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果树器官脱落及离区细胞壁代谢研究进展

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摘要: 器官脱落是植物生长发育过程中普遍存在的一种生理现象, 也是园艺植物重要的农艺性状。脱落发生的特定区域为离区, 离区形成是多种激素、基因共同参与的精细而复杂的过程, 是果树器官脱落的必备条件, 脱落启动受到脱落信号、成熟衰老、逆境等多种因素影响。本文从器官脱落阶段界定、参与离区形成的基因(JOINTLESS、BOP蛋白、MADS-box基因家族)、器官脱落调控信号(生长素、乙烯、脱落酸、IDA-Hae-HSL2等)及离区细胞壁降解相关基因(PME、PG、Cx、β-Gal)等方面阐述器官脱落过程及其机制的研究进展, 为防脱落技术研发、新品种选育、果实机械化采收等提供理论依据。

关键词: 器官; 脱落; 离区; 细胞壁; 调控

A review on organ abscission and cell wall metabolism in fruit trees

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Abstract: Organ abscission is a common phenomenon in plants, which is also an important agronomic trait for horticultural plants. The specific sites where abscission occurs are called abscission zones (AZs). Its formation is a complex and precise process regulated by several hormones and genes, which is indispensable for the abscission of fruit tree organs. Organ abscission launches with specific signals and is usually affected by many factors such as maturity, aging, adversity, etc. In this paper, the recent progress of organ abscission process and its mechanism was reviewed in the aspects of organ abscission stage definition, genes involved in AZ formation (JOINTLESS, BOP protein, and MADS-box gene family), organ abscission regulatory signals (auxin, ethylene, abscisic acid and IDA-Hae-HSL2), and genes related to AZ cell wall degradation (PME, PG, Cx and β-Gal). It will provide a theoretical scientific basis for research on organ abscission prevention technology, breeding of new fruit varieties and mechanized fruit harvesting.

Key words: organ; abscission; abscission zone; cell wall; regulation

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器官脱落是植物衰老或受损器官从母体分离的一种现象, 对于调节植物负荷、释放成熟果实、种子传播或器官重回土壤等具有重要意义(郝紫微等2020; Gao等2019; 文晓鹏等2018; Patharkar和Walker 2018)。按照产生原因可将其分为三类: 一是器官成熟或衰老引起的正常脱落, 如果实成熟、花和叶衰老脱落, 可有效减少植物养分浪费, 增强植物适应外界环境能力; 二是植物自身代谢引起的生理脱落, 如营养生长与生殖生长竞争引起的脱落(Sawicki等2015); 三是外界逆境引起的胁迫脱落, 如污染、水涝、干旱、病虫害等导致的器官非正常脱落。果树作物中部分品种果实成熟脱落不同步导致机械化采摘技术桎梏难以突破(Meng等2015), 而器官生理和胁迫脱落则会限制果树产量(Ying等2016), 在荔枝(Li等2019a)、桃(Wu等2018)、葡萄(Domingos等2015)和柑橘(Xie等2015)等上已有较多报道。果树器官脱落发生在离区(abscission zone, AZ), 接收内源信号后导致细胞间质和细胞壁发生降解。因此, 从离区形成过程中内源激素与细胞壁降解酶入手, 揭示植物器官脱落的机理, 可为果树新品种选育、器官脱落防控及果实机械化采收等提供科学依据。

1 植物器官脱落阶段界定

离区是由5~50层体积小且排列紧密的细胞构成, 其中1~2层细胞分化为离层从而触发脱落。植物器官首先产生离区, 然后在外力的作用下发生脱落。但也有例外, 如西藏半野生小麦在成熟期不需要外力就能自发断穗(冯翔2019)。虽然引起整个或部分器官脱落的触发因素不同, 但器官脱落步骤一般都分为4个阶段(Meir等2019), 主要包括: (1)细胞分化形成离区; (2)离区细胞对脱落信号做出反应; (3)脱落信号激活离区细胞, 细胞壁降解酶活性上升并促进细胞壁降解; (4)离区进一步分化产生离层和保护层, 导致器官脱落。

