International Journal of Pharmaceutical Science Invention
ISSN (Online): 2319 – 6718, ISSN (Print): 2319 – 670X
www.ijpsi.org Volume 8 Issue 1 ǁ Jan 2019 ǁ PP.01-07

Expression of Extracellular Proteins in Somatic Embryogenesis of Plants

Shuvam Bhuyan and Rajashree Bordoloi*
Department of Botany, Darrang College, Tezpur, Assam.
**Corresponding Author: Rajashree Bordoloi*

***ABSTRACT**: Somatic embryogenesis' is a process where somatic embryos are derived from somatic cells. The transition of somatic cells from a pro-embryonic mass (PEM) of cells to a somatic embryo requires several factors ranging from phytohormones, proteins, transcription factors and other related substances. Of them all, the extracellular proteins play an indispensable part in the differentiation and morphogenesis of the somatic cells. Despite this phenomenon being well-known, the mechanism of how these extracellular protein influences the cell fate during organogenesis is still unclear. Recent advances in proteomics and developmental biology allow us to explore new pathways in the development of somatic embryos from somatic cells.The various extracellular proteins employed during somatic embryogenesis and that have been reviewed in this article include xyloglucan endotransglycosylases (XET), Endochitinase, Arabinogalactan Proteins (AGPs), Non-Specific Lipid Transfer Proteins (LTPs), Heat shock proteins (HSPs), Lectins, Late embryogenesis abundant proteins (LEA), Citrins, Germins and Germin-like proteins (GLPs).*

***KEYWORDS:** Somatic Embryogenesis, Arabinogalactan proteins, Lipid transfer proteins, Germin and germin-like proteins.*

Date of Submission: 07-05-2019 Date of acceptance: 25-05-2019

I. INTRODUCTION

The developmental process associated with the restructuring of somatic cells to generate embryonic cells is called somatic embryogenesis. These somatic cells undergo a series of morpho-biochemical changes in them resulting in the formation of non-zygotic embryo capable of regenerating plants. The various stages of development in this process include the differentiation of cells, cell division activation and reprogramming of their physiology, metabolism and gene expression pattern (Xiyang and Zhang, 2010).The first study of somatic embryogenesis was documented in carrot cell suspension culture (Steward et al., 1958, Reinert, 1958). Extracellular proteins play a significant role in angiosperm embryology (Van Engien and de Vries, 1992, Kreuger and Holst, 1993). These proteins and their expressions have been associated with induction and initiation of somatic embryogenesis (Boyer et al., 1993). Carrot cell cultures secrete a wide range of proteins. Several studies have reported that extracellular proteins either play an inductive role (Hilbert et al., 1992) or inhibitory role (Gavish et al., 1992). The extracellular proteins are not secreted by embryogenic cells but from non embryogenic cells e.g. extracellular protein EPI (van Engelen et al., 1991). Chitinase may be involved in the generation of signal molecules which stimulate the somatic embryogenesis in carrot (de Jong et al., 1992). Extracellular protein β-1, 3-glucanase may be involved in the degradation of the callose wall surrounding embryogenic cells and small embryo (Helleboid et al., 1998). Protein β-1, 3-glucanase and chitinase cDNAs are expressed during the spruce somatic embryogenesis (Dong and Dunstan, 1997).

II. MATERIALS AND METHODS

We searched databases for the articles from relevant journals and books published from 1958 to 2014. This review article aims to focus on newer information and insights gained from all the research works that have been carried out on the role of extracellular proteins in somatic embryogenesis till date.

III. EXPRESSION OF EXTRACELLULAR PROTEIN IN SOMATIC CELLS

Xyloglucan endotransglycosylases

Up-regulation of xyloglucan endotransglycosylases (XET) modify cell wall during somatic embryogenesis [Malinowski and Filipecki 2002, Thibaud-Nissen et al., 2003, Rensing et al., 2005]. In Pinus radiata the modification in the structure and properties of the cell wall during somatic embryogenesis is due to the up regulation of **α**-d-galactosidase (SEPR1) which cleaves terminal **α**-galactosyl moieties of glycolipids and glycoproteins [Aquea and Arch-Johnson 2008].

