•综述•

植物开花时间的遗传调控通路研究进展

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摘要: 开花时间对植物的繁殖成功至关重要。广泛分布的物种经常发生开花时间的分化, 从而能够更好地适应不同的环境条件。为了探索植物开花行为发生适应性分化的分子机制, 首先要明确调控开花行为的遗传通路。本文梳理了植物各类群调控开花时间的遗传通路, 以期对开花时间适应性分化的分子机制研究提供依据。植物从营养生长向繁殖转变时, 其开花行为主要受到光照、温度、水分等外界环境因子和赤霉素等内在因素的影响。通过对模式植物拟南芥(*Arabidopsis thaliana*)和其他类群的研究, 总结出了调控植物开花时间的6条通路, 包括日照长度和光质影响开花的光依赖通路, 长时间冷暴露后促进植物开花的春化通路, 高温或低温环境影响开花的温度通路, 以及赤霉素通路、年龄通路和自主通路3条内部调节过程。植物开花时间调控的6条上游通路信号传递到下游的开花整合基因*FT* (*FLOWERING LOCUS T*)和*SOC1* (*SUPPRESSOR OF OVER-EXPRESSION OF CONSTANS 1*), 整合基因将这些复杂的调节因子整合后进一步传递到下游花分生组织, 从而启动开花。此外, 非编码RNA、转座子对开花时间的调控也具有重要作用。部分遗传通路被证实实在植物适应环境的过程中起到了重要作用。目前对植物开花调控的研究已经有一百多年历史, 理论相对成熟。然而, 仍然存在许多具有争议和未解决的问题, 如开花基因的表达方式、开花行为的特殊调控机制、开花时间变异的适应性意义等等, 需要更进一步的研究。

关键词: 开花基因; 开花时间; 适合度; 遗传调控; 遗传通路

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Advances in the genetic regulating pathways of plant flowering time

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ABSTRACT

Aims: Flowering time is critical for plant reproductive success. Plant species, especially which are widely distributed, are observed to exhibit significant differentiation in flowering time to maximize their fitness. In order to explore the molecular mechanism of adaptive differentiation of flowering time in plants, it is essential to clarify the regulating pathways of flowering. This paper summarizes the genetic pathways that regulate flowering time in various groups of plants, which can provide important reference for molecular mechanism research of adaptive differentiation of flowering time.

Progresses: As a vital transition from vegetative growth to reproduction in plants, the flowering time has been reported to be regulated by both extrinsic and intrinsic factors. Based on researches of the model plant *Arabidopsis thaliana* and other taxa, six pathways that regulate flowering time have been identified. The light-dependent pathway, vernalization pathway, and temperature pathway refer to the regulation of flowering time in response to day length or quality of light, a long period of cold exposure, and external high or low temperature, respectively. While the gibberellin pathway, the

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age pathway and the autonomic pathway are the endogenous pathways. Signals from the six upstream flowering regulation pathways are transmitted to the downstream flowering integrators *FT* (*FLOWERING LOCUS T*) and *SOC1* (*SUPPRESSOR OF OVEREXPRESSION OF CONSTANS 1*), assembled by these two integrators, and transmitted to the downstream flowering meristem where flowering initiates. In addition, most recent studies have shown that non-coding RNA and transposable elements also play important roles in the regulation of flowering time.

Prospect: The researches on the regulation of plant flowering have studied more than a hundred years ago, forming many mature theories. However, there are still many controversial and unresolved problems, such as the expression ways of flowering genes, the special regulatory mechanism of flowering, and the adaptive significance of differentiated flowering time, which require further study.

Key words: flowering gene; flowering time; fitness; genetic regulation; genetic pathway

开花是决定植物繁殖成功的重要过程, 植物必须准确地将内部信号和环境信号相结合然后启动开花过程。最优的开花时间对于植物适合度收益的最大化有着非常重要的影响, 在错误的时间开花可能会使植物开花时间与传粉环境不匹配, 导致不能够成功传粉, 从而产生更大的适合度代价(Kitamoto et al, 2006), 或者更易受到捕食者和致病菌的危害(Elzinga et al, 2007; Lemoine et al, 2017)。开花过早也可能导致植物没有充足的营养来完成繁殖(Elzinga et al, 2007)。有研究表明, 早开花导致入侵北欧的普通豚草(*Ambrosia artemisiifolia*)种子产量大幅度降低(Kralemann et al, 2018)。开花过晚可能会使得植物错过资源利用的最佳时期而不能在生长季结束之前完成繁殖过程, 也可能会因为相对于周围早开花植物的竞争力减弱而使得后代处于不利的环境中, 比如在植物高密度情况下对光照的竞争不足(Vermeulen, 2015)。广泛分布的物种面临多变的环境, 在适应不同环境的过程中, 很容易发生生活史性状的适应性进化, 尤其是开花时间的适应性进化(Barrett et al, 2008)。植物的开花时间受到自然环境和遗传机制的共同作用, 在种间和种内呈现出了丰富的多样性。研究者已开始探索开花时间多样性产生的遗传基础, 尤其是开花时间的遗传通路。

开花时间调控的研究已有100多年的历史(Kobayashi & Weigel, 2007), 涵盖了从基础的生理研究到深入的遗传分子水平、从种间比较发展到种间与种内相结合、从模式植物拟南芥(*Arabidopsis thaliana*)扩展到多种植物的研究。目前植物开花的调控通路已经有了比较成型的框架(图1)。基于模式植物拟南芥的研究发现, 开花时间受多种环境和内源途径调控, 主要有6条调控通路, 包括光依赖、自

主、春化、赤霉素(gibberellin acid, GA)、温度以及年龄通路(Fornara et al, 2010; Kinoshita & Richter, 2020)。近些年对开花时间调控的研究主要围绕以上6条通路开展。研究发现在花的诱导过程中, 有几个基因在多个组织中起作用, 它们将多个调节通路聚集在一起, 被称为整合基因(integrators)。这6条通路汇集到整合基因, 并由整合基因传递到下游的花分生组织基因(floral meristem identity gene)中, 决定花的形成。研究表明有上百个基因的突变会影响拟南芥的开花时间(Srikanth & Schmid, 2011)。有部分基因被证明是导致自然种群开花时间变异的主要原因, 主要涉及光受体基因、MADS转录因子基因、*FRI* (*FRIGIDA*)和*FRI-like*基因、昼夜节律基因、开花素编码基因和RNA加工基因等(Alonso-Blanco et al, 2009; Rosloski et al, 2010; Weigel, 2012; Méndez-Vigo et al, 2013)。近几年来一些新的研究方法应用于对开花时间遗传基础的研究当中, 并有了许多新的发现。例如, microRNA对开花时间有重要的影响, *miR156*和*miR172*调控年龄通路, *miR159*对赤霉素通路有重要作用(Yamaguchi & Abe, 2012)。近年来发现转座子也对开花行为有一定的影响(Tamaki et al, 2015)。有研究发现*FLC* (*FLOWERING LOCUS C*)基因中转座子元件的插入会影响其表达, 从而影响开花时间(Tamaki et al, 2015; Niu et al, 2019)。除此之外, 碳水化合物如蔗糖、海藻糖等, 也对开花行为有着显著影响(Bernler et al, 1993; Zhao et al, 2019)。综上所述, 调控开花时间的遗传通路错综复杂, 对开花时间调控通路的归纳有助于更好地厘清植物开花时间变化的分子机制及适应进化。

