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Progress in understanding the regulation and expression of genes during plant somatic embryogenesis: A review

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ABSTRACT

Based on the previous available documents involving molecular events during plant somatic embryogenesis, this report aims to review the advances that have been made for the past several years in the area of molecular mechanism of plant somatic embryogenesis. To begin with, studies suggest that the induction and differentiation of embryos from somatic tissue directly or through callusing involves the interaction of various cellular and molecular factors. Several intra- and extra-cellular proteins such as germins and germins-like proteins, lipid transfer proteins, heat-shock proteins, and late embryogenesis abundant proteins are known to regulate the induction of somatic embryos from the somatic cell. Simultaneously, regulation and expression of specific genes such as housekeeping genes *OsIAA* in rice; hormone-responsive genes *Dcarg-1*, *Dchsp-1*, *DcECP31*, *DcEMB1* in carrot; and *AtECP63*, Mt somatic embryo-related factor 1 in arabidopsis have been identified to play key roles during the process of somatic embryogenesis. These genes are known to express differentially for synthesis of new proteins during induction and development of somatic embryo. In addition, several transcription factors such as *leafy cotyledon* genes, *agamous-like15 (AGL15)* gene*,* ethylene-responsive element-binding protein (EREBPs), knotted1-like homeobox proteins, and RWP-RK group of plant-specific transcription factors are equally known that efficiently control the molecular events of somatic embryogenesis. Further, it is also now established that epigenetic factors such asDNA methylation, histone deacetylation/methylation, and microRNAs also influence the molecular mechanism of plant somatic embryogenesis.

1. INTRODUCTION

The process of embryogenesis has always been an important part of biological study which involves differentiation and development of a mature embryo from a fertilized egg cell. However, an alternative way of production of embryos from plant somatic cells without the involvement of gametes fusion known as somatic embryogenesis occurs in nature and also has been possible to achieve under *in vitro* conditions. Historically, the first study of somatic embryogenesis in plant was documented with carrot cell suspension cultures [1,2].

In general, plant somatic cells can restart *in vitro* embryogenesis when these cells are exposed to a wide range of severe abiotic stressors [3], and moreover, somatic cells could be induced to form somatic embryos by treating with abiotic stress-causing agents such as salt, hypochlorite, osmotic pressure, and heavy metal ions or high temperature in *Daucus carota* and in *Arabidopsis* [4]. In addition, synthetic auxins such as 2,4-D are also known as the most effective inducers of somatic embryogenesis in general and monocots in particular because it probably triggers both auxin-responsive genes and stress responses simultaneously [5].

Of late, somatic embryogenesis has emerged as a model system to understand the *in vitro* physiological and biochemical processes that occur during plant developmental processes. In recent years, considerable approaches have been made to identify the possible cellular and molecular factors that control the transition of a differentiated somatic cell into somatic embryo.

Moreover, understanding the interacting factors that initiate somatic embryogenesis still remains to be investigated. However, with the advent of new molecular techniques, several studies have been initiated to understand the molecular regulation of plant somatic embryogenesis. For instance, many embryo marker genes, including *babyboom1 (BBM1)*, *leafy cotyledon1 (LEC1)*, and *LEC2* have been identified using cDNA subtraction [6].

Further, microarray technology was also employed to identify key genes required to enhance somatic embryogenesis in *Arabidopsis* [7]. These genes encode proteins that play integral roles in hormone perception and signaling indicating the effects of differential gene expression during *in vitro* embryogenesis [8].

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Although much progress has been made in the past decade to understand the molecular regulation of plant somatic embryogenesis [8-17], these molecular events underlying early somatic embryo development remain still unclear. Based on the available past and recent reports, this review is thus an effort to understand the cellular and molecular factors that influence the events of somatic embryogenesis in plant.

2. REGULATORY ROLE OF CELLULAR PROTEINS DURING SOMATIC EMBRYOGENESIS

Somatic embryogenesis depends on several regulatory substances and some of these regulatory substances accumulate in the culture medium. Several studies have indicated that these cellular proteins either play an inductive [18,19] or inhibitory [20] roles in triggering embryogenic responses in plants.

