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# Central role of the LEAFY COTYLEDON1 transcription factor in seed development[FA]

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Invited Expert Review

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**Abstract** Seed development is a complex period of the flowering plant life cycle. After fertilization, the three main regions of the seed, embryo, endosperm and seed coat, undergo a series of developmental processes that result in the production of a mature seed that is developmentally arrested, desiccated, and metabolically quiescent. These processes are highly coordinated, both temporally and spatially, to ensure the proper growth and development of the seed. The transcription factor, LEAFY COTYLEDON1 (LEC1), is a central regulator that controls several aspects of embryo and endosperm development, including embryo morphogenesis, photosynthesis, and storage reserve accumulation. Thus, LEC1 regulates distinct sets of genes at different stages of seed development. Despite its critical importance for seed development, an understanding of the mechanisms underlying LEC1's multifunctionality is only beginning to be obtained. Recent studies describe the roles of specific transcription factors and the hormones, gibberellic acid and abscisic acid, in controlling the activity and transcriptional specificity of LEC1 across seed development. Moreover, studies indicate that LEC1 acts as a pioneer transcription factor to promote epigenetic reprogramming during embryogenesis. In this review, we discuss the mechanisms that enable LEC1 to serve as a central regulator of seed development.

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## INTRICACIES OF SEED DEVELOPMENT

### Overview of seed development

Seed development is a complex period of the flowering plant life cycle. As shown in Figure 1, the seed consists of three different regions, each with a distinct variation on a common genotype: diploid and filial embryo, triploid and filial endosperm, and diploid and maternal seed coat. Moreover, each region is comprised of distinct subregions, tissues, and cell types.

Seed development begins with the double fertilization of the egg and central cells of the embryo sac with two sperm cells that generate the embryo and endosperm, respectively (Goldberg et al. 1994). Fertilization also initiates seed coat development (Roszak and Kohler 2011).

Embryo and endosperm development can be divided temporally into two distinct phases: the morphogenesis phase, which is initiated immediately after fertilization, and the maturation phase, which partially overlaps and follows the morphogenesis phase (Figure 1). The morphogenesis phase is characterized by cell proliferation and differentiation that occur in both the embryo and endosperm. During this phase, the shoot and root apical meristems of the embryo are formed to set up the apical – basal plant axis, and the protoderm, ground meristem, and procambium develop as the tissue system progenitors that constitute the embryo's radial axis (reviewed by Lau et al.

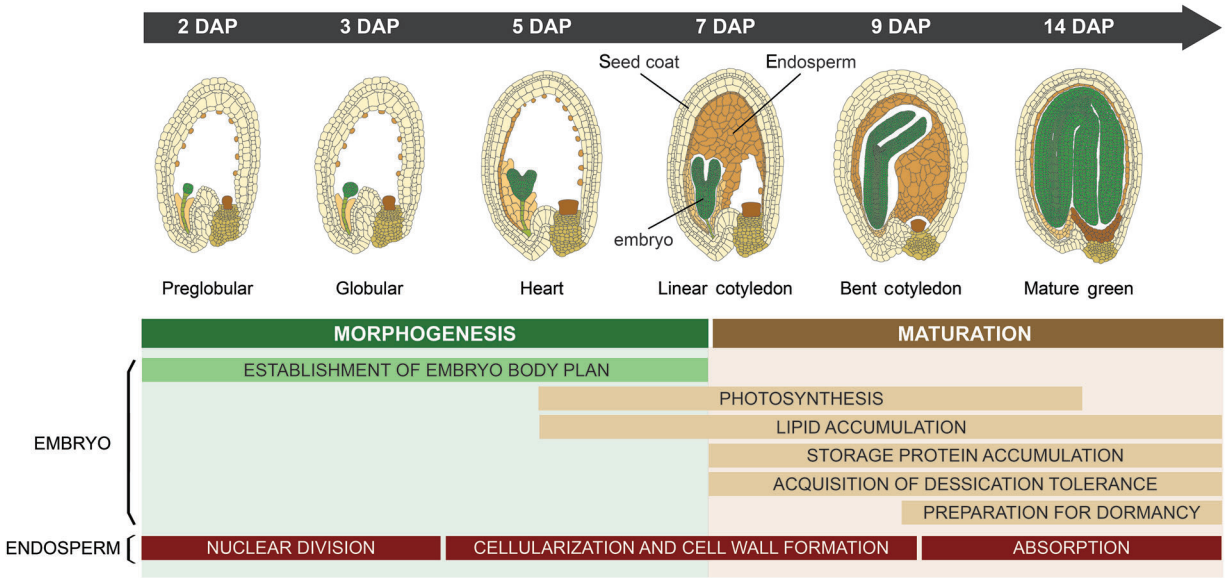


**Figure 1. Overview of the major biological events that occur during seed development**
Seed images diagram *Arabidopsis* seeds at the indicated stages and days after pollination (DAP). Bars indicate the morphogenesis and maturation phases and the major cellular processes that occur in embryos and endosperm.

2012; Palovaara et al. 2016). This basic body pattern which is established during embryogenesis is maintained throughout the sporophytic life cycle of the plant. The endosperm undergoes nuclear and cell proliferation, regionalization, and cell differentiation during the morphogenesis phase, and it develops into tissues that will provide nutrients for the developing embryo and/or postgerminative seedling (Li and Berger 2012).

By contrast, the maturation phase represents an interruption of the patterning, proliferation, and differentiation events that occur during the morphogenesis phase and that are reinitiated during seedling and vegetative development (Raz et al. 2001; Vicente-Carbajosa and Carbonero 2004). The maturation phase is characterized by the synthesis and massive accumulation of storage compounds, such as seed storage lipids and proteins (Harada 1997; Gutierrez et al. 2007; Baud et al. 2008). Storage compound accumulation results in cell expansion and a considerable increase in embryo cell size. It is also during the maturation phase that the embryo acquires the ability to survive desiccation that occurs at the latest stage of seed development through the accumulation of disaccharides, oligosaccharides, storage proteins, and late embryogenesis abundant proteins that preserve the integrity of membranes, proteins, and nucleic acids in the desiccated state (Angelovici et al. 2010; Leprince et al. 2017). Germination of the developing embryo is actively inhibited during the maturation phase, initially through accumulation of the hormone abscisic acid (ABA) and later through a reduction in water content (Kermode 1990). At the end of the maturation phase, the embryo and endosperm are developmentally arrested and metabolically quiescent, and they are typically maintained in this state until conditions favorable for germination are encountered.