Endochitinase

In an embryonic culture, endochitinases are expressed only in a morphologically distinct group of cells located outside the proembryonic mass and not in the developing somatic embryo. The transition from the globular to the heart-shaped stage in carrot embryonic culture is achieved by the extracellular glycosylated acidic class IV endochitinase or extracellular protein 3 (EP3) (de Jong et al., 1992). EP3 is a chitinase by function and is known to lift the arrest of somatic embryo growth in the temperature sensitive carrot embryogenic mutant ts11at the non permissive temperature condition (de Jong et al., 1992).Isozyme EP3-3 was able to lift the arrest at the globular stage and produced later stages of ts11 somatic embryos (Kragh et al., 1996). Endochitinase also play a nurturing role in the processing of signaling molecules during somatic embryogenesis. Apart from these, further investigations reveal endochitinase to be part of a phylogenetically conserved pathway as endochitinase isolated from sugar beet stimulate somatic embryogenesis in cell cultures of Picea abies (Egertsdotter and von Arnold, 1998). Sacco de Vries and his research team have shown that certain arabinogalactan proteins contain endochitinases cleavage site. Both arabinogalactans and endichitinases that are present in the carrot seeds or are secreted in the medium of suspension cultured cells can promote the formation of protoplast-derived somatic embryos (van Hengel, 1998).Pre-globular Pinus caribea embryos in culture contain a basic 48kDa chitinase-like protein ionically bound to their surface which digests embryo-specific AGPs secreted by these embryos as well as those from seeds but not AGPs from non-embryogenic lines (Domon et al. 2000). These modifications are likely to occur to either GlcN or GlcNAc residues which have been shown to be present within the structure of embryogenesis-inducing AGPs since the AGP molecules were also shown to contain an endochitinase cleavage site within their carbohydrate moiety (van Hengel et al., 2001).

Arabinogalactan Proteins

The Arabinogalactan proteins (AGPs) are a heterogenous group of proteo-glycans commonly found in the cell membrane, cell matrix and cell walls. Besides 90% of the macromolecule being composed of carbohydrates, AGPs are rich in hydroxyproline, alanine, glycine and serine amongst protein components (Majewska-Savka and Nothnagel, 2000). Numerous studies have been carried out demonstrating the signaling role ofAGPs in embryogenesis. They are reported to be involved in cell expansion (Welliats and Knox, 1996), cell proliferation (Nothnagel, 1997) and regulation of somatic embryo development (Kreuger and Van Holst, 1995). AGPs promote embryogenesis in a broad range of Angiospermic plants such as carrot (Stacey et al.,1990,van Hengel et al., 2001), Euphorbia (Saare et al., 2000), Wheat (Letarte et al.,2006), Chicory (Legrand et al., 2007) and also in gymnospermic species such as Picea abies (Filonova et al., 2000) and Pinus (Rocha et al., 2013, Domon et al., 2000).Purified AGPs in nanomolar concentration extracted from carrot embryogenesis suspension culture reinitiated embryogenic potential in non-embryonic cell lines (Kreuger and Van Holst, 1993). AGPs may be used in predicting the developmental fate of cells as they display developmentally regulated patterns of expression (Thmpson and Knox, 1998). The ability of the protoplast to form somatic embryos was found to decrease when AGPs bound to the cell wall were removed, whereas, addition of isolated extracellular AGPs reversed the effect of removal of AGPs from the cell wall partially (Van Hengel et al., 2001). Perturbation of AGPs have resulted in the alteration of somatic embryogenesis. For example, the addition of Yariv reagent blocks somatic embryogenesis in Daucus carota and Cichorium hybrid 474 by binding AGPs to the culture media (Thompson and Knox, 1998; Chapman et al., 2000). AGPs show a similar inhibitory effect on somatic embryo formation upon precipitating with an anti-AGP antibody (Butowt et al., 1999). Several immunocytochemistry experiments with AGPs isolated by using different monoclonal antibodies revealed that cells of embryonic suspension cultures of carrot showed a distinct temporal and spatial expression pattern of an AGP epitope detectable with the antibody JIM4 (Stacey et al., 1990), while JIM8-AGPs showed inhibition on the frequency of embryo development from single cells (Toonen et al., 1997). JIM4 reactive epitopes of AGPs have been reported from the embryonic cells of Daucus carota and Zea mays (Kreuger and van Holst, 1996; Samaj et al., 1999) whereas, JIM8 reactive epitopes of AGPs have been reported from a subpopulation of Daucus carota cells with a specific nursing function during somatic embryogenesis where isolated JIM8-negative cells developed into positive cells upon supplementation with media conditioned by JIM8-positive cells. This indicates that an active compound is released from JIM8-positive cells into the medium (McCabe et al., 1997). Isolated AGPs from the seeds of Daucus carota using their binding to the antibodies ZUM15 and ZUM18 showed that the ZUM15 reactive AGPs are inhibitory for somatic embryogenesis, while the ZUM18 reactive AGPs increases the percentage of embryonic cells. The frequency of somatic embryos in Cyclamen also enhanced upon treatment with ZUM18 reactive AGPs from Daucus carota (Kreuger and Van Holst, 1995).