2.1. Germins and Germins-like Proteins (GLPs)

GLPs belong to one of the most abundant groups of extracellular proteins found in embryogenic tissues, and these proteins were first discovered in wheat during germination [21]. Several studies have further demonstrated that the transcription of GLP encoding genes regulates in embryogenic lines of Caribbean pine, white lupin, and wheat [22-24] and their expression was evident only in embryogenic cells [17].

In another study, cell wall bound GLPs were found to be present in the pre-globular somatic embryos, whereas absent in non-embryogenic callus of *Pinus carribea*, and in subsequent studies, the presence of GLPs was treated as molecular markers of somatic embryogenesis. It was further suggested that GLPs may be probably involved in initiation and termination of cell wall expansion during somatic embryogenesis [9].

2.2. Lipid Transfer Proteins (LTPs)

The LTPs are tryptophan lacking small size (7–13 kDa) proteins and expression of *LTPs* genes was observed to be exclusively associated with the differentiation of first outer tissue layer or protoderm formation of somatic embryos [25]. This outer protoderm layer probably plays a regulatory role in controlling cell expansion during the development of embryos [15,26].

In addition, *LTPs* proteins expression was observed not only in embryogenic cell cultures but also in the shoot apex of seedlings, developing flowers, and maturing seeds. The expression of LTPs genes was further found to be uniform all the time in the pro-embryogenic masses, whereas in the non-embryogenic cell lines, their expressions were seen either limited or not at all. Moreover, the *LTP* expression level in cotton cell lines appears high before induction of embryogenesis as well as during the globular stage, while this expression declines during post-globular stages [17,27].

2.3. Arabinogalactan Proteins (AGPs)

AGPs are cell wall proteoglycans with a hydroxyproline-rich core protein and contain more than 90% carbohydrates such as arabinose and galactose along with the little amount of other sugars [28]. These proteins have been found widely distributed in higher plants and contribute multiple roles during cellular growth and development [29].

AGPs are known to promote embryogenesis in a broad range of angiospermic plants such as carrot [30,31], *Euphorbia* [32], wheat [33], chicory [34], and also in gymnospermic species such as *Picea abies* [35] and *Pinus* [16,19]. Significantly, embryogenesis also could be recorded in non-embryogenic cell lines when purified AGPs in nanomolar concentration extracted from carrot embryogenic suspension cultures were applied exogenously to non-embryogenic cells [36,37].

2.4. Heat-Shock Proteins (HSPs)

Many HSPs are known to be synthesized and accumulated during somatic embryo development in response to hormones such as 2,4-D [38,39]. In general, it is suggested that the heat-shock treatment arrests the growth of globular stage embryo, but such treatments have been failed to prove effective for other developmental stages of somatic embryogenesis [11,40-42].

The stage-specific syntheses of HSPs were initially reported in carrot embryogenic cultures [40] and simultaneously, also in tobacco cell suspension cultures [41]. In further studies, two cDNAs (*Mshsp18-1* and *Mshsp18-2*) were isolated from alfalfa suspension cultures that were involved in synthesis for small HSPs belonging to *hsp17* family. Hence, these studies together indicate that HSPs must play decisive roles during the development of plant cell [9,43].

2.5. Late Embryogenesis Abundant proteins (LEA)

At the molecular level, there is an expression of specific genes whose products are accumulated and are capable of surviving the period of desiccation during maturation of zygotic embryo. Since these proteins have been found to be abundant during the later stages of embryo maturation, therefore, these genes are known as LEA protein genes [9]. During initial studies, some of the *LEA* genes such as *Dc3*, *Dc8*, *DcECP31*, *DcECP40*, and *DcEMB1* were exclusively found to occur and characterized in carrot somatic embryogenesis [15,44].

