

# 果实中脱落酸的研究进展与展望

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**摘 要:** 综述了果实中脱落酸 (abscisic acid, ABA) 的生理作用、代谢及信号转导的研究进展, 并提出了果实中 ABA 从产生到作用的分子机制。果实中 ABA 的积累主要受 4 种关键酶的调控, 包括 NCEDs、CYP707As、GTs 和 BGs。在果实成熟过程中, ABA 信号的启动是通过 PYRs 等受体蛋白感知, 并通过 ABI1 和 SnRK2 等蛋白的可逆磷酸化作用将信号传递给下游转录因子和顺式元件, 最终促发果实软化、糖分积累及着色等成熟相关基因的表达。进一步深入研究 ABA 调控果实成熟的信号转导分子机制及 ABA、糖和乙烯交叉调控网络是未来重要的研究领域。

**关键词:** 果实发育和成熟; 脱落酸; 代谢; 信号转导

**中图分类号:** S 6

**文献标志码:** A

**文章编号:** 0513-353X (2015) 09-1664-09

## Research Advances and Prospects of ABA in Fleshy Fruit

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**Abstract:** This review summarizes abscisic acid (ABA) physiological function, metabolism and signaling transduction, and provides insight into the molecular mechanism of ABA from production to action. ABA accumulation in fruit is mainly regulated by four key enzymes, including NCEDs, CYP707As, GTs and BGs. In the processes of fruit ripening, ABA signal is perceived by some receptor proteins, such as PYRs, in turn is transmitted to the downstream transcription factors and *cis*-elements through protein reversible phosphorylation of ABI1 and SnRK2 to trigger the expression of the genes related to fruit ripening, such as softening, sugar accumulation and coloration. The molecular mechanisms of ABA in the regulation of fruit ripening and regulatory network of ABA, sugar and ethylene will be important research area in the future.

**Key words:** fruit development and ripening; abscisic acid; metabolism; signaling transduction

根据果实成熟过程中呼吸速率和乙烯释放高峰的有无, 可将其分为呼吸跃变型和非呼吸跃变型两种类型。以番茄 (*Solanum lycopersicum*) 果实为模式研究试材, 以乙烯合成及信号转导为理论基础, 呼吸跃变型果实成熟调控的分子机制已经阐明 (Alexander & Grierson, 2002; Adams-Phillips et

**收稿日期:** 2015-02-13; **修回日期:** 2015-08-07

**基金项目:** 国家自然科学基金项目 (31471837); 北京市属高等学校创新团队建设与教师职业发展计划项目 (IDHT20140509); “十二五”国家科技支撑计划项目 (2013BAD02B00)

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al., 2004; Prasanna et al., 2007; Gapper et al., 2013; Seymour et al., 2013; Perotti et al., 2014)。但非呼吸跃变型果实成熟的分子机制研究进展缓慢。

近年来, 模式植物拟南芥中 ABA 受体研究方面的突破 (Fujii et al., 2009; Ma et al., 2009; Melcher et al., 2009; Miyazono et al., 2009; Nishimura et al., 2009; Santiago et al., 2009; Shang et al., 2010), 极大促进了分子水平果实中 ABA 的研究, 并产生了一系列重要突破性成果, 不仅证实了 ABA 在非呼吸跃变型果实发育和成熟过程中发挥着重要的作用, 而且在呼吸跃变型果实发育中也起着一定的作用 (Zhang et al., 2009; Gambetta et al., 2010; Chai et al., 2011; Jia et al., 2011; Akagi et al., 2012; Romero et al., 2012; Sun et al., 2012a, 2012b; Li et al., 2013; Nicolas et al., 2014)。

本文中综述了果实中 ABA 的作用, 代谢及信号转导最新研究进展, 并展望果实成熟未来的研究方向, 以期对果实发育和成熟研究提供理论支撑。

## 1 ABA 对果实发育与成熟的调控作用

最早建立 ABA 与果实成熟关系主要是基于对葡萄 (*Vitis vinifera*) 果实的研究结果 (Coombe & Hale, 1973; Coombe, 1976; Inaba et al., 1976; Scienza et al., 1978; Cawthon & Morris, 1982; Palejwala et al., 1985; Davies et al., 1997)。ABA 可以明显加速葡萄果实的成熟过程, 包括着色、糖分积累、酸性下降和果肉变软 (Coombe & Hale, 1973; Inaba et al., 1976; Kataoka et al., 1982; Palejwala et al., 1985; Matsushima et al., 1989; Jeong et al., 2004)。近几年来, ABA 在调控葡萄果实成熟中的关键作用不断得到证实 (Yu et al., 2006; Wheeler et al., 2009; Gambetta et al., 2010; Giribaldi et al., 2010; Koyama et al., 2010; Gagné et al., 2011; Nicolas et al., 2014)。