Non-specific Lipid Transfer Proteins

Non-specific Lipid Transfer Proteins (LTPs) are secreted extracellularly are a class of small proteins (7-13kDa) that lack tryptophan and are secreted extracellularly (Stark et al., 1991). These proteins are characterized by their ability to transfer phospholipids from their place of synthesis in the endoplasmic

reticulum to various cellular locations (Kader, 1996). LTPs are ABA inducible and are found to be involved in plant defense, preventing water loss during stress and play an important role in the transport of signalling molecules through the apoplast and symplast (Stark et al., 1991; Smertenko and Bozhkov, 2014).The presence of five acidic LTP-like proteins found in the cell walls and conditioned media of microcluster cells derieved from embryonic suspension cultures of Draba glomerate helped distinguish between embryonic cells and non-embryonic cells (Tchorbadjieva et al., 2005). The expression of LTPs was observed to be present not only in embryogenic cell cultures but also in developing flowers, maturing seeds and in the shoot apex of seedlings .Expression of LTP gene product was reported to be exclusively associated with the first differentiated tissue of somatic embryo i.e., protoderm and is restricted to peripheral layer of young tissues and developing embryos (Stark et al., 1991; Sossountzov et al., 1991; Thoma et al., 1994). Overexpression of grapevine LTPs under the control of the 35S promoter, however, affects the establishment of bilateral symmetry of the embryos and disturbs epidermal cell layer morphology (Francois et al., 2008). EP2 was the first gene encoding an LTP to be isolated from carrot embryonic culture (Stark et al., 1991). This gene is expressed uniformly in PEMs, but diminishes its expression in non-embryonic cell lines (Chugh and Khurana, 2002). LTP genes were found to be necessary for the induction of normal somatic embryogenesis in Camellia leaf culture (Pedroso and Pais, 1995). The expression of LTP levels in Cotton was found to be highest in embryonic cells and pre-globular embryos, through transitional PEMs with higher expression but this expression declines during post-globular stages (Zeng et al., 2006).

Heat shock proteins

Heat shock proteins (HSPs) are a class of proteins that are produced in response to stress and are present in every cell of an individual organism (Li and Srivastava, 2003).During somatic embryo development many HSPs are known to be synthesized and accumulated in response to exposure of hormones such as 2, 4-D (Egertsdotter et al., 1995, Coca et al., 1994.). The HSPs are stage specific and were first reported in carrot embryogenic cultures (Kanabus et al., 1984.). The globular embryo exhibits lesser synthesis and accumulation of low molecular weight hsp mRNA than other developmental stages or undifferentiated callus culture (Zimmerman et al 1989). In yet other studies, two cDNAs (Mshsp 18-1 and 2) that were involved in the synthesis of small HSPs were isolated from Alfalfa suspension cultures. These small HSPs belonged to HSP17 family (Chugh et al., 2002, Gyorgyey et al., 1991). In the development of plant cells HSPs must play a decisive role (Chugh et al., 2002, Gyorgyey et al., 1991).

