常生长环境中的 *cyp707a3* 突变体内源ABA含量高于野生型、叶片蒸腾速率降低并对外源ABA敏感; 干旱促进突变体积累更多ABA, 植株耐旱性显著增强, 但过表达植株表型相反(Umezawa et al., 2006)。在正常生长环境中, *cyp707a1* 和 *cyp707a3* 突变体叶片的气孔导度都较低; 高湿环境显著增强 *AtCYP707A1/3* 表达、促进ABA降解, *cyp707a3* 突变体可以积累更高水平的ABA, 然而 *cyp707a1* 突变体的ABA水平与野生型相似。研究表明, 在高湿环境中 *AtCYP707A1* 使保卫细胞内的ABA失活, *AtCYP707A3* 则主要降解维管组织中移动的ABA, 植物气孔运动受到来自维管组织的ABA和保卫细胞内的ABA代谢共同调控(Okamoto et al., 2009)。

### 2.2 ABA代谢酶基因的表达调控

已有研究表明若干转录因子参与ABA代谢基因的表达调控。拟南芥CHO1 (CHOTTO1)为AP2/ERF型转

录因子, 促进 *AtABA1* 和 *AtNCED9*、抑制 *AtCYP707A2/3* 转录, 调控吸胀期种子ABA抑制的赤霉素合成(Yano et al., 2009)。AP2/ERF型转录因子ABI4促进ABA积累和种子休眠, 通过结合 *AtCYP707A1/2* 启动子并抑制其转录来实现(Shu et al., 2013)。拟南芥NLP8 (NIN-like protein 8)以硝酸盐依赖的方式结合 *AtCYP707A2* 的启动子并激活其转录, 降低种子ABA水平, 促进种子萌发(Matakiadis et al., 2009; Yan et al., 2016)。bZIP家族转录因子VIP1 (VirE2-interacting protein 1)为渗透胁迫的调节因子, VIP1直接结合 *AtCYP707A1/3* 启动子并激活其转录(Tsuguma et al., 2012)。拟南芥bHLH122是干旱、NaCl和渗透胁迫的正调节因子, bHLH122结合 *AtCYP707A3* 启动子G-/E-box元件并抑制其表达, 进而抑制ABA代谢(Liu et al., 2014)。拟南芥成花抑制因子SVP (short vegetative phase)直接结合 *AtCYP707A1/3* 和 *AtBG1* 启动子的CArG Motif元件, 抑制 *AtCYP707A1/3*, 促进 *AtBG1* 转录, 表明SVP是干旱胁迫下ABA代谢的重要调控因子(Wang et al., 2018)。

## 3 植物ABA可逆糖基化代谢的表达调控

内源ABA水平还受到ABA特异的葡萄糖基转移酶(ABA-uridine diphosphate glucosyltransferase, ABA-UGT)和 $\beta$ -葡萄糖苷酶( $\beta$ -glucosidase, BG)介导的可逆糖基化代谢调节。研究人员从赤豆(*V. angularis*)中克隆了编码ABA-UGT酶的基因AOG, UGT可催化ABA与UDPG结合生成ABA葡萄糖苷酯(ABA-glucoside ester, ABA-GE); ABA-GE缺乏生物学活性, 在液泡或质外体中积累(Xu et al., 2002; Priest et al., 2006)。拟南芥UGT家族的E亚家族中UGT71B6/7/8参与调节内源ABA水平, 影响 *AtCYP707A1-4* 表达, 在脱水和高盐胁迫以及种子萌发和生长发育进程中发挥重要调节作用(Dong et al., 2014)。此外, *AtUGT71C5* 也可催化ABA转化为ABA-GE, 与野生型相比, *ugt71c5* 突变体的种子萌发延迟且叶片气孔变小, 抗旱性增强(Liu et al., 2015)。

干旱条件下, 液泡或质外体贮存的ABA-GE迅速被BG水解, 生成活性ABA以适应变化的环境。拟南芥 *AtBG1* 在内质网将ABA-GE水解生成ABA, *bg1* 突变体内源ABA含量和抗旱性降低; 脱水迅速诱导BG1蛋白多聚化后显著增强BG活性, 从而加速ABA生成,

