

甘蓝类蔬菜抽薹开花调控相关基因研究进展

钟世浚, 颜文晨, 刘霄芸, 任雪松, 司 军, 宋洪元, 李勤菲
(西南大学园艺园林学院/长江上游农业生物安全与绿色生产教育部重点实验室, 重庆 400715)

摘要: 甘蓝类蔬菜是重要的蔬菜作物, 主要包含结球甘蓝、花椰菜、青花菜、苤蓝、抱子甘蓝和芥兰等多个变种。在生产和制种过程中, 该类蔬菜常发生未熟抽薹和亲本花期不遇等现象, 利用分子设计育种改良甘蓝的耐抽薹性, 可以有效地解决这些问题。然而甘蓝类蔬菜变种丰富, 开花习性差异大, 抽薹开花调控相关基因的研究相对分散。本文在简述了高等植物抽薹开花5种调控途径的基础上, 归纳了诱导甘蓝类蔬菜抽薹开花所需的最适环境条件, 总结了在春化途径、赤霉素途径和光周期途径中影响甘蓝类蔬菜抽薹开花的调控基因及其变异, 构建了甘蓝类蔬菜的抽薹开花调控基因网络, 并对甘蓝类蔬菜抽薹开花调控方面的后续研究提出了展望。本文为甘蓝类蔬菜耐抽薹性的改良提供参考。

关键词: 甘蓝类蔬菜; 抽薹开花; 开花时间; 基因

Research Progress of Genes Related to the Regulation of Bolting and Flowering in *Brassica oleracea* Vegetables

ZHONG Shijun, YAN Wenchen, LIU Xiaoyun, REN Xuesong, SI Jun, SONG Hongyuan, LI Qinfei
(College of Horticulture and Landscape Architecture, Southwest University/Key Laboratory of Agricultural Biosafety and Green Production of Upper Yangtze River, Ministry of Education, Chongqing 400715)

Abstract: *Brassica oleracea* vegetables, a group of leafy crops encompassing cabbage, cauliflower, broccoli, kohlrabi, brussels sprout, and kale, face persistent challenges in production and breeding, including premature bolting and asynchronous flowering between two parents. Improving bolting resistance by molecular design breeding strategies holds significant promise. However, the genetic complexity underlying flowering regulation in *B. oleracea* is compounded by the diverse flowering mechanisms across subspecies and fragmented knowledge of associated regulatory genes. This review concludes optimal environmental conditions for flowering of *B. oleracea* vegetables and summarizes genes and variants for flowering pathways which are mainly involved in gibberellin pathway, vernalization, and photoperiodic responses on the basis of five main flower regulation pathways in higher plants. The prospect of the follow-up research on the regulation of bolting and flowering of cabbage vegetables is also suggested. A conceptual gene interaction network that integrates key regulators of bolting and flowering of *B. oleracea* vegetables is proposed, providing a valuable reference for improving bolting resistance of *B. oleracea* vegetables.

Key words: *Brassica oleracea* vegetables; bolting and flowering; flowering time; genes

开花是植物完成生命周期、繁衍后代的重要过程。自20世纪初开始, 科学家们针对植物开花的机理开展了系列研究, 并在不同物种中发现了大量开

花调控基因。模式植物拟南芥的开花调控网络基本清晰^[1], 主要分为5条途径, 包括春化途径、光周期途径、赤霉素途径、自主途径和年龄途径^[2-3]。

收稿日期: 2024-08-03 网络出版日期: 2025-01-02

URL: <https://doi.org/10.13430/j.cnki.jpgr.20240803001>

第一作者研究方向为蔬菜种质创新与遗传育种, E-mail: zhongshijun1999@outlook.com

通信作者: 李勤菲, 研究方向为蔬菜种质创新与遗传育种, E-mail: feifei1984998@126.com

基金项目: 国家自然科学基金(32172569); 重庆市研究生科研创新项目(CYS23214)

Foundation projects: National Natural Science Foundation of China (32172569); Chongqing Graduate Research and Innovation Project (CYS23214)

在春化途径中,中心调控基因 *FLOWERING LOCUS C (FLC)* 通过抑制促花基因 *SUPPRESSOR OF OVEREXPRESSION OF CO 1 (SOC1)* 和 *FLOWERING LOCUS T (FT)* 的表达而抑制花芽分化^[4-5]。常温时, *FLC* 由 *FRIGIDA (FRI)* 等蛋白复合诱导 H3K4me3 及 H3K36me3 对其修饰,该类修饰由 *COOLAIR* 的 II 类选择性剪接子维持,使 *FLC* 继续表达,阻止植物开花^[6-9];低温春化时, *PLANT HOMEODOMAIN-POLYCOMB REPRESSIVE COMPLEX 2 (PHD-PRC2)* 蛋白复合体在染色体的 *FLC* 位点上富集 H3K27me3,并由 *COOLAIR* 的 I 类选择性剪切体去除 H3K4me3 修饰,沉默 *FLC* 表达,促进植株开花^[8-10]。

在光周期途径中,植物通过光敏色素 (phyA、phyB、phyC) 和隐花色素 (CRY1、CRY2) 感知红光、远红光和蓝光等光信号^[11-12]。通过 *ZEITLUPE (ZTL)*、*KELCH REPEAT F-BOX 1 (FKF1)* 和 *LOV KELCH PROTEIN 2 (LKP2)* 等蛋白群来协调植物的生物钟;生物钟信号通过 *CIRCADIAN CLOCK ASSOCIATED 1 (CCA1)*、*LATE ELONGATED HYPOCOTYL (LHY)* 和 *PSEUDO-RESPONSE REGULATORS (PRRs)* 交替传递输出至 *GIGANTEA (GI)* 和 *CONSTANS (CO)*^[13-16],诱导开花基因 *FT* 的表达,从而开启光信号对花的诱导,促进植株开花^[17-18]。

在赤霉素途径中,赤霉素 (GAs, gibberellins) 通过调节其信号转导途径的各类蛋白,影响植物生长发育。赤霉素广泛存在于植物中,目前已鉴定出 130 多种,但仅有 GA₁、GA₃、GA₄ 和 GA₇ 具生物活性。异戊二烯焦磷酸 (IPP, isopentenyl pyrophosphate) 经细胞色素 P450 酶及 GA13ox、GA20ox、GA3ox 等 GA 氧化酶作用,形成具生物活性的 GAs,发挥作用后由 GA2ox 降解^[19]。GAs 通过与 GIBBERELLIN-INSENSITIVE DWARF1 (GID1) 及 DELLA 蛋白结合形成三聚体,诱导 DELLA 蛋白泛素化降解,从而引起植株开花^[20]。

自主途径是植株缺乏光、温信号诱导,经历足够营养生长后仍能自主调控开花的途径。自主途径主要由 *FLOWERING LOCUS CA (FCA)*、*FLOWERING LOCUS Y (FY)*、*FLOWERING LOCUS KH DOMAIN (FLK)*、*FLOWERING LOCUS PA (FPA)*、*LUMINIDEPENDENS (LD)*、*FLOWERING LOCUS D (FLD)* 和 *FLOWERING LOCUS VE (FVE)* 等 7 个基因构成,它们通过抑制 *FLC* 的表达来促进

开花^[21]。

年龄途径发现较晚,是植物体内 miR156 丰度随植物生长而由高降低,最终影响开花的途径。在 miR156 下降过程中,miR156 靶基因 *SQUAMOSA PROMOTER BINDING PROTEIN-LIKEs (SPLs)* 的抑制逐渐被解除^[3]。*SPLs* 通过调控 miR172 表达,间接降低如 *AP2*、*SCHLAFMUTZE (SMZ)*、*TARGET OF EATs (TOE1、TOE2、TOE3)* 等 AP2-like 类基因表达,从而促进开花^[22]。

