REVIEW

LEAFY COTYLEDONs (LECs): master regulators in plant embryo development

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Abstract

In plants, somatic embryo development is regulated by a complex group or network of transcription factors (TFs). The *LEAFY COTYLEDON* (*LEC*) TFs are significant key regulators that promote the initiation of somatic embryo formation and biological processes of the embryo maturation phase. The *LEC* gene has been implicated to act as unique regulators in plant embryogenesis, growth and development via diverse signaling pathways. In the present review, we summarize the current advances in our understanding of the *LEC* TFs in plant biology including embryogenesis. Recent discoveries would be advantageous to unlock the mysteries of *LEC* TF genes of different molecular mechanisms in plant cells.

Keywords Embryogenesis · *LEAFY COTYLEDON* (*LEC*) · Transcription factor · Plant biotechnology · Seed development

Abbreviations

ABI3	*ABSCISIC ACID INSENSITIVE3*
BBM	*BABY BOOM*
FUS3	*FUSCA3*
AGL15	*Agamous-Like 15*
IAA30	Indole acetic acid inducible 30
LEC	*LEAFY COTYLEDON*
PGRs	Plant growth regulators
PKL	*PICKLE*
SD	Seed development
SE	Somatic embryogenesis
SERK	*SOMATIC EMBRYOGENESIS RECEPTOR LIKE KINASE*
TCL	TRICHOMELESS
TFs	Transcription factors
WUS	*WUSCHEL*

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Introduction

Embryogenesis is an essential stage which represents developmental plasticity in higher plant species (Yang and Zhang 2010). Somatic embryogenesis (SE) is an important in vitro regeneration method in modern crop breeding which describes the single cell differentiation into a mature embryo through different development periods (Kumar and Van Staden 2017). In the SE pathway, haploid or diploid somatic cells develop into differentiated plants through different embryological stages (globular, heart, torpedo and cotyle-donary-shaped) without fusion of gametes (Williams and Maheswaran 1986; Kumar and Van Staden 2017). In general, two distinct phases are involved in the whole process of plant embryogenesis; early morphogenesis phase which includes the formation of embryogenic cells and tissues, and maturation phase that permit the embryo to enter into a desiccated state (West and Harada 1993; Goldberg et al. 1994; Méndez-Hernández et al. 2019). Studies on the genetic mechanisms confirmed that a number of transcription factors (TFs) have been identified which are responsible for inducing somatic embryogenesis when ectopically expressed. A predominant number of SE-inducing genes encode TFs including *SOMATIC EMBRYOGENESIS RECEPTOR-LIKE KINASE* (*SERK*) (Schmidt et al. 1997; Kumar and Van Staden 2019), *BABY BOOM* (*BBM*) (Boutilier et al. 2002; Jha and Kumar 2018), *LEAFY COTYLEDON* (*LEC*) (Stone et al. 2001; Gaj et al. 2005), *AGAMOUS-LIKE 15* (*AGL15*) (Harding et al. 2003), *WUSCHEL* (*WUS*) (Zuo et al. 2002), and *EMBRYO*

MAKER (Tsuwamoto et al. 2010) have been identified, which are responsible for the induction of differentiated somatic cells and somatic embryo formation. Among the TF genes, the *LEC* genes are reported to have an important role in controlling several aspects of embryogenesis including embryo development (Gaj et al. 2005; Braybrook and Harada 2008 (Table 1)). The *LEC* TFs (*LEC1*, *LEC2* and *FUSCA3 (FUS3)*) are unique regulators of embryogenesis in that they are required to explain the molecular mechanisms for controlling embryo development, morphogenesis and embryo maturation (Harada 2001). The *LEC* TFs establish environments that encourage the initiation of somatic embryo formation and cellular processes of the maturation phase. The cessation of embryo morphogenesis, synthesis and storage of accumulated macromolecules, acquirement of desiccation tolerance and desiccation of the seed are the major features of the maturation phase (Harada 1997; Vicente-Carbajosa and Carbonaro 2005; Braybrook and Harada 2008). In early embryogenesis, *LEC* TFs are needed to specify suspensor cell fate and cotyledon identity (Lotan et al. 1998; Meinke et al. 1994; Keith et al. 1994; West et al. 1994; Stone et al. 2001), whereas during late embryogenesis *LEC* TFs are required for maturation phase for the expression of maturation-specific genes (West et al. 1994; Baumlein et al. 1994). Thus, *LEC* TFs are candidate gene regulators, which play a key role in controlling many aspects of embryogenesis including morphogenesis and maturation. The *LEC1*, *LEC2* and *FUS3* encode two distinct classes of TFs. The *LEC1* gene encodes an extensive sequence similarity to the HEMEACTIVATED PROTEIN 3 (HAP3) subunit of the CCAAT-binding TF, an isoform found in seed plants (Lotan et al. 1998; Stone et al. 2001; Kwong et al. 2003; Braybrook and Harada 2008). In *Arabidopsis thaliana*, based on sequence similarity HAP3 subunits can be divided into two different classes such as *LEC1*-type and the non-*LEC1*-type (Lee et al. 2003). Both the *LEC1* types are essential for embryogenesis and embryo development (Kwong et al. 2003). The *LEC2* and *FUS3* genes encodes B3 domain TFs, a DNA-binding motif, which acts in developing seeds (Luerssen et al. 1998; Stone et al. 2001). Ectopic expression of the *LEC* genes, *LEC1* and *LEC2* activate SE in vegetative cells and were found to be adequate in embryo development (Lotan et al. 1998; Stone et al. 2001). It was hypothesized that *Arabidopsis PICKLE* (*PKL*), which encodes a CHD3-chromatin-remodeling factor, is responsible for repression of the *LEC* genes during seed germination (Ogas et al. 1999; Rider et al. 2003). Consistent with expression of the *LEC* genes, *PKL* mutants accumulate storage products and promote embryonic identity in culture. These embryonic features are repressed by exogenous GA and enhanced by GA synthesis inhibitors (Ogas et al. 1997). The *LEC2* and *FUS3* TFs activates the genes involved in the accumulation of storage macromolecules in the embryo during maturation. In addition, *LEC2* and *FUS3* TFs are implicated in repression of GA biosynthesis during seed development (Gazzarrini et al. 2004; Curaba et al. 2004).

As shown in Fig. 1, *LEC1* gene activates *YUC10*, whereas *LEC2* induces *YUC2* and *YUC4*, an auxin biosynthesis enzyme (Stone et al. 2008). The *LEC2* gene also induces the *IAA30* (negative regulator of auxin signaling) (Braybrook et al. 2006; Kumar and Van Staden 2017; Jha and Kumar 2018). The activation of *YUC* genes increase the endogenous auxin levels which obviates the necessity for exogenous auxin and provides a critical insight into *LEC*-mediated SE.

The role of *LEC* genes in embryogenesis have been reported in many plant species such as *A. thaliana* (Lotan et al. 1998; Stone et al. 2001; Gaj et al. 2005; Wójcikowska et al. 2013), *Zea mays* (Zhang et al. 2002), *Daucus carota* hypocotyl (Yazawa et al. 2004), *Coffea canephora* seedlings (Nic-Can et al. 2013), *Medicago sativa* protoplasts (Domoki et al. 2006), *Medicago truncatula* leaves (Orlowska et al. 2017), *Theobroma cacao* leaf tissue (Alemanno et al. 2007; Fister et al. 2018) and *c* axillary buds (Brand et al. 2019). Additionally, few studies also revealed diverse biological processes of *LECs* such as regulation of gene sets, involved in seed development (Pelletier et al. 2017) and for enhancing oil yield in *Camelina* and *Arabidopsis* seeds (Zhu et al. 2018). The main purpose of this review is to provide brief insights on the recent discoveries and current advances of the *LEC* TFs in the area of plant embryogenesis.

Ectopic expression of *LEC* genes induces embryogenesis without exogenous auxin. Based on the articles reviewed we suggest that the endogenous auxin level was increased by *LEC1*-mediated activation of *YUC10* gene and *LEC2*-mediated activation of *YUC2* and *YUC4* gene that encodes auxin biosynthesis and *IAA30* (negative regular of auxin signaling), which modulate the auxin-mediated signaling during embryogenesis.