除了葡萄果实以外, 近年来一系列重要研究进展证实, ABA 在草莓果实成熟过程中也发挥着重要的作用 (Chai et al., 2011; Jia et al., 2011, 2013; Li et al., 2013)。水分胁迫草莓植株可显著提高草莓果实中 ABA 水平及糖酸比, 但却降低果实的大小 (Terry et al., 2007)。外源 ABA 可以明显促进果实成熟, 而 ABA 抑制剂氟啶酮 (fluridone) 则明显抑制果实成熟 (Jia et al., 2011)。大量的研究证实 ABA 是调控草莓果实成熟的重要激素 (Kano & Asahira, 1981; Manning, 1994; Perkins-Veazie, 1995; Jiang & Joyce, 2003; Terry et al., 2007; Jia et al., 2011; Li et al., 2013)。

值得关注的是, ABA 还参与多种果实发育的生理过程, 包括柿 (*Diospyros kaki*) 果实涩味的产生 (Akagi et al., 2012)、柑橘果皮的发育 (Romero et al., 2012)、樱桃 (*Prunus species*) 果实颜色的变化 (Ren et al., 2010)。

除了 ABA 在葡萄、草莓、柑橘和樱桃等非呼吸跃变型果实发育与成熟中的重要作用外, 近年来研究还证实 ABA 还参与呼吸跃变型果实的发育与成熟的调控。ABA 缺陷型番茄 (*high-pigment 3*) 果实含有更多的类胡萝卜素, 并且比野生类型果实积累更多的质体和番茄红素 (Galpaz et al., 2008), 表明 ABA 参与番茄果实的色素、软化及大小的调控 (Nitsch et al., 2012; Sun et al., 2012a, 2012b)。此外还发现, ABA 还参与番茄果实茎疤痕组织的栓化愈合 (Leide et al., 2012)、鳄梨果实生长 (Cowan et al., 1997) 及桃果实糖分积累 (Kobashi et al., 2001) 等生理过程。

总之, ABA 参与呼吸跃变型和非呼吸跃变型果实发育和成熟过程中多方面的生理调控, 包括果实的大小、果实的着色、糖分积累、酸性下降及果实的软化等, 是果实发育重要的调控激素。

## 2 果实中 ABA 信号的产生及代谢

高等植物细胞中的 ABA 水平是其合成—降解、结合—解离综合作用的结果 (Nambara & Marion-Poll, 2005)。ABA 合成主要是通过氧化裂解类胡萝卜素途径实现的, 其中 9 - 顺式 - 环氧类胡萝卜素双加氧酶 (NCED) 是 ABA 生物合成的关键酶; 而 ABA 的分解代谢主要是通过 8' - 羟化酶催化的 8' - 羟基化作用, 其中小家族的 P450 单加氧酶 CYP707A 是关键酶 (Zeevaert et al., 1999)。另外还发现, ABA 在糖基转移酶 (glycosyltransferases, GTs) 的作用下可转变为 ABA - 葡萄糖基酯 (ABA glucosyl ester, ABA-GE; Xu et al., 2002)。近年来证实, ABA-GE 在  $\beta$  - 葡萄糖苷酶 ( $\beta$ -glucosidases, BGs) 作用下可重新解离成游离的 ABA (Lee et al., 2006)。因此, NCED-CYP707A 和 GT-BG 分别从合成—分解及结合—解离途径调控了植物细胞内的 ABA 水平。结合—解离途径属于一步催化的化学反应, 更能迅速地改变 ABA 水平, 以满足植物发育与适应环境的需要。

借鉴模式植物 ABA 的代谢研究成果, 近年来果实中 ABA 积累的酶学调控机制也取得了重要的研究进展 (Jia et al., 2011; Li et al., 2011, 2013; Sun et al., 2012b)。利用病毒诱导基因沉默技术 (VIGS) 下调草莓果实中的 *FaNCED1* 基因的表达, 导致了 ABA 水平显著降低, 最终抑制了果实的着色, 证实 *FaNCED1* 是草莓果实中 ABA 生物合成的关键酶 (Jia et al., 2011)。同样, 调低草莓果实中的 *FaBG3* 基因的表达, 也显著降低了果实中 ABA 水平, 并且果实的成熟受到抑制 (Li et al., 2013)。这些研究表明, NCED 和 BG 在草莓果实成熟过程中发挥的重要作用。另外, 在番茄果实中也发现类似的研究结果, 果实中 ABA 水平受到 *SINCE1* 和 *SICYP707A1* 基因的共同调节 (Nitsch et al., 2009; Zhang et al., 2009)。通过 RNA 干扰技术抑制 *SINCE1* 的表达, 果实的保质期延长到了 3 周 (Sun et al., 2012b)。

