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Genes, proteins and other networks regulating somatic embryogenesis in plants

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Abstract

Background: Somatic embryogenesis (SE) is an intricate molecular and biochemical process principally based on cellular totipotency and a model in studying plant development. In this unique embryo-forming process, the vegetative cells acquire embryogenic competence under cellular stress conditions. The stress caused by plant growth regulators (PGRs), nutrient, oxygenic, or other signaling elements makes cellular reprogramming and transforms vegetative cells into embryos through activation/deactivation of a myriad of genes and transcriptional networks. Hundreds of genes have been directly linked to zygotic and somatic embryogeneses; some of them like *SOMATIC EMBRYOGENESIS LIKE RECEPTOR KINASE* (*SERK*), *LEAFY COTYLEDON* (*LEC*), *BABYBOOM* (*BBM*), and *AGAMOUS-LIKE 15* (*AGL15*) are very important and are part of molecular network.

Main text (observation): This article reviews various genes/orthologs isolated from different plants; encoded proteins and their possible role in regulating somatic embryogenesis of plants have been discussed. The role of SERK in regulating embryogenesis is also summarized. Different SE-related proteins identified through LC–MS at various stages of embryogenesis are also described; a few proteins like 14-3-3, chitinase, and LEA are used as potential SE markers. These networks are interconnected in a complicated manner, posing challenges for their complete elucidation.

Conclusions: The various gene networks and factors controlling somatic embryogenesis have been discussed and presented. The roles of stress, PGRs, and other signaling elements have been discussed. In the last two-to-three decades' progress, the challenges ahead and its future applications in various fields of research have been highlighted. The review also presents the need of high throughput, innovative techniques, and sensitive instruments in unraveling the mystery of SE.

Keywords: Auxin and cytokinin signaling, Plant growth regulators, *SERK* gene, Stress, Somatic embryo-specific proteins, Transcription factors

Background

Somatic embryogenesis (SE), the intricate multi-step process nowadays holds prime importance in tissue culture methodology, made big leaps ever since its first report in mid twentieth century [144]. This technique unveils diverse areas where its application is indispensible and provides significant insights in pathways and mechanisms underlying plant development. It is yet another way of mass propagation of plants vegetatively [32, 42]. The regeneration of a complete plant from a single or group of somatic cells is always remaining as the fundamental importance of SE [54]. The technique includes plant regeneration from cells that are already differentiated [62]. Hence, SE is a unique potentiality of plant cells and is triggered with acquired embryonic potential [75]. This paradigm shift occurs after reprogramming of developmental processes, enabling the cells to attain embryogenic competence [100]. The differentiated cells under plant growth regulator (PGR) treatments undergo several morphogenetic changes and attain embryogenic competence [75, 101, 102]. Similarly, the pre-

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embryogenic determined cells (PEDC) present in explant are committed to produce embryos and enter embryogenesis process under the influence of PGRs and other favorable conditions [75].

The process of SE has various phases like initiation, proliferation, maturation, and conversion [58]. Phase 0 is suggested to have competent single cells giving rise to embryogenic clusters under the influence of PGRs especially auxin [33, 150]. In this phase, different cell clusters acquire the competence to develop embryos. The phase 1 starts by transferring embryogenic cell clusters to an auxin-free medium, and the cell clumps proliferate slowly and do not differentiate [33]. This phase is followed by rapid cell division of cells, giving rise to globular embryos referred to as Phase 2. Embryos of different shapes (heart, torpedo, and others) constitute Phase 3 [33]. Drastic morphological, physiological, and biochemical changes set in during meristem (shoot, root) differentiation [135, 153]. The in vitro microenvironment is very stressful, and this could be osmotic and wounding and have micronutrient supply, desiccation, and PGR stress; and these adverse stresses trigger reprogramming of cellular development [28]. The already differentiated cells dedifferentiate or acquire embryogenic competence, and the entire phenomenon is often governed by hundreds of genes [28, 56, 115]. At different stages of SE, a distinct set of genes activate in developing embryos [64], and these genes regulate steps in switching from one development stage to the other [123]. Chromatin reorganization, the activation and deactivation of one or more genes (Fig. 1), carry out a cascade of activities and are perhaps the reason behind cellular transition. Only a few of these genes have been extensively studied while the other genes' role in embryogenesis is still a mystery [28].

The embryogenic cell/cells transforming embryos could histologically be distinguished from others by some characteristics like cell wall with cellulose, denser cytoplasm, fragmented vacuole, highly active nucleus with large nucleolus, high nucleus-to-cytoplasm ratio, and low level of heterochromatin [13, 147]. At molecular level, the features of embryogenic tissues have not been comprehensively distinguished because of the usage of the whole explant in expression analysis [13, 147]. Explants possess a variety of cells arranged in a complex fashion, posing problems in molecular marker-based identification of embryogenic cells.

Various embryo stages are present in the process of SE, named after the shape attained by the growing embryo in the course of development (Fig. 1). These stages are globular, heart, torpedo, and cotyledonary in most of the dicot plants, while globular, scutellar, and coleoptilar in monocots, and early immature, pre-cotyledonary, early cotyledonary, and late cotyledonary embryos in conifers [42, 103, 116]. Mikula et al. [98] reported three different morphogenetic stages of somatic embryos in fern—i.e., linear stage (spanning first cell division to several-celled proembryo), early embryonic leaf stage (until the emergence of first leaf), and late embryonic leaf stage (showing the appearance of second leaf). SE is induced either directly in explants or indirectly on callus [157]. In the former, SE occurs without forming any intervening callus, whereas indirect SE is always characterized by the formation of callus. In direct SE, the cells are determined to become embryos shortly after the reprogramming sets in without prior division of cells, while in indirect SE, embryogenic competence is attained comparatively later after formation of callus [115]. In certain cases, the embryogenic competence is often preceded by cell division, and induced embryogenic determined cells (IEDC) are formed by dedifferentiation of differentiated cells which lead to embryogenic development [141, 148]. Induction of SE is very difficult in the older tissue, and it may be of direct or indirect origin, but it is rather difficult to generate embryogenic competent cells from aged tissue as older cells take time to reprogram it [75]. This is perhaps the reason why developmentally older tissues take only the indirect route of embryogenic development [9]. The embryos are induced directly or indirectly on explants called primary somatic embryogenesis, while the formation of embryo on primary embryos is termed as secondary somatic embryogenesis. In this phenomenon, the primary embryo does not convert into a complete plantlet and instead gives rise to many secondary embryos [104]. Somatic embryos are bipolar structures and have no vascular connections with the underlying plant, one of the features distinguishing it from the other plant organs and zygotic embryos [149]. The bipolar structure contains an independent provascular system, and each of the pole has its own meristem [24, 68].