## Gene networks in seed development

The complexity of seed development suggests that the cellular processes that underlie specific seed functions must be highly coordinated both temporally and spatially. The onset and termination of these processes are controlled largely by changes in gene expression patterns. Therefore, understanding the mechanisms that control gene expression could aid in the development of strategies that can be used to modify the processes that occur during seed development and, potentially, improve seed quality in many important crop species.

The mRNA profiles of whole seeds and/or seed regions and subregions at different stages of development in several plant species have provided fundamental insights into the processes and regulatory

mechanisms that control seed development (Le et al. 2007; Benedito et al. 2008; Verdier and Thompson 2008; Xiang et al. 2011; Chen et al. 2012; Harada and Pelletier 2012; Belmonte et al. 2013; Terrasson et al. 2013; Becker et al. 2014; Chen et al. 2014; Khan et al. 2014; Li et al. 2014; Pradhan et al. 2014; Aghamirzaie et al. 2015; Gonzalez-Morales et al. 2016; Huang et al. 2017; Rangan et al. 2017). Gene expression patterns reflect spatial differences in seed regions and subregions and temporal differences in developmental stages. However, the most conspicuous change is a major reprogramming of gene expression that occurs in the embryo and endosperm during the transition between the morphogenesis and maturation phase of seed development (Verdier et al. 2008; Severin et al. 2010; Xiang et al. 2011; Chen et al. 2012; Belmonte et al. 2013; Chen et al. 2014). Many genes involved in patterning and morphological differentiation processes are preferentially expressed during the morphogenesis phase, whereas genes that are involved with seed storage macromolecule accumulation and desiccation tolerance are activated at the onset of the maturation phase. Although some aspects of gene expression are regulated posttranscriptionally in seeds (D'Ario et al. 2017), these findings suggest that transcriptional control mechanisms play major roles in regulating seed development.

### An introduction to LEAFY COTYLEDON1

Many transcription factors have been shown to regulate biological processes during seed development (reviewed by Le et al. 2007; Verdier and Thompson 2008; Le et al. 2010; Jia et al. 2014; Pradhan et al. 2014; Baud et al. 2016; Devic and Roscoe 2016). Among these transcription factors, LEAFY COTYLEDON1 (LEC1) has been identified as a key, central regulator of seed development (Meinke 1992; Meinke et al. 1994; West et al. 1994; Lotan et al. 1998; Harada 2001; To et al. 2006; Braybrook and Harada 2008; Pelletier et al. 2017). LEC1 is a novel subunit of the nuclear factor Y (NF-Y) transcription factor that accumulates primarily in the embryo and endosperm, specifically during seed development (Figure 2A) (Lotan et al. 1998; Calvenzani et al. 2012; Gnesutta et al. 2017b). Although LEC1 has long been considered to be a central regulator of seed development, we are only beginning to understand the mechanisms by which LEC1 controls several aspects of seed development, including the biosynthesis of storage macromolecules, desiccation tolerance, photosynthesis, and hormone biosynthesis. In this review, we discuss the multifunctionality of LEC1 during seed development and recent findings that describe potential mechanisms by which LEC1 can regulate distinct biological processes across seed development.

## LEC1 IS A KEY REGULATOR OF THE MATURATION PHASE

LEC1 is a central regulator of seed development that controls cellular processes that occur during the morphogenesis and maturation phases. Initial insights into LEC1 function were obtained through analyses of loss-of-function mutations of *Arabidopsis LEC1* that were identified in genetic screens for *embryo lethal* mutants (Harada 2001). Several characteristics of *lec1* mutants suggest that the transcription factor regulates several processes related to the maturation phase. First, LEC1 is required for embryos to acquire desiccation tolerance. Embryos with null mutations in *LEC1* die, because they do not survive maturation drying at the end of seed development (Meinke 1992; Meinke et al. 1994; West et al. 1994). Second, LEC1 is required for storage macromolecule accumulation. Storage protein and lipid accumulation are severely restricted in *lec1* mutants (Meinke 1992; Meinke et al. 1994; West et al. 1994). A genome-wide comparison of mRNA populations in wild type and *lec1* mutant seeds showed that the major difference in mRNA profiles is observed at the maturation phase of seed development (Pelletier et al. 2017). Genes involved with maturation processes, such as protein and lipid storage, desiccation tolerance, and seed dormancy, are downregulated in *lec1* mutant seeds. Third, postgerminative seedling development is suppressed during seed development by LEC1. The shoot apices of *lec1* mutant embryos are activated and possess leaf primordia, whereas wild type embryonic shoot apices are inactive and do not initiate leaf development (Meinke et al. 1994; West et al. 1994). One interpretation of these findings is that the maturation program prevents the precocious initiation of vegetative development during embryogenesis. Consistent with this interpretation, genes expressed seedling-specifically are prominently upregulated in *lec1* mutant embryos during the late stages of seed development (Pelletier et al. 2017). Thus, pleiotropic effects of the *lec1* mutation led to the conclusion that LEC1 is an essential

