



## Review

# Advancements in Molecular Mechanism Research on Bolting Traits in Vegetable Crops

Guo-Fei Tan <sup>1,2</sup>, Qing Luo <sup>1,2,3</sup>, Shun-Hua Zhu <sup>1,2</sup>, Xiu-Lai Zhong <sup>1,2</sup>, Ping-Hong Meng <sup>1</sup>, Meng-Yao Li <sup>4</sup> , Zhi-Feng Chen <sup>5,\*</sup> and Ai-Sheng Xiong <sup>3,\*</sup>

<sup>1</sup> Institute of Horticulture, Guizhou Academy of Agricultural Sciences/Guizhou Horticultural Engineering Technology Research Center, Guiyang 550006, China; tgfei@foxmail.com (G.-F.T.); lqing985@foxmail.com (Q.L.); zsh2801@163.com (S.-H.Z.); gzzyzxl@foxmail.com (X.-L.Z.); mengph322@163.com (P.-H.M.)

<sup>2</sup> Key Laboratory of Crop Gene Resources and Germplasm Innovation in Karst Mountain Area of Agriculture and Rural Ministry, Guiyang 550006, China

<sup>3</sup> State Key Laboratory of Crop Genetics & Germplasm Enhancement and Utilization, Ministry of Agriculture and Rural Affairs Key Laboratory of Biology and Germplasm Enhancement of Horticultural Crops in East China, College of Horticulture, Nanjing Agricultural University, Nanjing 210095, China

<sup>4</sup> College of Horticulture, Sichuan Agricultural University, Chengdu 611130, China; limy@sicau.edu.cn

<sup>5</sup> College of Biology and Agricultural Technology, Zunyi Normal College, Zunyi 563006, China

\* Correspondence: czf810@163.com (Z.-F.C.); xiongaisheng@njau.edu.cn (A.-S.X.)

**Abstract:** Bolting and flowering of vegetables are induced by vernalization in their early growth stage. This phenomenon is called premature bolting, and it has caused massive losses in production of vegetables such as cabbage, celery, carrot, radish, and spinach, etc. This review aimed to summarize studies on bolting and flowering pathways, physiological and biochemical changes, and underlined molecular mechanisms of various vegetable crop bolting involving genome and transcriptome analysis, and its association with vegetable breeding. This review could provide basic knowledge to carry out research on vegetable genetics and breeding and vegetable cultivation.

**Keywords:** vegetable crops; bolting and flowering; physiological and biochemical; molecular mechanism; vernalization



**Citation:** Tan, G.-F.; Luo, Q.; Zhu, S.-H.; Zhong, X.-L.; Meng, P.-H.; Li, M.-Y.; Chen, Z.-F.; Xiong, A.-S. Advancements in Molecular Mechanism Research on Bolting Traits in Vegetable Crops. *Horticulturae* **2024**, *10*, 670. <https://doi.org/10.3390/horticulturae10070670>

Academic Editor: Costas Delis

Received: 7 May 2024

Revised: 14 June 2024

Accepted: 21 June 2024

Published: 25 June 2024



**Copyright:** © 2024 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (<https://creativecommons.org/licenses/by/4.0/>).

## 1. Introduction

The flowering transition from vegetative to reproductive growth and the formation of floral organs in higher plants plays a central role in the development, reproduction, and evolution of plant species [1]. Many vegetable crops require low-temperature vernalization to produce flowers in the early growth stage, leading to flower bud differentiation and bolting [2]. Vegetable crops undergo bolting bloom before a knotting/non-knotting ball or fleshy root/stems are formed; this process is known as early or immature bolting [3]. It affects the yield and quality of the harvested products of vegetable crops, making it an important issue for breeders, researchers, and growers to address. They must study the early and late bolting of different plants according to the different needs of various vegetable crops [4].

Vegetable crops are widely cultivated in China and other countries due to their diverse types, high nutritional value, and strong adaptability. Although extensive research has been conducted on the bolting of vegetable crops worldwide, the most common subjects are leafy vegetables, including cabbage (*Brassica oleracea* L.) [5,6], turnip (*Brassica rapa* L.) [7], Chinese cabbage (*Brassica campestris* L.) [8], mustard (*Brassica juncea* L.) [9], celery (*Apium graveolens* L.) [10–13], lettuce (*Lactuca sativa* L.) [14], and spinach (*Spinacia oleracea* L.) [15]; succulent root vegetables such as carrot (*Daucus carota* L.) [16–20] and radish (*Raphanus sativus* L.) [21]; vegetable liverworts such as *B. rapa* var. *chinensis* ‘Parachinensis’ [22]; and

bulbous vegetables such as onion (*Allium cepa* L.) [23] and garlic (*Allium sativum* L.) [24] (Figure 1a).

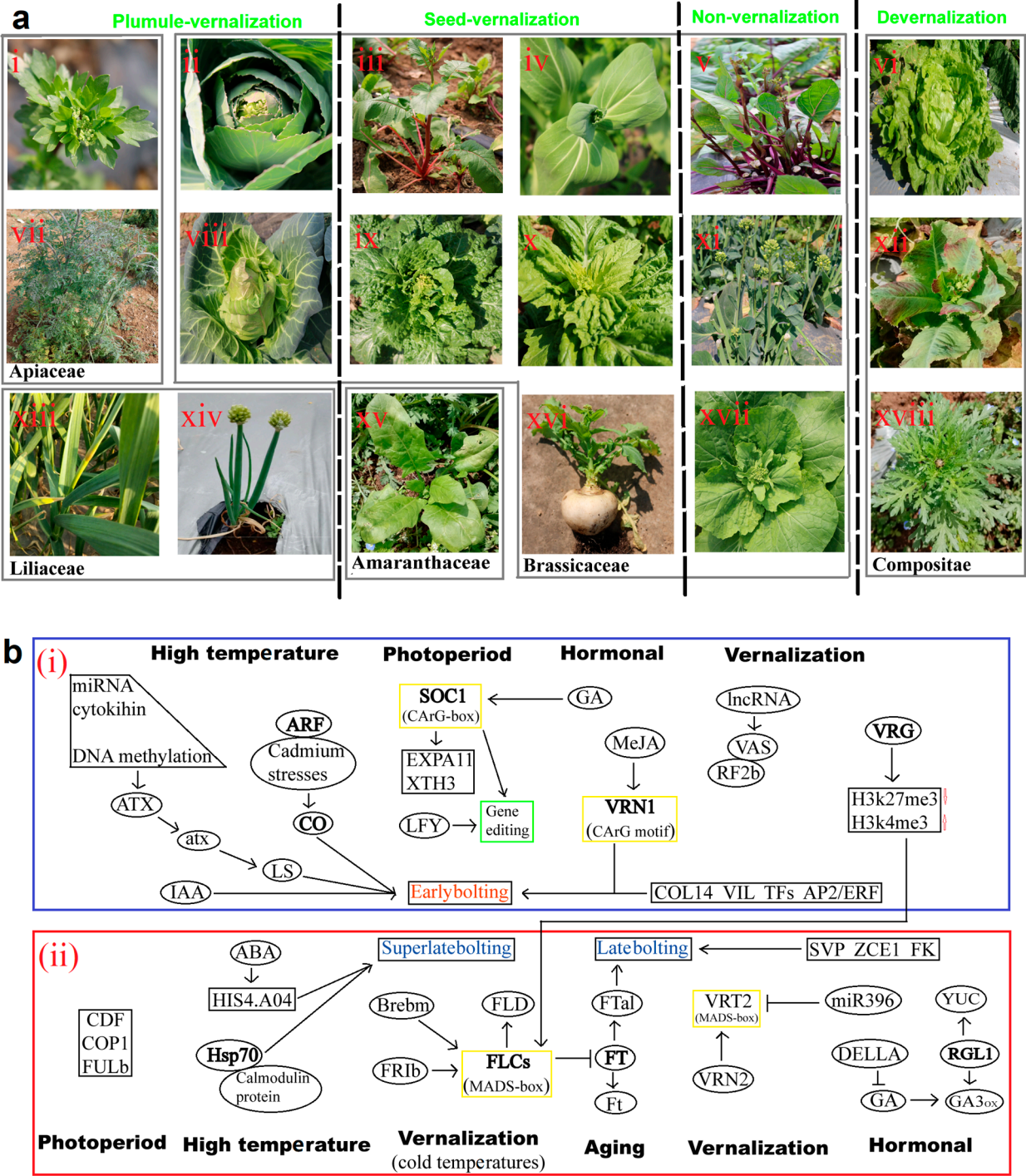


**Figure 1. Regulatory mechanism of bolting traits in different vegetable crops.** (a) Preconditions in bolting of various vegetable crops. (i): celery; (ii): cabbage; (iii): radish; (iv): choy sum; (v): red liverwort; (vi): lettuce; (vii): carrot; (viii): cauliflower; (ix): Chinese cabbage; (x): mustard; (xi): liverwort; (xii): asparagus lettuce; (xiii): garlic; (xiv): scallion; (xv): spinach; (xvi): turnip; (xvii): pakchoi; (xviii): garland chrysanthemum; (b) Regulatory genes. (i): promoting regulatory factors; (ii): inhibiting regulator factors. Gray frame: crops of different families; black dotted line: different vernalization; yellow frame: floral integrator that promotes flowering; green frame: gene editing; red

frame: positive regulation factors; blue frame: negative regulation factors; →: positive interaction; red arrows: increase or decrease of expression; ⇌: negative interaction. ATX: *Arabidopsis trithorax*; LS: leaf senescence; IAA: indoleacetic acid; ARF: auxin response factor; CO: CONSTANS; SOC1: suppressor of overexpression of constans 1; LFY: leafy; GA: gibberellin; MeJA: methyl jasmonate; VIN1: vernalization insensitive 1; lncRNA: long noncoding RNA; VAS: *VRN1* alter native splicing; VRN1: VERNALIZATION1; VRG: vernalization-related gene; ABA: abscisic acid; CDF: cycling dof factor; COP1: constitutive photomorphogenesis 1; FLD: FLOWERIG LOCUS D; FLC: FLOWERIG LOCUS C; FT: flowering locus T; Ft: floweringtime; VRT2: vegetative to reproductive transition 2; SVP: short vegetative phase; ZCE1: cis-CA (zusammen-CA)-enhanced 1; FK: FACKELL; VRN2: vernalization 2; COL14: CONSTANS-like 14; TFs: transcription factors; VIL: VIN3-like (VIN3: vernalization-insensitive 3); Brebm: early-bolting mutant in Chinese cabbage; FRILb: FRIGIDAb; miR396: microRNA396; HSP: heat shock protein; FTal: FT orthologue; RGL1: RGA-LIKE1; GA3ox: GA3-oxidase.

