LEAFY COTYLEDON 2: A Regulatory Factor of Plant Growth and Seed Development

Boling Liu †, Ge Sun †, Changju Liu and Shijuan Liu *

School of Life Science, Qufu Normal University, Qufu 273165, China; lblzzkk@126.com (B.L.); sungemakang@163.com (G.S.); kjsmkx@163.com (C.L.)
* Correspondence: sjliu@qfnu.edu.cn
† These authors contributed equally.

Abstract: Transcription factors are key molecules in the regulation of gene expression in all organisms. The transcription factor LEAFY COTYLEDON 2 (LEC2), which belongs to the DNA-binding protein family, contains a B3 domain. The transcription factor is involved in the regulation of important plant biological processes such as embryogenesis, somatic embryo formation, seed storage protein synthesis, fatty acid metabolism, and other important biological processes. Recent studies have shown that LEC2 regulates the formation of lateral roots and influences the embryonic resetting of the parental vernalization state. The orthologs of LEC2 and their regulatory effects have also been identified in some crops; however, their regulatory mechanism requires further investigation. Here, we summarize the most recent findings concerning the effects of LEC2 on plant growth and seed development. In addition, we discuss the potential molecular mechanisms of the action of the LEC2 gene during plant development.

Keywords: embryogenesis; somatic embryogenesis; plant growth; seed development; transcription factor; LEC2

1. Introduction

Seeds are the key means by which terrestrial plants adapt to changing environments in the processes of evolution and diversification, and seed development occurs after zygotic embryogenesis. When seeds are in the maturation stage of growth and development, energy reserves continue to accumulate, while the seeds gain desiccation tolerance [1]. This process is strictly controlled at the transcription level, involving the AFL (ABI3/FUS3/LEC2) (ABA INSENSITIVE3/FUSCA3/LEAFY COTYLEDON 2) subfamily of B3 transcription factors (TFs). Researchers have shown that the B3 TF gene family developed within the green algae family 1200–725 million years ago, and the genes are present in all photosynthetic organisms [2]. AFL members interact with LEC1 (LEAFY COTYLEDON1) and LEC1-LIKE, which belong to the CCAAT-binding factors of the HAP3 family to control seed growth and development [3–6]. These genes have been collectively named L-AFL [7]. Members of the L-AFL family are considered to be the key regulatory TFs during the seed maturity stage [8]. The LEC2 TF establishes an ideal cellular environment for the formation of the zygotic embryo and its later stages of development [9,10]. Early embryonic development is the main period of expression of LEC2; at times, it is also expressed in vegetative organs [11,12]. LEC2 contains two domains named B2 and B3 [13]. It appears that the plant-specific B3 domain encoded by the LEC2 gene recognizes the conserved RY motif to transcriptionally regulate the expression of zygotic embryogenesis-specific genes and that it promotes somatic embryo formation at the maturation stage [12,14,15]. The LEC2 gene could be directly repressed by E2FA binding to an E2F-binding site during the seed maturation phase [16]. A ChIP assay suggested that PHABULOSA acts directly on the LEC2 promoter during embryogenesis [17]. An analysis using reporter genes indicated that LEC2 is negatively regulated by miRNA pathways during early embryogenesis [18].
miRNA is responsible, directly or indirectly, for repressing LEC2 in the embryo until it is required [17–19]. Retinoblastoma-related proteins facilitate seedling establishment by directly or indirectly repressing the promoters of late embryogenesis genes, including LEC2, during seed germination [20].

LEC2 participates in a variety of signaling pathways and regulates the expression of numerous crucial genes during the growth and development of plants. Early studies have shown that the mutation of LEC2 in Arabidopsis thaliana altered the morphology of the embryo and caused certain local defects in the seed protein stockpile and its desiccation tolerance [12,21]. In addition, LEC2 mutations halted the ability of somatic embryos to emerge from A. thaliana explants [22]. Through further in-depth exploration of the biological functions of LEC2, it was shown that the ectopic expression of LEC2 caused the accumulation of seed storage lipids and proteins in plant nutritive organs [23,24], further inducing vegetative cells to form somatic embryos without exogenous auxin or seed-specific genes being expressed in the leaves [12,23]. In A. thaliana, the function of LEC2 has been explained in terms of many aspects (Table 1).