Somatic embryogenesis incidences and various networks

Embryogenesis and woody genera

In certain plant groups like woody genera, response is poor in developing callus and embryogenic tissues; the exudation of phenolics and similar other compounds aggravate the problem further [18]. With the growing knowledge and other technological advances, these problems were overcome in many plants, and consequently, many woody plants are now cultured in vitro. But most of the woody plants are still either completely reluctant or respond poorly to treatments for embryogenesis [42]. With the current high demand for woody plants (due to medicinal, aesthetic values, food, fiber, timber, fuel), plant conservation concerns and climate change attract researchers' attention in unveiling new strategies for

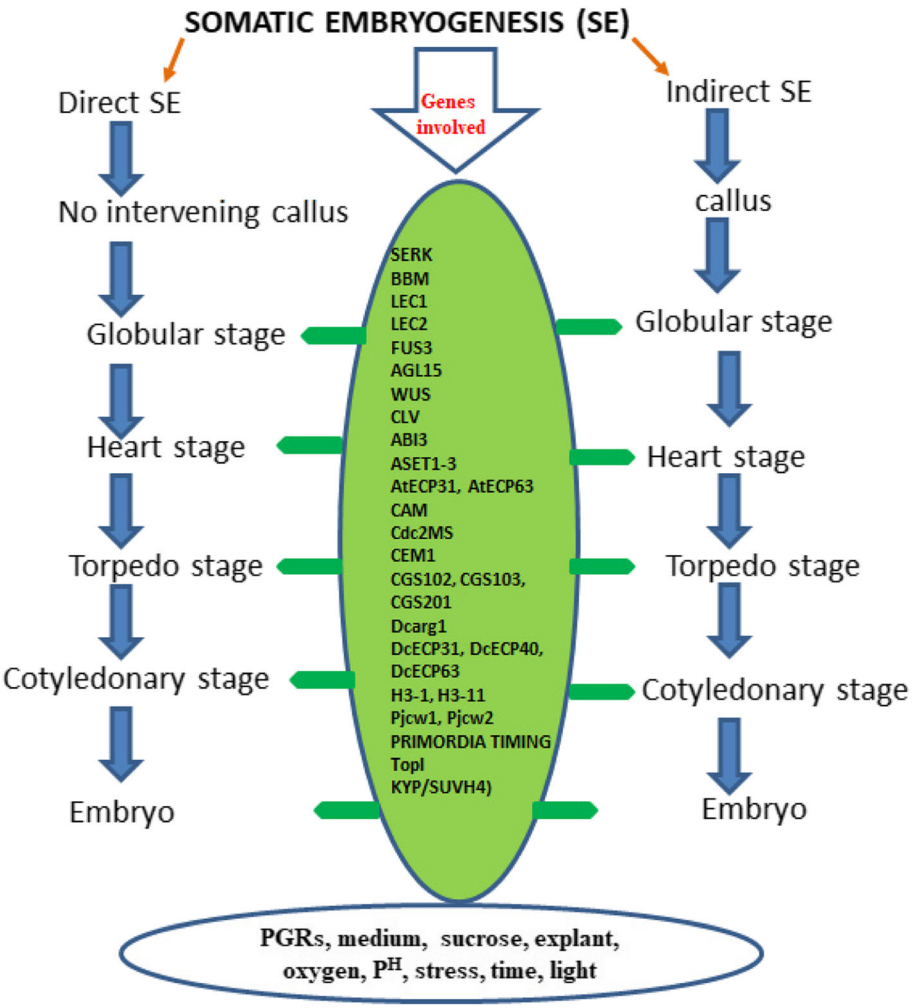

Fig. 1 *Two different pathways of SE in dicots (i.e., direct and indirect SE), different (i.e., globular, heart, torpedo and cotyledonary) stages of embryos, factors affecting SE are kept at bottom in oval, and one central green oval shows some genes involved in SE. SERK1-5 (SOMATIC EMBRYO RECEPTOR KINASE 1-5), LEC1, LEC2 (LEAFY COTYLEDON 1,2), BBM (BABY BOOM), FUS3 (FUSCA 3), ABI3(ABA INSENSITIVE 3), AGL15 (AGAMOUS LIKE 15), ASET1-3 (Alfalfa SE-specific transcripts), AtECP31 (Arabidopsis thaliana Embryogenic31), AtECP63 (Arabidopsis thaliana Embryogenic63 cell proteins), CaM genes (Calmodulin genes), Cdc2MS (Cell division cycle), CEM1 (elongation factor-1a), CGS102, CGS103, CGS201 (Carrot glutamine synthetase), Dcarg1 (Daucas carrotaauxin regulated gene), SAUR (small auxin up-regulated = Pjcw1, Top1 (topoisomerase1), DcECP31, DcECP40, DcECP63 (Daucus carota embryogenic cell protein), H3-1, H3-11 (Histone 3), KYP/SUVH4 (Kryptonite), LBD29 (LATERAL ORGAN BOUNDARIES DOMAIN 29), PRC 1(POLYCOMB REPRESSIVE COMPLEX1)*

rapid, mass propagation of such plants. Marker-assisted breeding, genetic transformation, etc. are also being targeted to improve plant quality [42, 82, 95]. SE is one of the methods being continuously upgraded and renovated to suit plant propagation particularly for those plants that have a long life cycle, produce less/no seeds, and do not reproduce vegetatively. This technique is preferred over the organogenesis because of bipolar embryo that does not need separate treatment for root or shoot induction [159]. The bipolar embryonal axis has both shoot and root ends and is directly grown to complete plants [24]. Various factors govern SE induction and embryo numbers such as plant genotype, type of explants, type and strength of stimulus, and age of tissue (e.g., juvenility) [113]. After acquisition of embryogenic competence, embryo development may not always reach the final stages of plantlet formation [164]. In plants, where embryos developed, a similar developmental pattern was observed for the attainment of other developmental stages. Thus, SE is suitable for forest and other groups of plant propagation, genetic engineering, and cryopreservation of elite germplasm [14, 95, 110].