To date, information obtained from germplasm resources through physiological and molecular research on various vegetable crops is limited. This review aims to summarize studies on environmental factors, physiological and biochemical changes, breeding, and molecular mechanisms in commonly used vegetable crops. We sincerely hope that this review can provide useful theoretical and practical information to assist research on bolting.

## 2. Bolting and Flowering Factors

### 2.1. Preconditions

During the transition from the vegetative growth stage to the reproductive growth stage, plants must go through a period of continuous low temperature, known as vernalization. This is a crucial process for the formation of flower organs and the regulation of flowering. The preconditions for bolting include seed vernalization [10,25–27], plumule vernalization [28–30], devernization [31,32], vernalization [1,2,33], and non-vernalization [34]. Liliaceae crops, such as garlic and scallion, and Apiaceae crops, such as carrot and celery, undergo plumule vernalization. Amaranthaceae crops, including spinach, and Brassicaceae crops, such as radish, Chinese cabbage, choy sum (*B. campestris* L. ssp. *chinensis* var. *utilis* Tsen et Lee), turnip, and mustard, primarily undergo seed vernalization. In contrast, crops like red liverwort, liverwort, and pakchoi exhibit non-vernalization [6]. Compositae crops, including asparagus lettuce, garland chrysanthemum, and lettuce, undergo devernization (Figure 1a).

### 2.2. Bolting and Flowering Pathways

Bolting, defined as stem elongation, is a prerequisite for flowering. Changes in environmental conditions, such as vernalization temperature and light, can lead to immature bolting in many vegetable crops, which reduces productivity and commercial value [8,35,36]. To understand the molecular mechanisms underlying floral transition, extensive research has been conducted on model plants [37]. This research has identified six flowering regulatory pathways mediated by photoreceptor-mediated environmental signaling in *Arabidopsis thaliana*: vernalization [1,38], photoperiodic [1,39,40], temperature [24], gibberellins (GAs) [14], autonomous [41], and age pathway [42] (Figure 1b).

### 2.3. Vernalization and Devernization Pathway

A low temperature promotes flower bud differentiation and flowering in vegetables such as celery [10], carrot [16,43], garlic [24], and wild lettuce (*Lactuca georgica*) [44]. Michael et al. [45] proposed that favorable temperatures could replace the photoperiod requirements for garlic, facilitating meristem transition, flowering, and bulbing under suboptimal photoperiod conditions. Suitable temperatures are another key factor inducing bolting and flowering in vegetable crops. High temperatures can induce early bolting, affecting both quality and production in crops like lettuce [44] and garlic [46].

Photoperiod pathway: Premature bolting in long-day plants such as Chinese cabbage [47], carrot [43,47], celery [48], and garlic [49] can be induced by extended light periods. Longer light durations are particularly beneficial for bolting in spinach and garlic [49].

Gibberellin (GA) pathway: GAs play a significant role in bolting regulation. In lettuce, for example, the expression of *BcSOC1* is significantly upregulated under exogenous GA3 and low-temperature treatments, leading to early bolting and flowering in Chinese cabbage [50,51].

Other factors: The sowing time of some vegetable crops can influence the bolting time and rate. Earlier sowing times lead to older plant leaves and higher bolting rates, as observed in carrots [44]. Mero and Honma [52] found a correlation between the number of true leaves and the bolting rate in kale.

### 3. Physiological and Biochemical Changes before and after Bolting

Many researchers have studied the physiological and biochemical changes before and after bud formation and bolting in plants, focusing on aspects such as carbohydrates, soluble proteins, endogenous hormones, and enzyme activity to theoretically explain the bolting mechanism [53,54].

#### 3.1. Carbohydrates

The carbohydrate mechanism in stem tips is closely related to vernalization and flower bud differentiation. High sugar levels in vernalized vegetable crops may accelerate flower initiation and development. In radish [55] and lettuce [14], the total soluble sugar content increases during the initial stages of floral bud differentiation before decreasing. Many researchers have identified a high sugar/carbohydrate ratio as a major determinant of the flowering process, as confirmed in studies on pakchoi [56]. Dai et al. [57] revealed that early bolting and faster flowering were caused by polysaccharide and sugar/carbohydrate metabolism.

#### 3.2. Soluble Proteins

Studies have found that low total nitrogen content and high soluble protein content in vegetable crops, such as radish [54], facilitate vernalization, which is crucial for the transition to the reproductive phase. Han et al. [14] identified 30 differentially accumulated proteins using proteomic analysis of bolting-resistant and bolting-sensitive lettuce lines. Wang et al. [58] demonstrated that soluble protein (S-Pr) plays an important role after the squaring stage in cabbage.

#### 3.3. Endogenous Hormones

The relationship between endogenous hormones and bolting has been extensively studied, suggesting that these physiological characteristics are highly associated with bolting in various vegetable crops [59,60]. Early-bolting cultivars maintain higher levels of cytokinin (CTK) and polyamines compared to late-bolting ones in spring Chinese cabbage [61]. Li et al. [59] found that GA content in shoot apical tissues increases in non-heading Chinese cabbage. Bolting in garlic is highly related to methyl jasmonate (MeJA) and endogenous phytohormones, particularly GAs [62]. Han et al. [14] found that chlorophyll, anthocyanin, and auxin levels were lower in a bolting lettuce line. High IAA content in the stem and GA content in the leaves promotes bolting in lettuce [63]. Higher ratios of GA4/ZR (Ribosylzeatin) and IAA/ZR lead to early bolting, whereas a high IAA content and low GA3 content play positive roles in early bolting of carrots [64]. Dai et al. [57] revealed that ABA, ethylene, and chitin-activated signaling pathways are enriched in late-bolting Chinese cabbage.

### 3.4. Enzyme Activity

Flower bud differentiation is accompanied by changes in enzyme activities in vegetable crops [65], such as SOD (superoxide dismutase) [66] and POD (peroxidase) [65]. Wang et al. [58] found that several indicators are important in bolting after vernalization, such as APX (ascorbate peroxidase) during the squaring stage, MDA after the squaring stage, and G-POD (guaiacol peroxidase) two weeks before the squaring stage in different cabbage genotypes.

### 3.5. Other Factors

DNA methylation/hypermethylation is critical to vernalization-induced flowering and provides a developmental control mechanism that prevents early flowering [38,59,67]. Yang et al. [68] reported that floral primordium initiation and development is caused by vernalization-induced hypermethylation. He et al. [69] found that partial hyper-acetylation of histones in *FLC* (*FLOWERING LOCUS C*) chromatin caused by lesions in *FLD* (*FLOWERING LOCUS D*) leads to extremely delayed flowering due to upregulation of *FLC* expression in the autonomous pathway in *Arabidopsis*.

## 4. Molecular Mechanism of Bolting

### 4.1. Molecular Markers

Researchers have analyzed the association between the flowering time of candidate loci using various molecular markers such as SSR (simple sequence repeat), RAPD (random amplified polymorphic DNA), SCAP (sequence-characterized amplified polymorphism), In-DEL (insertion/deletion), AFLP (amplified fragment length polymorphism), SCAR (sequence-characterized amplified regions), SNPs (single-nucleotide polymorphisms) [70,71], CAPS (cleaved amplified polymorphic sequence), and KASP (Kompetitive allele-specific PCR) [72]. They found that one or more flowering-related genes could be candidates in different vegetable crops [9,73], such as cabbage [5,74], Chinese cabbage [75], and radish [76]. VR-DE01 and VR-FT01 were detected on the top of A02 and were closely linked with *BrFLC2* in *B. rapa* [77]. Rosenta et al. [36] identified the environment-specific *LsFT* gene. Gan et al. [78] constructed a high-density genetic linkage map and detected five genes (*Rsa10025681*, *Rsa10025809*, *Rsa10025935*, *Rsa10035523* and *Rsa10025740*) with sequence variation between parental lines related to flowering and bolting. However, the detailed functions of these candidate genes during bolting and flowering of radish require further research. Some markers have been subjected to marker-assisted selection of flowering time in breeding *B. rapa*, such as *BrFLC1* [79] and *BrFLC5* [80]. Wang et al. [81] detected two QTLs in cabbage, located on chromosome C02 at 2.31–3.09 Mb and 33.57–34.40 Mb, respectively, with a total length of 1.61 Mb. In the study by Meng et al. [82], a major *qBT1.1*, was mapped on chromosome 1 in spinach and narrowed down to 0.56 Mb using KASP markers. Within this region, *SpCOL14* (*CONSTANS-LIKE*), a candidate gene for bolting, has multiple variations in the promoter.

### 4.2. Mining and Expression of Regulatory Genes

Many researchers have studied the molecular basis of vernalization and discovered that many genes, such as *CO* (*CONSTANS*) [9], *FLD* [69], *FLF* (*FLOWERING LOCUS F*) [83], *FLC* [84,85], *FRI* (*FRIGIDA*) [86], and *VRN* (vernalization) [87,88], regulate plant flowering [89–92]. Other genes related to bolting resistance have been gradually discovered and mined with the deepening of research on various vegetable crops (Table 1). Gu et al. [93] showed that the effects of the genome on bolting and budding were more than those from *BrFLCs*, while the background of the cabbage genome influenced the additional cabbage chromosome 4 on *BrFLC* expression. Han et al. [14] found that 12 flowering-promoting MADS-box genes were specifically induced in bolting-sensitive lines through GA treatment, suggesting that the *MADS-box* genes are responsible for bolting regulation in lettuce. Large families of regulators that comprise MADS-domain-containing transcription factors play diverse roles in plant development, including regulating flowering time (Figure 1b). The

expression of genes decreases/increases upon cold exposure, causing floral induction, which inhibits/promotes bolting and flowering. *FLC* is a key vernalization response gene but also a floral repressor. DELLA proteins negatively regulate the GA signaling pathway. H4 acetylation (a common regulator) connects drought and flowering regulation. SVP encodes an MADS-box gene family of transcription factors that repress floral transition. The AP2/ERF (APETALA2/ethylene-responsive element binding factors) gene super family demonstrates potential roles in plant flower development regulation and flower tissue formation [94–96].

