Research Progress on Bolting and Flowering Characteristics of Cruciferous Vegetables

Yue LIANG[1,2], **Xingsheng LI**[1], **Yangdong GUO**[2*], **Xiaowei YUAN**[1,2*]

1. Huasheng Agriculture Group Co., Ltd., Qingzhou 262500, China; 2. College of Horticulture, China Agricultural University, Beijing 100193, China

Abstract There are many varieties of vegetables in Cruciferae, which have a wide distribution and occupy an important position in the global vegetable industry. The bolting period is a crucial stage in the growth cycle of cruciferous plants, which directly affects the yield and quality of vegetable crops. This paper summarized the research progress on the physiological and biochemical characteristics, molecular genetic mechanisms and molecular markers of the flowering and bolting traits in cruciferous vegetables, in order to provide new ideas for revealing the regulatory mechanisms of flowering and bolting in cruciferous vegetables and to provide reference for the breeding of new varieties of cruciferous vegetables that are resistant to flowering.

Key words Cruciferae; Bolting; Flowering

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After a long period of low temperature environment and a period of long sunshine, plants begin to bolt and bloom, transitioning from vegetative growth to reproductive growth. Cruciferous vegetables are mostly consumed by leaves or swollen rhizomes, while premature bolting and flowering can lead to early termination of vegetative organ growth, which has a negative impact on vegetable quality and yield[1-2]. In recent years, with the market demand for cruciferous vegetables expanding continuously, the planting area has also increased year by year. However, due to various factors such as unstable temperature in early spring, cruciferous vegetables often exhibit immature bolting, causing serious economic losses to growers. Therefore, the research and application of molecular mechanisms and molecular markers for resistance to bolting in cruciferous vegetables will help improve the breeding efficiency of new varieties of high-quality bolting-resistant cruciferous vegetables, and contribute to the sustainable development of agriculture.

Physiological Indicators Related to Bolting and Flowering Traits in Cruciferous Vegetables

In the process of flower bud differentiation and bolting and flowering, a series of physiological and biochemical reactions will occur in plants, including changes in sugar content, soluble protein content, enzyme activity and plant hormones.

In plants, sugar is an important energy and carbon source, which supports their own growth and metabolism. High sugar content is necessary for flower bud differentiation[3]. In the hearts of *Brassica* vegetables, sugar accumulates continuously before flower bud differentiation, and after reaching the peak, plants begin flower bud differentiation[4]. Su *et al.*[5] found in their study on different varieties of lettuce that the soluble sugar in leaf lettuce with early bolting decreased to a minimum at the critical stage of bolting, while the content in late-bolting varieties was less at the initial stage of flower bud differentiation. During the flower bud differentiation of radish shoot tip, the total soluble sugar content showed a change law of first rising and then falling, and the sucrose content had a similar change trend with the total soluble sugar, and both of them recovered to the high levels in the early flower bud differentiation stage[6]. In rape, the soluble sugar content of early-bolting rape varieties is usually higher than that of late-bolting rapeseed varieties[7]. All the above results show that a high sugar content may be one of the factors that accelerate bolting and flowering of plants undergoing vernalization.

The soluble protein content shows an overall upward trend during plant growth and development[8]. In Chinese cabbage, soluble proteins continuously increase during growth and decrease during flower bud differentiation[11]. Yang *et al.*[12] proved that soluble proteins in the body gradually accumulated during the differentiation of cabbage flower buds, then decreased in the later stage until the differentiation ended, and increased again during the budding and bolting stages, showing an overall changing pattern of increasing, decreasing and increasing. With regard to the changes of enzyme activity in plants at the bolting stage, Zhang[13] found that the activity of phenylalanine ammonia-lyase (PAL), superoxide dismutase (SOD) and peroxidase (POD) all increased at the bolting stage, only the activity of catalase (CAT) weakened at the early bolting stage, and the changes of enzyme activity in different plant lines were obviously different. Du *et al.*[14] demonstrated in their experiments that the activity of SOD and POD in Chinese cabbage showed a decreasing, increasing and decreasing trend before and after bolting, and their changing patterns were not the same in materials that were resistant to and not resistant to bolting. It indicated that the activity changes of these enzymes

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Yue LIANG (2000 –), female, P. R. China, master, devoted to research about vegetable biotechnology breeding.