Genes regulating vegetative to embryonic (early stage) transition

LAFL network genes [*LEAFY COTYLEDON1*, LEC1/LEC1-LIKE (L1L), ABSCISIC ACID INSENSITIVE 3 (ABI3), *FUSCA3* (*FUS3*), and (*LEC2*)] are involved in the

initial steps of direct SE which is not true for indirect SE in *BABYBOOM* (*BBM*)-mediated LAFL [LEC1/LEC1-LIKE (L1L), *ABSCISIC ACID INSENSITIVE 3* (*ABI3*), *FUSCA3* (*FUS3*), and (*LEC2*)] gene expression [10]. Chromatin state of LAFL gene is one of the factors that determine direct or indirect SE. *LEC1/LEC1-LIKE* (*L1L*) and *LEC2* induce direct SE when constitutively overexpressed, while *LEC1* in particular is detected later after embryo appears on the callus surface [44].

Role of plant growth regulators (PGRs) in embryogenesis network

PGRs play a key role in both zygotic and somatic embryogeneses. Among all PGRs, auxin is most effective in the induction of SE [94, 112, 138]. Once SE is induced, auxin concentration is either to be lowered or completely omitted [117]. Different PGRs, their concentrations and combinations have different effects on the process of SE depending on the plant species. In most species, auxin, cytokinin, abscisic acid (ABA), and jasmonic acid (JA) are the key factors triggering the embryogenic response as these have a regulatory effect on cell cycle, division, and differentiation [29]. Auxin 2,4-dichlorophenoxyacetic acid (2,4-D), either alone or in combination with cytokinins, is used to induce somatic embryo in many plant species using seeds or zygotic embryos as explants [29, 61, 118]. Synthesis of jasmonic acid and abscisic acid (stress-related PGRs) was reported in *Medicago sativa* throughout the process of SE but differentially biosynthesized in different phases of SE. Gibberellins (GAs), usually gibberellic acid (GA_3), have a repressive role on the induction of SE in some plants as it significantly upregulates gibberellins 2-oxidase (GA2ox6), repressing GA synthesis (Elhiti et al. 2010).

LEAFY COTYLEDON 1 (LEC1) is a key player in abscisic acid (ABA)-mediated expression of *YUCCA10* (*YUC10*) in seedlings [72]. *YUC* mutants (YUC genes are involved in auxin biosynthesis) are less responsive to secondary SE, suggesting that the endogenous auxin is important for this process [151]. Adventitious shoot formation is induced in short auxin exposure while somatic embryo formation in long auxin exposure. This suggests the developmental continuum in somatic embryo and adventitious shoot formation, where critical threshold auxin signaling is crucial in in vitro induction and maintenance of embryo identity [112]. Auxin-mediated plant development involves changes in expression of auxin-responsive genes, encoding a family of transcription factors, AUXIN RESPONSE FACTORs (ARFs). The ARFs regulate the expression of target genes by binding to AUXIN RESPONSE ELEMENT (AuxRE) TCTCTC motif, present in promoters of auxin-responsive genes [150]. The ARFs bind promoters via a B3-type DNA binding domain, specific to plants. Molecular studies of *Arabidopsis thaliana* identified about 22 ARF genes and a pseudogene [86]. Among the different ARFs, ARF5, ARF6, ARF7, ARF8, and ARF19 activate the target gene expression, while ARF1, ARF2, ARF3, ARF4, and ARF9 repress the expression of target genes. Wójcikowska and Gaj [150] observed upregulation of four ARFs (ARF5, ARF6, ARF10, and ARF16) during the inductive phase of SE in *Arabidopsis*, while two ARFs (ARF8 and ARF17) were upregulated in advanced stages. A number of ARFs are being identified in different plants, and intensive research continues in this field to elucidate their role in plant developmental processes.

Plant genotype, explants, and oxygenation determining embryogenesis

The success in regenerating plant via SE is largely dependent on the genotype of the plant species [27, 65]. Different plant parts respond differently, while cultured in vitro or even different genotypes of a plant behave uniquely/differently. Sané et al. [124] reported that Ahmar and Amsekhsi cultivars were more callogenic than Tijib and Amaside, exhibiting response differences in primary callogenesis in different date palm cultivars. Similarly, woody plants are more recalcitrant in showing responses than the herbaceous groups of plants [18, 65].

Various types of explants are used for generating somatic embryos in different plants. The type and size of explant and plant species significantly influence the process of SE [140]. Kocak and co-workers [79] demonstrated that the leaves and petioles of *Cyclamen persicum* were more responsive compared to the ovule and ovary and took less time to induce callus; in carnation, callus followed by somatic embryos were obtained from petal explants in a number of cultivated varieties [76].

The dissolved oxygen concentration in culture flask has significant influence on the development of somatic embryos. It is observed that the concentration of oxygen in suspension had ostensible effects on the maturation process and the number of embryos [13, 22]. The 50% dissolved oxygen (DO) levels in medium showed maturated embryos with lower numbers, while at 80% DO concentration, opposite response (i.e., higher embryo numbers with less maturity) were noted in *Coffea arabica* [13].

Somaclonal variation, SE, and genetic integrity

Somaclonal variation (SV) is a phenomenon whereby the variations are manifested among the tissue culture-raised plants, and these variations include both phenotypic and genotypic alterations [99]. The genetic alterations occur spontaneously under stressed micro-environment and can continue to remain for several generations [20]. The changes are heritable and non-

heritable containing point mutation, chromosomal deletion, substitution, DNA breakage, and ploidy [97, 154]. The PGR-induced stress, nutrient, osmotic, humidity-transpiration imbalances, oxidative stress, and light stress are the forces generating these abnormalities [97]. Non-heritable genetic changes constitute some of the epigenetic changes, which are less stable, remain for a lesser period of time, and disappear on the cessation of stress condition [69]. DNA methylation, hypo- and hyperacetylation led some of the epigenetic changes occurring in in vitro-cultivated plant cells [25, 142]. Polycomb protein group modifies histone, and these proteins form conserve regulatory complexes that modify the chromatin state and gene expression during cellular transition from somatic to embryogenic cells. Two of such conserved regulatory complexes are Polycomb repressive complex 1 (PRC1) and PRC2. Trimethylation of histone 3 (H3K27me3) lysine 27 through SET-domain protein and subsequent binding of PRC1, which carry out ubiquitination of 119 lysine residues of histone H2A, improves compactness of the chromatin [109]. The state of chromatin determines binding of regulatory protein complexes and influences expression of genes.

