

Research Progress in Radish Bolting Biology and Breeding Strategies for Bolting Tolerance

Xiaowei YUAN^{1,2*}

1. Weifang Engineering Vocational College, Qingzhou 262500, China; 2. Huasheng Agricultural Group Co., Ltd., Qingzhou 262500, China

Abstract Premature bolting in radish (*Raphanus sativus* L.) is a major obstacle in spring radish production, severely reducing the commercial quality and economic value of the fleshy root. This paper systematically reviews the developmental process of radish bolting, molecular and genetic regulatory mechanisms, physiological and biochemical basis, and environmental interaction effects. It focuses on the structure and function of the FLC gene family (a key repressor in the vernalization pathway), the epigenetic regulatory mechanisms, and the key regulatory gene RsMIPS3 identified based on T2T genome analysis. In addition, the paper summarizes the research progress in screening for bolting-tolerant germplasm, marker-assisted selection breeding, and gene editing technologies, and introduces representative bolting-tolerant varieties developed in recent years. The challenges currently facing research and future development directions are also discussed, aiming to provide a theoretical reference for the genetic improvement and production application of bolting traits in radish.

Key words Radish; Bolting; FLC gene; Vernalization

DOI:10.19759/j.cnki.2164-4993.2026.04.003

Radish (*Raphanus sativus* L.) is an important cruciferous vegetable crop in China, with a long cultivation history, rich nutrition, and diverse uses. The planting area of radish in China is approximately 1.2 million hm², with an annual output of 40.68 million t, ranking first in the world. Radish is a biennial plant that requires low-temperature vernalization under natural conditions to transition from vegetative growth to reproductive growth. In production, if the fleshy root bolts and flowers prematurely before it has fully expanded, it is referred to as "premature bolting". Premature bolting leads to hollowing and lignification of the fleshy root, resulting in a significant decline in commercial value, and in severe cases, complete loss of edibility^[1].

Premature bolting is particularly prominent in spring production. For a long time, there has been a shortage of bolting-tolerant radish varieties, and production has primarily relied on varieties imported from Japan and South Korea, which are costly and have limited adaptability. The bolting trait is regulated by multiple genes and interacts closely with environmental factors, and its genetic mechanism has long remained incompletely elucidated^[2]. In recent years, with the rapid development of genomics, molecular biology, and bioinformatics technologies, several important breakthroughs have been achieved in radish bolting research. This paper systematically reviews the progress in this field, hoping to provide a reference for future research and breeding practices against bolting.

Radish Bolting Development Process and Its Biological Significance

The bolting and flowering process in radish can be divided into three consecutive stages: floral differentiation, bolting, and flowering. Floral differentiation marks the initiation of reproductive growth, referring to the transition of the shoot apical meristem from a vegetative cone to a reproductive cone under suitable inductive conditions. Cytological observation has shown that floral differentiation in the radish shoot apical meristem is characterized by the formation of single floral primordia on the surface of the growth cone, gradually followed by the differentiation of sepal primordia, stamen primordia, pistil primordia, and petal primordia in sequence^[3]. Bolting is initiated after the completion of floral differentiation, and the flower stalk elongates rapidly, marking the plant's formal entry into the reproductive growth stage. Low temperature is the basic ecological condition for floral differentiation. After floral differentiation is completed, long sunshine and higher temperature promote bolting and flowering.

From the perspective of agricultural production, the edible organ of radish is the fleshy root, the expansion of which needs a long time of nutrient growth and accumulation. If the plant encounters low-temperature vernalization before the fleshy root has fully expanded, it shifts to reproductive growth, which will inhibit the development of the fleshy root and significantly reduce its commercial value. Therefore, in-depth elucidation of the development and regulatory mechanisms of bolting and flowering is of great significance for guiding production practice and breeding improvement.

Molecular and Genetic Regulatory Mechanisms of Bolting

Structure and function of the FLC gene family

The FLC (Flowering Locus C) gene belongs to the MADSbox

Received: March 12, 2026 Accepted: June 20, 2026

Supported by Weifang Science and Technology Development Program (2024GX073); Agricultural Variety Improvement Project of Shandong Province (2024LZGCQY017).