ABA正反馈激活BG1蛋白多聚化(Lee et al., 2006)。AtBG2以复合物形式储存在中央液泡,脱水诱导AtBG2表达,bg2突变体对脱水和盐胁迫敏感,AtBG2过表达可互补bg1表型(Xu et al., 2012)。在低湿环境下,拟南芥aba3-1突变体中AtBG1转录水平极显著高于野生型,说明细胞内ABA-GE水解机制可部分补偿ABA从头合成的缺陷(Bauer et al., 2013)。此外,AtBGLU10编码的BG酶分布在液泡中,bglu10突变体的BG酶活性和ABA含量均降低,且叶面温度和胁迫反应基因表达量也降低,而AtBGLU10过表达株系抗旱性增强(Wang et al., 2011a)。

## 4 植物ABA转运的表达调控

### 4.1 ABA合成位点和作用位点

ABA从头合成途径的最后步骤由SDR1和AAO酶催化,因此,检测SDR1和AAO蛋白定位就可确定ABA合成位点。GFP-和免疫荧光显示,拟南芥AAO3在根尖、韧皮部伴胞细胞和木质部薄壁细胞中含量最高,保卫细胞也有少量蛋白(Koiwai et al., 2004)。免疫组化也发现叶脉薄壁细胞含有大量的AAO3和ABA2蛋白,失水可使薄壁细胞内NCED3蛋白显著增加,证明干旱胁迫下NCED3酶是ABA合成的关键酶(Endo et al., 2008)。GUS染色证明NCED3基因在叶肉细胞、保卫细胞、维管束及根系中都有表达,在根尖表达量最高,证明NCED3酶促进根源ABA合成,但保卫细胞ABA合成量低于其它组织(Tan et al., 2003)。进一步研究表明,保卫细胞ABA合成受到维管细胞合成的ABA正反馈调节,低湿环境下保卫细胞合成的ABA是诱导气孔关闭充分且必要因子(Bauer et al., 2013)。种子内源ABA分别来源于母体维管组织、胚和胚乳细胞(Lefebvre et al., 2006)。总之,植物ABA合成位点包括根尖、维管束伴胞细胞和薄壁细胞、叶肉细胞、保卫细胞、种胚和胚乳细胞。

已证明ABA既在合成位点起作用,也在合成位点周围的靶细胞或远距离靶细胞发挥功能。番茄*flacca*突变体和野生型双向嫁接实验显示,正常环境下嫁接植株叶中ABA浓度不依赖砧木基因型,但根中ABA受到接穗基因型影响,*flacca*接穗植株的ABA含量较低;盐胁迫促进ABA长距离从根向叶转运,砧木基因型影

响接穗的气孔导度,*flacca*砧木的嫁接植株叶面积减少,表明ABA长距离转运影响特定组织的ABA水平(Li et al., 2018)。

### 4.2 ABA转运蛋白

近年来,植物ABC(ATP-binding cassette)蛋白家族的AtABCG40/25/22/30/31、硝酸盐转运蛋白AtNRT1.2(nitrate transporter 1.2)/AIT1(ABA-importing transporter 1)和MATE家族的AtDTX50(detoxification efflux carrier 50)蛋白相继被鉴定为ABA转运蛋白,调控植物内源ABA水平和信号。植物细胞中不同的ABA转运蛋白具有不同的转运功能,一些转运蛋白存在功能冗余。例如,拟南芥AtABCG40和AtNRT1.2为ABA输入转运蛋白(importer),而AtABCG25和AtDXT50为ABA输出转运蛋白(exporter)(Boursiac et al., 2013; Kuromori et al., 2018)。

AtABCG40/PDR12(pleiotropic drug resistance 12)定位在保卫细胞和其它细胞的质膜,*abcg40*突变体原生质体对ABA吸收能力显著下降(Kang et al., 2010)。AtABCG25是ABA输出转运蛋白,AtABCG25在维管组织中表达,过表达植株保卫细胞ABA信号增强、植株水分利用率提高(Kuromori et al., 2010, 2016)。AtNRT1.2/AIT1介导质膜ABA输入转运,*nrt-1.2/ait1*突变体对外源ABA敏感性降低(Kanno et al., 2012)。AtABCG40和AtNRT1.2/AIT1介导细胞吸收ABA的空间表达谱不同,AtABCG40在保卫细胞中表达,而AtNRT1.2/AIT1在维管细胞中表达;AtNRT1.2/AIT1与AtABCG25共同调节维管组织向保卫细胞转运ABA,且AtNRT1.2/AIT1介导ABA进入维管组织可能与植物通过木质部和韧皮部进行ABA再分配相关(Kuromori et al., 2018)。拟南芥MATE(DTX/multidrug and toxin compound extrusion)家族成员DTX50蛋白定位在维管细胞和保卫细胞质膜,介导维管细胞和保卫细胞向外转运ABA;外源ABA促进DTX50表达,*dtx50*突变体对ABA敏感、气孔导度较低、抗旱性增强(Zhang et al., 2014)。AtABCG22定位于质膜,具有ABA转运功能,参与ABA转运、合成和信号转导(Kuromori et al., 2011)。此外,研究表明AtABCG25/31/30/40协同参与种子的ABA转运,其中胚乳表达的AtABCG25/31为ABA输出转运蛋白,协同将胚乳细胞合成的ABA转运出去,而种胚表达的