对植物开花时间调控的研究多集中于模式植物拟南芥。但是拟南芥是一种长日照植物, 而光周期对于开花具有很强的影响, 所以需要研究短日照

图1 调控开花行为的遗传通路(以拟南芥为例)。图中自上而下分为三部分: 上游调控通路、下游开花整合基因和花分生组织基因。虚线方框内代表拟南芥调控开花的6个通路以及相关的基因。方框内的大写字母代表基因的简称, 椭圆框内的字母代表蛋白的简称。带箭头的实线代表促进作用, 平端的虚线代表抑制作用。改自Banta和Purugganan (2011)。

Fig. 1 The genetic pathways regulating flowering (take *Arabidopsis thaliana* as an example). The figure includes three parts from top to bottom: upstream regulatory pathway, downstream floral integrators and floral meristem identity genes. Six pathways and related genes that regulate flowering in *Arabidopsis thaliana* are enclosed in the dashed boxes separately. The letters in the boxes stand for abbreviation of genes, and the letters in the ovals stand for abbreviation of proteins. Lines with arrows indicate activation, and broken lines with blunt ends indicate repression. Modified from Banta & Purugganan (2011).

植物和日中性植物开花的调控过程, 并分析开花调控通路的保守性和差别性。目前对其他植物研究最多的是水稻(*Oryza sativa*)、荠菜(*Capsella rubella*)、豌豆(*Pisum sativum*)、烟草(*Nicotiana tabacum*)、番茄(*Solanum lycopersicum*)等。经研究发现, 水稻作为短日照植物的代表, 有许多与拟南芥功能相同的开花相关基因。其他植物也具有许多与拟南芥同源的开花基因, 证明了从拟南芥中发现的开花通路具有显著的保守性; 但是其他植物也有自己独特的开花调控基因, 说明了开花时间调控具有物种差异性。本文将以拟南芥为代表综述主要的6个开花时间调控通路和相应的开花时间调控基因, 并总结其他植物在开花调控通路上的研究进展, 比较其在物种间的保守性和差异性, 阐述此类研究中仍然存在的争议和问题。

1 开花调控上游通路

1.1 光依赖通路

1.1.1 拟南芥中调控开花时间的光依赖通路基因

光是植物开花的主要环境调节因子之一。光周

期(昼夜长短)作为季节更替的重要信号, 能够诱导植物进入繁殖期。光周期调控是开花时间调控的重要机制。开花的光周期信号通路由三部分组成: 光信号输入、节律钟(circadian clock)和信号输出(Shim et al, 2017)。高等陆生植物的光信号由红光/远红光受体(光敏色素PHYA-E, PHYTOCHROME A-E)、蓝光/UV-A受体(隐花色素CRY1-2, CRYPTOCHROME 1-2)、向光素PHOT1-2 (PHOTOTROPIN 1-2)、ZTL (ZEITLUPE)/FKF1 (FLAVIN-BINDING, KELCH REPEAT, F-BOX 1)/LKP2 (LOV KELCH PROTEIN 2)蛋白家族, 还有一种UV-B紫外光受体UVR8 (UV RESISTANCE LOCUS 8)感知(Mawphlang & Kharshiing, 2017; Sanchez et al, 2020)。植物的节律钟系统主要由复杂的信号网络形成, 其核心组分通常具有转录活性, 通过具有时间特异性的多重反馈调控(部分基因在特定的时间对另一部分基因产生调控, 形成周期性的调控回路)形成节律性振荡(oscillator), 调节下游输出基因的表达, 进而调控植物各种生理反应的时机(Shim et al, 2017)。节律钟的核心组分包括起抑制作用的转录因子CCA1

(*CIRCADIAN CLOCK ASSOCIATED 1*)、*LHY* (*LATE ELONGATED HYPOCOTYL*)、*PRR9* (*PSEUDO-RESPONSE REGULATORS 9*)、*PRR7*、*PRR5*、*ELF3* (*EARLY FLOWERING 3*)、*ELF4*、*LUX* (*LUX ARR-HYTHMO*)和*TOC1* (*TIMING OF CAB EXPRESSION 1*)，以及激活因子*LWD1* (*LIGHT-REGULATED WD 1*)、*LWD2*和*RVE8* (*REVEILLE 8*) (Shim et al, 2017)。植物对光周期的感知需要光信号和节律钟系统共同作用来完成。光信号通过光受体影响节律性振荡的节律期(period)和相位(phase)，使得节律钟控制的过程能够精确地与太阳活动周期相匹配(Yanovsky & Kay, 2001)。同时，节律钟又通过调控某些光信号组件(如*GI* (*GIGANTEA*)，*ELF3*)来影响光对节律钟的调控，最终形成一定的昼夜节律，直接或间接影响下游基因的表达，使植物能够适应环境的周期性变化(Yanovsky & Kay, 2001)。

CO (*CONSTANS*)是光周期路径的关键下游基因。在长日照下*CO*的表达被三种蛋白的活性修饰：*GI*、*FKF1*、*CDF1* (*CYCLING DOF FACTOR 1*) (Imaizumi et al, 2005; Sawa et al, 2007; Fornara et al, 2009)。这三个基因本身受昼夜节律钟的调控。*CDFs*属于转录调节因子家族，通过直接与*CO*调节区域结合作为*CO*转录的抑制因子(Fornara et al, 2009)。在昼夜节律钟的调控下，*CDFs*、*GI*和*FKF1*先后表达，*FKF1*与抑制*CO*转录的*CDF1-GI*复合物相互作用，并通过其F-Box结构域使*CDF1*降解(Sawa et al, 2007)，一旦*CDF*被降解，*FBHs* (*FLOWERING BHLHs*)和*TCPs* (*TEOSINTE BRANCHED/CYCLOID EA/PROLIFERATING CELL NUCLEAR ANTIGEN FACTORS*)将诱导*CO*的转录(Ito et al, 2012; Kubota et al, 2017)。*CO*不仅在转录水平上受到调控，其蛋白质稳定性和积累水平也受到调控(图2A)。晚上，*COP1-SPA1* (*CONSTITUTIVE PHOTOMORPHOGENIC 1-SUPPRESSOR OF PHYA 1*)复合物降解*CO*蛋白，以抑制在短日照下的开花(Jang et al, 2008)。而存在蓝光时，蓝光受体*CRY2*与*COP1-SPA1*复合物结合能够抑制对*CO*蛋白的降解作用(Zuo et al, 2011)。除此之外，还有依赖*ZTL/FKF1*的调节机制，早上，*ZTL*可能与*GI*一起降低*CO*的稳定性(Song et al, 2014)；下午，*FKF1*通过抑制功能性*COP1*的同源二聚化来增加*CO*蛋白(Lee et al, 2017)。由于*GI*也与*CO*直接相互作用，*FKF1*、*GI*和*CO*可能形成三聚体