Further, the study reveals that *LEA* gene *Dc8* expression was also involved in the process of somatic embryogenesis but was not dependent on it [45]. Similarly, another *LEA* gene *EMB1* cDNA from carrot was also seen to express only in embryogenic tissues during the transition of globular and torpedo stage embryos and accumulates specifically in the meristematic regions [46].

2.6. Lectins and Storage Proteins

Lectins are carbohydrate-binding proteins that are commonly found in microbes, animals, and plants [47]. Citrin, a citrus seed storage protein shows differential expression during embryogenesis and the citrin encoding gene expresses at the early globular stage in the zygotic embryos, whereas these transcripts accumulate during the later stages of somatic embryogenesis [48]. In addition, differential expression of lectins was also recorded during various stages of somatic and zygotic embryo development in alfalfa. These results thus indicate that the lectins and other storage proteins are significantly involved during plant embryogenesis [9].

3. REGULATORY ROLE OF GENES DURING SOMATIC EMBRYOGENESIS

Various structural and functional genes are known today that are significantly associated with the regulation of plant somatic embryogenesis, and these regulatory genes have been further identified and characterized.

3.1. Cellular-Housekeeping Genes

In general, housekeeping genes of the cells are mainly associated with regulation of important cellular metabolic activities, but these genes were also found to exhibit significant roles during the process of embryogenesis [49]. It was observed that a globular embryo-specific gene elongation factor-1a, *CEM1* was found in the active and dividing cells [50], while another gene *CEM6*, specifically expresses during the pre-globular and globular stages of carrot somatic embryogenesis. These results further suggest that probably these genes specifically contribute in cell wall biogenesis during embryogenesis [15,51].

3.2. Hormone-Responsive Genes

It is documented that hormones play the key roles in mediating the signal transduction pathway leading to the reprogramming of gene expression. These phytohormones are generally involved in switching on/off the specific target genes during the developmental stages of somatic embryogenesis through coordinated interactions with other signaling pathways that are involved in cell development [11].

3.2.1. Auxin-inducible genes

It is suggested that reactivation of cell division in somatic plant cells is the most essential part for the establishment of embryogenic callus and somatic embryo formation. Simultaneously, it is also proved that the exposure of high auxin pulse treatment serves as a triggering factor to induce cell division in the epidermal cells, and it probably promotes their further differentiation into somatic embryos [52-55].

In the molecular study of carrot somatic embryogenesis, the transcript of auxin-regulated specific gene *Dcarg-1* was found to occur only during the early induction period of somatic embryos while during the later stages of somatic embryogenesis, expression was not observed. However, in another study, other auxin-responsive gene *Dchsp-1* expresses constantly during the entire period of carrot somatic embryogenesis [39].

In addition, *OsIAA1,* an early auxin-inducible gene was characterized from the rice and also suggested that the gene *OsIAA1* may be involved putatively in cell division [56]. In further study, expression pattern of three carrot cDNA clones coding for the three isoforms of the enzyme glutamine synthetase (GS) (*CGS102*, *CGS103,* and *CGS201*) was investigated during somatic as well as zygotic embryogenesis [57].

Moreover, transcript levels of *CGS102* and *CGS201* were found to be increased during the early stages of somatic embryogenesis and also during the seed development, whereas *CGS103* expression was recorded only in the later stages of seed development and senescent leaves. Interestingly, its expression was not observed in somatic embryos or young leaves. In addition, the expression of *CGS102* and *CGS201* was found to decline in the presence of medium supplemented with glutamine as nitrogen source, indicating transcriptional regulation of GS activity. This also signifies the involvement of a common regulatory system for nitrogen metabolism in somatic and zygotic embryogenesis [9,15,57].

3.2.2. Abscisic acid (ABA)-inducible genes

It is established that an exogenous application of ABA causes induction of somatic embryogenesis and exogenous ABA treatment probably enhances the endogenous cellular level of indole-3-acetic acid [58,59]. Further, ABA-inducible genes have been also isolated and characterized that express specifically in embryos or embryogenic cells [60,61]. During the early embryogenesis stages, a carrot homolog of *ABI* (*C-ABI3*) gene appears to regulate the expression of embryogenic cell protein genes, and these proteins later were found to be involved in the process to achieve the somatic cell embryogenic competency [16].

