



## REVIEW

# LEAFY COTYLEDONs: old genes with new roles beyond seed development [version 1; peer review: 2 approved]

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## Abstract

Seed development is a complex process and consists of two phases: embryo morphogenesis and seed maturation. LEAFY COTYLEDON (LEC) transcription factors, first discovered in *Arabidopsis thaliana* several decades ago, are master regulators of seed development. Here, we first summarize molecular genetic mechanisms underlying the control of embryogenesis and seed maturation by LECs and then provide a brief review of recent findings in the role of LECs in embryonic resetting of the parental 'memory of winter cold' in *Arabidopsis*. In addition, we discuss various chromatin-based mechanisms underlying developmental silencing of LEC genes throughout the post-embryonic development to terminate the embryonic developmental program.

## Keywords

Seed development, LEC1, LEC2, FUS3, pioneer transcription factor, embryonic reprogramming, vernalization, FLC

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## Introduction

Plant seeds are composed mainly of three distinct compartments: embryo, endosperm, and seed coat. Seed development is a complex and critical stage in the life cycle of higher plants. This development process is classified generally into two different phases: a morphogenesis phase, which is initiated after fertilization and consists of cell division and differentiation, apical–basal plant axis establishment, and organogenesis, and a maturation phase, which includes organ expansion, storage macromolecule accumulation, and acquisition of desiccation tolerance<sup>1,2</sup>. Each stage of seed development is regulated by a number of transcription factors (TFs), among which are *LEAFY COTYLEDON (LEC1)*, *LEC2*, and *FUSCA3 (FUS3)*<sup>2</sup>. These three genes, first identified in *Arabidopsis*, are master transcriptional regulators in seed development<sup>1,2</sup>. Loss-of-function mutations in *LEC1*, *LEC2*, or *FUS3* lead to a partial loss of embryo identity and give rise to a homeotic ‘leafy cotyledon’ phenotype: embryos with cotyledons characteristic of leaf traits (for example, trichome development and anthocyanin accumulation)<sup>1,2</sup>. When ectopically expressed during vegetative phases, these genes can induce somatic embryogenesis. Hence, these genes constitute the group of *LEC* genes and appear to be evolutionarily conserved across angiosperms to control seed development from embryogenesis through seed maturation<sup>2,3</sup>.

## Old story: *LEC* genes are master regulators of seed development

*LEC1* encodes a subunit of a trimeric nuclear factor Y (NF-Y) TF and its expression is *de novo* activated shortly after fertilization<sup>4</sup>. Both *LEC2* and *FUS3* encode plant-specific B3-domain TFs and their expression in early embryos is *de novo* activated within 2 and 3 days after fertilization (DAFs), respectively<sup>4,6</sup>. *LEC1* partly promotes the expression of both *LEC2* and *FUS3*<sup>1,2</sup>. These three master TFs regulate thousands of genes from early through late stages during seed development in *Arabidopsis*<sup>7–9</sup> and function in partial redundancy as well as synergistically to control seed development<sup>1,2</sup>.

The *LEC1*-bearing heterotrimeric NF-Y, through a DNA-binding subunit (NF-YA), binds the CCAAT motif of the target gene to regulate their expression<sup>7</sup>. Various genetic and molecular analyses reveal that *LEC1* is a central regulator of seed development and controls embryonic morphogenesis such as to maintain sensor identity and specifying cotyledon identity and seed maturation, including biosynthesis of storage macromolecules, acquiring desiccation tolerance, and seed dormancy<sup>1,2</sup>. Recent studies show that *LEC1* sequentially regulates distinct sets of genes involved in seed development from early through late stages by coordinating with distinctive TFs and hormones at different stages<sup>7</sup>. In early embryogenesis, *LEC1* directly regulates the expression of the HD-ZP III TFs *PHAVOLUTA* and *PHABULOSA* (functioning as apical fate master regulators), and the basic leucine zipper (bZIP) TF *SCARECROW* that controls root architecture<sup>7,10,11</sup>, to promote the establishment of the apical–basal plant axis in embryogenesis. In addition, upon a high level of GA accumulation and consequent degradation of the DELLA protein (a *LEC1* part-

ner), *LEC1* is released to activate the expression of the auxin-biosynthesis genes, including *YUC4* and *YUC10*, leading to auxin accumulation to facilitate embryo morphogenesis<sup>12</sup>. In the embryo/seed maturation phase, for instance, *LEC1* activates the expression of *CRUCIFERIN* (encoding a seed storage protein) and *FATTY ACID DESTATURASE3*, leading to the accumulation of seed storage macromolecules<sup>13,14</sup>.