甘蓝类蔬菜是世界上重要的蔬菜作物之一,包含不同的变种,如结球甘蓝、花椰菜、青花菜、苤蓝、抱子甘蓝和芥兰等。我国甘蓝类蔬菜产量较大,据联合国粮农组织 (FAO, Food and Agriculture Organization of the United Nations) 统计数据 (https://www.fao.org/faostat/en/#rankings/countries_by_commodity),2022 年我国结球甘蓝产量近 3500 万吨,花椰菜和青花菜产量近 960 万吨,均居于世界首位。然而我国在甘蓝类蔬菜育种和生产过程中,仍有许多问题亟待解决,抽薹开花调控是育种家们重点关注的问题之一。以结球甘蓝为例,结球甘蓝是绿体春化型植物,生产过程中如遇低温,可能造成未熟抽薹,严重影响产量和品质,导致巨大的经济损失。目前甘蓝类蔬菜主要利用杂种优势育种,在甘蓝品种繁育过程中,如两亲本花期不遇,就难以获得稳定的杂交种,严重影响育种进度^[23]。利用分子设计育种快速改良亲本的耐抽薹性是实现杂种迭代更新的重要手段。尽管甘蓝类蔬菜与拟南芥同属十字花科植物,但是甘蓝类蔬菜丰富的变种类型,造成其开花习性的差异,有关开花调控的研究分散,未成体系。因此,本文将在总结甘蓝类蔬菜现有开花调控基因的基础上,参考拟南芥开花调控网络,梳理甘蓝类蔬菜的开花调控途径,构建甘蓝类蔬菜的开花调控基因网络,从基因层面上解析甘蓝类蔬菜抽薹开花的分子机制,为改良甘蓝类蔬菜耐抽薹性提供参考。

1 甘蓝类蔬菜抽薹开花差异

甘蓝类蔬菜是十字花科芸薹属植物,包含多个变种类型,不同变种表现不同的开花习性。以叶球或肉质茎等营养器官为商品的结球甘蓝^[24]、抱子甘蓝^[25]和苤蓝^[26]等,属于典型的绿体春化型植物,植株需要生长至一定大小才能响应低温,并经过一段时间持续低温,才能诱导开花。目前普遍认为结球

甘蓝植株生长至6~10片真叶或者茎粗0.6~1.0 cm以上才能响应低温,经历4℃~10℃低温一定时间才能完成春化,抽薹开花;易抽薹品种仅需30 d即可完成春化,而耐抽薹品种需经过60 d,甚至更长时间才能完成春化^[24, 27-30]。苤蓝和抱子甘蓝的开花最适诱导条件仍缺乏研究。以花球为商品的青花菜和花椰菜中,部分品种需要经历低温完成春化才能抽薹开花,而另外一些品种无需低温也能抽薹开花^[31-32]。花椰菜一般需生长至4~6片真叶,在17℃以下才能顺利春化;多数青花菜需要生长至3~5片真叶,在10℃~13℃环境下通过春化,但仍有适应高温的青花菜在高达25℃时也能抽薹开花^[33]。以花苔为商品的芥兰,无需春化就能抽薹开花^[34]。不同的甘蓝类蔬菜抽薹开花习性不同,诱导抽薹开花的最适光、温条件也不相同。

2 甘蓝类蔬菜抽薹开花调控基因的研究

目前,甘蓝类蔬菜抽薹开花调控基因的研究主要集中在春化途径上,赤霉素途径和光周期途径也有一定研究,而自主途径和年龄途径研究极少。本文主要针对甘蓝类蔬菜的春化途径、赤霉素途径和光周期途径展开集中论述。

2.1 春化途径

在甘蓝类蔬菜的春化途径中,*BoFLCs*是目前研究最为深入的基因。甘蓝类蔬菜中共发现5个*FLC*同源基因,分别被命名为*BoFLC1*^[35]、*BoFLC2*^[36]、*BoFLC3*^[35]、*BoFLC4*^[37]和*BoFLC5*^[35]。但Okazaki等^[37]认为,因选择的参考氨基酸序列不足,*BoFLC4*与*BoFLC2*应是同一基因。上述基因中对春化影响最大的是*BoFLC2*,该基因的表达与极端抽薹时间表型存在强正相关,且在不需春化的甘蓝(TO1000)中缺少*BoFLC2*^[38]。*BoFLC2*中第四外显子的单碱基缺失突变影响该基因功能,导致甘蓝对低温的敏感性提高,低温沉默*BoFLC2*的速度更快,造成突变体快速通过春化,甚至无需春化,即能抽薹^[37, 39]。晚花结球甘蓝中*BoFLC2*第一内含子中的215 bp碱基缺失突变,也能减缓*BoFLC2*沉默速度,导致结球甘蓝的晚花^[40]。Tang等^[41]在羽衣甘蓝中发现了9325 bp的区段缺失,导致*BoFLC2*完全丢失,使得羽衣甘蓝不需春化也能开花。

除*BoFLC2*外,*BoFLC1*和*BoFLC3*对春化也有影响。Itabashi等^[42]将*BoFLC1*和*BoFLC3*分别在拟南芥中过表达,发现二者均会导致拟南芥晚花,且

在冷处理后*BoFLC3*表达下调。Abuyusuf等^[43]发现,*BoFLC1*第二内含子中存在67 bp的插入突变时,结球甘蓝春化更快,开花时间更早。Kinoshita等^[44]在由极难开花结球甘蓝nfc与2种结球甘蓝和1种羽衣甘蓝杂交产生的F₂分离群体中,定位到影响甘蓝抽薹时间的基因*BoFLC1*。Lin等^[45]在由早花青花菜BLM29和晚花青花菜BLM25杂交获得的F₂分离群体中,定位到*BoFLC3*参与调节开花期,并且*BoFLC3*第二、四外显子的非同义替换或第一内含子的255 bp缺失及50 bp插入均会引起开花时间改变。而*BoFLC5*在甘蓝类蔬菜中的表达量极低,可能是因为过早出现终止密码子导致基因功能异常,且在早、晚花甘蓝中缺乏多态性,因此*BoFLC5*被认为是一个假基因^[46]。

拟南芥中,*FLC*的反义转录本lncRNA *COOLAIR*参与开花途径。青花菜中也发现了由*BoFLC1*、*BoFLC2*和*BoFLC3*反义转录生成的*COOLAIR*。*BoFLC1*、*BoFLC2*生成的I类*COOLAIR*均受低温诱导,且*BoFLC2*生成的I类*COOLAIR*转录量大,II类*COOLAIR*仅在温暖环境下表达;但*BoFLC3*生成的2类*COOLAIR*均在温暖条件下表达,在低温下未测出;II类*COOLAIR*中,靠近5'端的数个结构域是保守的,这可能与它们的功能相关^[47]。然而,*COOLAIR*在甘蓝类蔬菜的春化途径中发挥的具体功能仍待探索。