Lectins

Lectins are a class of carbohydrate-binding proteins that are found in microbes, plants and also animals (Sharon et al., 1998). Lectins were recorded to show differential expressions during various stages of somatic embryo development in Alfalfa. This indicates their involvement in plant embryogenesis although not enough studies have been conducted so far and knowledge about lectins is limited.

Late embryogenesis abundant proteins

Late embryogenesis abundant proteins (LEA) are a class of proteins which are expressed in abundance in the later stages of embryonic development. These proteins are accumulated and are capable of surviving the period of desiccation in the developing embryo. The LEA genes are regulated by exogenous ABA treatment and show high levels of sequence homology among them. LEA genes were first identified in carrot somatic embryo. These genes are viz. Dc 3, Dc ECP31, Dc 8, Dc ECP40, Dc EMB1 (Hatzopoulos et al., 1990). Due to their temporal and spatial expression pattern during various stages of somatic embryogenesis, these genes are used to distinguish between direct and indirect somatic embryogenesis (Corre et al., 1996). During the transition from globular to torpedo stage embryo, EMB1 cDNA from carrot was expressed and accumulated specifically in the meristematic regions (Wurtele et al., 1993). The expression of Dc 8 gene was also found but it was reported that it was dependent on somatic embryogenesis (Cheng et al., 1996).

Citrins

Citrins are citrus seed storage proteins that show differential expression during embryogenesis. Transcripts of citrin coding genes were found to accumulate during the later stages of somatic embryogenesis (Koltunow et al., 1996).

Germins and Germin-like proteins (GLPs)

Germin and Germin-like proteins are one of the most abundant groups of extracellular proteins distributed widely in the plant Kingdom. Although, functionally diverse, structurally, these proteins are related to the members of the cupin superfamily. The naming of these proteins was done on the basis of their conserved β-barrel mature cupin domain (Dunwell et al., 2001; Rajavel et al., 2008; Dunwell et al., 2008). They were

named germin following their initial identification as germination-specific markers in wheat (Thompson and Lane, 1980; Grzelezak and Lane, 1984). GLPs have been found to play a significant role in somatic and zygotic embryogenesis (Domon et al., 1995, Neutelings et al., 1998, Patnaik and Khurana, 2001).Cell wall bound GLPs were found to be present in the pre-globular somatic embryos but were found absent in non-embryonic callus of Pinus carribea. The identification of the first GLP in somatic embryogenesis was achieved comparing profiles of extracellular proteins of non-embryonic and embryonic cell lines in Pinus caribea (Domon et al., 1995). In later studies, its cDNA PcGERI was isolated and its expression was analysed to confirm the embryonic specificity of this GLP (Neutelengs et al., 1998) and its relation to the cell cycle (Mathew et al., 2003; Lane, 2002). The isolation of a similar GLP cDNA from Pinus radiata showed high mRNA transcription levels in embryogenic tissues and little no expression in non-embryogenic tissue (Bishop - Harley et al., 2003). In several other studies, the upregulation of transcription of GLP encoding genes was also demonstrated in embryonic lines of Caribbean pine and white lupin (Neutelings et al., 1998, Wojtaszek et al., 1998, Caliskan et al., 2004). It was suggested that during somatic embryogenesis GLPs are probably involved in initiation and termination of cell wall expansion (Chugh et al., 2002). It was also proposed that the GLP expressing gene of hybrid larch namely LmGER1 plays an important role in somatic embryo formation by regulating remodeling of cell wall necessary for correct development (Mathew et al., 2006). In order to quantitatively assess the expression levels of proteins in the four stages of embryo development, proteomic methods were employed (Lippert et al., 2005) which showed a significant change in GLP abundance as early as day 7 of embryo development. Several germin and GLP genes such as AtGER2 in Arabidopsis(Neutelings et al.,1998), pseudogermin in wheat (Lane et al.,1993.) and GP111, GP103 and GP94 in Pine (Domon et al.,2000.) were reported in plant embryogenesis but their specific function in embryo development are unknown. Germins and GLPs are characterized as glycoproteins with oxalate oxidase activity (Lane et al., 1993; Lane, 2000; Schweizer et al., 1999) and are often retained in the extracellular matrix by ionic bonds (Faye and Chrispeels, 1988, Jaikaran et al., 1990). Further investigations reveal the wide role that germins and GLPs play as enzymes, structural proteins and receptors during somatic embryogenesis, salt stress and in response to pathogen attack (Dunwell et al., 2000; Bernier and Berna, 2001; Lane, 2000).

