

脱落酸调控果实成熟的分子及信号转导机制研究进展

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摘要:脱落酸(abscisic acid, ABA)作为一种重要的植物激素,不仅涉及许多植物发育过程和逆境胁迫,而且在果实成熟,尤其是非呼吸跃变型果实成熟中发挥关键作用。随着植物中ABA合成、代谢和作用机制的解析及其受体识别和核心信号转导模型的建立,极大地推动了ABA在果实成熟和品质形成中的研究。一般来讲,褪绿和着色是果实成熟过程中普遍存在的现象,这一过程涉及了ABA早期信号和多种激素的协同作用并组成了复杂的网络调控机制。总之,ABA是调控果实成熟的核心机制,其中存在着乙烯依赖(呼吸跃变型)和不依赖(非呼吸跃变型)类型。综述了ABA在植物体内的合成、代谢及作用的分子机制,构建了ABA调控果实成熟的分子网络模型,为果实的品质改善和保鲜奠定理论基础。

关键词:果实成熟;脱落酸;(非)呼吸跃变型;乙烯;生长素;信号转导

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Molecular mechanism of abscisic acid in regulating fruit ripening

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Abstract: Abscisic acid (ABA), as an important plant hormone, not only participates in a variety of plant developmental processes and stresses, but also plays a major role in fruit ripening, especially in non-climacteric fruit ripening. With the continuous study of ABA biosynthesis, metabolism and physiological effect in plants, especially the establishment of models for ABA perception and signaling transduction, the research on ABA in fruit development and ripening has been greatly promoted. De-greening and coloration are common process during fruit ripening, which involves the synergistic role of ABA and the early signals as well as multiple hormones, constituting a complex regulatory network. This paper reviewed the molecular mechanism of ABA biosynthesis, metabolism and physiological roles in plants. Finally, a model of ABA in regulating fruit ripening was proposed to lay a theoretical foundation for improving fruit quality and shelf-life. Hormones are important factors in regulating fruit ripening. According to whether the fruit ripening depends on ethylene or not, it can be divided into ethylene dependent (climacteric) and independent (non-climacteric) types. For the climacteric fruits (such as tomatoes and bananas), both respiratory intensity and the release rate of ethylene reach to peak at ripening. However, there is no such peak in non-climacteric fruits (such as grapes and strawberries), whose ripening is mainly controlled by ABA. ABA plays an important role in regulating fruit ripening, especially in non-climacteric fruits. For example, ABA content in strawberry receptacle increases during strawberry fruit ripening and exogenous ABA treatment can accelerate strawberry ripening, indicating that ABA may participate in the regulation of strawberry ripening. In addition, exogenous ABA can also promote the ripening of grapes, avocados, tomatoes, cucumbers, oranges, figs and so on. In a word, ABA is a core hormone in regulating fruits ripening. The synergetic regulation of ABA from biosynthe-