第一阶段细胞分化形成离区, 主要受细胞分化相关转录因子和蛋白调控, 未完成分化的离层细胞不具备感知脱落信号的能力。番茄离区发育控制基因J (JOINTLESS)突变后, 离区消失, 而*jointless-2*延缓了离区的发育和形成(Malabarba等2020; Roldan等2017)。*JOINTLESS*与MADS-box基因家族的2个成员*MACROCALYX* (*MC*)和*SlMBP21*互作形成SLMBP21-J-MC复合物, 参与花梗离层发育(Liu等2014), 也可以与SlFYFL互作参与离区的形成(Xie等2014)。*SHAT1*和*SH4*是水稻小穗发育前期种子离区识别的关键基因, 持续表达可以促进离区的发育和分化(Zhou等2012)。BOP (BLADE-ON-PETIOLE)蛋白在新生区和离层起着特异分化的功能, 其中, BOP2可以调节烟草花冠离层的分化(Wu等2012), *GhBOP1*能通过影响陆地棉离层的分化进而参与整个叶片的脱落进程(常璟等2015)。第二阶段为离层细胞接收脱落信号并做出反应, 启动器官脱落, 主要包括乙烯与生长素信号、花发育信号、细胞凋亡信号、ROS信号等。第三和第四阶段主要是离区细胞壁代谢相关酶活性提高导致细胞壁组分降解, 进而促进器官脱落, 比如果胶甲酯酶和多聚半乳糖醛酸酶的活性上调, 在蓝莓(Chea等2019)和冬枣(李红卫等2014)等花朵脱落、果实成熟过程中起到重要作用。

2 细胞壁降解酶参与果树器官脱落

落花落果、异常落叶现象在葡萄(韩先焱2019)、荔枝(杜艺2016)和柑橘(董倩倩等2018)等果树生产过程中普遍存在, 对于果树丰产稳产具有重要影响。果树落果包括受精不完全导致胚和胚乳发育受限的幼果脱落、果实成熟正常脱落以及非生物胁迫导致的脱落等, 主要是由细胞壁降解引起的。细胞壁的解体是果树离区形成的必经过程。细胞壁是由果胶、纤维素、半纤维素和结构蛋白通过氢键、共价键、离子键、疏水作用力等方式相互联系在一起形成的多糖网络结构(张元薇等2019)。脱落过程中果胶甲酯酶(pectin methylesterase, PME)、多聚半乳糖醛酸酶(polygalacturonase, PG)、纤维素酶(cellulase, CE)等活性上调从而加速破坏细胞之间的粘附力(文晓鹏等2018), 原果胶溶解为可溶性果胶, 纤维素、半纤维素含量不断下降, 这在黑莓(Zhang等2019a)、樱桃(沈颖等2020)、梨(许娟等2015; 霍宏亮等2016)、番荔枝(Ren等2020)、蓝莓(Chea等2019)、冬枣(李红卫等2014)和苹果(高滋艺等2016)等果树上均有相关研究报道。

2.1 果胶酶

果胶酶是一种可分解果胶的多酶复合物, 包括果胶甲酯酶(PME)、多聚半乳糖醛酸酶(PG)、β-半乳糖苷酶(β-galactosidase, β-Gal)和α-L-阿拉伯呋喃糖苷酶(α-L-arabinofuranosidase, α-Af)等。果实发育初期PME活性急剧上升, ‘琯溪蜜柚’果实中*CmPME1*表达量逐渐升高(刘志发等2015), *PaPME2*基因沉默可延缓甜樱桃果实成熟(齐希梁等2020)。PME去酯化后, PG通过水解果胶分子多聚半乳糖醛酸链使原果胶转化成可溶性果胶, 参与初生细胞壁松弛促进果树的落花落果。冬枣半红期*ZjPG07*表达量上调导致细胞壁果胶含量减少(何颖等2021); *CisPG21*参与柑橘离区细胞壁降解促进果实脱落(Tong等2020); *PpPG1*和*PpPG2*均参与翠冠梨果实衰老过程(李慧等2012)。

影响果实发育早期细胞壁代谢的还有β-Gal, 如桃β-Gal基因表达量较高, 通过降解果胶多聚醛酸侧链的半乳糖残基, 促进果实中果胶物质溶解(张元薇等2019); 但也有β-Gal在果实发育后期起作用的报道, 如β-Gal在苹果、猕猴桃、龙眼和甜樱桃成熟期表达量增加较快(冯新等2019), 加速果胶的降解导致果实硬度快速下降(张元薇等2019; 赵云峰等2014)。α-Af影响果实发育后期的细胞壁代谢活动, 在甜樱桃和桃果实中活性较高, 通过降解阿拉伯糖残基使果胶溶解, 受到乙烯和1-甲基环丙烯(1-methylcyclopropene, 1-MCP)调控(张元薇等2019; 张敏等2015)。