**Table 1.** Expression and functional characteristics of gene and regulatory factors.

| Families     | Species                             | Gene                                                  | Characteristic of Genes, Expression, and Regulation                                                                                                                                                              | References |
|--------------|-------------------------------------|-------------------------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|------------|
| Brassicaceae | <i>Cabbage (B. oleracea L.)</i>     | <i>BoFLC2</i>                                         | Negative regulation                                                                                                                                                                                              | [97,98]    |
|              |                                     | <i>BoVIN3</i>                                         | Stems; gene length was 1680 bp; amino acid was 560 aa; isoelectric point was 6.56                                                                                                                                | [99]       |
|              |                                     | <i>BoFLC(1,2,3)</i>                                   | Conserved with the MADS-box domain                                                                                                                                                                               | [42]       |
|              |                                     | <i>AGL18, HDA9</i>                                    | Gene length was 777 and 1281 bp, conserved region was MIKC/HDAC; amino acids were 258 and 426 aa; negative regulation                                                                                            | [100]      |
|              |                                     | <i>AGL19, SOC1, AGL24</i>                             | Amino acids were 221, 221, and 214 bp, conserved region was MIKC; AGL19 and SOC1 were SOC1/TM3 subfamily; positive regulation                                                                                    | [101,102]  |
|              | <i>Chinese cabbage (B. rapa L.)</i> | <i>BrFLC5</i>                                         | Weak positive regulator                                                                                                                                                                                          | [103]      |
|              |                                     | <i>BrFLC2</i>                                         | A candidate gene for a vernalization                                                                                                                                                                             | [99]       |
|              |                                     | <i>BrFLC, BrMAF, BrVIP, BrVRN</i>                     | Negative regulation, response to vernalization; <i>BrVRN</i> and <i>BrVIP</i> genes showed different expression patterns                                                                                         | [33]       |
|              |                                     | <i>BrHIS4.A04</i>                                     | A histone H4 gene; prevents premature bolting by weakening the expression of flowering genes under drought conditions through the ABA signaling pathway                                                          | [104]      |
|              |                                     | <i>BrEb-1</i>                                         | Positive regulation; an incomplete dominant gene, mapped from 20,070,000 to 25,290,000 bp (5.22 Mb) and harbored on chromosome A07                                                                               | [105]      |
|              |                                     | <i>BrPIF4, BrPIF5, BrFLCs, BrFRL, BrMAF1s, BrCOLs</i> | <i>BrPIF4</i> , <i>BrPIF5</i> , and <i>BrCOLs</i> were predominantly expressed in core tissues, promoting bolting, <i>BrFLCs</i> , <i>BrFRL</i> , and <i>BrMAF1s</i> were predominantly expressed in core tissue | [106]      |
|              |                                     | <i>BrSVP</i>                                          | Negative regulation; repressed the expression of the floral integrator genes <i>AGL20</i> , <i>AGL24</i> , and <i>FT</i> during vernalization                                                                    | [107]      |
|              | <i>B. rapa ssp. pekinensis</i>      | <i>BrpFLC</i>                                         | Negative regulation; gene length was 851 bp and contained a 591 bp ORF; amino acid length was 197 aa; conserved region was MADS-box; belongs to a multi-gene family                                              | [108]      |
|              | <i>B. campestris ssp. chinensis</i> | <i>BcFLC-1, BcFLC-2, BcFLC3</i>                       | Negative regulation, responded to low-temperature vernalization in leaves; gene length was 1017 bp; conserved region was MADS-box; amino acid length was 197 aa; isoelectric point was 9.36; multi-copy          | [109,110]  |

Table 1. Cont.

| Families                       | Species         | Gene                                                                    | Characteristic of Genes, Expression, and Regulation                                                                                                                                                  | References |
|--------------------------------|-----------------|-------------------------------------------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|------------|
|                                | Chinese cabbage | <i>BcSOC1</i>                                                           | Positive regulation; promoted stem elongation and bolting in flowering Chinese cabbage                                                                                                               | [51]       |
|                                |                 | <i>DELLA</i>                                                            | Negative regulation of GA signal transduction; its proteins contained VHYNP-, DELLA-, SAW-, and VHIID-conserved domains; tissue-specific expression                                                  | [111]      |
| Radish ( <i>R. Sativus</i> L.) |                 | <i>BrcuFRI</i> , <i>BrcuFLC</i>                                         | <i>BrcuFRI</i> in stems and leaves, while <i>BrcuFLC</i> in roots; Gen Bank accession number was EU700362/EF138603                                                                                   | [86]       |
|                                |                 | <i>RsFLC</i> , <i>RsSOC1</i>                                            | <i>RsFLC</i> was <i>Ft</i> genes; negative regulation; <i>RsSOC1</i> positive negative                                                                                                               | [112]      |
|                                |                 | <i>RsFLC2</i>                                                           | A late-bolting gene was detected in a 1.1 cM on chromosome R02; contains a 1627 bp insertion; weakened gene repression                                                                               | [113]      |
|                                |                 | <i>FLC1.1</i> , <i>FLC1.2</i> , <i>VRN1</i> , <i>VRN2</i> , <i>SOC1</i> | <i>FLC1.1</i> and <i>FLC1.2</i> induced positive regulation while <i>VRN1</i> , <i>VRN2</i> , and <i>SOC1</i> induced negative regulation                                                            | [54]       |
| Carrot ( <i>D. carota</i> L.)  |                 | <i>DcFLC1</i> , <i>DcFLC2</i> , <i>DcFLC3</i>                           | <i>DcFLC1</i> and <i>DcFLC3</i> responded to low temperature in late bolting while <i>DcFLC2</i> responded to light; amino acid length was 209, 212, and 219 aa; conserved region was MADS-box/K-box | [114]      |
|                                |                 | <i>Vrn1</i> , <i>Rf1</i>                                                | Early-flowering gene, mapped to chromosomes 2 and 9 with flanking markers from 0.70 to 4.38 cM and 0.46 to 1.12 cM                                                                                   | [115]      |
|                                |                 | <i>DcSOC1-1</i> , <i>DcSOC1-2</i>                                       | <i>DcSOC1-1</i> promoted by long day early-bolting; amino acids were 217 and 211 aa, conserved region was MADS-box/K-box, sub cellular location was SOC1/TM3 subfamily                               | [116]      |
| Lettuce ( <i>L. sativa</i> L.) |                 | <i>LsARF3</i>                                                           | Response to high temperature; activate the expression of <i>LsCO</i>                                                                                                                                 | [117]      |
|                                |                 | <i>LsARF8a</i>                                                          | 24 <i>LsARFs</i> in the lettuce genome; have been classified into three clusters; respond to heat                                                                                                    | [118]      |
|                                |                 | <i>LsRGL1</i>                                                           | One of the DELLA-encoding genes; negatively regulates the GA pathway; interacts with <i>LsGA3ox</i> and the <i>LsYUC4</i> promoter region                                                            | [50]       |
|                                |                 | <i>LsFT</i>                                                             | Over expression of it recovered the late-flowering phenotype of <i>ft-2</i> mutant and it was promoted by heat treatment; knockdown of it by RNA interference dramatically delayed bolting           | [119]      |

FLC: FLOWERIG LOCUS C; VIN: vernalization insensitive; AGL: agamous-like; HAD 9: histone deacetylase 9; SOC1: suppressor of overexpression on constans 1; MAF1: MADS AFFECTING FLOWERING1; VIP: VERNALIZATION INDEPENDENCE; VRN: VERNALIZATION; PIF: PHYTOCHROME-INTERACTINGFACTOR; FRL: FRIGIDA-LIKE; SVP: short vegetative phase; FRI: FRIGIDA; COL1: CONSTANS-like 1; CLF: curly leaf; VRT-2: vegetative transition gene 2; ARF: auxin response factor; RGL1: RGA-LIKE1; FT: FLOWERING LOCUS T.

#### 4.3. Protein and Protein Interaction Regulation

Interactions between proteins such as SVP, FLC, SOC, and AGL are crucial in flowering regulation. In *B. juncea*, specific amino acid sites regulate these interactions. For example, HDA9 regulates flowering signal integrators SOC1 and AGL24, while DELLA proteins interact with BcGID1b, affecting GA signal transduction in Chinese cabbage. Heat shock proteins and calmodulin interactions under high temperatures also influence GA levels and bolting in lettuce.

### 5. Genome and Transcriptome Analysis

#### 5.1. Genome and Transcriptome

Genome-wide and transcriptome analyses have identified numerous genes related to bolting and flowering across various crops. For example, radish transcriptome profiling revealed genes involved in vernalization, and candidate genes for bolting in Chinese cabbage have been isolated. DNA methylation and miRNAs play roles in controlling gene expression during bolting, as seen in high-temperature-induced bolting in lettuce.

#### 5.2. RNA (miRNAs/lncRNAs/circRNAs/ceRNA)

miRNAs, lncRNAs, and circRNAs are involved in the regulation of flowering time and bolting. For instance, differential expression of transcription factors in lettuce and miRNA-DEG pairs in radish are significant. ceRNA networks reveal interactions between various RNA molecules and vernalization-related genes, indicating complex regulatory mechanisms.

#### 5.3. Functional Verification and Genetic Transformation

Functional studies of genes like *BrFLC1* and *BrFLC3* in *Brassica* crops have shown delayed bolting times in transgenic plants. Such studies enhance the understanding of bolting mechanisms and contribute to breeding strategies for improved bolting resistance.

### 6. Identification of Bolting and Breeding

#### 6.1. Investigating Epigenetics

Epigenetic modifications such as DNA methylation and histone modifications regulate gene transcription related to bolting and adaptation to environmental stresses. These modifications play a role in vernalization and flowering in *Brassica* vegetables [120–122].

#### 6.2. Identification of the Bolting Properties

To identify bolting properties, methods like principal component analysis (PCA) and subordinate function analysis have been used [68]. These methods evaluate the tolerance to bolting in radish and other crops, helping to select germplasms with desired bolting resistance [123,124]. Zhang et al. [125] divided 64 germplasms into three groups using the membership function method and screened 40 germplasms with moderate bolting tolerance.

#### 6.3. Heritability and Hereditary Effects

Bolting traits in crops are influenced by major genes and polygenes, with significant environmental variance. Genetic analyses reveal additive–dominant–epistatic effects in crops like Chinese cabbage and cabbage, aiding in the selection of bolting tolerance in early generations [105,126–128]. Two major genes expressed in the mode of additive–dominant–epistatic (D-2) effects mainly controlled the bolting trait, and the additive effects of the two major genes were similar in Chinese cabbage [105,126–128], cabbage [51,129], pakchoi [130], and carrot [16,20]. However, the environmental variance was high in total variance, so selecting for bolting tolerance was in its early stages [130]. The average heritability of major genes and polygenes was 93.41% in cabbage [51]. Ji et al., [127] indicated that in *B. rapa*, one or two major genes controlled the bolting trait. Genetic analysis revealed that in Chinese cabbage, an incomplete dominant gene *BrLb-1* controlled the late-bolting to early-bolting trait [106].

#### 6.4. Breeding Methods

Breeding methods, including crossbreeding and mutation breeding, are essential for developing new plant species and varieties that meet specific needs, such as delayed bolting.

Crossbreeding: Gu et al. [94] obtained cabbage plants with different chromosome counts ( $2n = 21$  and  $2n = 20$ ) through cross combinations. Plants with  $2n = 21$  chromosomes bolted later than those with  $2n = 20$  from the same hybridized combination. Motoki et al. [131] explored whether transmissible agents from rootstocks could induce flowering in cabbage without low-temperature treatment. They concluded that the pathway to vernalization in these plants is independent of cabbage *BoFT* and *BoFT* expression from the scion.