## *LEC* TFs genes are crucial during somatic embryogenesis

SE developmental pathway comprises complex network of cellular processes and expression of several signaling pathways. A considerable number of studies related to molecular genetics confirmed that induction of spontaneous embryogenesis is due to ectopic expression of TF genes (Salvo et al. 2014; Horstman et al. 2017a; Jha and Kumar 2018). *LECs* TFs are central regulators of plant cell totipotency (Gaj et al. 2005), are responsible for initiation and control of maturation phase during embryogenesis and cause formation of somatic embryos when expressed ectopically (Braybrook and Harada 2008). During embryogenesis the zygote undergoes two different developmental stages i.e. morphogenesis and maturation. In morphogenesis, the basic plant

Table 1 Showing *LECs* TF gene and their biological functions in different plant species

Plant species	Eudicot/Monocot	Gene type	Name of gene	Biological function	References
A. thaliana	Eudicot	*LEC*	*LEC2*	To induce embryo development in vegetative cells; Induction of direct somatic embryogenesis	Lotan et al. (1998)
A. thaliana	Eudicot	*LEC*	*LEC2*	To induce embryo development	Stone et al. (2001)
A. thaliana	Eudicot	*LEC*	*LEC1/2; FUS3*	Induction of somatic embryogenesis	Gaj et al. (2005)
A. thaliana	Eudicot	*LEC*	*LEC2*	Promote somatic embryogenesis induction	Wójcikowska et al. (2013)
A. thaliana	Eudicot	*LEC*	*LEC2*	Rapid changes in auxin activity and induce cell-dedifferentiation in the maturation phase of embryogenesis	Stone et al. (2008)
A. thaliana	Eudicot	*LEC*	*LEC2*	Trigger the accumulation of oil and seed specific mRNAs	Mendoza et al. (2005)
A. thaliana	Eudicot	*LEC*	*LEC2*	Seed maturation	Kim et al. (2014)
A. thaliana	Eudicot	*LEC*	*LEC1*	To induce plant embryo development	Suzuki et al. (2007)
A. thaliana	Eudicot	*LEC*	*LEC1; FUS3*	Somatic embryogenesis dedifferentiation and development	Ledwoń and Gaj (2011)
A. thaliana	Eudicot	*LEC*	*LEC1*	Involved in controlling late embryogenesis develement	West et al. (1994)
A. thaliana	Eudicot	*LEC*	*LEC1*	Essential for embryo development	Kwong et al. (2003)
A. thaliana	Eudicot	*LEC*	*LEC2*	Induces a leaf anatomy and development	Feeney et al. (2013)
A. thaliana	Eudicot	*LEC*	*LEC1*	Regulates trichome development and controls cell fate determination	Huang et al. (2015a)
A. thaliana	Eudicot	*LEC*	*ZmLEC1*	Essential for enhancing oil yield	Zhu et al. (2018)
A. thaliana	Eudicot	*LEC*	*FUS3*	Seed development	Wang and Perry (2013)
A. thaliana	Eudicot	*LEC*	*FUS3*	Seed development	Roscoe et al. (2019)
A. thaliana	Eudicot	*LEC*	*FUS3–LEC2 complex*	Essential to control lateral root formation	Tang et al. (2016)
A. thaliana	Eudicot	*LEC*	*LEC1/ LEC2/ FUS3*	Induction of somatic embryogenesis	Horstman et al. (2017b)
A. thaliana	Eudicot	*LEC*	*LEC1*	Promotes epigenetic reprogramming during early embryogenesis	Tao et al. (2017)
A. thaliana	Eudicot	*LEC*	*LEC2/ FUS3*	Involved in early embryogenesis	Tao et al. (2019)
Z. mays	Monocot	*LEC*	*ZmLEC1*	Induction of zygotic and somatic embryogenesis	Zhang et al. (2002)
Z. mays	Monocot	*LEC*	*ZmLEC1*	Increases seed oil production in maize	Shen et al. (2010)
D. carota	Eudicot	*LEC*	*DcLEC1*	Induction of zygotic and somatic embryogenesis	Yazawa et al. (2004)
M. sativa	Eudicot	*LEC*	*MsLEC1*	Somatic embryogenesis induction from leaf protoplast cells	Domoki et al. (2006)
C. sativa	Eudicot	*LEC*	*ZmLEC1*	Essential for enhancing oil yield	Zhu et al. (2018)
T. cacao	Eudicot	*LEC*	*LEC1*	Induction of somatic embryogenesis	Alemanno et al. (2007)
T. cacao	Eudicot	*LEC*	*LEC2*	Induction of somatic embryogenesis	Shires et al. (2017)
T. cacao	Eudicot	*LEC*	*LEC2*	Induction of somatic embryogenesis in leaf tissue	Fister et al. (2018)
G. hirsutum	Eudicot	*LEC*	*LEC1*	Regulates somatic embryogenesis by regulating auxin homeostatis	Min et al. (2015)
C. annuum	Eudicot	*LEC*	*LEC1*	Induction of somatic embryogenesis	Irikova et al. (2012)
C. sinensis	Eudicot	*LEC*	*LEC1*	To induce embryo-like structures	Zhu et al. (2014)
M. trunculata	Eudicot	*LEC*	*LEC1*	Induction of somatic embryogenesis	Orlowska et al. (2017)
G. max	Eudicot	*LEC*	*LEC1*	Regulates gene sets and involved in seed development	Pelletier et al. (2017)
G. max	Eudicot	*LEC*	*LEC2*	Regulates gene sets and involved in seed development	Manan et al. (2017)
B. napus	Eudicot	*LEC*	*LEC1& LEC-1LIKE*	Enhanced seed oil production	Tan et al. (2011)

Table 1 (continued)

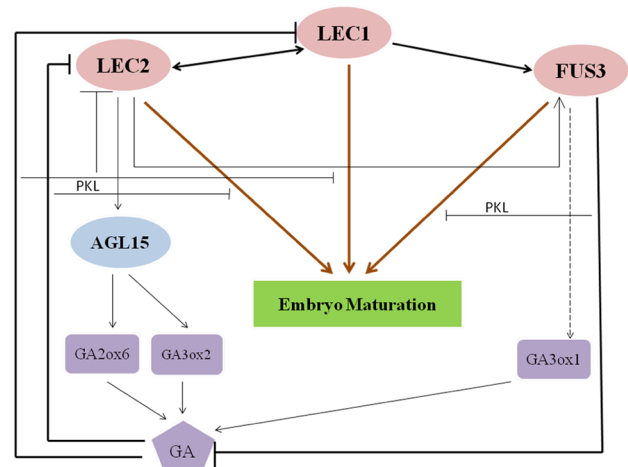| Plant species	Eudicot/Monocot	Gene type	Name of gene	Biological function	References
M. esculenta	Eudicot	*LEC*	*MeLEC1* *MeLEC2*	Induction of somatic embryogenesis	Brand et al. (2019)
S.moellendorffii	Lycophyte	*LEC*	*LEC1*	Seed development	Kirkbride et al. (2013)
C. sinensis	Rutaceae	*FUSCA3*	*CsFUS3*	Promotes somatic embryogenesis	Liu et al. (2018)
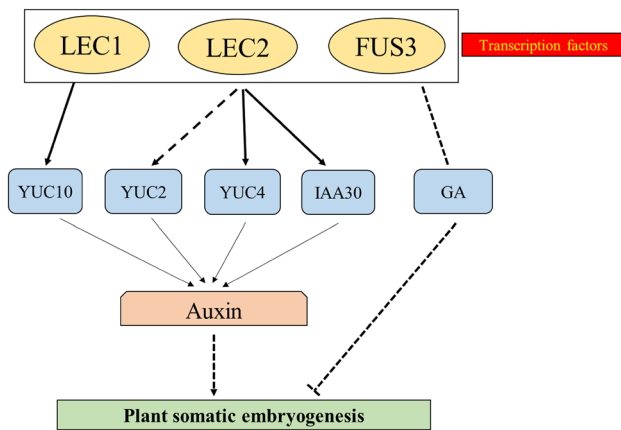
Fig. 1 Schematic model which explain the role of *LEC* TFs in somatic embryogenesis. Ectopic expression of *LEC* genes induces embryogenesis without exogenous auxin. Based on the articles reviewed we suggest that the endogenous auxin level was increased by *LEC1*-mediated activation of *YUC10* gene and *LEC2*-mediated activation of *YUC2* and *YUC4* gene that encodes auxin biosynthesis and *IAA30* (negative regular of auxin signaling), which modulate the auxin-mediated signaling during embryogenesis. The *FUS3* repressed biosynthesis of GA. Arrows with dotted line indicate transcriptional regulation that molecular mechanisms are not clear and arrows with solid line indicates direct transcriptional regulation by molecular evidence

Fig. 2 Schematic overview of regulation of the embryo maturation phase by *LEC* TFs. During embryo maturation phase *LEC* TFs exhibit complex regulatory interrelationship to activate several genes to induce maturation. The *LEC2* activates both *LEC1* and *FUS3* (Stone et al. 2008), whereas, *LEC1* activates *LEC2* and *FUS3* (Kagaya et al. 2005b; To et al. 2006). *LEC* TFs interact with GA; *LEC2* directly induces and activates *AGL15* (Braybrook et al. 2006). The *AGL15* positively activates GA degrading enzyme GA$_3$ox2 (Wang et al. 2004; Kumar and Van Staden 2017). The *FUS3* represses the GA$_3$ox1 and GA$_3$ox2 (GA biosynthesis genes) (Gazzarrini et al. 2004; Curaba et al. 2004). *PKL* represses *LEC* genes in seedlings (Ogas et al. 1997; Rider et al. 2003). *pkl* mutants express *LEC* genes ectopically and the overexpression of *LEC* genes is enhanced by GA synthesis inhibitors. However, *PKL*-mediated repression of maturation process is still unclear

body is established and the embryo is expressed as a shoot (plumule) and root (radicle) axis. (Harada 2001; Laux and Jurgens 1997). During maturation phase several metabolic activities allow the embryo to germinate (Harada 1997). Storage proteins and lipids are stored in protein and lipid bodies throughout the embryo and these are utilized by the growing seedling as a nutrient source.

In addition, at this stage the embryo acquires the ability to withstand desiccation; seeds desiccate at the late development of embryogenesis (Harada 2001).

It is so that the *LEC1/2* and *FUS3* participate in an important role in controlling several aspects of embryogenesis including early morphogenesis and late maturation phase (Harada 2001; Parcy et al. 1997; Nambara et al. 2000; Kroj et al. 2003; Gaj et al. 2005). The *LEC* genes are essential to maintain suspensor cell identity during morphogenesis phase in embryogenesis (Meinke and Yeung 1993). A further function during morphogenesis of the *LEC* genes is the specification of cotyledon identity (Meinke 1992; Meinke et al. 1994; West et al. 1994). Cotyledons are reverting partially to a leaf-like organ and incompletely specified in the absence of *LEC* gene activity.