IV. CONCLUSION

Somatic embryogenesis is either directly or indirectly depends on various factors including phytohormones, regulatory proteins, genes, transcription and epigenetic factors.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. Previous studies on molecular regulation of somatic embryogenesis indicated that differential gene expression is required for the synthesis of new mRNAs and proteins during somatic embryogenesis. On the basis of previous studies it has been found that molecular understanding of somatic embryogenesis has been greatly based on experiments with different culture systems, such as carrot (Aleith and Richter, 1991; Dodeman and Ducreux, 1996; Komamine et al., 2005), alfalfa (1990; Domoki et al.., 2006;), Arabidopsis(Jenik et al., 2007; Park and Harada, 2008), and conifers (Mathieu et al., 2006; Cairney and Pullman, 2007).With the advancement of molecular knowledge, it is necessary to investigate the molecular factors which are involved in the process of somatic embryogenesis.

n this review, we highlighted the main factors involved in all steps of the SE, providing a synthesis of our current understanding of gene expression patterns during this unique developmental pathway. SE is a suitable platform to increase our knowledge of the molecular aspects of the transition events involved in transforming plant somatic cells into mature embryos. A lot of progress has been achieved in the molecular genetics of this process over the past years. Several embryogenic-specific markers have been identified such as SERKs, BBM and LECs. In addition, proteome and transcriptome approaches used in recent years for study of SE allowed large-scale identification of genes associated with the development of somatic embryos, increasing the level of complexity of the devel- opmental regulation of this process through an integration of multiple response pathways. Improving our ability to understand the molecular basis of plant SE will not only help to establish and optimize in vitro regeneration pro- tocols for many commercial crop species, but will also ultimately improve our ability to access a major biological conundrum such as the reprogramming o n this review, we highlighted the main factors involved in all steps of the SE, providing a synthesis of our current understanding of gene expression patterns during this unique developmental pathway. SE is a suitable platform to increase our knowledge of the molecular aspects of the transition events involved in transforming plant somatic cells into mature embryos. A lot of progress has been achieved in the molecular genetics of this process over the past years. Several embryogenic-specific markers have been identified such as SERKs, BBM and LECs. In addition, proteome and transcriptome approaches used in recent years for study of SE allowed large-scale identification of genes associated with the development of somatic embryos, increasing the level of complexity of the devel- opmental regulation of this process through an integration of multiple response pathways. Improving our ability to

understand the molecular basis of plant SE will not only help to establish and optimize in vitro regeneration protocols for many commercial crop species, but will also ultimately improve our ability to access a major biological conundrum such as the reprogramming o

REFERENCES

[1]. Aleith, F., and Richter, G. 1991. Gene expression during induction of somaticembryogenesis in carrot cell suspensions. Planta 183: 17–24

[2]. Aquea, F., and Arce-Johnson, P. 2008. Identification of genes expressed during early somatic embryogenesis in Pinus radiata. Plant Physiol. Biochem. 46: 559–568.

[3]. Bernier, P.W. and Berna, A., 2001. Germin and germin like proteins: plant-do-all proteins, but what do they do exactly? Plant Physiol Biochem. 39:545-554.

