Epigenetic Regulation of Flowering Time

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Introduction

Transition to flowering at the appropriate time of the life cycle of the plant is crucial for reproductive success of many species of plants, and it has special relevance in short season agroecological zones for successful reproduction.

Flowering time is controlled by a set of nearly 300 genes belonging to eight different pathways responding to external cues (photoperiod and temperature) and internal signals (hormones, sugars, etc.). Master regulatory genes governing flowering time includes *CONSTANS* (*CO*), *FLOWERING LOCUS T* (*FT*), *FLOWERING LOCUS C* (*FLC*), *APETALA 1* (*AP1*) and *LEAFY* (*LFY*) and epigenetic mechanisms play a crucial role in the regulation of expression of some of these genes.

In this poster, we present the current understanding about the genetic and epigenetic control of flowering time since early flowering lines have implications in breeding for early maturing cultivars in crops including flax (Figure 1).

Figure 1.A. Commercial flax field near Grenfell Saskatchewan (photo: Helen Booker); **B.** the flax growing areas of Western Canada (**Source:** Flax Council of Canada)

Definitions

Epigenetics: is mainly described as the heritable alteration to gene expression without any change to the underlying DNA sequence and can be transmitted through both mitosis and meiosis.

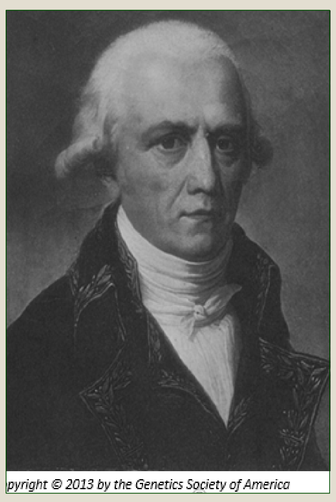


Figure 2: Jean-Baptiste de Lamarck (1744-1829), a French biologist is considered as a pioneer in Epigenetics.

Jean-Baptise de Lamarck (1803 ; Figure 2) proposed the theory of inheritance of acquired traits, popularly known as '**Lamarckism'.**

Epialleles: can be defined as variation in the levels of DNA methylation at a specific gene locus and may underlie heritable phenotypic variation across several generations.

Transgenerational epigenetic inheritance:
(i) Meiotically heritable.
(ii) No change in DNA sequence.
(iii) Is stable without initial stimulus.

Genetic Control of Flowering Time

In *Arabidopsis thaliana*, flowering time is controlled by vernalization, autonomous, photoperiod, and gibberellin pathways (Figure 3).

The *FT* gene expressed in the companion cells of the phloem is transported to shoot apical meristem (SAM) through phloem sieve elements, and this FT-protein is the 'florigen' the systemic signal hypothesized in 1930s by Chaïlakhyan (Nakamura et al, 2014).

- The list of major genes associated with flowering time is given in the Table 1.

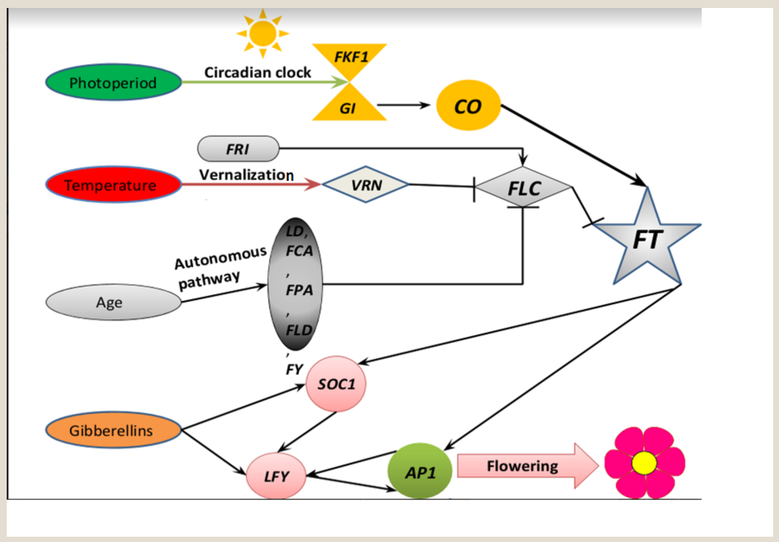


Figure 3. Proposed genetic control of flowering in *Arabidopsis thaliana*, vernalization, autonomous, photoperiod, and gibberellin pathways together affect the gene multiplication. Photoperiod affects *FKF1* and *GI*, while *GI* promotes *CO* which increases *FT*. *FRI* assist *FLC* duplication that suppress *FT*. In autonomous, *LD*, *FCA*, *FPA*, *FLD*, *FY* as well as *VRN* in vernalization repress *FLC*. Gibberellins affect both *SOC1* and *LFY* positively, in addition, *FT* enhance *LFY* through increasing *SOC1*. Both *LFY* and *FT* contribute to *AP1* duplication, thus inducing transition from vegetative to flowering stage

