

· 热点评述 ·

长寿与短命：十字花科植物中MADS-box基因的长袖善舞

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摘要 开花基因决定植物的一年生或多年生开花习性。已在不同植物中鉴定到多个开花基因, 然而关于开花基因如何驱动十字花科植物一年生与多年生生活史策略转变的进化机制仍不清楚。最近一项研究聚焦十字花科不同属的自然变异, 发现3个亲缘关系密切的MADS-box类转录因子编码基因(即FLC、FLM和MAF)与其一年生/多年生习性转变相关, 并解析了其分子机制, 提出十字花科植物生活史策略(即多年生/二年生/一年生之间的转换)是由FLC类MADS-box基因剂量叠加所决定的连续过程。研究结果初步明确了十字花科植物一年生与多年生生活史策略转变的进化机制和轨迹, 为培育多年生油菜品种奠定了理论基础, 也为其它十字花科作物的多年生化遗传改良提供借鉴。

关键词 十字花科, 生活史策略, MADS-box, 多年生, 一年生, 转换

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经过近万年的人工选择, 许多作物从多年生野生近缘种驯化成一年生栽培种, 产量提高且品质改善, 为人类粮食安全提供了重要保障(Jackson, 1980)。然而, 一年生作物每年耕作的生产方式也带来了种子成本增加、农药化肥施用增多、水土流失加剧以及土壤养分失衡等生态环境问题(Crews et al., 2018)。因此, 作物的多年生化(perennialization)是未来农业可持续发展的方向, 有助于实现粮食安全和生态安全的平衡(Cox et al., 2006; Glover et al., 2010; Zhang et al., 2023)。

种子植物按其生活史可分为一年生和多年生2种类型。一年生植物从种子萌发开始的营养生长到开花结实的生殖生长, 完成一个完整的生命周期; 多年生植物则在连续多次的营养生长和生殖生长之间交替, 形成多次结实的多年生习性。开花是植物从营养生长向生殖生长转变的重要节点, 也是一年生和多年生转换(transition)的重要标志之一, 对植物的生长发育和生殖繁衍具有重要意义(Stearns and Fawcett, 2013; Friedman and Rubin, 2015; Friedman, 2020)。春化作用(vernalization)是诱导包括十字花科在内许多植

物开花的重要路径(Sheldon et al., 1999; Xu and Chong, 2018; Luo and He, 2020; Gao and He, 2024)。尽管对于一年生植物开花途径的调控机制已有深入研究, 十字花科模式植物拟南芥(*Arabidopsis thaliana*)开花途径中保守的信号元件同时参与多年生的调节机制, 但多年生植物具有较长的生长周期及复杂多样的开花机制, 一年生植物的开花调控机制并不能完全解释多年生植物的特性, 特别是多年生植物向一年生植物演化的机理尚不清楚(Hu et al., 2003; Tan and Swain, 2006; Li et al., 2022)。

十多年前, Zhou等(2013)通过对多年生草本植物十字花科碎米荠属(*Cardamine*)的研究, 揭示了年龄途径和春化途径共同参与调控开花的分子机理。弯曲碎米荠(*C. flexuosa*)为两年生或多年生草本植物, 其成花诱导需要经历一段时间持续低温的春化作用, 年龄途径和春化途径共同调控开花, 与多年生植物的生长习性密切相关, 这一机制确保多年生草本植物可以在获得足够的生物量后, 通过感受外界环境变化启动开花结实(Zhou et al., 2013)。最近, Zhai等(2024)揭示了十字花科植物多年生与一年生生活习性转换的

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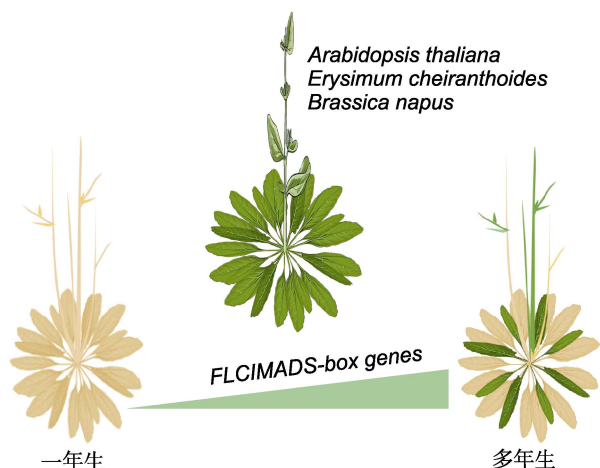


