

激素调控植物成花机理研究进展

邹礼平, 潘钺, 王梦馨, 崔林, 韩宝瑜

中国计量大学, 浙江省生物计量及检验检疫技术重点实验室, 杭州 310018

摘要:开花是植物对环境的适应性表现, 是在多种外源和内源信号形成的复杂成花调控网络下完成。植物激素作为最重要的内源信号参与者, 在成花进程中扮演着重要角色。近年来, 光周期等成花途径和表观遗传调控中激素的作用机理不断被解析。研究发现激素间存在协同和拮抗作用, 并证实多种激素参与赤霉素(gibberellins, GA)途径中 DELLA 蛋白介导的多种成花调控途径。本文主要综述了 GA 在植物成花中的调控机理, 同时探讨了脱落酸(abscisic acid, ABA)、生长素(auxin, IAA)、细胞分裂素(cytokinin, CTK)、水杨酸(salicylic acid, SA)、茉莉酸(jasmonic acid, JA)和乙烯(ethylene, ET)等其他内源激素在成花中的作用及其与 DELLA、miRNAs 和转录因子(transcription factor, TFs)等通路串联调控, 为全面解析激素调控植物成花的网络提供参考。

关键词: 植物激素; 花芽分化; 成花调控; 信号传导

Progress on the mechanism of hormones regulating plant flower formation

Liping Zou, Cheng Pan, Mengxin Wang, Lin Cui, Baoyu Han

Zhejiang Provincial Key Laboratory of Biometrology and Inspection & Quarantine, China Jiliang University, Hangzhou 310018, China

Abstract: Flowering is the adaptability of plants in response to the environment, which is regulated by the complex flowering control network formed by a variety of exogenous and endogenous signals. Plant hormones, the most important endogenous signal participants, play important roles in the process of plant flowering. Recent reports reveal the pivotal roles of hormones in the epigenetic regulation and flowering promotion pathway. In addition, synergistic or antagonistic interaction has been observed among many hormones. Numerous hormones have been found to be involved in the regulation of the multiple flowering development regulation and signaling pathways mediated by DELLA protein in the gibberellin (GA) pathway. In this review, we summarize the recent advances of the flowering mechanisms related to GA pathway and discuss the effects of abscisic acid (ABA), auxin (IAA), cytokinin (CTK), salicylic acid (SA), jasmonic acid (JA), and

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作者简介: 邹礼平, 在读硕士研究生, 专业方向: 生物化学与分子生物学。E-mail: 1223760931@qq.com

通讯作者: 韩宝瑜, 博士, 教授, 研究方向: 化学生态与分子生物学。E-mail: hanby15@163.com

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ethylene (ET) on flowering, including their cross-regulation with DELLA, miRNAs, and transcription factor (TFs). This review provides a reference for further comprehensive analysis of the hormone-regulated network of plant flower formation.

Keywords: plant hormone; flower bud differentiation; floral regulation; signal transduction

开花是植物对环境的适应性表现,是植物从营养生长向生殖发育的转变,是决定植物繁殖成功与否的重要环节,本质是茎顶端分生组织(shoot apical meristem, SAM)由营养生长期分化产生叶片转变为生殖发育时期形成花、果实和种子的过程^[1]。植物成花过程可分为花的诱导、花芽分化和花器官的发育 3 个阶段,此过程与开花时间、开花数量、开花质量和花期长短密切相关,同时还对植物的观赏、食用和药用的经济价值产生直接影响^[2]。成花过程是一个复杂的生理过程,该过程受外部和内部因素的共同调控,如光周期、温度以及内源激素介导的多种途径调控^[2~4]。在过去几十年,通过对拟南芥(*Arabidopsis thaliana*)的成花生理和分子机制的研究,发现光周期途径、春化途径和环境温度途径主要传递光和温度等外部信号;而自主途径、赤霉素途径和年龄途径在很大程度上以内源信号为主^[1,2,5~7]。可见,在自然状态下植物成花是对多种环境和内源信号识别和整合后作出的应答。