Mutation breeding: Ipek et al. [132] discovered a 1403 bp mitochondrial DNA marker associated with bolting in garlic, speculating that it resulted from an insertion mutation during garlic's evolution. Li et al. [133] developed a new cultivar of non-heading Chinese cabbage named Yanchun using space mutation combined with traditional breeding methods. Wang et al. [114] identified an *RsFLC2* gene with a 1627 bp insertion near its first intron, linked to latebolting in radish. Liu et al. [124] demonstrated that a 1628 bp insertion in the *FLC2* gene's first intron in radish significantly impacted late bolting, with homozygous mutations having a more pronounced effect than heterozygous ones. Abuyusuf et al. [134] used the InDel method to design molecular markers (*BolPrx.2*) to characterize bolting time variations in cabbage, predicting about 84% of the variation within commercial and population lines. Fu et al. [135] found an early-bolting mutant in Chinese cabbage caused by a single-nucleotide C-to-T substitution in the *BrFLC2* gene, controlled by a recessive nuclear gene. Li et al. [136] identified a 215 bp deletion in the *BoFLC2* gene intron I, which slowed its silencing activity, leading to late flowering in cabbage. Tang et al. [137] noted that the 9325 bp loss of the *BoFLC* gene caused a non-vernalization requirement, leading to the development of its codominant marker for breeding *B. oleracea* crops.

Gene editing: Shin et al. [138] used CRISPR/Cas9 to edit *AGL19* and *AGL24* genes in Chinese cabbage, resulting in late-bolting T-DNA free lines. Shin and Park [139] edited the *BrLEAFY* (*BrLFY*) gene using CRISPR/Cas9, producing T-DNA-free *E1 LFY*-edited lines that showed continuous vegetative growth and late bolting. Choi et al. [140] conducted CRISPR/Cas9-mediated single-base mutation in the *SOC1* gene of lettuce, delaying the formation of the first flower bud and lowering the expression of several floral regulatory genes (*LsFUL*, *LsAPL1*, *LsAPL2*, and *LsLFY*).

### 7. Discussion

#### 7.1. Studying Blooming in Other Crops

Research on bolting and blooming spans various crops, highlighting the importance of shoot apical meristem transitions to inflorescence and floral meristems. This process is crucial for seed production but can negatively affect the plant's medicinal, market, and economic value. Studies have been conducted on medicinal plants (e.g., *Angelica sinensis*) [141], oil crops (*B. rapa*) [142], commercial crops (sugar beet) [143], grain crops (barley, rice, wheat) [144–146], flower crops (*Agave thaliana*, *Dendrobium nobile*, *Lilium longiflorum*, and *Aquilegia coerulea*) [147–150], and forage crops (*Medicago truncatula*, orchard grass) [94,151]. Shojaei et al. [152] identified *COP1* and *CDF* in the photoperiod pathways of sugar beet. Kane et al. [153] found that *TaVRN1* transcription in wheat was repressed by *TaVRT2*. Takada et al. [154] indicated that *BrFRILb* functions as an activator of *BrFLC* in *B. rapa*, showing that H3K27me3 accumulation represses *BrFLCs*. Liang et al. [155] uncovered differentially expressed lncRNAs and mRNAs in *B. vulgaris*, revealing candidate vernalization genes encoding B3-domain-containing proteins.

#### 7.2. Advantages and Disadvantages of Early and Late Bolting

Understanding the molecular mechanism of vernalization is crucial for breeding high bolting resistance. Preferences for early or late bolting depend on market needs.

Early bolting: Suitable for quality seed production, but may damage the economic potential of leafy, fleshy root, and succulent stem vegetable crops.

Late bolting: Increases market value by allowing more extensive vegetative growth and is ideal for leafy, root, and stem crops. Bolting time is often linked to leaf senescence (LS). Early LS is associated with early bolting, while late LS is associated with late bolting. The *A. trithorax* (ATX) enzymes, for instance, regulate transitions between vegetative and reproductive phases: Hinckley and Brusslan [156] generated an *atx1*, *atx3*, and *atx4* triple-T-DNA-insertion mutant showing both early LS and early bolting in *Arabidopsis*. Dai et al. [57] revealed that leaf senescence is related to bolting and flowering in Chinese cabbage, with several hub genes (e.g., *CPRD49*, *AAP8*, *MTHFR2*, *BXLs*, *WRKYs*, *GATLs*) regulating vernalization.

## 8. The Concluding Overview

Research on bolting and flowering in vegetables has gained traction, with notable studies on plants like water dropwort, flowering Chinese cabbage, watercress, and *Brasenia schreberi*. There is a need to balance the cultivation of bolting-resistant vegetables with market demand for characteristic vegetables that bolt easily.

Despite advancements in controlling bolting through improved facility conditions, open-field cultivation still faces significant challenges, particularly in developing regions like southwestern China. Future research should focus on genomics, molecular markers, and gene editing techniques to develop early- or late-bolting varieties tailored to the vegetable industry's needs.

**Author Contributions:** G.-F.T., Q.L., Z.-F.C. and A.-S.X. conceived the paper; G.-F.T. wrote the manuscript; G.-F.T., S.-H.Z., X.-L.Z., P.-H.M. and M.-Y.L. collected and cultured the plant material; Q.L. and G.-F.T. conducted analysis; Q.L., Z.-F.C., A.-S.X. and G.-F.T. contributed substantially to revisions. All authors commented on the manuscript. All authors have read and agreed to the published version of the manuscript.

**Funding:** The research was supported by The Construction of Biological Breeding Platform for Important Crops in Karst Mountain Areas of Guizhou Province (Qian Ke He Zhong Yin Di [2023]033); Project of Guizhou Provincial Department of Science and Technology (Qiankehe Foundation-ZK [2024] General 543; Qiankehe Fuqi No. [2022] 005; Guizhou Provincial Key Technology R&D Program ([2021] No. 207); Project of Guizhou Academy of Agricultural Sciences (Science and Technology Innovation of Qiannongkeyuan No. [2022] 07); Jiangsu Seed Industry Revitalization Project (JBGS(2021)068).

**Conflicts of Interest:** The authors declare no conflicts of interest.

## References

1. Coustham, V.; Li, P.J.; Strange, A.; Lister, C.; Song, J.; Dean, C. Quantitative modulation of polycomb silencing underlies natural variation in vernalization. *Science* **2012**, *337*, 584–587. [\[CrossRef\]](#) [\[PubMed\]](#)
2. Elers, B.; Wiebe, H.J. Flower formation of Chinese cabbage. I. Response to vernalization and photoperiods. *Sci. Hortic.* **1984**, *22*, 219–231. [\[CrossRef\]](#)
3. Yang, P.; Yang, H.J.; Yang, J.C.; Xu, C.; Zhang, K.H.; Ma, X.C. Identification and evaluation of bolting characters of turnip (*Brassicarapa* L.) germplasm resources. *Mol. Plant Breed.* **2022**, *20*, 1363–1372.
4. Yui, S.; Yoshikawa, H. Bolting resistant breeding of Chinese cabbage. 1. flower induction of late bolting variety without chilling treatment. *Euphytica* **1991**, *52*, 171–176. [\[CrossRef\]](#)
5. Bohuon, E.J.R.; Ramsay, L.D.; Craft, J.A.; Arthur, D.F.; Marshall, D.F.; Lydiate, D.J. The association of flowering time quantitative trait loci with duplicated regions and candidate loci in *Brassica oleracea*. *Genetics* **1998**, *50*, 393–401. [\[CrossRef\]](#) [\[PubMed\]](#)
6. 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 Physiol.* **2005**, *137*, 1037–1048. [\[CrossRef\]](#) [\[PubMed\]](#)
7. Nishioka, M.; Tamura, K.; Hayashi, M.; Fujimori, Y.; Ohkawa, Y.; Kuginuki, Y. Mapping of QTLs for bolting time in *Brassica rapa* (syn. *campestris*) under different environmental conditions. *Breed. Sci.* **2005**, *55*, 127–133. [\[CrossRef\]](#)
8. Moe, R.; Guttormsen, G. Effect of photoperiod and temperature on bolting in Chinese cabbage. *Sci. Hortic.* **1985**, *27*, 49–54. [\[CrossRef\]](#)
9. Axelsson, T.; Shavorskaya, O.; Lagercrantz, U. Multiple flowering time QTLs with in several *Brassica* species could be the result of duplicated copies of oneance stralgene. *Genome* **2001**, *44*, 856–864. [\[CrossRef\]](#)
10. Thomas, T.H. Relationship between bolting-resistance and seed dormancy of different celery cultivars. *Sci. Hortic.* **1978**, *9*, 311–316. [\[CrossRef\]](#)