In SV, the frequency of variations increases with the age of cultures, number of subcultures, and duration of stress [108]. The variations noted in plants regenerated through SE have both advantages and disadvantages. SV is a big problem where plants' genetic and phenotypic integrity and purity are aimed at. In such cases, the genetic purity is ensured by taking the explants from authenticated, registered sources while the SV is also widely used in plant improvement programs [6]. The easily available variations among the regenerated plants could be profitable only when maintained stably for generations. The main problem of SV is the non-beneficial, redundant, and unstable variations, restricting the progress of breeding, and most of the regenerated plants showed poor agronomic performance [80, 81].

Carbohydrates and underlying mechanism of SE

The reprogramming of signaling and communication of callus cells seem to be chemical in nature, and the analysis of callus exudates in the medium shows compounds like sugars, growth regulators, low molecular weight compounds, amino acids, and vitamins [16, 17]. Different carbohydrates were used as energy source in various media, of which sucrose and glucose are observed to be the most efficient for better cultural growth. In some plants, SE is absent until sucrose was added to the media, confirming its importance in embryo induction [75, 83]. For example, the expanded cotyledons of melon were noted to induce somatic embryos only in the presence of sucrose [52]. Sucrose or glucose may be substituted by other carbohydrates as carbon sources depending upon the tissue, plant, and species from which explants are taken [71]. Grzyb et al. [41] noted many fold effects of increased soluble sucrose at developmental transition to SE expression phase. Species-specific storage products are also accumulated during SE process and are absent in other stages of development [157].

Somatic Embryogenesis Receptor Kinase, *SERK*, and other genes regulating SE

SERK is involved in embryogenic competence acquisition [152, 159]; the gene encodes protein and was isolated initially from carrot, named as *DcSERK*. Later, *SERK* homologues were also reported in many other plants (Table 1). Structurally, *SERK* consists of serine–proline-rich leucine zipper, kinase domain, signal peptide, leucine-rich region, transmembrane domain, and C-terminal region [152]. *SERK*, a cell surface receptor, triggers a signal cascade after binding to the ligand through the leucine-rich repeat (LRR) domain and with the help of intracellular domains reaches to the nucleus. This cascade alters gene expression pattern via chromatin remodelling [159]. Activity of genes is often altered either by repressing specific or selective genes and activating/changing the expression of others. *SERK* overexpression is observed during embryogenic induction till the globular stage and together with other genes like *BBM* and *LEC* promotes transition to embryogenic cells from non-embryogenic tissues [132].

LEAFY COTYLEDON (*LEC*) is one among the most important genes, playing a central role in both zygotic and somatic embryogeneses. Loss of functional mutation in *LEC* largely impaired the embryonic development [56]. The *LEC* mutant shows significantly reduced or total repression of embryogenic response as observed in double and triple mutants in *A. thaliana* [34]. The impairment is most ostensible in the maintenance of embryonic cell fate and specification of cotyledon identity. Overexpression of *LEC2* affects several target genes including the *AGAMOUS-like 15 (AGL15)* TF gene and auxin pathway genes [151]. *LEC2* mutants do not acquire desiccation tolerance and do not accumulate storage reserves in cotyledon tips [136]. Studies suggested that *FUSCA3* (*FUS3*), *LEC1*, and *LEC2* do not play a major role in the induction of SE, but during late stages of embryogenesis, their function has a significant say [56, 136]. Watery callus and root hairs are produced in *LEC1* single mutant, while *LEC1* and *FUS3* double and triple mutants negatively affect the SE process. Embryo identity and maturation are regulated by the network of LAFL proteins LEC1/LEC1-LIKE (L1L), ABSCISIC ACID INSENSITIVE 3 (ABI3), FUSCA3 (FUS3), and (LEC2) where B9 and B3 domains are encoded by *LEC1* and *LEC2* genes, respectively [145]. B9 is a subunit of

Table 1 Genes/orthologs regulating somatic embryogenesis in various investigated plants