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sis to signaling transduction is the key to plant growth and fruit ripening. In higher plants, “biosynthesis-degradation” and “binding-dissociation” pathways synergistically regulate the level of ABA, and 9-cis-epoxycarotenoid dioxygenase (NCED) is the first step specific to ABA biosynthesis. In the whole process of strawberry fruit development, the level of ABA and the expression of the *FaNCED1* show the same tendency, suggesting that NCED is the key enzyme determining ABA level in strawberry fruit, especially exogenous ABA can restore the coloration of the *FaNCED1*-RNAi, but cannot restore the coloration of the *FaCHLH/ABAR*-RNAi fruit. 8'-hydroxylation is the main pathway of ABA oxidative catabolism. The UDP-glycosyltransferases (UGTs) can catalyze ABA to ABA glucose ester (ABA-GE). The β -Glucosidase (BGs) can catalyze the dissociation of ABA glucose esters into free ABA. Comparing with *de novo* synthesis, the rapid metabolic mode make plant quickly change the level of endogenous ABA to adapt to changes of the environment. In conclusion, NCED, UGT71, CYP707A and BG play important roles in strawberry ripening, revealing that ABA is the key plant hormone in regulating fruit ripening. The ABA receptors play a critical role in ABA perception, and protein reversible phosphorylation plays a key role in ABA signaling transduction pathway. The core signal components of “PP2C-SnRK2” are the key to strawberry fruit ripening. FaPYR1 is closely related to initiate and quality format in fruit ripening. “PYR1-PP2C-SnRK2” is a conservative mechanism for regulating fruit ripening. CHLH/ABAR has multiple biological functions, including chlorophyll biosynthesis, plastid-nuclear retrograde signaling and ABA signaling transduction. As a co-receptor of FaABAR, FaRIPK1 participates in the initiation of strawberry fruit ripening, and FaABAR regulates fruit ripening, confirming that FaABAR/CHLH is a positive regulator for fruit ripening. In a word, the core signaling component “ABA-PYR1-PP2C-SnRK2” is the conservative mechanism in regulating fruit ripening, while “ABA-ABAR-RIPK1-ABI4” is a new mechanism for regulating strawberry fruit ripening, suggesting that ABA regulation network is complex, conservative and diverse. The development of fruit includes early cell division and expansion, followed by chlorophyll degradation, cell wall softening, and metabolism changes including phenylpropionic acid, flavonoids, starch/sucrose, and carotenoid during ripening. These processes are strictly controlled by plant hormones, emphasizing on the role of ethylene in climacteric and ABA in non-climacteric fruit ripening, as well as two interactions. In the study of fig fruit, a special type of ripening, ABA can promote the accumulation of ethylene and initiate fruit ripening, and the regulation of fruit ripening by ethylene depends on the perception of ABA receptors. Therefore, the role of ABA is closely related to ethylene system I / II. In conclusion, this paper tried to propose the molecular mechanism of ABA regulating fruit ripening. With the initiation of fruit ripening, the development signals such as sugar, NO, Ca²⁺ and environmental signals such as light would lead to the accumulation of ROS, triggering the biosynthesis and accumulation of ABA. At the same time, they would synergistically inhibit the biosynthesis and effect of GA, IAA and CTK, and synergistically promote the biosynthesis and effect of ethylene, JA, PA and BR. All these hormones could constitute a complex regulatory network, in which ABA is the core hormone in regulating fruit ripening. In the past decade, the research on plant molecular biology in China has made rapid progress, and has begun to transform from model plants to fruit and woody plants. However, the long time of cultivation of fruit trees and the bottleneck of genetic transformation system have restricted the development of fruit tree molecular biology. In the future, the combination of the genomics, transcriptomics, proteomics, metabonomics and epigenetics, as well as the gene knockout technology CRISPR/Cas9, in-depth analysis of the commonness and specificity of the hormone regulation mechanism in fruit ripening will be an important direction, so does the molecular mechanism of seed and pulp synergetic regulation network.

Key words: Fruit ripening; Abscisic acid; (Non) Climatic fruits; Ethylene; Auxin; Signal transduction

果实成熟是指果实发育后期完成生长膨大后内部发生的一系列生理生化反应,包括果皮褪绿、叶绿素降解、花色苷及类胡萝卜素合成、香气合成及果实变软等典型特征,这其中涉及一系列复杂的代谢过程,并伴随着多种次生物质的产生。在自然界中,成熟过程不仅有助于食用水果的动物散播种子,而且在人类的营养和健康中发挥重要作用,还有利于控制果实衰老进程,减轻水果在运输和保鲜中的腐烂变质。

激素是调节果实成熟的重要因子,可以显著影响果实发育和成熟的进程。根据果实成熟过程中呼吸强度及乙烯释放速率的生理特点,果实主要分为两种类型:呼吸跃变型及非呼吸跃变型^[1-2]。在跃变型果实(如番茄和香蕉)中呼吸和乙烯水平均在成熟期达到峰值;而非呼吸跃变型果实(如葡萄和草莓)中没有出现此类峰值,其成熟受脱落酸(ABA)以不依赖乙烯的方式控制^[1-2]。另外,脱落酸还参与了种子成熟和休眠及逆境胁迫响应,在调控营养生长和生殖生长平衡中发挥关键作用^[3-5]。因此,ABA在非呼吸跃变型和呼吸跃变型果实成熟过程中都发挥着重要作用^[6-7]。综述了果实发育中ABA合成、代谢及作用的分子机制,并提出了ABA调控果实成熟的分子网络模型,以期为果实成熟、品质形成和采后保鲜奠定基础。

1 ABA在果实成熟过程中发挥重要作用

ABA是果实发育和成熟过程中重要的内源激素之一^[8-10]。与乙烯相比,ABA在非呼吸跃变型果实成熟和衰老过程中起着更为重要的作用^[11]。外源施加ABA能够促进果实的成熟进程,主要体现在果实的糖酸比提高、硬度下降、可溶性固形物和糖类的积累、果实色泽的形成等方面。草莓是一种典型的非呼吸跃变型果实,它的成熟和衰老涉及基因表达和代谢变化,是一个基因编程的复杂过程^[12-13]。在果实成熟过程中,草莓花托中ABA含量会呈现上升趋势,这是成熟果实中ABA生物合成的增加和氧化作用的降低共同作用的结果^[13]。检测不同西瓜品种成熟过程中游离态及结合态ABA的含量发现,西瓜果实的成熟及品质进化过程也与ABA含量高度相关^[14]。