11. Jiang, Q.; Wang, F.; Li, M.Y.; Tan, H.W.; Ma, J.; Xiong, A.S. High-throughput analysis of small RNAs and characterization of novel microRNAs affected by abiotic stress in a local celery cultivar. *Sci. Hortic.* **2014**, *169*, 36–43. [\[CrossRef\]](#)
12. Jia, X.L.; Li, M.Y.; Jiang, Q.; Xu, Z.S.; Wang, F.; Xiong, A.S. High-throughput sequencing of small RNAs and anatomical characteristics associated with leaf development in celery. *Sci. Rep.* **2015**, *5*, e11093. [\[CrossRef\]](#) [\[PubMed\]](#)
13. Li, M.Y.; Hou, X.L.; Wang, F.; Tan, G.F.; Xu, Z.S.; Xiong, A.S. Advances in the research of celery, an important Apiaceae vegetable crop. *Crit. Rev. Biotechnol.* **2018**, *38*, 172–183. [\[CrossRef\]](#) [\[PubMed\]](#)
14. Han, Y.Y.; Chen, Z.J.; Lv, S.S.; Ning, K.; Ji, X.L.; Liu, X.Y.; Wang, Q.; Liu, R.Y.; Fan, S.X.; Zhang, X.L. MADS-box genes and gibberellins regulate bolting in lettuce (*Lactuca sativa* L.). *Front. Plant Sci.* **2016**, *7*, e1889. [\[CrossRef\]](#) [\[PubMed\]](#)
15. Abolghasemi, R.; Haghighi, M.; Etemadi, N.; Wang, S.; Soorni, A. Transcriptome architecture reveals genetic networks of bolting regulation in spinach. *BMC Plant Biol.* **2021**, *21*, 179. [\[CrossRef\]](#) [\[PubMed\]](#)
16. Alessandro, M.S.; Galmarini, C.R. Inheritance of vernalization requirement in carrot. *J. Am. Soc. Hort. Sci.* **2007**, *132*, 525–529. [\[CrossRef\]](#)
17. Ma, J.; Xu, Z.S.; Tan, G.F.; Wang, F.; Xiong, A.S. Distinct transcription profile of genes involved in carotenoid biosynthesis among six different color carrot (*Daucus carota* L.) cultivars. *Acta Biochim. Biophys. Sin.* **2017**, *49*, 817–826. [\[CrossRef\]](#)
18. Tan, G.F.; Wang, F.; Zhang, X.Y.; Xiong, A.S. Different lengths, copies and expression levels of the mitochondrial *atp6* gene in male sterile and fertile lines of carrot (*Daucus carota* L.). *Mitochondrial DNA* **2018**, *29*, 446–454. [\[CrossRef\]](#) [\[PubMed\]](#)
19. Que, F.; Hou, X.L.; Wang, G.L.; Xu, Z.S.; Tan, G.F.; Li, T.; Xiong, A.S. Advances in research on the carrot, an important root vegetable in the Apiaceae family. *Hortic. Res.* **2019**, *6*, 860–874. [\[CrossRef\]](#)
20. Wang, X.J.; Luo, Q.; Li, T.; Meng, P.H.; Pu, Y.T.; Liu, J.X.; Tan, G.F. Origin, evolution, breeding, and omics of Apiaceae: A family of vegetables and medicinal plants. *Hortic. Res.* **2022**, *9*, uhac076. [\[CrossRef\]](#)
21. Sheen, T.F. Effect of day and night temperature variation and of high temperature on devernalization in radish. *Acta Hortic.* **2000**, *5*, 157–162. [\[CrossRef\]](#)
22. Curtis, G.J.; Hornes, K.G. Graft-transmissible induction of bolting and flowering in scions of sugar-beet red for resistance to bolting. *Nature* **1964**, *202*, 1238. [\[CrossRef\]](#)
23. Gupta, A.J.; Mahajan, V.; Lawande, K.E. Genotypic response to bolting tolerance in short day onion (*Allium cepa* L.). *Veg. Sci.* **2018**, *45*, 92–96.
24. Wu, C.N.; Wang, M.Y.; Dong, Y.X.; Cheng, Z.H.; Meng, H.W. Growth, bolting and yield of garlic (*Allium sativum* L.) in response to clove chilling treatment. *Sci. Hortic.* **2015**, *194*, 43–52. [\[CrossRef\]](#)
25. Ellis, R.H.; Summerfield, R.J.; Roberts, E.H. Effects of temperature, photoperiod and seed vernalization on flowering in faba bean. *Ann. Bot.* **1988**, *61*, 17–27. [\[CrossRef\]](#)
26. Fujime, Y.; Mesuda, Y.; Okuda, N.; Varadhan, W. Promotive effects of seed vernalization on flowering and pod setting of some broad bean cultivars. *Acta Hortic.* **2000**, *533*, 75–82. [\[CrossRef\]](#)
27. Filek, W.; Kościelniak, J.; Grzesiak, S. The effect of seed vernalization and irradiation on growth and photosynthesis of field bean plants (*Vicia faba* L. *minor*) and on nitrogenase activity of root nodules. *J. Agron. Crop. Sci.* **2010**, *185*, 229–236. [\[CrossRef\]](#)
28. Jiang, X.M.; Wu, M.X.; Yu, X.H.; Liu, S.C.; Xu, W. Effect of vernalization on nucleic acid content of *Brassica oleracea* L. var. *italica* Plenck. *China Veg.* **2011**, *10*, 41–44.
29. Yu, R.F.; Su, T.B.; Yu, S.C.; Zhang, F.L.; Yu, Y.J.; Zhang, D.S. Effects of plumule-vernalization and seedling-vernalization on bolting and flowering times of different Chinese cabbage varieties. *China Veg.* **2016**, *5*, 27–32.
30. Dai, Y.; Li, G.L.; Gao, X.Y.; Wang, S.X.; Li, Z.; Song, C. Identification of long noncoding RNAs involved in plumule-vernalization of Chinese cabbage. *Front. Plant Sci.* **2023**, *14*, e1147494. [\[CrossRef\]](#) [\[PubMed\]](#)
31. Jiang, X.M.; Zhao, R.Q.; Yu, X.H. Effect of devernalization on nucleic acid content of cabbage. *Acta Physiol. Plant* **2009**, *45*, 673–676. [\[CrossRef\]](#)
32. Yu, X.H.; Li, W.P.; Jiang, X.M.; Liu, D.; Zhang, Y. Changes of endogenous hormone during devernalization in cabbage. *China Veg.* **2010**, *20*, 38–41. [\[CrossRef\]](#)
33. Akter, A.; Miyazaki, J.; Shea, D.J.; Nishida, N.; Takada, S.; Miyaji, N. Gene expression analysis in response to vernalization in Chinese cabbage (*Brassica rapa* L.). *Hortic. J.* **2020**, *89*, 268–277. [\[CrossRef\]](#)
34. Chen, G.P.; Hu, G.L.; Hu, Z.L.; Li, Y.; Gu, F. Cloning and expression of vernalization-related genes in purple flowering stalk (*Brassica campestris* ssp. *chinensis* var. *pupurea* Hort.). *LSR* **2010**, *14*, 27–33. [\[CrossRef\]](#)
35. Ma, C.F.; Dai, S.L. Advances in photoreceptor-mediated signaling transduction in flowering time regulation. *Chin. Bull. Bot.* **2019**, *54*, 9–22. (In Chinese with English Title and Abstract) [\[CrossRef\]](#)
36. Rosental, L.; Still, D.W.; You, Y.; Hayes, R.J.; Simko, L. Mapping and identification of genetic loci affecting earliness of bolting and flowering in lettuce. *Theor. Appl. Genet.* **2021**, *134*, 3319–3337. [\[CrossRef\]](#)
37. Kim, D.H. Current understanding of flowering pathways in plants: Focusing on the vernalization pathway in *Arabidopsis* and several vegetable crop plants. *Hortic. Environ. Biot.* **2020**, *61*, 133–143. [\[CrossRef\]](#)
38. Burn, J.E.; Bagnall, D.J.; Metzger, J.D.; Dennis, E.S.; Peacock, W.J. DNA methylation, vernalization, and the initiation of flowering. *Proc. Natl. Acad. Sci. USA* **1993**, *90*, 287–291. [\[CrossRef\]](#)
39. Fornara, F.; Panigrahi, K.C.S.; Gissot, L.; Sauerbrunn, N.; Rühl, M.; Jarillo, J.A. *Arabidopsis* DOF transcription factors act redundantly to reduce *CONSTANS* expression and are essential for a photoperiodic flowering response. *Dev. Cell* **2009**, *17*, 75–86. [\[CrossRef\]](#)

40. Bendix, C.; Marshall, C.; Harmon, F. Circadian clock genes universally control key agricultural traits. *Mol. Plant* **2015**, *8*, 1135–1152. [\[CrossRef\]](#)
41. Wang, Q.; Zuo, Z.C.; Wang, X.; Gu, L.F.; Yoshizumi, T.; Yang, Z.H. Photo activation and inactivation of *Arabidopsis* cryptochrome2. *Science* **2016**, *354*, 343–347. [\[CrossRef\]](#)
42. Itabashi, E.; Shea, D.J.; Fukino, N.; Fujimoto, R.; Okazaki, K.; Kakizaki, T. Comparison of cold responses for orthologs of cabbage vernalization-related genes. *Hortic. J.* **2019**, *88*, 462–470. [\[CrossRef\]](#)
43. Mao, J.H.; Mao, S.M.; Zhuang, F.Y.; Ou, C.G.; Zhao, Z.W.; Bao, S.Y. Heredity and environmental regulation of premature bolting in carrot. *Acta Agric. Boreal-Occident Sin.* **2013**, *28*, 67–72.
44. Beharav, A.; Hellier, B. Bolting and flowering response of *Lactuca georgica*, a wild lettuce relative, to low temperatures. *Am. J. Plant Sci.* **2020**, *11*, 2139–2154. [\[CrossRef\]](#)
45. Michael, B.; Shemesh-Mayer, T.; Kimhi, E.; Gershberg, S.; Forer, C.; Avila, I. Temporal and spatial effect of low pre-planting temperatures on plant architecture and flowering in bolting garlic. *Sci. Hortic.* **2018**, *242*, 69–75. [\[CrossRef\]](#)
46. Mayer, E.S.; Ben-Michael, T.; Kimhi, S.; Forer, I.; Rabinowitch, H.D.; Kamenetsky, R. Effects of different temperature regimes on flower development, microsporogenesis and fertility in bolting garlic (*Allium sativum*). *Funct. Plant Biol.* **2015**, *42*, 514–526. [\[CrossRef\]](#)
47. Bao, S.Y.; Ou, C.G.; Zhuang, F.Y.; Chen, J.F.; Zhao, Z.W. Study of premature bolting of carrot in spring cultivation. *China Veg.* **2010**, *6*, 38–42.
48. Pressman, E.; Negbi, M. The effect of day length on the response of celery to vernalization. *J. Exp. Bot.* **1980**, *31*, 1291–1296. [\[CrossRef\]](#)
49. Huang, Z.J.; Liu, S.Q.; Zhang, Z.K.; Chen, Y.C.; Zhang, Y.; Ma, L. Effect of prolonged photoperiod on bolting of garlic. *Acta Agric. Boreal-Occident Sin.* **2010**, *20*, 100–103. (In Chinese with English Title and Abstract)
50. Wang, S.L.; Luo, C.; Sun, L.; Ning, K.; Chen, Z.J.; Yang, J.J. *LsRGL1* controls the bolting and flowering times of lettuce by modulating the gibberellin pathway. *Plant Sci.* **2022**, *316*, e111175. [\[CrossRef\]](#)
51. Wang, Y.D.; Huang, X.; Huang, X.M.; Su, W.; Hao, Y.W.; Liu, H.C. *BcSOC1* promotes bolting and stem elongation in flowering Chinese cabbage. *Int. J. Mol. Sci.* **2022**, *23*, 3459. [\[CrossRef\]](#)
52. Mero, C.E.; Honma, S. A method for evaluating bolting-resistance in *Brassica* species. *Sci. Hortic.* **1984**, *24*, 13–19. [\[CrossRef\]](#)
53. Bernier, G.; Havelange, A.; Houssa, C.; Petitjean, A.; Lejeune, P. Physiological signals that induce flowering. *Plant Cell* **1993**, *5*, 1147–1155. [\[CrossRef\]](#)
54. He, L.; Yao, N.; Pei, Y.; Yu, T.; Zu, G.D.; Zhang, W.P. Physiological and biochemical changes and spatial and temporal expressions of flowering genes in radish (*Raphanus sativus* L.) during bolting. *Mol. Plant Breed.* **2020**, *18*, 6837–6843.
55. Wang, B.L.; Deng, J.Y.; Zeng, G.W. Changes in carbohydrate content of stem apices and leaves during floral bud differentiation in radish (*Raphanus sativus* L.). *Acta Hortic. Sin.* **2004**, *31*, 375–377.
56. Wang, Z.Z.; Hou, R.X.; Li, X.F.; Zhu, H.F.; Zhu, Y.Y.; Hou, X.L. Analysis of carbon and nitrogen indexes among different in bred lines during bolting in pak-choi. *Plant Physiol. J.* **2011**, *47*, 893–898. [\[CrossRef\]](#)
57. Dai, Y.; Sun, X.; Wang, C.G.; Li, F.; Zhang, S.F.; Zhang, H. Geneco-expression net work analysis reveals key pathways and hubgenes in Chinese cabbage (*Brassica rapa* L.) during vernalization. *BMC Genom.* **2021**, *22*, 236. [\[CrossRef\]](#)
58. Wang, S.Y.; Yu, F.W.; Zhang, W.; Yu, L.; Li, J.B. Change of anti-oxidative indexes and protein during bolting process of cabbage (*Brassica oleracea* L. var. *capitata* L.). *Acta Agric. Boreal-Occident Sin.* **2023**, *32*, 101–108. (In Chinese with English Title and Abstract) [\[CrossRef\]](#)
59. Li, M.L.; Wang, Q.M.; Zhu, Z.J.; Zeng, G.W. Studies on the changes of DNA methylation level, GA content and protein in non-heading Chinese cabbage during vernalization. *Acta Hortic. Sin.* **2002**, *29*, 353–357. (In Chinese with English Title and Abstract) [\[CrossRef\]](#)
60. Oka, M.; Tasaka, Y.; Iwabuchi, M.; Mino, M. Elevated sensitivity to gibberellins by vernalization in the vegetative rosette plants of *Eustoma grandiflorum* and *Arabidopsis thaliana*. *Plant Sci.* **2001**, *160*, 1237–1245. [\[CrossRef\]](#)
61. Cheng, F.; Zhang, S.N.; Sun, C.H.; Li, S.J.; Chen, G.F. Study on index of morphology and physiology for spring Chinese cabbage. *Acta Hortic. Sin.* **1999**, *26*, 120–122. (In Chinese with English Title and Abstract). [\[CrossRef\]](#)
62. Wu, C.N.; Wang, M.Y.; Cheng, Z.H.; Meng, H.W. Response of garlic (*Allium sativum* L.) bolting and bulbing to temperature and photoperiod treatments. *Biol. Open.* **2016**, *5*, 507–518. [\[CrossRef\]](#)
63. Liu, X.Y.; Lv, S.S.; Liu, R.; Fan, S.X.; Liu, C.J.; Liu, R.Y. Transcriptomic analysis reveals the roles of gibberellin-regulated genes and transcription factors in regulating bolting in lettuce (*Lactuca sativa* L.). *PLoS ONE* **2018**, *13*, e0191518. [\[CrossRef\]](#)
64. Yang, Y.G.; Zhang, H.S.; Li, Y.L.; Wang, X.W.; Yu, J.H.; Wang, X.L. Endogenous hormone content of fleshy root in relation to early bolting in summer cultivated carrot on plateau. *Acta Hortic. Sin.* **2010**, *37*, 1102–1108. [\[CrossRef\]](#)
65. Wu, C.; Wang, M.; Dong, Y.; Cheng, Z.; Meng, H. Effect of plant age and vernalization on bolting, plant growth and enzyme activity of garlic (*Allium sativum* L.). *Sci. Hortic.* **2016**, *201*, 295–305. [\[CrossRef\]](#)
66. Guo, H.Y.; Liu, Y.J.; Yuan, S.H.; Yue, J.R.; Li, Y.M.; Liao, X.Z. Superoxide dismutase promotes early flowering in *Triticum aestivum* L. *Agric. Commun.* **2023**, *1*, e100007. [\[CrossRef\]](#)
67. Finnegan, E.J.; Genger, R.K.; Kovac, K.; Peacock, W.J.; Dennis, E.S. DNA methylation and the promotion of flowering by vernalization. *Proc. Natl. Acad. Sci. USA* **1988**, *95*, 5824–5829. [\[CrossRef\]](#)