植物内源激素(plant endogenous hormones)参与植物的整个生命过程,通过在植物体内构建复杂完整的信号网络,传递外源或内源信号来调控植物的生长发育。因此,激素信号对于成花的影响非常重要^[8,9]。在特定的条件下,激素信号的调控往往是将不同激素信号汇集后通过改变关键成花基因的表达水平来实现^[10]。赤霉素(gibberellins, GA)作为赤霉素途径中主要的信号因子,在成花过程必然发挥着关键性的作用,但其他激素如脱落酸(abscisic acid, ABA)、生长素(auxin, IAA)、细胞分裂素(cytokinin, CTK)、水杨酸(salicylic acid, SA)、茉莉酸(jasmonic acid, JA)和乙烯(ethylene, ET)等,也是参与激素调控网络不可缺少的部分^[3,11]。对于温室种植或精细化管理的作物而言,通过光周期和温度等控制外部信号可实现对成花的调控;但是对于大田种植的作物而言,则存在易被干扰、成本较高和可操作性差等缺点。因此,研究成花过程中激素的调控作用,解析植物体内信号调控网络,可为大田作物生产提供指

导借鉴。本文主要对激素调控植物成花的机理研究进行了综述,并总结出部分激素互作通路模式图(图 1),以期为更好地研究植物花的诱导、花芽分化和花器官发育中激素作用机理和调控机制提供参考。

1 赤霉素途径

GA 是一类四环二萜类化合物,在植物生长发育过程中起着重要的调节作用。迄今为止,自然界中发现的 GA 形态结构超过 136 种,但是只有 GA₁、GA₃、GA₄ 和 GA₇ 少数形态具有生理活性^[12]。近年来,随着分子遗传学和功能基因组学的不断发展,GA 调控植物生长发育的模式被解析的十分透彻^[13,14]。越来越多的研究表明,GA 在去抑制和信号转导等方面发挥着重要的作用^[14,15]。GA 信号转导主要借助于 GID1 (GA insensitive dwarf 1)、DELLA 蛋白和介导 DELLA 蛋白降解的其他调控因子实现,可见 DELLA 蛋白是 GA 合成及其信号转导过程中的核心因子,在 GA 合成以及其信号转导中发挥着重要作用。

1.1 GA 与植物成花

赤霉素途径调控成花是最早被发现的 4 条成花途径之一,拟南芥内源 GA 合成受阻或者破坏 GA 在体内的信号转导过程,成花进程均会受到影响^[16]。GA 信号转导是由活性 GA 激活的,而 GA 作为可移动的分子,可通过细胞膜在细胞间进行运输^[17]。细胞间 GA 的动态平衡主要由 GA 合成途径中关键限速酶基因 *GA20ox* 和 *GA3ox*、失活和降解途径中 *GA20ox* 氧化酶基因调控。GA 信号转导依赖一类核蛋白 DELLA 的介导^[18],DELLA 蛋白被认为是植物生长发育和成花的抑制因子。水稻(*Oryza sativa* L.)中仅存在一个基因编码 DELLA 蛋白^[19,20],而拟南芥存在 5 个特异性的 *DELLA* 基因,包括 *GAI* (GA insensitive)、*RGA* (repressor of *GAL-3*)和 3 个 *gal-3-like* 蛋白的抑制基因(*RGL1*、*RGL2* 和 *RGL3*),这些基因既存在功能的冗余又具有特异性^[8,21]。拟南芥突变体