2.2 淀粉酶和脂氧合酶

淀粉酶(amylase, AM)可将淀粉转化为可溶性糖, 导致细胞膨胀力下降, 细胞之间连接减少, 细胞离散。淀粉酶主要有2种, 即α-淀粉酶和β-淀粉酶, 二者协同降解淀粉。AM活性和*MdAM*基因表达的快速上升可促进淀粉降解, 在‘嘎拉’苹果果实软化初期具有重要作用(齐秀东等2015)。低温结合1-MCP处理能显著抑制苹果AM活性, 保持果实细胞壁完整(鲁乐2020)。也有研究证明AM活性与‘山农脆’梨果实硬度变化呈极显著负相关(艾静2014), 在桃果实的衰老过程中也有相似报道(陈凯路2015)。

脂氧合酶(lipoxygenase, LOX)是果实中与膜降解有关的含非血红素铁的酶, 其活性上升会产生活性氧、自由基和氢过氧化物等, 从而加速植物组织衰老。‘富平尖柿’中LOX活性呈现“上升-下降”的趋势, 其中*DkLOX3*在果实发育前期表达量极低, 但随着果实的成熟表达量逐渐升高, 至乙烯跃变时出现表达高峰, 说明该基因可能与乙烯协同作用, 促进柿果实的成熟衰老(侯亚莉2016)。

2.3 纤维素酶和松弛因子

纤维素酶(CE)通过分解半纤维素基质多糖, 导致果胶外露更易受水解酶影响, 细胞壁结构松懈, 加速落花落果(赵云峰等2020)。兔眼蓝莓离区CE活性随着果实发育逐渐增加, 赤霉素处理抑制CE活性, 而乙烯显著增强果实离区CE活性(李婷2019)。*CisCEL16*在柑橘离区中表达水平上调, *LcCEL2*和*LcCEL8*在荔枝果实脱落阶段表达显著上调, 促进纤维素酶活性增加, 导致细胞壁降解加快, 果实脱落加速(何颖等2021; Li等2019a, b)。

细胞壁降解还与细胞壁松弛因子(expansin, EXP)有关, 通过破坏氢键促进果实软化(Valenzuela-Riffo等2020)。*EXP1*过表达可促进桃果实提前软化, 而沉默*EXP1*会提高果实硬度和延缓果实成熟, 这与*Exp1*在榴莲和番荔枝果实中的作用一致(Palapol等2015; 陈晶晶等2015)。

3 植物激素信号对器官脱落的调控

植物激素包括生长素、乙烯、脱落酸等, 作为信号对器官脱落进程有促进或抑制作用, 尤其是生长素和乙烯的平衡是调节离区脱落信号获取的关键因素, 当离区感受到脱落信号之后, 该区域细胞才会进一步分化, 通过下一级通路传递下去, 导致离区细胞壁降解相关酶类活性增加, 细胞壁降解(Nakano等2014)。

3.1 生长素调控植物器官脱落

生长素对植物器官脱落有抑制作用, 并以自上而下的极性运输方式使远轴端生长素含量高于近轴端, 阻止或延缓离区形成; 当远轴端生长素含量低于近轴端, 启动离区形成。免疫定位法发现黄色羽扇豆花器官离区生长素含量的变化与脱落有关, 其在脱落前含量下降, 脱落后含量增加(Kućko等2019)。

调控植物器官生长素水平可影响脱落, 如月季*RhIAA16*表达上升会减少生长素的含量, 促进器官脱落, 在花瓣、花托、雌雄蕊以及离层部位均有表达, 且在离层启动前期阶段表达量最高(Gao等2016)。番茄花柄离区生长素运输载体SlPIN1和SlLIN4促进生长素极性运输, 加快离区生长素耗竭, 促进脱落(史自航2018; 韩新奇2018)。外施生长素处理增加了黄色羽扇豆离区生长素含量从而延缓脱落(Kućko等2019)。果实离区生长素反应因子SlARF受SlBL4调控, 使果实离区生长素含量积累, 抑制果实脱落(Yan等2021), 其中SlARF10、SlARF16和SlARF17受SlmiR160影响, 使番茄花器官生长素含量下降, 促进花器官脱落(Damodharan等2016)。作为一种气体信号分子, H_2S可以诱导*TOFZY3*在番茄花柄远轴端和离区表达, 抑制*TOFZY4*在整个花柄中的表达, 从而调控生长素水平(李佳宁等2020)。GH3家族多个蛋白可以催化游离的生长素同氨基酸结合形成结合态生长素, 而Aux/IAA家族成员可以通过与生长素应答因子(auxin response factor, ARF)结合来抑制生长素信号的转导, 从而降低活性生长素的浓度(Peer 2013)。生长素的含量也可以通过乙烯来调控, 从而影响器官脱落(李家寅2017)。