68. Yang, Z.F.; Yan, H.D.; Wang, J.P.; Nie, G.; Feng, G.Y.; Xu, X.H. DNA hyper methylation promotes the flowering of orchard grass during vernalization. *Plant Physiol.* **2022**, *190*, 1490–1505. [CrossRef]
69. He, Y.H.; Michaels, S.D.; Amasino, R.M. Regulation of flowering time by histone acetylation in *Arabidopsis*. *Science* **2003**, *302*, 1751–1754. Available online: <https://www.researchgate.net/publication/9030793> (accessed on 5 December 2003). [CrossRef]
70. Osborn, T.C.; Kole, C.; Parkin, I.A.P.; Kuiper, M.; Lydiat, D.J.; Trick, M. Comparison of flowering time genes in *Brassica rapa*, *B. napus* and *Arabidopsis thaliana*. *Genetics* **1997**, *146*, 1123–1129. [CrossRef]
71. Li, F.; Kitashiba, H.; Inaba, K.; Nishiio, T. A *Brassica rapa* linkage map of EST-based SNP markers for identification of candidate genes controlling flowering time and leaf morphological traits. *DNA Res.* **2009**, *16*, 311–323. [CrossRef]
72. Yang, S.J.; Wang, Z.Y.; Zhao, Y.Y.; Wei, X.C.; Yuan, Y.X.; Zhang, X.W. Development of KASP marker for bolting related gene *BrFLC1* in Chinese cabbage (*Brassica rapa* L. ssp. *pekinensis*). *J. Nucl. Agric. Sci.* **2020**, *34*, 265–272. [CrossRef]
73. Yang, X.; Yu, Y.J.; Zhang, F.L.; Zou, Z.R.; Zhao, X.Y.; Zhang, D.S. Link age map construction and quantitative trait loci analysis for bolting based on a double haploid population of *Brassica rapa*. *J. Integr. Plant Biol.* **2007**, *49*, 664–671. [CrossRef]
74. 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*. *Mol. Plant Breed.* **2020**, *18*, 1529–1534. [CrossRef]
75. Kakizaki, T.; Kato, T.; Fukino, N.; Ishida, M.; Hatakeyama, K.; Matsumoto, S. Identification of quantitative trait loci controlling late bolting in Chinese cabbage (*Brassica rapa* L.) parental line Nou 6 gou. *Breed. Sci.* **2011**, *61*, 151–159. [CrossRef]
76. Xu, W.L.; Wang, S.F.; Mu, J.H.; Wang, C.H.; Liu, X.X. Identification of AFLP and SCAR molecular markers linked to bolting trait in radish. *Mol. Plant Breed.* **2009**, *7*, 743–749. [CrossRef]
77. Liu, Y.T.; Zhang, L.; Ji, X.H.; Lv, X.X.; Yang, Y.G.; Feng, H. QTL mapping of vernalization requirement in *Brassica rapa*. *Agric. Biotechnol.* **2015**, *4*, 1–5. [CrossRef]
78. Gan, C.X.; Cui, L.; Pang, W.X.; Wang, A.H.; Yu, X.Q.; Deng, X.H. QTL mapping of bolting and flowering traits based on high density genetic map of radish. *Acta Hortic. Sin.* **2021**, *48*, 1273–1281. [CrossRef]
79. Yuan, Y.X.; Sun, R.F.; Zhang, X.W.; Wu, J.; Xu, D.H.; Zhang, H. A caps marker linked to bolting related gene *BrFLC1* in *Brassica rapa*. *Acta Hortic. Sin.* **2008**, *35*, 1635–1640.
80. Zhang, X.M.; Liu, B.; Hu, Y.Y.; Liu, J.; Wang, X.W.; Wu, J. Development of dCAPs marker for *BrFLC5* related with flowering time in *Brassica rapa*. *Acta Hortic. Sin.* **2014**, *41*, 2035–2042.
81. Wang, W.H.; Wang, J.L.; Li, B.Y.; Wei, Q.Z.; Hu, T.H.; Hu, H.J. Genetic and QTL mapping analysis of bolting time in cabbage (*Brassica oleracea*). *Acta Hortic. Sin.* **2022**, *47*, 974–982. [CrossRef]
82. Meng, Q.; Liu, Z.Y.; Feng, C.D.; Zhang, H.L.; Xu, Z.S.; Wang, X.W. Quantitative trait locus mapping and identification of candidate genes controlling bolting in spinach (*Spinacia oleracea* L.). *Front. Plant Sci.* **2022**, *13*, e850810. [CrossRef] [PubMed]
83. Sheldon, C.C.; Burn, J.; Perez, P.P.; Metzger, J.; Edwards, J.A.; Peacock, W.J. The FLMADS boxgene: A repressor of flowering in *Arabidopsis* regulated by vernalization and methylation. *Plant Cell* **1999**, *11*, 445–458. [CrossRef] [PubMed]
84. Michaels, S.D.; Amasino, M.R. *Flowering Locus C* encodes a novel MADS domain protein that acts as a repressor of flowering. *Plant Cell* **1999**, *11*, 949–956. [CrossRef] [PubMed]
85. Sheldon, C.C.; Conn, A.B.; Dennis, E.S.; Peacock, W.J. Different regulatory regions are required for the vernalization-induced repression of *Flowering Locus C* and for the epigenetic maintenance of repression. *Plant Cell* **2002**, *14*, 2527–2537. [CrossRef] [PubMed]
86. Xiao, X.F.; Cao, B.H.; Wang, Y.; Chen, G.J.; Lei, J.J. Study on flower bud differentiation and cloning and expression of *BrcuFLC* in *Brassica campestris* L. ssp. Chinese (L.) makino var utilis. *Acta Hortic. Sin.* **2008**, *35*, 827–832. [CrossRef]
87. Basualdo, J.; Díaz, M.L.; Cuppari, S.; Cardone, S.; Soresi, D.; Camargo, G.P.; Carrera, A.; Jung, C. Allelic variation and differential expression of *VRN-A1* in durum wheat genotypes varying in the vernalization response. *Plant Breed.* **2015**, *134*, 520–528. [CrossRef]
88. Zitzewitz, J.V.; Szucs, P.; Dubcovsky, J.; Yan, L.L.; Francia, E.; Pecchioni, N. Molecular and structural characterization of barley vernalization genes. *Plant Mol. Biol.* **2005**, *59*, 449–467. [CrossRef]
89. Putterill, J.; Laurie, R.; Macknight, R. It's time to flower: The genetic control of flowering time. *Bioessays* **2004**, *26*, 363–373. [CrossRef]
90. Fornara, F.; Montaigne, A.D.; Coupland, G. Snap Shot: Control of flowering in *Arabidopsis*. *Cell* **2010**, *141*, 550. [CrossRef]
91. Guo, D.; Wong, W.S.; Xu, W.Z.; Sun, F.F.; Qing, D.J.; Li, N. *Cis-cinnamic acid-enhanced 1* gene plays a role in regulation of *Arabidopsis* bolting. *Plant Mol. Biol.* **2011**, *75*, 481–495. [CrossRef] [PubMed]
92. Huang, B.Y.; Qian, P.P.; Gao, N.; Shen, J.; Hou, S.W. Fackel interacts with gibberellic acid signaling and vernalization to mediate flowering in *Arabidopsis*. *Planta* **2017**, *245*, 939–950. [CrossRef]
93. Gu, A.X.; Zhang, Y.K.; Zhao, J.J.; Wang, Y.H.; Chen, X.P.; Shen, S.X. Effects of the added cabbage chromosome 4 on bolting time and *BrFLCs* expression of Chinese cabbage. *Acta Hortic. Sin.* **2015**, *42*, 2405–2411. [CrossRef]
94. Feng, G.Y.; Xu, L.; Wang, J.P.; Nie, G.; Bushman, B.S.; Xie, W.G. Integration of small RNAs and transcriptome sequencing uncovers a complex regulatory network during vernalization and heading stages of orchard grass (*Dactylis glomerata* L.). *BMC Genom.* **2018**, *19*, 727. [CrossRef]
95. Shim, Y.; Lim, C.; Seong, G.; Choi, Y.; Kang, K.; Paek, N.C. The AP2/ERF transcription factor LATE FLOWERING SEMI-DWARF suppresses long-day-dependent repression of flowering. *Plant Cell Environ.* **2022**, *45*, 2446–2459. [CrossRef] [PubMed]