在*FLC*沉默过程中,蛋白复合体Polycomb Repressive Complex 2 (PRC2)负责招募H3K27me3富集在*FLC*染色质上,并催化*FLC*沉默^[48],但在甘蓝类蔬菜中该复合体功能尚无报道。PRC2的辅助因子VERNALIZATION INSENSITIVE 3 (VIN3)在甘蓝类蔬菜中有少量研究。*VIN3*为诱导型表达基因,仅在低温处理时表达,翻译后蛋白包含1个PHD结构域,有观点认为该结构域能与*FLC*染色体上某些三甲基化位点结合,减少*FLC*转录,但该功能是否在甘蓝中存在仍有争议^[48]。赵荣秋^[49]首次从结球甘蓝中克隆出*AtVIN3*的2种同源基因*BoVIN3-1*和*BoVIN3-2*,均编码含560个氨基酸的蛋白质,且均需要低温处理达到春化要求后才会茎尖表达;反义表达实验及半定量RT-PCR分析表明,*BoVIN3-1*直接参与春化过程,在早、晚花结球甘蓝春化过程中,早花甘蓝中的*BoVIN3*表达量率先达到峰值,通过抑制*BoFLC*表达而促进春化。春化途径的另一个热点基因是*FRI*。青花菜中共发现*AtFRI*的2种同源基因,分别命名为*BoFRIa*和*BoFRIb*(表1)。

BoFRIa 和 BoFRIb 均含有 2 个保守结构域: 其一是含 23 个氨基酸的 FRI 蛋白家族特征结构域, 它能影响 BoFRI 蛋白质活性; 另一个结构域由 37 个氨基酸构成, 可能参与蛋白质寡聚化。相较 BoFRIa, BoFRIb 缺失一个螺旋结构域, 但二者均能使 *fri* 缺失的拟南芥开花时间恢复正常, 且无显著差异^[50-51]。

表 1 甘蓝类蔬菜中春化途径相关基因
Table 1 Genes involved in vernalization in *B. oleracea* vegetables

基因名称 Gene name	BRAD 数据库序号 Number in BRAD database	染色体位置(bp) Chr. location	与拟南芥基因一致度(%) Identity with <i>Arabidopsis thaliana</i> gene	参考文献 Reference
<i>BoFLC1</i>	BolC09g062620.2J	63395901~63399910	85.427	[35]
<i>BoFLC2</i>	BolC02g004040.2J	2542284~2545548	82.741	[36]
<i>BoFLC3</i>	BolC03g004550.2J	2244866~2248179	83.417	[35]
<i>BoVIN3-1</i>	BolC03g013830.2J	7260993~7263556	68.960	[49]
<i>BoVIN3-2</i>	BolC02g015310.2J	10887788~10892097	58.013	[49]
<i>BoFRIa</i>	BolC03g017480.2J	9633856~9636028	57.241	[50]
<i>BoFRIb</i>	BolC09g037260.2J	40382470~40384598	59.011	[50]

2.2 赤霉素途径

目前虽已从各种植物中鉴定出百余种赤霉素, 但从甘蓝中获得的仅有 GA₁、GA₄、GA₁₂ 和 GA₁₅ 等 9 种, 其中 GA₄ 对甘蓝花芽发育的影响相对较大^[52]。测序结果显示, 甘蓝共有 12 个 *Gibberellin 20 oxidase* (*BoGA20ox*)、4 个 *Gibberellin 3-beta-dioxygenase* (*BoGA3ox*) 和 14 个 *Gibberellin 2-beta-dioxygenase* (*BoGA2ox*) 拷贝, 其中 2 个 *BoGA3ox* 和 7 个 *BoGA2ox* 基因仅余留部分序列, 呈截断状态, 此

类截断型基因其是否发挥功能尚待研究^[53]。GA INSENSITIVE DWARF1 (*GID1*) 能够结合 GAs 而诱导 DELLA 蛋白被泛素化降解, 引起植株开花。与拟南芥类似, 甘蓝类蔬菜中也存在 5 个 *GID1* 基因, 分别为 *BoGID1a*、*BoGID1b-1/2/3* 及 *BoGID1c*^[53]。晚花因子 DELLA 在甘蓝中共存在 5 个, 分别为 BoRGA1、BoRGA2、BoRGL1、BoRGL2 和 BoRGL3, 但不存在 GA INSENSITIVE (*GAI*)^[54] (表 2)。

表 2 甘蓝类蔬菜中 GA 信号转导相关基因
Table 2 GA pathway genes in *Brassica oleracea* vegetables

基因名称 Gene name	BRAD 数据库序号 Number in BRAD database	染色体位置(bp) Chr. location	与拟南芥基因一致度(%) Identity with <i>A. thaliana</i> gene	参考文献 Reference
<i>BoGID1a</i>	BolC05g060470.2J	55275185~55276562	84.770	[53]
<i>BoGID1b-1</i>	BolC08g045880.2J	43466928~43468248	91.389	[53]
<i>BoGID1b-2</i>	BolC04g030280.2J	31287613~31288803	89.118	[53]
<i>BoGID1b-3</i>	BolC06g027340.2J	29529812~29531056	87.778	[53]
<i>BoGID1c</i>	BolC07g039220.2J	42725133~42726810	92.754	[53]
<i>BoRGA1</i>	BolC07g031500.2J	36431939~36433669	82.412	[54]
<i>BoRGA2</i>	BolC09g027430.2J	24522236~24523945	81.636	[54]
<i>BoRGL1</i>	BolC02g022360.2J	18385313~18386836	84.496	[54]
<i>BoRGL2</i>	BolC05g063590.2J	57356636~57358267	82.364	[54]
<i>BoRGL3</i>	BolC09g055750.2J	59207584~59209161	82.243	[54]

2.3 光周期途径

光周期调控植株开花大体可分 3 个阶段: 一是植物对光信号的接收; 二是生物钟对光信号的转

导; 三是光信号输出并影响植株开花^[55]。在甘蓝类蔬菜中, 光信号接收相关基因的功能研究鲜有报道。TIMING OF CAB EXPRESSION1 (*BoTOC1*)、

BoPRR3 和 *BoCCAI* 等部分生物钟信号转导基因已在羽衣甘蓝与西兰花杂交产生的 F_1 代甘蓝中定位^[56]。后续研究发现,*BoPRRs* 类基因响应低温、干旱及盐分等非生物胁迫^[57],*BoCCAI* 基因响应低温胁迫^[58],但这些基因对甘蓝类蔬菜抽薹开花的影响却鲜有报道。

GI 和 *CO* 是光信号从生物钟输出,调控植株开花过程中的重要基因。拟南芥、白菜及甘蓝的 *GI* 高度保守,均为 1 个拷贝^[59]。Thiruvengadam 等^[60]将青花菜的部分 *BoGI* 序列反义表达转入正常青花菜后,

转基因植株的开花期显著延迟。但是,结球甘蓝中缺少与 *BoGI* 相互作用的 *ZTL* 和 *FKF1* 蛋白,*BoGI* 通过与 *BoLKP2* 互作来行使功能^[61]。*BoGI-BoLKP2* 复合体通过抑制 *CYCLING DOF FACTOR 1 (BoCDF1)* 间接提高 *BoCO* 的表达。Schiessl 等^[62]对结球甘蓝进行重测序,发现 1 号、3 号和 9 号染色体上各包含 1 个 *CO* 的同源拷贝;2 号和 3 号染色体上各包含 1 个 *CDF1* 的同源拷贝。但更新的结球甘蓝基因组测序结果显示,仅在 9 号染色体上有 1 个 *CO* 的拷贝^[63](表 3)。

表 3 甘蓝类蔬菜中光周期途径相关基因
Table 3 Photoperiod pathway genes in *Brassica oleracea* vegetables