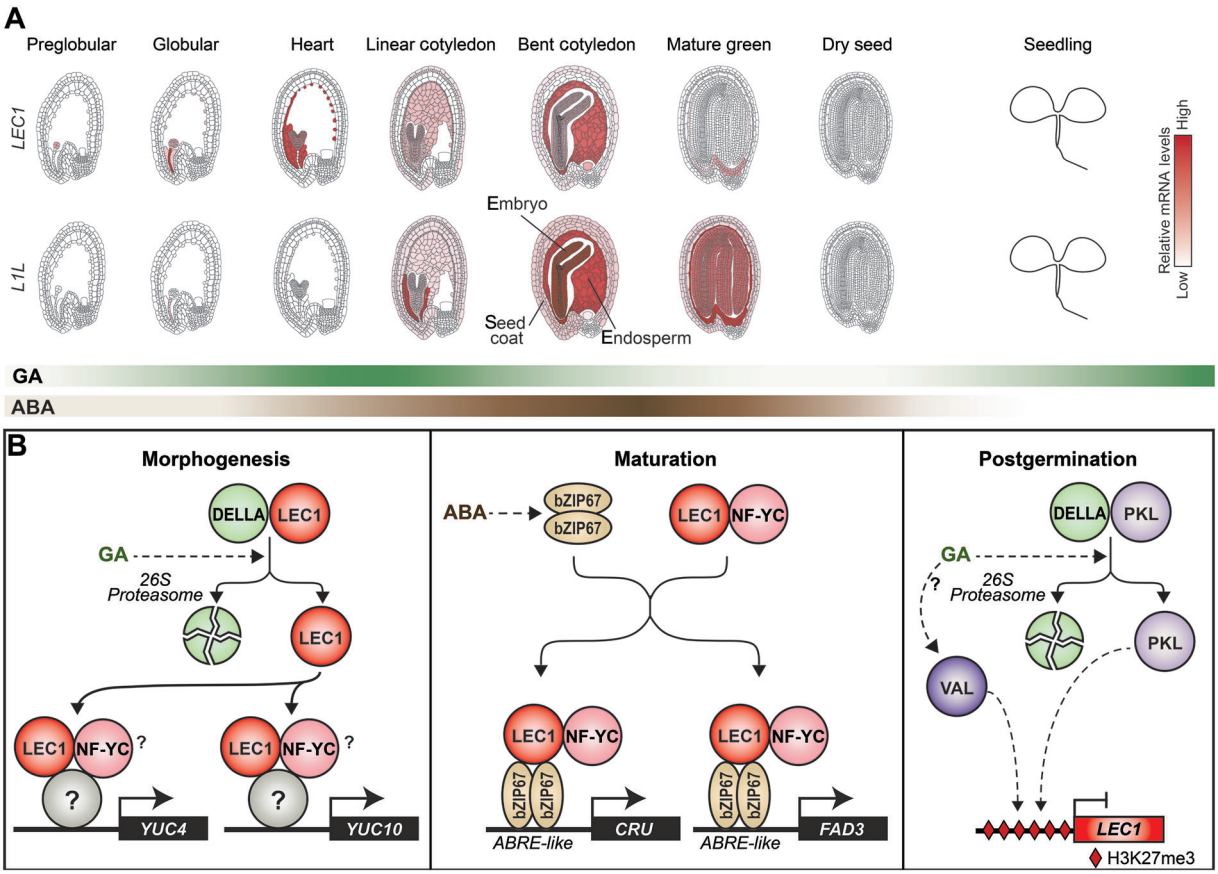


**Figure 2. Modulation of LEC1 activity during seed development**

**(A)** Heat map representations of *LEC1* and *L1L* mRNA levels in embryo, endosperm, and seed coat subregions during *Arabidopsis* seed development (top panel) and GA and ABA levels at the indicated stages of seed and postgerminative development, with darker colors indicating higher relative hormone levels (bottom panel). mRNA data are taken from Belmonte et al. (2013). **(B)** Mechanistic effects of GA and ABA on LEC1 activity. Morphogenesis panel. Because bioactive GA levels are high, DELLA is degraded, releasing LEC1 to activate gene encoding auxin biosynthetic enzymes, *YUC4* and *YUC10*, although the subunits with which LEC1 interacts is not known. Maturation panel. ABA levels are high, and the ABA-inducible transcription factor bZIP67 accumulates and forms a complex with a LEC1-NF-YC (or L1L-NF-YC) dimer. The complex binds *ABRE-like* DNA sequence motifs and activates maturation genes, such as *CRU* and *FAD3*. Postgermination panel. DELLA is degraded, because GA levels become high prior to and during germination and postgermination. PKL is released, resulting in an increase in H3K27me3 occupancy of the *LEC1* promoter and silencing of the *LEC1* gene. An increase in VAL activity, which is thought to be mediated by GA, also results in an increase in H3K27me3 occupancy.

regulator of the maturation phase (Meinke et al. 1994; West et al. 1994; Lotan et al. 1998; Harada 2001; To et al. 2006; Braybrook and Harada 2008; Lepiniec et al. 2018).

LEC1's role during the maturation phase was also demonstrated in gain-of-function genetic experiments. Ectopic expression of *LEC1* in *Arabidopsis* results in the upregulation of several genes involved in processes that occur during the maturation phase, such as seed storage proteins and lipid accumulation, desiccation tolerance, and seed dormancy (Lotan et al. 1998). For example, overexpression of *LEC1* in developing seeds results in the upregulation of key genes involved in fatty acid biosynthesis and storage and an increase in lipid content in a number of plant species (Kagaya et al. 2005; Mu et al. 2008; Tan et al. 2011; Elahi et al. 2016; Pelletier et al. 2017; Tang et al. 2018). These findings open the possibility that manipulating LEC1 expression might be useful to enhance the seed quality of crop plants.

The phenotypes induced by loss- and gain-of-function mutations suggest that LEC1 is a key regulator of the

maturation phase. Genome-wide characterization of LEC1 binding sites revealed that LEC1 can directly regulate several genes involved in processes that occur during the maturation phase of developing *Arabidopsis* and soybean seeds (Junker et al. 2012; Pelletier et al. 2017).

LEC1 has been implicated to have played a critical role in the evolution of the seed habit. In contrast to plant lineages that do not produce seeds, seed plant embryos undergo biochemical and physiological changes during the maturation phase that allow them to withstand maturation drying and metabolic quiescence and undergo the reinitiation of growth after germination. The processes that occur during the maturation phase account, in part, for the evolutionary success of seed plants (Steeves 1983; Harada 2001; Vicente-Carbajosa and Carbonero 2004). Thus, understanding the regulatory circuitry controlling seed maturation could provide insights into the mechanisms that underlie evolution of the seed habit. The requirement of LEC1 to regulate maturation processes opens the possibility that LEC1 may have played a critical role in the evolution of the maturation phase and the seed habit. Consistent with this possibility, phylogenetic analysis revealed that *LEC1*-type genes, which are shared among all spermatophytes, are first detected among basal land plant lineages in lycophytes (Xie et al. 2008; Kirkbride et al. 2013; Cagliari et al. 2014; Fang et al. 2017; Han et al. 2017), suggesting that LEC1 originated at least 30 million years before the appearance of seed plants in the fossil record. Based on their expression patterns, *LEC1*orthologs have been suggested to play roles in promoting desiccation tolerance and lipid accumulation in *Selaginella* (lycophyte) species and storage macromolecule accumulation in reproductive organs of the fern, *Adiantumcapillus-veneris* (Xie et al. 2008; Kirkbride et al. 2013; Fang et al. 2017; Han et al. 2017). Further studies of LEC1 function in basal plants could advance our understanding of seed plant evolution.

