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甘蓝类蔬菜抽薹开花调控相关基因研究进展

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摘要：甘蓝类蔬菜是重要的蔬菜作物，在生产和制种过程中，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，抽薹开花调控基因研究相对分散。本文在简述了植物抽薹开花 5 种途径的基础上，归纳总结了春化途径、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，并构建了抽薹开花调控基因网络，该工作将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

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Abstract: *Brassica oleracea* vegetables are important vegetative crops. Premature bolting and mismatched flowering time between two parents are commonly occurred during the process of production and breeding in *B. oleracea* vegetables. Improving bolting resistance of *B. oleracea* vegetables by molecular design breeding will resolve these problems. However, diverse subspecies of *B. oleracea* vegetables exhibit various flowering times, and research on the genes regulating bolting and flowering is scattered. This article summarized genes and variants for flowering pathways which are mainly involved in gibberellin pathway, vernalization pathway, and photoperiod pathways of *B. oleracea* vegetables on the basis of five main flower regulation pathways in plants. And a gene network that regulates bolting and flowering of *B. oleracea* vegetables is constructed, which will provide 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。自上世纪初开始，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，即春化途径、光周期途径、赤霉素途径、自主途径和年龄途径[2, 3]。

在春化途径中，中心调控基因 *FLOWERING LOCUS C* (*FLC*)通过抑制促花基因 *SOC1* 和 *FT* 的表达而抑制花芽分化[4, 5]。常温时，*FLC* 由 FRIGIDA(FRI)等蛋白复合物诱导 H3K4me3 及 H3K36me3 对其修饰，该类

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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，PHD-PRC2 蛋白复合体于染色体的 *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 ASSOCIATED1(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 *FLOWERING LOCUS T (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 Gibberellins(GAs)通过调节其信号转导途径的各类蛋白，影响植物生长发育。GAs 广泛存在于植物中，目前已鉴定出 130 多种，但仅有 GA_1、GA_3、GA_4 和 GA_7 具生物活性。异戊二烯焦磷酸 (IPP)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 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 *FLOWERING LOCUS C(FLC)*表达来促进开花[21]。

年龄途径发现较晚，是随植物生长，体内 miR156 丰度由高降低，从而影响开花的途径。随植物生长，*miR156* 标靶基因 *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，据世界粮农组织(FAO)统计数据，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，抽薹开花调控即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，若两亲本花期不遇，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，以至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，为育种者改良甘蓝类蔬菜耐抽薹性奠定基础。

1　甘蓝类蔬菜抽薹开花差异

甘蓝类蔬菜为十字花科芸薹属植物，包含结球甘蓝、花椰菜、青花菜、抱子甘蓝、苤蓝和芥兰等丰富的变种类型，表现不同的开花习性。以叶球等营养器官为商品的结球甘蓝[24]、苤蓝[25]和抱子甘蓝[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，方能诱导开花。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 cm ~ 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，一些品种需要经历低温完成春化才能抽薹开花，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，诱导开花抽薹的最适光、温也不相同。

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，对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*、*BoFLC2*、*BoFLC3*、*BoFLC4* 和 *BoFLC5*[35-37]。但 Okazaki 等认为，因选择的参考氨基酸序列不足，*BoFLC4* 与 *BoFLC2* 应是同一基因[37]。上述基因中对春化影响最大的是 *BoFLC2*，该基因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会影响该基因功能，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 215bp 缺失突变，也能减缓 *BoFLC2* 沉默速度，导致结球甘蓝的晚花[40]。Tang 等在羽衣甘蓝中发现了 9325bp 区段缺失，造成 *BoFLC2* 完全丢失，使得羽衣甘蓝不需春化也能开花[41]。

除 *BoFLC2* 外，*BoFLC1* 和 *BoFLC3* 对春化亦有影响。Itabashi 等将 *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[42]。Abuyusuf 等发现，*BoFLC1*

第二内含子中存在 67bp 插入突变时，结球甘蓝春化更快，开花时间更早[43]。Kinoshita 等在极难开花结球甘蓝 nfc 与 2 种结球甘蓝和 1 种羽衣甘蓝杂交产生的 F2 代分离群体中，定位到影响甘蓝抽薹时间的基因 *BoFLC1*[44]。Lin 等在早花青花菜 BLM29 和晚花青花菜 BLM25 杂交 F2 代分离群体中，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 255bp 缺失及 50bp 插入均会引起开花时间改变[45]。而 *BoFLC5* 在甘蓝类蔬菜中的表达量极低，可能因过早出现终止密码子而导致基因功能异常，且在早、晚花甘蓝中缺乏多态性，故 *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。青花菜中发现也有 *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，却在低温下未测出；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 富集于 *FLC* 染色质上，并催化 *FLC* 沉默，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]。赵荣秋首次从结球甘蓝中克隆出 2 条 *VIN3* 同源物 *BoVIN3-1* 和 *BoVIN3-2*，均编码含 560 个氨基酸的蛋白质，两基因只在低温处理达到春化要求后才会在茎尖表达。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、晚花结球甘蓝中春化过程中，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[49]。春化途径的另一个热点基因是 *FRI*。青花菜中共发现 2 种 *FRI* 同源物，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，但二者均能恢复 *fri* 缺失拟南芥的开花时间，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 Vernalization pathway genes in *Brassica oleracea* vegetables

