Green Carbon 3 (2025) 110–112

Contents lists available at ScienceDirect

Green Carbon

journal homepage: www.keaipublishing.com/en/journals/green-carbon/

Commentary

MADS-box transcription factors as green-revolution regulators for plant longevity and biomass production

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During long-term evolution, plants have signified a shift in their life-history strategy from perenniality to annuality to rapidly complete their reproduction in variable climatic environments. However, as the human population is rapidly increasing and fossil fuels are being increasingly consumed, it becomes essential to develop low-carbon agriculture and sustainable industries. Therefore, it is important to improve plant perennial flowering behavior to upgrade biomass production and maintain biodiversity as a green revolution and carbon neutralization strategy [1].

In principle, annual plants have a relatively short lifecycle for completing their entire life period within a single growing season, whereas perennial plants span multiple seasons and repeat their flowering and fruiting periods over several years. Because plant flowering process symbolizes the transition from nutritional growth phase to reproductive period, it is defined as a crucial step in accounting for perennial characteristics. Although it has been recognized that repeating the nutritional growth phase after the flowering stage determines the ability of plants to retain perennial traits, the evolutionary motivation behind the different life history strategies remains unclear.

As a physiological process induced by low temperatures, the vernalization response plays a decisive role in the initiation of reproductive growth and is indispensable for flowering in many plants. Through vernalization, plants can sense and respond to environmental signals, such as winter cold and spring thaw, and dynamically enter the reproductive growth stage. Vernalization collaborates with age-dependent pathways to regulate the initiation of plant flowering, which is intimately associated with the growth patterns and characteristics of perennial plants. This regulatory mechanism guarantees that perennial herbaceous plants can commence flowering and fruiting once they have accumulated adequate biomass triggered by external environmental alterations. Therefore, a recent article titled "Reciprocal conversion between annual and polycarpic perennial flowering behavior in the *Brassicaceae*" accomplished an in-depth exploration of the transformation between different life-history strategies in *Brassicaceae* [2]. Zhai et al. identified two perennial model species of *Brassicaceae* (*C. himalaica* and *E. nevadense*) and employed forward genetics methods to identify three crucial MADS box transcription factors that regulate the transformation of plant life history strategies such as *FLOWERING LOCUS C (FLC)*, *FLOWERING LOCUS M* (*FLM*), and *MADS AFFECTING FLOWERING* (*MAF*). These three transcription factors are highly homologous and functionally redundant, and each gene can independently respond to vernalization to inhibit flowering and restore plant nutritional growth. Based on their expression patterns, protein functions and epigenetic modifications, *FLC*, *FLM* and *MAF* enable the determination of the evolution of different life-history strategies in *Brassicaceae* plants. In particular, the inhibitory histone modification H3K27me3 induced by vernalization restricts the expression of *FLC*, *FLM*, and *MAF* genes to promote flowering after vernalization in perennial *Brassicaceae* plants. However, the modification of H3K27me3 is gradually relieved after vernalization, and these three types of genes resume expression to promote the transition of plants to vegetative growth. In annual *Brassicaceae* plants, there are either functional defects in the proteins encoded by *FLC*, *FLM* and *MAF*, or stable maintenance of H3K27me3 modification, which prevents the transition from flowering to nutrient growth. While CRISPR-Cas9 technology has been employed to simultaneously knock out three genes, *ChFLC*, *ChFLM* and *ChMAF* in the perennial *Brassicaceae* plant (*C. himalaica*), the plant

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https://doi.org/10.1016/j.greenca.2024.09.007
Received 8 July 2024; Received in revised form 2 September 2024; Accepted 11 September 2024
Available online 30 October 2024