Genes/orthologs	Encoded products and possible role	Investigated plant	References
ABI3 (*ABA INSENSITIVE 3*)	B2, B3 domain transcription factors; regulate embryo-specific ABA-inducible genes	*Arabidopsis thaliana*	Ikeda et al. [61]
AGL15 (*AGAMOUS LIKE 15*)	MADS-box transcription factor; promote somatic embryogenesis	*Brassica napus*	Zhu and Perry [165]
ASET1-3 (Alfalfa SE-specific transcripts)	Specific transcript, (product unknown); expressed at early stages of embryogenesis	*Medicago sativa*	Giroux and Pauls [39]
AtECP31, *AtECP63*	Embryogenic 31 and 63 cell proteins; expression during torpedo stage of embryogenesis, ABA-responsive genes	*A. thaliana*	Yang et al. [156]
BBM (*BABY BOOM*)	AP2/ERF Transcription factors; activates LEC1-ABI3-FUS3-LEC2 network to induce somatic embryogenesis	*B. napus*	Boutilier et al. [11] Hortsman [55]
CaM (Calmodulin genes)	Kinase type protein; accumulates during early embryogenesis through Ca-mediated signaling	Many plants	[5]
Cdc2 (*Cell division cycle 2*)	Cdc protein; regulation of cell cycle progression	*M. sativa*	[96]
CEM1	Polypeptide, similar to translational elongation-factor 1α Expressed strongly pro-globular and globular stage	*Daucus carota*	[77]
CGS102, *CGS103*, *CGS201*	Glutamine synthetase; enzyme, expression during early SE stages	*D. carota*	[53]
DcARG1 (*Auxin regulated Gene 1*)	Protein specific to auxin; expression at early induction stage	*D. carota*	[15]
DcECP31, *DcECP40*, *DcECP63*	Embryogenic cell protein; expression at torpedo stage of SE	*D. carota*	[15]
FUS3 (*FUSCA 3*)	Transcriptional factor family protein; regulate synthesis of storage proteins and lipids	*A. thaliana*	[73]
H3-1, *H3-11* (Histone 3,11)	H3-1 gene transcript, auxin responsive	*M. sativa*	[74]
Kryptonite (*KYP/SUVH4*)	Methyl transferase; role in dedifferentiation	*A. thaliana*	[26]
LATERAL ORGAN BOUNDARIES DOMAIN 29 (*LBD29*)	Transcription factor; dedifferentiation of cells, role in early embryogenesis	*A. thaliana*	[89]
LEC1, LEC2 (*LEAFY COTYLEDON 1,2*)	B3 domain transcription factor; essential for somatic embryogenesis	*A. thaliana*	[21]
PICKLE	ATP-dependent chromatin remodeler; inhibits SE	*A. thaliana*	[120]
PJCW1, PJCW2 = SAUR, SMALL AUXIN UP-REGULATED GENE	Protein product, influence cell elongation	*Glycine max*	[45]
POLYCOMB REPRESSIVE COMPLEX1 (*PRC 1*)	Epigenetic effector proteins; stem cell self-renewal, pluripotency, gene silencing; repressive effect on dedifferentiation ability of cells	*A. thaliana*	[26]
PRIMORDIA TIMING	Gene product; help in flower development; increases SAM cell population	*A. thaliana*	[49]
SERK1-5 (*SOMATIC EMBRYO RECEPTOR KINASE 1-5*)	Receptor like kinase protein; acquisition of embryogenic competence	Many plants	[105]
TOPI (*Topoisomerase1*)	Constitutively expressed during cellular proliferative activities and at torpedo stage of SE development	*D. carota*	[7]
WUSCHEL	Homeo-domain transcription factor; Promote "vegetative to embryonic" transition	*A. thaliana*	[166]

NUCLEAR factor Y (NF-Y-B9), and B3 is a domain which contains transcription factor LEC2 [160] playing a role in maintaining the morphology of suspensor, progression via maturation phase, cotyledon identity specification, and suppressing premature germination [46]. Accumulation of storage macromolecules, desiccation tolerance, and cotyledon development are defective in zygotic embryos where loss of function mutation occurs in *LAFL* genes. LAFL proteins regulate the expression of BBM which gets reduced in case of *LAFL* mutant seeds [55]. *LEC2* have central role in maturation phase of SE; *LEC2* up regulates *AGL15* which is involved in the formation of somatic embryos from embryogenic tissues like zygotic embryos. *AGL15* and *LEC2* are involved in the activation of *INDOLE-3-ACETIC ACID INDUCIBLE 30* (*IAA30*) which when mutated affects the *AGL15*-mediated SE that normally shows enhancement under its effect [163]. Embryo development is switched on in the vegetative cells that acquire embryogenic competence under the influence of ectopic expression of *LEC* [29, 90, 137]. The *LEC* genes in turn seem to be regulated by *PICKLE* by causing chromatin remodelling, repressing the embryonic identity regulators during germination [84, 121].

BABYBOOM (*BBM*) is a transcription factor of AINTEGUMENTA-LIKE (AIL) APETALA2/ethylene-responsive element (AP2/ERF) family, isolated from *Brassica napus* embryos developed from pollen grains [11]. Ectopic expression of *BBM* in *A. thaliana* seedlings induces somatic embryos without the exogenous stress or growth regulator treatment. *BBM* along with other AP2/ERF family of transcription factors help in maintaining meristematic state of shoot and root meristems [56, 57]. It regulates cell growth and identity and promotes morphogenesis and cellular proliferation by exploiting AIL and LAFL proteins while mediating embryogenesis. Ectopic expression of *BBM* has an inductive effect in the formation of "somatic embryo-like structures" in *Arabidopsis*. *BBM* in SE binds to *YUCCA3* (*YUC3*), *YUC8*, and *TRYPTOPHAN AMINOTRANSFERASE OF ARABIDOPSIS1 (TAA1)* and promotes auxin biosynthesis, suggesting its role in endogenous auxin synthesis [151, 161]. *FUS3* and *LEC1* mutants completely abolish BBM-induced SE, suggesting their crucial role in *BBM*-induced SE pathway. Beside adventitious root, shoot formation, and SE induction, neoplastic growth (cell proliferation), deformed flowers, and leaves are the pleiotropic phenotypes of *BBM*. In *Theobroma cacao*, a higher level of *TcBBM* expression was noted during somatic embryogenesis than during zygotic embryogenesis time [30]. *BBM* also transcriptionally regulates *LEC*, *FUSCA3 (FUS3)*, and *ABI 45 INSENSITIVE3 (ABI3)* genes and induces cellular totipotency through LAFL network during seed germination [56]. *BBM* regulates the expression of *AGL15* and *LAFL* by binding to promoter of genes. This is evident from the observation where *AGL15* and *LEC2* mutants show reduced *BBM*-mediated SE.