Further, all *LEA* genes show high sequence homology and are regulated by ABA. In general, *LEA* genes play significant roles in desiccation tolerance in different species. However, the main features of the *LEA* genes involve by their premature induction and expression by exogenous ABA treatment, and thus, ABA-inducible genes such as *Dc3*, *Dc8*, *DcECP31*, *DcECP40*, and *DcEMB1* in carrot and *AtECP31* and *AtECP63* from *Arabidopsis* were identified and found to express during late stages of the embryo development. It was further observed that ABA-inducible *LEA* genes expression increases during the torpedo stage of somatic embryos but not during the seedling stage [39,62]. These results thus indicate that regulation of *LEA* genes is caused by ABA in association with some other unknown embryo-specific factors [9].

3.2.3. Ethylene-inducible genes

Based on the previous studies, ethylene is known to act positively during somatic embryogenesis in many species such as *Coffea canephora* [63], *Oncidium* sp. [64], *Medicago sativa* [65], *Pinus sylvestris* [66], and *Quercus ilex* [67]. However, in some other plant species such as black spruce [68] and *Leucojum aestivum* [69] ethylene behaves negatively during somatic embryo development.

It is thus established fact that ethylene plays a crucial role during somatic embryo maturation, and moreover, Mt somatic embryo-related factor 1 (*MtSERF1*) was found to be induced and expressed by ethylene in *Medicago truncatula* embryogenic callus, and it was suggested that *MtSERF1* promoter region contains putative binding sites related to auxin, cytokinin, and ethylene responses. Therefore, this indicates that ethylene-signaling pathways probably interact with auxin and cytokinin pathways [70,71].

3.3. Maturation and Protein Storage Genes

It is well documented that the expression of various genes performs key roles during the maturation stages of somatic embryo differentiation. Moreover, the expression of these genes is maturation stage-specific and bears similarity with the zygotic embryo maturation genes. In a study on carrot somatic embryogenesis, *Dc2.15* gene expression was found to be maximal at the heart stage and torpedo stage [72], while maximum level of other lipoxygenase gene expression in soybean was observed during maturation of somatic embryos [73]. Similarly, another seed storage citrin protein gene shows differential expression during the late stage of somatic embryogenesis in citrus [48].

In addition, differential gene expression of lectin and other seed storage protein was observed during various stages of somatic embryo development in alfalfa, while the *globulin-1* gene expression was noticed in regenerable *Zea mays* callus [74]. Moreover, it appears that lectins are likely involved in growth regulation during embryogenic pattern formation. In another study, accumulation of *MsLEC1* and *MsLEC2* mRNAs was also found to increase during the later stages of embryogenesis in alfalfa; therefore, these results suggest that these genes play significant roles during embryo development [9,11,75].

4. ROLE OF TRANSCRIPTION FACTORS DURING SOMATIC EMBRYOGENESIS

Based on the previous studies in plant somatic embryogenesis at molecular level, various transcription factors have been identified that are found to be involved in the process of induction and development of somatic embryos in many plant species.

4.1. Leafy Cotyledons *(LEC)* Genes

Leafy Cotyledon *(LEC)* genes such as *LEC1*, *LEC2*, and *FUSCA3* (*FUS3*) are known as transcription factors that regulate plant embryogenesis [76], and specifically, *LEC2* gene was proved to play an important role during the induction phase of somatic embryogenesis [77,78]. It is suggested that *LEC2* gene probably provides a condition which is required to achieve the cellular embryogenic competency [16,78]. However, overexpression of *LEC2* gene in *Nicotiana tabacum* exhibits abnormal development like ectopic callus production which further fails to differentiate into somatic embryos [79].