果实硬度下降是果实成熟的重要标志。施加外源ABA可加速果实硬度的下降,这可能是ABA增

强了细胞壁降解酶、果胶甲酯酶和多聚半乳糖醛酸酶等能够改变果实细胞壁结构的酶的活性,最终促使果实软化^[15]。外源ABA可以促进葡萄^[16-18]、草莓^[19]、无花果^[20]等多种果实的软化和品质提升。

ABA对果实着色发挥重要作用。果实成熟过程中的颜色变化是通过叶绿素降解和次生颜色代谢产物如类胡萝卜素和花色苷的生物合成实现的,而果皮颜色是果品商品价值的重要品质指标^[21]。如施用ABA迅速启动荔枝果实叶绿素分解,ABA浓度峰值与随后合成的花青素水平一致,证明ABA对荔枝果实成熟起重要作用^[22]。内源ABA通过上调乙烯的产生和苯丙氨酸解氨酶(phenylalanine ammonia-lyase, PAL)的活性,提升草莓的花色苷和酚类含量,促进草莓果实着色^[9]。同样,外源ABA也可以促进葡萄、荔枝和甜樱桃等非呼吸跃变型果实成熟过程中花色苷的生物合成及果实着色^[23-25]。

糖类的积累也是决定果实品质和消费的一个核心要素。葡萄果实成熟启动(花青素积累开始)与糖积累密切相关,并伴随着ABA浓度的显著增加^[26]。例如,外源ABA处理后,植物果实的总淀粉量和直链淀粉量均可增加,表明ABA可能调控淀粉合成基因的表达^[14]。同时,ABA还参与呼吸跃变型果实的膨大、软化和糖分积累等^[6,27]。外源ABA能够通过增强库容的方式使叶片中的光合产物向苹果果实运输,从而提高果实中可溶性糖的积累^[28];而抑制ABA合成关键酶9-顺环氧类胡萝卜素双加氧酶(9-cis-epoxycarotenoid dioxygenase, NCED)的表达,会导致果胶在成熟过程中的积累,减缓番茄的软化过程^[28]。

总之,ABA参与果实成熟调控涉及一系列复杂的生理变化,如色素合成、糖分积累和果实软化等;大量的研究证实,ABA在调控非呼吸跃变型和呼吸跃变型果实成熟及品质形成中都发挥着重要作用。

2 果实中ABA的代谢及作用机制

2.1 ABA生物合成及代谢

细胞内ABA生物合成和分解代谢涉及了前馈和反馈调控。反馈和前馈与抑制*FveCYP707A4a*表达(cytochrome P450, ABA降解的关键)和促进*FveNCED*表达(ABA生物合成的关键)密切相关,并涉及草莓果实成熟的起始^[29]。ABA从生物合成到信号转导的协同调控是植物生长发育和果实成熟的

核心机制。

ABA的生物合成始于质体,止于细胞质,其水平通过不同的途径进行调节。近年来,ABA在高等植物中的合成及其调控机制得到了广泛的关注^[30]。在高等植物中,“合成-降解”“结合-解离”途径协同调控ABA的水平,NCED为ABA生物合成的限制酶^[31-33]。在草莓果实发育整个过程中,ABA水平和*FaNCED1*的表达呈相同的变化趋势,暗示*FaNCED1*是决定草莓果实中ABA水平的关键酶。这一结论通过瞬时转基因体系调低*FaNCED1*表达量抑制成熟得到证实。同时,通过瞬时转基因体系调低ABA受体基因*FaABAR*表达量也抑制成熟,尤其外源ABA可以恢复*FaNCED1*-RNAi果实着色,但不能恢复*FaCHLH/ABAR*-RNAi果实着色,证实ABA在调控草莓果实成熟中发挥重要作用^[34]。值得关注的是,在早熟柑橘成熟过程中,ABA具有类似乙烯合成系统II的反馈调节机制,能够在转录水平和翻译水平诱导自身的生物合成^[35-36]。目前这一结论在呼吸跃变型和非呼吸跃变型果实,如鳄梨^[37]、柿子^[38]、草莓^[39]上都得到证实。8'-羟基化是ABA氧化分解代谢的主要途径,P450单加氧酶CYP707A是其中的关键酶;糖基转移酶(UDP-glucosyltransferase, GTs)能够催化ABA形成ABA-葡萄糖基酯(ABA glucosyl ester, ABA-GE);而 β -葡萄糖苷酶(β -glucosidases, BGs)能够催化ABA-葡萄糖基酯解离为游离的ABA^[40]。植物依靠这种“结合-解离”代谢快速模式,与从头合成相比,能迅速改变内源ABA水平,以便快速适应环境和果实发育的变化。