AtABCG30/40为输入转运蛋白, 共同将ABA转运入种胚细胞(Kang et al., 2015)。

研究表明, 细胞质膜上ABA转运蛋白水平的变化能够调控植物ABA的转运。生物胁迫能够以ABA不依赖方式增强网格蛋白介导的胞吞和内体腔囊泡转运, 减少质膜AtABCG25蛋白水平; 外源ABA则是以ABA依赖方式激活胞内体再循环, 提高质膜AtABCG25蛋白水平。研究表明, 质膜上AtABCG25蛋白存在ABA依赖和ABA不依赖2种调节途径, 在调控植物内源ABA水平中发挥重要作用(Park et al., 2016)。

## 5 小结和展望

目前, 高等植物ABA合成、代谢和转运机制研究取得重要突破和进展, 已揭示植物具备维持细胞内源ABA稳态的复杂且精巧的调控机制, 用于平衡植物生长发育和逆境响应的生理过程。植物ABA合成、代谢和转运途径发生在植物体不同组织细胞及亚细胞器, 由各种催化酶和转运蛋白共同参与(图1A)。ABA从头合成和ABA-GE去糖基化途径可以提高靶细胞内源ABA水平; 相反, ABA羟基化代谢和糖基化修饰则会降低ABA水平。ABA可逆糖基化代谢仅需一步反应就可快速改变靶细胞活性ABA水平, 有利于植物对逆境的快速响应。不同的ABA转运蛋白协同地将不同合成场所的ABA转运到靶细胞, 从而提高靶细胞ABA水平, 增强ABA反应。

近年来, ABA合成与代谢酶基因的表达调控研究取得了重要进展(图1B), 已鉴定出许多转录因子、调节蛋白和物理化学因子参与ABA合成代谢基因的转录和表达调控, 但大部分集中在植物对非生物胁迫响应方面。ABA糖基化途径的UGT和BG酶及ABA转运蛋白的表达调控机制尚未见报道。因此, 今后应加强正常生理和生物胁迫条件下植物ABA合成代谢基因的表达调控、ABA糖基化和ABA转运途径的表达调控以及ABA与其它植物激素(如赤霉素和生长素)的互作等领域研究。植物内源ABA水平的动态调控机制研究可为提高农作物抗逆性和增加粮食产量的遗传和分子设计育种提供理论依据。

## 参考文献

任慧波, 范意娟, 魏开发, 高志晖, 李桂芬, 刘静, 李冰冰, 胡建芳, 贾文锁 (2007). *NCED3*基因的持续诱导及ABA合成

与代谢的协同调控在拟南芥ABA信号积累中的作用. 科学通报 52, 59–66.

魏开发, 陈娟, 陈艳峰, 吴凌娟, 贾文锁 (2012). 内源ABA信号水平动态调控的分子机制. 遗传 34, 296–306.

伍静辉, 谢楚萍, 田长恩, 周玉萍 (2018). 脱落酸调控种子休眠和萌发的分子机制. 植物学报 53, 542–555.

Barrero JM, Piqueras P, González-Guzmán M, Serrano R, Rodríguez PL, Ponce MR, Micol JL (2005). A mutational analysis of the *ABA1* gene of *Arabidopsis thaliana* highlights the involvement of ABA in vegetative development. *J Exp Bot* 56, 2071–2083.

Bauer H, Ache P, Lautner S, Fromm J, Hartung W, Al-Rasheid KA, Sonnewald S, Sonnewald U, Kneitz S, Lachmann N, Mendel RR, Bittner F, Hetherington AM, Hedrich R (2013). The stomatal response to reduced relative humidity requires guard cell-autonomous ABA synthesis. *Curr Biol* 23, 53–57.