## BEYOND MATURATION – ROLES FOR LEC1 IN OTHER ASPECTS OF SEED DEVELOPMENT

### Importance of LEC1 for embryo morphogenesis

Although LEC1 is a key regulator of the maturation phase, several lines of evidence indicate that LEC1 also acts as a regulator during the morphogenesis phase of seed development. First, LEC1 is expressed within 24 h after fertilization, suggesting that it functions at the earliest stages of seed development (Figure 2A) (Lotan et al. 1998). Second, LEC1 is required to maintain embryonic suspensor identity early in seed development. The wild-type *Arabidopsis* suspensor is a transient structure comprised of a single file of six to eight cells. *lec1* mutant suspensors undergo abnormal cell divisions and often consist of more than eight cells (Lotan et al. 1998). Furthermore, combining the *lec1* mutation with mutations in *ABA INSENSITIVE3* (*ABI3*) or *FUSCA3* (*FUS3*) genes that encode other seed development regulators results in polyembryony, in which a second embryo proper forms from cells derived from proliferating suspensor cells (Vernon and Meinke 1994; Lotan et al. 1998). Thus, LEC1 is required to suppress the embryogenic potential of the suspensor early in embryo development. Third, LEC1 is required to specify cotyledon identity during embryogenesis (Meinke 1992; Meinke et al. 1994; West et al. 1994). *lec1* mutant embryo cotyledons, unlike wild type, undergo a heterochronic conversion in which they acquire leaf traits, such as trichomes on their adaxial surfaces and a cellular organization that is intermediate between cotyledons and leaves (Meinke et al. 1994; West et al. 1994). Consistent with this interpretation, trichome development is suppressed in plants overexpressing *LEC1* (Lotan et al. 1998; Huang et al. 2015a). Fourth, LEC1 regulates the expression of genes involved in embryo morphogenesis, including those encoding the transcription factors PHAVOLUTA and SCARECROW, and in auxin biosynthesis in *Arabidopsis* and soybean embryos early in seed development (Junker et al. 2012; Pelletier et al. 2017; Hu et al. 2018). Finally, a striking indication of LEC1's role in embryo morphogenesis is its ability to induce somatic embryo development in vegetative tissues of several plant species (Lotan et al. 1998; Lowe et al. 2003; Yang and Zhang 2010; Ledwon and Gaj 2011; Guo et al. 2013; Nic-Can et al. 2013; Orlowska et al. 2017). The mechanisms that underlie LEC1's ability to promote somatic embryogenesis are not fully understood, but it has been speculated that it acts to enhance embryogenic competence.

### Involvement of LEC1 in photosynthesis and chloroplast development during seed development

Embryos of many angiosperm taxa possess chloroplasts that are highly shade adapted because of the light

quality to which they are exposed but that, nonetheless, photosynthesize during embryo development (reviewed by Puthur et al. 2013). In oilseeds, photosynthesis generates oxygen, which is limited in the internal tissues of the embryo, for mitochondria respiration, and it may aid in recycling carbon dioxide that is lost with each cycle of fatty acid elongation (Vigeolas et al. 2003; Rolletschek et al. 2005; Allen et al. 2009). LEC1 has been implicated to regulate photosynthesis and chloroplast biogenesis during seed development. *Arabidopsis lec1* mutants have a paler green coloration than wild-type embryos, suggesting that LEC1 promotes but is not absolutely required for proper chloroplast biogenesis during embryogenesis (Meinke 1992; West et al. 1994; Junker et al. 2012; Pelletier et al. 2017). LEC1 also transcriptionally activates the expression of representatives of most genes encoding the light-reaction components of photosystems I and II and of many other genes involved in chloroplast biogenesis in *Arabidopsis* and soybean embryos (Pelletier et al. 2017). These findings indicate a role for LEC1 in controlling photosynthesis and chloroplast biogenesis during seed development.

### LEC1 plays a role in controlling endosperm development

mRNA profiles of *Arabidopsis* seeds revealed an extensive overlap in gene activity between embryo and endosperm subregions (Belmonte et al. 2013). Many of the same genes that are involved in processes that occur during the morphogenesis and maturation phases in the embryo are also expressed in the endosperm. The findings that chloroplasts and storage protein and oil bodies are present not only in the embryo but also in the endosperm support the functional significance of this overlap in gene expression programs (Belmonte et al. 2013).

*LEC1* is expressed in the endosperm of many plant species, including *Arabidopsis*, maize, rapeseed, rice, and soybean (Figure 2A) (Lotan et al. 1998; Huang et al. 2009; Belmonte et al. 2013; Zhan et al. 2015; Pelletier et al. 2017; E et al. 2018). Moreover, *Arabidopsis* LEC1 directly activates genes that act both in the embryo and endosperm in processes related to the morphogenesis and maturation phases, suggesting the LEC1 regulates aspects of endosperm development, although the *lec1* mutant does not display obvious morphological defects in endosperm (Meinke 1992; Meinke et al. 1994; Lotan et al. 1998). Similarly, it was proposed that LEC1 can control endosperm development in rice through its interaction with AP2 transcription factors (Zhang and Xue 2013; Xu et al. 2016).

Thus, substantial evidence indicates that LEC1's role in seed development extends beyond simply control of the maturation phase. The ability of LEC1 to regulate cellular processes during both the morphogenesis and maturation phases and in distinct regions of the seed demonstrates that LEC1 is a central regulator of seed development.

## TEMPORAL REGULATION OF LEC1 ACTIVITY BY HORMONES DURING SEED DEVELOPMENT

LEC1 regulates distinct processes at different stages of seed development, and its activity must be repressed after germination to promote vegetative development (Figure 2A, 2B). Thus, LEC1 activity must be highly temporally regulated during plant development.

Recent findings provide insight into the mechanisms by which LEC1 responds to the physiological cues that govern seed development. For example, gibberellic acid (GA) regulates LEC1 activity during seed development (Hu et al. 2018). As shown in Figure 2A, bioactive GA isoforms display a dynamic accumulation pattern, achieving highest levels during the early stages of seed development. In the absence of GAs, LEC1's ability to activate at least some of its target genes is repressed through its interaction with DELLA proteins, which are repressors of GA signaling pathways (Figure 2B). Bioactive GAs promote the degradation of DELLA proteins, releasing LEC1 to activate gene transcription. GAs have been shown to release LEC1 to activate the expression of *YUCCA* (*YUC*) genes involved in auxin biosynthesis (Hu et al. 2018).