过去大量的研究证实,ABA是调节非呼吸跃变型果实成熟的关键激素。在越橘(*Vaccinium myrtillus*)果实的成熟过程中,ABA生物合成关键酶NCED发挥重要作用^[41]。黄瓜ABA从头合成基因(*CsNCEDs*)、分解代谢基因(*CsCYP707A1*)和解离基因(*CsBGs*)均在果肉中高表达,协同调节ABA含量及果实成熟进程^[42]。从绿熟期开始,ABA在草莓果实中快速合成,其含量受到合成基因*FaNCED2*和*FaNCED1*及代谢基因*FaCYP707A1*的调控^[33-34, 39, 43]。草莓中*FaBG3*的表达与ABA含量的变化基本一致,均在成熟阶段出现高峰,经过*FaBG3*-RNAi处理的草莓果实中*FaBG3*的表达量显著降低,ABA含量低于对照,说明其在转录水平上参与了果实的成熟过程^[44]。另外,通过对草莓中葡萄糖

苷酶1(BG1)的酶活性表明分析,其能催化ABA糖基酯(ABA-GE)水解,释放具有生物活性的游离ABA。进一步研究发现,草莓果实着色的开始伴随着*FaBG1*表达的急剧升高,而*FaBG1*的下调导致内源性ABA的显著下降,从而抑制果实成熟^[45]。总之,NCED、UGT71、CYP707A和BG在草莓成熟过程中发挥了重要的作用^[34,46-47],揭示了ABA是调控果实成熟的关键激素。

2.2 ABA调控非呼吸跃变型果实成熟分子机制

近十年来,模式植物拟南芥ABA核心信号转导分子机制的阐明^[48]极大地促进了非呼吸跃变型果实成熟的机制研究,拓展了ABA的生物学功能。拟南芥中ABA受体蛋白为PYR1/PYLs/RCAR(pyrabactin resistance/pyr1-like/regulatory components of ABA receptor),大量研究揭示了“ABA-PYR1/PYLs/RCAR-PP2C(type 2C protein phosphatase)-SnRK2(sucrose non-fermenting 1-related protein kinase 2)”核心信号转导机制^[49-50]。受体PYR与ABA结合能促进形成“ABA-PYR-PP2C”信号复合体,抑制PP2Cs活性并依次激活蛋白激酶SnRK2、转录因子ABF(ABRE binding factors)及一系列下游应答基因,最终激活ABA的多种生理反应^[51]。因此,在ABA信号转导过程中,ABA受体介导的信号感知过程发挥了核心作用,蛋白可逆磷酸化发挥着关键作用^[52]。

植物中蛋白可逆磷酸化涉及了蛋白激酶和蛋白磷酸酶:激酶包括CDPKs(Ca²⁺-dependent protein kinases,钙依赖的蛋白激酶)、SnRKs(SNF1-related kinases,SNF1相关蛋白激酶)、MAPKs(mitogen-activated protein kinases,丝裂原活化蛋白激酶)、RPKs(receptor-type kinases,受体蛋白激酶);磷酸酶主要为PP2Cs(protein phosphatase 2C,PP2Cs蛋白磷酸酶)^[4]。SnRK2和ABI1(ABA insensitive1)涉及的蛋白可逆磷酸化是ABA信号转导的核心机制^[49],在草莓果实成熟调控中存在保守性^[53]。例如,蛋白激酶FaSnRK2.6能够与蛋白磷酸酶FaABI1发生相互作用,在草莓果实成熟中发挥负调控作用^[54]。“PP2C-SnRK2核心信号组分”是调控草莓果实成熟的关键环节^[55]。在缺乏ABA的情况下,PP2C家族成员如ABI1、ABI2和HAB1(hypersensitive to ABA1)负调控SnRK2激酶家族的成员如SnRK2.6、SnRK2.2和SnRK2.3的激活。而当ABA受体与ABA结合后,其疏水表面暴露,PP2Cs的活性受到ABA受体的抑