Xiaowei YUAN (1983–), female, P. R. China, researcher, PhD, devoted to research about vegetable biotechnology breeding.

* Corresponding author.

transcription factor family and is a key repressor of flowering time in the vernalization pathway. In *Arabidopsis thaliana*, *FLC* delays flowering by suppressing the expression of flowering-promoting genes such as *FT* and *SOC1*. Prolonged low-temperature treatment (vernalization) silences *FLC* expression through epigenetic mechanisms, thereby relieving the inhibition of flowering^[4].

In radish, the *FLC*-homologous *RsFLC* gene has been successfully isolated. Its sequence analysis revealed that *RsFLC* shares high homology with *FLC* genes from other cruciferous vegetables, and the encoded protein contains conserved MADS-box and Kbox domains. Expression analysis shows that *RsFLC* is highly expressed in the shoot tip, but not in the root. Vernalization treatment significantly reduces its expression level, with the extent of reduction varying among varieties with different winteriness. The stronger the winteriness, the less the reduction in the expression level of *RsFLC*. When the expression of *RsFLC* decreases to an almost undetectable level, the shoot tip has already transitioned to reproductive growth^[5-6].

In addition to *RsFLC*, multiple *FLC* family members have been identified in the radish genome. A study conducted a genome-wide identification of flowering-related genes in radish, yielding a total of 638 flowering-related genes, among which *RsFLC3* was successfully cloned. Subcellular localization revealed that its encoded protein is localized in the nucleus^[2]. During the bolting and flowering process, the expression level of *RsFLC3* generally shows a decreasing trend, but the expression levels vary considerably among different varieties at various stages, indicating that multiple members of the *FLC* family are coordinately involved in fine regulation.

Epigenetic regulatory mechanisms

The molecular essence of vernalization-induced silencing of the *FLC* gene is the dynamic changes in epigenetic modifications at the chromatin level. In *A. thaliana*, vernalization achieves stable repression of *FLC* through H3K27me3 histone methylation modification mediated by Polycomb Repressive Complex 2 (PRC2). In recent years, similar mechanisms have also been identified in radish.

Recent studies have found that an insertion mutation in the *RsFLC2* gene region of radish disrupts vernalization-induced intragenic looping and the enrichment of H3K27me3 on chromatin. Using the normal-flowering cultivar ‘Jinjudaepeung’ (JD) and the extremely late-bolting inbred line ‘Simu’ (SM) as materials, it was found that *RsFLC2* was significantly upregulated in SM and was not affected by vernalization. In the SM material, two DNA insertion fragments (1 037 bp and 1 627 bp in length, respectively) were detected, located in the proximal promoter and the first intron region of *RsFLC2*. Transgenic plants containing these insertions exhibited a more pronounced lateflowering phenotype in *A. thaliana*. Compared with JD, PRC2-mediated H3K27me3 deposition in SM was significantly impaired, and vernalization-induced intragenic looping was also markedly disrupted^[8]. This study revealed the molecular basis of functional differentiation of

the *FLC* gene and the formation of bolting-tolerant traits.

Discovery of the key regulatory gene *RsMIPS3*

It has been difficult to elucidate the genetic mechanisms regulating bolting in radish for a long time due to the complexity of its genome. In 2026, the team of Yang Feng at Sichuan Academy of Agricultural Sciences, in collaboration with the teams of Professors Lin Honghui and Zhang Dawei at Sichuan University, completed the high-quality and gap-free genome assembly of radish at the telomere-to-telomere (T2T) level for the first time. The genome size is 472.71 Mb, comprising nine chromosomes, with a total of 49 768 protein-coding genes identified, 97.38% of which have been functionally annotated, and repetitive sequences account for 59.72% of the genome^[8].