复合物并稳定*CO* (Song et al, 2014)。除了与光周期相关的调节外，*CO*蛋白的积累还受到光受体的影响。红光受体*PHYB*在早上与*HOS1* (*HIGH EXPRESSION OF OSMOTICALLY RESPONSIVE GENES 1*)形成复合物抑制*CO*蛋白的积累(Lazaro et al, 2015)；远红光受体*PHYA*促进*CO*蛋白的积累(Valverde et al, 2004)；*CRY2*感知蓝光并稳定*CO* (Zuo et al, 2011)。最终使得长日照下*CO*在黎明和下午表达，进而使得*FT*转录水平上调并诱导开花；而短日照下，高水平的*CO*表达在黑暗中发生，不会上调*FT*，从而导致开花延迟(Putterill et al, 2004)。*CO*还能诱导与*FT*转运相关的*NaKR1* (*SODIUM POTASSIUM ROOT DEFECTIVE 1*)的表达，从而促进*FT*向茎尖分生组织转运，最终诱导花芽的形成(Shim et al, 2017)。在光周期通路中，除了通过*CO*途径影响下游基因外，*GI*也能通过*miR172*间接激活*FT*，或通过与*FT*启动子结合并与*FT*抑制因子形成复合物来直接激活*FT*，从而促进开花(Sawa & Kay, 2011)。最近有研究鉴定到两种新的*FT*转录增强子*Block E*和*Block C*，它们能够影响*FT*表达对光周期的响应(Zicola et al, 2019)。

1.1.2 光依赖通路在其他植物中的保守性和差异性

在其他植物中也鉴定到了光依赖途径相关基因。例如在水稻中发现了许多拟南芥开花相关基因的同源基因，如*Hd1* (*HEADING DATE 1*)是*CO*的同源基因(Yano et al, 2000)，*Hd3a*和*RFT1* (*RICE FLOWERING LOCUS T 1*)是*FT*的同源基因(Kojima et al, 2002)，*Hd6*是编码拟南芥CK2 (*CASEIN KINASE 2*，调节拟南芥生物钟活动和开花时间的物质)的同源基因(Sugano et al, 1999)，表明了开花光依赖通路的保守性。然而由于水稻是短日照植物，调控机制可能有所不同。如长日照下，水稻中*OsGI*的过度表达会促进*Hd1*的表达，随后*Hd1*抑制*Hd3a*的表达，从而导致开花延迟；而在拟南芥中*GI*的过度表达会促进*CO*表达，进而促进*FT*的表达，使得开花提前。在短日照下，水稻中*Hd1*促进*Hd3a*的表达从而促进开花，而拟南芥*CO*则不会影响开花(Putterill et al, 2004)。此外，水稻中存在特有的调控途径：在短日照和长日照条件下，*Ehd1* (*EARLY HEADING DATE 1*，*CO*的同源基因)上调*Hd3a*和*RFT1*的表达促进开花(Doi et al, 2004)；*Ghd7* (*GRAIN NUMBER*，

图2 拟南芥开花调控各通路的详细图解。(A)光周期通路;(B)春化通路;(C)温度通路;(D)赤霉素通路;(E)年龄通路。黑色填充方框代表外界调节因子。方框内的字母代表基因的简称,椭圆框内的字母代表蛋白的简称。带箭头实线代表促进作用,平端实线代表抑制作用。双向箭头代表相互作用。在图(A)中,圆角矩形框指开花素转运到的位置,带箭头的虚线代表转运过程。

Fig. 2 Detailed diagrams of the regulation pathways of flowering in *Arabidopsis thaliana*. (A) The photoperiodic pathway; (B) The vernalization pathway; (C) The temperature pathway; (D) The gibberellin pathway; (E) The age pathway. The black-filled box represents external regulating factors. The letters in the boxes stand for abbreviation of genes, and the letters in the ovals stand for abbreviation of proteins. Lines with arrows and blunt ends indicate activation and repression, respectively. The two-way arrows represent interactions. In figure (A), rectangle with rounded corners indicates the position where the florigen to be transferred, and the broken lines with arrows represent the transport process.

PLANT HEIGHT, AND HEADING DATE 7)的表达随日照长度增加而增加,该基因可下调*Ehd1*的表达(Itoh et al, 2010); *Ghd8*通过下调*Hd3a*表达抑制水稻在长日照条件下的开花,而最近的一项研究提出*Ghd8*与*Ghd7*的启动子结合,可以诱导*Ghd7*的表达(Wang P et al, 2019)。此外,即使短日照植物之间,光周期的调控机制也有所不同,例如在菊花(*Chrysanthemum seticuspe*)中,长日照条件下*CsGI*(*GI*在菊花的同源基因)的过度表达会促进*AFT*(*ANTI-FLORIGENIC FT/TFL1 FAMILY PROTEIN*, *AFT*与*FT*作用相反, *AFT*是开花抑制因子)的表达,进而抑制开花(Oda et al, 2020),这与水稻的*OsGI*抑制*Hd3a*的表达从而导致开花延迟不同。牵牛花(*Pharbitis nil*)也是短日照植物,白天向夜晚转变的生物钟系统引起花的转变, *FT*的表达促进开花,但是与拟南芥不同的是,牵牛花的*FT*表达与*CO*无关,在牵牛花中可能存在着其他的节律调控响应光周期(Hayama et al, 2007, 2018)。芒果(*Mangifera indica*)、番荔枝(*Annona squamosa*)中也发现了与开花时间有关的*GI*、*ELF3*、*CRY*的同源基因(Liu KD et al, 2016; Yadav et al, 2020)。在甘野菊(*Chrysanthemum eticuspe*)中鉴定到了拟南芥的大多数光依赖途径相关基因,如光受体、昼夜节律基因等,但是与拟南芥和水稻相比,甘野菊的光依赖开花途径取决于绝对黑暗持续时间,并且对午夜的光照敏感(Hirakawa et al, 2019)。台湾枇杷(*Eriobotrya deflexa* f. *koshunensis*)中基因*EdGI*和*EdCO*可能起着与拟南芥中*GI*和*CO*相似的作用,并调节枇杷的开花,但是*EdCO*的日变化规律与拟南芥不同,枇杷可能已经进化出不同的调控机制来控制*EdCO*在不同光周期条件下的昼夜表达(Zhang L et al, 2019)。这些研究表明光依赖开花途径中的相关基因组成在不同的物种中相对保守,但每个基因的调控作用可能不同,以此来应对不同的环境条件。