制。被PP2Cs抑制的SnRK2.6、SnRK2.2和SnRK2.3可以重新激活下游ABA响应元件SLAC1(slow anion channel-associated 1),打开S型阴离子通道^[56]。另外,草莓果实中FaMRLK47,作为一种FERONIA-like受体激酶,在草莓果实成熟过程中发挥着至关重要的作用^[56]。总之,FaPYR1与果实成熟启动及品质形成密切相关^[57-58],"PYR1-PP2C-SnRK2"是调节果实成熟的核心信号转导机制^[59-60]。

在草莓FaPYR/PYLs和FaPP2C家族成员中,只有FaPYL2/4/9/11和FaABI1/FaPP2C16相互作用,FaPYL2与FaABI1的相互作用可能在草莓果实成熟过程中发挥作用^[51]。值得注意的是,SnRK2.6蛋白在拟南芥保卫细胞中充当CHLH/ABAR(Mg-chelatase H subunit/ABA receptor)和PYR/PYL/RCAR之间的耦合因子^[61]。因此,草莓果实成熟过程中ABAR与PYR/PYL/RCAR的关系有待进一步研究。CHLH/ABAR具有多种生物学功能,涉及了叶绿素合成、质核逆向信号及ABA信号转导^[61]。例如,在拟南芥中,CHLH/ABAR通过ABA-ABAR-WRKY40-ABI5/ABI4以不同的途径调节气孔运动、种子萌发和幼苗生长^[62]。为了进一步探索FaABAR在草莓果实成熟中的作用机制,通过酵母双杂交技术鉴定到了一个与FaABAR互作的富含亮氨酸重复序列(LRR)受体类激酶,即成熟调控蛋白激酶FaRIPK1(red-initial protein kinase 1)^[63]。FaRIPK1作为FaABAR的共受体,协同调控草莓果实的成熟,即FaRIPK1参与草莓果实成熟的启动并调控了果实的成熟,证实了FaABAR/CHLH是果实成熟的正向调节因子。FaMYB10(R2R3 MYB)是一个重要的转录因子,它介导ABAR感知下游的信号转导,从而刺激草莓果实成熟期间花青素的生物合成,FaMYB10和FaGAMYB参与了成熟多种生理过程调控,如着色、软化和香气,其中涉及重要转录因子FaABI4和FaABI5^[39,64-68]。

另外,在其他非呼吸跃变型果实上ABA核心信号转导机制的研究也取得重要进展。在对柑橘研究中,CsPYL4和CsPYL5在成熟过程中表达模式与ABA积累相反,而CsPP2CA和CsSnRK2的表达在成熟过程中持续下降^[69]。在黄瓜果实发育中,CsPYL2及CsPP2C2表达量较高并在花后27 d达到峰值,变化趋势与ABA水平一致,表明CsPYL2及CsPP2C2可能在黄瓜成熟过程中发挥重要作用,揭

示了ABA参与黄瓜果实的成熟调控^[70]。在甜樱桃中,ABA处理显著促进果实中花青素的积累,发现PacPP2C1与6个PacSnRK2s相互作用^[25]。受ABA诱导的荔枝LcASR蛋白定位于细胞核中并参与了果实的成熟调控^[71]。

总之,"ABA-PYR1-PP2C-SnRK2"核心信号组分是ABA调控果实成熟的保守机制^[72-73];同时"ABA-ABAR-RIPK1-ABI4"是调控草莓果实的成熟新机制^[35,62,74],表明ABA作用机制的复杂性、保守性和多样性。

2.3 ABA通过多种协同机制调控非呼吸跃变型果实成熟

在草莓果实成熟过程中,ABA和生长素(indoleacetic acid, IAA)是重要的协同调控激素,乙烯和赤霉素的作用较弱^[75]。在果实发育过程中,IAA和赤霉素GA4(gibberellic acid 4)含量均以小绿时期的草莓果实最高,并随着发育过程逐渐降低;ABA含量随果实成熟迅速增加,与着色变化趋势一致;茉莉酸甲酯浓度随时间变化不明显,水杨酸含量逐渐增加;茉莉酸(jasmonic acid, JA)和乙烯含量太低,无法量化^[39]。IAA主要在瘦果中产生,而ABA、乙烯、细胞分裂素(cytokinin, CTK)和赤霉素主要在花托中合成;赤霉素在一定程度上延缓了成熟,而细胞分裂素和乙烯似乎参与了成熟的后期调控^[13]。随着草莓果实成熟的开始,ABA、乙烯和多胺的作用增强,而GA和IAA的作用减弱^[76]。此外,JA参与果实花青素积累、细胞壁软化及乙烯的生物合成,最终加速了草莓果实的成熟^[77]。总之,非呼吸跃变型果实成熟的调控是一个复杂的过程,涉及了多种激素的协同调控。