Boursiac Y, Leran S, Corratgé-Faillie C, Gojon A, Krouk G, Lacombe B (2013). ABA transport and transporters. *Trends Plant Sci* 18, 325–333.

Cao MJ, Wang Z, Zhao Q, Mao JL, Speiser A, Wirtz M, Hell R, Zhu JK, Xiang CB (2014). Sulfate availability affects ABA levels and germination response to ABA and salt stress in *Arabidopsis thaliana*. *Plant J* 77, 604–615.

Chen HY, Hsieh EJ, Cheng MC, Chen CY, Hwang SY, Lin TP (2016). ORA47 (octadecanoid-responsive AP2/ERF-domain transcription factor 47) regulates jasmonic acid and abscisic acid biosynthesis and signaling through binding to a novel *cis*-element. *New Phytol* 211, 599–613.

Cui P, Zhang S, Ding F, Ali S, Xiong L (2014). Dynamic regulation of genome-wide pre-mRNA splicing and stress tolerance by the Sm-like protein LSM5 in *Arabidopsis*. *Genome Biol* 15, R1.

Dong T, Xu ZY, Park Y, Kim DH, Lee Y, Hwang I (2014). Abscisic acid uridine diphosphate glucosyltransferases play a crucial role in abscisic acid homeostasis in *Arabidopsis*. *Plant Physiol* 165, 277–289.

Endo A, Okamoto M, Koshiba T (2014). ABA biosynthetic and catabolic pathways. In: Zhang DP, ed. *Abscisic Acid: Metabolism, Transport and Signaling*. Dordrecht: Springer Press. pp. 21–45.

Endo A, Sawada Y, Takahashi H, Okamoto M, Ikegami K, Koiwai H, Seo M, Toyomasu T, Mitsunashi W, Shinozaki K, Nakazono M, Kamiya Y, Koshiba T, Nambara E (2008). Drought induction of *Arabidopsis* 9-*cis*-epoxycarotenoid dioxygenase occurs in vascular parenchyma cells. *Plant Physiol* 147, 1984–1993.