Table 1. Biological function of LEC2 transcription factor in A. thaliana.

| Biological Function                                                                 | Reference |
|-----------------------------------------------------------------------------------|-----------|
| Induces somatic embryos and embryonic development in vegetative cells             | [4]       |
| Initiates somatic embryo development                                               | [12]      |
| Regulates the expression of storage protein genes                                  | [11]      |
| Induces somatic embryogenesis                                                      | [22]      |
| Triggers the stockpile of oil and seed-specific mRNAs                              | [23]      |
| Induces maturation traits and auxin activity                                       | [24]      |
| Affects the contents of oil and protein, starch, and sucrose                       | [25]      |
| Changes the shape and anatomy of leaves                                            | [26]      |
| Triggers the expression of genes encoding seed maturation and oil body protein regulators in trophic organization | [27]      |
| Promotes embryogenic callus formation in roots                                     | [28]      |
| Controls the formation of lateral roots                                            | [29]      |
| Involved in early embryogenesis                                                    | [30]      |
| Participates in the development of somatic embryos                                 | [31]      |

Although major advances have been made concerning LEC2, its regulatory mechanism at the cellular and molecular levels remains unclear. Here, we discuss the impact of LEC2 on the growth and development of plants.

2. The Effect of LEC2 on Plant Early Embryo Morphogenesis

The development of seeds can be loosely divided into two stages: early embryonic development and maturation. In general, plants achieve desiccation tolerance by accumulating stored materials at the later stage of seed maturity. Embryogenesis is an important stage in the development of higher plants, and the LEC2 TF plays a pivotal regulatory role in controlling embryogenesis in Arabidopsis.

In the process of plant early embryogenesis, specialized leaves called cotyledons are produced. Compared with ordinary leaves, these embryonic leaves have large differences in morphology and gene expression patterns. When AtLEC2 is mutated, the cotyledons undergo certain changes, including rounding in shape and the development of abnormal protrusions on the surface. Mutant cotyledons produce trichomes characteristic of leaves, indicating that AtLEC2 is important for maintaining cotyledon traits during early embryogenesis [32].

Recent research has shed new light on AtLEC2’s involvement in the development of early embryos. When plants undergo a long winter, the polycomb protein silences the potent flower repressor FLOWERING LOCUS C (FLC) that induces flowers to undergo vernalization. VIVIPAROUS1/ABI3-LIKE1 (VAL1) and VAL2 are necessary for this process [33,34]. LEC2 and FUS3 are also required for embryonic FLC reactivation in early
embryos following parental vernalization [30]. Late flowering is dependent on FLC in non-vernalized plants. However, this phenomenon is suppressed in LEC2 and FUS3 seeds. Hence, LEC2 and FUS3 are involved in embryonic FLC reactivation. FLC reactivation is also suppressed by LEC2 in vernalized seedlings. In addition, the parental vernalization of T2 progeny from FUS3 plants caused a reduction in FLC expression in the seedlings of T3 progeny [30]. LEC2 and FUS3 bind to the cold memory element of FLC to reactivate FLC expression in early embryos following parental vernalization. The ectopic induction of LEC2 or FUS3 activity can antagonize FLC repression mediated by VAL1 and VAL2 in seedlings. The B3 domain TFs LEC2 and FUS3 can replace VAL1 and VAL2 to reverse the chromatin-mediated silencing of FLC by polycomb proteins, thereby preventing the enrichment of histone 3 lysine 27 trimethylation and eliminating the parental retention of winter cold memory during early embryogenesis [30].

3. The Effect of LEC2 on the Maturation of Plant Seeds

In the maturation stage after embryogenesis, certain storage products are accumulated during the seed filling process in order for growth to be restored under favorable environmental conditions [35,36]. The seed has three different regions: the filial embryo, the filial endosperm, and the maternal seed coat, which have major differences in terms of their genotypes [37]. In various plant species, fatty acids, sugars, starch, and storage proteins accumulate in the endosperm or embryo of the seeds [38]. LEC2 imparts a regulatory effect on the formation of storage compounds during plant seed development. Studies have shown that FUS3 in the L-AFL family could inhibit the expression of GA3ox1 and GA3ox2 (GA biosynthesis genes) [39,40], while LEC2 could activate LEC1 and FUS3 genes to induce embryo maturation [24]. In addition, LEC2 directly induces AGL15 (AGAMOUS-LIKE15) [14], and AGL15 regulates the expression of the GA-related genes GA3ox2 and GA2ox6 [41,42]. These findings indicate that LEC2 regulates genes that are related to GA biosynthesis to affect the embryonic maturation stage of seeds.