Similarly, ectopic expression of *LEC1* gene in transgenic plants induces the formation of somatic embryo-like structures [80] and exhibits a differential expression pattern during the entire course of somatic embryogenesis in *Arabidopsis*. It was thus suggested that possibly *LEC1* gene is involved in the process of differentiation and development, rather than in the induction of somatic embryos [81].

4.2. Agamous-like15 (*AGL15*)

Transcription factor *AGL15* belongs to a family of eukaryotic transcription factors and are commonly found in yeast, plants, and humans. All members of this family contain a conserved MADS-box motif within their DNA binding domain. In plant somatic embryogenesis, *AGL15* expression was found to be at a maximal level during embryo development, particularly at the beginning of globular stage [17], and it was thus suggested that AGL15 can directly bind to promoter regions of different target genes [82].

Significantly, embryogenic cultures exhibit high levels of *AGL15* expression [83] and further studies, reveal that consistent ectopic expression of *AGL15* increases the efficiency of both direct and indirect somatic embryogenesis in *Arabidopsis thaliana* and soybean [83,84], while knock-out of *AGL15* gene reduces the efficiency of somatic embryogenesis [83].

4.3. Ethylene-responsive Element-binding Protein (EREBP)

Ethylene-responsive factor (ERF) belongs to a family of plant-specific transcription factors that are involved in the regulation of a set of developmental processes [85], and the EREBP has been considered as one of the largest families of *Arabidopsis* transcription factors. It is documented that the EREBP includes almost 150 members and these are probably involved in various critical processes during plant development [17].

ERFs were initially identified as binding factors mediating ethylene response [86], and it is established that several members of the ERF family regulate somatic embryogenesis. In Medicago, *MtSERF1*, a homolog of *A. thaliana* ERF, is an ethylene-inducible gene that was found to be expressed in zygotic embryos and also involved in the proliferation of embryogenic cultures as well as somatic embryogenesis [70,71]. Furthermore, another member, *A. thaliana* embryomaker (*EMK*), was observed to be functional in early and mature embryos and probably has a redundant role in maintaining embryonic cell identity [87].

In additional, another ethylene-inducible *BBM* gene expression was recorded during all stages of zygotic embryos from the globular stage to mature seeds in *A. thaliana* and *BBM* gene was thus recognized as a marker of somatic embryogenesis in cell cultures of *Brassica napus* [88]. Moreover, ectopic expression of *BBM* gene was found to enhance the rate of somatic embryogenesis and other morphogenic responses on medium lacking plant growth regulators (PGRs) [88,89]. In contrast, overexpression of *BBM* gene results in the induction of indirect somatic embryogenesis in tobacco [90] and poplar *Populus tomentosa* [91] while in *Capsicum annum*, *BBM* gene expression proves to be recalcitrant [92].

4.4. Homeodomain Transcription Factors

Homeobox genes are the key regulatory genes controlling pattern formation and morphological differentiation in multicellular organisms. Homeotic genes contain a characteristic conserved nucleotide sequence called the homeobox. The encoded homeodomain codes a transcription factor involving a conserved 60 amino acid long sequence with DNA-binding activities and is also associated with pattern formation in plants [93].

4.4.1. Carrot homeobox (CHB)

During initial studies, six homeobox-containing genes (*CHB1*, *CHB2*, *CHB3*, *CHB4*, *CHB5*, and *CHB6*) were identified from carrot somatic embryos, and specifically, *CHB1* gene expression was constantly observed in undifferentiated cell clusters. In contrast, *CHB2* gene expression was found to be enhanced after globular stage and the maximum level of expression was seen at heart and during early torpedo stage of somatic embryogenesis [94].

In addition, a chromobox gene *DcB1* was also isolated and characterized from embryogenic cell clusters of carrot and its expression increases during early stages of somatic embryos, whereas, low level of transcripts were also detected in both torpedo-shaped somatic embryo and during seed-setting stage [15,95].