基因名称 Gene name	BRAD 数据库序号 Number in BRAD database	染色体位置(bp) Chr. location	与拟南芥基因一致性(%) Identity with <i>A. thaliana</i> gene	参考文献 Reference
<i>BoPRR1</i>	BolC07g043430.2J	45523619~45525750	70.108	[57]
<i>BoPRR2</i>	BolC09g007640.2J	5022510~5024832	71.865	[57]
<i>BoPRR3</i>	BolC09g049260.2J	53732329~53734477	71.705	[57]
<i>BoPRR4</i>	BolC09g006740.2J	4416343~4418837	70.789	[57]
<i>BoPRR5</i>	BolC07g041680.2J	44330275~44332645	75.309	[57]
<i>BoPRR6</i>	BolC02g059060.2J	62363399~62365472	71.067	[57]
<i>BoPRR7</i>	BolC02g000830.2J	657915~660633	80.082	[57]
<i>BoPRR8</i>	BolC09g068830.2J	66790565~66793543	81.165	[57]
<i>BoPRR9</i>	BolC04g001840.2J	1431380~1432882	68.615	[57]
<i>BoPRR10</i>	BolC04g068220.2J	65033411~65035606	73.967	[57]
<i>BoCCAI</i>	BolC04g001800.2J	1415998~1421969	65.846	[58]
<i>BoGI</i>	BolC05g021100.2J	13896504~13901184	91.709	[60]
<i>BoCDF1-1</i>	BolC02g061010.2J	64012310~64013817	76.159	[62]
<i>BoCDF1-2</i>	BolC03g058640.2J	42769905~42771304	70.627	[62]
<i>BoCO</i>	BolC09g057360.2J	60256399~60257685	70.341	[63]

2.4 其他影响因素

另外,在研究甘蓝类蔬菜抽薹开花调控过程中还发现了一些无法归属途径的基因,它们对甘蓝类蔬菜的抽薹开花也有显著影响。Abuyusuf 等^[64]在早花结球甘蓝 BN7115 和晚花结球甘蓝 BN4730 杂交产生的 F_2 分离群体中,定位到影响抽薹的编码过氧化物酶的基因 *BolPrx.2*,该基因在晚花结球甘蓝中的表达量显著高于早花结球甘蓝,第一内含子中 27 bp 缺失、2 bp 插入是导致结球甘蓝晚花的主要影响因素。Wang 等^[65]通过分析早花结球甘蓝 C491、晚花结球甘蓝 B602 以及二者杂交 F_2 的转录组,发现 *SEPALLATA2 (BoSEP2-1)* 和 *BoSEP2-2* 与开花时间密切相关,晚花甘蓝 B602 中 *BoSEP2-1* CDS 序列存

在 3 处 SNP,*BoSEP2-2* CDS 序列存在 1 处 SNP,二者表达量均显著低于早花甘蓝。Shu 等^[66]在早花青花菜 93219 和晚花结球甘蓝 195 的杂交分离后代群体中,定位到与开花时间相关的 *G-BOX REGULATING FACTOR 6 (BoGRF6)* 基因;相较晚花甘蓝的 *BoGRF6*,该基因在早花甘蓝中 C 端更长,多编码 13 个氨基酸,并存在 1 个氨基酸突变,其在早花甘蓝中表达量显著高于晚花甘蓝。还有研究发现,在青花菜中,AGAMOUS-LIKE 18 (AGL18)^[67]与 AGAMOUS-LIKE 19 (AGL19)^[68]均能够与 AGL24 互作而间接影响开花整合因子 SOC1 的功能,从而影响开花时间(表 4)。综上,将甘蓝类蔬菜抽薹开花调控网络总结为图 1。

表 4 甘蓝类蔬菜中尚未归属途径的抽薹开花调节基因
Table 4 Flowering regulatory genes in *Brassica oleracea* vegetables that have not yet been assigned pathways

基因名称 Gene name	BRAD 数据库序号 Number in BRAD database	染色体位置(bp) Chr. location	与拟南芥基因一致度(%) Identity with <i>A. thaliana</i> gene	参考文献 Reference
<i>BolPrx.2</i>	BolC03g002350.2J	1166288~1167985	74.769	[64]
<i>BoSEP2-1</i>	BolC01g057100.2J	51965015~51966909	92.885	[65]
<i>BoSEP2-2</i>	BolC05g062690.2J	56731949~56734008	92.829	[65]
<i>BoGRF6</i>	BolC02g004210.2J	2639811~2643131	88.077	[66]
<i>BoAGL18</i>	BolC04g034740.2J	35717984~35719596	75.385	[67]
<i>BoAGL19</i>	BolC03g078380.2J	66859691~66868426	82.432	[68]
<i>BoAGL24</i>	BolC01g018940.2J	13074521~13077176	86.486	[68]

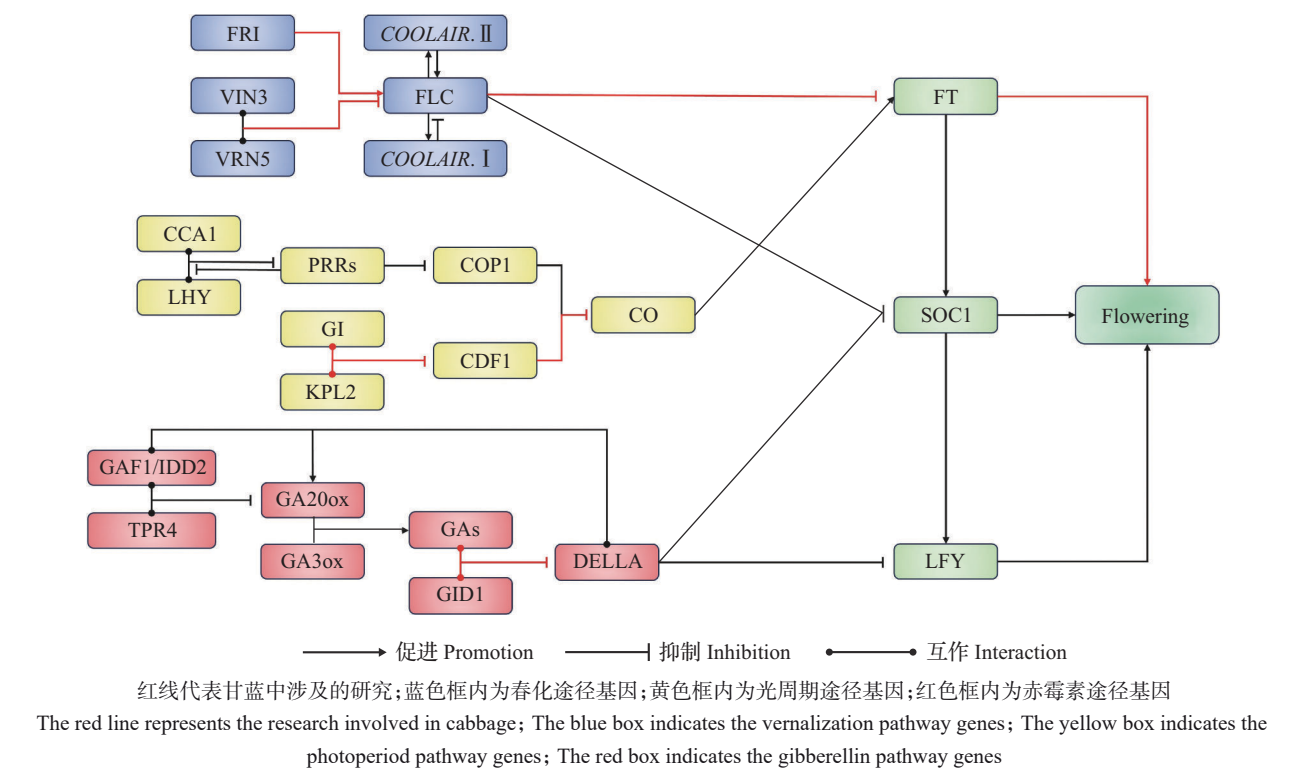


图 1 甘蓝类蔬菜抽薹开花调控基因网络
Fig. 1 Bolting and flowering time regulatory genes network in *B. oleracea*