1.1.3 光依赖途径与开花行为的多样性

研究发现,很多物种开花行为的变异与光依赖途径相关基因的变异有关。在拟南芥、水稻、玉米(*Zea mays*)、大麦(*Hordeum vulgare*)等植物中发现了多个能够解释开花光周期响应多样性的基因,包括光受体基因*CRY2*、*PHYC*、*PHYD*、*CO*及其同源基因,以及其他的一些调控基因,如水稻中的*Ghd7*、玉米中的*Vgt1* (*VEGETATIVE TO GENERATIVE*

TRANSITION 1)等(Alonso-Blanco et al, 2009)。此外,近期研究又发现了一些导致开花时间多样性的光依赖途径相关基因。例如大豆(*Glycine max*)中的*PRR3b*和*PRR37*抑制开花,而*E11* (*a newly discovered QTL on chromosome 7*)促进开花(Wang FF et al, 2019; Li et al, 2020; Wang LW et al, 2020)。小麦(*Triticum turgidum*)中的*PPD1* (*PHOTOPERIOD 1*)和*PRR1*会影响开花时间(Shaw et al, 2020; Sun et al, 2020)。蔓菁(*Brassica rapa*)中*CCA1*基因的变异导致了开花时间的分化(Yi et al, 2017)。水稻中的*SDG701* (*SET DOMAIN GROUP 701*)、*ROC4* (*RICE OUTERMOST CELL-SPECIFIC GENE 4*)和*Hd18*对开花有促进作用(Shibaya et al, 2016; Wei et al, 2016; Liu et al, 2017)。这些基因的变异最终使得植株在不同的光周期条件下表现出不同的开花行为,并增强植物在不同环境下的适合度。如大麦中*Ppd-H1* (*PHOTOPERIOD-H1*)可促进在长日照下开花。中东地区的大麦因携带这种基因而在春季迅速开花,以应对漫长的白天和夏季干旱;而北欧的大麦主要携带突变的*Ppd-H1*等位基因,这些等位基因减少了其对长日照的反应,从而使该植物能够在该地区较温和的夏季生长,并产生较高的种子产量(Turner et al, 2005)。

1.2 春化通路

Chourde在1960年将春化定义为“通过低温处理获得或加速开花的能力”(Srikanth & Schmid, 2011)。一般来说,夏季一年生植物具有兼性春化反应,即不进行低温处理也能够开花;而冬季一年生植物具有专性春化要求,即需要经过一段长时间的冷处理才能够开花。基因*FLC*与*FRI*一直是春化通路研究的重点,两者都是开花的抑制因子。*FLC*抑制下游开花整合基因*FT*和*SOC1*的表达,从而抑制开花。*FRI*基因能上调*FLC*的表达,它的缺失会使*FLC*表达降低以促进开花(Michaels & Amasino, 2001)。*FRI*编码一种含有卷曲螺旋域的蛋白(Johanson et al, 2000),它与其他转录因子结合形成超级蛋白复合体,*FRI*超级复合体通过在*FLC*的5'端形成一个具有活跃染色质修饰和拓扑结构的局部染色体环境,进而促进*FLC*的形成(Li et al, 2018)。

春化作用能够降低*FLC* mRNA水平以促进开花(Sheldon et al, 2000)。在温度升高后,*FLC* mRNA依然保持低水平,但减数分裂后*FLC* mRNA重新分

配回到正常值(Simpson & Dean, 2002), 因此这种春化状态不能由亲本传给子代。*FLC*的转录激活因子对于在春化植物胚胎中重新激活*FLC*的表达很重要, 确保幼苗不受亲本春化作用的影响(Yun et al, 2011)。在拟南芥中鉴定出了3个*FLC*的调节因子:*VRN1* (*VERNALISATION 1*)、*VRN2* 以及 *VIN3* (*VERNALISATION INSENSITIVE 3*), 它们都是*FLC*的负调节因子。有研究表明*FLC*在响应春化时是表观沉默的。在寒冷时,*VRN1*和*VRN2*维持*FLC*的沉默(Gendall et al, 2001); 而*VIN3*抑制*FLC*的表达, *VIN3*在寒冷时能够被瞬间诱导产生(Sung & Amasino, 2004)。另外还发现非编码RNA是一类新的基因表达调控因子, 也能够调节*FLC*。例如在拟南芥中的*COOLAIR* (*COLD INDUCED LONG ANTISENSE INTRAGENIC RNA*)和*COLD AIR* (*COLD ASSISTED INTRONIC NONCODING RNA*): 在寒冷条件下, *COOLAIR*在*VIN3*发挥作用之前先转录, 抑制*FLC*的转录(Swiezewski et al, 2009); *COLD AIR*在*FLC*被抑制时激活, 进一步抑制*FLC* (Heo & Sung, 2011)。有研究发现, 许多与*FLC*相关的转录因子如*MAF1-5* (*MADS AFFECTING FLOWERING 1-5*)和*AGL24* (*AGAMOUS-LIKE 24*) 在春化反应中受到的调控独立于*FLC*, 这些基因可能在调节春化反应中起着重要的作用(Alexandre & Hennig, 2008) (图2B)。如在青菜(*Brassica rapa* var. *chinensis*)中, *BcMAF2*能够直接与*BcTEM1* (青菜的*TEMPRANILLO 1*同源基因)结合并促进其表达, 从而抑制开花(Huang et al, 2019)。拟南芥在春化作用下, *AGL24*和*SOC1*能够上调彼此的表达, 以独立于*FLC*的方式介导春化促进开花(Michaels et al, 2003)。

除了十字花科植物以外, 很多植物中都发现了*FLC*的同源基因, 包括双子叶植物和单子叶植物(Reeves et al, 2007; Ruelens et al, 2013)。然而, 在3种豆科植物(*Lotus corniculatus* var. *japonicus*, *Medicago truncatula*和*Glycine max*)中并未发现*FLC*的同源基因(Kim et al, 2013)。在藜属植物*Chenopodium quinoa* Willd.中存在几个春化相关基因, 但并未鉴定到*FLC*的同源基因(Golicz et al, 2020)。小麦、大麦等单子叶温带谷物由3个位点(*VRN1-3*, 与拟南芥的*FLC*的调节因子不相关只是名字相同)决定春季和冬季习性; 基因*VRN1*、*VRN3*分别与拟南芥*API* (*APETALA 1*)和*FT*同源, 而*VRN2*