* Corresponding author. E-mail: yuanxiaowei-yuan@163.com; yaguo@cau.edu.cn.

were related to the bolting characteristics of vegetables to a certain extent. The research results of Tian[15] are relatively consistent with those of other scholars, such as Li[9], and they believe that the activity levels of CAT and POD gradually increase before bolting and decrease after bolting. However, there are differences in the changes in CAT content compared with the results obtained by Zhang[13]. In mustard, plant bolting is influenced by SOD activity and soluble sugar content in the leaves, both of which can accelerate bolting. In addition, there is a significant correlation between bolting rate and POD and CAT activity, which plays a negative regulatory role in mustard bolting and flowering[16].

Various hormones within plants coordinate with each other and work together on bolting and flowering[17]. In plants that require low temperatures to complete vernalization, and endogenous hormones GAs are involved in the process of bolting and flowering[18]. Studies have shown that gibberellin (GA) and auxin (IAA) have dual effects on flower formation, that is, low concentrations promote flower bud differentiation, while high concentrations inhibit it[19]. Shortly before flowering, GAs and sucrose are transported from the outside to the top of branches, and the GA4 level increased sharply at the top of branches[20]. The research results of Guan *et al.*[21] showed that spraying gibberellin at different growth stages of plants produced different effects. Spraying GA3 when cauliflower reaches the second true leaf stage can promote flowering but not bolting. However, spraying gibberellin at the third true leaf stage could not only promote bolting but also promote flowering. The application time and growth stage of gibberellin could affect the growth and development of plants. The experiment of Xia *et al.*[22] showed that the IAA content in Chinese cabbage changed obviously at the bolting stage. In the vegetative growth stage, the IAA content was high, and when flower buds was about to differentiate, the IAA content decreased. Auxin could promote the vegetative growth of Chinese cabbage, but inhibit flower bud differentiation[23]. Song *et al.*[24] also came to the conclusion that IAA inhibited reproductive growth in the study of hormone content changes during bolting and flowering of radish.

Molecular Genetic Mechanism of Bolting and Flowering Traits

The bolting and flowering traits of cruciferous vegetables have complex genetic backgrounds, exhibit genetic characteristics of quantitative traits, which are usually influenced by environmental factors such as sunshine length and temperature[25]. Analyzing the regulatory mechanisms of bolting and flowering at the molecular level is the foundation and prerequisite for realizing the breeding of cruciferous varieties that are resistant to bolting.

The study on the genetic mechanism of plant bolting and flowering was first conducted in the model organism *Arabidopsis thaliana*[26]. Major genes interact with other auxiliary genes in *A. thaliana* as well as environmental factors to regulate the bolting trait together[27]. Cheng *et al.*[28] found that the bolting traits of Chinese cabbage were jointly controlled by multiple genes. The early bolting trait is to some extent dominant, while environmental factors have a relatively small impact on bolting traits. The late bolting trait can be relatively stably transmitted to offspring. There is currently no conclusive conclusion on the genetic mode of bolting traits, and there are still differences in major gene + polygene genetic models for cruciferous vegetables' bolting. Li *et al.*[29] thought that the bolting traits of flowering Chinese cabbage was controlled by gene pleiotropy or contiguous genes. Cao *et al.*[30] found in the study on late bolting of *Brassica oleracea* var. *capitata* Linnaeus that the number ratio of early-bolting plants, intermediate plants and late-bolting plants followed the separation ratio of 1 : 2 : 1, which is consistent with the genetic characteristics of quality traits and conflicted with previous research results. Zhuo, Guo and Wang[31-33] studied the bolting traits of Chinese cabbage and head cabbage, and proved that they conformed to the two pairs of additive-dominant-epistatic major genes + additive-dominant-epistatic polygene model. Studies of Zhang and Du[13-14] showed that these traits were controlled by a pair of additive major genes + additive-dominant polygene model. Li *et al.*[34] included the squaring stage and flowering stage in the identification indexes of bolting and flowering characters, and obtained the same results as Zhuo *et al.*, and there were obvious additive, dominant and epistatic effects among genes.