基因名称 Gene name	BRAD 数据库序号 No. in BRAD database	染色体位置 Chr. Location (bp)	与拟南芥基因一致度（%） The identity with A. thaliana gene	参考文献 Reference
BoFLC1	BolC09g062620.2J	63395901-63399910	85.427	[35]
BoFLC2	BolC02g004040.2J	2542284-2545548	82.741	[36]

BoFLC3	BolC03g004550.2J	2244866-2248179	83.417	[35]
BoVIN3-1	BolC03g013830.2J	7260993-7263556	68.960	[49]
BoVIN3-2	BolC02g015310.2J	10887788-10892097	58.013	[49]
BoFRIa	BolC03g017480.2J	9633856-9636028	57.241	[50]
BoFRIb	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 GA_1、GA_4、GA_{12} 和 GA_{15} 等共 9 种，其中 GA_4 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 *GA3ox* 和 7 个 *GA2ox* 基因仅余留部分序列，呈截断状态，该种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)*基因[54]。

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 No. in BRAD database	染色体位置(bp) Chr. Location	与拟南芥基因一致度（%） The identity with A. thaliana gene	参考文献 Reference
BoGID1a	BolC05g060470.2J	55275185-55276562	84.770	[53]
BoGID1b-1	BolC08g045880.2J	43466928-43468248	91.389	[53]
BoGID1b-2	BolC04g030280.2J	31287613-31288803	89.118	[53]
BoGID1b-3	BolC06g027340.2J	29529812-29531056	87.778	[53]
BoGID1c	BolC07g039220.2J	42725133-42726810	92.754	[53]
BoRGA1	BolC07g031500.2J	36431939-36433669	82.412	[54]
BoRGA2	BolC09g027430.2J	24522236-24523945	81.636	[54]
BoRGL1	BolC02g022360.2J	18385313-18386836	84.496	[54]
BoRGL2	BolC05g063590.2J	57356636-57358267	82.364	[54]
BoRGL3	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三个阶段：其一是植物对光信号的接收；其二是生物钟对光信号的转导；其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。*BoTOC1*、*BoPRR3* 和 *BoCCA1* 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 F1 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，*BoCCA1* 基因响应低温胁迫，但这些基因对甘蓝类蔬菜抽薹开花的影响却鲜有报道[57, 58]。

GI 和 *CO* 是光信号从生物钟输出，调控植株开花的过程中的重要基因。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[60]。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 BoCDF1 间接提高 *BoCO* 的表达。Schiessl 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[62]；但更新的结球甘蓝基因组测序结果认为，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 No. in BRAD database	染色体位置(bp) Chr. Location	与拟南芥基因一致度（%） The identity with A. thaliana gene	参考文献 Reference
BoPRR1	BolC07g043430.2J	45523619-45525750	70.108	[59]
BoPRR2	BolC09g007640.2J	5022510-5024832	71.865	[59]
BoPRR3	BolC09g049260.2J	53732329-53734477	71.705	[59]
BoPRR4	BolC09g006740.2J	4416343-4418837	70.789	[59]
BoPRR5	BolC07g041680.2J	44330275-44332645	75.309	[59]
BoPRR6	BolC02g059060.2J	62363399-62365472	71.067	[59]
BoPRR7	BolC02g000830.2J	657915-660633	80.082	[59]
BoPRR8	BolC09g068830.2J	66790565-66793543	81.165	[59]
BoPRR9	BolC04g001840.2J	1431380-1432882	68.615	[59]
BoPRR10	BolC04g068220.2J	65033411-65035606	73.967	[59]
BoCCA1	BolC04g001800.2J	1415998-1421969	65.846	[59]
BoGI	BolC05g021100.2J	13896504-13901184	91.709	[60]

BoCDF1-1	BolC02g061010.2J	64012310-64013817	76.159	[62]
BoCDF1-2	BolC03g058640.2J	42769905-42771304	70.627	[62]
BoCO	BolC09g057360.2J	60256399-60257685	70.341	[63]