[4]. Bishop-Harley, S.L., Gardner, R.C., and Walter, C. 2003. Isolation and molecular characterization of genes expressed during somatic embryo development in Pinus radiata. Plant Cell Tissue Org. Cult. 74: 267-280.

[5]. Boyer, C., Hilbert, J.L. andVassseur, J., Plant Sci.,1993, 93, 41-53.

[6]. Butowt R., Niklas A., Rodrigues-Garcia M.I. & Majewskasawka A. 1999 Involvement of JIM13 and JIM8responsive carbohydrate epitopes in early stages of cell wall formation. J.Plant.Res.112,107-116

[7]. Cairey, J., Zheng, L., Cowels, A., Hsiao, J., Zismann, V., Liu, J., Ouyang,S., Thibaud-Nissen, F., Hamilton, J., Childs, K., Pullman, G. S., Zhang, Y.,Oh, T., and Buell, C. R. 2006. Expressed sequence tags from loblolly pine embryos reveal similarities with angiosperm embryogenesis. Plant Mol. Biol.62: 485-501

[8]. Çaliskan M, Turet M, Cuming AC. Formation of wheat (Triticum aestivum L.) embryogenic callus involves peroxide- generating germin-likeoxalate oxidase. Planta 2004; 219:132-40.

[9]. Chapman, A., Blervacq, A. S., Vasseur, J., and Hilbert, J. L. 2000. Arabinogalactan-proteins in Cichorium somatic embryogenesis: effect of ßglucosyl Yariv reagent and epitope localisation during embryo development. Planta 211: 305–314.

[10]. Cheng JC, Seeley KA, Goupil P, Sung ZR. Expression of DC8 is associated with, but not dependent on embryogenesis. Plant Mol Biol., 1996, 31, 127-141.

[11]. Chugh A, Khurana P. Gene expression during somatic embryogenesis–Recent advances. Curr Sci 2002; 86:715-30.

[12]. Coca MA, Almoguera C, Jordano J. Expression of sunflower low embryogenesis. Plant Molecular Biology, 22:367-377, 1993.

[13]. Coca MA, Almoguera C, Jordano J. Expression of sunflower low molecular-weight heat-shock proteins during embryogenesis and persistence after germination: Localization and possible functional implications. Plant Mol Biol 1994; 25:479-92.

[14]. Corre, I., Henry, Y., Rode, A. and Hartmann, C. 1996. Em gene expression during somatic embryogenesis in the monocot Triticum aestivum L. Plant Sci. 117, 139-149.

[15]. De Jong,A.J., Cordewener.J., Lo Schiavo, F.,Terzi.M.J., Van Kanmen.A., De Vries.S.C.(1992). A carrot somatic embryo mutant is rescued by chitinase. Plant Cell.4: 425-433.

[16]. Deng W, Luo KM, Li ZG, Yang YW. A novel method for induction of plant regeneration via somatic embryogenesis. Plant Sci 2009;177:43-8

[17]. Dodeman VL, Ducreux G, Kreis M. Zygotic embryogenesis versus somatic embryogenesis. J Exp Bot 1997; 48:1493-509.

[18]. Dodeman, V. L., and Ducreux, G. 1996. Total protein pattern expression during induction and development of carrot somatic embryos. Plant Sci. 120: 57–69.

[19]. Dodeman, V. L., Ducreux, G., and Kreis, M. 1997. Zygotic embryogenesis versus somatic embryogenesis, J. Exp. Bot. 48: 1493–1509

[20]. Domoki, M., Gyorgyey, J., and Biro, J. 2006. Identification and characterization of genes associated with the induction of embryogenic competence in leaf protoplast-derived alfalfa cells. Biochim. Biophys. Acta. 1759: 543-551.

[21]. Domon, J. M., Neutelings, G., Roger, D., David, A., and David, H. 2000. A basic chitinase-like protein secreted by embryogenic tissues of Pinus caribaea acts on arabinogalactan proteins extracted from the same cell line. J. PlantPhysiol. 156: 33–39.