The transformation process of cruciferous vegetables from vegetative growth to reproductive development is regulated by interaction between genes of different flowering pathways[35]. Among them, more than 300 genes related to flowering complexity have been identified in *A. thaliana*, which affect bolting and flowering by participating in multiple flowering pathways such as photoperiod, vernalization, age, autonomy and hormones[36]. Many different flowering pathways are regulated by several key genes such as *FLOWERING LOCUS C* (*FLC*), *FLOWERING LOCUS T* (*FT*) and *LEAFY* (*LFY*)[37] (Fig. 1).

FLC is a transcription factor of MADS-box, which participates in the integration of autonomous pathway and vernalization pathway, and plays a role in inhibiting bolting and flowering[38]. Under long-term low temperature conditions, in order to prevent plants from flowering prematurely in cold environment, the expression of gene *FLC* is up-regulated, thus delaying flowering time[39]. At this time, FRIGIDA (FRI) is activated, which is a unique gene in *A. thaliana* which positively regulates vernalization reaction. With the extension of low temperature period, the expression of FLC is affected by FRI, which promotes bolting and flowering[40]. In addition to *A. thaliana*, the inhibitory effect of *FLC* homologous genes on bolting and flowering process has been reported in many cruciferous vegetables such as rape, cabbage and radish. Among them, rape has six homologous genes for flowering trait[41]. Yi *et al.*[42-43] isolated from radish three *FLC* homologous genes, the effect of which are similar to the *FLC* gene in *A. thaliana*, and these three genes negatively regulate the flowering process in radish. There are five *FLC* homologous genes in Chinese cabbage genome, and the influence of each gene copy on bolting and flowering is still controversial. M. Eric[44] deemed that BrFLC1, BrFLC2 and BrFLC5 were co-separated from the flowering time locus, and regulated flowering time in an additive way. Yuan *et al.* [45] demonstrated that there were mutation sites in gene *BrFLC1* closely related to the bolting trait in plants, while genes *BrFLC2*, *BrFLC3* and *BrFLC5* had no obvious linkage with bolting time, and *BrFLC1* was closely linked with QTLs that can best explain phenotypic variation. Kitamoto *et al.* [46] showed that the polymorphism of *BrFLC1* had little effect on flowering time, but the polymorphism of *BrFLC2* gene had an obvious effect on flowering time after low temperature treatment, and *BrFLC2* was the key candidate gene for flowering time and cold treatment reaction of *Brassica napus*, which was closely linked with QTL locus. The research results of Kitamoto *et al.* [46] showed that the polymorphism of *BrFLC1* had little effect on flowering time, but the polymorphism of gene *BrFLC2* had a significant effect on flowering time after undergoing low temperature treatment. *BrFLC2* is the key candidate gene for flowering time and cold treatment response in *Brassica rapa* var. *oleifera* DC., closely linked to the QTLs. *BcFLC2* regulates plant flowering by regulating the transcription factor of *SUSPENSOR 1* (*TSM1*) and *SEPALLATA3* (*SEP3*) genes[47]. In addition, Li *et al.* [48] found that there were two variants of gene *BoFLC2* in head cabbage, with *BoFLC2E* associated with early flowering and *BoFLC2L* associated with late flowering. A 215bp insertion/deletion was found in the intron region of the gene, which affected the silencing rate of *BoFLC2L* during vernalization and led to a delay in flowering time. XU *et al.* [49] studied genes *RsFLC1* and *RsFLC2* in early- and late-bolting white radish, and found that there were differences in the promoter region between the two, with TCA elements and GARE motif cis regulatory elements only presenting in *PRsFLC1*. These differences led to the diversity of core elements in the promoter, which explains the differences in bolting and flowering time among different white radish varieties at the genetic level.