Table 1: **Regulatory genes governing transition from vegetative to reproductive phase**

Gene name	Function
FLOWERING LOCUS T (*FT*)	The key factor controlling floral inductive signals
FLOWERING LOCUS C (*FRI*)	A key repressor of *FT*
FRIGIDA (*FLC*)	Upregulates and increase *FLC* expression
LEAFY and *APETALA1* (*AP1* & *LFY*)	Both induces transition from vegetative to flowering stage
GIGANTEA (*GI*), *FLAVIN KELCH F BOX 1* (*FKF1*), *CO* and *FT*	The prime sensing unit of light/photoperiod
FLC, *SHORT VEGETATIVE PHASE* (*SVP*), *TEMPRANILLO 1* (*TEM1*) and *SCHLAFMUTZE* (*SMZ*)	*FT* repressors
Mutations in *EARLY FLOWERING7* (*ELF7*), *VERNALIZATION INDEPENDENCE 4* (*VIP4*), *PHOTOPERIOD-INDEPENDENT EARLY FLOWERING1* (*PIE1*) and *EARLY FLOWERING IN SHORT DAYS* (*SDG8*);	*FLC* repressors group 1
FRI-LIKE1 (*FRL1*), *FRIGIDA-ESSENTIAL1* (*FES1*), and *SUPPRESSOR OF FRIGIDA4* (*SUF4*) .	*FLC* repressors group 2- directly repressing *FRI*

Epigenetic Control of Flowering Time

Histone modification such as acetylation, methylation, and phosphorylation of histones mediate epigenetic regulation of gene expression.

- Histone methylation governs winter memory through a protein complex that changes the tail of histone H3 by tri-methylating lysine 27 (H3K27me3, Figure 4).
- In general, hypoacetylated histones are associated with gene repression, whereas hyperacetylated histones are related to gene activation.

DNA methylation is catalyzed by a group of methyltransferases that transfer a methyl group from S-adenosylmethionine (SAM) to adenine purine ring or cytosine pyrimidine ring (in CG, CHG, and CHH sequence contexts) in DNA, and this methylation mark can cause a functional loss of the locus with an adverse impact on plant growth (Penterman et al., 2007). A flowering time mutant resulting from hypomethylation has been observed in *Bambusa multiplexcanes* (Yuan et al., 2012). 5-azacytidine induced hypomethylation significantly advanced flowering time in species such as *Linum usitatissimum* (Fieldes and Amyot, 1999).

Transposable elements which occupy a large portion of plant genomes also mediate epigenetic regulation of phenotypic traits including flowering time. In cereal genomes like maize and sorghum, DNA methylation variation found at *Vgt1* allele harboring a miniature inverted repeat transposable element (MITE) conditions an early flowering phenotype.