During maturation phase, the *LEC* genes regulate and are responsible for the storage of macromolecule synthesis and accumulation. The *LEC* genes ectopically expressed in plants accumulates lipids and proteins characteristic of seeds in reproductive and vegetative tissues (Stone et al. 2001, 2008; Mendoza et al. 2005; Baud et al. 2007; Wang et al. 2007a, b). Storage protein synthesis and lipid accumulation is defective in loss-of-function *LEC* mutants, however, these *LEC* mutants are involved in the accumulation of starch grains and protein in the distal tips and in basal regions respectively (Meinke et al.

1994; Ikeda et al. 2006). Likewise, a number of researchers have identified that the expression of genes usually active during maturation phase, including genes related to storage lipid and protein accumulation, is defective in *LEC* mutants (Harada 2001; Bäumlein et al. 1994; Parcy et al. 1997).

The *LEC* TFs directly target the genes involved in the synthesis of storage macromolecule. The *LEC2* and *FUS3* TF genes bind with the RY sequence repeats, which is conserved in the 5′ flanking regions of seed protein genes and involved in the regulation of transcription of these genes (Dickinson et al. 1988; Kroj et al. 2003; Reidt et al. 2000; Monke et al. 2004; Braybrook et al. 2006). During maturation phase, *ABSCISIC ACID INSENSITIVE3* (*ABI3*) interacts with *LEC* genes to regulate the seed protein genes (Kroj et al. 2003; To et al. 2006). Activation of *LEC1* seed protein gene is dependent on the *ABI3* and other *LEC* genes. Ectopic expression of *LEC1* activates the *ABI*, *LEC2* and *FUS3* genes (Kagaya et al. 2005a).

A complex relationship among the *LEC* TFs for the regulation of embryo maturation has been shown in Fig. 2. During embryo maturation phase *LEC* TFs exhibit complex regulatory interrelationships to activate several genes to induce maturation. The *LEC2* activates both *LEC1* and *FUS3* (Stone et al. 2008), whereas, *LEC1* activates *LEC2* and FUS3 (Kagaya et al. 2005b; To et al. 2006). *LE*C TFs interact with GA; *LEC2* directly induces and activates *AGL15* (Braybrook et al. 2006). The *AGL15* positively activates GA degrading enzyme GA$_3$ox2 (Wang et al. 2004; Kumar and Van Staden 2017). The *FUS3* represses the GA$_3$ox1 and GA$_3$ox2 (GA biosynthesis genes) (Gazzarrini et al. 2004; Curaba et al. 2004). *PKL* represses *LEC* genes in seedlings (Ogas et al. 1997; Rider Jr. et al. 2003). *PKL* mutants express *LEC* genes ectopically and the overexpression of *LEC* genes is enhanced by GA synthesis inhibitors. However, *PKL*-mediated repression of the maturation process is still unclear. These characteristics revealed that the *LEC* TF genes play an essential role in controlling embryogenesis processes in plants. The *LEC* genes have distinct differences, although they share similar mutant phenotypes. Finally, the *LEC* genes are candidate markers that coordinate embryogenesis being involved in both morphogenesis and maturation stages.

Other transcription factor genes controlling plant embryogenesis

SE consists of various developmental phases which initiates with embryonic induction. While the cells are in induction phase, several genes are functional, possibly due to biotic or abiotic stresses or extrinsic hormones. The induction phase can further be classified into three sub stages: embryogenic dedifferentiation, totipotency expression and embryogenic commitment. Cell dedifferentiation is a cellular regression

process in which mature cells are converted into transient stages.

As discussed above, *LEC* genes have been found to be key regulators for embryogenesis when ectopically expressed. However, other TF genes have also been recognized to promote embryogenesis which includes *SERK* (Schmidt et al. 1997; Hecht et al. 2001), *BBM* (Boutilier et al. 2002), *AGL15* (Harding et al. 2002), *WUS* (Zuo et al. 2002), and *EMBRYO MAKER* (Tsuwamoto et al. 2010).

SERK role is identified during embryogenesis in several plant species such as *A. thaliana* (Hecht et al. 2001), *Z. mays* (Zhang et al. 2011), *M. truncatula* (Nolan et al. 2009), *T. cacao* (Santos et al. 2005) and *T. nigrescens* (Pilarska et al. 2016). In a study on *Arabidopsis*, by Hecht et al. (2001), *AtSERK1* was found to be highly expressed during early embryogenesis. The study suggested that *AtSERK1* gene is initially expressed during megasporogenesis in the megaspore and in cells of embryo sac till fertilization stage. However, least expression of the same gene has been found in matured vascular tissues. *ZmSERK1* and *ZmSERK2* genes isolated from *Z. mays*, has been found to express during embryogenesis (Zhang et al. 2011). Interestingly, *ZmSERKs* genes expression are associated to embryo development and hormone signaling. These studies indicates that *SERK* gene is involved in cell to embryonic transition in plant cells.

WUS encodes the homoeodomain TF, reported to play an important role in plant embryogenesis. It has been observed that *WUS* is positively up-regulated during SE in various plant species (Zuo et al. 2002; Zheng et al. 2014; Tvorogova et al. 2019). Ectopic expression of *WUS* gene was shown to be involved in vegetative-to-embryonic transition in all tissues (leaf petiole, leaves, stem and root), without adding exogenous growth hormones in *A. thaliana* (Zuo et al. 2002). In *C. canephora*, overexpression of *WUS* significantly enhanced the embryo development up to 400%, and also increased the SE in a heterologous system, however exogenous PGRs were essential for the initiation of SE (Arroyo-Herrera et al. 2008).

A. thaliana WUS (*AtWUS*) significantly increased embryogenic callus formation (47.75%) in *G. hirsutum* (cotton), when ectopically expressed (Zheng et al. 2014), and also positively upregulated *LEC1*, *LEC2* and *FUS3* in the embryogenic callus. Similarly, Bouchabké-Coussa et al. (2013) also revealed that *WUS* overexpression significantly promoted (×3) embryogenic capacity and triggered in vitro regeneration competence in cotton when *WUS* was expressed ectopically. However, these researchers also examined that *WUS* overexpression resulted in the initiation of embryo-like structures (abnormal) and that leaf-like structures developed on the somatic embryos (Bouchabké-Coussa et al. 2013).

In tobacco, Zhou et al. (2018) uncovered a novel function of *WOXs* in regulating embryo patterning, and confirmed by expression pattern analysis that *WOX2* and *WOX9* are

essential for early embryo patterning. In a recent report with *M. truncatula*, it was showed that the *WOX9* homolog, *MtWOX9-1*, participates in embryogenesis and its overexpression enhances embryogenic capacity by changing the expression levels of various SE-associated genes (Tvorogova et al. 2019). These findings confirmed that *WUS* and *WOX* family members have an important impact on improving SE competence in plant cells.

BBM TF is a master regulator, which induces embryo development without any exogenous PGRs (Boutilier et al. 2002; Jha and Kumar 2018). In a breakthrough report, it was observed that *BBM* transcriptionally regulates *LEC1/2*, *ABI3* and *FUS3* network during plant embryogenesis (Horstman et al. 2017b). This observation indicates that *LEC1* and *FUS3* are crucial for embryo development, where as *ABI3* and *LEC2* positively regulates *BBM*-mediated SE. However, it is a context and dose-dependent mechanism. In a breakthrough report by Boutilier et al. (2002), it was found that in *Arabidopsis* an ortholog gene (*AtBBM*) and in *B. napus* two ortholog genes (*BnBBM1* and *BnBBM2*) were recognized and it was revealed that overexpression of these ortholog genes encourage embryo development. A transgene constructs *35S::BBM* and *UBI::BBM* were used for transformation in *Arabidopsis* and *B. napus* respectively and responsible for cotyledon-shaped embryo development on post-germination organs. Interestingly, in *P. tomentosa*, overexpression of *BBM*-mediated embryogenesis significantly improved regeneration pathway (Deng et al. 2009). BBM induces embryo development from *P. tomentosa* calli, when expressed ectopically. Approximately 12 embryo were developed from 6 calli after 28 days, however, among 12 only 6 embryo survived and developed into complete plantlets (Deng et al. 2009). Similarly, in *T. cacao*, an ortholog gene (*TcBBM*) has been identified, which is found to promote the vegetative to embryonic transition of *T. cacao* somatic cells (Florez et al. 2015).

Expression level of *TcBBM* gene was found throughout the embryogenesis process including several stages such as globular-stage, heart-stage, early and late torpedo stage and cotyledonary stages. These expression levels led to phenotype in *T. cacao*, without any exogenous PGRs for direct embryogenesis, however, *TcBBM* overexpression enhanced embryonic potential significantly. Overall, these findings showed that *TcBBM* transcriptional level plays a vital role in embryogenesis and it could use as marker gene in *T. cacao* tissue for embryonic growth (Florez et al. 2015).