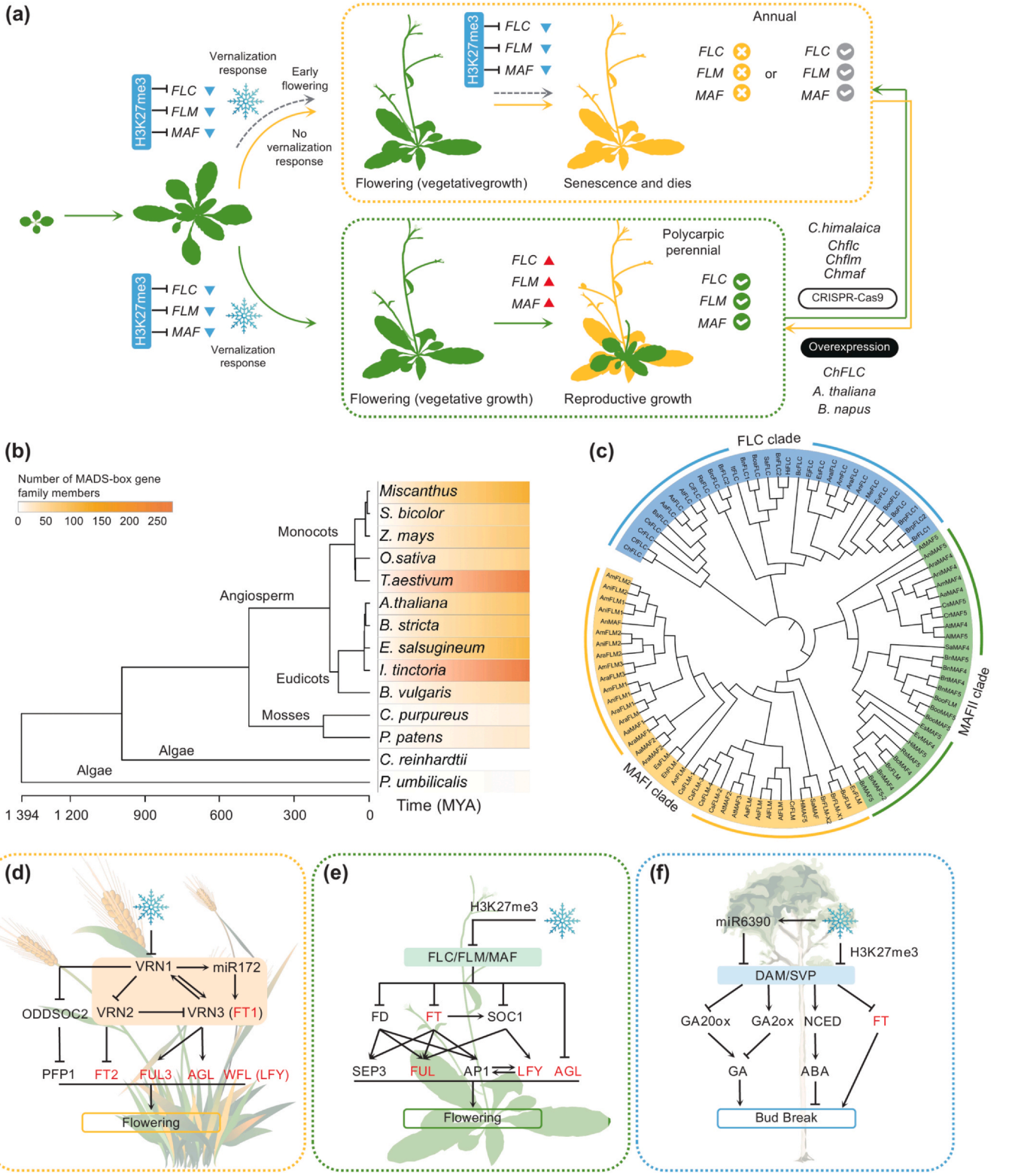

Fig. 1. MADS-box genes play a crucial role in perennial flowering habits of plants. (a) The transition model of *Brassicaceae* plants between annuality and perenniality. The *FLC*, *FLM,* and *MAF* genes encode the proteins that suppress flowering to promote nutritional growth in plants, but their expressions are repressed by the histone modification of H3K27me3 induced by vernalization responses. In polycarpic perennial *Brassicaceae*, the restoration of H3K27me3 modification after vernalization enables re-expressions of those three genes to re-promote the nutritional growth for maintaining perennial habit (marked as green arrow). In annual *Brassicaceae,* either functional deficiencies in *FLC*, *FLM*, and *MAF* proteins (yellow arrow) or the stable maintenance of H3K27me3 modification results in stable repression of those three genes after flowering (grey arrow), preventing the recovery of nutritional growth as annual life cycle. **(b)** The duplication events of MADS-box genes during plant evolutionary process. Members of the MADS-box gene family could increase their copy numbers in the genome through gene duplication mechanisms, which plays an important role in plant functional differentiation and morphogenesis. **(c)** Phylogenetic tree of *FLC*-like genes in *Brassicaceae* plants. **(d, e)** Regulatory networks of vernalization responses and flowerings in wheat (**d**) and *Brassicaceae* (**e**). **(f)** Regulatory network of dormancy in woody plants.