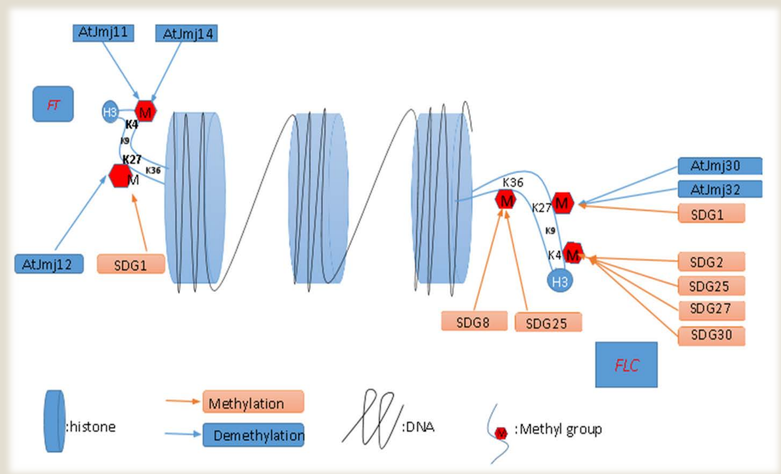
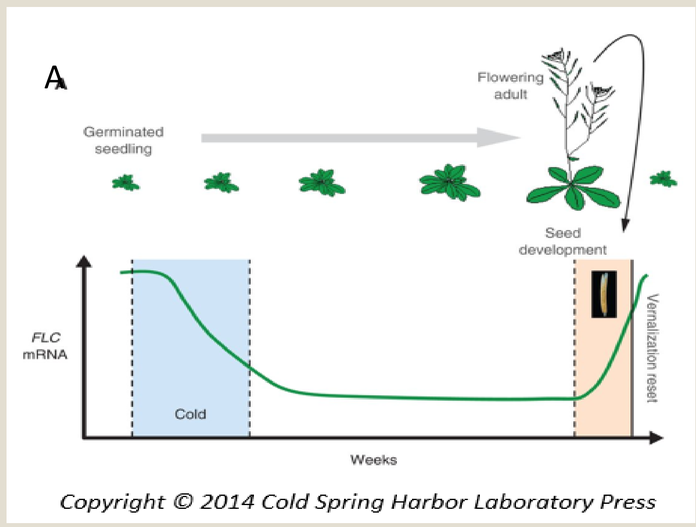


Figure 4: Histone methylation is mainly associated with different lysine residues on H3. AtJmj groups cause demethylation to K4, K27; while SDG family lead to methylation on K4, K27, K36. These epi-modifications affect the expression of both FT and FLC thereby affecting flowering time.

Vernalization

Exposure to cold period to initiate flowering was reported in *Hyoscyamus niger* (Lang, 1965). The cells in shoot apical meristem (SAM) directly sense cold and are vernalized, and the vernalized state stably inherited through mitotic divisions (Amasino, 2010, Figure 5).



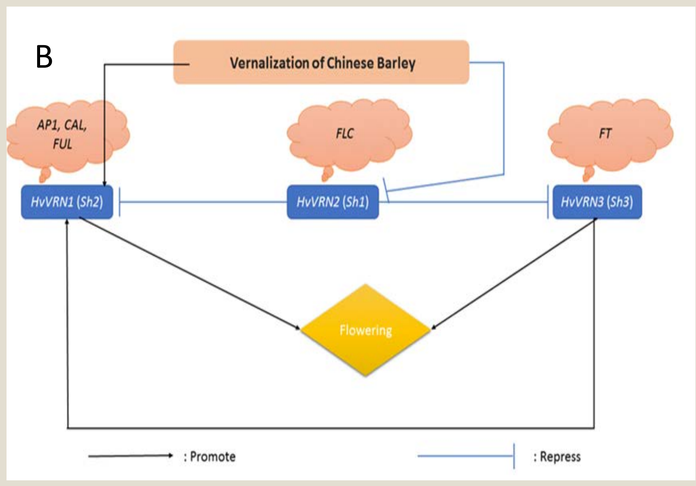


Figure 5: A. Vernalization. FLC expression is epigenetically silenced by cold and reset during embryo development. The floral repressor gene, FLC, is highly expressed in young seedlings. As plants perceive cold, the expression is quantitatively repressed, dependent on the length of cold experienced. As temperatures warm in spring, the repression is epigenetically maintained until seed development when it is reset. This ensures that each generation of seedlings requires vernalization. **B.** The orthologues of Arabidopsis flowering genes found in Chinese barley: *Sh2* is functioning like *AP1*, *CAL*, and *FUL*, acting with *Sh3-FT* to introduce flowering, but *Sh1* works like *FLC* that repress both *Sh2* and *Sh3* to delay flowering. Vernalization will repress *Sh1* and promote *Sh2*, thereby inducing flowering.

Conclusion

Flax is one of the last crops to mature in the northern prairies of Canada. Flax farmers face a potential risk of an early frost in fall, cultivation of earlier flowering varieties can potentially reduce this risk. Epigenetic mechanisms only change the gene expression without modifying the underlying DNA sequence, thus the stringent regulations adopted for genetically modified plants (GMOs) need not be applied for epigenetically derived seeds by government regulators and bringing these cultivars to the market is comparatively cheaper.

References

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Acknowledgements

Lei Chen would like to thank the AgBio Faculty, his Professors and Teaching Assistants for providing an enriching experience and for their advice. Guidance by the course coordinators Drs. Graham Scoles and Tim Sharbel is also gratefully acknowledged.