96. Jiang, Q.; Wang, Z.; Hu, G.M.; Yao, X.H. Genome-wide identification and characterization of AP2/ERF gene super family during flower development in *Actinidia eriantha*. *BMC Genom.* **2022**, *23*, 650. [[CrossRef](#)] [[PubMed](#)]
97. Okazaki, K.; Sakamoto, K.; Kikuchi, R.; Saito, A.; Togashi, E.; Kuginuki, Y.; Hirai, S.M. Mapping and characterization of *FLC* homologs and QTL analysis of flowering time in *Brassica oleracea*. *Theor. Appl. Genet.* **2007**, *114*, 595–608. [[CrossRef](#)]
98. Razi, H.; Howell, E.C.; Newbury, H.J.; Kearesy, M.J. Does sequence polymorphism of *FLC* paralogues underlie flowering time QTL in *Brassica oleracea*? *Theor. Appl. Genet.* **2008**, *116*, 179–192. [[CrossRef](#)]
99. Zhao, R.Q.; Hu, Y.; Jiang, X.M.; Yu, X.H. Clone and expression analysis of *BoVIN3* from Cabbage. *Acta Hortic. Sin.* **2012**, *39*, 1099–1106.
100. Wang, Y.; Jiang, W.; Yan, K.; Zhou, W.W.; Wang, Z.M.; Wei, D.Y. Protein interactions of flowering inhibitors AGL18 and HDA9 with integrator factors in *Brassica oleracea* var. *italica*. *Acta Hortic. Sin.* **2018**, *45*, 2383–2394. [[CrossRef](#)]
101. Jiang, W.; Zhou, W.W.; Li, C.C.; Yan, K.; Wang, Y.; Wang, Z.M. Interactions of flowering promoting factor AGL19 with integrator factors AGL24 and SOC1 in *Brassica oleracea* var. *italica*. *Acta Hortic. Sin.* **2017**, *44*, 1905–1913. [[CrossRef](#)]
102. Michaels, S.D.; Ditta, G.; Gustafson-Brown, C.; Pelaz, S.; Yanofsky, M.; Amasino, R.M. *AGL24* acts as a promoter of flowering in *Arabidopsis* and is positively regulated by vernalization. *Plant J.* **2003**, *33*, 867–874. [[CrossRef](#)] [[PubMed](#)]
103. Xi, X.; Wei, K.Y.; Gao, B.Z.; Liu, J.H.; Liang, J.L.; Cheng, F. *BrFLC5*: A weak regulator of flowering time in *Brassica rapa*. *Theor. Appl. Genet.* **2018**, *131*, 2107–2116. [[CrossRef](#)] [[PubMed](#)]
104. Xin, X.Y.; Su, T.B.; Li, P.R.; Wang, W.H.; Zhao, X.Y.; Yu, Y.J. A histone H4 gene prevents drought-induced bolting in Chinese cabbage by attenuating the expression of flowering genes. *J. Exp. Bot.* **2020**, *72*, 623–635. [[CrossRef](#)] [[PubMed](#)]
105. Wei, X.C.; Rahim, M.A.; Zhao, Y.Y.; Yang, S.J.; Wang, Z.Y.; Su, H.N. Inheritance and genetic mapping of late-bolting to early-bolting gene, *BrEb-1*, in Chinese cabbage (*Brassica rapa* L.). *Agronomy* **2022**, *12*, 1048. [[CrossRef](#)]
106. Dong, X.S.; Yi, H.; Han, C.T.; Nou, I.S.; Swaraz, A.M.; Hur, Y. Genome-wide analysis of genes associated with bolting in heading type Chinese cabbage. *Euphytica* **2016**, *212*, 65–82. [[CrossRef](#)]
107. Hong, J.K.; Park, S.R.; Suh, E.J.; Park, J.; Lee, Y.H. Effects of over expression of *Brassica Rapa Short Vegetative Phase* gene on flowering time. *Kor. J. Breed. Sci.* **2020**, *52*, 244–251. [[CrossRef](#)]
108. Li, Z.G.; Zhao, L.X.; Cui, C.S.; Kai, G.Y.; Zhang, L.D.; Sun, X.F. Molecular cloning and characterization of an anti-bolting related gene (*BrpFLC*) from *Brassica rapa* ssp. *Pekinensis*. *Plant Sci.* **2005**, *168*, 407–413. [[CrossRef](#)]
109. Huang, J.S.; Li, J.Y.; Yu, X.L.; Sun, B.J.; Cao, J.S. Cloning and expression analysis of vernalization-related gene *BcFLC* in *Brassica campestris*. *Acta Hortic. Sin.* **2007**, *34*, 1169–1176. [[CrossRef](#)]
110. Rong, Z.L.; Hou, X.L.; Shi, G.J.; Xiao, D.; Wang, Q.; Zhang, L. Cloning and expression analysis of late bolting *BcFLC3* gene from *Brassica campestris* ssp. *Chinensis*. *Acta Bot Boreal-Occident Sin.* **2010**, *12*, 2373–2378, (In Chinese with English Title and Abstract).
111. Guan, H.L.; Huang, X.M.; Zhu, Y.N.; Xie, B.X.; Liu, H.C.; Song, S.W. Identification of *DELLA* genes and key stage for GA sensitivity in bolting and flowering of flowering Chinese cabbage. *Int. J. Mol. Sci.* **2021**, *22*, 12092. [[CrossRef](#)] [[PubMed](#)]
112. Jung, W.Y.; Park, H.J.; Lee, A.; Lee, S.S.; Kim, Y.S.; Cho, H.S. Identification of flowering-related genes responsible for differences in bolting time between two radish in bred lines. *Front. Plant Sci.* **2016**, *7*, e1844. [[CrossRef](#)] [[PubMed](#)]
113. Wang, Q.B.; Zhang, Y.J.; Zhang, L.B. A naturally occurring insertion in the *RsFLC2* gene associated with late-bolting trait in radish (*Raphanus sativus* L.). *Mol. Breed.* **2018**, *38*, e137. [[CrossRef](#)]
114. Mao, J.H.; Zhuang, F.Y.; Ou, C.G.; Zhao, Z.W.; Wang, H.; Ma, Z.G. Expression analysis of *FLC* homologues responding to low temperature and photoperiod in carrot. *Acta Hortic. Sin.* **2013**, *40*, 2453–2462.
115. Alessandro, M.S.; Galmarini, C.R.; Iorizzo, M.; Simon, P.W. Molecular mapping of vernalization requirement and fertility restoration genes in carrot. *Theor. Appl. Genet.* **2013**, *126*, 415–423. [[CrossRef](#)] [[PubMed](#)]
116. Liu, L.J.; Ou, C.G.; Zhao, Z.W.; Sun, T.T.; Zhuang, F.Y. Function analysis of carrot *SOC1* homologues responding to photoperiod. *Acta Hortic. Sin.* **2016**, *43*, 1099–1106. [[CrossRef](#)]
117. Li, Y.F.; Zhu, J.Q.; Feng, Y.X.; Li, Z.F.; Ren, Z.; Liu, C.J. *LsARF3* mediates thermally induced bolting through promoting the expression of *LsCO* in lettuce (*Lactuca sativa* L.). *Front. Plant Sci.* **2022**, *13*, e958833. [[CrossRef](#)] [[PubMed](#)]
118. Hu, M.M.; Qi, Z.Y.; Ren, Z.; Tong, J.; Wang, B.J.; Wu, Z.H. Genome-wide analysis of auxin response factors in lettuce (*Lactuca sativa* L.) reveals the positive roles of *LsARF8a* in thermally induced bolting. *Int. J. Mol. Sci.* **2023**, *23*, 13509. [[CrossRef](#)] [[PubMed](#)]
119. Chen, Z.J.; Han, Y.Y.; Ning, K.; Ding, Y.Y.; Zhao, W.S.; Yan, S.S. Inflorescence development and the role of *LsFT* in regulating bolting in lettuce (*Lactuca sativa* L.). *Front. Plant Sci.* **2017**, *8*, e2248. [[CrossRef](#)]
120. Fu, D.; Dunbar, M.; Dubcovsky, J. Wheat *VIN3*-like PHD finger genes are up-regulated by vernalization. *Mol. Genet. Genomics* **2007**, *277*, 301–313. [[CrossRef](#)]
121. Schmitz, R.J.; Amasino, R.M. Vernalization: A model for investigating epigenetics and eukaryotic gene regulation in plants. *Biochim. Et Biophys. Acta* **2007**, *1769*, 269–275. [[CrossRef](#)] [[PubMed](#)]
122. Kamiya, Y.; Shiraki, S.; Fujiwara, K.; Akter, M.A.; Akter, A.; Fujimoto, R. The role of epigenetic transcriptional regulation in *Brassica* vegetables: A potential resource for epigenetic breeding. In *Smart Plant Breeding for Vegetable Crops in Post-Genomics Era*; Springer Nature Singapore Pte Ltd.: Singapore, 2023; pp. 1–24. [[CrossRef](#)]
123. Zhang, S.J.; Qiu, Y.; Song, J.P.; Wang, H.P.; Zhang, X.H.; Shen, D. Identification for the tolerance to bolting of radish germplasm resources. *J. Plant. Genet. Res.* **2014**, *15*, 262–269. (In Chinese with English Title and Abstract)