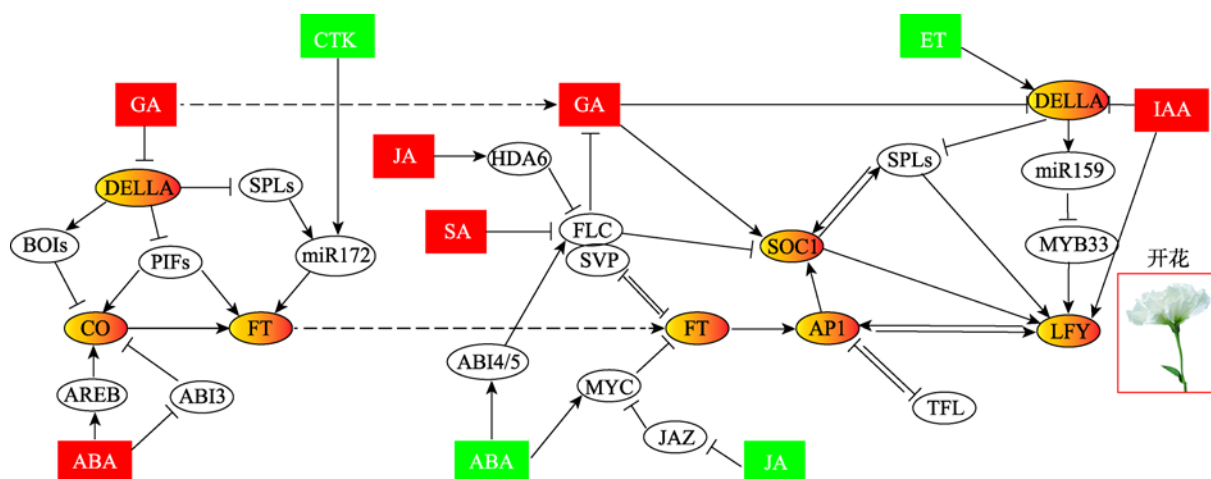


图1 激素在植物成花中的交互机制

Fig. 1 The interaction mechanism of hormones in plant flower formation

成花途径关键基因用黄色高亮标记, 红色和绿色分别代表激素的作用, 红色代表促进、绿色代表抑制; 虚线箭头代表迁移, \rightarrow 代表正调控, \vdash 代表负调控, 双向符号代表互相作用。GA: 赤霉素; ABA: 脱落酸; IAA: 生长素; CTK: 细胞分裂素; SA: 水杨酸; JA: 茉莉酸; ET: 乙烯。CO: constans; FT: flowering locus T; AP1: apetala 1; SOC1: suppressor of overexpression of constans; LFY: leafy; SPLs: squamosa promoter binding protein-like; BOIs: botrytis susceptible1 interactors; PIFs: phytochrome interacting factor; AREB: ABA responsive element binding protein; ABI: abscisic acid-insensitive; HDA6: histone deacetylase 6; FLC: flowering locus C; SVP: short vegetative phase; MYC: myelocytomatosis proteins; JAZ: jasmonate ZIM-domain protein; MYB33: MYB domain protein 33; TFL: terminal flower。

gal-3 在短日照下不开花, 在长日照下呈现中度晚花现象^[22]。该现象揭示赤霉素途径调控低于光周期调控, 当光周期调控不起主导作用时, 赤霉素途径的重要性被凸显出来。但是近期研究发现, 无论光周期调控信号是否存在, GA 都具有独特的调控模式促进成花。Porri 等^[23]发现长日照下 GA 也可以上调 FT (flowering locus T) 和 TSF (twin sister of FT) 蛋白的表达水平促进成花。Galvão 等^[24]发现环境温度途径诱导拟南芥成花需要借助 GA 信号转导, DELLA 在长日照下可沉默叶片中 miR172 和茎尖的 *MADS* 基因参与自主途径抑制成花^[25], DELLA 也下调年龄途径中 miR156 的靶基因 *SPLs* (squamosa promoter binding protein-like) 参与成花^[22]。可见 GA 信号参与年龄、自主和环境温度等途径的调控^[22,24,26~28]。FT 蛋白的合成部位在叶片, 但其被运送至 SAM 中才发挥作用^[11], 因此 GA 调控成花的作用部位分为叶片和 SAM。

1.2 叶片中的 GA 调控

众多的研究表明, 当植物体内 GA 含量较低或者 GA 信号传递受阻的情况下, FT 基因表达水平处于较低水平; 而当叶面上外源喷洒 GA 或恢复 GA

信号传递时, FT 基因表达水平上调^[23,24,27~29]。这些结果支持长日照下 GA 可增强 FT 基因的转录活性这一观点。但也有研究发现叶面喷洒 GA 既不能改变野生型植株在短日照下 FT 基因的转录水平, 也不能改变长日照下 *co* 突变体 FT 基因的转录水平^[29,30]。所以, 长日照下 GA 是否调控 FT 基因的表达量还需要更多的研究来验证。

GA 可通过多种机制调节 FT 基因的表达水平实现成花调控^[23,24,27,28]。AP2 (apetala 2) 类蛋白负调节叶片中 FT 基因的转录活性, 而叶片中 DELLA 可抑制 miR172 的表达, 实现对 miR172 靶基因 AP2 的上调^[31~33]。Yu 等^[27]也发现 GA 对 miR172 的调控是借助于 DELLA 和 miR172 的正调控因子 SPLs 来实现。当然部分 SPLs (如 *SPL3*) 基因编码序列可直接与 FT 基因序列结合, 并激活 FT 基因转录^[34]。Yu 等^[27]还指出 DELLA 组成型激活表达后, miR172 的表达量被显著下调, 可能是由于 DELLA 与 SPLs 蛋白结合引起的, 同时会引起 FT 基因转录水平下调。在突变体 *SUC2: ΔDELLA* 中过表达 miR172 可改善其晚花现象^[31], 这也证明 DELLA 可能是通过 *SPL-miR172* 调控模式增强对 FT 的转录抑制。