In A. thaliana, the main storage compounds of seeds are lipids and seed storage proteins (SSP) [43]. Studies of the regulation of gene expression in plants have demonstrated that SSP is strictly regulated in time and space. Previous research has shown that AtLEC2 regulates the expression of SSP genes. At2S3 is a storage protein gene. Through yeast hybrid screening, the TFs LEC2 and FUS3 were shown to directly activate the expression of the At2S3 promoter and regulate it in a partially redundant manner [11]. Moreover, LEC2 also has a regulatory effect on fatty acid metabolism, mainly because it could influence the WRINKLED1 (WRI1) factor that encodes the transcription of fatty acids [44].

LEC2 is preferentially expressed during seed maturation. The mutation of the LEC2 gene in A. thaliana resulted in reductions in protein and oil content by 15% and 30%, respectively, whereas sucrose and starch content were sharply increased by 140% and 500% relative to the wild type [25]. For the phenomenon of increased sucrose, studies have shown that the sucrose synthase (SUS) gene in A. thaliana is regulated by LEC2. SUSs play a central role in carbon metabolism in plant heterotrophic tissues. Among these, AtSUS2 (At5g49190) and AtSUS3 (At4g02280), members of the SUS gene family, are upregulated in A. thaliana seeds [45–48]. During the growth and development of the seeds, the contents of AtSUS2 and AtSUS3 gradually accumulate when AtLEC2 is mutated. This result indicates that AtLEC2 has an epistatic effect on the two sucrose synthase genes [49].

There has been some progress in understanding the mechanism of LEC2 in the regulation of lipids and oil in seeds. Lipids and oils extracted from plants are extremely important renewable bioenergy materials. In plants, the main component of oil in seeds is triacylglycerol (TAG), and its synthesis can be enhanced by artificial modification. Meanwhile, the synthesis of fatty acids can also be artificially regulated. A recent study discovered an interesting phenomenon in A. thaliana: LEC2 could trigger the stockpiling of oil in leaves and seed-specific mRNA. OLEOSIN, the main structural protein of oil bodies during seed development, is highly expressed in seeds [50]. A previous study demonstrated that the effective expression of OLEOSIN in A. thaliana requires the activation of two adjacent
RY elements of the LEC2 promoter [51]. LEC2 acts synergistically with ABI3 and LEC1 to enhance the activation of the OLEOSIN promoter in the developing embryo [52]. In summary, LEC2 regulates many genes that participate in different events and signaling pathways of early embryonic development and seed maturation (Figure 1).

The LEC2 gene is involved in the regulation of both embryonic formation and maturation in A. thaliana. The heterologous expression of the AtLEC2 gene in tobacco results in abnormal tobacco seedlings. Digital gene expression profile analysis has shown that the ectopic expression of the AtLEC2 gene in tobacco could activate several genes and metabolic processes, including SSP, late embryogenesis abundant (LEA) protein, fatty acid biosynthesis, and sugar accumulation; in addition, AtLEC2 can activate key regulatory genes such as MADS-box protein 9, LIL, SERK1, and HAM. The ectopic expression of AtLEC2 affects the contents of stored substances and induces somatic embryogenesis in tobacco [53]. The latest research shows that the induced expression of AtLEC2 could also trigger the formation of embryogenic calli in tobacco [54].

Castor bean is an essential oil crop that is capable of accumulating a large amount of TAG in its seeds. The LEC2 gene identified in castor bean seeds is named RcLEC2 and consists of six exons and five introns that are substantially homologous to the LEC2 gene of A. thaliana. The heterologous expression of RcLEC2 in A. thaliana induces the expression of related TFs that influence seed maturity, as well as the seed fatty acid biosynthesis gene WR11 (Figure 1), thereby resulting in an increase in TAG content [27]. The above results may facilitate the characterization of the regulatory mechanism of fatty acid and lipid synthesis during the growth and development of castor beans.

Similarly, three putative homologs of the LEC2 gene in A. thaliana were identified in the monocot plant maize and were designated as ZmAFL4, ZmAFL5, and ZmAFL6. The ZmAFL5 and ZmAFL6 genes had the highest activity in ovules and kernels, and both genes exhibited constitutive gene reactivity. The ZmAFL4 gene has preferential expression in corn tassels and pollen, and its expression profile is consistent with that of LEC2. The analysis of ZmAFL4 gene expression in maize seeds indicated that its transcripts are abundant in the endosperm but are barely expressed in embryos, different from the active expression site of LEC2 in A. thaliana. In addition, metabolomics analysis suggests that the reduction in ZmAFL4 gene activity affects the carbon metabolism in corn kernels; the starch content of transgenic corn kernels at 20 DAP showed the most significant reduction. More importantly, ZmAFL4 does not seem to be involved in the TFs that regulate maize seed storage proteins. These results indicate that the function of LEC2 homologs of A. thaliana is not conserved, and no LEC2 functional homolog has been found in monocots [13,55].