3.2 乙烯调控植物器官脱落

乙烯被认为是植物主要的脱落诱导因子, 其通过信号转导机制被传导下去, 导致ERF (ethylene response factor)、EBF等乙烯应答转录因子激活, 引起离区细胞壁水解酶活性增强, 促进果胶和半乳糖醛酸长链降解, 导致器官脱落(刘畅宇等2019; Do等2016; Cheng等2015)。已有报道表明木瓜跃变期产生大量乙烯, 加速新陈代谢, 促进果实成熟(Ding等2019)。无花果接近成熟时乙烯含量快速升高, 释放高峰与呼吸峰同步出现, 促进果实快速成熟(李春丽和沈元月2016)。

ACC合酶(ACC synthase, ACS)和ACC氧化酶(ACC oxidase, ACO)是乙烯生物合成过程中的两个关键酶, 有效调控乙烯的合成(吴建阳等2017)。生长素能够调控乙烯合成, 外施生长素能提高拟南芥中*ACS4*基因的表达水平, 合成更多的乙烯(岳鹏涛2020)。生长素类似物萘乙酸(1-naphthylacetic acid, NAA)处理, 能诱导苹果*Md-ARF5*与*MdACS3a*的启动子区域结合从而促进其转录, 促进乙烯合成(岳鹏涛2020)。KNOTTED1-LIKE homeobox (KNOX)蛋白LcKNAT1能够和荔枝果实中*LcACS1*、*LcACS7*和*LcACO2*基因启动子区域结合从而抑制其转录, 抑制乙烯合成, 进而延缓荔枝果实脱落(Zhao等2020; 吴建阳等2017)。HDZIPI转录因子LcHB2、LcHB3能和*LcACO2/3*、*LcACS1/4/7*基因的启动子结合, 激活其表达, 促进荔枝果粒脱落(Li等2019a, b)。外施乙烯处理可通过上调相关基因*BcCEL*、*BcPG*、*BcPME*和乙烯受体*BcERS1*、*BcETR2*等表达水平, 增加白菜叶片离区乙烯含量, 促进大白菜叶片脱落(孟娇2019)。也有报道称植物离区H_2O_2含量与乙烯有关, 进而调控果实脱落(李婷2019)。乙烯响应因子Sl-ERF52与*SlTIP1*启动子结合调控H_2O_2积累, 增加了番茄花梗离区中乙烯含量, 促进花器官脱落(Wang等2021)。H_2O_2处理也可以促进乙烯积累, 通过调控纤维素酶相关基因的表达促进番茄叶脱落(王禹佳2020)。

3.3 脱落酸调控植物器官脱落

脱落酸是植物体内发现的半萜类化合物, 能够调控植物的多种生理反应, 包括促进落花落果、气孔关闭等。脱落酸的积累与植物器官脱落密切相关, 如‘糯米糍’荔枝采前落果显著高于‘桂味’的原因在于前者脱落酸含量更高, 主要受*LcNCES1*、*LcNCED3*和*LcNCED5K*等关键基因的调控(王丹2018)。脱落酸还能增加纤维素酶的活性, 参与细胞壁降解(Chen等2016)。

有研究表明脱落酸的作用是通过乙烯间接实现的。脱落酸可以抑制生长素的极性运输或提高*ACS1*和*ACO1*基因表达来促进乙烯的合成, 从而加速脱落(Botton和Ruperti 2019)。外源脱落酸提高了羽扇豆花梗离区乙烯合成基因*LlACS*和*LlACO*的表达水平, 显著增加离区乙烯含量, 促进了花脱落(Wilmowicz等2016)。脱落酸还促进了苹果*MdACO1*启动子与*MdHB1*结合, 加快乙烯合成(刘悬烁2019)。反之, 乙烯也可以促进脱落酸的合成。乙烯响应因子*PpERF3*直接调控脱落酸合成相关基因*PpNCED2/3*表达来提高脱落酸的合成(Wang等2019)。但也有报道认为高浓度的脱落酸对某些植物器官脱落不起作用, 如新疆‘纸皮’扁桃新稍高浓度脱落