DELLA 除了可激活 FT 基因的抑制因子外, 还

会干扰 *FT* 关键转录激活因子 CO (constans) 蛋白的功能。DELLA 可与 CO 或含有 CO 结构域类似物结合, 使其与 DNA 互作而丧失功能^[35,36]。因此, 不论是 GA 含量降低还是增强 DELLA 蛋白水平, 其最终结果都是导致 *FT* 和 *TSF* 的转录水平降低, 这与 CO 蛋白的稳定性恰好一致^[23,30]。体外研究发现, DELLA 可阻止 CO 和 NFYB(nuclear transcription factor Y subunit B)互相结合, 从而使 CO 失去激活 *FT* 的功能^[35,37]。CO 与 NFY (nuclear transcription factor Y)复合物的主要功能是维持染色体上 *FT* 位点的特异性结构, 从而有利于 *FT* 的转录激活^[38]。因此, DELLA 可通过降低 CO 蛋白功能来阻止染色体上 *FT* 位点的特异性结构的形成^[30]。但是, Hou 等^[28]提出 DELLA 与 NFYB 和 NFYC 也可以互相结合, 所以 DELLA 的调控机制可能更为复杂。

DELLA 蛋白可与多种转录因子结合同时抑制 CO 蛋白功能和 *FT* 基因的转录激活, 其本质是通过与转录因子结合互作的方式降低与 DNA 的结合能力^[39]。如光敏色素互作因子 *PIF4* (phytochrome interacting factor 4)是 *FT* 的激活因子, 在温敏途径中 CO 蛋白也可被 *PIF4* 互作激活。DELLA 与 *PIF4* 结合后, *PIF4* 的功能被抑制^[40~42]。可见, GA 利用 DELLA 与 *PIF4* 或 *PIFs* 类转录因子的互作机制调控植物成花时间^[43]。

除了结合互作的方式外, DELLA 还可通过其他机制影响转录因子^[39]。Li 等^[44]研究发现, DELLA 与转录因子 *PIF4* 的结合, 不但产生“隔离”的作用, 还能降解 *PIF4*。DELLA 还可以引导转录抑制因子作用于特定的基因位点, 如 BOIs (botrytis susceptible1 interactors)蛋白^[45]。BOIs 蛋白在花芽分化期富集, 但需要依赖于 DELLA 才能被引导至 *FT* 启动子区域富集并与 *FT* 位点结合, 抑制 *FT* 的转录^[46]。除了依赖于 DELLA 的方式外, BOIs 蛋白也可通过其 CCT 结构域与 CO 蛋白结合, 干扰 CO 与 DNA 的识别机制^[46]。同样, DELLA 蛋白还可与 FLC (flowering locus C)形成复合物阻碍 *FT* 基因的转录激活^[47]。

1.3 SAM 中的 GA 调控

SAM 是 GA 调控成花的另一个作用部位。外源

喷洒 GA 不能激活短日照下叶片内 *FT* 基因的表达, 但却可以促进野生型、*co* 突变体和 *ft tsf* 突变体成花^[23,29,48,49]。非成花条件下, 叶片中高含量 GA 诱导 SAM 成花, 因此 Hisamatsu 和 King^[29]提出 GA 成花调控途径不借助于叶片中的成花基因。这可能是叶片中合成的 GA 被运输至 SAM 才激活成花基因表达, 也可能是 GA 拥有不依赖于叶片中 FT 蛋白的调控机制^[17]。Zhu 等^[50]发现叶片中合成 FT 蛋白在 NaKR1 (sodium potassium root defective 1)蛋白作用下被运输至 SAM 中发挥作用。虽然 GA 在植物体内的精准分布情况还缺乏研究, 但是 GA 可在细胞间被主动运输已被广泛认可^[51,52]。研究发现 GA₄ 含量会在 SAM 花芽分化期急剧上升, 与成花进程密切相关; 但是通过分子水平的研究发现, 该阶段 SAM 中与 GA₄ 生物合成相关基因并未提前呈现上调趋势, 因此 GA₄ 含量的增加是由于 SAM 以外的部位运输补充^[17]。NFL (no flowering in short day)转录因子是短日照下 GA 稳态的关键调控因子, *nfl* 突变体的 SAM 中 GA 生物合成和分解代谢相关基因相对野生型分别呈现下调和上调的现象, 这表明该突变体的 SAM 中 GA 呈现低活性状态; 但在长日照条件下, *nfl* 突变体与野生型类似, 表现为开花表型, 因此 NFL 及其靶基因的调控与光周期调控也密切相关^[53]。