- Frey A, Effroy D, Lefebvre V, Seo M, Perreau F, Berger A, Sechet J, To A, North HM, Marion-Poll A (2012). Epoxycarotenoid cleavage by NCED5 fine-tunes ABA accumulation and affects seed dormancy and drought tolerance with other NCED family members. *Plant J* **70**, 501–512.
- Hao GP, Zhang XH, Wang YQ, Wu ZY, Huang CL (2009). Nucleotide variation in the NCED3 region of *Arabidopsis thaliana* and its association study with abscisic acid content under drought stress. *J Integr Plant Biol* **51**, 175–183.
- Harrison E, Burbidge A, Okyere JP, Thompson AJ, Taylor IB (2011). Identification of the tomato ABA-deficient mutant sitiens as a member of the ABA-aldehyde oxidase gene family using genetic and genomic analysis. *Plant Growth Regul* **64**, 301–309.
- Je J, Chen H, Song C, Lim CO (2014). *Arabidopsis* DREB2C modulates ABA biosynthesis during germination. *Biochem Biophys Res Commun* **452**, 91–98.
- Jensen MK, Lindemose S, de Masi F, Reimer JJ, Nielsen M, Perera V, Workman CT, Turck F, Grant MR, Mundy J, Petersen M, Skriver K (2013). ATAF1 transcription factor directly regulates abscisic acid biosynthetic gene NCED3 in *Arabidopsis thaliana*. *FEBS Open Biol* **3**, 321–327.
- Jiang YJ, Liang G, Yu DQ (2012). Activated expression of WRKY57 confers drought tolerance in *Arabidopsis*. *Mol Plant* **5**, 1375–1388.
- Kang J, Hwang JU, Lee M, Kim YY, Assmann SM, Martinoia E, Lee Y (2010). PDR-type ABC transporter mediates cellular uptake of the phytohormone abscisic acid. *Proc Natl Acad Sci USA* **107**, 2355–2360.
- Kang J, Yim S, Choi H, Kim A, Lee KP, Lopez-Molina L, Martinoia E, Lee Y (2015). Abscisic acid transporters cooperate to control seed germination. *Nat Commun* **6**, 8113.
- Kanno Y, Hanada A, Chiba Y, Ichikawa T, Nakazawa M, Matsui M, Koshiba T, Kamiya Y, Seo M (2012). Identification of an abscisic acid transporter by functional screening using the receptor complex as a sensor. *Proc Natl Acad Sci USA* **109**, 9653–9658.
- Ko JH, Yang SH, Han KH (2006). Upregulation of an *Arabidopsis* RING-H2 gene, *XERICO*, confers drought tolerance through increased abscisic acid biosynthesis. *Plant J* **47**, 343–355.
- Koiwai H, Nakaminami K, Seo M, Mitsuhashi W, Toyomasu T, Koshiba T (2004). Tissue-specific localization of an abscisic acid biosynthetic enzyme, AAO3, in *Arabidopsis*. *Plant Physiol* **134**, 1697–1707.
- Kuromori T, Fujita M, Urano K, Tanabata T, Sugimoto E, Shinozaki K (2016). Overexpression of *AtABCG25* enhances the abscisic acid signal in guard cells and improves plant water use efficiency. *Plant Sci* **251**, 75–81.
- Kuromori T, Miyaji T, Yabuuchi H, Shimizu H, Sugimoto E, Kamiya A, Moriyama Y, Shinozaki K (2010). ABC transporter *AtABCG25* is involved in abscisic acid transport and responses. *Proc Natl Acad Sci USA* **107**, 2361–2366.
- Kuromori T, Seo M, Shinozaki K (2018). ABA transport and plant water stress responses. *Trends Plant Sci* **23**, 513–522.
- Kuromori T, Sugimoto E, Shinozaki K (2011). *Arabidopsis* mutants of *AtABCG22*, an ABC transporter gene, increase water transpiration and drought susceptibility. *Plant J* **67**, 885–894.
- Kushiro T, Okamoto M, Nakabayashi K, Yamagishi K, Kitamura S, Asami T, Hirai N, Koshiba T, Kamiya Y, Nambara E (2004). The *Arabidopsis* cytochrome P450 CYP707A encodes ABA 8'-hydroxylases: key enzymes in ABA catabolism. *EMBO J* **23**, 1647–1656.
- Le Hir R, Castelain M, Chakraborti D, Moritz T, Dinant S, Bellini C (2017). At bHLH68 transcription factor contributes to the regulation of ABA homeostasis and drought stress tolerance in *Arabidopsis thaliana*. *Physiol Plant* **160**, 312–327.
- Lee HG, Lee K, Seo PJ (2015). The *Arabidopsis* MYB96 transcription factor plays a role in seed dormancy. *Plant Mol Biol* **87**, 371–381.
- Lee KH, Piao HL, Kim HY, Choi SM, Jiang F, Hartung W, Hwang I, Kwak JM, Lee IJ, Hwang I (2006). Activation of glucosidase via stress-induced polymerization rapidly increases active pools of abscisic acid. *Cell* **126**, 1109–1120.
- Lefebvre V, North H, Frey A, Sotta B, Seo M, Okamoto M, Nambara E, Marion-Poll A (2006). Functional analysis of *Arabidopsis* NCED6 and NCED9 genes indicates that ABA synthesized in the endosperm is involved in the induction of seed dormancy. *Plant J* **45**, 309–319.
- Li W, De Ollas C, Dodd IC (2018). Long-distance ABA transport can mediate distal tissue responses by affecting local ABA concentrations. *J Integr Plant Biol* **60**, 16–33.
- Lin PC, Hwang SG, Endo A, Okamoto M, Koshiba T, Cheng WH (2007). Ectopic expression of *ABSCISIC ACID 2/GLUCOSE INSENSITIVE 1* in *Arabidopsis* promotes seed dormancy and stress tolerance. *Plant Physiol*