exhibits an annualized phenotype. In contrast, perennial habit is achieved by overexpressing *ChFLC* in annual *Brassicaceae* plants (*Arabidopsis thaliana* and *Brassica napus*) (Fig. 1(a)). Hence, this study is the first to achieve free conversion between perennial and annual life-history strategies in *Brassicaceae* plants, providing a theoretical foundation for the precise design and targeted cultivation of perennial rapeseed crops to adapt for specific climatic and geographical environments in the future. It also contributes to the sustainable development of agriculture by promoting biomass production and reducing water and fertilizer supply. Nonetheless, Zhai et al. have also pointed out that multiple flowering is a prerequisite for the perennial habit of cruciferous plants. In addition to the flowering habit, it is necessary to consider the effective utilization of bioenergy by plant tissues, such as leaves and roots, via a regulatory source-sink drive or the interactions among multiple traits from the growth and development of underground plant organs.

During plant evolution, MADS-box genes have been involved in multiple gene duplication events, leading to their expansion into important gene families in angiosperms (Fig. 1(b)). Notably, the MADS-box gene family plays a core role in driving flower morphological diversity, regulating reproductive organ development, promoting seed germination, and enhancing plant adaptability to environmental changes [3]. In terms of the evolutionary process of *Brassicaceae* plants, MADS-box genes such as *FLC*, *FLM* and *MAF*, form a unique branch that enables the creation of a characteristic flowering pathway (Fig. 1(c,e)). Despite distinct flowering processes in *Brassicaceae* plants, MADS-box genes have similar functions in other plant species. For example, a group of crucial MADS-box genes have been identified in wheat including *TaVRN1* and *TaVRN2*, which constitute the core of the vernalization-flowering regulation network. As *TaVRN1* serves as a key factor in the response to vernalization by sensing and responding to low winter temperatures, its downregulation could relieve the inhibitory effect on the flowering repressor *TaVRN2*. When the expression level of *TaVRN2* is excessively high, it directly suppresses the expression of the *Flowering Locus T* (*FT*), thereby delaying or preventing plants from entering the flowering stage (Fig. 1(d)) [4]. Moreover, the MADS-box gene *DAM6* in woody plants functions similarly to *FLC*, and its expression is suppressed by the cold-induced repressive histone modification H3K27me3. When woody plants enter dormancy, *DAM* proteins inhibit the expression of *FT2* and the GA synthetic enzyme *GA20OXs* genes, suppressing bud sprouting to maintain the dormant state. During the accumulation of low temperatures, *DAM* gene expression is significantly downregulated by inhibiting the expression of *FT2* and *GA20OXs* genes, which promote the release of dormancy within buds and the sprouting of buds (Fig. 1(f)) [5]. Therefore, the transformation of different life history strategies in crucifers provides insights into models for other plant species. In addition, *FT* , *LEAFY* (*LFY*), *FRUITFULL* (*FUL*), *AGAMOUS-LIKE* (*AGL*) and other genes were direct targets of the regulator *FLC* in the flowering control network (Fig. 1(d–f)). These genes have shown functional conservation across different plant species, which indicates a theoretical basis and practical approach to precisely regulate plant life history strategies for enhancing plant longevity and biomass production via heterologous expression of the *FLC* gene.

CRediT authorship contribution statement

Liangcai Peng: Writing – review & editing, Project administration, Conceptualization. **Chunxiang Fu:** Investigation. **Xifeng Ren:** Data curation. **Jingyuan Liu:** Writing – original draft, Formal analysis. **Yixiang Wang:** Writing – original draft, Visualization, Software, Formal analysis. **Yanting Wang:** Writing – review & editing, Project administration, Methodology.

Declaration of competing interest

Liangcai Peng is an associate editor for Green Carbon and was not involved in the editorial review or the decision to publish this article. The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This work was supported by the National Natural Science Foundation of China (32101701, 32470273, 32170268), Hubei Provincial Natural Science Foundation of China for Excellent Young Scientists (2024 AFA100), National 111 Project of the Ministry of Education of China (BP0820035), and an Initiative Grant of Hubei University of Technology for High-level Talents (GCC20230001).

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