Leveraging this T2T genome, the research team constructed a high-density genetic linkage map using an F₂ population derived from a cross between earlybolting and late-bolting radish lines, and mapped seven QTLs associated with bolting and flowering. Through combined transcriptome sequencing and qRTPCR analysis, the key regulatory gene *RsMIPS3* was successfully identified. The expression level of this gene significantly decreased during the bolting process, and its expression level in late-bolting materials was significantly higher than in earlybolting materials. Overexpression of *RsMIPS3* in *A. thaliana* significantly delayed bolting time, while the *mips3* mutant exhibited earlier bolting, confirming that *RsMIPS3* is a negative regulator of bolting^[8]. This finding provides a new entry point for understanding the polygenic regulatory mechanism of bolting in radish and offers a valuable target for molecular breeding of late-bolting traits.

Physiological and Biochemical Basis and Environmental Regulation of Bolting

Physiological changes during low-temperature vernalization

Differences in vernalization requirements among radish varieties are reflected in the duration of low-temperature exposure and the minimum effective temperature. Spring radish is a seed-vernalization type crop. From the germination of seeds, exposure to low temperatures between 0 and 12 °C for 10 to 20 d is sufficient to pass through the vernalization stage, with the optimal temperature being approximately 4 °C. Temperatures above 12 °C make it difficult to complete vernalization. The varieties that are prone to bolting can even sense low temperatures and initiate floral differentiation as early as the 2–3 true-leaf stage^[9-10].

During vernalization, the contents of soluble protein and free amino acids in the shoot apical meristem gradually increase, while soluble sugar content decreases. The soluble protein and soluble sugar contents in the bolting-tolerant variety ‘Changchun Daxing’ were significantly lower than those in the variety ‘Duanye Shisan’ prone to bolting, while the free amino acid content showed the opposite trend. Both gibberellin and auxin exhibited pronounced peaks at the onset of floral differentiation^[12]. These physiological indicators can serve as references for screening bolting-tolerant germplasm.

Regulatory roles of light, temperature, and cultivation factors

Photoperiod is another key factor influencing bolting. Long-day conditions (day length > 14 h) significantly promote bolting and flowering after floral differentiation. In spring production, the combined effect of low temperature and long sunshine greatly increases the risk of premature bolting. In addition, factors such as excessively low planting density, uneven water and fertilizer supply, and insufficient nitrogen fertilizer can induce premature bolting to some extent. Appropriate close planting, maintaining soil moisture, and increasing potassium and organic fertilizers are conducive to rapid enlargement of the fleshy root and can inhibit floral differentiation^[11]. Timely sowing, plastic film mulching for heat preservation, and other cultivation measures play important roles in controlling bolting.

Technical Strategies for Bolting-tolerant Breeding

Germplasm resource evaluation and screening

The team at Nanjing Agricultural University systematically evaluated over 1 600 radish germplasm resources, established the Chinese Radish Germplasm Resource Information System (CR-GRIS), and conducted evaluations of late-bolting, heat tolerance, downy mildew resistance, and quality traits in 362 germplasm resources^[12]. Autumn-winter radish varieties are mostly late-maturing and have relatively strong bolting tolerance, whereas spring radish varieties are prone to premature bolting. The bolting type can be rapidly identified by determining the time required for floral differentiation initiation after low-temperature treatment at the seedling stage. Using the minimum duration of low-temperature treatment needed for floral differentiation in plants at the stage of two leaves and one bud as an indicator can effectively evaluate the bolting characteristics of germplasm.

Marker-assisted selection breeding

Molecular markers developed based on key regulatory genes have provided tools for efficient selection of bolting-tolerant traits. By comparing the *RsFLC* sequences of radish lines with different bolting characteristics, InDel differences significantly associated with bolting traits were identified in Intron 1 and Intron 2 regions, and molecular markers for early-bolting and late-bolting types were developed. Field validation showed high consistency with phenotypic identification^[5]. Another study found that the first intron of *FLC2* contains an insertion mutation of approximately 1 628 bp in the late-bolting donor ‘Baiyuchun’. The promoting effect on late-bolting is greater in homozygous insertion mutants than in heterozygotes. Using PCR amplification based on this insertion mutation, homozygous late-bolting plants can be accurately identified at the flowering stage, effectively preventing trait segregation^[6].