在拟南芥中没有同源基因, 但在春化过程中起着类似*FLC*的作用(Yan et al, 2003, 2004, 2006)。在这些温带谷物中, *VRN3*被*VRN2*抑制, 寒冷暴露期间*VRN2*水平降低, *VRN1*水平升高, 从而促进*VRN3*的表达和分生组织的转变(Sasani et al, 2009)。

拟南芥的春化需求是由*FRI*的显性活性赋予的(Shindo et al, 2005), 而对荠菜的研究表明*FLC*是主要的调控因素(Yang et al, 2018)。在甜菜(*Beta vulgaris*)中, 有3个基因*BvBTC1* (*BOLTING TIME CONTROL 1*)、*BvFT1*和*BvFT2*在春化中起作用, 其中*BvFT1*和*BvFT2*与*FT*最相关, *BvBTC1*的显性等位基因产生一年生品种, 而隐性等位基因产生需要春化的两年生品种(Pin et al, 2010, 2012)。这与拟南芥相反。在拟南芥中, *FRI*的缺失使春化途径的需求最小化, 因而产生一年生的品系(Johanson et al, 2000)。因此, 比起保守性强的光周期通路, 春化通路的差异性更强, 反映了植物对不同环境条件的适应。

1.3 温度通路

除了春化作用外, 外界环境温度还直接影响开花行为。一般来说, 高环境温度促进开花, 而低环境温度延迟开花(Jagadish et al, 2016)。拟南芥在较高的环境温度下开花较早, 且在拟南芥的其他生活型中, 较高的温度可以作为诱导性长日照的替代, 比如*PHYB*突变体在23°C比在16°C时开花早(Halliday et al, 2003)。对拟南芥的研究发现, 不同温度下*FLM* (*FLOWERING LOCUS M*)的可变剪切体和*SVP* (*SHORT VEGETATIVE PHASE*)的稳定性影响了开花行为, 同时发现*H2A.Z*、*PIF4* (*PHYTOCHROME INTERACTING FACTOR 4*)、*miR399-PHO2* (*microRNA399-PHOSPHATE 2*)和*miR172*基因介导了高温对开花行为的影响, 而*miR156*则是低温下抑制开花的负调节因子(Verhage et al, 2014) (图2C)。*FLM*属于*FLC*家族, 在不同的环境温度下具有不同的可变剪切体(Balasubramanian et al, 2006)。其两个主要剪切体形成的蛋白通过与*SVP*相互作用而发挥拮抗作用, 在低温下产生的剪切体*FLM-β*是一种开花抑制因子, 而高温下产生的剪切体*FLM-δ*是开花的激活因子(Posé et al, 2013)。*SVP*蛋白在高温下不稳定。在较低温度下, 相对增加的*SVP*蛋白与*FLM-β*相互作用, 通过直接结合下游靶基因抑制开花。长日照下的寒冷夜晚条件下*FT*的表达会受到

抑制, 导致开花延迟, 这主要是由于上述 *SVP-FLM- β* 复合物的增加所导致的 (Kinmonth-Schultz et al, 2016)。 *FT*、*TSF* (*TWIN SISTER OF FT*, *FT*的姊妹基因)和*SOC1*是开花行为对环境温度响应过程中*SVP*、*FLM*和*FLC*基因的主要下游靶点。*SVP*对*FLC*没有调节作用但它们可能协同作用。两者在时间和空间上表现出相似的表达, 在*FT*和*SOC1*上有共同的结合位点, 因此*SVP*可能以依赖*FLC*的方式调节这些基因的表达 (Li et al, 2008)。*MYB*转录因子*EFM* (*EARLY FLOWERING MYB PROTEIN*)也介导环境温度对开花的影响, 直接抑制叶片维管中*FT*的表达。*SVP*和*EFM*主要在同一调控途径中起着抑制开花的作用。*EFM*介导*SVP*对温度响应通路下游的影响, 其表达受到*SVP*的上调从而抑制开花, 并通过*H3K36me2*去甲基酶*JMJ30*与光响应的昼夜节律钟相互作用 (Yan et al, 2014)。在相对高温和短日照的环境下, 转录因子*PIF4*结合并激活*FT*, 另外对*FT*位点具有抑制性作用的*H2A.Z*核小体的富集率降低, 从而促进开花 (Kumar et al, 2012)。此外, 拟南芥在较高温(23°C)和长日照条件下, *miR399b*的过度表达和其靶基因*PHO2*功能等位基因的缺失导致开花提前 (Kim et al, 2011)。研究认为*miR399-PHO2*维持了磷稳态, 并通过增加*TSF*的表达来调节开花时间 (Kim et al, 2011)。然而, 在*miR399*过量表达*PHO2*突变体植物中磷酸盐毒性的间接后果也可能导致早开花, 需要进一步研究 (Spanudakis & Jackson, 2014)。温度也能够调节*miR156*和*miR172*的表达水平: 在较低温度(16°C)下, *miR156*的表达受到促进导致开花延迟, 在较高的温度(23°C)下, *miR156*表达受到抑制, 而*miR172*则相反 (Lee et al, 2010; Kim et al, 2012)。温度对*miR172*的调控受到*SVP*的影响, *SVP*抑制*miR172*的表达, 而*miR172*则有可能通过抑制*FLC*来促进开花 (Lee et al, 2010)。此外, 有研究发现*ICA* (*ICARUS*)编码转运RNA加工相关酶的基因, 其不同的基因型能够改变拟南芥开花时间对温度的响应行为 (Méndez-Vigo et al, 2019)。

在中国水仙(*Narcissus tazetta* var. *chinensis*)中, 温度升高也促进了开花, 并且*FT*同源基因*NFT1*在高温下表达上调 (Li et al, 2013)。郁金香(*Tulipa gesneriana*)和麝香百合(*Lilium longiflorum*)的开花分别受高温和低温的诱导, 并且研究发现从麝香百

合中鉴定到的*LIFT*基因以及从郁金香中分离出的*TgFT2*基因与从郁金香中分离出的*TgFT1*和*TgFT3*基因对开花时间的影响完全相反 (Leeggangers et al, 2018)。另一方面, 有研究发现小麦和大麦在高温(25°C)条件下, 在长日照下进行生殖发育, 而在短日照下*FT-like*基因不表达, 表明高温和日照时长条件之间存在密切的相互作用, 并且研究发现*FPF1-like* (*FLOWERING PROMOTING FACTOR1-like*)、*RNase-S-like*和*VER2-like*基因可能介导了开花对高温的响应 (Hemming et al, 2012)。对春兰(*Cymbidium goeringii*)的研究发现, *CgSVP*基因作用于*CgAPI*和*CgSOC1*, 在低温诱导开花行为的早期可能起到了重要作用 (Yang et al, 2019)。