SAM 中 GA 含量变化受到多种成花基因的影响。Andrés 等^[54]发现长日照下 SAM 中 GA 合成关键酶基因 *GA20ox2* (gibberellin 20-oxidase 2)表达量在花芽分化期显著增加, 他们认为 *GA20ox2* 基因表达的积累与 FT 蛋白的激活有关, FT 蛋白通过下调成花抑制因子 SVP (short vegetative phase)的表达水平来增加 *GA20ox2* 的表达量。因此, 在长日照下 FT 信号运输至 SAM 后, 可促进 GA 积累, 促进花芽分化。Li 等^[55]发现高 GA 含量又可反馈抑制 SVP 基因表达, 他们认为 SVP 是 SAM 中 GA 生物合成相关基因的关键调控者。FLC/SVP 复合物可上调 *GA2ox* (gibberellin 2-oxidase)的表达促进 GA 的降解, 还可促进 GA 合成关键酶 *GA3ox* (gibberellin 3-oxidase)的抑制因子 *TEM1* (tempranillo 1)和 *TEM2* 的表达^[47,54]。因此, SVP/FLC 复合物可以影响 GA 合成和代谢相关酶来调控 GA 在 SAM 中的动态平衡。除了调控 GA 生物合成和分解代谢的方式外, DELLA 可将 GA 信

号传递到多种调控途径。DELLA 可激活 miR159 的转录表达, 抑制 MYB33 (MYB domain protein 33) 的活性, 从而完成对花分生组织特异性基因 *LFY* (leafy) 的抑制, 延缓成花进程^[56-59]。也有研究指出, GA 信号可直接上调 *LFY* 的激活因子 *SOC1* (suppressor of overexpression of constans) 的表达, 实现对 *LFY* 的激活, 该过程不依赖于 DELLA 和 miR159/MYB33 调控途径^[56,60]。但是, Yu 等^[27]发现 DELLA 可抑制 SPLs 的转录来下调 *SOC1* 的表达水平; 也有研究指出在长日照条件下, 在花芽分化期 *SOC1* 可引起 SAM 中部分 SPLs 表达量的上调, 从而实现自我调节的反馈回路^[23,61]。可见, GA 对 *LFY* 的调控存在多种复杂的调控机制。

GA 也参与 SAM 中由 miR156 及其靶基因 SPLs 调控的年龄途径^[62]。miR156-SPLs 调控模式在进化上较为保守, 随着植物生长发育逐渐下调 miR156 的水平导致 SPLs 的积累增加; SPLs 拥有众多参与 SAM 成花调控的靶基因, 如 miR172、*SOC1*、*API* (apetala 1) 和 *FUL* (fruitful) 等成花基因^[62-64]。外源喷洒 GA 仅能轻微缓解过表达 miR156 植株的晚花表型^[27,65], 可见在 SPLs 积累过少时, GA 对 DELLA 蛋白的降解并不能激活成花。所以, GA 参与年龄途径的调控发生在 miR156 表达量降低后, 参与增加 SPLs 的积累调控。DELLA 蛋白对 SPLs 的调控可分为转录和转录后两个水平。DELLA 蛋白抑制茎尖不同 SPLs 基因的转录激活^[23,24]。Park 等^[66]和 Zhang 等^[67]均发现 DELLA 与染色质重塑因子 PKL (pickle) 的拮抗结合可抑制 SPL 基因的转录。而转录后的调控是 DELLA 蛋白直接与 SPLs 结合, 降低 SPLs 结合靶基因的活性^[27,65]。越来越多的研究已经证实 GA 通过 DELLA-SPLs 互作机制调控成花, 在短日照条件下这种互作机制尤为显著^[27,65,68,69], 但 GA 的具体作用与 SPLs 的种类密切相关。在短日照下 *spl15* 突变体与 GA 缺陷型突变体均呈现为极晚花表型, 因此 Hyun 等^[65]认为 *SPL15* 是 DELLA 在短日照下调控的关键性靶基因, 只有当 GA 充足并消除 DELLA 对 *SPL15* 的抑制作用, *SPL15* 与 *SOC1* 才能协同诱导 *FUL* 的表达, 影响 SAM 其他成花基因的表达。但 Xu 等^[69]的研究结果指出短日照下 *SPL15* 的成花调控作用不是唯一的, 原因是 SPLs 序列存在高度的冗