- 143, 745–758.
- Lisso J, Schröder F, Fisahn J, Müssig C** (2011). NFX1-LIKE2 (NFXL2) suppresses abscisic acid accumulation and stomatal closure in *Arabidopsis thaliana*. *PLoS One* **6**, e26982.
- Lisso J, Schröder F, Schippers JHM, Müssig C** (2012). Nfxl2 modifies cuticle properties in *Arabidopsis*. *Plant Signaling Behavior* **7**, 551–555.
- Liu S, Li M, Su L, Ge K, Li L, Li X, Liu X, Li L** (2016). Negative feedback regulation of ABA biosynthesis in peanut (*Arachis hypogaea*): a transcription factor complex inhibits *AhNCED1* expression during water stress. *Sci Rep* **6**, 37943.
- Liu W, Tai H, Li S, Gao W, Zhao M, Xie C, Li WX** (2014). bHLH122 is important for drought and osmotic stress resistance in *Arabidopsis* and in the repression of ABA catabolism. *New Phytol* **201**, 1192–1204.
- Liu Z, Yan JP, Li DK, Luo Q, Yan Q, Liu ZB, Ye LM, Wang JM, Li XF, Yang Y** (2015). UDP-glucosyltransferase-71C5, a major glucosyltransferase, mediates abscisic acid homeostasis in *Arabidopsis*. *Plant Physiol* **167**, 1659–1670.
- Ma YL, Cao J, He JH, Chen QQ, Li XF, Yang Y** (2018). Molecular mechanism for the regulation of ABA homeostasis during plant development and stress responses. *Int J Mol Sci* **19**, 3643.
- Malcheska F, Ahmad A, Batool S, Müller HM, Ludwig-Müller J, Kreuzwieser J, Randewig D, Hänsch R, Mendel RR, Hell R, Wirtz M, Geiger D, Ache P, Hedrich R, Herschbach C, Rennenberg H** (2017). Drought-enhanced xylem sap sulfate closes stomata by affecting ALMT-12 and guard cell ABA synthesis. *Plant Physiol* **174**, 798–814.
- Matakiadis T, Alboresi A, Jikumaru Y, Tatematsu K, Pichon O, Renou JP, Kamiya Y, Nambara E, Truong HN** (2009). The *Arabidopsis* abscisic acid catabolic gene *CYP707A2* plays a key role in nitrate control of seed dormancy. *Plant Physiol* **149**, 949–960.
- Nambara E, Marion-Poll A** (2005). Abscisic acid biosynthesis and catabolism. *Annu Rev Plant Biol* **56**, 165–185.
- North HM, De Almeida A, Boutin JP, Frey A, To A, Botran L, Sotta B, Marion-Poll A** (2007). The *Arabidopsis* ABA-deficient mutant *aba4* demonstrates that the major route for stress-induced ABA accumulation is via neoxanthin isomers. *Plant J* **50**, 810–824.
- Okamoto M, Kuwahara A, Seo M, Kushiro T, Asami T, Hirai N, Kamiya Y, Koshiba T, Nambara E** (2006). *CYP707A1* and *CYP707A2*, which encode abscisic acid 8'-hydroxylases, are indispensable for proper control of seed dormancy and germination in *Arabidopsis*. *Plant Physiol* **141**, 97–107.
- Okamoto M, Tanaka Y, Abrams SR, Kamiya Y, Seki M, Nambara E** (2009). High humidity induces abscisic acid 8'-hydroxylase in stomata and vasculature to regulate local and systemic abscisic acid responses in *Arabidopsis*. *Plant Physiol* **149**, 825–834.
- Park HY, Seok HY, Park BK, Kim SH, Goh CH, Lee BH, Lee CH, Moon YH** (2008). Overexpression of *Arabidopsis* *ZEP* enhances tolerance to osmotic stress. *Biochem Biophys Res Commun* **375**, 80–85.
- Park Y, Xu ZY, Kim SY, Lee J, Choi B, Lee J, Kim H, Sim HJ, Hwang I** (2016). Spatial regulation of ABCG25, an ABA exporter, is an important component of the mechanism controlling cellular ABA levels. *Plant Cell* **28**, 2528–2544.
- Perea-Resa C, Carrasco-López C, Catalá R, Turečková V, Novak O, Zhang W, Sieburth L, Jiménez-Gómez JM, Salinas J** (2016). The LSM1-7 complex differentially regulates *Arabidopsis* tolerance to abiotic stress conditions by promoting selective mRNA decapping. *Plant Cell* **28**, 505–520.
- Priest DM, Ambrose SJ, Vaistij FE, Elias L, Higgins GS, Ross ARS, Abrams S, Bowles DJ** (2006). Use of the glucosyltransferase UGT71B6 to disturb abscisic acid homeostasis in *Arabidopsis thaliana*. *Plant J* **46**, 492–502.
- Ren T, Wang J, Zhao M, Gong X, Wang S, Wang G, Zhou C** (2018). Involvement of NAC transcription factor SiNAC1 in a positive feedback loop via ABA biosynthesis and leaf senescence in foxtail millet. *Planta* **247**, 53–68.
- Sato H, Takasaki H, Takahashi F, Suzuki T, Iuchi S, Mitsuda N, Ohme-Takagi M, Ikeda M, Seo M, Yamaguchi-Shinozaki K, Shinozaki K** (2018). *Arabidopsis thaliana* NGATHA1 transcription factor induces ABA biosynthesis by activating *NCED3* gene during dehydration stress. *Proc Natl Acad Sci USA* **115**, E11178–E11187.
- Scholz SS, Reichelt M, Vadassery J, Mithöfer A** (2015). Calmodulin-like protein CML37 is a positive regulator of ABA during drought stress in *Arabidopsis*. *Plant Signal Behav* **10**, e1011951.
- Schwartz SH, Tan BC, Gage DA, Zeevaart JAD, McCarty DR** (1997). Specific oxidative cleavage of carotenoids by VP14 of maize. *Science* **276**, 1872–1874.
- Seo M, Aoki K, Koiwai H, Kamiya Y, Nambara E, Koshiba T** (2004). Comparative studies on the *Arabidopsis* alde-