In soybeans, the LEC2 homolog GmLEC2a regulates carbohydrate catabolism and triacylglycerol (TAG) biosynthesis; it also plays an important role in the development of plant seeds. Studies have shown that the ectopic expression of GmLEC2a in soybean hairy
roots causes the upregulation of the GmLEC1, GmFUS3, GmABI3, GmDof11, and GmWRI1 genes, which in turn enhance TAG biosynthesis. In addition, its ectopic expression also negatively regulated the expression of TAG lipase genes [56].

The finding that LEC2 TFs regulate lipids, sucrose, starch, oils, and proteins in various plant seeds of dicots indicates that LEC2 plays a major role in the maturation stage of seed development. Future research is warranted to understand how the LEC2 gene participates in the regulation of various storage material synthesis pathways during seed maturation.

4. The LEC2 Gene Plays a Crucial Role in Somatic Embryogenesis

Plant cells exhibit unique developmental plasticity that is related to totipotency. For example, the occurrence of somatic embryos is a good indicator of the pluripotency of plant cells. The formation of somatic embryos can be induced by treating cultured somatic cells with auxins and inducing the cells to differentiate in vitro [57]. Numerous studies have shown that the ectopic expression of TFs and their associated genes could induce spontaneous embryogenesis [58–60], among which the TF LEC2 is instrumental in inducing the formation of somatic embryos.

In A. thaliana, the LEC2 gene was cloned and expressed ectopically, and the results revealed that it was preferentially expressed during embryogenesis and that it has the ability to induce the formation of somatic embryos [12]. It has been suggested that auxin-induced plant somatic embryogenesis is a key factor in somatic embryo formation, i.e., LEC2 may affect the occurrence of somatic embryos by regulating auxin [61]. A previous study has suggested that AtLEC2 could activate auxin in response to the expression of the INDOLE-3-ACETIC ACID INDUCIBLE30 (IAA30) gene during embryogenesis [14]. Shortly afterward, when LEC2 was ectopically expressed in Arabidopsis seedlings, somatic embryos were formed in the seedlings, and AtLEC2 also activated the expression of the YUCCA2 (YUC2) and YUCCA4 (YUC4) genes for auxin biosynthesis [24]. The above findings imply that the ability of LEC2 to induce the formation of somatic embryos may be derived from the activation of the YUC2 and YUC4 genes that mediate auxin biosynthesis, and that LEC2 acts as a negative regulator of the auxin signal transduction-related IAA30 gene [41,59]. Although the overexpression of LEC2 in plants could induce the formation of somatic embryos, explants treated with auxin in vitro have produced damaged embryos. To better understand this phenomenon, 35S::LEC2-GR transgenic explants were treated with different concentrations of auxin. The results demonstrated that AtLEC2 augments endogenous auxin in the cultured explants, and the expression of three YUCCA genes (YUC1, YUC4, and YUC10) in the IPA-YUC auxin biosynthesis pathway related to somatic embryo induction also showed some correlation with AtLEC2 [62]. Through RT-PCR analysis of the embryogenesis cultures of the explants described above, AtLEC2 was found to be a key regulator that could stimulate the transcription of the YUC1, YUC4, and YUC10 genes. The overexpression of AtLEC2 could also significantly upregulate the expression levels of these three genes when explants were cultured in an auxin-free medium. The increase in endogenous auxin is due to the activation of the YUC gene that regulates the presence and function of exogenous auxin. These findings provide an important perspective for the study of the LEC2-mediated formation of somatic embryos [63].