Abscisic acid (ABA) accumulation during the late stages of seed development is at least partially responsible for the onset of the maturation phase and other developmental changes (Figure 2A) (Finkelstein et al. 2002; Gutierrez et al. 2007; Holdsworth et al. 2008; Nakashima and Yamaguchi-Shinozaki 2013). Given the importance of LEC1 and ABA in controlling the maturation phase, it is not surprising that ABA has been shown to augment LEC1's activation of genes involved in maturation. For example, ABA enhances the ability of LEC1 to activate the expression of the storage protein gene, *CRUCIFERIN* (*CRU*), and the lipid biosynthesis gene, *FATTY ACID DESATURASE3*

(*FAD3*), by promoting the activity of ABA RESPONSIVE ELEMENT BINDING (AREB) proteins, such as the transcription factor, BASIC LEUCINE ZIPPER67 (bZIP67) (Figure 2B) (Yamamoto et al. 2009; Mendes et al. 2013). It is not clear, however, if promotion results from enhanced *bZIP67* transcription or posttranslational phosphorylation of bZIP67, as has been shown to occur for another bZIP transcription factor, ABA INSENSITIVE5 (Lopez-Molina et al. 2001; Nakashima et al. 2009). The mechanistic relationship between LEC1 and bZIP transcription factors will be discussed, but it is likely that ABA modulates LEC1 function at least in part, by inducing AREB protein activity.

The central role of LEC1 in promoting seed development emphasizes a requirement to repress LEC1 activity during vegetative development. For example, ectopic *LEC1* expression in seedlings results in the repression of vegetative growth and the development of embryo-like seedlings (Lotan et al. 1998). Two lines of evidence indicate that chromatin conformation plays integral roles in regulating LEC1 expression postgermination (Jia et al. 2014; Pu and Sung 2015; Lepiniec et al. 2018). First, PICKLE (PKL), a CHD3 chromatin remodeling factor, negatively regulates *LEC1* expression and, therefore, embryonic programs during seedling development (Ogas et al. 1999; Dean Rider et al. 2003; Li et al. 2005). The seedling roots of *pkl* mutants display characteristics of embryos and accumulate storage lipids and proteins normally found in seeds. This phenotype results from the ectopic expression of LEC1 and other maturation regulators in *pkl* seedlings (Ogas et al. 1997; Henderson et al. 2004). Moreover, *pkl* mutants show spontaneous development of somatic embryos in postgerminative roots (Ogas et al. 1997). Second, the VIVIPAROUS ABI3-LIKE (VAL) proteins, also act to repress LEC1 activity during postgerminative development. *VAL1* and *VAL2* genes, also known as *HIGH-LEVEL EXPRESSION OF SUGAR-INDUCIBLE GENE2* (*HSI2*) and *HSI2-LIKE* genes, respectively, are B3 domain transcription factors that contain conserved CW and PHD domains frequently found in chromatin remodeling factors (Suzuki et al. 2007; Tsukagoshi et al. 2007). Monogenic *val* mutants do not display striking mutant phenotypes, however, *val1 val2* double mutants develop somatic embryos in shoot apical meristem regions of germinating seedlings (Suzuki et al. 2007). Although not normally active in wild-type seedlings, *LEC1* is expressed in *val1 val2* seedlings after germination, indicating that *VAL1* and *VAL2* inhibit embryonic development by repressing the expression of *LEC1* and other transcriptional regulators of maturation during seedling growth (Suzuki et al. 2007; Tsukagoshi et al. 2007).

Both PKL and VAL act epigenetically to repress *LEC1* expression (Figure 2B) (Jia et al. 2014; Pu and Sung 2015; Lepiniec et al. 2018). Repression of seed maturation genes by PKL is mediated through the trimethylation of the lysine 27 residue of histone H3 (H3K27me3), a repressive epigenetic mark, as indicated by the observation that *pkl* mutants display reduced H3K27me3 occupancy on *LEC1* postgermination (Zhang et al. 2008; Zhang et al. 2012). Similarly, *val1 val2* mutants show reduced accumulation of H3K27me3 and increased accumulation of active histone marks, such as histone H3 lysine 4 trimethylation, histone H3 acetylation, and histone H4 acetylation, in the promoter and coding regions of *LEC1* during seed germination (Zhou et al. 2013). VAL1 and VAL2 interact with HISTONE DEACETYLASE19 and 6, respectively, to inhibit *LEC1* activity (Zhou et al. 2013; Chhun et al. 2016). VAL2 binds with the promoter and coding/intron regions of *LEC1* to recruit HDA6 and suppress *LEC1* activity during seed germination.

The concerted actions of PKL and VAL1/VAL2 emphasize the importance of repressing the activities of LEC1 and other maturation regulators and, consequently, the embryonic program during vegetative development. GAs have been proposed to play an important role in controlling PKL and VAL activities (Figure 2B) (Ogas et al. 1997; Ogas et al. 1999; Suzuki et al. 2007; Zhang et al. 2014). An increase in GA levels prior to germination is responsible for breaking seed dormancy and promoting seed germination. In *pkl* mutant and *val1 val2* double mutant seedlings, the development of embryo-like structures is enhanced by GA biosynthesis inhibitors (Ogas et al. 1997; Suzuki et al. 2007). In addition, DELLA proteins interact with PKL to negatively regulate PKL activity (Figure 2B) (Zhang et al. 2014). Thus, GA induced degradation of DELLA proteins appears to activate PKL to repress embryonic gene expression after germination. The mechanism by which GAs influence VAL function remains to be determined. Nevertheless, the GA-mediated repression of LEC1 and other maturation regulators by PKL and VAL1 provides insight into the transition between seed and vegetative development in spermatophytes.

Together, these findings indicate that hormones play important roles in modulating LEC1 activity during seed development in response to physiological changes.

## LEC1 REGULATES SEED DEVELOPMENT DIRECTLY AND INDIRECTLY THROUGH THE ACTIVATION OF OTHER KEY TRANSCRIPTION FACTORS

Genome-wide characterization of LEC1 occupancy coupled with gene expression analyses indicates that LEC1 can directly regulate many genes involved in the processes that occur during seed development (Junker et al. 2012; Pelletier et al. 2017). For instance, LEC1 directly regulates genes encoding enzymes involved in hormone biosynthesis and seed storage macromolecule accumulation. These studies also show that LEC1's involvement in controlling distinct processes during seed development may reflect, in part, its ability to regulate different sets of downstream transcription factors.

LEC1's function early in seed development is mediated, at least in part, through its direct activation of transcription factors involved in morphogenetic processes (Junker et al. 2012; Pelletier et al. 2017; Hu et al. 2018). For example, LEC1 directly regulates the transcription of the HD-ZIPIII transcription factors, *PHABULOSA* and *PHAVOLUTA*, that have been characterized as master regulators of apical fate early in embryogenesis and of *SCARECROW*, a key regulator of root architecture (Di Laurenzio et al. 1996; Smith and Long 2010; Pelletier et al. 2017). Moreover, LEC1 regulates genes involved in the biosynthesis of auxin, a hormone that plays key roles in embryonic pattern formation (Junker et al. 2012). Thus, LEC1 regulates the establishment of embryo body pattern by controlling the expression of genes involved in embryonic axis differentiation.