4.4.2. Knotted1-like homeobox (KNOX)

Another group of homeodomain fold transcription factors consists of KNOX family proteins and plays a significant role during plant somatic embryogenesis. These proteins regulate a balance between cell proliferation and cell differentiation during tissue patterning, and therefore, are very important for plant development [96]. Moreover, the soybean homeobox-containing gene sphingoid base hydroxylases (*SBH)* expression was apparent during early somatic embryogenesis in soybean, while the maximum transcripts level of *SBH* gene was recorded at the cotyledonary stage, and thereafter, its expression decreases [17,97].

Furthermore, *HBK2,* a homolog of homeobox of *KNOX* class (*HBK*) was treated as marker and important regulator of somatic embryogenesis in *P. abies* where its expression was seen in somatic embryos, but in non-embryogenic cell lines, the expression was lacking [98].

Similarly, expressions of other homolog of *HBK* (*HBK1* and *HBK3*) were found to be upregulated immediately after initiation of somatic embryogenesis in a medium lacking PGRs [99]. Interestingly, ectopic expression of *HBK3* was found to enhance the yield of somatic embryos, while the downregulation of *HBK3* was seen to inhibit embryogenesis [100].

Significantly, the shoot meristemless (*STM*) member of the *arabidopsis* KNOXI group was also found to be involved in somatic embryogenesis and ectopic expression of *B. napus STM* promotes somatic embryogenesis [7,17]. Similarly, in *C. canephora*, ectopic expression of *A. thaliana* wuschel was observed to promote hormone-induced formation of callus and 400 times increase in the formation of somatic embryos was also recorded [101].

4.4.3. RKD4--(RWP-RK domain 4)

Arabidopsis RKD4 belongs to the RWP-RK group of plant-specific conserved transcription factors, and its transcription has been detected in all cells during early embryogenesis. Significantly, it was found that expression starts from the late globular stage, and gradually, it restricts to the embryo suspensor cells [102].

Moreover, induction of ectopic expression of *RKD4* for 8 days was found to switch on the embryogenesis-related genes expression which further causes to promotion in somatic embryogenesis, whereas constitutive ectopic expression of *RKD4* results in continuous proliferation without differentiation [102].

5. ROLE OF EPIGENETIC FACTORS DURING SOMATIC EMBRYOGENESIS

The event of plant somatic embryogenesis was also found to be regulated by epigenetic factors and some epigenetic factors such as DNA methylation, histone deacetylation/methylation, and microRNAs (miRNAs) pathways are known today that control the process of somatic embryogenesis in plants.

5.1. Methylation of DNA

Methylation of DNA plays a significant role in somatic embryogenesis by causing gene silencing, and it was observed that the promoter region of *LEC1* gene becomes hypomethylated just before initiation of somatic embryogenesis, while the methylation level subsequently increases during embryo maturation as well as vegetative growth period. Similarly, hypermethylation of a region within the promoter of *LEC1* gene using RNA-directed DNA methylation downregulates its transcription [103], and therefore, indicates that transcription of *LEC1* gene is regulated by methylation of its promoter [17].

Furthermore, application of 5-azacitidine, a methylation inhibitor was found to inhibit or block the somatic embryogenesis in carrot cultures [104]; however, the drug 5-aza-2′ deoxycytidine promotes embryogenesis by inhibiting methyltransferase 1 activity, and it also increases transcription of a key embryogenesis regulator *STM* [7].

5.2. Deacetylation of Histone Protein

Deacetylation of histone protein is also known to cause transcription repression, and thus, it serves as an alternative way to prevent the untimely onset of somatic embryogenesis. Moreover, it was observed that treatment of trichostatin A (TSA), an inhibitor of histone deacetylases, produces embryo-like structures from true leaves in *Arabidopsis* [105].

Furthermore, TSA in combination with heat treatment was proved to significantly enhance the efficiency of somatic embryogenesis from *B. napus* microspores [106] and suggested that heat stress and histone deacetylation jointly converges on the upregulation of embryonic regulators to initiate the embryonic program [5].