AGL15 encodes a MADS domain TF that is expressed during embryogenesis, although not exclusively (Heck et al. 1995; Rounsley et al. 1995; Perry et al. 1999; Wang et al. 2004; Zheng et al. 2016). In *Arabidopsis*, *AGL15* can stimulate SE and lead to extended periods (over 12–19 years to date), when expressed ectopically (Harding et al. 2003; Thakare et al.2008; Zheng et al. 2016). A transgene (*35S promoter:AGL15*), promotes SE from apical region of shoots which is germinated in the medium supplemented with 2,4-D (Harding et al. 2003; Thakare et al.2008). In addition, overexpression of *AGL15-like* TF gene is responsible for early embryogenesis in *Zea mays* (Salvo et al. 2014). Moreover, gene encoding putative ortholog, *GmAGL15* (isolated from *Glycine max*) can enhance embryo development in *Arabidopsis* (Thakare et al. 2008). However, loss-of-function alleles of agl15 showed significant reduction in SE (Thakare et al. 2008). Finally, the different TF genes are master regulators that coordinate SE being involved in both early and late embryo development.

LEC TFs gene mediated oil content accumulation

Oilseed crop improvement is one of the major objectives to fulfil the ever-increasing oil needs by humans and for biodiesel production. A number of plants accumulate oils in the seeds with several beneficial effects. Mainly plant oil is synthesized as triacylglycerols (TAGs) from fatty acyl-CoA and glycerol-3-phosphate (Ohlrogge and Browse 1995; Shen et al. 2010).

Seed oil content in plants is controlled by several phases in the oil biosynthetic pathway. Oilseed accumulation and biosynthesis are influenced by various genes which are involved directly or indirectly in embryo or seed development (Wang et al. 2007a, b; Shen et al. 2010; Tan et al. 2011; Zhu et al. 2018). In *A. thaliana*, two important TFs *LEC1* and *WRINKLED1* (*WRI1*) have been found which are involved in the regulation of oil accumulation (Lotan et al. 1998; Cernac and Benning 2004). Several studies by pioneer scientists have been documented that overexpression of TFs enhance the oil production in plants when compared to the overexpression of pathway enzymes (Broun 2004; Grotewold 2008; Van Erp et al. 2014). The *LEC* TFs are key regulators of embryogenesis and are also involved in fatty acid biosynthesis by increasing the expression of genes.

In *Zea mays* (maize), *ZmLEC1* (*maize LEC1*) is overexpressed as a key regulator and increases the seed oil production (Shen et al. 2010). The *ZmLEC1* gene homolog exhibited 41% identity to *Arabidopsis LEC1* in amino acid sequence. Overexpression of *ZmLEC1* enhanced the oil content by 48.7% in transgenic maize, however, seed germination and leaf growth reduced significantly (Shen et al. 2010). The transgenic leaves were 40–50% shorter, and were narrow and dark green in colour. Transgenic *ZmLEC1* seedlings shoot and root growth were slower, resulting in reduced height of the plant in the field.

In a recent promising report, *LEC* gene was shown to increase oil production in *Arabidopsis* and *Camelina* seeds (Zhu et al. 2018). By using *Agrobacterium*-mediated floral

dip method *ZmLEC1* binary vector were constructed, driven by seed-specific serine carboxypeptidase-like (SCPL17) and acyl carrier protein (ACP5) promoters and introduced into *Arabidopsis* and *Camelina* for expression. The overexpression of *ZmLEC1* enhanced the total oil content by < 20% in *Arabidopsis* and < 26% in *Camelina* mature seeds (Zhu et al. 2018). Interestingly, there was no phenotypic variation or abnormal growth identified throughout the life cycle of both the plants. These results suggest that *ZmLEC1*, a master regulator, trigger and increases the oil content in *Arabidopsis* and *Camelina* seeds and might be useful for the enhancement of oil production in different crops or oilseed crop improvement. Similarly, in *Brassica napus*, overexpression of *BnLEC1* and *Bn LEC1-like* TFs significantly increases the total seed oil content by 2–20% in transgenic seeds without any abnormal effects on agronomic traits (Tan et al. 2011). In a report by Angeles-Núñez and Tiessen (2011), they proposed that overexpression of *LEC2* TF reduced the seed oil content by 30% while maintaining high levels of sucrose (140%) and starch (> fivefold more) in transgenic *Arabidopsis* seeds. Future research with more extensive analysis may help to understand the molecular mechanisms on how *LEC* genes are involved in the expression of genes for fatty acid biosynthesis.

LEC crucial for seed development

Seed development (SD) is a critical and complex phase of the higher plant life cycle. A seed comprises three different regions (filial embryo, filial endosperm and maternal seed coat) with distinct variation on a common genotype (Jo et al. 2019). Furthermore, each region contains distinct subregions, cell and tissues. SD process starts with a double fertilization event that generate the zygote and endosperm (Goldberg et al. 1994; Harada 2001). Many TFs have been shown to express and regulate diverse processes during SD (Pradhan et al. 2014; Jia et al. 2014; Devic and Roscoe 2016; Jo et al. 2019). Among the TFs involved in SD, *LEC1* has been considered to be a central regulator of SD (Harada 2001; To et al. 2006; Braybrook and Harada 2008; Pelletier et al. 2017; Jo et al. 2019). *LEC1* TF acts sequentially and controls diverse processes at several stages of SD (Pelletier et al. 2017). During SD, *LEC1* acts indirectly to regulate diverse processes by activating TFs controlling structural genes, however, *LEC1* also regulate directly by establishing a feed-forward loop (FFL) network with association of other TFs (Mangan and Alon 2003). In addition, *LEC1* also interacts with several other TFs and activates a particular set of genes during SD (Huang et al. 2015b).

LEC1 is also positively involved in chloroplast biogenesis and photosynthesis during SD (Pelletier et al. 2017;

Jo et al. 2019). In *Arabidpsis* and *Glycine max* (soybean) embryos, *LEC1* TF transcriptionally activates and expressed a genes encoding the light-reaction components of photosystems I and II and other set of genes involved in photosynthesis and chloroplast biogenesis (Pelletier et al. 2017). It was also identified that *LEC1* TF also regulates and control endosperm development (Lotan et al. 1998). In rice, *LEC1* control endosperm development through its interaction with *AP2* TFs (Zhang and Xue 2013; Xu et al. 2016).

It was found that *LEC1* may regulate directly or indirectly different TFs to regulate gene sets involved in early and late stages of SD (Junker et al. 2012; Pelletier et al. 2017; Jo et al. 2019). The *LEC1* directly regulates the *LEC2*, *ABI3* and *FUS3* TFs, which all are master regulators of seed maturation (Santos-Mendoza et al. 2008; Braybrook and Harada 2008; Boulard et al. 2017, 2018). It confirms that *LEC1* transcriptionally regulates *ABI3* and *FUS*3 and together they form a feed-forward loop (FFL) network, a three-gene pattern and regulates a target gene (Mangan and Alon 2003). Similarly, *LEC1* directly regulates *WRINKLED1* (*WRI1*) (TF which plays a key role in seed maturation), and make a FFL network and directly regulate genes involved in the fatty acid accumulation during SD in *Arabidopsis* (Baud et al. 2007; To et al. 2012; Jo et al. 2019). Moreover, *LEC1* TF also control SD indirectly by regulating the expression of TFs that independently control SD.

Few studies suggested that *LEC1* may interact with other TFs to regulate diverse development processes during SD (Parcy et al. 1997; To et al. 2006; Pelletier et al. 2017; Jo et al. 2019). In a recent report published in PNAS, they propose that *LEC1* acts sequentially and interacts with different TFs and respond to different developmental signals during seed development (Pelletier et al. 2017). *LEC1* interacts with *LEC2*, *ABI3* and *FUS3* TFs and control gene expression in seeds and are involved in the regulation of diverse processes during seed maturation (Devic and Roscoe 2016; Boulard et al. 2018; Lepiniec et al. 2018).

LEC1 control the maturation phase by interacting with B3 and bZIP (basic leucine zipper TF) TFs which accumulate during SD (Mendes et al. 2013; Baud et al. 2016).

In addition, *LEC1* interacts with *PHYTOCHROME INTERACTING FACTOR4* (*PIF4*) (a transcriptional modulator), which is responsible for the expression of hypocotyl elongation related genes through G box element (Huang et al. 2015b). *LEC1* also interacts with *TCL2* to repress trichome formation during embryogenesis (Huang et al. 2015a). Finally, the interaction of *LEC1* with many other TFs provides an outline to define how *LEC1* regulate and express distinct gene sets during different phases of SD. In future, *LEC1* interaction with all TFs and their impact on *LEC1* could provide novel insights into the multitasking of *LEC1* during SD. In *A. thaliana*, *FUS3* phosphorylation at

SnRK1 (conserved eukaryotic kinase complex) sites positively regulates seed yield and plant growth at heat stress (Chan et al. 2017). They concluded that *FUS3* phosphorylation plays an important role for SD and plant growth at high temperature. However, the molecular mechanism by which *FUS3* regulates is still elusive. Finally, *LEC1* TF has been identified as a central regulator of SD, however, very little is known about the mechanisms by which *LEC1* controls and regulates diverse biological processes of SD.

Multi-functionality of *LEC* TFs during plant development

The *LEC* TFs acts as a master regulator and are involved in diverse functions including plant embryogenesis, growth and development. In *A. thaliana*, Junker and Baumlein 2012 and Junker et al. 2012 identified that *LEC1* TF affects light and brassinosteroid (BR) signaling during embryogenesis. In addition, *LEC1* expression has also been detected in etiolated seedlings (Warpeha et al. 2007; Siefers et al. 2009; Junker et al. 2012).