酸诱导叶片中营养物质向幼果流动从而减缓幼果脱落(杨波等2015)。

3.4 其他信号通路参与器官脱落的调控

拟南芥IDA突变体在乙烯感知或信号转导过程中受损, 表现为器官延迟脱落, 由此推测存在一种调节器官脱落信号, 由ABSCSIAT (IDA)信号肽、HAESA (HAE)和HAESA-like2 (HSL2)激酶复合物控制(Meir等2019)。IDA-HAE-HSL2复合物作用于乙烯的下游, 是器官脱落后期步骤所必需的, 而不是脱落过程的诱导阶段所必需的, 在细胞分离和细胞壁降解过程中起到积极的调节作用, 如可受离区积累的乙烯激活, 增强细胞壁降解酶活性, 导致细胞壁降解和器官脱落(图1) (Botton和Ruperti 2019)。IDA信号肽通过受体HAE和HSL2行使功能, 主要是促进果胶水解和细胞壁降解。拟南芥IDA家族成员*CitIDA3*在器官离区过表达促进离区细胞增大, 而IDL6能够诱导PG2的表达, 降低细胞壁的强度(Estornell等2015; 王鑫2016)。遗传学研究表明, HAE受体复合物的下游是一个由MKK4/5和MPK3/6组成的丝裂原活化蛋白激酶(MAPK)级联反应, 激活Class I KNOX类转录因子和MADS结构域转录因子AGAMOUS-LIKE 15 (AGL15) (Cho等2008)。KNOX基因包括KNAT1/BP、KNAT2、KNAT6等, 其中, KNAT1/BP位于IDA-HAE-HSL2信号转导的下游, 通过抑制KN-AT2和KNAT6表达来调控器官脱落(Ma等2015; Cho等2008)。已有证据表明过表达AGL15可抑制器官脱落, 但不改变离区的形成, 说明它是脱落的负调控因子。AGL15还通过MKK4/5差异磷酸化促使HAE表达, 从而完成一个控制HAE表达的正反馈回路(Patharkar和Walker 2015)。这些因素被认为可以诱导细胞壁重塑和降解酶的转录。

细胞分离阶段还存在一个NEVERSHED (NEV)途径, 编码ADP核糖基化因子GTP酶激活蛋白(ADP-ribosylation factor GTPase-activating protein, ARF-GAP), 突变体离区能够正常分化, 但器官不能脱落。NEV信号途径中断影响脱落启动过程所需的HAE和HSL2信号分子定位、细胞壁修饰酶分泌等(Liu等2013), 其突变改变高尔基体结构, 影响反式高尔基体网络的位置, 将HAE和其他蛋白质移动到质膜, 或促使NEV在囊泡积累, 阻断了细胞分离所需信号转导与相关酶的运输, 细胞分离中止, 器官脱落受到抑制, 此过程中离区细胞有明显增大现象(Groner等2016)。研究发现, EVERSHED (EVR)、SOMATIC EMBRYOGENESIS RECEPTOR-LIKE KINASE1 (SERK1)和CAST AWAY (CST)基因突变可以减少NEV在囊泡的积累, 间接恢复高尔基体结构, 使HAE-HSL2信号不受阻碍, 促进器官脱落(Taylor和Walker 2018; Patharkar和Walker 2018)。另外, NEV也参与IDA平行途径促进细胞分离, 如当KNAT1