Other genes like *LATE EMBRYO ABUNDANT (LEA)* are noted to be abundantly expressed during later phases of embryogenesis [107]. The LEA proteins are hydrophilic and are regulated by ABA [60]. The LEA proteins influence the developmental processes of zygotic and somatic embryogeneses and also to stress-related responses. In almost all instances, their expression is observed in embryogenic tissue and not in vegetative cells. In addition to LEA proteins, some other genes like *WUSCHEL* are active during SE; *WUS* develops somatic embryos indirectly, and ectopic expression of *WUS* also produces somatic embryo directly and promotes organogenesis on exogenous auxin-amended or PGR-free cultures as evidenced in *WUS* mutants [88]. The emergence of shoots forming embryos similarly occurs in ectopically expressed *WUS* explants in auxin-free and *CLAVATA (CLV)* mutants in 2,4-D (auxin)–added medium [164]. *WUS* and *CLV* normally function to maintain stem cells and cell differentiation in shoot meristem [166]. Cell differentiation is also regulated by these genes in the shoot apical meristem (SAM) of *CLV* mutants where somatic embryos are formed by some non-committed cells [61, 166]. *WOUND INDUCED DEDIFFERENTIATION1 (WIND1)* or RAP2-4 (Protein RELATED to APETALA2 4) induces SE and play a role in callus formation in tissue damage and wounding [63]. *PLETHORA2 (PLT2)* plays a major role in the induction and specification of root pole in SE [11, 146]. Reverse glycosylating protein (RGP-1), a membrane protein, encourages plant cell wall development by facilitating polysaccharide metabolism, and in early phases of somatic embryogenesis, it is thought to participate in structural reorganization [37]. *AGAMOUS-like 15* (*AGL 15*) is isolated as a MADS-box gene, detected in many plants (e.g., *B. napus*, *Arabidopsis*, *Taraxacum*), and in alfalfa, it is detected in somatic embryos [60]. *AGL15* regulates the expression of several genes during the process of SE by encoding MADS-box family of transcription factors. For example, AtGA2ox6 is encoded by a gene, controlled by *AGL15* [60]. Overexpression of *AGL15* induces SE in embryogenic tissue like zygotic embryos and could not induce SE spontaneously in *Arabidopsis* seedlings. Ectopic expression of *AGL15* under CaMV35S promoter induces embryo formation in seedling in which 2,4-D and *AGL15* both regulate expression [165].

Among the different RKD (RWP-RK domain-containing) proteins, only RWP-RK DOMAIN-CONTAINING 4 (RKD4) is noted to produce embryos; RWP-RK DOMAIN-CONTAINING 4 (RKD4)/

GROUNDED (GRD) also induces embryos and is thought to be expressed in maximum in suspensors and early stages of embryos [57]. On the overexpression of *RKD4,* SE develops into seedlings by stimulating root cells to proliferate; and in *RKD4* mutants, embryo development is arrested, and suspensor remains short [55]. Different genes/transcription factors (TFs) playing various roles at different stages of embryogenesis are shown in Fig. 2.

The mystery behind the SE is being gradually unfolded by the use of molecular approach. Over 700 TFs and genes are being extensively studied during the process of SE in *Arabidopsis thaliana* and other plants, suggesting the very significant role of TF in competence acquisition via embryogenic reprogramming [40]. Some of the genes and TFs having a role in SE are enlisted in Table 2. Studies suggest that the basic mechanism behind the somatic and zygotic embryogenesis is the same, and the genes regulating zygotic embryogenesis have very similar effect on SE. Differentially expressed genes *DEG1* and *DEG2* associated with embryogenesis were identified in *Dactylis glomerata* [3]; *DEG*s express in the embryogenic leaf (not in non-embryogenic cells) and is noted in both directly and indirectly induced cultures, while *DEG2* expression is noted only in directly induced tissues. The ectopic expression of various zygotic embryogenic genes significantly increased the somatic embryo development in several investigated plants. Similarly, the chromatin remodeling determines spatial and temporal expression of genes and influences the development of SE to a large extent [4]. Indirect SE requires more extensive chromatin modification than that of direct SE as was shown by differential expression of chromatin modifiers after 2,4-D–mediated callus formation [23]

SE-related proteins

Currently, a novel combination of techniques is being utilized for the identification and quantification of embryo-specific proteins, which cannot otherwise be identified by conventional gel-based methodologies. Liquid chromatography–mass spectroscopy (LC–MS) is a technique in which liquid chromatography and mass spectroscopy operate together and in tandem. In this technique, the protein sample is processed/digested into