- hyde oxidase (AAO) gene family revealed a major role of AAO3 in ABA biosynthesis in seeds. *Plant Cell Physiol* **45**, 1694–1703.
- Shu K, Zhang H, Wang S, Chen M, Wu Y, Tang S, Liu C, Feng Y, Cao X, Xie Q** (2013). ABI4 regulates primary seed dormancy by regulating the biogenesis of abscisic acid and gibberellins in *Arabidopsis*. *PLoS Genet* **9**, e1003577.
- Sussmilch FC, Brodribb TJ, Mcadam SAM** (2017). Up-regulation of NCED3 and ABA biosynthesis occur within minutes of a decrease in leaf turgor but AHK1 is not required. *J Exp Bot* **68**, 2913–2918.
- Takahashi F, Suzuki T, Osakabe Y, Betsuyaku S, Kondo Y, Dohmae N, Fukuda H, Yamaguchi-Shinozaki K, Shinozaki K** (2018). A small peptide modulates stomatal control via abscisic acid in long-distance signaling. *Nature* **556**, 235–238.
- Tan BC, Joseph LM, Deng WT, Liu LJ, Li QB, Cline K, McCarty DR** (2003). Molecular characterization of the *Arabidopsis* 9-*cis* epoxycarotenoid dioxygenase gene family. *Plant J* **35**, 44–56.
- Tan BC, Schwartz SH, Zeevaart JAD, McCarty DR** (1997). Genetic control of abscisic acid biosynthesis in maize. *Proc Natl Acad Sci USA* **94**, 12235–12240.
- Tan WR, Zhang DW, Zhou HP, Zheng T, Yin YH, Lin HH** (2018). Transcription factor HAT1 is a substrate of SnRK-2.3 kinase and negatively regulates ABA synthesis and signaling in *Arabidopsis* responding to drought. *PLoS Genet* **14**, e1007336.
- Tsugama D, Liu SK, Takano T** (2012). A bZIP protein, VIP1, is a regulator of osmosensory signaling in *Arabidopsis*. *Plant Physiol* **159**, 144–155.
- Umezawa T, Okamoto M, Kushiro T, Nambara E, Oono Y, Seki M, Kobayashi M, Koshiba T, Kamiya Y, Shinozaki K** (2006). CYP707A3, a major ABA 8-hydroxylase involved in dehydration and rehydration response in *Arabidopsis thaliana*. *Plant J* **46**, 171–182.
- Vallabhaneni R, Wurtzel ET** (2010). From epoxycarotenoids to ABA: the role of ABA 8'-hydroxylases in drought-stressed maize roots. *Arch Biochem Biophys* **504**, 112–117.
- Wang PT, Liu H, Hua HJ, Wang L, Song CP** (2011a). A vacuole localized  $\beta$ -glucosidase contributes to drought tolerance in *Arabidopsis*. *Chin Sci Bull* **56**, 3538–3546.
- Wang Z, Wang FX, Hong YC, Yao JJ, Ren ZZ, Shi HZ, Zhu JK** (2018). The flowering repressor SVP confers drought resistance in *Arabidopsis* by regulating abscisic acid catabolism. *Mol Plant* **11**, 1184–1197.
- Wang ZY, Xiong L, Li W, Zhu JK, Zhu J** (2011b). The plant cuticle is required for osmotic stress regulation of abscisic acid biosynthesis and osmotic stress tolerance in *Arabidopsis*. *Plant Cell* **23**, 1971–1984.
- Xiong L, Gong Z, Rock CD, Subramanian S, Guo Y, Xu W, Galbraith D, Zhu JK** (2001). Modulation of abscisic acid signal transduction and biosynthesis by an smlike protein in *Arabidopsis*. *Cell* **1**, 771–781.
- Xu ZJ, Nakajima M, Suzuki Y, Yamaguchi I** (2002). Cloning and characterization of the abscisic acid-specific glucosyltransferase gene from adzuki bean seedlings. *Plant Physiol* **129**, 1285–1295.