ABA 的代谢研究除了在草莓和番茄果实中取得重要进展外, 关于其他物种的果实也有相似的研究报告。在玫瑰香葡萄果实发育后期, *VvNCED1* 和 *VvBG1* 基因的高水平表达, 同时伴随 *VvCYP1* 和 *VvGT* 基因的低水平表达, 协同促进了 ABA 的持续积累, 尤其是在着色阶段, *VvBG1* 转录比 *VvNCED1* 增加更快, *VvBG1* 蛋白具有很高的酶活性, 表明其在果实成熟期发挥着更重要的作用 (Sun et al., 2015)。Chernys 和 Zeevaert (2000) 研究发现, 鳄梨果实中 ABA 的生物合成受类胡萝卜素裂解水平的调节, *PaNCED1* 和 *PaNCED3* 高表达促进了果实的成熟。在柑橘果皮和液囊中, *CitNCED2* 和/或 *CitNCED3* 表达量的增加, 与 ABA 的大量积累相一致 (Kato et al., 2006)。西瓜 *CIBG1*、*CINCE4* 和 *CICYP707A1* 基因的表达量随着果实成熟迅速增加, 并在收获期达到最高水平 (Li et al., 2012)。甜樱桃果实中内源 ABA 含量受 *PacNCED1*、*PacCYP707A1* 和 *PacCYP707A3* 的协同调控 (Ren et al., 2010)。桃果实成熟过程中, *PpNCED1* 是促发 ABA 生物合成的关键酶 (Zhang et al., 2009)。

综上所述, 在大多数肉质果实中 ABA 的积累与果实的成熟密切相关。ABA 水平的调节主要是通过 NCED1 和 CYP707A1 进行的。在果实发育后期,  $\beta$  - 葡萄糖苷酶 (BGs) 发挥着重要的作用。

## 3 果实中的 ABA 受体识别及信号转导

### 3.1 ABA 受体

目前在模式植物拟南芥上已鉴定出 3 种 ABA 受体, 并提出了两个核心 ABA 信号转导途径: 受体包括质膜上的 GTG1/GTG2 (Pandey et al., 2009)、胞质内的 PYR/PYL/RCAR (Ma et al., 2009;

Park et al., 2009) 和叶绿体内的镁整合酶 H 亚基 ABAR/CHLH (Shen et al., 2006; Wu et al., 2009; Shang et al., 2010); 信号途径包括 “ABA-PYR/PYL/RCAR-PP2C-SnRK2” 通路 (Fujii et al., 2009) 和 “ABA-ABAR-WRKY40-ABI5” 通路 (Shang et al., 2010)。

早期关于果实 ABA 受体识别的研究发现, 在葡萄浆果微粒体的内膜上存在特异的 ABA 受体 ( $K_d$ :  $17.5 \sim 50 \text{ nmol} \cdot \text{L}^{-1}$ ), 而细胞质膜或细胞质中则检测不到结合活性 (Zhang et al., 1999)。在苹果果肉微粒体的细胞质中检测到高亲和力 ( $K_d$ :  $2.3 \text{ nmol} \cdot \text{L}^{-1}$ ) 和低亲和力 ( $K_d$ :  $58.8 \text{ nmol} \cdot \text{L}^{-1}$ ) ABA 结合活性 (Zhang et al., 2001), 表明果实中 ABA 受体的存在。借鉴拟南芥 ABA 受体研究结果, 下调草莓果实中 *FaPYR1* 或 *FaCHLH/ABAR* 的表达量, 都能抑制果实成熟 (Chai et al., 2011; Jia et al., 2011); 而下调 2C 型蛋白磷酸酶基因 *FaABI1* 却促进了草莓果实的成熟 (Jia et al., 2013), 表明 *FaPYR1* 或 *FaCHLH/ABAR* 作为正调控因子参与了草莓果实的成熟, 而 *FaABI1* 作为负调控因子参与草莓果实的成熟, “ABA-*FaPYR1*-*FaPP2C*-*FaSnRK2*” 信号系统可能是 ABA 调节草莓果实成熟过程中的核心机制。以草莓果实为试验材料, 以 ABA 受体及其信号转导为理论基础, 提出了非呼吸跃变型果实成熟调控的分子机制 (Li et al., 2011)。