2.3.1 ABA与乙烯的相互作用 尽管乙烯是跃变型果实成熟的关键调节因子^[78],但这种气体分子也通过与ABA的相互作用参与非呼吸跃变型果实成熟^[79-80]。在采后草莓果实中,乙烯促进ABA在花托组织中的积累,但不影响ABA分解代谢^[80]。乙烯反应调节因子FveERF的超表达激活草莓果实成熟期间的酰基转移酶(alcohol acyltransferase, AAT)基因的转录和酯积累^[79]。呼吸跃变型李果实及其非呼吸跃变型突变体果实的ACSI(ACC synthase1)启动子区序列差异较小;然而ABI5在非呼吸跃变型突变体李果实成熟期间的表达低于呼吸跃变型李果实,表明ABA在乙烯合成中起着至关重要的作用^[81]。黄

瓜 MADS-box 蛋白 CsSHP 通过 ABA 介导 CsSEPs (SEPARALATA) 调控^[59]。ABA 和乙烯相关基因在葡萄浆果成熟过程中受到一组转录因子的差异调控,包括 MADS-box、MYB、NAC、AP2/ERF、bHLH 和 ZIP^[82]。因此,ABA 与乙烯的相互作用在非呼吸跃变型果实成熟过程中起着重要作用。

2.3.2 ABA 与 IAA 的相互作用 在葡萄果实发育过程中,乙烯和 IAA 之间存在“拮抗调控作用”,ABA 和 IAA 之间存在“协同调控作用”,在激素生物合成和信号转导水平上形成一个精确的调控分子网络^[83]。在果实成熟前期,葡萄果实种子中的 IAA 含量比果皮中高出多倍,种子/果实鲜质量比率高的果皮具有较高的 IAA/ABA 水平,而比率低的浆果中 *NCED* 和 *MYB* 表达量显著升高^[84]。在葡萄果实中发现了 *GH3.1*,它编码一个生长素-氨基酸合成酶 (IAA-amino synthetase),能使 IAA-氨基酸结合并导致游离生长素含量降低,最终促进成熟,这种调控机制在呼吸跃变型及非呼吸跃变型果实中普遍存在^[85]。

在草莓果实发育过程中,IAA 和 ABA 是主导激素并以协同或独立的方式发挥作用:IAA 决定花托发育而 ABA 决定成熟;乙烯和 GA 基本不起作用^[76,86]。高水平的生长素促进了种子组织的发育,生长素响应因子基因的转录产物在果皮组织中积累;而在成熟后期,生长素作用减弱,ABA 作用逐步增强,表明生长期间 IAA/ABA 比率较高,成熟期间比率较低^[87]。草莓瘦果中 IAA 含量的降低可加速成熟进度^[88]。ABA 及 IAA 在瘦果中的含量显著高于花托,协同调控了种子及果肉的生理成熟^[86,89]。

发育的瘦果中 IAA 和 ABA 的积累量大于花托中 IAA 和 ABA 的积累量,这可以表明这两种激素调控草莓果实成熟的机制是复杂的^[86]。研究发现,花托中 IAA 依赖于瘦果中输出的 IAA,后期果实的膨大依赖于多种植物激素的协同调控,包括 GA、ABA 和乙烯等^[90]。IAA 和 ABA 在果实成熟中的重要作用涉及了多种生理过程^[91-92],如 *FaRGlyase1* (鼠李糖半乳糖醛酸裂解酶基因)^[93],*FaSHP* (一种 C-type MADS-box 基因)^[94],*FaβGal4* (β -半乳糖苷酶基因)^[95] 和 *Fa-NIP1;1* (质膜水通道蛋白基因)^[96],这些基因在草莓果实成熟期间受到 ABA 的正调控与生长素的负调控。此外,膜联蛋白 *FaAnn5* 和 *FaAnn8* 可能通过钙信号,参与草莓果实生长和成熟过程中 ABA 和 IAA 的协同调节;受体激酶和泛素连接酶对 IAA 和 ABA 都有

反应,并可能在两种激素的互作中发挥关键作用^[92]。综上所述,IAA 和 ABA 是草莓果实成熟的关键调控因子,ABA 和 IAA 通过一个复杂的分子网络在非呼吸跃变型果实成熟调控中发挥核心作用^[97]。