Apart from the CCAAT motif, recent genome-wide analyses of *LEC1* occupancy reveal that other *cis*-regulatory elements are enriched in *LEC1* target genes in seed development, including RY (CATGCA), ABRE [(C/G/T) ACGTG(G/T)(A/C)] and G-box (CACGTG)<sup>7,15</sup>. This indicates that *LEC1* may partner with other DNA-binding proteins to regulate seed gene expression. It has recently been shown that *LEC1* can interact with *LEC2* to form a ternary complex that regulates seed gene expression<sup>16,17</sup>; in addition, *LEC2* and *FUS3* can form a heterodimer<sup>18</sup>. The DNA-binding B3 domains in both *LEC2* and *FUS3* recognize the RY motif or its variants<sup>8,9,19</sup>; hence, it is not surprising that the RY motif or variants are enriched in *LEC1*-binding sites. Consistent with similar seed phenotypes in *lec1*, *lec2*, and *fus3*, these three genes regulate common sets of genes that are involved in embryogenesis or seed maturation or both<sup>7,8</sup>. Nevertheless, these three genes each have distinct targets in seed development<sup>7–9</sup>. Thus, these genes have partially overlapping as well as synergistic functions in the control of seed development.

## New function: *LEC* genes reset the parental ‘memory of winter cold’ in early embryogenesis

Many over-wintering plants in temperate climates acquire competence to flower in spring after experiencing winter cold (prolonged cold exposure) through a process known as vernalization<sup>20,21</sup>. The vernalization pathways shut down the expression of a potent floral repressor and this vernalization-mediated repression or ‘vernalized state’ is maintained in cell divisions during subsequent growth and development when the temperature rises in spring, namely epigenetic ‘memory of winter cold’, enabling plants to flower in spring<sup>21,22</sup>. However, the ‘memory of winter cold’ must be reset/erased in the next generation to ensure that each generation or growth cycle experiences winter cold prior to flowering and thus flowers at a right season to maximize reproductive success<sup>22,23</sup>. In crucifers such as *Arabidopsis thaliana*, the vernalization pathway represses the expression of the potent floral repressor *FLOWERING LOCUS C (FLC)* to enable spring flowering<sup>21</sup>. Recent studies reveal that shortly after fertilization *LEC1* functions as a pioneer TF to initiate *FLC* resetting/re-activation and that *LEC2* and *FUS3* subsequently function together with *LEC1* to fully re-activate *FLC* expression in early embryogenesis<sup>19,24</sup>. Hence, these three *LEC* genes act to reset the parental ‘memory of winter cold’ during early embryogenesis in *Arabidopsis*.

In *Arabidopsis* winter annuals, *FLC*, encoding a MADS-box TF, is upregulated by *FRIGIDA (FRI)* to a high level to inhibit precocious flowering in young seedlings prior to winter cold exposure<sup>25,26</sup>. *FRI*, a plant-specific scaffold protein, is enriched at the *FLC* locus and functions as ‘molecular glue’ to recruit

active chromatin modifiers such as the histone 3 lysine 4 (H3K4) methyltransferase complex COMPASS-like and the histone 3 lysine 36 (H3K36) methyltransferase EARLY FLOWERING IN SHORT DAYS (EFS, also called as SDG8) and histone acetyltransferases<sup>27–29</sup>. This leads to the establishment of an active chromatin environment with multiple active chromatin marks, including H3K4me3, H3K36me3, and histone acetylation, resulting in a high level of *FLC* expression<sup>29</sup>. When the temperature drops in winter, two homologous B3-bearing proteins VP1/ABI3-LIKE 1 (VAL1) and VAL2 are specifically enriched at a 47–base pair *cis*-regulatory element encompassing two canonical RY motifs (known as ‘cold memory element’ or CME), located near the 5’ end of the first intron of *FLC*, to mediate *FLC* silencing by vernalization<sup>30,31</sup>. VAL proteins further recruit Polycomb group (PcG) proteins such as Polycomb repressive complex 2 (PRC2, an H3K27 methyltransferase complex) that deposits the repressive histone mark H3K27 trimethylation (H3K27me3), leading to a silenced chromatin state at *FLC* and consequent *FLC* silencing by vernalization<sup>31</sup>. After return to warmth, the silenced *FLC* chromatin is stably maintained or ‘memorized’ through cell divisions during subsequent growth and development through DNA replication-coupled H3K27 trimethylation by PRC2<sup>32,33</sup>.

The epigenetic ‘memory of winter cold’ is reset in the next generation. A recent study has revealed that a *LEC1*-bearing NF-Y (*LEC1* NF-Y) pioneer TF initiates *FLC* re-activation/resetting shortly after fertilization<sup>24</sup>. Loss of *LEC1* function disables *FLC* resetting in early embryogenesis and thus *FLC* remained silenced in the next generation in the absence of winter cold exposure. *LEC1* NF-Y binds to CCAAT motifs located in a distal *FLC* 5’ promoter region, enabling the CME to be accessible to *LEC2* and *FUS3*<sup>19</sup>. The B3 domains of *LEC2*, *FUS3*, *VAL1*, and *VAL2* bind to CME in an identical manner<sup>19</sup>. In early embryogenesis, *LEC2* and *FUS3* are progressively enriched at the CME region, whereas the levels of *VAL* proteins at CME are progressively reduced, resulting in a disruption of PcG-mediated silencing at *FLC* inherited from the vernalized parents<sup>19</sup>. On the other hand, *LEC2* and *FUS3* further recruit FRI in complex with active chromatin modifiers to establish an active *FLC* chromatin state, resulting in embryonic *FLC* re-activation/resetting<sup>19</sup>. The active embryonic *FLC* chromatin state can be transmitted to young seedlings upon seed germination and a high-level expression of *FLC* prevents precocious flowering prior to winter cold exposure<sup>24</sup>.