值得关注的是, ABA 受体核心信号机制的研究除了在草莓果实中有重要进展外, 在其他果实上也得到证实。葡萄中 *VvPYL1*、*VvRCAR6* 和 *VvRCAR5* 是 ABA 识别的主要受体, 信号主要是通过 *VvPP2C4* 传递 (Boneh et al., 2011; Li et al., 2012)。番茄果实中, *SIPYL1* 和 *SIPYL2* 在果实发育与成熟的整个阶段都处在高水平表达, *SIPP2C1* 和 *SIPP2C5* 在始红期高表达, 而 *SlSnRK2.2*、*SlSnRK2.3*、*SlSnRK2.4* 和 *SlSnRK2C* 在成熟过程中也处在高水平表达 (Sun et al., 2011)。

## 3.2 ABA 信号转导的下游信号组分

### 3.2.1 蛋白激酶和磷酸酶

植物蛋白激酶和磷酸酶包括  $\text{Ca}^{2+}$  依赖蛋白激酶 (CDPKs)、SNF1 相关的蛋白激酶 (SnRKs)、分裂原活化蛋白激酶 (MAPKs)、受体型激酶 (RPKs) 和蛋白磷酸酶 PP2Cs (Hirayama & Shinozaki, 2007)。拟南芥中 SnRK2 和磷酸化酶 ABI1 的相互作用在 ABA 信号转导过程中发挥着重要的作用 (Fujii et al., 2009)。

关于果实中蛋白激酶和磷酸酶的研究, 除了在草莓果实成熟过程中已鉴定的 PP2C-SnRK2 核心磷酸化信号系统 (Jia et al., 2013) 外, 早期的研究 (Shen et al., 2004) 还发现, 在葡萄浆果中存在钙依赖蛋白激酶 (CDPK) 和分裂原活化蛋白激酶 (MAPK)。后续的研究鉴定了一个 58 kD 的定位于原生质膜和叶绿体/质体上的受 ABA 激活的钙依赖蛋白激酶 ACPK1, 并发现 ACPK1 调控了原生质膜上  $\text{H}^+$ -ATP 酶的活性, 正调控葡萄果实的发育 (Yu et al., 2006)。另外, 葡萄浆果中蛋白激酶 *VvSK1* 随着果实积累可溶糖和 ABA 而强烈表达, *VvSK1* 过量表达导致了单糖转运体 (*VvHT3*、*VvHT4*、*VvHT5* 和 *VvHT6*) 的转录水平上调, 葡萄糖摄入速率增加 5 倍, 证实 *VvSK1* 通过糖/ABA 诱导蛋白激酶控制糖分的运输与积累 (Lecourieux et al., 2010)。Wang 等 (2010) 证实了苹果果实中存在受 ABA 激活的 MAPK 信号级联 (MdMKK1-MdMPK1) 反应, MdMPK1 通过特殊残基 Ser314, 使得 ABI5 蛋白磷酸化, Ser 残基使 ABI5 蛋白成为 ABA 信号转导过程中 MAPK 的直接靶点。

### 3.2.2 转录因子、顺式元件及靶基因

近年来, 果实中许多参与 ABA 信号相关的转录因子、顺式元件和靶基因得到鉴定。柿果实中 DkbZIP5 在 DkMyb4 的启动子区域识别 ABA 应答元件, 并以依赖 ABA 的作用方式参与原花青素 (PA) 的合成调控 (Akagi et al., 2012)。番茄中, *SIAREB1* 超表达株系中已糖积累可能与液泡转化

酶及蔗糖合酶的基因高水平表达有关,表明通过 AREB 介导的 ABA 信号转导影响番茄果实发育的糖代谢 (Bastías et al., 2011, 2014)。ABA 通过影响调节番茄果实成熟过程中细胞壁分解代谢相关酶 (SIPG、SIPME、SITBG、SIXET、SICels 和 SIExp) 基因的表达,从而影响番茄果实的保鲜期 (Sun et al., 2012b)。调控草莓果实中 *FaABI1* 转录水平可以调节 ABA 应答相关基因的表达 (包括 *ABI3*、*ABI4*、*ABI5*、*SnRK2*、*ABRE1*、*CHS*、*PG1*、*PL*、*CHI*、*F3H*、*DFR*、*ANS* 和 *UFGT*),最终影响了果实成熟,包括硬度、色泽和糖含量等 (Jia et al., 2013)。一个受 ABA 胁迫和成熟诱导 *FaASR* 基因被证实草莓果实成熟过程中发挥着重要作用 (Chen et al., 2011)。最近研究发现,转录因子 PcMYBA 和 VvABF2 在 ABA 诱导甜樱桃和葡萄果实成熟过程中发挥着重要的作用 (Nicolas et al., 2014; Shen et al., 2014)。