总的来说, 对植物开花温度通路的研究相对较少, 主要集中在模式植物拟南芥中, 且在拟南芥中也存在许多未解决的问题, 如*bHLH-PIFs* (*PIF3*, *PIF4*, *PIF5*)和*microRNAs*等转录调节因子对开花基因的差异调控。对其他植物的研究较少且发现的机制也不完全一致。有的植物对于温度的反应可能与拟南芥相反或者没有响应。在全球变暖的环境下, 植物如何响应变化的温度是值得关注的问题。

1.4 自主通路

除环境因素外, 植物的内部信号也参与调节开花。自主通路相关基因的突变体*FCA* (*FLOWERING LOCUS CA*)、*FY* (*FLOWERING LOCUS Y*)、*FPA* (*FLOWERING LOCUS PA*)、*LD* (*LUMINIDEPENDENS*)、*FLD* (*FLOWERING LOCUS D*)、*FLK* (*FLOWERING LOCUS KH DOMAIN*)和*FVE* (*FLOWERING LOCUS VE*) 在长日照和短日照条件下开花都较晚 (Simpson, 2004; Srikanth & Schmid, 2011), 但是这种晚开花的表型可以通过春化来恢复 (Abou-Elwafa et al, 2011)。近年来已经鉴定出了许多新的自主通路相关基因。自主通路的关键调节因子包括 *FCA*、*FPA*、*FVE*、*FLD*、*PCFS4* (*PCF11P-SIMILAR PROTEIN 4*)、*PEP* (*PEPPER*)、*FLK*、*HDA5* (*HISTONE DEACETYLASE 5*)、*HDA6*、*PRMT5* (*PROTEIN ARGININE METHYLTRANSFERASE 5*)、*PRMT10*、*DRM2* (*DOMAINS REARRANGED METHYLTRANSFERASE 2*)、*CK2*等 (Cheng et al, 2017)。与春化通路的基因一样, 自主通路的主要靶基因也是*FLC*, 独立于光周期和温度通过抑制*FLC*的表达来促进开花 (Cheng et al, 2017)。自主通路基

因主要通过调节*FLC*的mRNA形成过程、染色质表观遗传修饰和对*FLC*翻译后调控来发挥作用(Cheng et al, 2017)。*FCA*、*FPA*、*FVE*以及*FLD*共同作用, 调节*FLC*的沉默(Liu et al, 2007; Bäurle & Dean, 2008); *PCFS4*通过调控*FCA*的选择性加工, 促进开花(Xing et al, 2008); *PEP*与*FLK*功能拮抗, 通过转录和转录后调控上调*FLC* (Ripoll et al, 2009); *HDA5*、*FVE*、*FLD*和*HDA6*通过对*FLC*染色质中的H3K4去甲基化和H3或H4去乙酰化抑制*FLC*表达(Luo et al, 2015); *PRMT5*和*PRMT10*通过不对称组蛋白精氨酸甲基微调*FLC*的表达来控制开花, 并且两者的功能是独立的(Niu et al, 2007); *DRM2*通过DNA甲基化参与了表观遗传调控机制(Zhong et al, 2014); *CK2*通过磷酸化和去磷酸化抑制*FLC*, 以翻译后的方式调节*FLC*蛋白(Heidari et al, 2013; Mulekar & Huq, 2015)。最近有研究发现了两种富含甘氨酸的RNA结合蛋白, 能同时与*FCA*、*FPA*和*FLK*作用, 并且还可以调控*FLM*的可变剪切, 参与开花的自主和温度两个通路(Steffen et al, 2019)。

在除了拟南芥以外的其他植物中也鉴定到了自主通路的同源基因。例如在藜属植物*Chenopodium quinoa*中鉴定到了拟南芥自主途径关键基因*FCA*、*FPA*、*FY*、*FVE*、*FLD*、*LD*的同源基因, 但是缺失自主途径靶基因*FLC* (Golicz et al, 2020)。在牡丹(*Paeonia suffruticosa*)中鉴定到了*FLD*的同源基因(Wang SL et al, 2019)。此外, 在甜菜中鉴定到了*FLK*、*FVE*、*LD*和*LDLI*基因。*BvFLK*与拟南芥的*FLK*基因功能相同, 但是*BvFVE1*的功能却与拟南芥中的*FVE*不同, *BvFVE1*受昼夜节律钟的调控(Abou-Elwafa et al, 2011), 说明自主通路具有一定的保守性, 但不同植物中的作用机制存在一定差异。

1.5 赤霉素通路

赤霉素是调节植物休眠、萌发、茎伸长和开花等发育过程的植物激素。它不仅能刺激植物器官的生长, 还能诱导发育阶段的转变(Mutasa-Göttgens & Hedden, 2009)。赤霉素在某些植物(如拟南芥)中促进开花, 而在其他植物(如苹果*Malus × domestica*)中抑制开花, 因此赤霉素对于不同植物的作用具有差异性(Zhang SW et al, 2019)。拟南芥中, 在短日照条件下, 赤霉素促进开花作用最强(Porri et al, 2012)。在叶中, 赤霉素信号被*GIDI* (*GA INSENSI-*

TIVE DWARF 1)感知, *GIDI*经历构象变化后使赤霉素与*DELLA* (*Asp-Glu-Leu-Leu-Ala*)蛋白相互作用, 赤霉素启动*DELLA*蛋白的降解从而促进开花(Sun, 2010) (图2D)。*SPY* (*SPINDLY*)蛋白作为赤霉素信号转导的抑制因子, 可能通过岩藻糖基化上调*DELLAs*蛋白来延迟开花(Jacobsen et al, 1998; Zentella et al, 2017)。*DELLA*蛋白能直接与*CO*结合从而下调*FT* (Wang et al, 2016; Xu F et al, 2016), 还能够与*PIF4*相互作用而抑制*FT*的表达(de Lucas et al, 2008)。除此之外, *DELLA*蛋白还能够与*FT*的抑制因子相互作用来抑制*FT*的表达, 如*MYC3*与*DELLA*蛋白相互作用直接抑制*FT* (Bao et al, 2019)。另外, *DELLA*蛋白很可能与富集*PRC2* (*POLYCOM REPRESSIVE COMPLEX 2*)的*PKL* (*PICKLE*)相互作用, *PRC2*会提高*FLC*中的组蛋白标记*H3K27me3*的水平, 使得*FLC*沉默, 从而调节*FT*和*SOC1*等靶基因, 进而调控开花行为(Li et al, 2016; Campos-Rivero et al, 2017)。赤霉素还会通过抑制*DELLA*蛋白对*miR159*产生影响, 随后影响*miR159*的靶序列*MYB*, 最终影响*LFY* (*LEAFY*)的表达(Achard et al, 2004)。除了通过*DELLA*蛋白的作用, 赤霉素还能够通过影响赤霉素的生物合成和运输来调控开花, 主要与赤霉素氧化酶有关, 它们能够将赤霉素前体转化为赤霉素活性物质, 进而促进开花(Mitchum et al, 2006)。另一方面, 赤霉素通过促进*SOC1*诱导基因(如*AGL24*)的表达、下调植物开花抑制因子(如*SVP*)等多个途径来调节*SOC1*的表达, 影响*LFY*的表达进而影响开花(Li et al, 2008)。有研究发现*SVP*能够抑制赤霉素的合成酶*GA20ox2* (*GIBBERELLIN 20 OXIDASE 2*), 导致赤霉素含量降低, 从而抑制开花(Andrés et al, 2014)。