Among genes directly regulated by LEC1 are the "AFL" B3 domain transcription factors, ABI3, FUS3, and LEAFY COTYLEDON2 (LEC2), which are all key regulators of seed maturation (Braybrook and Harada 2008; Santos-Mendoza et al. 2008; Boulard et al. 2017). Single mutants for each gene display phenotypic similarities to *lec1* mutants and to each other (Finkelstein and Somerville 1990; Meinke 1992; Keith et al. 1994; Meinke et al. 1994; West et al. 1994; Harada 2001). The lack of redundancy among *AFL* genes indicates that they play similar though not identical roles during seed maturation. For example, *abi3* and *lec1* mutants but not *fus3* and *lec2* mutants have reduced sensitivity to exogenous ABA (To et al. 2006). *lec1, abi3* and *fus3* mutants are embryo lethal mutants, because they are desiccation intolerant, whereas *lec2* mutant embryos display only partial desiccation intolerance (Nambara et al. 1995; Harada 2001). LEC1 appears to act upstream of *ABI3, FUS3,* and *LEC2* in that *ABI3* and *FUS3* expression is reduced in *lec1* mutants, and overexpression of *LEC1* results in increased *ABI3* and *FUS3* expression in *Arabidopsis* seeds (Parcy et al. 1997; Kagaya et al. 2005; To et al. 2006; Mu et al. 2008; Pelletier et al. 2017). Moreover, *Arabidopsis ABI3, FUS3,* and *LEC2* are directly transcriptionally regulated by LEC1 (Pelletier et al. 2017).

Many maturation genes that are direct targets of LEC1 are also direct targets of ABI3 and FUS3 (Monke et al. 2012; Wang and Perry 2013; Pelletier et al. 2017). Thus, it appears that LEC1 activates both ABI3 and FUS3, and all three transcription factors act to promote maturation gene transcription during seed development. This type of network architecture is known as a feed-forward loop that can accelerate the response time of target gene expression following induction (Mangan and Alon 2003). Another potential example of a feed-forward loop is the relationship between LEC1 and WRINKLED1 (WRI1), another transcription factor that plays a key role in the maturation phase. WRI1 is a direct target of LEC1, and it is thought to directly regulate genes involved with fatty acid accumulation in *Arabidopsis* seeds that are also directly regulated by LEC1 (Baud et al. 2007; To et al. 2012; Pelletier et al. 2017). Thus, LEC1 works in concert with WRI1 to control fatty acid biosynthesis during seed development.

LEC1 indirectly controls seed development by regulating the expression of transcription factors that control independent developmental programs during seed development. However, LEC1's ability to directly regulate many of the structural genes in the regulatory network that are, in turn, regulated by its downstream transcription factor suggests a feed-forward mechanism of regulation that reinforces specific gene expression programs during seed development.

## LEC1 FUNCTION IS MODULATED BY INTERACTIONS WITH OTHER TRANSCRIPTION FACTORS

The finding that LEC1 regulates distinct processes at different stages of development prompted the

question of how a single transcription factor can control different sets of genes. Genetic analyses suggested that LEC1 may interact synergistically with other transcription factors to regulate different processes during seed development (Parcy et al. 1997; To et al. 2006). Recent studies suggest that LEC1 acts sequentially during seed development to respond to different developmental signals by interacting with different combinations of transcription factors to alter the transcriptional specificity of LEC1 (Pelletier et al. 2017). In this section, we discuss LEC1's interactions with other transcription factors during seed development.

**LEC1 as a subunit of a Nuclear Factor-Y transcription factor**

LEC1 is a novel NF-YB subunit of the NF-Y complex, a transcription factor that is conserved among eukaryotes and binds the CCAAT DNA motif (Lotan et al. 1998; Calvenzani et al. 2012; Dolfini et al. 2012). In addition to NF-YB, the NF-Y complex is comprised of two other subunits, NF-YA and NY-YC (Petroni et al. 2012; Zhao et al. 2016). Different from other organisms, such as animals and yeast which contain only one gene for each subunit, plants possess NF-Y subunit gene families that consist of 8 to 14 members (Petroni et al. 2012; Zhao et al. 2016). This diversity of subunits offers the potential for the functional specialization of different combinations of NF-Y subunits (Siefers et al. 2009; Laloum et al. 2013). Seed plants possess two types of NF-YB subunits: the non-LEC1 type with B domains that are conserved across eukaryotes and the LEC1-type that, in *Arabidopsis*, consists of LEC1 (NF-YB9) and its paralog, LEC1-LIKE (L1L, NF-YB6), although LEC1 and L1L exhibit distinct accumulation patterns (Figure 2A) (Kwong et al. 2003b). LEC1-type subunits confer LEC1 activity whereas the non-LEC1 subunits do not (Kwong et al. 2003a; Lee et al. 2003). The B domains of LEC1-type subunits share sequence similarity with non-LEC1 type subunits, but they also possess unique amino acid residues. These unique residues are responsible for conferring LEC1 activity only to NF-Y complexes containing the LEC1-type subunits (Lee et al. 2003). The LEC1-type NF-YB subunits are found primarily in seed plants although they appear to have originated in land plant lineages in lycophytes (Xie et al. 2008; Kirkbride et al. 2013; Cagliari et al. 2014). Thus, non-LEC1 type and LEC1 type NF-YB subunits appear to have fundamentally different function.

The ability of NF-Y complexes containing non-LEC1-type NF-YB subunits to bind the CCAAT motif and to regulate gene transcription has been extensively studied in yeast, mammals and plants (Dolfini et al. 2012; Zhao et al. 2016; Myers and Holt 2018). The initial step in NF-Y complex formation involves dimerization between NF-YB and NF-YC through their histone-fold domains. NF-YC subunits possess nuclear localization sequences, whereas NF-YB subunits do not. Therefore, NF-YB/NF-YC dimers localize to the nucleus (Frontini et al. 2002; Kahle et al. 2005). The nuclear localized NF-YA subunit binds with the NF-YB/NF-YC dimer to form a functional transcription factor that binds the CCAAT DNA motif. All three subunits, particularly NF-YA, confer DNA binding specificity to the complex (Sinha et al. 1996; Zemzoumi et al. 1999).