- Xu ZY, Lee KH, Dong T, Jeong JC, Jin JB, Kanno Y, Kim DH, Kim SY, Seo M, Bressan RA, Yun DJ, Hwang I** (2012). A vacuolar  $\beta$ -glucosidase homolog that possesses glucose-conjugated abscisic acid hydrolyzing activity plays an important role in osmotic stress responses in *Arabidopsis*. *Plant Cell* **24**, 2184–2199.
- Yan D, Easwaran V, Chau V, Okamoto M, Ierullo M, Kimura M, Endo A, Yano R, Pasha A, Gong Y, Bi YM, Provart N, Guttman D, Krapp A, Rothstein SJ, Nambara E** (2016). NIN-like protein 8 is a master regulator of nitrate-promoted seed germination in *Arabidopsis*. *Nat Commun* **7**, 13179.
- Yang J, Worley E, Udvardi M** (2014). A NAP-AAO3 regulatory module promotes chlorophyll degradation via ABA biosynthesis in *Arabidopsis* leaves. *Plant Cell* **26**, 4862–4874.
- Yano R, Kanno Y, Jikumaru Y, Nakabayashi K, Kamiya Y, Nambara E** (2009). CHOTTO1, a putative double APET-ALA2 repeat transcription factor, is involved in abscisic acid-mediated repression of gibberellin biosynthesis during seed germination in *Arabidopsis*. *Plant Physiol* **151**, 641–654.
- Yue Y, Zhang M, Zhang J, Tian X, Duan L, Li Z** (2012). Overexpression of the *AtLOS5* gene increased abscisic acid level and drought tolerance in transgenic cotton. *J Exp Bot* **63**, 3741–3748.
- Zdunek-Zastocka E, Sobczak M** (2013). Expression of *Pisum sativum* PsAO3 gene, which encodes an aldehyde oxidase utilizing abscisic aldehyde, is induced under progressively but not rapidly imposed drought stress. *Plant Physiol Biochem* **71**(2), 57–66.
- Zhang H, Zhu H, Pan Y, Yu Y, Luan S, Li L** (2014). A DTX/MATE-type transporter facilitates abscisic acid efflux and modulates ABA sensitivity and drought tolerance in *Arabidopsis*. *Mol Plant* **7**, 1522–1532.

Zhou YP, Wu JH, Xiao WH, Chen W, Chen QH, Fan T, Xie CP, Tian CE (2018). *Arabidopsis* IQM4, a novel calmodulin-binding protein, is involved with seed dormancy and germination in *Arabidopsis*. *Front Plant Sci* **9**, 721.

Zhu G, Ye N, Zhang J (2009). Glucose-induced delay of seed germination in rice is mediated by the suppression of ABA catabolism rather than an enhancement of ABA biosynthesis. *Plant Cell Physiol* **50**, 644–651.

## The Dynamic Regulation Mechanism of the Endogenous ABA in Plant

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**Abstract** Absciscic acid (ABA) plays important roles in regulating plant growth and development, and in responding rapidly to various environmental stimuli. The endogenous ABA level in plants is regulated sophisticatedly by the ABA biosynthesis, catabolism, and transportation pathways. This paper reviewed the most recent advancements in ABA *de novo* biosynthesis, ABA hydroxylation catabolism, reversible glycosylation metabolism, and ABA transportation pathway in plants, with emphasis on the expression regulation mechanism of the ABA biosynthetic and catabolic genes. Prospectives for research directions in the future were also suggested.

**Key words** abscisic acid, ABA biosynthesis, ABA metabolism, ABA transportation

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