余。相反, 在花分生组织中当 DELLA 与 SPL9 结合后, 有助于激活 *AP1* 启动子的转录表达^[70]。因此, DELLA 与 SPLs 的互作需要根据 SPL 的种类及其调控的 DNA 序列具体分析。

2 其他激素途径

2.1 JA

JA 及其衍生物属于脂质类植物激素, JA 类衍生物的信号途径及应对逆境胁迫的反应机制被研究的较为透彻^[71,72], 但在花期调控中的作用研究较少。拟南芥中参与 JA 应答的 HDA6 (histone deacetylase 6) 参与 *FLC* 染色质的去乙酰化过程, 抑制 *FLC* 基因表达, 这表明 HDA6 是 JA 参与成花调控的关键因子^[73-75]。有研究显示, 拟南芥 JA 合成缺陷型突变体表现为雄性不育, 同时发现突变体的花丝延伸能力、花粉成熟和花药开裂程度均受到影响^[76,77]。同时, *arf6 arf8* 双基因突变体也呈现短花瓣、短雄蕊花丝和花药不开裂等现象^[78]。而外源喷洒 JA 后, 随着 JA 含量增多调节花丝成熟的 *ARF6* (auxin response factor 6) 和 *ARF8* 基因在花药开裂期大量表达, 可见 JA 可促进雄蕊和雌蕊成熟^[78]。研究表明, *ARF6* 和 *ARF8* 分别是 miR167 和 miR160 的靶基因^[78,79], 因此 JA 与 miR167 和 miR160 共同控制 *ARF6* 和 *ARF8* 参与成花调控^[80]。Zhai 等^[81]还发现 JA 可借助 JAZ (jasmonate ZIM-domain protein) 蛋白将信号传递给转录因子 MYCs (myelocytomatosis proteins), 来抑制 *FT* 的表达并延迟成花。虽然以上结果显示 JA 参与花器官发育或抑制 *FT* 的表达, 但其在成花途径中的作用还缺乏研究, 与其他激素是否存在串联调控机制也未被证实。

2.2 ABA

ABA 是一类倍半萜类植物激素, 参与植物蛋白质和脂质合成、种子脱水耐受、种子休眠和成花等生长发育过程^[82], 同时 ABA 还参与多种非生物胁迫应答^[83,84]。目前, ABA 信号是否参与花芽分化仍存在争议, 很多报道相互对立^[85,86]。生理研究发现, ABA 积累被认可有利于木本植物温州蜜柑 (*Satsuma Mandarin*) 的花芽孕育^[87]; 但是在温州蜜柑花芽诱导

期, ABA 处于较低水平, 在花原基形成时才上升到较高水平, 故 ABA 对花芽分化的作用因所处阶段而异^[88]。ABA 在陆地棉(*Gossypium hirsutum*)^[89]、苹果(*Malus domestica*)^[90]的花芽分化期含量逐渐增高, 可见高浓度 ABA 有利于花芽分化; 但高含量的 ABA 不利于龙眼(*Dimocarpus longana*)的花芽形成^[91]。在草本植物中, 内源 ABA 是打破百合花(*Longiflorum hybrids*)鳞茎休眠促进花芽分化的关键物质^[92], ABA 在菊花(*Chrysanthemum morifolium*)花芽分化期呈现为逐渐升高的现象^[93]。基因的研究发现, ABA 可激活 *FT* 和 *TSF* 基因表达, 有利于拟南芥的花芽分化^[94,95]。在长日照下, *aba1* 和 *aba2* 突变体呈现晚花现象, 而在短日照条件下表现正常^[94,95]。

ABA 信号可能参与激活 *CO* 转录或增强 *CO* 蛋白功能。ABA 可磷酸化激活 ABA 反应元件结合蛋白(ABA responsive element binding protein, AREB)来促进 *CO* 的转录^[96-99]。*areb2 abf3 abf1* 突变体中 *CO* 转录处于低水平并呈现晚花表型^[100,101]; 但在 ABA 缺陷型的突变体中, *CO* 表达量虽然呈现下调趋势, 却呈现极早花表型^[100,102]。因此, ABA 是否通过 *AREB* 调控 *CO* 转录有待进一步研究。ABA 还影响 *CO* 蛋白功能和信号传递^[95]。ABA 可泛素化降解 ABI3 (abscisic acid-insensitive 3), 释放与 ABI3 结合的 *CO* 蛋白来促进成花^[35,103,104]。ABA 还调控 MYCs 转录因子抑制 *FT* 蛋白表达, *GA* 也存在 MYC3-*FT* 调控模式, *JA* 调控也存在类似机制, 因此 ABA、*GA* 和 *JA* 存在串联调节 *CO*、*FT* 蛋白功能的现象^[11,81,105]。ABA 还可负调控 *FT* 下游基因延迟成花。ABA 可上调 bZIP 转录因子 ABI5 (abscisic acid-insensitive 5) 和 AP2 结构域转录因子 ABI4 (abscisic acid-insensitive 4) 的表达来激活 *FLC* 转录^[106,107], 降低 *SOC1* 表达量, 延迟拟南芥成花。而 *SOC1* 的表达可被 *GA* 上调^[56,60], 可见 *SOC1* 可能是 *GA* 和 ABA 信号进行串联调控的关键点之一。