FT is an important switch for flowering induction and one of the important components of the flowering pathway[50]. CONSTANS (CO) is mainly involved in the regulation of photoperiod. Under the stimulation of long sunlight, the level of CO protein in plants sharply increases, and acts as a transcription regulatory factor to stimulate the expression of downstream target gene flowering locus T, producing FT protein and accelerating plant flowering[51]. Subsequently, the FT protein moves to the leaf axil and interacts with the SUPERRESSOR OF OVEREXPRESSION OF CONSTANS 1 (SOC1) protein to activate SOC1 expression and further activate other flowering-related genes, forming a key chain in the photoperiodic pathway that synergistically regulates plant flowering[52]. Ubiquitin ligase (COP1) under dark conditions and photosensitive pigment B (phyB) under light conditions can both degrade CO, thereby achieving the goal of inhibiting flowering[36] (Fig. 1). Ayako *et al.* [53] investigated in detail the action mechanism of the nearest homolog of FT, TWIN SISTER OF FT (TSF), and found that overexpression of TSF promoted early flowering in plants. Both TSF and FT are similarly regulated by other factors such as Calcium And Integratin Binding 1 (CLB1) and SHORT VEGATIVE PHASE (SVP)[36]. In addition to the aforementioned regulatory factors, some transcription factors of the Related to ABI3/VP1 (RAV) family, such as the APETALA2 (AP2) transcription factor genes *TEMPOILLO 1* (*TEM1*), *TEMPOILLO 2* (*TEM2*), *TARGET OF EAT1* (*TOE1*), *TARGET OF EAT2* (*TOE2*), *SCHNARCHZAPFEN* (*SNZ*) and *SCHLAFMUTZE* (*SMZ*) harboring miR172 binding sites, can also affect the expression of gene FT[54]. Overexpression of any of these four genes can delay flowering, and *TEM1* and *SMZ* can directly inhibit the expression of gene *FT*[55].

In cruciferous vegetables such as *A. thaliana*, Chinese cabbage and radish, the genes regulating bolting and flowering are usually homologous[42]. *Brassica* and radish crops have experienced genome triplication during evolution, and there are multiple copies homologous to *A. thaliana* genes[56]. Xiao *et al.* [57] confirmed that genome triplication is not a random process, but that specific genes are preferentially reserved, and among them, gene *FT* is preferentially reserved in the rape genome to regulate its flowering time. However, the research on specific regulatory mechanisms is not yet in-depth enough. Vollrath *et al.* [58] identified QTL loci for generalized genetic bolting and flowering, which are located in the A02 and C02 intervals. Through sequencing analysis, it was found that there was a 288 bp deletion on the *FT* gene *Bna FT. A02*, which may be related to the flowering period of rape. The *BnaFTA02* gene did not need to be affected by low temperature when regulating flowering time, but had a certain dependence on the length of sunlight.

Vernalization signals and photoperiodic signals can both affect the expression of LFY. The transcription factors encoded by LFY play an important role in the development of leaves and flowers[59], and their activity is regulated by the complex regulation of BLADE-ON-PETILE BOPs and Cullin3-RING ubiquitin ligase (CRL3)[60]. The expression of LFY is also regulated by gibberellins, and GA-dependent flowering can be explained by the roles of two key genes, *LFY* and *SOC1*[20]. Moreover, key factors in the age pathway, miR156 and SQUAMOSA PROMOTER BINDING PROTEIN-LIKE (SPLs), can also activate the *LFY* gene[52]. The MADS-box transcription factor family is the main regulatory factor controlling flower transformation in *A. thaliana*, and they are involved in the development of flower organs[61]. *SOC1* and *AGAMOUS-LIKE 24* (*AGL24*) belong to the MADS-box family genes, and their interaction directly regulates the expression of LFY, thereby determining the flowering time of bolting[62-63] (Fig. 1). Furthermore, Nie *et al.* [64] also identified other MADS family members, such as AGAMOUS-LIKE (AGL), APETALA1 (AP1), AP2, SVP, and FLOWERING LOCUS M (FLM), which may be involved in the development and flowering regulation of radish.