2.3.3 ABA 与糖的相互作用 糖在果实成熟和品质调控中发挥重要作用,因为糖的代谢和积累对风味有很大的影响。蔗糖能够作为一种信号,通过刺激 ABA 的产生和积累促进草莓果实成熟^[34,53]。ABA 和蔗糖都能诱导葡萄浆果成熟,蔗糖以 ABA 依赖和非依赖两种方式发挥作用^[6]。葡萄浆果在没有外源脱落酸的情况下,2%蔗糖显著促进花色苷的积累^[98]。糖-ABA 信号转导耦合因子,如 PP2C 及转录因子 WRKY 和 HOMEBOX,是葡萄果实成熟的核心组分^[26]。

另外,研究还发现蔗糖通过 ABA 调控果实的成熟^[34,53]。如用蔗糖处理大绿果草莓果实会促进 ABA 合成并诱导成熟,且这种诱导在采后储存的第一天最为明显^[99]。ABA 和蔗糖会抑制糖酵解,并促进草莓果实成熟,表明 ABA 与蔗糖的相互作用是通过抑制糖酵解而影响成熟的^[100]。此外,糖酵解关键酶 *FaGAPC2* (胞质甘油醛-3-磷酸脱氢酶)/*FaGAPCp1* (质体甘油醛-3-磷酸脱氢酶)对草莓果实中 ABA 和蔗糖介导的成熟具有负调控作用^[100]。转录因子 ABA-stress-ripening (ASR) 参与 ABA 和蔗糖信号转导^[101-102],ASR 通过 ABA 和蔗糖之间的耦合调节草莓果实的成熟^[102]。因此,ABA 与糖的相互作用在非呼吸跃变型果实成熟过程中发挥至关重要的作用。

2.3.4 ABA 与多胺的相互作用 在草莓果实成熟期间,多胺 (polyamines, PA),尤其是精胺 (spermine, Spm),以 ABA 为主导的和 IAA-乙烯协同参与的方式调控草莓果实的成熟^[89]。在草莓果实成熟开始时期,*NCED3* 转录促进 ABA 的快速积累,从而抑制多胺氧化酶 *FaPAO5* 的表达,导致精胺和亚精胺的积累^[103]。有趣的是,精胺和亚精胺 (spermidine, Spd) 含量的增加触发了 SAM 脱羧酶 *SAMDC*、亚精胺合酶 *SPDS* 和精胺合酶 *SPMS* 基因的表达,进一步加速了精胺和亚精胺的积累和果实成熟^[103]。以上研究揭示了 ABA 和多胺的相互作用在草莓果实成熟调控中发挥重要作用。总之,*FaPAO5* 介导的多胺代谢 Spd/Spm 产生 H_2O_2 ,与 ABA、乙烯、NO、 Ca^{2+} 构成复杂网络:Put 和乙烯在果实成熟过程中形成负协调环,Spd/Spm 和 ABA 组成了一个正调控环,揭示了