综上所述,近年来果实中的 ABA 信号转导分子机制研究取得了很大的进展,鉴定了一些重要的相关蛋白,包括 ABA 受体、蛋白激酶、蛋白磷酸化酶、转录因子、顺式元件及靶基因,尤其确立了几个重要的核心信号转导组分及其重要的靶基因,核心信号转导组分包括草莓果实“ABA-FaPYR1-FaPP2C-FaSnRK2”,葡萄果实“ABA-VvACPK1-H<sup>+</sup>-ATPase”和“ABA-VvSK1-VvHTs”,苹果果实“ABA-MdMKK1-MdMPK1-ABI5”,柿果实“ABA-DkbZIP5-DkMyb4-PA”;靶基因包括与果实软化 (*PG*、*PL*、*PME*、*TBG*、*XET*、*Cels* 和 *Exp*)、糖代谢 (*VvHTs* 和 *MiADH2*)、色素积累 (*PA*、*CHS*、*CHI*、*F3H*、*DFR*、*ANS* 和 *UFGT*) 等相关基因。

#### 4 ABA 调控果实成熟的协同机制

值得关注的是,近年来研究发现,ABA、乙烯和糖在果实的成熟过程中存在相互作用,并可能共同调控果实成熟 (Gambetta et al., 2010; Jia et al., 2011, 2013; Nitsch et al., 2012; Sun et al., 2012b; Klie et al., 2014)。

早期的研究发现,ABA 可能通过提高乙烯的敏感性 (Jiang et al., 2000) 或者乙烯水平 (Riov et al., 1990) 调控果实的成熟。在葡萄果实成熟中,糖和 ABA 可以激活共同的调节因子,包括蔗糖传感器 SUT2、核心 G 蛋白信号组件 GPA1 和 RGS1、己糖激酶 (HXK)、PP2C 蛋白磷酸激酶、Snf1 相关激酶 (SnRK) 和糖相关的 WRKY、ABRE 结合因子 (ABF) 和 AP2 转录因子 (Gambetta et al., 2010)。在果实成熟过程中,不同种类的果实存在保守的代谢途径 (Klie et al., 2014)。在番茄果实生长阶段,ABA 通过抑制乙烯的合成刺激细胞膨大 (Nitsch et al., 2012; Sun et al., 2012b);在果实成熟阶段,ABA 合成显著降低,导致了 ABA 生物合成的上游物质 (包括番茄红素、胡萝卜素) 的积累,从而促进果实着色 (Sun et al., 2012a, 2012b)。在柑橘类果实中,ABA 在转录水平诱导自身生物合成,导致柑橘液囊中类胡萝卜素含量下降 (Zhang et al., 2012)。草莓中,蔗糖可以作为信号分子促进 *FaNCED1* 表达,并在 ABA 积累和果实成熟过程中发挥着重要的作用 (Jia et al., 2011, 2013)。

综上所述,为了适应果实发育和响应环境的需要,肉质果实可以合成 ABA。肉质果实中 ABA 的积累主要受 4 种关键酶的调控,包括 NCEDs、CYP707As、GTs 和 BGs。在果实成熟过程中,ABA、乙烯和糖类的相互作用发生在生理及分子水平上。ABA 信号的启动是通过 PYRs 和 ABAR 受体感知触发的,进而通过 ABI1、SnRK2、ACPK1、SK1、MKK1 和 MPK1 等蛋白的可逆磷酸化作用将信号传递给下游转录因子及顺式元件,包括 bZIP5、MYb4、ABI3、ABI4、ABI5 和 ABRE 等,并诱导果实软化、糖分积累及着色等成熟相关基因的表达,最终促进果实成熟。

## 5 展望

近年来, 虽然证实 ABA 在非呼吸跃变型果实成熟调控中发挥着重要的作用, 但其调控的分子机理目前仍不十分清楚。以非呼吸跃变型草莓果实为模式材料, 通过转录组学、蛋白组学和代谢组学研究发现 ABA 调控非呼吸跃变型果实成熟的新的信号组分, 包括 ABA 受体、蛋白激酶、转录因子等, 有助于进一步阐明 ABA 作用的分子机制。鉴于非呼吸跃变型果实成熟调控的复杂性, 研究 ABA、乙烯和糖之间的相互作用及其对果实成熟的交叉调控机制, 是未来重要的研究领域。另外, 通过 T-DNA 插入和 EMS 化学诱变发现新的与果实成熟相关的草莓突变体, 并完善草莓稳定遗传转化体系, 是未来亟待解决的重要问题。

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