124. Liu, C.X.; Sui, M.; Liu, C.X.; Cao, H.X.; Chang, T.L.; Yin, C.L. Back cross breeding of late bolting and detection of first intron PCR amplification of *FLC2* gene in radish. *Acta Agric. Boreal-Occident Sin.* **2019**, *34*, 83–92. (In Chinese with English Title and Abstract) [[CrossRef](#)]
125. Zhang, S.X.; Fan, W.Q.; Zheng, S.Y.; Wang, C.N.; Hua, D.P.; Zhang, H. Identification of bolting tolerance and genetic relationship analysis of green radish germplasm resources. *Mol. Plant Breed.* **2022**, *20*, 6566–6576. (In Chinese with English Title and Abstract)
126. Zhuo, Z.C.; Wan, E.M.; Zhang, L.G.; Zhang, M.K.; Hui, M.X. Major gene plus poly gene inheritance analysis of bolting trait in heading Chinese cabbage. *Acta Bot. Boreal-Occident Sin.* **2009**, *29*, 867–873. [[CrossRef](#)]
127. Ji, X.H.; Zhang, L.; Lu, X.X.; Liu, Y.T.; Wang, Y.G.; Feng, H. Inheritance analysis of bolting associated traits using mixed major gene plus polygenemodel in *Brassica rapa*. *Agric. Biotechnol.* **2013**, *2*, 26–30. [[CrossRef](#)]
128. Li, X.F.; Zhu, H.F.; Zhu, Y.Y.; Hou, R.X. Combining ability and heritability analysis of bolting character of non-heading Chinese cabbage. *Plant Div. Res.* **2015**, *37*, 788–792.
129. Li, M.; Liu, Y.M.; Fang, Z.H.; Yang, L.M.; Zhuang, M.; Zhang, Y.Y. Combining ability and heritability analysis of bolting and flowering characters in cabbage (*Brassica oleracea* var. *capitata*). *Acta Agric. Boreal-Occident Sin.* **2009**, *24*, 86–89. (In Chinese with English Title and Abstract)
130. Li, X.F.; Zhu, H.F.; Zhu, Y.Y.; Hou, R.X.; Zhai, W. Inheritance of major gene plus polygene underlying bolting and flowering traits in pak-choi. *J. Nucl. Agric. Sci.* **2016**, *12*, 2318–2325. (In Chinese with English Title and Abstract) [[CrossRef](#)]
131. Motoki, K.; Kinoshita, Y.; Hosokawa, M. Non-vernalization flowering and seed set of cabbage induced by grafting onto radish roots stocks. *Front. Plant Sci.* **2019**, *9*, e1967. [[CrossRef](#)]
132. Ipek, M.; Ipek, A.; Senalik, D.; Simon, P.W. Characterization of an unusual cytoplasmic chimera detected in bolting garlic clones. *J. Am. Soc. Hortic. Sci.* **2007**, *132*, 664–669. [[CrossRef](#)]
133. Li, X.F.; Zhu, H.F.; Zhu, Y.Y.; Hou, R.X. Development of a new late-bolting germplasm and breeding a new cultivar yanchun of pak-choi by using space mutation. *J. Nucl. Agric. Sci.* **2018**, *32*, 1249–1255. [[CrossRef](#)]
134. 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 Mol. Biol. Rep.* **2018**, *36*, 725–737. [[CrossRef](#)]
135. Fu, W.; Huang, S.S.; Liu, Z.Y.; Gao, Y.; Zhang, M.D.; Wang, N. Fine mapping of *Breb6*, a gene conferring the early-bolting phenotype in Chinese cabbage (*Brassica rapa* ssp. *pekinensis*). *Veg. Res.* **2021**, *1*, e7. [[CrossRef](#)]
136. Li, Q.F.; Peng, A.; Yang, J.Q.; Zheng, S.D.; Li, Z.P.; Mu, Y.H. A 215-bp in delatrintron I of *BoFLC2* affects flowering time in *Brassica oleracea* var. *capitata* during vernalization. *Theor. Appl. Genet.* **2022**, *135*, 2785–2797. [[CrossRef](#)]
137. Tang, Q.W.; Kuang, H.H.; Yu, C.C.; An, G.H.; Tao, R.; Zhang, W.Y. Non-vernalization requirement in Chinese kale caused by loss of *BoFLC* and low expressions of its paralogs. *Theor. Appl. Genet.* **2022**, *135*, 473–483. [[CrossRef](#)]
138. Shin, Y.H.; Lee, H.M.; Park, Y.D. CRISPR/Cas9-mediated editing of *Agamous-like* genes results in a late-bolting phenotype in Chinese cabbage (*Brassica rapa* ssp. *pekinensis*). *Int. J. Mol. Sci.* **2022**, *23*, 15009. [[CrossRef](#)]
139. Shin, Y.H.; Park, Y.D. CRISPR/Cas9-mediated mutagenesis of *BrLEAFY* delays the bolting time in Chinese cabbage (*Brassica rapa* L. ssp. *pekinensis*). *Int. J. Mol. Sci.* **2023**, *24*, 541. [[CrossRef](#)]
140. Choi, S.H.; Ahn, W.S.; Jie, E.Y.; Cho, H.S.; Kim, S.W. Development of late-bolting plants by CRISPR/Cas9-mediated genome editing from mesophyll protoplasts of lettuce. *Plant Cell Rep.* **2022**, *41*, 1627–1630. [[CrossRef](#)]
141. Fan, S.T.; Li, Y.; Luo, X.Y.; Zong, Y.; Liu, B.L.; Li, J.M. Bioinformatics analysis of key genes *FT* and *SOC1* in radish *Angelica sinensis*. *Mol. Plant Breed.* **2022**, *20*, 3562–3569. (In Chinese with English Title and Abstract)
142. Kitamoto, N.; Yui, S.; Nishikawa, K.; Takahata, Y.; Yokoi, S. A naturally occurring long insertion in the first intron in the *Brassica rapa FLC2* gene causes delayed bolting. *Euphytica* **2014**, *196*, 213–223. [[CrossRef](#)]
143. Chia, T.Y.P.; Müller, A.; Jung, C.; Mutasa-Göttgens, E.S. Sugar beet contains a large *CONSTANS-Like* gene family including a CO homologue that is independent of the early-bolting (*B*) gene locus. *J. Exp. Bot.* **2008**, *59*, 2735–2748. [[CrossRef](#)] [[PubMed](#)]
144. Szűcs, P.; Karsai, I.; Zitzewitz, J.V.; Meszaros, K.; Cooper, L.L.D.; Gu, Y.Q. Positional relationships between photoperiod response QTL and photoreceptor and vernalization genes in barley. *Theor. Appl. Genet.* **2006**, *112*, 1277–1285. [[CrossRef](#)]
145. Liu, S.N.; Ma, T.F.; Ma, L.Y.; Lin, X.C. Ectopic expression of *PvSOC1*, a homolog of *SOC1* from *Phyllostachys violascens*, promotes flowering in *Arabidopsis* and rice. *Acta Physiol. Plant* **2016**, *38*, 166. [[CrossRef](#)]
146. Xu, S.J.; Dong, Q.; Deng, M.; Lin, D.X.; Xiao, J.; Cheng, P.L. The vernalization-induced long non-coding RNA *VAS* functions with the transcription factor *TaRF2b* to promote *TaVRN1* expression for flowering in hexaploid wheat. *Mol. Plant* **2021**, *14*, 1525–1538. [[CrossRef](#)]
147. Dios, E.A.D.; Delaye, L.; Simpson, J. Transcriptome analysis of bolting in *A. tequilana* reveals roles for florigen, MADS, fructans and gibberellins. *BMC Genomics* **2019**, *20*, 473. [[CrossRef](#)]
148. Wen, Z.Z.; Guo, W.Z.; Li, J.C.; Lin, H.S.; He, C.M.; Liu, Y.Q. Comparative transcriptomic analysis of vernalization and cytokinin induced floral transition in *Dendrobium nobile*. *Sci. Rep.* **2017**, *7*, e45748. [[CrossRef](#)]
149. Yan, X.; Wang, L.J.; Zhao, Y.Q.; Jia, G.X. Expression patterns of key genes in the photoperiod and vernalization flowering pathways in *Lilium longiflorum* with different bulb sizes. *Int. J. Mol. Sci.* **2022**, *15*, 8341. [[CrossRef](#)]
150. Sharma, B.; Batz, T.A.; Kaundal, R.; Kramer, E.M.; Sanders, U.R.; Mellano, V.J. Developmental and molecular changes underlying the vernalization-induced transition of lowering in *Aquilegia coerulea* (James). *Genes* **2019**, *10*, 734. [[CrossRef](#)]
151. Jaudal, M.; Yeoh, C.C.; Zhang, L.L.; Stockum, C.; Mysore, K.S.; Ratet, P. Retroelement insertions at the medicago *FTa1* locus in spring mutants eliminate vernalisation but not long-day requirements for early flowering. *Plant J.* **2013**, *76*, 580–591. [[CrossRef](#)]

152. Shojaei, E.; Mirzaie-Asl, A.; Mahmoudi, S.B.; Nazeri, S. Identification of sugar beet flowering genes based on *Arabidopsis* homologous genes. *J. Agric. Sci. Technol.* **2017**, *19*, 719–729.
153. Kane, N.A.; Agharbaoui, Z.; Diallo, A.O.; Adam, H.; Tominaga, Y.; Ouellet, F. *TaVRT2* represses transcription of the wheat vernalization gene *TaVRN1*. *Plant J.* **2007**, *51*, 670–680. [[CrossRef](#)]
154. Takada, S.; Akter, A.; Itabashi, E.; Nishida, N.; Shea, D.J.; Miyaji, N. The role of *Frigida* and *Flowering Locus C* genes in flowering time of *Brassica rapa* leafy vegetables. *Sci. Rep.* **2019**, *9*, e13843. [[CrossRef](#)]
155. Liang, N.G.; Cheng, D.Y.; Zhao, L.; Lu, H.D.; Xu, L.; Bi, Y.H. Identification of the genes encoding B3 domain-containing proteins related to vernalization of *Beta vulgaris*. *Genes* **2022**, *13*, 2217. [[CrossRef](#)] [[PubMed](#)]
156. Hinckley, W.E.; Brusslan, J.A. Gene expression changes occurring at bolting time are associated with leaf senescence in *Arabidopsis*. *Plant Direct.* **2020**, *4*, e00279. [[CrossRef](#)] [[PubMed](#)]

**Disclaimer/Publisher’s Note:** The statements, opinions and data contained in all publications are solely those of the individual author(s) and contributor(s) and not of MDPI and/or the editor(s). MDPI and/or the editor(s) disclaim responsibility for any injury to people or property resulting from any ideas, methods, instructions or products referred to in the content.