### Developmental silencing of *LEC* genes throughout post-embryonic development

*LEC* genes are specifically or primarily expressed in seed development and silenced throughout post-embryonic development under normal growth conditions<sup>2,4</sup>. This terminates the embryonic developmental program. Following seed germination, plants enter vegetative growth and development. Furthermore, the silencing of *LECs* at seedling stages enables *VAL1* and *VAL2* to bind to CME at the *FLC* locus to mediate *FLC* silencing again by vernalization when winter cold comes<sup>19</sup>,

ensuring that each generation acquires competence to flower after experiencing winter.

*LEC* genes are silenced by chromatin-mediated mechanisms through repressive chromatin modifications throughout post-embryonic development<sup>2</sup>. Following seed germination, histone deacetylases such as HDA6 and HDA19 are enriched at the *LEC* loci for histone deacetylation<sup>34,35</sup>. In addition, Polycomb repressive complex 1 (PRC1), containing an E3 ubiquitin ligase AtBMI1A/AtBMI1B, is enriched at *LEC* loci to mediate histone H2A monoubiquitination (H2Aub), and after H2Aub marking, an H3K27 methyltransferase complex, PRC2, is recruited to deposit the repressive H3K27me3 for transcriptional repression at the *LEC* loci<sup>36–40</sup>. In addition to the H2Aub marking, *cis*-regulatory DNA elements, Polycomb responsive elements (PREs), are required for PRC2 recruitment to both *LEC2* and *FUS3* chromatin<sup>2,41–43</sup>; moreover, H3K27 trimethylation at *LECs* requires ATP-dependent nucleosome remodeling by PICKLE<sup>44</sup>. The H3K27me3 mark at the *LEC* loci is read by LIKE HETEROCHROMATIN PROTEIN 1 (LHP1) and two Bromo adjacent homology (BAH) domain-bearing proteins known as EARLY BOLTING IN SHORT DAYS (EBS) and SHORT LIFE (SHL)<sup>39,45</sup>. These readers further associate with the plant-specific EMBRYONIC FLOWER 1 (EMF1) that mediates chromatin compaction for transcriptional repression<sup>45–47</sup>. In short, PRC1-mediated H2A monoubiquitination initiates the repression of *LECs*, followed by H3K27me3 deposition by PRC2 to establish stable silencing of *LECs*. This results in the switch from embryonic to post-germinative growth and development and thus termination of the embryonic developmental program.

### Perspectives

*LEC1*, *LEC2*, and *FUS3* play essential roles to regulate seed development from early through late stages. Although there is considerable understanding of the regulatory network of *LECs*, important questions remain to be answered. For example, how *LECs* and other transcriptional regulators function together to sequentially regulate various aspects of seed development at different stages. How is the expression of each *LEC* gene *de novo* activated in early embryogenesis? Within hours after fertilization, the expression of *LEC1*, functioning as a pioneer TF, is activated, but the underlying molecular and chromatin mechanisms are essentially unknown.

Plants are sessile and must endure diverse environmental challenges (for example, winter cold) by reprogramming transcriptional circuitries typically through chromatin modifications. At certain loci, some environment-induced chromatin marks are heritable through cell divisions after relief from environmental inputs. In addition to resetting/erasing of the winter cold-induced H3K27me3 at *FLC*, do *LEC* genes function to erase H3K27me3 at other loci and/or other chromatin marks in the Arabidopsis genome in early embryogenesis? Seeds are essential resources of nutrients for humans and animals. Addressing these and related questions will advance the molecular,

genetic, and epigenetic understanding of seed development, providing effective strategies for genetic manipulation of seed development toward high yield and better nutrients.

## Abbreviations

CME, cold memory element; FLC, FLOWERING LOCUS C; FRI, FRIGIDA; FUS3, FUSCA3; H2Aub, histone H2A

monoubiquitination; H3K27me3, histone 3 lysine-27 trimethylation; LEC1, LEAFY COTYLEDON 1; LEC2, LEAFY COTYLEDON 2; LEC, LEAFY COTYLEDON; NF-Y, nuclear factor Y; PcG, Polycomb group; PRC1, Polycomb repressive complex 1; PRC2, Polycomb repressive complex 2; TF, transcription factor; VAL1, VIVIPAROUS/ABI3-LIKE 1; VAL2, VIVIPAROUS/ABI3-LIKE 2

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### Version 1

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**Competing Interests:** No competing interests were disclosed.

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