5.3. Methylation of Histone Protein

Methylation of histone protein also causes the modification of chromatin packing, but it depends on the site of methylation in the histone molecule and it is documented that methylated histone protein causes either an inhibitory or stimulatory effects on gene transcription. Moreover, it is suggested that *S*-adenosylmethionine (SAM)-dependent transmethylation causes modulation in the expression of regulators that are involved in the cell-cycle program [107].

In addition, several members of the SAM metabolic pathways have been also found to be upregulated during early stages of cellular de-differentiation before the establishment of somatic embryogenesis in cotton [108] and also during early embryogenesis in *P. abies* [109].

5.4. MicroRNAs (miRNAs) Mediated Gene Silencing

miRNAs are known as small, single-stranded, endogenous transcripts that may cause target gene silencing by cleavage of target gene mRNA or inhibit translation of target mRNA. Furthermore, it is suggested that miRNAs interact with the target transcription factors in a co-ordinated manner to regulate gene expression during cell differentiation and proliferation [110,111].

In addition, miRNAs are also known to play significant roles in the regulation of cell proliferation during somatic embryogenesis and based on miRNA constitution during successive stages of somatic embryogenesis, several members of miRNAs have been identified in sweet orange that are unique during early embryo development (miR156, 168, and 171), the globular embryo stage (miR159, 164, 390, and 397), the cotyledonary-stage embryo (miR166, 167, and 398). These miRNAs were also found even in cell lines that were lacking embryogenic potentials (miR164, 166, and 397) [17,112] [Table 1].

Table 1: Some regulators involved in somatic embryogenesis [17].

Name	Functions	Species	Overexpression phenotypes	References
STM	Homeobox domain TF	*B. oleraceae*	Enhanced efficiency of indirect somatic embryogenesis	[7]
azadC	Inhibitor of DNA methylation	*A. thaliana*	Upregulation of *STM* and higher yield of somatic embryos	[7]
LEC2	B3 domain TF	*A. thaliana*	Induction of direct somatic embryogenesis without auxin	[81]
AGL15	MADS-box TF	*G. max*	Enhanced indirect embryogenesis	[83]
EMK	AP2/ERF family TF	*A. thaliana*	Enhanced direct and indirect embryogenesis	[87]
BBM1	AP2/ERF family TF	*A. thaliana*	Direct somatic embryogenesis on seedlings	[89]
		P. tomentosa	Indirect somatic embryogenesis	[91]
		C. annum	Indirect somatic embryogenesis	[92]
HBK3	Homeobox domain TF	*P. abies*	Increased somatic embryogenesis yield	[100]
WUS	Homeobox domain TF	*C. canephora*	Enhanced efficiency of indirect somatic embryogenesis	[101]
RKD4	RWP-RK domain TF	*A. thaliana*	Short-term expression promotes somatic embryogenesis without auxin	[102]

STM: Shoot meristemless, azadC: 5-Aza-2′ deoxycytidine, *LEC2*: Leafy cotyledon 2, *AGL15*: Agamous-like15, *EMK*: Embryomaker, *BBM1*: Baby boom, WUS: Wuschel, *B. oleraceae: Brassica oleraceae, A. thaliana: Arabidopsis thaliana, G. max: Glycine max, P. tomentosa: Populus tomentosa, C. annum: Capsicum annum, P. abies: Picea abies, C. canephora: Coffea canephora.*

6. CONCLUSION

Based on previous studies involving the results on molecular regulation of somatic embryogenesis, it indicates that differential gene expression is required for the synthesis of new mRNAs and proteins during somatic embryogenesis. Further, several chemical substances also act in gene expression as signals and the interactions between phytohormone and various cellular factors (regulatory proteins and genes, transcription and epigenetic factors) in coordinate manner are likely to play an important part during the induction and development of somatic embryos.

Simultaneously, many genes have been identified and characterized in many plant species which express differentially during somatic embryogenesis and synthesize the specific proteins that are required for somatic embryo development. In addition, with the advancements in the cellular and molecular knowledge and also the advent of new techniques, the future study needs to be undertaken to investigate additional cellular and molecular factors that might be involved during the process of somatic embryogenesis in plants.

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