Lateral root development is critical for higher plants and is responsible for the uptake of water and nutrient acquisition for the growth and development of plants (Charlton 1996; Tang et al. 2016). Embryonic master regulators *LEC2* and *FUS3* are involved in the lateral root formation by regulating *YUC* functions (Tang et al. 2016). In *A. thaliana*, a *FUS3* and *LEC2* complex function synergistically and activates auxin biosynthesis and *YUC* gene during lateral root formation. However, expression of *FUS3* during lateral root formation is activated by *LEC2* (Tang et al. 2016). In future, more extensive studies will hopefully provide novel findings for the better understanding of the molecular mechanisms of lateral root formation.

A number of studies have been reported that during post-embryonic development cell fate determination is controlled by TFs (Peris et al. 2010; Perianez-Rodriguez et al. 2014). Few researchers documented a significant role of *LEC1* in post-embryonic cell differentiation, including formation of trichomes, mesophyll cells and vascular tissue (Junker and Baumlein 2012; Junker et al. 2012). The regulation of trichome formation by different TFs has been well studied by several researchers (Marks and Feldmann 1989; Oppenheimer et al. 1991; Wang and Chen 2014; Zhao et al. 2008; Zhou et al. 2014). Huang et al. (2015a) documented that *LEC1* is positively involved in cell fate determination during post-embryonic development in *A. thaliana*. They found that *LEC1* interacts in vitro with transcription repressors such as TRICHOMELESS1/2 (*TCL1/2*), CAPPICE (*CPC*) and ENHANCER OF TRY AND CPC1 (*ETC1*) to repress trichome formation. It was identified that *TCL1* was highly expressed in developing seeds, whereas *TCL2* in cotyledons

(Wang et al. 2007a, b; Gan et al. 2011). The interaction with these repressors provides a mechanism by which *LEC1* regulates cell fate determination.

In a recent breakthrough report by Tao et al. (2019), they discovered that *LEC2* and *FUS3* TFs are involved in expression of key flowering gene and embryonic resetting in *Arabidopsis*. The *LEC2* and *FUS3* TFs compete against *VAL1* and *VAL2* (epigenome readers) to disrupt the Polycomb silencing during early embryogenesis. Furthermore, *LEC2* and *FUS3* recruit the FRIGIDA (scaffold protein) in order to establish an active chromatin state, resulting in the activation of *FLC* (*FLOWERING LOCUC C*, a floral repressor) and erasing the parental memory in early somatic embryos during winter cold. However, *LEC2* and *FUS3* were silenced during post-embryonic phase (Tao et al. 2019). Reprogramming of epigenetic mechanisms during embryogenesis by *LEC* TF is well reported (Tao et al. 2017).

Further research will help to unlock the different biological and molecular mechanism underlying these processes. These results suggest that over-expression of *LEC* gene has been used for multifunction in different plant species. Increasing current advances and better understanding of the mechanism of *LEC* genes will lead to new opportunities and development of different biological applications.

Conclusions and future perspectives

The findings presented reveal that the *LEC* transcription factor genes have emerged as a master regulator that controls diverse aspects of somatic embryogenesis and has potential application in the plant biology. The *LEC* TFs are used as candidate markers to define the molecular mechanisms that control the initiation and maturation phase of SE. The expression of the *LEC* gene provides clear evidence of its role in embryogenesis and diverse developmental signaling pathways including oil content accumulation, cell fate determination, lateral root development and chloroplast biogenesis and photosynthesis during seed development. The *LEC* gene acts as a master regulator to participate in initiation and maturation of somatic embryos but how the *LEC*-mediated cellular process initiates the maturation phase is still unclear. In addition, how the *LEC* TFs control signaling transmission specificity to regulate initiation and maturation of somatic embryo at the molecular level remains unclear. In addition, *LEC* also acts as a pioneer TF gene, which activates different sets of genes and controls diverse biological processes during SD. However, we are only at the beginning to understand the potential insight and molecular mechanism by which *LEC1* regulates diverse functions of SD. Recent discoveries have explored the multiple roles of *LEC* TFs in diverse

aspects of plant growth and development. However, a few future challenges still need to be clarified such as *LEC1* and *LEC2* are involved in the diverse signaling pathways related to embryogenesis including embryo morphogenesis and maturation, but how these pathways are regulated remains unclear. In addition, how is the specificity of these *LEC TFs* obtained? Apart from known processes, what additional physiological and biological processes are regulated by *LEC* TFs? The underlying molecular mechanism by which *LEC* regulates diverse biological processes of SD is still unclear. Therefore, research should shed some light on how these *LEC* TFs control embryogenesis and several aspects of plant dynamics. In order to decode these regulatory networks, a single-molecule imaging technology will be required to understand the diverse functions of individual *LECs* in different signaling pathways. Together, structural studies of different *LECs* may open new roadmaps for better understanding their signaling specificity and developmental plasticity. It would also help to find new insights into the molecular mechanisms and unexplored signaling pathways for the better understanding of the functions of *LEC* TFs in plant cells.

Compliance with ethical standards

Conflict of interest All authors declare that they have no conflict of interest.

References

Alemanno L, Devic M, Niemenak N, Sanier C, Guilleminot J, Rio M, Verdeil JL, Montoro P (2007) Characterization of *leafy cotyledon1*-like during embryogenesis in *Theobroma cacao* L. Planta 227:853–866

Angeles-Núñez JG, Tiessen A (2011) Mutation of the transcription factor *LEAFY COTYLEDON 2* alters the chemical composition of *Arabidopsis* seeds, decreasing oil and protein content, while maintaining high levels of starch and sucrose in mature seeds. J Plant Physiol 168:1891–1900

Arroyo-Herrera A, Gonzalez AK, Moo RC, Quiroz-Figueroa F, Loyola-Vargas V, Rodriguez-Zapata L, Burgeff D'Hondt C, Suárez-Solís VM, Castano E (2008) Expression of *WUSCHEL* in *Coffea canephora* causes ectopic morphogenesis and increases somatic embryogenesis. Plant Cell Tissue Organ Cult 94:171–180

Baud S, Mendoza MS, To A, Harscoët E, Lepiniec L, Dubreucq B (2007) *WRINKLED1* specifies the regulatory action of *LEAFY COTYLEDON2* towards fatty acid metabolism during seed maturation in *Arabidopsis*. Plant J 50:825–838

Baud S, Kelemen Z, Thevenin J, Boulard C, Blanchet S, To A, Payre M, Berger N, Effroy-Cuzzi D, Franco-Zorrilla JM, Godoy M, Solano R, Thevenon E, Parcy F, Lepiniec L, Dubreucq B (2016)

Deciphering the molecular mechanisms underpinning the transcriptional control of gene expression by master transcriptional regulators in *Arabidopsis* seed. Plant Physiol 171:1099–1112

Bäumlein H, Miséra S, Leurben H, Kölle K, Horstman C, Wobus U, Müller AJ (1994) The *FUS3* gene of *Arabidopsis thaliana* is a regulator of gene expression during late embryogenesis. Plant J 6:379–387

Bouchabké-Coussa O, Obellianne M, Linderme D, Montes E, Maia-Grondard A, Vilaine F, Pannetier C (2013) *Wuschel* overexpression promotes somatic embryogenesis and induces organogenesis in cotton (*Gossypium hirsutum* L.) tissues cultured in vitro. Plant Cell Rep 32:675–686

Boulard C, Fatihi A, Lepiniec L, Dubreucq B (2017) Regulation and evolution of the interaction of the seed B3 transcription factors with NF-Y subunits. Biochim Biophys Acta Gene Regul Mech 1860:1069–1078

Boulard C, Thevenin J, Tranquet O, Laporte V, Lepiniec L, Dubreucq B (2018) *LEC1* (NF-YB9) directly interacts with *LEC2* to control gene expression in seed. Biochim Biophys Acta 1861:443–450

Boutilier K, Offringa R, Sharma VK, Kieft H, Ouellet T, Zhang L, Hattori J, Liu C, van Lammeren AAM, Miki BLA, Custers JBM, van Lookeren Campagne MM (2002) Ectopic Expression of *BABY BOOM* Triggers a Conversion from Vegetative to Embryonic Growth. Plant Cell 14:1737–1749

Brand A, Quimbaya M, Tohme J, Chavariagga-Aguirre P (2019) *Arabidopsis LEC1* and *LEC2* orthologous genes are key regulators of somatic embryogenesis in Cassava. Front Plant Sci 10:673

Braybrook SA, Harada JJ (2008) *LECs* go crazy in embryo development. Trends Plant Sci 13:624–630

Braybrook SA, Stone SL, Park S, Bui AQ, Le BH, Fischer RL, Goldberg RB, Harada JJ (2006) Genes directly regulated by *LEAFY COTYLEDON2* provide insight into the control of embryo maturation and somatic embryogenesis. Proc Natl Acad Sci USA 103:3468–3473

Broun P (2004) Transcription factors as tools for metabolic engineering in plants. Curr Opin Plant Biol 7:202–209

Cernac A, Benning C (2004) *WRINKLED1* encodes an AP2/EREB domain protein involved in the control of storage compound biosynthesis in *Arabidopsis*. Plant J 40:575–585

Chan A, Carianopol C, Tsai AY, Varatharajah K, Chiu RS, Gazzarrini S (2017) SnRK1 phosphorylation of *FUSCA3* positively regulates embryogenesis, seed yield, and plant growth at high temperature in *Arabidopsis*. J Exp Bot 68:4219–4231

Charlton WA (1996) Lateral root initiation. In: Waisel Y, Eshel A, Kafkafi U (eds) Plant roots: the hidden half. Marcel Dekker, New York, pp 149–174