2.3 ET

植物催熟激素 ET 与果实成熟、叶片衰老、胁迫应答和成花过程都密切相关^[108]。ET 在植物组织内分布具有广泛性, 但只有当叶片损伤、成熟或被切除才会造成 ET 的合成增加。有研究发现 ET 合成受抑制的拟南芥突变体呈现出早花表型^[109], 而 ET 组

成型表达的 *ctr1* 突变体在短日照条件下呈晚花表型, 可见 ET 可抑制拟南芥成花。Achard 等^[110]认为 ET 可促进 DELLE 蛋白的积累, 抑制 *GA* 信号并延迟成花。低温环境下的成花延迟现象被认为属于 ET 调控, Alonso 等^[111]认为由于 ET 的抑制作用, 虽然春化途径后拟南芥体内促进成花的 miRNA 被激活, 但不呈现开花现象。ET 可上调甘蓝型油菜(*Brassica napus*)中 *HAD19* 的表达表达量, 在增强植物抗病性同时可促进 *FLC* 的表达来延迟成花^[112]。虽然 ET 可调控 DELLA 和 *HAD19* 蛋白实现对花期的调控, 但 ET 与其他激素在成花途径中的串联作用机制还需要深入研究。

2.4 IAA

IAA 是最早被鉴定的植物激素, 影响植物细胞的伸长、分化, 参与种子发育、侧根形成、根和叶片的生长发育等多种生理过程^[19]。同时 IAA 也参与植物成花调控。Mai 等^[113]发现与 IAA 缺陷型突变体 *axr2* (auxin resistant 2)在短日照下延迟成花。外源施加不同浓度 IAA 溶液会影响花朵的正常发育^[114]。IAA 是局部合成, 经过极性运输至作用部位, 在植物体内呈现梯度分布, 这种动态分布与成花进程密切相关^[115]。PIN (pin-formed)蛋白家族与 IAA 的极性运输密切相关^[25], 拟南芥 *pin1-1* 突变体缺失 IAA 的极性运输能力, 出现针状花序, 花、维管组织发育缺陷^[26], 外源喷洒 IAA 可以逆转这种情况诱导成花^[116]。Przemeck 等^[117]发现 *arf5* 突变体仅能形成裸花序柄, 因此 IAA 响应因子 ARF5 (auxin response factor 5)活性被认为与花原基的启动密切相关。与花器官发育相关基因 *LFY*、*ANT* (aintegumenta)和 *AIL6* (aintegumenta-like 6)均属于 ARF5 的靶基因^[118]。ARFs 和 IAA 还可以通过促进 *GA20ox* 和 *GA3ox* 的表达^[119,120]、抑制 DELLA 蛋白表达^[121]的形式参与到 *GA* 生物合成和信号传导的过程。可见, IAA 可以通过调节 *GA* 含量和促进 DELLA 降解的方式促进成花。

2.5 CTK

CTK 是一类 N6-取代的嘌呤衍生物, 参与细胞的增殖和分化, 与植物生长发育密切相关, 在开花植物中 CTK 具有延缓衰老的作用^[122]。尽管 CTK 是否参与成花转变目前还存在争议, 但 CTK 调控花分

生组织细胞的分裂和分化已被证实^[123]。CKX (cytokinin oxidase/dehydrogenase enzymes) 是催化降解 CTK 的关键酶, *ckx3ckx5* 双突变体呈现异常膨大的花序和花分生长组织, 因此 CTK 参与花芽分化中细胞分化的调控^[124]。Corbesier 等^[125]发现成花刺激后叶片和韧皮部中内源 CTK 含量迅速增加; 在短日照下, 外源施加 CTK 可诱导营养生长期植物在细胞层面进行成花转变^[126]。可见, CTK 含量增加与成花转变的存在密切联系。此外, CTK 可下调 *miR172* 的表达水平, 促进 AP2 蛋白表达, 使植物呈现花瓣增加、雄蕊和心皮增殖等缺陷型花型^[31]。可见 CTK 与 GA 信号在 *miR172* 和 AP2 途径实现串联调控, 但 CTK 参与成花调控的机制尚未被完全解析^[127]。