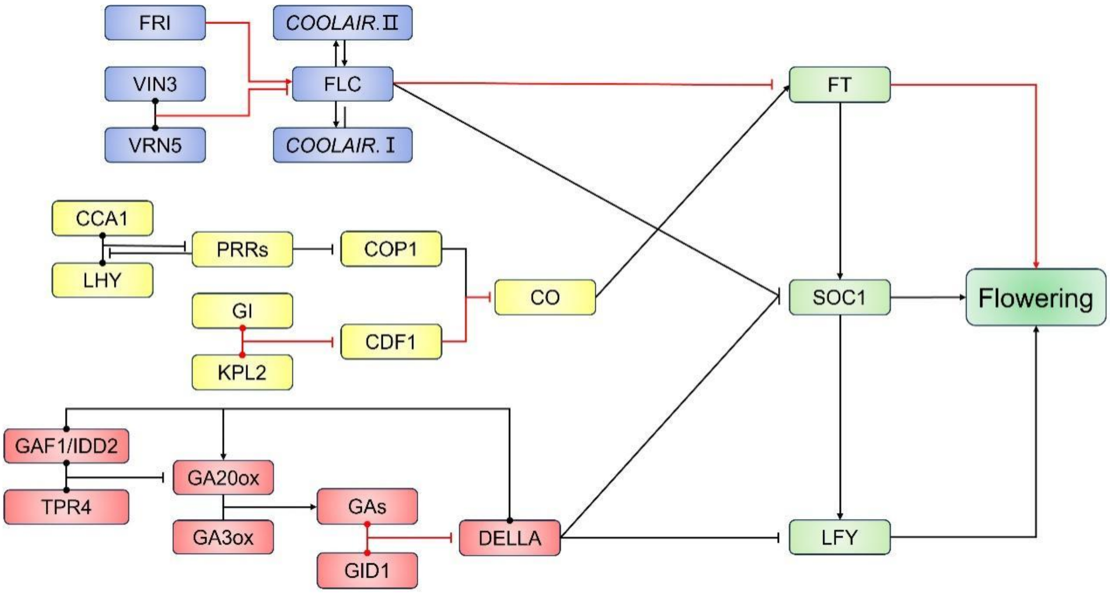
2.4 其他影响因子

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，他们对甘蓝类蔬菜的抽薹开花也有显著影响。Abuyusuf 等在早花结球甘蓝 BN7115 和晚花结球甘蓝 BN4730 杂交产生的 F2 代分离群体中，定位到影响抽薹的编码过氧化物酶基因 *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 27bp 缺失、2bp 插入是导致结球甘蓝晚花的主要影响因素[64]。Wang 等通过分析早花结球甘蓝 C491、晚花结球甘蓝 B602 以及二者杂交 F2 代的转录组，发现 *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[65]。Shu 等在早花青花菜 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 *BoGRF6* 基因，该基因的 C 端在早花甘蓝中比晚花甘蓝多 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[66]。还有研究发现，在青花菜中，AGL18 与 AGL19 均能够与 AGL24 互作而间接影响开花整合因子 SUPPRESSOR OF OVEREXPRESSION OF CO 1(SOC1)的功能，从而影响开花时间[67, 68]（表 4）。

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 No. in BRAD database	染色体位置(bp) Chr. Location	与拟南芥基因一致度（%） The identity with A. thaliana gene	参考文献 Reference
BolPrx.2	BolC03g002350.2J	1166288-1167985	74.769	[64]
BoSEP2-1	BolC01g057100.2J	51965015-51966909	92.885	[65]
BoSEP2-2	BolC05g062690.2J	56731949-56734008	92.829	[65]
BoGRF6	BolC02g004210.2J	2639811-2643131	88.077	[66]
BoAGL18	BolC04g034740.2J	35717984-35719596	75.385	[67]
BoAGL19	BolC03g078380.2J	66859691-66868426	82.432	[68]
BoAGL24	BolC01g018940.2J	13074521-13077176	86.486	[68]



红线代表甘蓝中涉及的研究；蓝色框内为春化途径基因；黄色框内为光周期途径基因；红色框内为赤霉素途径基因

The red line represents the research involved in cabbage; the blue box indicates the vernalization pathway genes; the yellow box indicates the photoperiod pathway genes; the red box indicates the gibberellin pathway genes

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，各地农民逐渐涌现出对优质、适应性强甘蓝品种的需求。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 沉默技术至 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。该文通过构建的甘蓝类蔬菜抽薹开花调控基因网络，将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；芥蓝的商品器官是花苔；结球甘蓝的商品器官是叶球；抱子甘蓝的商品器官腋芽小球；苤蓝的商品器官肉质膨大茎；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，5 大调控途径的各个因子亦存在相互串

联，故整合多个途径的基因研究而形成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，故油菜的 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]。目前已有研究将位于油菜 C 亚基因组的 *BnCO*、*BnSPA3*、*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，故可参考拟南芥抽薹开花调控网络按图索骥[74]。综上，参考油菜、拟南芥等植物的研究成果搭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(图 1)，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，然而在甘蓝类蔬菜中开发的分子标记仍然较少，标记所针对的基因仍不够全面。早期研究中，曹维荣等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[75]。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。王娇等针对 *BoFLC1* 和 *BoFLC5* 分别创制了 1 个 KASP 标记，针对 *BoFLC3* 创制了 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 天[78]。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，应加大力度探索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]。通过大量分析基因组文件所包含的信息，结合 GWAS 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。

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