3 问题与展望

随着我国国民生活水平的不断提高,人们对蔬菜提出了各式各样的品质要求。甘蓝类蔬菜作为重要的蔬菜作物之一,未熟抽薹等现象严重制约着甘蓝生产,各地农民对优质、适应性强甘蓝品种的需求逐渐增加。因此,推进甘蓝类蔬菜良种选育仍十分迫切。从过表达技术、VIGS 沉默技术到 CRISPR/Cas9 基因编辑技术等生物育种技术的蓬勃发展,为利用分子设计育种途径加速甘蓝育种提供了可能。然而,分子设计育种中,目标基因的选择

是关键。本文构建了甘蓝类蔬菜抽薹开花调控基因网络,可为改良现有甘蓝类蔬菜优良品种耐抽薹性提供重要参考,推进甘蓝良种培育。

自野生甘蓝被人类驯化以来,甘蓝已分化出多个变种,且每个变种的商品器官多有不同,如花椰菜、青花菜的商品器官是花球;芥兰的商品器官是花苔;结球甘蓝的商品器官是叶球;抱子甘蓝的商品器官是腋芽小球;苤蓝的商品器官是肉质膨大茎;羽衣甘蓝的商品器官是叶片,也是主要的观赏部位。对于每个变种而言,抽薹开花的意义各有不同,如食用花球的甘蓝类蔬菜需要促使花芽分化、

花球大而饱满;食用叶球的结球甘蓝则需要培育耐抽薹品种,延长其营养生长阶段,从而提高产量^[69]。通过构建甘蓝类蔬菜的抽薹开花调控基因网络,能更有针对性地应对各变种的育种需求,加快良种的开发进度。

参与植物抽薹开花的基因调控网络是一个高度复杂的动态系统,五大调控途径的各个因子之间存在相互串联,因此整合多个途径的基因研究进而构建甘蓝类蔬菜的抽薹开花调控基因网络是十分必要的。在芸苔属植物中,油菜的抽薹开花调控基因研究进度相对更快,且油菜的C亚基因组多与甘蓝基因组共线,因此油菜的C亚基因组研究内容对建立甘蓝类蔬菜的抽薹开花途径基因网络有较大参考价值^[70]。目前已有研究将油菜C亚基因组的*BnCO*、*SPAI-RELATED3 (BnSP3)*、*BnCDF1*等光周期途径基因克隆,并将其功能确定^[71-73]。另外,十字花科模式植物拟南芥的抽薹开花调控网络已有较深探索,甘蓝类蔬菜与拟南芥同属十字花科,同科植物基因同源度较高且功能接近,因此也可参考拟南芥抽薹开花调控网络验证甘蓝类蔬菜的抽薹开花调控网络^[74]。综上,参考油菜、拟南芥等植物的研究成果构建甘蓝类蔬菜抽薹开花基因网络,是加快该基因网络构建的重要手段之一。本文在简述调控植物抽薹开花5种途径的基础上,分析在甘蓝类蔬菜中发现的抽薹调控基因及其变异,梳理了甘蓝类蔬菜的抽薹开花调控基因网络,为解决甘蓝类蔬菜良种选育问题提供参考。

虽然甘蓝类蔬菜抽薹开花调控基因逐渐被发现,但在甘蓝类蔬菜中开发的分子标记仍然较少,且标记所针对的基因仍不够全面。早期研究中,曹维荣等^[75]利用混合分离群体法得到了一个与结球甘蓝晚抽薹相关基因的连锁的RAPD标记。在后续研究中,该标记被先后改进为稳定性和精确性更强的SCAR标记^[76]及CAPS标记^[77],然而与该标记连锁的调控抽薹基因始终未被揭示。王娇等^[78]针对*BoFLC1*和*BoFLC5*分别开发了1个KASP标记,针对*BoFLC3*开发了1个Indel标记,并依靠这3个标记成功育出耐抽薹结球甘蓝,其平均抽薹时间比早花型抽薹晚11.33 d。此外,也有针对结球甘蓝*BoFLC2*开发的Indel标记^[79]。除结球甘蓝外,基于芥兰及羽衣甘蓝*BoGRF6*序列差异设计的Indel标记能鉴别出开花需春化的晚花品种及不需春化的早花品种^[80]。从上述研究结果可见,甘蓝类蔬菜的抽薹开花相关分子标记在结球甘蓝中探索相对更

多,在芥兰及羽衣甘蓝中有少量研究,而在花椰菜和青花菜中鲜有相关报道,并且与标记连锁的基因多与春化途径相关。随着甘蓝类蔬菜抽薹开花调控基因网络的逐步建立,应加大力度开发更多与抽薹开花相关基因连锁的分子标记。另外,还应加强对青花菜和花椰菜中相关分子标记的探索,填补该领域的空白。

相较模式植物,甘蓝类蔬菜抽薹开花调控基因挖掘程度仍有较大不足。随着甘蓝全基因组测序的不断完善,包含花椰菜、青花菜、羽衣甘蓝和结球甘蓝等多个甘蓝变种的全基因组测序文件在近期均已公开发布^[81]。通过分析基因组文件所包含的信息,结合全基因组关联分析,能加快甘蓝类蔬菜抽薹开花调控相关基因的挖掘进度,从而提高甘蓝类蔬菜抽薹开花调控基因网络的构建速度及完整性。

参考文献

- [1] Blumel M, Dally N, Jung C. Flowering time regulation in crops-what did we learn from Arabidopsis? Current Opinion in Biotechnology, 2015, 32: 121-129
- [2] Freytes S N, Canelo M, Cerdan P D. Regulation of lowering time: When and where? Current Opinion in Plant Biology, 2021, 63: 102049
- [3] Wang J W, Czech B, Weigel D. miR156-Regulated SPL transcription factors define an endogenous flowering pathway in *Arabidopsis thaliana*. Cell, 2009, 138(4): 738-749
- [4] Sheldon C C, Rouse D T, Finnegan E J, Peacock W J, Dennis E S. The molecular basis of vernalization: The central role of *FLOWERING LOCUS C (FLC)*. Proceedings of the National Academy of Sciences, 2000, 97(7): 3753-3758
- [5] Lee H, Suh S S, Park E, Cho E, Ahn J H, Kim S G, Lee J S, Kwon Y M, Lee I. The AGAMOUS-LIKE 20 MADS domain protein integrates floral inductive pathways in *Arabidopsis*. Genes Development, 2000, 14(18): 2366-2376
- [6] Liu F, Marquardt S, Lister C, Swiezewski S, Dean C. Targeted 3' processing of antisense transcripts triggers *Arabidopsis FLC* chromatin silencing. Science, 2010, 327(5961): 94-97
- [7] Marquardt S, Raitskin O, Wu Z, Liu F, Sun Q, Dwan C. Functional consequences of splicing of the antisense transcript *COOLAIR* on *FLC* transcription. Molecular Cell, 2014, 54(1): 156-165
- [8] Choi K, Kim J, Hwang H J, Kim S, Park C, Kim S Y, Lee I. The FRIGIDA complex activates transcription of *FLC*, a strong flowering repressor in *Arabidopsis*, by recruiting chromatin modification factors. Plant Cell, 2011, 23(1): 289-303
- [9] Pien S, Fleury D, Mylne J S, Crevillen P, Inze D, Avramova