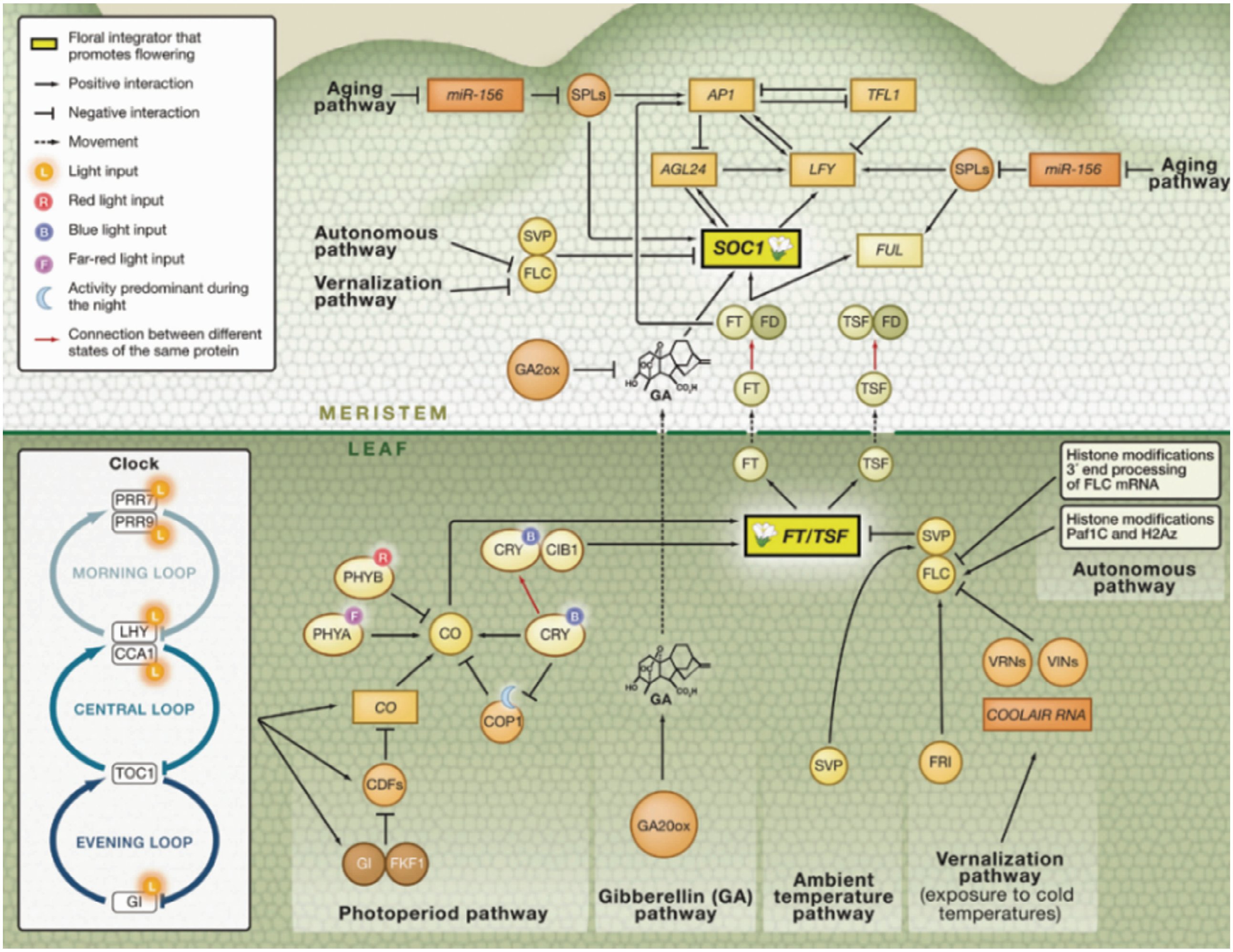

Fig. 1 Main regulatory pathways for bolting and flowering

Development of Molecular Markers for Bolting Tolerance in Cruciferous Vegetables

Late bolting is an important breeding goal for root vegetables, stem vegetables and leafy vegetables[65]. In recent years, with the development of biotechnology, molecular markers have become increasingly mature and play an important role in field variety identification, precise gene localization, and genetic diversity assessment of vegetable crops.