2.6 SA

SA 可促进成花、调节种子发芽、抑制顶端优势、促进侧生长、调节膜透性等多种植物生长发育^[22]。目前, 有关 SA 调控成花的研究报道越来越多。如 4 $\mu\text{mol/L}$ 浓度的 SA 可促进烟草(*Nicotiana tabacum*) 愈伤组织形成花蕾^[128]。苍耳属植物韧皮部的 SA 含量仅在开花期能检测到^[129]。外源喷洒浓度为 3~10 $\mu\text{mol/L}$ 的 SA 溶液, 可刺激对光周期不敏感的柠檬属植物成花^[130]。这些发现均显示出 SA 含量增加在诱导成花或促进花器官发育中的作用。但是外源施加 SA 又可缓解由营养不良胁迫引起的牵牛(*Pharbitis nil*) 的早花现象^[131], 因此 SA 对成花的调控与植物所处状态密切相关^[131,132]。外源施加 SA 溶液或紫外照射可诱导 SA 的积累, 来抑制野生型拟南芥 *FLC* 转录因子的表达, 从而促进成花^[130]。但在 SA 缺陷型突变体中 SA 是否存在抑制 *FLC* 转录并促进成花的机制仍有争议, 这是由于 *CO* 和 *SOC1* 的表达在短日照和长日照条件下是不同的。在长日照条件下, SA 缺乏植物的 *CO* 和 *SOC1* 的表达水平与野生型相比下降约 50%; 在短日照条件下, SA 缺乏植物的 *CO* 表达量与野生型相比增加 2~3 倍, 但 *SOC1* 的表达两者间无显著差异^[130]。同时, 外源施加 SA 可逆转突变株 *co-1* 的晚花表型, 但在长日照下对突变株 *soc1* 无显著改善现象^[133]。可见, SA 参与成花调控网络的串联点可能位于 *CO* 下游和 *SOC1* 上游区域, 但具体机制以及 SA 是否参与成花调控还有待进行深入研究。

3 结语与展望

植物成花调控不仅受外界环境因子影响, 而且植物体内的各种激素存在互相协同和拮抗作用, 是一个复杂的调控过程。植物激素调控是植物感受外部环境变化信号, 利用多种激素的协同或拮抗的作用调整自身的生长和分化进程, 增强对环境适应能力的调控方式。最新的研究表明, 以 DELLA 介导的 GA 信号调节中枢及其调控的多种成花因子(如 *CO*、*FT*、*LFY* 和 *SOC1* 等), 在 GA 和其他成花途径或激素信号途径关键调控因子的互相作用中发挥着重要作用。目前, 对于激素调节植物成花的机制还未被深入解析, 在不同植物的成花进程和花器官发育中激素调控机制、激素的动态变化以及在不同组织或细胞的精准分布都尚待进一步阐明。随着高通量测序技术的发展以及转录组、蛋白质组和代谢组等手段在成花调控研究中的应用, 必将会全面解析激素调控植物成花的网络途径。

今后对激素调控成花机理的研究可能主要集中在以下几个方面: (1) 进一步阐明激素在不同环境下与各种成花途径互作的分子机制, 以及多种激素在时间和空间上协同或拮抗的串联互作机制。(2) 表观遗传机制及其对植物成花的生理、代谢和分子调控影响, 解析激素调控成花的表观遗传规律。随着气候变化的加剧, 表观遗传对成花诱导的影响越来越显著, 而植物激素信号在表观遗传调控营养期到生殖期的转变过程中不可或缺。DNA 甲基化、组蛋白翻译后修饰和 miRNAs 剪切等表观遗传调控将指导人们更好地开发适应新环境挑战的植物。(3) 应用外源激素调控花芽分化或花器官发育的可行性。不同物种、品种等激素调控的差异性较大, 对开花植物特别是附加值较高的花卉植物的调控可借助温室大棚调控光周期或温度等手段来实现。但是对于大田种植或附加值较低的植物, 此方法成本较高。因此研究开发和应用外源激素控制成花对指导农业生产具有重要意义。

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