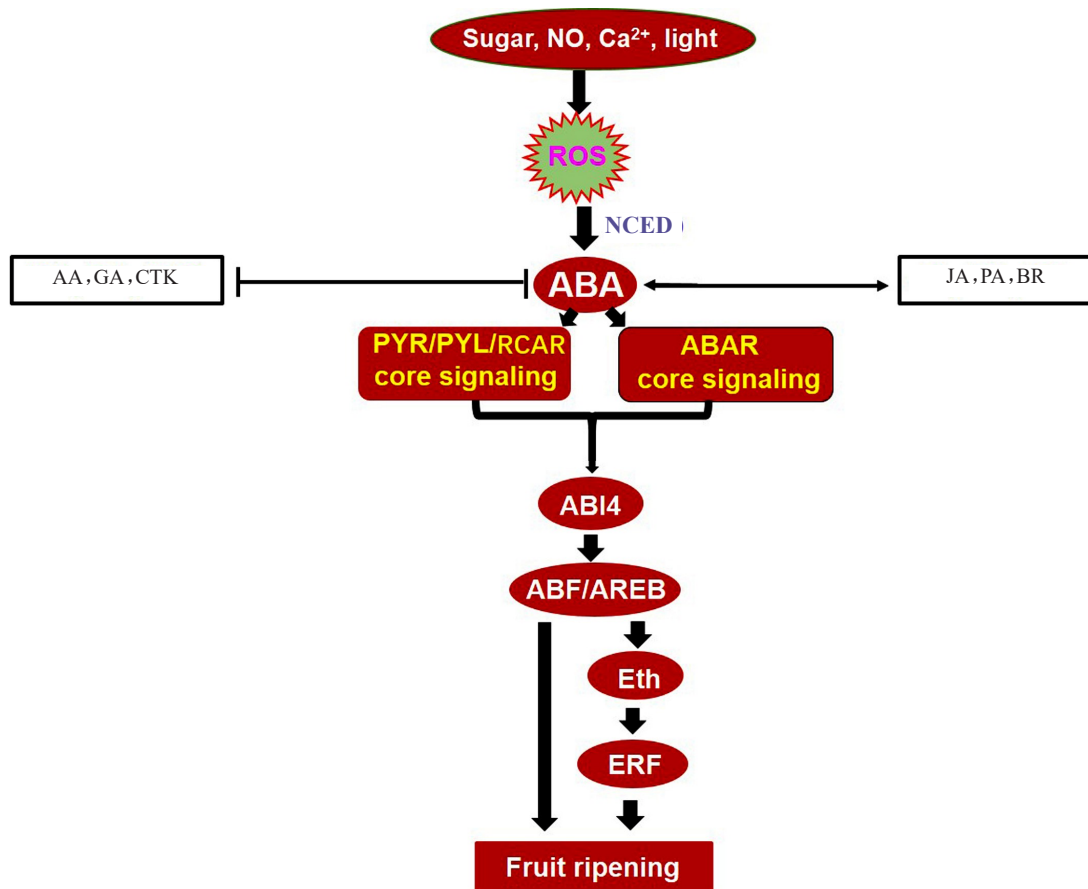
ABA 和多胺的相互作用在草莓果实成熟调控中产生重要影响^[104]。

3 结论和展望

果实的发育过程包括早期的细胞分裂和膨大,随后叶绿素降解、细胞壁软化,以及成熟过程中苯丙酸、类黄酮、淀粉/蔗糖和类胡萝卜素代谢的变化。这些过程受植物激素严格控制,主要包括乙烯在呼吸跃变型果实成熟中的作用、ABA 在非呼吸跃变型果实成熟中的作用以及二者的相互作用^[105-107]。在中间成熟类型无花果中的研究表明,ABA 能促进乙烯的积累及果实的成熟启动,而乙烯调控果实的成熟依赖于 ABA 受体识别,ABA 的作用方式与乙烯的系统 I /II 密切相关^[108]。综上所述,笔者提出了脱落

酸调控果实成熟的分子机制(图1)。随着果实启动成熟,糖、NO、Ca²⁺等发育信号及光等环境信号导致 ROS 积累,进而触发 ABA 合成及积累,同时协同抑制 GA、IAA 和 CTK 的合成和作用,并协同促进乙烯、JA、PA 及 BR(油菜素内酯)的合成及作用。这些激素组成了复杂的调控网络,其中 ABA 是调控果实成熟的核心机制,存在着乙烯依赖(呼吸跃变型)和不依赖(非呼吸跃变型)类型。总之,ABA、乙烯和 IAA 的协同调控主要表现为非呼吸跃变型果实中 ABA-IAA 互作、呼吸跃变型果实中的乙烯-IAA 互作以及两类果实中的 ABA-乙烯互作,他们在果实成熟中协同发挥关键的调控作用。

总之,近十年来,我国植物分子生物学研究取得了较大的进展,并且已开始从模式植物向果树木本



褪绿和着色是果实成熟过程中普遍存在的现象,这一过程涉及了 ABA 及早期信号和多种激素(糖、NO、Ca²⁺、光、JA、PA、BR、GA、IAA、CTK)的协同作用并组成了复杂的网络调控机制,ABA 是调控果实成熟的核心机制,其中存在着乙烯依赖(呼吸跃变型)和不依赖(非呼吸跃变型)类型。

Chlorosis and coloration are common phenomena during fruit ripening, which involves the synergistic effect of ABA and the early signals as well as multiple hormones (such as sugar, NO, Ca²⁺, light, JA, PA, BR, GA, IAA, CTK), constituting a complex regulatory network. ABA is the core player in regulating fruit ripening in the ethylene-dependent (climacteric) and ethylene-independent (non-climacteric) manner.

图1 植物激素协同调控果实成熟的分子机制

Fig. 1 Molecular mechanism of plant hormones in synergistically regulating fruit ripening

植物转变,但果树栽培周期长及遗传转化体系瓶颈限制了果树分子生物学发展。未来,结合基因组学、转录组学、蛋白组学、代谢组学和表观遗传学的发展及基因敲除 CRISPR/Cas9 等最新技术的应用,深入剖析果实成熟激素调控分子机制的共性和特异性,及种子和果肉的协同调控分子机制是未来重要的研究方向。

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