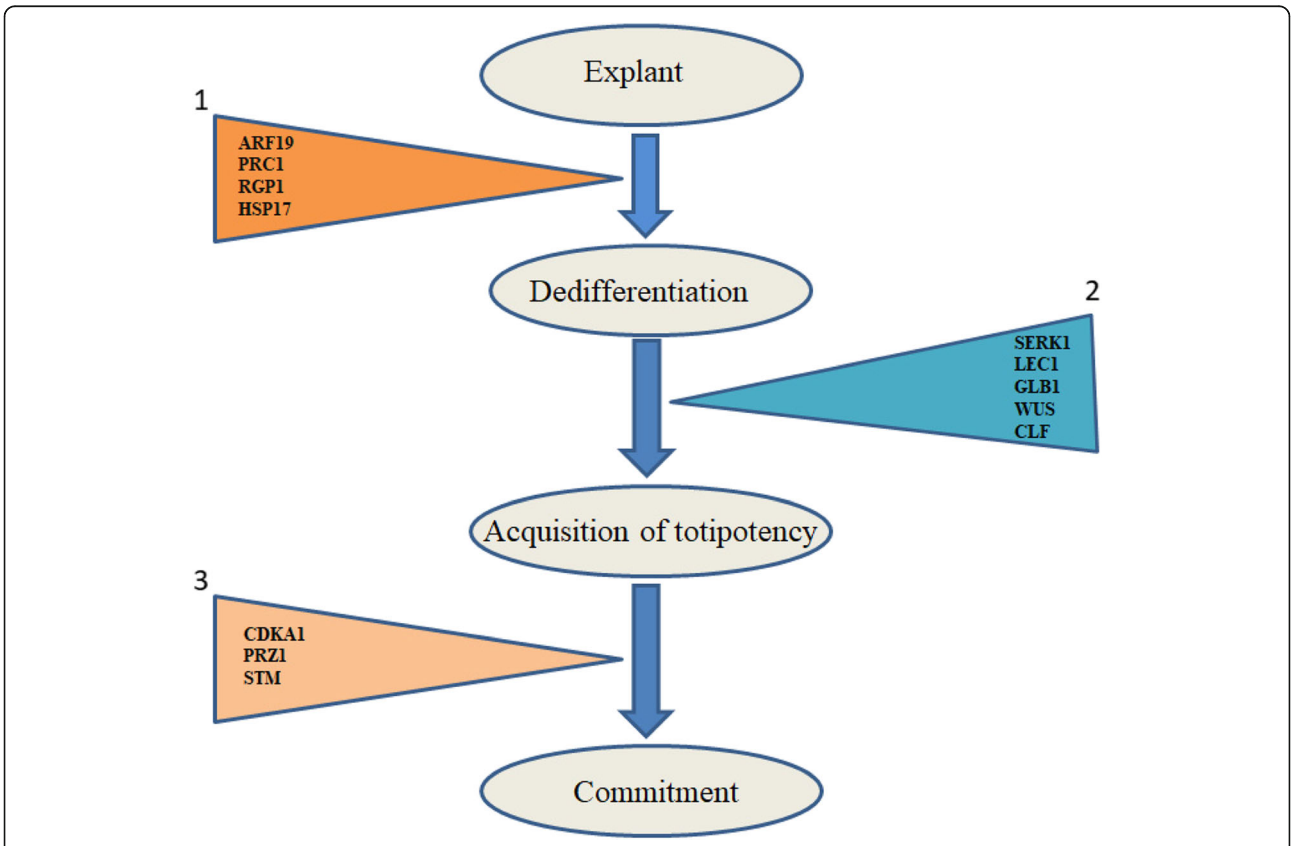

Fig. 2 *Different genes at different stages of SE pathway. Triangle 1 in yellow shows genes involved in dedifferentiation; triangle 2 shows genes involved in acquisition of totipotency by the cells; and triangle 3 shows genes expressed in commitment of totipotent cells to embryogenic state. AUXIN RESPONSE FACTOR 19 (ARF19), POLYCOMB REPRESSIVE COMPLEX 1 (PRC1), REVERSIBILY GLYCOSYLATED POLYPEPTIDE 1 (RGP1), HEAT SHOCK PROTEIN 17 (HSP17), SOMATIC EMBRYOGENESIS LIKE RECEPTOR KINASE (SERK1), LEAFY COTYLEDON1 (LEC1), GALACTOSIDASE BETA 1 (GLB1), WUSCHEL (WUS), CURLY LEAF (CLF), CYCLIN DEPENDENT KINASE A1 (CDKA1), PROPORZ1 (PRZ1), SHOOT MERISTEMLESS (STM)*

Table 2 *SOMATIC EMBRYOGENESIS RECEPTOR KINASE* (*SERK*) gene regulating embryogenesis in different studied plant materials

Name of plant	Common name	*SERK* gene	References
Adiantum capillus-veneris	Maidenhair fern	*AcvSERK*	[87]
Ananas comosus	Pineapple	*Ac SERK1–3*	[91]
Arabidopsis thaliana	Thale cress	*At SERK1–5*	[47]
Citrus sinensis	Orange	*Cs SERK*	[38]
Citrus unshiu	Tangerine	*Cu SERK*	[131]
Cocos nucifera	Coconut	*Cn SERK*	[114]
Cucurma alismatifolia	Summer tulip	*CaSERK*	[139]
Cyclamen persicum	Persian cyclamen	*Cp SERK1–2*	[128]
Cyrtochilum loxense	Not available	*Cl SERK*	[19]
Dactylis glomerata	Orchard grass	*DgSERK*	[134]
Daucus carota	Carrot	*Dc SERK*	[129]
Dimocarpus longan	Longan	*Dl SERK*	[1]
Garcinia mangostana	Magnosteen	*Mangosteen SERK*	[122]
Glycine max	Soya bean	*Gm SERK1–2*	[155]
Gossypium hirsutum	Cotton	*Gh SERK1–3*	[111]
Helianthus annuus	Sunflower	*HaSERK*	[143]
Marchantia polymorpha	Common liverwort	*Mp SERK*	[127]
Medicago truncatula	Barrel clover	*Mt SERK1–6*	[105]
Musa acuminata	Banana	*MaSERK*	[59]
Nicotiana benthamiana	Tobacco	*Nb SERK3A, Nb SERK3B*	[93]
Ocotea catharinensis	Not available	*OcoteaSERK*	[125]
Oryza sativa	Rice	*OsbiSERK, Os SERK, Os SERKlike1, Os SERKlike2*	[66]
Physcomitrella patens	Moss	*Pp SERK1–3*	[1]
Poa pratensis	Common meadow grass	*Poap SERKlike1–2*	[2]
Populus trichocarpa	Black cottonwood	*Pp SERK1-4*	Aan den Toorn et al. [1]
Prunus persica	Peach	*Persica SERK**	[67]
Prunus salicina	Japenese plum	*PsSERK*	[67]
Rosa canina	Dog rose	*RcSERK*	x [78]
Rosa hybrid	Hybrid tea rose	*RhSERK1–4*	[158]
Selaginella moellendorffii	Club moss	*Sm SERK1–4*	[1]
Solanum lycopersicum	Tomato	*Sl SERK1, Sl SERK3A, Sl SERK3B*	[93]
Solanum peruvianum	Wild tomato	*Sp SERK*	[1]
Solanum tuberosum	Potato	*St SERK*	[130]
Sorghum bicolor	Sorghum	*Sb SERK1–3*	[1]
Theobroma cacao	Cocoa tree	*TcSERK*	[126]
Triticum aestivum	Wheat	*Ta SERK1, Ta SERK2, Ta SERKlike3*	Singla et al. [133]
Vitis vinifera	Grape	*Vv SERK1–3*	[92]
Zea mays	Maize	*Zm SERK1–3*	[8]

Modified and courtesy: [141]

small fragments and separated after loading in the LC column; and subsequent analysis is made based on mass/charge ratio (m/z). The technique is used for the identification of proteins using different softwares like SEQUEST, MASCOT, and Proteome discoverer. Helleboid [48] reported glucanases, chitinases, and osmotin-like proteins (also called pathogen-related or PR proteins) which accumulate during SE of *Cichorium*. These and other similar proteins were isolated from different plants including tobacco during the hypersensitive reactions against the tobacco mosaic virus, classified into five major groups PR1–PR5. Later, it was established that

such proteins accumulate during stress conditions like injury, heavy metals, plant hormones, and UV. Similarly, other SE-related proteins were reported in different plants [e.g., *Zea mays* [35], *Araucaria angustifolia* [31], *Coffea arabica* [12], *Picea asperata* [70], *Gossypium hirsutum* [36], *Larix principis-rupprechtii* [162], *Picea balfouriana* [85], *Saccharum* spp. [50], and *Catharanthus roseus* [43]]. One class of 14-3-3 proteins play a significant role in plant immunity, cell cycle control, metabolism, stress responses, transcription, signal transduction, programmed cell death protein trafficking, and SE [106]. These are acidic regulatory proteins, binding in a phosphorylation-dependent manner to target proteins like phosphothreonine and phosphoserine and thus have a significant role in plant growth and development. Heat shock proteins, peroxidase, catalase, superoxide dismutase, etc. are some other proteins that are common in many plants, accumulate in SE tissues, and are studied via gel-free shotgun proteomics. Several proteins isolated during SE are stress proteins suggesting that stressed microenvironment is the driving force for SE induction. Of these different proteins, several were identified as proteomic markers. The most common proteins identified as potential markers of SE are listed in Table 3.