Achievements in new variety breeding

In recent years, significant progress has been made in breeding new bolting-tolerant radish varieties. The radish breeding team of Huasheng Agricultural Group Co., Ltd. has developed late-bolting varieties such as ‘Tianshanxue No. 2’ and ‘Tianshanxue 679’, which are comparable to the bolting-tolerant Korean variety

‘Baiyuchun’, and have largely replaced imports of Korean radish varieties. The team at Nanjing Agricultural University has utilized heterosis combined with marker-assisted selection to develop late-bolting varieties including ‘Nanchunbai No. 1’, ‘Nanchunbai No. 5’, ‘Nanchunbai No. 6’, and ‘Nanchunhong No. 2’^[12]. In 2025, the new radish line ‘C30114’, bred by the radish team of the Rice and Sorghum Research Institute of Sichuan Academy of Agricultural Sciences, passed technical appraisal by a provincial expert panel. Its average period from sowing to bolting in Pingba District, Sichuan Province reached 182.5 d, comparable to the bolting-tolerant Korean variety ‘Baiyuchun’. It also exhibits excellent self-compatibility, and the hybrid combination achieved a yield increase of 5.53% over ‘Baiyuchun’^[7].

Prospects for gene editing and novel breeding technology

The resolution of the T2T complete genome has laid a solid foundation for the application of gene editing technologies. Based on this genome, a number of excellent candidate genes related to bolting tolerance, hollowness tolerance, and quality have been preliminarily identified^[8]. The gene editing technology based on CRISPR/Cas9 can precisely modify bolting tolerance-related genes to create new germplasms with targeted improvements in target traits. The invention patent “An m6A Demethylase-Regulated Bolting and Flowering Gene *RsSUF4* in Radish and Its Application”, published in 2025, clarified the functions of the m6A demethylase *RsALKBH10B* and the flowering repressor gene *RsSUF4* in flowering regulation for the first time; overexpression of *RsALKBH10B* reduces m6A modification levels and promotes bolting and flowering, whereas overexpression of *RsSUF4* delays bolting and flowering. This provides novel molecular targets for bolting-tolerant breeding.

Prospects and Discussion

Overall, radish bolting is a complex trait regulated by multiple genes and closely interacting with environmental factors. In recent years, significant progress has been made in this field, including the successful assembly of the T2T complete genome, the discovery of key regulatory genes such as *RsMIPS3*, in-depth elucidation of *FLC* family functions and epigenetic regulatory mechanisms, the development and application of molecular markers, and the breeding of multiple new bolting-tolerant varieties. However, several challenges remain in current research. The number of key regulatory genes identified is still limited, and substantial work is still required to move from QTL mapping to fine analysis of functional genes. The interactive mechanisms among different regulatory pathways, including the vernalization pathway, photoperiod pathway, and gibberellin pathway, remain unclear. Moreover, existing bolting-tolerant varieties are still primarily developed through traditional breeding approaches, and the deep integration of modern biotechnology and conventional breeding urgently needs to be strengthened.

Looking to the future, it is recommended to focus on breakthroughs in the directions below. First, fine QTL mapping and

map-based cloning should be deepened to systematically uncover key functional genes in the bolting regulatory network. Second, the dynamic regulatory mechanisms of epigenetic modifications in vernalization memory maintenance and bolting initiation should be systematically elucidated, with particular attention to the functional conservation and species specificity of PRC2-mediated histone modification pathways in radish. Third, a marker-assisted selection system based on genome-wide association studies should be established to improve the efficiency of selecting bolting-tolerant traits. Fourth, the ecological adaptability evaluation of bolting-tolerant varieties and the integration of supporting cultivation techniques should be strengthened to promote the transformation of research findings into production applications. With the continued development of genomics, epigenetics, and gene editing technologies, the molecular code of radish bolting is expected to be fully deciphered. The independent breeding of bolting-tolerant radish varieties is set to enter a fast track, providing strong scientific and technological support for the stable development and year-round balanced supply of China's radish industry.

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Editor: Yingzhi GUANG

Proofreader: Xinxiu ZHU



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Editor: Yingzhi GUANG

Proofreader: Xinxiu ZHU