The continuous upgrading and improvement of molecular marker technology has brought strong impetus to the study of bolting traits in cruciferous vegetables. At present, the main focus is on the development of bolting tolerance markers for Brassica vegetables such as *Brassica oleracea* var. *capitata* Linnaeus and Chinese cabbage, and research on radish markers has also made progress. Zhang[13] selected a pair of markers closely linked to late bolting genes from 182 pairs of simple sequence repeat (SSR) primers, with a genetic distance of 5.7 cM. Rao *et al.*[66] found a pair of SSR dominant markers in 62 pairs of SSR primers that have a certain linkage relationship with the bolting trait of Chinese cabbage, and the genetic linkage distance between this marker and the early bolting gene was 7.2 cM. At present, the development of molecular markers for bolting tolerance in Chinese cabbage is mostly based on phenotypic traits, but the bolting phenotype is easily influenced by environmental factors, subjective intentions, etc., and a unified identification standard has not yet been formed. Zhang *et al.*[67] conducted genotyping, field phenotype and artificial vernalization indoor phenotype identification using single nucleotide polymorphism (SNP) markers on 32 core germplasm resources of Chinese cabbage. They found that the genotype identification results were highly consistent with the phenotype identification results of other two methods, and it could be used for auxiliary screening and evaluation of new varieties of Chinese cabbage that are resistant to bolting to improve the accuracy of phenotype identification results at the genetic level.

Cao *et al.* developed a randomly amplified polymorphic DNA (RAPD) marker named N1-750 with a linkage distance of 7.9 cM in the study of molecular markers for bolting tolerance in *B. oleracea* var. *capitata* Linnaeus. However, the application of RAPD markers has complexity and randomness. Wu *et al.*[68] transformed the obtained RAPD markers linked to late bolting genes in *Brassica* *oleracea* L. var. *capitata* L. into more effective sequence characterized amplified region (SCAR) markers, named SCAN1. However, when specific fragments that control bolting traits mutate, SCAR markers are no longer applicable. To improve the shortcomings of SCAR markers, Li *et al.*[69] successfully transformed the SCAR marker SCN1/248 into an cleaved amplified polymorphic sequence (CAPS) marker, further enhancing the accuracy of molecular marker-assisted selection. Zhao[70] screened six RAPD markers associated with radish bolting tolerance genes, one sequence-related amplified polymorphism (SRAP) marker and one simple sequence repeat (ISSR) marker. Liu *et al.*[71] used population segregation analysis to screen SRAP markers closely linked to radish bolting tolerance genes in 288 pairs of primer combinations, with a genetic distance of 5.7 cM between genes. Xu *et al.*[72] applied amplified fragment length polymorphism (AFLP) molecular marker technique to develop two markers linked to radish bolting tolerance genes, ACT-CTG, with a genetic distance of 9.1 cM; and the genetic distance of ACG-CAG was 14.6 cM, and the former was transformed into an SCAR marker with a genetic distance of 7.5 cM. Due to the genetic diversity of different populations, currently-developed molecular markers do not have universality. Therefore, when applying these markers to agricultural production, further specific screening and validation are required.

Prospects

The study on material changes during the bolting process and the exploration of the bolting mechanism in cruciferous vegetables are related to vegetable breeding and the development of the vegetable industry. Thoroughly studying the molecular mechanisms of plant growth and development is of great significance for improving the stress resistance of vegetables and guiding breeding for bolting tolerance. However, there is currently relatively little quantitative research on the physiological and biochemical indicators of bolting tolerance in cruciferous plants, and the exploration of growth and development mechanisms is still limited, which may lead to the situation that bred bolting-tolerant varieties are greatly affected by climate and environment and their stability is insufficient.

There are many varieties in the family of cruciferous plants, but the coverage of studied varieties is relatively low, and more extensive investigation of species and varieties is needed to gain a more comprehensive understanding of cruciferous plants. Furthermore, it is also a challenge to successfully apply research results to actual breeding. The advent of the gene era is pushing breeding towards a more scientific direction. It is necessary to make full use of the frontier progress of molecular marker technology to accelerate the breeding of varieties and comprehensively improve the breeding of bolting-resistant cruciferous vegetables, so as to adapt to the needs of modern agriculture.

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