- Z, Dean C, Grossniklaus U. ARABIDOPSIS TRITHORAX1 dynamically regulates *FLOWERING LOCUS C* activation via histone 3 lysine 4 trimethylation. *Plant Cell*, 2008, 20(3): 580-588
- [10] Sharma N, Geuten K, Giri B S, Varma A. The molecular mechanism of vernalization in *Arabidopsis* and cereals: Role of Flowering Locus C and its homologs. *Physiologia Plantarum*, 2020, 170(3): 373-383
- [11] Legris M, Ince Y C, Fankhauser C. Molecular mechanisms underlying phytochrome-controlled morphogenesis in plants. *Nature Communications*, 2019, 10(1): 5219
- [12] Galvão V C, Fankhauser C. Sensing the light environment in plants: Photoreceptors and early signaling steps. *Current Opinion in Neurobiology*, 2015, 34: 46-53
- [13] Johansson M, Staiger D. Time to flower: Interplay between photoperiod and the circadian clock. *Journal of Experimental Botany*, 2015, 66(3): 719-730
- [14] Anwer M U, Davis A, Davis S J, Quint M. Photoperiod sensing of the circadian clock is controlled by *EARLY FLOWERING 3* and *GIGANTEA*. *Plant Journal*, 2020, 101(6): 1397-1410
- [15] Nakamichi N, Kiba T, Henriques R, Mizuno T, Chua N H, Sakakibara H. PSEUDO-RESPONSE REGULATORS 9, 7, and 5 are transcriptional repressors in the *Arabidopsis* circadian clock. *Plant Cell*, 2010, 22(3): 594-605
- [16] Luo X, Yin M, He Y. Molecular genetic understanding of photoperiodic regulation of flowering time in *Arabidopsis* and soybean. *International Journal of Molecular Sciences*, 2021, 23(1): 466
- [17] Sawa M, Kay S A. GIGANTEA directly activates *Flowering Locus T* in *Arabidopsis thaliana*. *Proceedings of the National Academy of Sciences*, 2011, 108(28): 11698-11703
- [18] Tiwari S B, Shen Y, Chang H C, Hou Y, Harris A, Ma S F, Mcpartland M, Hymus G J, Adam L, Marion C, Belachew A, Repetti P P, Reuber T L, Ratcliffe O J. The flowering time regulator CONSTANS is recruited to the *FLOWERING LOCUS T* promoter via a unique cis-element. *New Phytologist*, 2010, 187(1): 57-66
- [19] Hedden P. The current status of research on gibberellin biosynthesis. *Plant Cell Physiology*, 2020, 61(11): 1832-1849
- [20] Bao S, Hua C, Shen L, Yu H. New insights into gibberellin signaling in regulating flowering in *Arabidopsis*. *Journal of Integrative Plant Biology*, 2020, 62(1): 118-131
- [21] Simpson G G. The autonomous pathway: Epigenetic and post-transcriptional gene regulation in the control of *Arabidopsis* flowering time. *Current Opinion in Plant Biology*, 2004, 7(5): 570-574
- [22] Wang J W. Regulation of flowering time by the miR156-mediated age pathway. *Journal of Experimental Botany*, 2014, 65(17): 4723-4730
- [23] 汤青林, 王小佳, 宋明, 张洪, 任雪松, 牛义. 芥菜和甘蓝启动抽薹的温光诱导体系研究. *西南大学学报: 自然科学版*, 2007, 29(12): 113-117
- Tang Q L, Wang X J, Song M, Zhang H, Ren X S, Niu Y. Research on bolting-inducing system of mustard (*Brassica juncea*) and cabbage (*Brassica oleracea*) with temperature and photoperiod. *Journal of Southwest University: Natural Science Edition*, 2007, 29(12): 113-117
- [24] 杨小明, 李成琼, 宋洪元. 春甘蓝耐抽薹性研究进展. *北方园艺*, 2009(1): 111-114
- Yang X M, Li C Q, Song H Y. The progress of study on the bolting tolerance in spring cabbage. *Northern Horticulture*, 2009(1): 111-114
- [25] De Z D, Leopold A C. Altering juvenility with auxin. *Science*, 1955, 122(3176): 925-926
- [26] Wiebe H J, Habegger R, Liebig H P. Quantification of vernalization and devernization effects for kohlrabi (*Brassica oleracea* convar. acephala var. gongylodes L.). *Scientia Horticulturae*, 1992, 50(1): 11-20
- [27] 吴国平, 王建华, 王丽娟, 毛忠良, 陈智超, 刘小凤. 幼苗春化特性对结球甘蓝开花及繁种的影响. *江苏农业科学*, 2013, 41(6): 121-122
- Wu G P, Wang J H, Wang L J, Mao Z L, Chen Z C, Liu X F. Effects of seedling vernalization characteristics on flowering and propagation of cabbage. *Jiangsu Agricultural Sciences*, 2013, 41(6): 121-122
- [28] 徐磊, 林碧英, 林义章. 春化作用与甘蓝类蔬菜的生育障碍(综述). *亚热带植物科学*, 2002, 31(4): 73-76
- Xu L, Lin B Y, Lin Y Z. Relationship between breeding disturbance and vernalization in cabbage vegetable. *Subtropical Plant Science*, 2002, 31(4): 73-76
- [29] Adžić S, Girek Z, Pavlović N, Zdravković J, Cvikić D, Pavlović S, Prodanović S. Vernalization and seed yield of late head cabbage in different phases of rosette development by applying GA3 in vivo. *Acta Horticulturae*, 2013, 1005: 369-374
- [30] 王超, 张韬, 吴世昌. 春甘蓝抽薹特性的研究(I)——抽薹鉴定的方法. *东北农业大学学报*, 2003, 34(2): 129-132
- Wang C, Zhang T, Wu S C. Study on the method screening for bolting resistance in spring cabbages. *Journal of Northeast Agricultural University*, 2003, 34(2): 129-132
- [31] 刘奎彬, 方文惠, 张宝珍, 李素文, 孙德岭, 赵前程. 不同播种期花椰菜生长发育特性. *华北农学报*, 2002, 17(1): 64-68
- Liu K B, Fang W H, Zhang B Z, Li S W, Sun D L, Zhao Q C. Study on growth and development characteristics in cauliflower at different sowing date. *Acta Agriculturae Boreali-Sinica*, 2002, 17(1): 64-68
- [32] Farnham M W, Bjorkman T. Breeding vegetables adapted to high temperatures: A case study with broccoli. *HortScience*, 2011, 46(8): 1093-1097
- [33] Lindemann-zutz K, Fricke A, Stützel H. Prediction of time to harvest and its variability in broccoli (*Brassica oleracea* var. italica) Part I. Plant developmental variation and forecast of time to head induction. *Scientia Horticulturae*, 2016, 198: 424-433