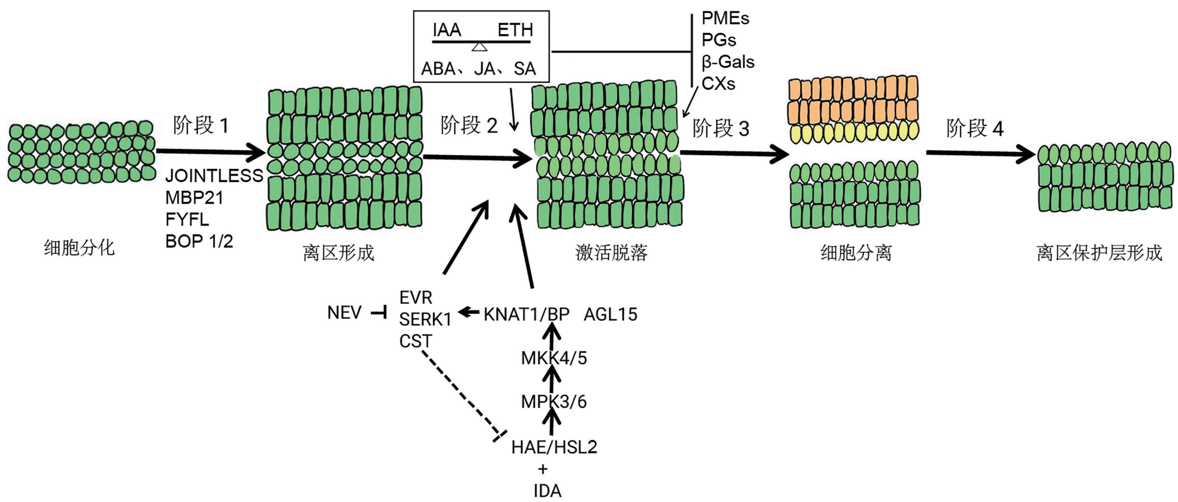

图1 离区形成和器官脱落模型

Fig. 1 Model of AZ formation and organ exfoliation

作为IDA-HAE-HSL2信号通路的下游效应被抑制时, EVR的表达水平降低, KNAT2和KNAT6的转录抑制解除, 从而促进脱落(Liu等2013)。

综合上述, 器官脱落过程并不是单一的途径调控, 而是受多个信号途径共同影响(图1)。另外水杨酸(salicylic acid, SA)和茉莉酸甲酯(methyl jasmonate, MeJA)也能够促进植物组织中乙烯的合成, 在离区累积, 引起器官脱落(Kućko等2019)。但多种植物激素如何交叉作用调控植物器官脱落尚有待进一步研究。

4 研究展望

植物器官脱落在自然界中普遍存在。对果树而言, 正常的器官脱落有利于及时调整源库关系, 但严重的落花落果会导致减产, 农民收入下降, 因此, 研究器官脱落在基础理论研究和生产实践应用上都具有重要意义。果树中器官脱落基因家族研究已有较多报道, 如, 梨中鉴定出61个PG基因、23个LOX基因(Luo等2021; Zhang等2019b), 猕猴桃中鉴定出51个PG基因、6个LOX基因(Huang等2020; 张曾等2017), 柑橘中鉴定出38个PG基因(Ge等2019), 桃中鉴定出13个LOX基因、45个PG基因(钱铭2017; 郭绍雷等2016)。但器官脱落相关基因在不同树种中的作用机制及是否存在协同作用等方面, 仍需要进一步研究。另外, 前人报道激素对器官脱落相关基因有调控作用, 如乙烯可以抑制PMEs基因的表达, 促进PGs和β-Gals基因的表达, 生长素能抑制PGs基因的表达, 促进PMEs基因的表达, 但具体的调节方式还有待深入研究。

在果实采收过程中, 同期成熟是一个重要研究课题, 关系到果实机械化采收和成功销售。了解各种果树生长发育规律, 使用生物技术手段结合传统育种, 采用精准栽培管理技术, 可以促使果实同期成熟, 如, 喷施褪黑素可减少葡萄未成熟和过度成熟果实数量, 增强种植区域果实成熟的同步性(Meng等2015)。喷施脱落酸能促进甜樱桃花青素的积累, 促进果实色泽同期均匀变红, 有利于果园机械化同期采收(Tijero等2016)。国内外学者虽已在果实成熟脱落机制方面进行了大量的研究, 但仍有许多科学问题需要进一步解决。但对具有总状花序的果树而言, 果实成熟具有不同期性的特点, 如蓝莓, 如何调控花序或果实发育实现同期成熟仍有待深入研究。

另外, 多数果树遗传转化体系还不完善, 研究脱落相关基因功能比较困难, 但随着梨(Jia等2019)、柑橘(Osakabe等2018)、苹果(Malabarba等2020)、葡萄(Ren等2021)等遗传转化体系和CRISPR/Cas9基因编辑技术的日趋成熟, 使果树器官脱落的特异性机制研究成为可能, 将为果树新品种选育、器官脱落防控技术研发及果实机械化采收提供有力支撑。

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