Curaba J, Moritz T, Blervaque R, Parcy F, Raz V, Herzog M, Vachon G (2004) AtGA3ox2, a key gene responsible for bioactive gibberellin biosynthesis, is regulated during embryogenesis by *LEAFY COTYLEDON2* and *FUSCA3* in *Arabidopsis*. Plant Physiol 136:3660–3669

Deng W, Luo KM, Li ZG, Yang YW (2009) A novel method for induction of plant regeneration via somatic embryogenesis. Plant Sci 177:43–48

Devic M, Roscoe T (2016) Seed maturation: simplification of control networks in plants. Plant Sci 252:335–346

Dickinson CD, Evans RP, Nielsen NC (1988) RY repeats are conserved in the 5'-flanking regions of legume seed-protein genes. Nucleic Acids Res 16:371

Domoki M, Györgyey J, Bíró J, Pasternak TP, Zvara Á, Bottka S, Puskás LG, Dudits D, Fehér A (2006) Identification and characterization of genes associated with the induction of embryonic competence in leaf-protoplast-derived alfalfa cells. Biochimet Biophys Acta 1759:543–551

Feeney M, Frigerio L, Cui Y, Menassa R (2013) Following vegetative to embryonic cellular changes in leaves of

Arabidopsis overexpressing *LEAFY COTYLEDON2*. Plant Physiol 162:1881–1896

Fister AS, Landherr L, Perryman M, Zhang Y, Guiltinan MJ, Maximova SN (2018) Glucocorticoid receptor-regulated *TcLEC2* expression triggers somatic embryogenesis in *Theobroma cacao* leaf tissue. PLoS ONE 13:e0207666

Florez SL, Erwin RL, Maximova SN, Guiltinan MJ, Curtis WR (2015) Enhanced somatic embryogenesis in *Theobroma cacao* using the homologous BABY BOOM transcription factor. BMC Plant Biol 15:121

Gaj MD, Zhang S, Harada JJ, Lemaux PG (2005) *LEAFY COTYLEDON* genes are essential for induction of somatic embryogenesis of *Arabidopsis*. Planta 222:977–988

Gan LJ, Xia K, Chen JG, Wang SC (2011) Functional characterization of *TRICHOMELESS2*, a new single-repeat R3 MYB transcription factor in the regulation of trichome patterning in *Arabidopsis*. BMC Plant Biol 11:176

Gazzarrini S, Tsuchiya Y, Lumba S, Okamoto M, McCourt P (2004) The transcription factor *FUSCA3* controls developmental timing in *Arabidopsis* through the hormones gibberellin and abscisic acid. Dev Cell 7:373–385

Goldberg RB, De Paiva G, Yadegari R (1994) Plant embryogenesis: zygote to seed. Science 266:605–614

Grotewold E (2008) Transcription factors for predictive plant metabolic engineering: are we there yet? Curr Opin Biotechnol 19:138–144

Harada JJ (1997) Seed maturation and control of germination. In: Larkins BA, Vasi IK (eds) Advances in cellular and molecular biology of plants cellular and molecular biology of seed development, vol 4. Kluwer Academic Publishers, Dordrecht, pp 545–592

Harada JJ (2001) Role of Arabidopsis *LEAFY COTYLEDON* genes in seed development. J. Plant Physiol 158:405–409

Harding EW, Tang W, Nichols KW, Fernandez DE, Perry SE (2003) Expression and maintenance of embryogenic potential is enhanced through constitutive expression of *AGAMOUSLIKE15*. Plant Physiol 133:653–663

Hecht V, Vielle-Calzada JP, Hartog MV, Schmidt ED, Boutilier K, Grossniklaus U, de Vries SC (2001) The Arabidopsis S*OMATIC EMBRYOGENESIS RECEPTOR KINASE 1* gene is ex- pressed in developing ovules and embryos and enhances embryogenic competence in culture. Plant Physiol 127:803–816

Heck GR, Perry SE, Nichols KW, Fernandez DE (1995) AGL15, a MADS domain protein expressed in developing embryos. Plant Cell 7:1271–1282

Horstman A, Bemer M, Boutilier K (2017a) A transcriptional view on somatic embryogenesis. Regeneration 4:201–216

Horstman A, Li M, Heidmann I, Weemen M, Chen B, Muino JM, Angenent GC, Boutilier K (2017b) The *BABY BOOM* transcription factor activates the *LEC1-ABI3-FUS3-LEC2* network to induce somatic embryogenesis. Plant Physiol 175:848–857

Huang M, Hu Y, Liu X, Li Y, Hou X (2015a) *ArabidopsisLEAFY COTYLEDON1* controls cell fate determination during postembryonic development. Front Plant Sci 6:955

Huang M, Hu Y, Liu X, Li Y, Hou X (2015b) *Arabidopsis LEAFY COTYLEDON1* mediates postembryonic development via interacting with PHYTOCHROME-INTERACTING FACTOR4. Plant Cell 27:3099–3111

Ikeda M, Umehara M, Kamada H (2006) Embryogenesis-related genes; its expression and roles during somatic and zygotic embryogenesis in carrot and *Arabidopsis*. Plant Biotechnol 23:153–161

Irikova T, Grozeva S, Denev I (2012) Identification of *BABY BOOM* and *LEAFY COTYLEDON* genes in sweet pepper (*Capsicum annuum* L.) genome by their partialgene sequences. Plant Grow Regul 67:191–198

Jha P, Kumar V (2018) *BABY BOOM* (*BBM*): a candidate transcription factor gene in plant biotechnology. Biotechnol Lett 40:1467–1475

Jia H, Suzuki M, McCarty DR (2014) Regulation of the seed to seedling developmental phase transition by the *LAFL* and *VAL* transcription factor networks. Wiley Interdiscip Rev Dev Biol 3:135–145

Jo L, Pelletier JM, Harada JJ (2019) Central role of the *LEAFY COTYLEDON1* transcription factor in seed development. J Integ Plant Biol 61:564–580

Jr Rider SD, Henderson JT, Jerome RE, Edenberg HJ, Romero- Severson J, Ogas J (2003) Coordinate repression of regulators of embryogenic identity by *PICKLE* during germination in *Arabidopsis*. Plant J 35:33–43

Junker A, Bäumlein H (2012) Multifunctionality of the *LEC1* transcription factor during plant development. Plant Signal Behav 7:1718–1720

Junker A, Mönke G, Rutten T, Keilwagen J, Seifert M, Thi TMN, Renou JP, Balzergue S, Viehöver P, Hähnel U, Ludwig-Müller J, Altschmied L, Conrad U, Weisshaar B, Bäumlein H (2012) Elongation-related functions of *LEAFY COTYLEDON1* during the development of *Arabidopsis thaliana*. Plant J 71:427–442

Kagaya Y, Okuda R, Ban A, Toyoshima R, Tsutsumida K, Usui H, Yamamoto A, Hattori T (2005a) Indirect ABA-dependent regulation of seed storage protein genes by *FUSCA3* transcription factor in *Arabidopsis*. Plant Cell Physiol 46:300–311

Kagaya Y, Toyoshima R, Okuda R, Usui H, Yamamoto A, Hattori T (2005b) *LEAFY COTYLEDON1* controls seed storage protein genes through its regulation of *FUSCA3* and *ABSCISIC ACID INSENSITIVE3*. Plant Cell Physiol 46:399–406

Keith K, Kraml M, Dengler NG, McCourt P (1994) *fusca3*: a heterochronic mutation affecting late embryo development in *Arabidopsis*. Plant Cell 6:589–600

Kim HU, Jung SJ, Lee KR, Kim EH, Lee SM, Roh KH, Kim JB (2014) Ectopic overexpression of castor bean *LEAFY COTYLEDON2* (*LEC2*) in *Arabidopsis* triggers the expression of genes that encode regulators of seed maturation and oil body proteins in vegetative tissues. FEBS Open Bio 4:25–32

Kirkbride RC, Fischer RL, Harada JJ (2013) *LEAFY COTYLEDON1*, a key regulator of seed development, is expressed in vegetative and sexual propagules of *Selaginella moellendorffii*. PLoS ONE 8:e67971

Kroj T, Savino G, Valon C, Giraudat J, Parcy F (2003) Regulation of storage protein gene expression in *Arabidopsis*. Development 130:6065–6073

Kumar V, Van Staden J (2017) New insights into plant somatic embryogenesis: an epigenetic view. Acta Physiol Plant 39:194

Kumar V, Van Staden J (2019) Multi-tasking of *SERK*-like kinases in plant embryogenesis, growth and development: current advances and biotechnological applications. Acta Physiol Plant 41:31

Kwong RW, Bui AQ, Lee H, Kwong LW, Fischer RL, Goldberg RB, Harada JJ (2003) *LEAFY COTYLEDON1-LIKE* defines a class of regulators essential for embryo development. Plant Cell 15:5–18

Laux T, Jurgens G (1997) Embryogenesis: a new start in life. Plant Cell 9:989–1000

Ledwoń A, Gaj MD (2011) *LEAFY COTYLEDON1*, *FUSCA3* expression and auxin treatment in relation to somatic embryogenesis induction in *Arabidopsis*. Plant Grow Regul 65:157–167

Lee H, Fischer RL, Goldberg RB, Harada JJ (2003) *Arabidopsis* LEAFY COTYLEDON1 represents a functionally specialized subunit of the CCAAT binding transcription factor. Proc Natl Acad Sci USA 100:2152–2156