Regarding the fact that LEC2 can induce somatic embryos, in addition to the possibility that it could regulate growth hormones, other hormones such as gibberellic acid and ethylene have been considered. Among these, ethylene, a gaseous plant hormone, participates in and controls the processes of plant growth and development [64,65]. Ethylene is regulated by ERF022, a gene that can induce effective embryogenesis in explants [66]. After mutating ERF022 in A. thaliana seedlings, the content of ethylene was increased, and the ability of embryogenesis was reduced [67]. In a breakthrough report, researchers have documented that auxin–ethylene interactions are controlled by ERF022 and AtLEC2 and their targets during somatic embryo formation [66]. This provides information concerning the underlying mechanism by which LEC2 regulates somatic embryo formation.
AtLEC2 also influences somatic embryo formation in other plant species. Using the leaf disc method to transform AtLEC2 into tobacco, embryogenic calli appeared on the stem apex meristems of tobacco [54], and then the structures of somatic embryos formed in the callus. This indicates that ectopic AtLEC2 expression induces the formation of somatic embryos in tobacco [53]. Similarly, when AtLEC2 was transferred to Brassica napus, somatic embryos with cotyledon-like and hypocotyl-like organ systems were formed on the cotyledon petioles, and their morphology and structure were similar to those of zygotic embryos [68].

Recent studies have shown that TcLEC2 induces the formation of a large number of somatic embryos on the leaves of Theobroma cacao [69,70]. In cassava, an orthologous gene of A. thaliana LEC2 has been identified and named MeLEC2. An analysis of the effect of its overexpression during somatic embryogenesis revealed that MeLEC2 was unregulated in somatic embryos compared with differentiated mature plant tissues. Furthermore, qRT-PCR analysis has shown that MeLEC2 plays a role in somatic embryogenesis in cassava. In addition, somatic embryogenesis, which is similar to zygotic embryogenesis, was observed in MeLEC2 transgenic cassava leaves. This result demonstrated that MeLEC2 has the ability to program vegetative cells to induce somatic embryogenesis [71].

In the legume Medicago truncatula, the LEC2 gene has been identified and named MtLEC2. There are two near-isogenic types in M. truncatula; one is M9-10a with embryogenic ability, and the other was named M9 and had very low embryogenic ability [72,73]. The two genotypes of M. truncatula were introduced into leaflet explants in vitro and then detected by qRT-PCR during the formation of somatic embryos. The final results showed that the MtLEC2 gene was highly expressed in the M9-10a explants, while the MtLEC2 gene in M9 explants displayed a low level of expression. Expression profiling has shown that MtLEC2 is involved in the occurrence of M. truncatula somatic embryos [31].

Taken together, these studies show that LEC2 has a significant effect on plant somatic embryogenesis. However, further exploration of the regulatory effect of LEC2 on somatic embryo formation at the molecular level is needed.

5. The Function of LEC2 during Other Plant Developmental Stages

LEC2 acts as the master regulatory factor in the processes of plant growth and development. It influences the occurrence of somatic embryos and also plays an important role in the growth phase of other plant structures. Studies have shown that LEC2 is also closely related to the formation of lateral roots. LEC2 activated the transcription of the NAC gene family. NAC proteins play roles in plant developmental processes such as lateral root development [74]. AtLEC2 also interacts with AtFUS3 to activate the expression of the auxin biosynthesis gene YUCCA4 (YUC4), which in turn promotes the generation of lateral roots in A. thaliana [29]. LEC2 and FUS3 have different binding sites in the YUC4 promoter. They can both directly bind to different RY elements of the YUC4 promoter. The FUS3–LEC2 interaction may enhance the ability of binding to RY elements to synergistically activate YUC4 transcription. In the initial stages of lateral root formation, AtLEC2 also activates AtFUS3 expression [29]. The lateral root formation induced by LEC2 was partially attributable to the enhanced FUS3 expression.

In addition, AtLEC2 could induce leaf reprogramming during development. The overexpression of the LEC2 gene in Arabidopsis resulted in alterations of the morphological characteristics of leaves [26]. The leaves became smaller and curled, and developed into cotyledons. Furthermore, the leaves were less fleshy, and the number of trichomes was reduced. Based on the lack of research at the cellular level, this phenomenon could not be further analyzed. After the leaves were sectioned and stained with toluidine blue-O (TBO) dye solution, changes in the anatomical structure of the leaves were assessed. Leaf cells showed a tighter arrangement, and vacuoles were sharply decreased in number and were lightly stained by the dye solution [26].

When LEC2 was overexpressed in the senescent leaves of A. thaliana, TAG content was augmented threefold compared with the wild type, and there were no negative effects on
plant growth and development [75]. More importantly, LEC2 upregulated the expression of multiple genes related to fatty acid and TAG synthesis in senescent leaves. Therefore, we deduced that LEC2 regulates genes that are involved in the key metabolic steps of TAG and fatty acid synthesis, thereby greatly increasing TAG content in vegetative organs.