在其他物种中发现了拟南芥赤霉素途径相关基因的同源基因, 说明该途径具有一定的保守性。在豚草的研究中发现, 中国北方的豚草(开花早)中的*SPY*表达随着时间的推移而增加, 并且在开花后高于南方的植物。因为*SPY*的表达可能阻断赤霉素信号传导或赤霉素生物合成, 因此发育过程中*SPY*水平的增加可能与发育的转变有关(Li et al, 2015)。在对芒果的研究中发现, 正常花芽与畸形花芽相比, *MYB*、*ALG24*以及赤霉素氧化相关基因的表达具有显著差异, 说明花芽的发育与赤霉素途径密切相关(Yadav et al, 2020)。在藜属植物*Chenopodium quinoa*

中,也鉴定到了许多*GIDI*和降解*DELLA*蛋白的同源基因(Golicz et al, 2020)。Yano等(2015)的研究证明在水稻中所有赤霉素调控途径都是由*GIDI-DELLA*系统调控的。

1.6 年龄通路

年龄通路为内源的开花调节通路,主要由*miR156-SPL (SQUAMOSA PROMOTER-BINDING PROTEIN-LIKE)*和*miR172-AP2 (APETALA 2)*调节(Hyun et al, 2017)。*miR156*抑制*SPL*,它能调节营养阶段的生长,受到糖有关的信号分子影响,其表达随着植物年龄的增长而减少,使得*SPLs*表达增加,促进植物开花并向成熟期过渡(He et al, 2018)。在拟南芥中,*SPL*基因可分为两大类,其中*miR156*识别的有与开花相关的*SPL2*、*SPL9*、*SPL10*、*SPL11*、*SPL13*和*SPL15*,以及促进花分生组织分化的*SPL3*、*SPL4*和*SPL5* (Hyun et al, 2016; Xu ML et al, 2016)。*SPL9*和*SPL15*结合*miR172b*基因的启动子促进其表达,再通过抑制开花抑制基因*AP2-like*的表达促进开花,*AP2-like*基因*TOE1 (TARGET OF EARLY ACTIVATION TAGGED 1)*、*TOE2*、*SNZ (SCHNARCHZAPFEN)*、*SMZ (SCHLAFMUTZE)*都被证明是开花抑制因子,它们抑制*FT*的表达(Mathieu et al, 2009; Zhu & Helliwell, 2011; Song et al, 2013) (图2E)。

萝卜(*Raphanus sativus*)中也发现了与年龄途径有关的基因,如*SPL1*、*SPL2*、*SPL3*、*SPL9*、*SPL13*和*SPL15*,它们与抽苔和开花有关(Nie et al, 2016)。而在藜属植物*Chenopodium quinoa*中鉴定到了*SPL9*的同源基因,它作为相对保守的*miR156*的靶基因,可能参与控制开花行为(Golicz et al, 2020)。对柳枝稷(*Panicum virgatum*)的研究发现,*SPL7*和*SPL8*通过直接上调*SEP3 (SEPALLATA 3)*和*MADS32*诱导开花,而下调*SPL7*和*SPL8*会导致植株开花延迟或不开花,这与拟南芥十分不同,因此*SPL7/8*的调节代表了一种禾本科的新的调控机制(Gou et al, 2019)。另外,*SPL7/8*基因的下调能够逆转花序由生长向生殖的转换,在其他禾本科植物中没有发现这一现象(Gou et al, 2019)。

对开花调控年龄通路的研究还存在许多问题,如在*SPLs*家族中还有许多成员的功能未知。*SPLs*在禾本科植物开花中的作用仍不明确(Gou et al, 2019)。此外,年龄通路与糖的调节关系也需要进一

步研究。

2 开花调控通路的下游基因

2.1 开花整合基因

在拟南芥中6条开花通路汇集到开花整合基因中,开花整合基因接收上游的信号并通过激活参与花形成过程的下游基因来促使开花行为的发生。其中两个基因*FT*和*SOC1*作为关键的开花转变基因启动花的发育。

*SOC1*在分生组织中产生,为开花的正调控因子,其表达能影响下游基因的表达并促进开花。*SOC1*将上游多条通路的信号整合,传递到下游花分生组织基因如*LFY*、*FUL (FRUITFULL)*中,以启动花的发育。*SOC1*受*CO*、赤霉素信号和*miR156/SPL*的正向调节(Moon et al, 2003; Fernández et al, 2016)。同时,*SOC1*是*FLC*的靶基因,*FLC*通过抑制*SOC1*的表达抑制开花。另外,*SOC1*与另一种*MADS-box*蛋白*AGL24*的活性密切相关,两者之间相互影响,而*AGL24*的表达受到光依赖途径、春化通路和赤霉素途径的正向调节(Srikanth & Schmid, 2011)。

在拟南芥中,*FT*的表达能够促进开花。*FT*具有多个转录调节因子,其中*CO*是*FT*的正调节因子,能够促进*FT*的表达以促进开花。*RAV*家族的两个包含*AP2*域的转录因子(*TEM1*, *TEM2*)和*euAP2*基因家族的6个基因(*AP2*, *SMZ*, *SNZ*, *TOE1*, *TOE2*, *TOE3*),它们作为*FT*的抑制因子抑制开花(Kim et al, 2006)。除了这些类似*AP2*的转录因子外,*FT*还受到*SVP*、*FLC*的抑制(Srikanth & Schmid, 2011)。对拟南芥的研究发现,*FT*蛋白至少是开花素的一部分(Andrés & Coupland, 2012),开花素是由叶片产生的在茎尖诱导花芽形成的可传递信号,通过韧皮部从叶片移动到顶端(Corbesier et al, 2007)。与*SOC1*在分生组织产生并发挥作用不同的是,*FT*作为一种长距离信号诱导开花(Corbesier et al, 2007),*FT*在叶片的韧皮部表达,*FT*蛋白经韧皮部的伴胞运输到分生组织,与*FD (FLOWERING LOCUS D)*相互作用形成*FT-FD*复合物促进下游花分生组织基因*API*的表达,从而启动植株的开花,随后*FT-FD*复合物含量下降(Abe et al, 2019)。