图1 十字花科开花植物从一年生向多年生转换的机制
十字花科开花植物从多年生向二年生/一年生的转变由3个密切相关的MADS-box基因决定,这3个基因中的1个基因就能够将1次结实一年生十字花科植物转化为多年生多次开花植物。MADS-box基因剂量在开花特性进化中扮演关键角色,丰富的多年生开花植物表型与MADS-box基因的表达水平相关。

Figure 1 The mechanism of annual transforming into polycarpic perennial flowering plants in Brassicaceae
The transition of Brassicaceae plants from a polycarpic perennial life cycle to biennial and annual flowering behavior is controlled by three closely related MADS-box genes. Notably, a single gene among these three is sufficient to convert annual Brassicaceae plants into polycarpic perennial flowering plants. The dosage of MADS-box genes plays a pivotal role in the evolution of flowering behavior, as the phenotypes of diverse perennial flowering plants observed may be attributed to differential expression levels of MADS-box genes in Brassicaceae.

机理:从十字花科须弥芥属(*Crucihimalaya*)和糖芥属(*Erysimum*)生活史表型差异定位到3个均编码一类亲缘关系密切的MADS-box转录因子基因*FLC* (*FLOWERING LOCUS C*)、*FLM* (*FLOWERING LOCUS M*)和*MAF* (*MADS AFFECTING FLOWERING*),说明十字花科植物的生活史策略演化具有跨物种的保守性;他们进一步构建了喜马拉雅须弥芥(*C. himalaica*)的*Chflc/Chflm/Chmaf*三突变体,使其表型从多次结实多年生野生型转换为1次结实一年生突变型,而这3个基因的单突或双突材料表现为两年生的兼性表型;与之相反,在一年生小花糖芥(*E. cheiranthoides*)中超表达*FLC*类MADS-box基因,其生活习性由1次结实一年生转换为多次结实多年生。上述研究表明,十字花科植物生活史策略的演变(即多年生/二年

生/一年生之间的转换)是由*FLC*类MADS-box基因剂量叠加后表现出的表型连续变化过程,可能是十字花科植物多年生生活习性建立的充分必要条件(图1)。此外,结合H3K27me3组蛋白甲基化检测,发现多年生内华达糖芥(*E. nevadense*)*FLC*类MADS-box基因在春化后的抑制性组蛋白修饰H3K27me3无法稳定维持;而一年生植物小花糖芥中的*FLC*类MADS-box基因能够稳定维持春化诱导产生的H3K27me3,使得*FLC*在春化后处于抑制状态(Zhai et al., 2024)。研究结果阐明了十字花科植物一年生与多年生生活史策略转换的进化机制和轨迹,为培育多年生油菜品种奠定了理论基础,也为其它近缘关系物种的多年生化遗传改良提供了借鉴。

拟南芥中已有研究表明,开花途径中保守的信号元件也参与多年生的调节机制(Tan and Swain, 2006),通过在拟南芥中导入多年生*FLC*基因,拟南芥出现由1次结实一年生向多次结实多年生的表型转换。然而,正如Zhai等(2024)指出的多次开花仅是十字花科植物多年生习性的一个前置条件。对于植物的多年生习性与一年生习性的进化机制而言,除开花习性外,还有必要考虑植物的叶片和根组织结构、植物对能量的有效利用、源库驱动的调节作用以及地下茎器官的生长发育(Hu et al., 2003)等许多性状之间的互作对于多年生与一年生转换的作用。

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MADS-box Genes Driven Life History Strategy Diversity in Brassicaceae

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Abstract The numerous flowering genes that have been identified in different plants play a crucial role in determining whether a plant is annual or perennial. However, the evolutionary mechanism by which these flowering genes drive the transition between annual and perennial life history strategies in Brassicaceae plants remains poorly understood. A recent study focused on natural variations in different genera of Brassicaceae. They identified three closely related MADS-box transcription factor genes, namely *FLC*, *FLM*, and *MAF*, and elucidated their molecular mechanisms associated with the transition between annual and perennial behavior. Their findings suggest that the life-history strategy in Brassicaceae plants (i.e., the conversion between perennial, biennial, and annual behavior) is a continuum determined by the dosage of *FLC*-like MADS-box genes. The study elucidates the evolutionary mechanisms and trajectories underlying the reciprocal conversion of life history strategies from annual to perennial in Brassicaceae, providing a theoretical foundation for breeding perennial rapeseed varieties and offering insights for Brassicaceae crops improved towards perennial grain.

Key words Brassicaceae, life history strategy, MADS-box, perennial, annual, transition

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