Lepiniec L, Devic M, Roscoe TJ, Bouyer D, Zhou DX, Boulard C, Baud S, Dubreucq B (2018) Molecular and epigenetic regulations

and functions of the *LAFL* transcriptional regulators that control seed development. Plant Reprod 31:291–307

Liu Z, Ge XX, Qiu WM, Long JM, Jia HH, Yang W, Dutt M, Wu XM, Guo WW (2018) Overexpression of the *CsFUS3* gene encoding a B3 transcription factor promotes somatic embryogenesis in *Citrus*. Plant Sci 277:121–131

Lotan T, Ohto M, Yee KM, West MAL, Lo R, Kwong RW, Tamagishi K, Fisher RL, Goldberg RB, Harada JJ (1998) *Arabidopsis LEAFY COTYLEDON1* is sufficient to induce embryo development in vegetative cells. Cell 93:1195–1205

Luerssen H, Kirik V, Herrmann P, Miséra S (1998) *FUSCA3* encodes a protein with a conserved VP1/AB13-like B3 domain which is of functional importance for the regulation of seed maturation in *Arabidopsis thaliana*. Plant J 15:755–764

Manan S, Ahmad MZ, Zhang G, Chen B, Haq BU, Yang J, Zhao J (2017) Soybean *LEC2* regulates subsets of genes involved in controlling the biosynthesis and catabolism of seed storage substances and seed development. Front Plant Sci 8:1604

Mangan S, Alon U (2003) Structure and function of the feed-forward loop network motif. Proc Natl Acad Sci USA 100:11980–11985

Marks MD, Feldmann KA (1989) Trichome development in *Arabidopsis-thaliana*.1. T-DNA tagging of the Glabrous1 gene. Plant Cell 1:1043–1050

Meinke DW (1992) A homoeotic mutant of *Arabidopsis thaliana* with leafy cotyledons. Science 258:1647–1650

Meinke DW, Yeung EC (1993) Embryogenesis in angiosperms: development of the suspensor. Plant Cell 5:1371–1381

Meinke DW, Franzmann LH, Yeung EC (1994) *Leafy Cotyledon* mutants of *Arabidopsis*. Plant Cell 6:1049–1064

Mendes A, Kelly AA, van Erp H, Shaw E, Powers SJ, Kurup S, Eastmond PJ (2013) bZIP67 regulates the omega-3 fatty acid content of Arabidopsis seed oil by activating fatty acid desaturase3. Plant Cell 25:3104–3116

Méndez-Hernández HA, Ledezma-Rodríguez M, Avilez-Montalvo RN, Juárez-Gómez YL, Skeete A, Avilez-Montalvo J, De-la-Peña C, Loyola-Vargas VM (2019) Signaling overview of plant somatic embryogenesis. Front Plant Sci 10:77

Mendoza MS, Dubreucq B, Miquel M, Caboche M, lepineic L, (2005) *LEAFY COTYLEDON 2* activation is sufficient to trigger the accumulation of oil and seed specific mRNAs in *Arabidopsis* leaves. FEBS Lett 579:4666–4670

Min L, Hu Q, Li Y, Xu J, Ma Y, Zhu L, Yang X, Zhang X (2015) *LEAFY COTYLEDON1*-CASEIN KINASE I-TCP15-PHYTOCHROME INTERACTING FACTOR4 network regulates somatic embryogenesis by regulating auxin homeostasis. Plant Physiol 169:2805–2821

Mönke G, Altschmied L, Tewes A, Reidt W, Mock HP, Bäumlein H, Conrad U (2004) Seed-specific transcription factors *ABI3* and *FUS3*: molecular interaction with DNA. Planta 219:158–166

Nambara E, Hayama R, Tsuchiya Y, Nishimura M, Kawaide H, Kamiya Y, Naito S (2000) The role of *ABI3* and *FUS3* loci in *Arabidopsis thaliana* on phase transition from late embryo development to germination. Dev Biol 220:412–413

Nic-Can GI, López-Torres A, Barredo-Poll F, Wrobel K, LoyolaVargas VM, Rojas-Herrera R, De-la-Peña C (2013) New Insights into somatic embryogenesis: *LEAFY COTYLEDON1*, *BABY BOOM1* and *WUSCHEL-RELATED HOMEOBOX4* are epigenetically regulated in *Coffea canephora*. PLoS ONE 8:e72160

Nolan KE, Kurdyukov S, Rose RJ (2009) Expression of the *SOMATIC EMBRYOGENESIS RECEPTOR-LIKE LINASE1* (*SERK1*) gene is associated with developmental change in the life cycle of the model legume *Medicago truncatulata*. J Exp Bot 60:1759–1771

Ogas J, Cheng JC, Sung ZR, Somerville C (1997) Cellular differentiation regulated by gibberellin in the *Arabidopsis thaliana* pickle mutant. Science 277:91–94

Ogas J, Kaufmann S, Henderson J, Somerville C (1999) PICKLE is a CHD3 chromatin-remodeling factor that regulates the transition from embryonic to vegetative development in *Arabidopsis*. Proc Natl Acad Sci USA 96:13839–13844

Ohlrogge J, Browse J (1995) Lipid biosynthesis. Plant Cell 7:957–970

Oppenheimer DG, Herman PL, Sivakumaran S, Esch J, Marks MD (1991) A myb gene required for leaf trichome differentiation in *Arabidopsis* is expressed in stipules. Cell 67:483–493

Orlowska A, Igielska R, Lagowska K, Kepczynska E (2017) Identification of *LEC1*, *L1L* and *Polycomb Repressive Complex 2* genes and their expression during the induction phase of *Medicago truncatula* Gaertn. somatic embryogenesis. Plant Cell Tiss Organ Cult 129:119–132

Parcy F, Valon C, Kohara A, Misera S, Giraudat J (1997) The *ABSCISIC ACID-INSENSITIVE3*, *FUSCA3*, and *LEAFY COTYLEDON1* loci act in concert to control multiple aspects of *Arabidopsis* seed development. Plant Cell 9:1265–1277

Pelletier JM, Kwong RW, Park S, Le BH, Baden R, Cagliari A, Hashimoto M, Munoz MD, Fischer RL, Goldberg RB, Harada JJ (2017) *LEC1* sequentially regulates the transcription of genes involved in diverse developmental processes during seed development. Proc Natl Acad Sci USA 114:6710–6719

Perianez-Rodriguez J, Manzano C, Moreno-Risueno MA (2014) Post-embryonic organogenesis and plant regeneration from tissues: two sides of the same coin? Front Plant Sci 5:219

Peris CIL, Rademacher EH, Weijers D (2010) Green beginnings—pattern formation in the early plant embryo. Plant Dev 91:1–27

Perry SE, Lehti MD, Fernandez DE (1999) The MADS-domain protein AGAMOUS-like 15 accumulates in embryonic tissues with diverse origins. Plant Physiol 120:121–129

Pilarska M, Malec P, Salaj J, Bartnicki F, Konieczny R (2016) High expression of SOMATIC EMBRYOGENESIS RECEPTOR-LIKE KINASE coincides with initiation of various developmental pathways in in vitro culture of *Trifolium nigrescens*. Protoplasma 253:345–355

Pradhan S, Bandhiwal N, Shah N, Kant C, Gaur R, Bhatia S (2014) Global transcriptome analysis of developing chickpea (*Cicer arietinum* L.) seeds. Front Plant Sci 5:698

Reidt W, Wohlfarth T, Ellerstrom M, Czihal A, Tewes A, Ezcurra I, Rask L, Bäumlein H (2000) Gene regulation during late embryogenesis: the RY motif of maturation-specific gene promoters is a direct target of the *FUS3* gene product. Plant J 21:401–408

Roscoe TJ, Vaissayre V, Paszkiewicz G, Clavijo F, Kelemen Z, Michaud C, Lepiniec L, Dubreucq B, Zhou DX, Devic M (2019) Regulation of *FUSCA3* expression during seed development in *Arabidopsis*. Plant Cell Physiol 60:476–487

Rounsley SD, Ditta GS, Yanofsky MF (1995) Diverse roles for MADS box genes in Arabidopsis development. Plant Cell 7:1259–1269

Salvo SAGD, Hirsch CN, Buell CR, Kaeppler SM, Kaeppler HF (2014) Whole transcriptome profiling of maize during early somatic embryogenesis reveals altered expression of stress factors and embryogenesis-related genes. PLoS ONE 29:e111407

Santos MO, Romanoa E, Yotoko KSC, Tinoco MLP, Dias BBA, Aragao FJL (2005) Characterization of the cacao somatic embryogenesis receptor-like kinase (SERK) gene expressed during somatic embryogenesis. Plant Sci 168:723–729

Santos-Mendoza M, Dubreucq B, Baud S, Parcy F, Caboche M, Lepiniec L (2008) Deciphering gene regulatory networks that control seed development and maturation in *Arabidopsis*. Plant J 54:608–620

Schmidt ED, Guzzo F, Toonen MA, de Vries SC (1997) A leucine rich repeat containing receptor-like kinase marks somatic plant cells competent to form embryos. Development 124:2049–2062

Shen B, Allen WB, Zheng P, Li C, Glassman K, Ranch J, Nubel D, Tarczynski MC (2010) Expression of *ZmLEC1* and *ZmWRI1* increases seed oil production in maize. Plant Physiol 153:980–987

Shires ME, Florez SL, Lai TS, Curtis WR (2017) Inducible somatic embryogenesis in *Theobroma cacao* achieved using the DEX-activatable transcription factor-glucocorticoid receptor fusion. Biotechnol Lett 39:1747–1755