- [34] 关佩聪, 梁承愈. 芥兰花芽分化与品种、播种期和春化条件的关系. 华南农业大学学报, 1989, 10(2): 60-66
Guan P C, Liang C Y. Flower bud differentiation of Chinese Kale (*Brassica albolabra* Bailey) and its relation to cultivar sowing time and vernalization. Journal of South China Agricultural University, 1989, 10(2): 60-66
- [35] Schranz M E, Quijada P, Sung S-B, Lukens L, Amasino R, Osborn T C. Characterization and effects of the replicated flowering time gene *FLC* in *Brassica rapa*. Genetics, 2002, 162(3): 1457-1468
- [36] Okazaki K, Sakamoto K, Kikuchi R, Saito A, Togashi E, Kuginuki Y, Matsumoto S, Hirai M. Mapping and characterization of *FLC* homologs and QTL analysis of flowering time in *Brassica oleracea*. Theoretical and Applied Genetics, 2007, 114(4): 595-608
- [37] Lin S I, Wang J G, Poon S Y, Su C L, Wang S S, Chiou T J. Differential regulation of *FLOWERING LOCUS C* expression by vernalization in cabbage and *Arabidopsis*. Plant Physiology, 2005, 137(3): 1037-1048
- [38] Woodhouse S, He Z, Woelfenden H, Steuernagel B, Haerty W, Bancroft I, Irwin J A, Morris R J, Wells R. Validation of a novel associative transcriptomics pipeline in *Brassica oleracea*: Identifying candidates for vernalisation response. BMC Genomics, 2021, 22(1): 539
- [39] Irwin J A, Soumpourou E, Lister C, Ligthart J D, Kennedy S, Dean C. Nucleotide polymorphism affecting *FLC* expression underpins heading date variation in horticultural brassicas. The Plant Journal, 2016, 87(6): 597-605
- [40] Li Q, Peng A, Yang J, Zheng S, Li Z, Mu Y, Chen L, Si J, Ren X, Song H. A 215-bp indel at intron I of *BoFLC2* affects flowering time in *Brassica oleracea* var. *capitata* during vernalization. Theoretical and Applied Genetics, 2022, 135(8): 2785-2797
- [41] Tang Q, Kuang H, Yu C, An G, Tao R, Zhang W, Jia Y. Non-vernalization requirement in Chinese kale caused by loss of *BoFLC* and low expressions of its paralogs. Theoretical and Applied Genetics, 2022, 135(2): 473-483
- [42] Itabashi E, J. Shea D, Fukino N, Fujimoto R, Okazaki K, Kakizaki T, Ohara T. Comparison of cold responses for orthologs of cabbage vernalization-related genes. The Horticulture Journal, 2019, 88(4): 462-470
- [43] Abuyusuf M, Nath U K, Kim H T, Islam M R, Park J I, Nou I S. Molecular markers based on sequence variation in *BoFLC1*. C9 for characterizing early- and late-flowering cabbage genotypes. BMC Genetics, 2019, 20(1): 42
- [44] Kinoshita Y, Motoki K, Hosokawa M. Upregulation of tandem duplicated *BoFLC1* genes is associated with the non-flowering trait in *Brassica oleracea* var. *capitata*. Theoretical and Applied Genetics, 2023, 136(3): 41
- [45] Lin Y R, Lee J Y, Tseng M C, Lee C Y, Shen C H, Wang C S, Liou C C, Shuang L S, Paterson A H, Hwu K K. Subtropical adaptation of a temperate plant (*Brassica oleracea* var. *italica*) utilizes non-vernalization-responsive QTLs. Scientific Reports, 2018, 8(1): 13609
- [46] Razi H, Howell E C, Newbury H J, Kearsey M J. Does sequence polymorphism of *FLC* paralogues underlie flowering time QTL in *Brassica oleracea*? Theoretical and Applied Genetics, 2008, 116(2): 179-192
- [47] Hawkes E. Conservation and function of COOLAIR long non-coding RNAs in *Brassica* flowering time control. Norwich: University of East Anglia, 2017
- [48] Nielsen M. Deciphering the role of PRC2 accessory proteins in promoting cold-induced epigenetic switching in *Arabidopsis thaliana*. Norwich: University of East Anglia, 2021
- [49] 赵荣秋. 甘蓝春化相关基因 *BoVIN3* 的克隆及分析. 哈尔滨: 东北农业大学, 2013
Zhao R Q. Clone vernalization related gene *BoVIN3* from cabbage and analysis. Harbin: Northeast Agricultural University, 2013
- [50] Irwin J A, Lister C, Soumpourou E, Zhang Y, Howell E C, Teakle G, Dean C. Functional alleles of the flowering time regulator *FRIGIDA* in the *Brassica oleracea* genome. BMC Plant Biology, 2012, 12(1): 21
- [51] Фаина О А. Структурные особенности гена *FRIGIDA* у видов *Brassica*. Москва: Всероссийский научно-исследовательский институт сельскохозяйственной биотехнологии, 2014
- [52] Hamano M, Yamato Y, Yamazaki H, Miura H. Endogenous gibberellins and their effects on flowering and stem elongation in cabbage (*Brassica oleracea* var. *capitata*). The Journal of Horticultural Science and Biotechnology, 2015, 77(2): 220-225
- [53] Hajime Ohyanagi, Kentaro Yano, Eiji Yamamoto, Ai Kitazumi. Plant omics advances in big data biology. Wallingford: CABI, 2022: 151-171
- [54] 李必元, 赵彦婷, 岳智臣, 雷娟利, 胡齐赞, 陶鹏. 甘蓝 *DELLA* 基因家族鉴定及其 mRNA 在嫁接体中的运输分析. 遗传, 2023, 45(2): 156-164
Li B Y, Zhao Y T, Yue Z C, Lei J L, Hu Q Z, Tao P. Identification of *DELLA* gene family in head cabbage and analysis of mRNA transport in the heterograft. Hereditas, 2023, 45(2): 156-164
- [55] 田素波, 郭春晓, 郑成淑. 光周期诱导植物成花的分子调控机制. 园艺学报, 2010, 37(2): 325-330
Tian S B, Guo C X, Zheng C S. Molecular mechanism of controlling flower formation by photoperiod inducement in plants. Acta Horticulturae Sinica, 2010, 37(2): 325-330
- [56] Salathia N, Lynn J R, Millar A J, King G J. Detection and resolution of genetic loci affecting circadian period in *Brassica oleracea*. Theoretical and Applied Genetics, 2007, 114(4): 683-692
- [57] Xing Y Y, Jiang Y J, Muhammad A R, Song J S. Genome-wide identification of pseudo-response regulator (PRR) family members in cabbage (*Brassica oleracea* var. *capitata* L.) and their expression in response to abiotic stress. The Journal of