The wheat EST sequence was queried in the databases, and a homolog of the *A. thaliana* seed maturation regulator LEC2 was detected and named *TaL2L* (LEC2-LIKE) [76]. Numerous LEC2 orthologs have been identified in dicotyledonous plants, and *TaL2LA* was the first LEC2 ortholog identified in monocotyledonous plants [76]. Researchers have reported that the *DELAY OF GERMINATION1* (DOG1) gene regulated seed dormancy in *A. thaliana* [77]. Several studies have suggested that the DOG1 promoter contains the RY element. This implies that DOG1 would be regulated by LEC2 as in *Arabidopsis*, as the RY element is the target site of the TF, containing the B3 domain [11,14,77,78]. The germination index (GI) could be used to assess the influence of each TF in seed dormancy. In wheat, except for the dormant cultivars, the expression level of *TaL2LA* is significantly correlated with the GI of seed dormancy levels. The expression of *TaDOG1* in wheat is also significantly correlated with seed dormancy, suggesting that *TaL2LA* influences wheat seed maturity and dormancy by regulating the expression of the *TaDOG1* gene [76].

The cellulose synthase 8A protein (PtdCesA8A) of poplar trees is highly expressed in the xylem cells of poplar trees [79] and also shows high activity in the xylem of transgenic tobacco plants. The *A. thaliana DGAT1* and LEC2 genes are linked to the xylem-specific promoter PtdCesA8A, and these were transformed into transgenic tobacco plants. The results demonstrated that a large supply of fatty acids and TAGs accumulate in the stems of tobacco, and no abnormalities in the growth and development of the plant were observed [80].

The above results indicate that the LEC2 gene plays a regulatory role in other developmental processes of different plant species, indicating the versatility of the LEC2 gene. However, LEC2 is expressed from the early globular stage until the early torpedo stage. Although LEC2 has been shown to control OLEOSIN genes, its pattern does not fit with the late embryogenesis and heavy fat reserve accumulation that are the foci of ABI3 regulation. The current research is focused on the biological significance and regulatory molecular mechanisms underlying these biological processes.

6. Conclusions and Future Perspectives

The molecular mechanisms that affect plant growth and development regulatory networks have been explored in depth. Among these, the functional expression of the LEC2 gene in plants has resulted in significant progress in plant biology and the application of biotechnology to transgenic plants.

Studies in the model plant *A. thaliana* indicate that LEC2 is the main regulatory factor involved in the growth and development of plant seeds. The expression of LEC2 can induce the occurrence of somatic embryos throughout the development process. Various lines of evidence indicate that the expression of LEC2 is involved in important biological processes such as embryogenesis, synthesis of storage proteins, fatty acids, and TAGs, as well as in the formation of lateral roots during seed growth and development. LEC2 is not only a direct transcription activator but also acts as a leading TF gene in various plant species. LEC2 participates in a variety of signaling pathways and regulates the expression of multiple key genes. The above research results demonstrate that the functions of the TF LEC2 are diverse and are important in many aspects of plant development.

In addition, the orthologs of the *Arabidopsis* LEC2 gene and the characterization of their functions have been identified in crops such as maize and wheat. Although the LEC2 orthologs identified in cassava and soybeans show functional conservation, these have certain differences compared to the orthologs in maize, allowing us to better understand the functions of LEC2 homologs in different species. At the same time, the discovery of orthologs of the LEC2 gene in wheat could facilitate a better understanding of the process of regulating seed dormancy. The above studies improve our understanding of
the conservation and functional differences of LEC2 genes in different plant species and provide us with a broader perspective of the functions of the LEC2 genes.

However, there are still many problems to be further explored and solved. For example, in addition to embryological processes, does LEC2 regulate other unknown biological processes in plant development? Continuous in-depth research on LEC2 may result in the identification of new signaling pathways and thus improve our understanding of the biological function of LEC2.

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Abbreviations

LEC2 LEAFY COTYLEDON 2
ABI3 ABA INSENSITIVE3
FUS3 FUSCA3
LEC1 LEAFY COTYLEDON1
TAG Triacylglycerol
SSP Seed storage protein
AGL15 AGAMOUS-LIKE15
HAM Hairy meristem
IAA30 Indole acetic acid inducible 30
SUS Sucrose synthase
LEA Late embryogenesis abundant
DOG1 DELAY OF GERMINATION1

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