Despite their difference from non-LEC1 subunits, both *Arabidopsis* LEC1 and L1L form functional NF-Y complexes, as diagramed in Figure 3 (Calvenzani et al. 2012; Gnesutta et al. 2017b). Assembly of the LEC1 NF-Y complex appears to occur similarly with non-LEC1 NF-Y complexes in that rice LEC1 preferentially localizes to tobacco epidermal cells nuclei only when a rice NF-YC subunit is coexpressed, suggesting that LEC1 lacks a nuclear localization sequence (E et al. 2018). Protein crystallography studies predict that the structure of the NF-Y complex containing L1L is very similar to NF-Y complexes from animals, and NF-Y complexes containing LEC1 or L1L bind CCAAT DNA motifs (Calvenzani et al. 2012; Nardini et al. 2013; Gnesutta et al. 2017b). Consistent with this finding, the CCAAT DNA motif is overrepresented in the promoter of several genes that are regulated by LEC1 during the early stages of embryo development in *Arabidopsis* and soybean (Pelletier et al. 2017). Thus, it is likely that LEC1 promotes transcription as a functional NF-Y complex during seed development.

**LEC1 interactions with other transcription factors**

Genome-wide analysis of LEC1 binding sites in the upstream regions of *Arabidopsis* and soybean genes that are transcriptionally regulated by LEC1 revealed a distinct set of DNA sequence motifs that were enriched in their promoter regions (Pelletier et al. 2017). The CCAAT DNA motif is enriched in genes that are LEC1 regulated early in seed development. By contrast, LEC1 regulated genes expressed at later stages of seed development were overrepresented for DNA motifs that resemble the G-Box (CACGTG), ABRE-like ((C/G/T)

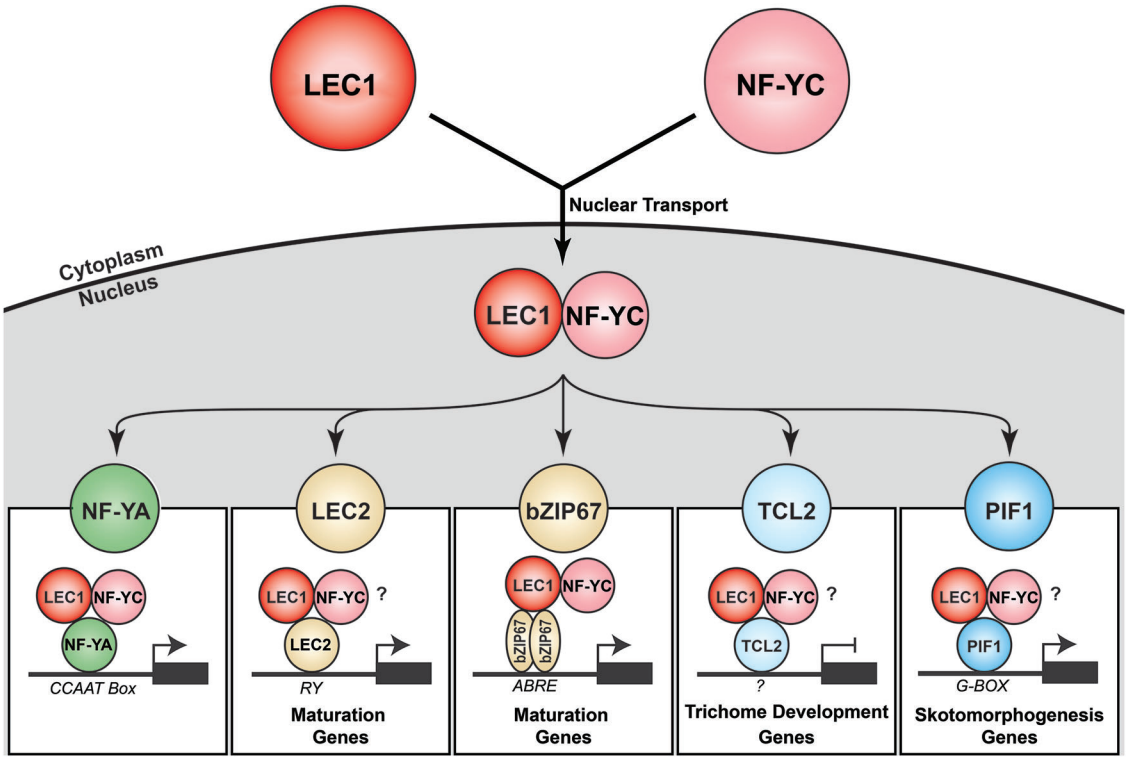


**Figure 3. LEC1 regulates distinct processes during seed development through its interaction with other transcription factors**

Binding of LEC1 with NF-YC enables transport of the dimer into the nucleus where it can interact with the indicated transcription factors, dependent on developmental stage. NF-YC subunits marked with a question mark indicate that NF-YC has not been shown to be required for the interaction of LEC1 with the transcription factor. In many cases, L1L may replace LEC1 in the complexes. The DNA sequence motif bound by TCL2 is not known.

ACGTG(G/T)(A/C)), RY (CATGCA) and BPC1 ((A/G)GA(A/G)AG(A/G)(A/G)A) *cis*-regulatory elements (Pelletier et al. 2017). Because NF-Y complexes bind CCAAT DNA motifs, it is hypothesized that LEC1 can interact with several other transcription factors and that these interactions specify which set of genes are regulated by LEC1 (Pelletier et al. 2017). Interactions between NF-Y subunits and other transcription factors have been reported extensively for plants and animals, and these interactions are important to specify the activity of these other transcription factors (Dolfini et al. 2012; Zhao et al. 2016; Myers and Holt 2018). Here, we discuss interactions between LEC1 and other transcription factors.

Studies of the B-BOX-type zinc finger transcription factor, CONSTANS (CO) that controls flowering in plants, provide insight into a potential mechanism by which the transcriptional specificity of LEC1 may be modulated. CO interacts with a NF-YB/NF-YC dimer to form a functional transcription factor by essentially replacing NF-YA in the NF-Y complex (Gnesutta et al. 2017a). Given that the NF-YA subunit participates in determining the DNA binding specificity of NF-Y complexes, the CO/NF-YB2/NF-YC3 complex does not bind the CCAAT DNA motif, but rather it binds the CORE element (CCACA) in the promoter regions of the CO target gene, *FLOWERING LOCUS T*. Interestingly, CO competes with NF-YA subunits for the NF-YB/YC dimer (Gnesutta et al. 2017a).