- Horticultural Science and Biotechnology, 2023, 99 (2) : 168-178
- [58] Song H, Yi H, Han C T, Park J I, Hur Y. Allelic variation in *Brassica oleracea* *CIRCADIAN CLOCK ASSOCIATED 1* (*BoCCA1*) is associated with freezing tolerance. Horticulture, Environment, and Biotechnology, 2018, 59(3): 423-434
- [59] Liu S, Liu Y, Yang X, Tong C, Edwards D, Parkin I A, Zhao M, Ma J, Yu J, Huang S, Wang X, Wang J, Lu K, Fang Z, Bancroft I, Yang T J, Hu Q, Wang X, Yue Z, Li H, Yang L, Wu J, Zhou Q, Wang W, King G J, Pires J C, Lu C, Wu Z, Sampath P, Wang Z, Guo H, Pan S, Yang L, Min J, Zhang D, Jin D, Li W, Belcram H, Tu J, Guan M, Qi C, Du D, Li J, Jiang L, Batley J, Sharpe A G, Park B S, Ruperao P, Cheng F, Waminal N E, Huang Y, Dong C, Wang L, Li J, Hu Z, Zhuang M, Huang Y, Huang J, Shi J, Mei D, Liu J, Lee T H, Wang J, Jin H, Li Z, Li X, Zhang J, Xiao L, Zhou Y, Liu Z, Liu X, Qin R, Tang X, Liu W, Wang Y, Zhang Y, Lee J, Kim H H, Denoeud F, Xu X, Liang X, Hua W, Wang X, Wang J, Chalhoub B, Paterson A H. The *Brassica oleracea* genome reveals the asymmetrical evolution of polyploid genomes. Nature Communications, 2014, 5: 3930
- [60] Thiruvengadam M, Shih C F, Yang C H. Expression of an antisense *Brassica oleracea* *GIGANTEA* (*BoGI*) gene in transgenic broccoli causes delayed flowering, leaf senescence, and post-harvest yellowing retardation. Plant Molecular Biology Reporter, 2015, 33(5): 1499-1509
- [61] Lou P, Wu J, Cheng F, Cressman L G, Wang X, McClung C R. Preferential retention of circadian clock genes during diploidization following whole genome triplication in *Brassica rapa*. Plant Cell, 2012, 24(6): 2415-2426
- [62] Schiessl S V, Huettel B, Kuehn D, Reinhardt R, Snowdon R J. Flowering time gene variation in *Brassica* species shows evolutionary principles. Frontiers in Plant Science, 2017, 8: 1742
- [63] Cai X, Wu J, Liang J, Lin R, Zhang K, Cheng F, Wang X. Improved *Brassica oleracea* JZS assembly reveals significant changing of LTR-RT dynamics in different morphotypes. Theoretical and Applied Genetics, 2020, 133(11): 3187-3199
- [64] Abuyusuf M, Nath U K, Kim H-T, Biswas M K, Park J-I, Nou I-S. Intronic sequence variations in a gene with peroxidase domain alter bolting time in cabbage (*Brassica oleracea* var. *capitata*). Plant Molecular Biology Reporter, 2018, 36(5-6): 725-737
- [65] Wang J, Zhang B, Guo H, Chen L, Han F, Yan C, Yang L, Zhuang M, Lv H, Wang Y, Ji J, Zhang Y. Transcriptome analysis reveals key genes and pathways associated with the regulation of flowering time in cabbage (*Brassica oleracea* L. var. *capitata*). Plants, 2023, 12(19): 3413
- [66] Shu J, Liu Y, Zhang L, Li Z, Fang Z, Yang L, Zhuang M, Zhang Y, Lv H. QTL-seq for rapid identification of candidate genes for flowering time in broccoli×cabbage. Theoretical and Applied Genetics, 2018, 131(4): 917-928
- [67] 王宇, 蒋伟, 闫凯, 周雯文, 王志敏, 魏大勇, 汤青林. 青花菜 AGL18 及 HDA9 与开花信号整合子互作研究. 园艺学报, 2018, 45(12): 2383-2394
- Wang Y, Jiang W, Yan K, Zhou W W, Wang Z M, Wei D Y, Tang Q L. Protein interactions of flowering inhibitors AGL18 and HDA9 with integrator factors in *Brassica oleracea* var. *italica*. Acta Horticulturae Sinica, 2018, 45(12): 2383-2394
- [68] 蒋伟, 周雯文, 李朝闯, 闫凯, 王宇, 王志敏, 宋明, 汤青林. 青花菜开花促进因子 AGL19 与整合子 AGL24 和 SOC1 的互作研究. 园艺学报, 2017, 44(10): 1905-1913
- Jiang W, Zhou W W, Li C C, Yan K, Wang Y, Wang Z M, Song M, Tang Q L. Interactions of flowering promoting factor AGL19 with integrator factors AGL24 and SOC1 in *Brassica oleracea* var. *italica*. Acta Horticulturae Sinica, 2017, 44(10): 1905-1913
- [69] Lin X, Liu B, Weller J L, Abe J, Kong F. Molecular mechanisms for the photoperiodic regulation of flowering in soybean. Journal of Integrative Plant Biology, 2021, 63(6): 981-994
- [70] Bohuon E J R, Keith D J, Parkin I A P, Sharpe A G, Lydiat D J. Alignment of the conserved C genomes of *Brassica oleracea* and *Brassica napus*. Theoretical and Applied Genetics, 1996, 93(5): 833-839
- [71] 伍向苹, 王直新, 卓宸剑, 文静, 易斌, 马朝芝, 沈金雄, 傅廷栋, 涂金星. 甘蓝型油菜 CO 同源基因功能初步研究. 中国油料作物学报, 2021, 43(2): 186-194
- Wu X P, Wang Z X, Zhuo C J, Wen J, Yi B, Ma C Z, Shen J X, Fu T D, Tu J X. Preliminary study on function of CO homologs in *Brassica napus*. Chinese Journal of Oil Crop Sciences, 2021, 43(2): 186-194
- [72] Yu K, Wang X, Chen F, Chen S, Peng Q, Li H, Zhang W, Hu M, Chu P, Zhang J, Guan R. Genome-wide transcriptomic analysis uncovers the molecular basis underlying early flowering and apetalous characteristic in *Brassica napus* L.. Scientific Reports, 2016, 6: 30576
- [73] Xu J, Dai H. *Brassica napus* Cycling Dof Factor1 (*BnCDF1*) is involved in flowering time and freezing tolerance. Plant Growth Regulation, 2016, 80(3): 315-322
- [74] Osborn T C, Kole C, Parkin I A P, Sharpe A G, Kuiper M, Lydiat D J, Trick M. Comparison of flowering time genes in *Brassica rapa*, *B. napus* and *Arabidopsis thaliana*. Genetics, 1997, 146(3): 1123-1129
- [75] 曹维荣, 王超. 甘蓝迟抽薹基因的 RAPD 标记. 生物技术通报, 2007 (5): 167-169
- Cao W R, Wang C. RAPD marker of later bolting gene on cabbage. Biotechnology Bulletin, 2007 (5): 167-169
- [76] 乌兰, 王超. 结球甘蓝迟抽薹基因 RAPD 标记转 SCAR 标记. 分子植物育种, 2010, 8(2): 307-311
- Wu L, Wang C. A SCAR marker derived from the RAPD marker linked to later bolting gene in headed cabbage. Molecular Plant Breeding, 2010, 8(2): 307-311

- [77] 李江丽, 王超, 张晓烜, 姜凯旋, 赵乐杰. 结球甘蓝 (*Brassica oleracea* var. *capitata*) 迟抽薹基因 SCAR 标记转 CAPS 标记. 分子植物育种, 2020, 18(5): 1529-1534
Li J L, Wang C, Zhang X X, Jiang K X, Zhao L J. A CAPS marker derived from the SCAR marker linked to later bolting gene in *Brassica oleracea* var. *capitata*. Molecular Plant Breeding, 2020, 18(5): 1529-1534
- [78] 王娇, 张斌, 吴元康, 杨丽梅, 庄木, 吕红豪, 王勇, 季家磊, 闫超, 张扬勇. 甘蓝 *BoFLCs* 基因标记开发及优异单倍型聚合. 中国蔬菜, 2024 (5): 40-50
Wang J, Zhang B, Wu Y K, Yang L M, Zhuang M, Lyu H H, Wang Y, Ji J L, Yan C, Zhang Y Y, Development of *BoFLCs* gene markers and pyramiding of elite haplotypes in cabbage (*Brassica oleracea* L. var. *capitata*), China Vegetables, 2024 (5): 40-50
- [79] 宋洪元, 李勤菲, 李樟萍, 任雪松, 司军. CN107190092B 用于鉴定结球甘蓝开花早晚的分子标记、引物对及分子标记方法与应用. 2020-11-24
Song H Y, Li Q F, Li Z P, Ren X S, Si J. CN107190092B Molecular marker, primer pair and molecular marker method and application for identification of flowering time and evening of cabbage. 2020-11-24
- [80] 陈炯炯, 唐其蔚, 匡汉晖. CN112410464A 用于羽衣甘蓝和芥蓝花期鉴定的分子标记引物及应用. 2022-04-22
Chen J J, Tang Q W, Kuang H H. CN112410464A Molecular marker primers for identification of flowering period of kale and kale and their application. 2022-04-22
- [81] Li X, Wang Y, Cai C, Ji J, Han F, Zhang L, Chen S, Zhang L, Yang Y, Tang Q, Bucher J, Wang X, Yang L, Zhuang M, Zhang K, Lv H, Bonnema G, Zhang Y, Cheng F. Large-scale gene expression alterations introduced by structural variation drive morphotype diversification in *Brassica oleracea*. Nature Genetics, 2024 (56): 517-529