Siefers N, Dang KK, Kumimoto RW, Bynum WE, Tayrose G, Holt BF (2009) Tissue-specific expression patterns of *Arabidopsis* NF-Y transcription factors suggest potential for extensive combinatorial complexity. Plant Physiol 149:625–641

Stone SL, Kwong LW, Yee KM, Pelletier J, Lepiniec L, Fischer RL, Goldberg RB, Harada JJ (2001) *LEAFY COTYLEDON2* encodes B3 domain transcription factor that induces embryo development. Proc Natl Acad Sci USA 98:11806–11811

Stone SL, Braybrook SA, Paula SL, Kwong LW, Meuser J, Pelletier J, Hsieh T, Fischer RL, Goldberg RB, Harada JJ (2008) *Arabidopsis LEAFY COTYLEDON2* induces maturation traits and auxin activity: Implications for somatic embryogenesis. Proc Natl Acad Sci USA 105:3151–3156

Suzuki M, Wang HHY, McCarty DR (2007) Repression of the *LEAFY COTYLEDON 1/B3* Regulatory Network in Plant Embryo Development by *VP1/ABSCISIC ACID INSENSITIVE 3-LIKE* B3 Genes. Plant Physiol 143:902–911

Tan H, Yang X, Zhang F, Zheng X, Qu C, Mu J, Fu F, Li J, Guan R, Zhang H, Wang G, Zuo J (2011) Enhanced seed oil production in canola by conditional expression of *Brassica napus LEAFY COTYLEDON1* and *LEC1-LIKE* in developing seeds. Plant Physiol 156:1577–1588

Tang LP, Zhou C, Wang SS, Yuan J, Zhang XS, Su YH (2016) *FUSCA3* interacting with *LEAFY COTYLEDON2* controls lateral root formation through regulating *YUCCA4* gene expression in *Arabidopsis thaliana*. New Phyt 213:1740–1754

Tao Z, Shen L, Gu X, Wang Y, Yu H, He Y (2017) Embryonic epigenetic reprogramming by a pioneer transcription factor in plants. Nat 551:124–128

Tao Z, Hu H, Luo X, Jia B, Du J, He Y (2019) Embryonic resetting of the parental vernalized state by two B3 domain transcription factors in *Arabidopsis*. Nat Plant 5:424–435

Thakare D, Tang W, Hill K, Perry SE (2008) The MADS-domain transcriptional regulator AGAMOUS-Like 15 promotes somatic embryo development in Arabidopsis and soybean. Plant Physiol 146:1663–1672

To A, Valon C, Savino G, Guilleminot J, Devic M, Giraudat J, Parcy F (2006) A network of local and redundant gene regulation governs *Arabidopsis* seed maturation. Plant Cell 18:1642–1651

To A, Joubes J, Barthole G, Lecureuil A, Scagnelli A, Jasinski S, Lepiniec L, Baud S (2012) *WRINKLED* transcription factors orchestrate tissue-specific regulation of fatty acid biosynthesis in *Arabidopsis*. Plant Cell 24:5007–5023

Tsuwamoto R, Yokoi S, Takahata Y (2010) *Arabidopsis EMBRYOMAKER* encoding an AP2 domain transcription factor plays a key role in developmental change from vegetative to embryonic phase. Plant Mol Biol 73:481–492

Tvorogova VE, Fedorova YA, Potsenkovskaya EA, Kudriashov AA, Efremova EP, Kvitkovskaya VA, Wolabu TW, Zhang F, Tadege M, Lutova LA (2019) The *WUSCHEL*-related homeobox transcription factor *MtWOX9-1* stimulates somatic embryogenesis in *Medicago truncatula*. Plant Cell Tissue Organ Cult 138:517–527

Van Erp H, Kelly AA, Menard G, Eastmond PJ (2014) Multigene engineering of triacylglycerol metabolism boosts seed oil content in *Arabidopsis*. Plant Physiol 165:30–36

Vicente-Carbajosa J, Carbonaro P (2005) Seed maturation: developing an intrusive phase to accomplish a quiescent state. Int J Plant Sci 49:645–651

Wang SC, Chen JG (2014) Regulation of cell fate determination by single-repeat R3 MYB transcription factors in *Arabidopsis*. Front Plant Sci 5:133

Wang F, Perry SE (2013) Identification of direct targets of *FUSCA3*, a key regulator of *Arabidopsis* seed development. Plant Physiol 161:1251–1264

Wang H, Caruso LV, Downie AB, Perry SE (2004) The embryo MADS domain protein AGAMOUS-Like 15 directly regulates expression of a gene encoding an enzyme involved in gibberellins metabolism. Plant Cell 16:1206–1219

Wang H, Guo J, Lambert KN, Lin Y (2007a) Developmental control of *Arabidopsis* seed oil biosynthesis. Planta 226:773–783

Wang SC, Kwak SH, Zeng QN, Ellis BE, Chen XY, Schiefelbein J, Chen JG (2007b) *TRICHOMELESS1* regulates trichome patterning by suppressing GLABRA1 in *Arabidopsis*. Development 134:3873–3882

Warpeha KM, Upadhyay S, Yeh J, Adamiak J, Hawkins SI, Lapik YR, Anderson MB, Kaufman LS (2007) The GCR1, GPA1, PRN1, NF-Y signal chain mediates both blue light and abscisic acid responses in *Arabidopsis*. Plant Physiol 143:1590–1600

West MAL, Harada JJ (1993) Embryogenesis in higher plants: an overview. Plant Cell 5:1361–1369

West MAL, Yee KM, Danao J, Zimmerman JL, Fischer RL, Goldberg RB, Harada JJ (1994) *LEAFY COTYLEDON1* is an essential regulator of late embryogenesis and cotyledon Identity in *Arabidopsis*. Plant Cell 6:1731–1745

Williams EG, Maheswaran G (1986) Somatic embryogenesis: factors influencing coordinated behaviour of cells as an embryogenic group. Ann Bot 57:443–462

Wójcikowska B, Jaskóla K, Gasiorek P, Meus M, Nowak K, Gaj MD (2013) *LEAFY COTYLEDON2* (*LEC2*) promotes embryogenic induction in somatic tissues of *Arabidopsis*, via *YUCCA*-mediated auxin biosynthesis. Planta 238:425–440

Xu JJ, Zhang XF, Xue HW (2016) Rice aleurone layer specific OsNF-YB1 regulates grain filling and endosperm development by interacting with an ERF transcription factor. J Exp Bot 67:6399–6411

Yang X, Zhang X (2010) Regulation of somatic embryogenesis in higher plants. Crit Rev Plant Sci 29:36–57

Yazawa K, Takahata K, Kamada H (2004) Isolation of the gene encoding Carrot *leafy cotyledon 1* and expression analysis during somatic and zygotic embryogenesis. Plant Physiol Biochem 42:215–223

Zhang JJ, Xue HW (2013) *OsLEC1/OsHAP3E* participates in the determination of meristem identity in both vegetative and reproductive developments of rice. J Integr Plant Biol 55:232–249

Zhang SB, Wong L, Meng L, Lemaux PG (2002) Similarity expression patterns of knotted1 and *ZmLEC1* during somatic and zygotic embryogenesis in Maize (*Zea mays* L.). Planta 215:191–194

Zhang S, Liu X, Lin Y, Xie G, Fu F, Liu H, Wang J, Gao S, Lan H, Rong T (2011) Characterization of a *ZmSERK* gene and its relationship to somatic embryogenesis in a maize culture. Plant Cell Tiss Org Cult 105:29–37

Zhao M, Morohashi K, Hatlestad G, Grotewold E, Lloyd A (2008) The TTG1-bHLH-MYB complex controls trichome cell fate and patterning through direct targeting of regulatory loci. Development 135:1991–1999

Zheng W, Zhang X, Yang Z, Wu J, Li F, Duan L, Liu C, Lu L, Zhang C, Li F (2014) *AtWuschel* promotes formation of the embryogenic callus in *Gossypium hirsutum*. PLoS ONE 9:e87502

Zheng Q, Zheng Y, Ji H, Burnie W, Perry SE (2016) Gene regulation by the AGL15 transcription factor reveals hormone interactions in somatic embryogenesis. Plant Physiol 172:2374–2387

Zhou LM, Zheng KJ, Wang XY, Tian HN, Wang XL, Wang SC (2014) Control of trichome formation in *Arabidopsis* by poplar single-repeat R3 MYB transcription factors. Front Plant Sci 5:262

Zhou X, Guo Y, Zhao P, Sun M (2018) Comparative analysis of *WUSCHEL*-related homeobox genes revealed their parent-of-origin and cell type-specific expression pattern during early embryogenesis in Tobacco. Front Plant Sci 9:311

Zhu S, Wang J, Ye J, Zhu A, Guo W, Deng X (2014) Isolation and characterization of *LEAFY COTYLEDON 1-LIKE* gene related to embryogenic competence in *Citrus sinensis*. Plant Cell Tiss Organ Cult 119:1–13

Zhu Y, Xie L, Chen GQ, Lee MY, Loque D, Scheller HV (2018) A transgene design for enhancing oil content in *Arabidopsis* and *Camelina* seeds. Biotechnol Biofuels 11:46

Zuo J, Niu QW, Frugis G, Chua NH (2002) The *WUSCHEL* gene promotes vegetative-to-embryonic transition in *Arabidopsis*. Plant J 30:349–359