在对开花素的研究中,不管是长日照植物还是短日照植物或是日中性植物,都鉴定到了*FT*的同源

基因, 并且都为开花调控通路的整合基因, 且大多数能够促进开花, 说明了 FT 功能的保守性(Shim & Jang, 2020)。在与拟南芥同属芸苔属的其他物种如蔓菁(*Brassica rapa*)和野甘蓝(*B. oleracea*)中, 只发现了部分拟南芥开花基因, 这可能与芸苔属进化的复杂性有关(Schiessl et al, 2017)。例如欧洲油菜(*Brassica napus*)中鉴定到了 FT 的同源基因, 但大部分基因发生了结构改变进而导致功能的改变(Schiessl et al, 2017)。在短日照植物水稻中鉴定到了其特有的基因 $RFT1$, 当 $Hd3a$ 的功能受到抑制时, $RFT1$ 作为 $Hd3a$ 的功能辅助基因, 能够确保植株开花以繁衍后代(Komiya et al, 2008)。在对豚草的研究中发现了两个 FT 的同源基因 $AaFTL1$ 和 $AaFTL2$ (Kralemann et al, 2018)。两者具有不同的功能: $AaFTL1$ 是开花激活因子, $AaFTL2$ 是开花抑制因子(Kralemann et al, 2018)。除了被子植物, 在裸子植物如华山松(*Pinus armandii*)、粗榧(*Cephalotaxus sinensis*)、银杏(*Ginkgo biloba*)中, 也鉴定到了 FT 的同源基因, 并且它们在生长和繁殖中起着与 FT 相似的作用, 但是在有的植物如粗榧中 FT -like基因起抑制开花的作用(Liu YY et al, 2016)。

2.2 花分生组织基因

花分生组织基因的分子功能是DNA转录因子。上游的花整合基因传递到下游的花分生组织基因, 花分生组织基因在茎尖分生组织中上调, 从而诱导开花。如拟南芥中, FT 和 TSF 基因从叶片传输到茎尖分生组织, 它们与 FD 形成一个复合物, 激活花分生组织基因(包括 API 和 FUL)的过表达(Perrella et al, 2020)。对拟南芥的突变体研究已经鉴定出 LFY 、 API 、 CAL (*CAULIFLOWER*)基因参与花原基的形成(Busch et al, 1999)。 LFY 基因的组成性表达可加速开花, 同时 LFY 还可以诱导 API 和 CAL 的表达(Liljgren et al, 1999)。花分生组织基因在植物之间保守性强, 如在牡丹、豚草中鉴定到了花分生组织基因 CAL 和 API 诱导开花(Mátyás et al, 2019; Wang SL et al, 2019)。在茶树(*Camellia sinensis*)中 LFY 的表达也与花芽的形成相关(Liu et al, 2020)。

3 展望

开花行为的发生是环境条件和遗传调控共同作用的结果, 因此在实验中, 特别是在受控条件下, 通过选择个体的环境条件, 如光周期、温度、光质

量、营养或其他实验变量, 可以观察到某一等位基因功能缺失产生的表型, 从而揭示它们在开花时间调控中的作用。目前对开花调控的研究已经有一百多年的历史, 相比其他性状具有更成熟的理论, 但是仍然存在许多具有争议和未解决的问题。

首先, 开花相关基因的表达部位和表达时间是否具有一定的特异性? 为什么存在这种特异性? 例如, 研究发现 FT 基因只在韧皮部伴胞表达(Takada & Goto, 2003)。那么表达 FT 的韧皮部伴胞是否能相互传递信号使得 FT 的表达在组织内和组织间同步? FT 在叶片中产生, 后作为开花信号被运输到茎尖, FT 是通过什么方式从叶片韧皮部到达茎尖分生组织? 有研究认为 FT 是通过胞间连丝运输的, 并且鉴定到有两种膜相关蛋白 $FTIP1$ (*FT-Interacting Protein 1*)和 $NaKRI$ 作为 FT 运动的分子转运蛋白(Liu et al, 2012; Zhu et al, 2016)。但是对于 FT 蛋白的运动仍然存在很多疑问, 仍需要进一步的研究。从表达时间看, 为什么拟南芥植物在早晨具有多种 CO 抑制机制? 这是否意味着植物可以在早晨根据各种外部和内部条件来微调 CO 的活性?

其次, 开花通路调控的分子机制有哪些? 除了一些常见的基因、转录因子的调控外, 还有一些特殊的调控机制, 如 $microRNA$ 、转座子、可变剪切的调控等等。目前已发现 $miR172$ 、 $miR156$ 等 $microRNA$ 在环境温度、赤霉素和年龄调节开花时间的途径中起到了重要作用, 但具体机制还需要进一步研究(Lee et al, 2010; Kim et al, 2012; Verhage et al, 2014)。已有研究发现转座子能够调控开花时间。如拟南芥3'UTR中的转座子可以通过甲基化来改变基因表达, 而水稻的转座子可以改变基因的翻译效率。对荠菜的研究发现在 FLC 的3'UTR处插入转座子会影响 FLC mRNA的稳定性, 降低 FLC 的表达水平并导致开花提前(Niu et al, 2019)。转座子的功能以及它在其他物种中的作用还不清楚, 有待进一步研究。此外, 对mRNA的剪切是转录后调控的重要步骤。虽然研究发现很少有剪切因子参与到开花转变中, 但是仍然存在可变剪切参与开花调控的可能(Wang P et al, 2020)。最近有研究发现, 椰子(*Cocos nucifera*)有需要7-8年才能开花的高椰子和2-3年就能开花的矮椰子两种生活型, 短的 FT 可变剪切体只存在于矮椰子中, 证明了 FT 的可变剪切可能与椰子的开花时间的遗传调控有关(Xia et al, 2020)。但这

种调控作用有待进一步研究。

开花时间的变异直接关系到植物对环境的适应, 因此了解不同物种开花时间变异的分子机制至关重要。例如最近发现在水稻中4个关键的开花基因(*Hd1*、*OsPRR37*、*DTH8*、*Hd6*)参与了温度对开花时间的可塑性的调控, 使得水稻能够适应不同温度条件, 这可能与开花基因发生遗传变异有关(Guo et al, 2020)。由于植物自身发育过程的不同阶段之间相互影响(如萌发时间的差异会使植物处于不同的环境中, 从而影响开花行为), 再加上基因具有多效性机制(如开花相关基因也会影响种子的萌发情况), 因此在研究开花时间调控机制时, 还应考虑基因通过环境产生的多效性间接作用。

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