By analogy to the CO/NF-YB/NF-YC complex, the LEC1/NF-YC dimer appears to interact with other transcription factors to modulate LEC1 activity as shown in Figure 3. Consistent with the finding that G-box motifs are enriched in LEC1 binding regions in LEC1 target gene promoters, the basic leucine zipper transcription factor, bZIP67, has been shown to interact with the L1L/NF-YC2 dimer (Yamamoto et al. 2009). The LEC1/NF-YC2/bZIP67 complex binds the ABRE DNA motif, which has a G-box

core, but not the CCAAT DNA motif, in the promoters of genes involved in the maturation phase, such as *CRUCIFERIN C*, *FATTY ACID DESATURASE3*, and *SUCROSE SYNTHASE 2* (Yamamoto et al. 2009; Mendes et al. 2013). Similar to the CO/NF-YB/NF-YC complex, NF-YA strongly inhibits the activity of the LEC1 complex with *CRUCIFERIN C*, suggesting a competition between NF-YA and bZIP67 for the LEC1/NF-YC dimer (Yamamoto et al. 2009).

LEC1 also interacts with LEC2 (Figure 3) (Baud et al. 2016; Boulard et al. 2018). LEC2 is a B3 transcription factor that together with other B3 proteins, ABI3 and FUS3, regulates several processes during the maturation phase (Devic and Roscoe 2016; Lepiniec et al. 2018). LEC1, LEC2 and ABI3 synergistically promote the expression of the *OLEOSIN1* gene through RY and ABRE DNA motifs (Baud et al. 2016). Thus, LEC1's ability to control the maturation phase likely occurs through interactions with B3 and bZIP transcription factors that accumulate during the late stages of seed development.

LEC1 also interacts with other transcription factors to regulate diverse development processes (Figure 3). For example, LEC1 interacts with PHYTOCHROME INTERACTING FACTOR1 (PIF1) that is important for the expression of skotomorphogenesis genes through the G box element (Junker et al. 2012; Huang et al. 2015b). LEC1 also interacts with TRICHOMELESS2 (TCL2) to repress the expression of genes involved with trichome development during embryogenesis (Huang et al. 2015a).

Together, the ability of LEC1 to interact with many transcription factors provides potential mechanisms to explain how LEC1 can regulate distinct gene sets at different stages of seed development. Defining all of the transcription factors that interact with LEC1 during seed development and their impact on LEC1 activity could provide useful insights into the multifunctionality of LEC1 during seed development.

## LEC1 AS A PIONEER TRANSCRIPTION FACTOR

The transition from the morphogenesis to the maturation phase represents a reprogramming of cellular identity. Cellular reprogramming in animals is often mediated, in part, by pioneer transcription factors that are involved in the initial steps that allow silenced genes to become competent for transcription (Guo and Morris 2017). Pioneer transcription factors have the capacity to bind compacted or "closed" chromatin and initiate chromatin remodeling, resulting in an increase in target site accessibility and facilitating the recruitment of other transcription factors to genes in the newly opened chromatin (reviewed by Zaret and Carroll 2011; Mayran and Drouin 2018; Sartorelli and Puri 2018).

LEC1 is the first pioneer transcription factor to be identified in plants based on its involvement in activating *FLOWERING LOCUS C* (*FLC*) (Figure 4) (Tao et al. 2017). FLC is a flowering repressor that undergoes epigenetic silencing during vernalization, resulting in the transition from vegetative to reproductive development (reviewed by Andres and Coupland 2012; Whittaker and Dean 2017). After plants flower, *FLC* remains silenced and in a repressed chromatin state, and it is maintained as such through gametogenesis (Sheldon et al. 2008). However, *FLC* expression must be

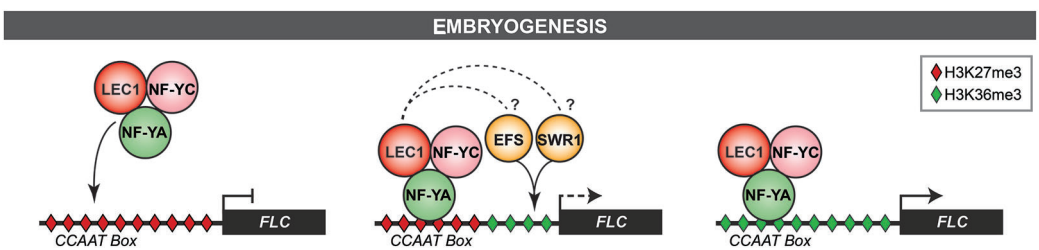


**Figure 4. LEC1 is a pioneer transcription factor that promotes *FLC* transcription during embryogenesis**
An NF-Y complex containing LEC1 binds the CCAAT DNA sequence motif in the *FLC* promoter in a closed chromatin conformation, as indicated by its occupancy by H3K27me3. The LEC1 NF-Y complex works through EFS and the SWR1 complex to initiate the establishment of an active chromatin state as indicated by occupancy of the active chromatin mark, H3K36me3.

reestablished to repress flowering prior to vernalization. As shown in Figure 4, LEC1 promotes the initial establishment of an active chromatin state at *FLC* in embryos (Tao et al. 2017). LEC1 binding at the *FLC* promoter is essential to engage EARLY FLOWERING IN SHORT DAYS (EFS) and the SWR1 complex to enhance chromatin accessibility and facilitate the recruitment of active histone marks on the *FLC* promoter, although the mechanistic relationship between LEC1 and the chromatin remodelers remains to be determined.

The characterization of LEC1 as a pioneer transcription factor opens the possibility that LEC1 may serve a similar function during seed development. Thus, LEC1 may bind compacted chromatin and promote chromatin conformational changes that allow other transcription factors to bind, in part, through their interactions with LEC1. Further analysis of the relationship between LEC1 and epigenetic changes that occur during seed development could provide insights into LEC1 role as a pioneer transcription factor.

## CONCLUSION AND PERSPECTIVES

In this review, we have summarized recent findings that emphasize the role of LEC1 as a central regulator of seed development. LEC1 controls distinct processes at different stages of development. Therefore, its activity must sequentially regulate different sets of genes during seed development. The hormones GA and ABA may be involved in modulating LEC1 function in response to different physiological cues.

How does LEC1 regulate diverse sets of genes? First, LEC1 acts indirectly to regulate cellular processes during seed development by activating genes encoding transcription factors controlling structural genes that underlie these processes. In some cases, LEC1 also directly activates the same structural genes that are regulated by its downstream transcription factors, establishing a feed-forward loop that potentially promotes gene expression. LEC1 also interacts with different transcription factors at different stages of development, and the concerted actions of these transcription factor complexes may specify the particular set of genes that are activated. Moreover, the recent finding that LEC1 acts as a pioneer transcription factor provides potential insight into understanding LEC1 function to promote the activation of different gene sets during seed development.

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