Conclusions

Since the first report of SE, this intricate process has been studied extensively in a large number of plant genera of dicots, monocots, gymnosperms, and fern. Various stages of embryogenesis (i.e., embryo origin, development, maturation, and germination into plantlets) have also been unveiled. The factors controlling somatic embryogenesis have also been identified; some of them are plant genotype, explant, medium composition, carbohydrate type, oxygen concentration, PGRs, and various stresses. Although the molecular mechanism is still not well elucidated, chromatin remodeling, activation and deactivation of genes, and complicated transcription networks are linked with somatic and zygotic embryogenesis processes. A number of genes or orthologs which have important say in early cellular transition from somatic to embryogenic cells are *AUXIN RESPONSE FACTORs, POLYCOMB REPRESSIVE COMPLEX 1* (*PRC1*), *REVERSIBILY GLYCOSYLATED POLYPEPTIDE 1* (*RGP1*), and *HEAT SHOCK PROTEIN 17* (*HSP17*), *SOMATIC EMBRYOGENESIS LIKE RECEPTOR KINASE* (*SERK1*), *LEAFY COTYLEDON1* (*LEC1*), *WUSCHEL* (*WUS*), *CURLY LEAF* (*CLF*). The expression of *SHOOT MERISTEMLESS* (*STM*) gene influences in other stages

Table 3 Plants and different SE related proteins, identified through LC-MS

Some important SE-related proteins	Plant/species	References
Alcohol dehydrogenase, allene oxide synthase, ATP synthase, glyceraldehyde-3-phosphate dehydrogenase, GH3 protein, glutathione-S transferases, heat shock proteins, indole-3-acetic acid-amidosynthetase, late embryogenesis abundant, lipid transfer protein, peroxidase, photosystem II proteins, ribosomal proteins, ribulose-1,5 bisphosphate carboxylase, superoxide dismutase, sucrose synthase	*Gossypium hirsutum*	[36]
14-3-3 protein, 6-phosphogluconate dehydrogenase, actin, aldose 1-epimerase, annexin, ADP-ribosylation factor GTPase-activating proteins, ATP synthase, calmodulin, catalase, chitinase, citrate synthase, clathrin, elongation factors, eukaryotic initiation factors, glyceraldehyde-3-phosphate dehydrogenase, glycine-rich RNA-binding proteins, heat shock cognate proteins, histones, heat shock proteins, importin, superoxide dismutase, triosephosphateisomerase, tubulin, peroxidase, ubiquitin	*Larix principis-rupprechtii*	[162]
14-3-3 protein, actin, aldose 1-epimerase, annexin, ATP synthase, ADP-ribosylation factor GTPase-activating proteins, calmodulin, chitinase, citrate synthase, glycine-rich RNA-binding proteins, heat shock cognate proteins, heat shock proteins, importin, peroxidase, triosephosphateisomerase, tubulin	*Larix principis-rupprechtii*	[162]
Calmodulin, germin-like proteins, glutathione-S transferases, peroxidase, ribosomal proteins, superoxide dismutase	*Picea balfouriana*	[85]
Actin, aldolase, catalase, germin-like proteins, late embryogenesis abundant, secreted protein, tubulin	*Saccharum* spp.	[50]
14-3-3 proteins, actin, alcohol dehydrogenase, ATP synthase, chitinase, elongation factors, glyceraldehyde-3 phosphate dehydrogenase, glutathione-S transferases, histones, heat shock proteins, PIN-like protein, ribulose-1,5-bisphosphate carboxylase, ubiquitin	*Araucaria angustifolia*	[31]
Aldolase, chitinase, glyceraldehyde-3-phosphate dehydrogenase, peroxidase	*Coffea arabica*	[12]
14-3-3 proteins, arabinogalactan proteins, glutathione-S transferases, heat shock proteins, indole-3-acetic acid-amidosynthetase, late embryogenesis abundant, peroxidase, ubiquitin	*Saccharum* spp.	[119]
Alcohol dehydrogenase, aldose 1-epimerase, allene oxide synthase, catalase, chitinase, glutathione-S transferases, heat shock proteins, indole-3-acid-amidosynthetase, late embryogenesis abundant, peroxidase, photosystem II proteins, ribosomal proteins, ribulose-1,5-bisphosphate carboxylase, sucrose synthase, tubulin	*Picea asperata*	[70]
6-phosphogluconate dehydrogenase, annexin, clathrin, eIFs, histones, heat shock proteins, lipid transfer protein, peroxidase, ribosomal proteins	*Saccharum* spp	[51]
14-3-3 proteins, chitinase, GH3 protein, glutathione-S transferases, indole-3-acetic acid-amidosynthetase, peroxidase, tubulin	*Zea mays*	[35]
14-3-3 proteins, chitinase, GH3 protein, glutathione-S transferases, peroxidase, tubulin, annexin, clathrin, eIFs, histones, heat shock proteins, late embryogenesis abundant, chitinase, PR proteins, importin, catalase, etc.	*Catharanthus roseus*	[43]

of somatic embryogenesis. Several proteins may act as potential markers for the process of SE (e.g., 14-3-3 protein, chitinase, LEA, etc.). At the time of genetically uniform plant propagation, genetic transformation, artificial seed production, plant regeneration from protoplast, and in biodiversity conservation, the SE information will be very indispensable. Flow cytometry, nano LC–MS, real-time PCR, and other sensitive molecular techniques have a scope in understanding the molecular mechanism underlying SE. These may refine the process, scale up the progress of research in SE, and may increase its application in other novel fields.

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