[22]. Domon, J. M., Neutelings, G., Roger, D., David, A., and David, H. 1995. Three glycosylated polypeptides secreted by several embryogenic cell cultures of show highly specific serological affinity to antibodies directed against the wheat germin apoprotein monomer. Plant Physiol. 108: 141–148.

[23]. Dong JZ, Dunstan DI. 1997. Endochitinase and beta-1,3-glucanase genes are developmentally regulated during somatic embryogenesis in Picea glauca. Planta 201, 189-194.

[24]. Dunwell, J.,Khuri, S., And Gane, P. 2000. Microbial relatives of the seed storage proteins of higher plants: Conservation of structure and diversification of function during evolution of the cupin super-family. Microbial. Mol. Biol. 12: 475-486.

[25]. Dunwell, J.M.,Culham, A., Carter, C.E., Sosa-Aguirre, C.R., and Goodenough, P.W.2001. Evolution of functional diversity in the cupin superfamily. Trends biochem. Sci 26: 740-746.

[26]. Dunwell, J.M., Gibblings, J.G., Mahmood, T., and Naqvi, S.M.S.2008. germin and germin like proteins: evolution, structure and function. Crit.Rev. Plant Sci. 27:342-375.

[27]. Dyachok J.V., Tobin A.E., Price N.P.J. & Von Arnold S. 2000 Rhizobial Nod factors stimulate somatic embryo development in Piceaabies. Plant Cell Rep. 19, 290-297.

[28]. Dyachok J.V., Wiweger M., Kenne L. & Von Arnold S. 2002 Endogenous Nod-factor-like signal molecules promoteearly somatic embryo development in Norway spruce. PlantPhysiol. 128, 523-533.

[29]. Egertsdotter U, von Arnold S. Importance of arabinogalactan proteins for development of somatic embryos of Norway spruce (Picea abies). Physiol Plant 1995; 93:334-45. 38.

[30]. Faye, L., and Chrispeels, M. J. 1988. Common antigen determinants in the glycoproteins of plants, molluscs and insects. Glycoconjugate J. 5: 245–256.

[31]. Filonova LH, Bozhkov PV, von Arnold S. Developmental pathway of somatic embryogenesis in Picea abies as revealed by time-lapse tracking. J Exp Bot 2000; 51:249-64.

[32]. Gavish, H., Vardi, A., and Fluhr, R. 1992. Suppression of somatic embryogenesis in Citrus cell cultures by extracellular proteins. Planta 186: 511–517.

[33]. Grzelczak.,Z. F., and Lane, B.G. 1984. Signal resistance of a soluble protein to enzymic proteolysis. An unorthodox approach to the isolation and purification of germin, a rare growth-related protein. Can J. Biochem. Cell Biol, 62: 1351-1353.

[34]. Györgyey J, Gartner A, Németh K, Magyar Z, Hirt H, Heberle-Bors E, et al. Alfalfa heat shock genes are differentially expressed during somatic embryogenesis. Plant Mol Biol 1991; 16:999-1007.

[35]. Hatzopoulos P, Fong F, Sung ZR. Abscisic acid regulation of DC8, a carrot embryonic gene. Plant Physiol 1990; 94:690-5.

[36]. Helleboid S, Bauw G, Belingheri L, Vasseur J, Hilbert JL. Extracellular β-1, 3-glucanases are induced during early somatic embryogenesis in Cichorium. Planta 205, 56-63.
[37]. Hilbert,J. L., Dubois, T. and Vasseur, J., Plant Physiol. Biochem., 1992, 30, 733-741.
[38]. Jaikaran, A. S. I., Kennedy, T. D., Dratewka-Kos, E., and Lane, B. G. 1990. Covalently bonded and adventitious glycans in germin. J. Biol. Chem. 265:12503–12512.
[39]. Jenik P. D., Gilmor, C. S., and Lukowitz, W. 2007. Embryonic patterning in Arabidopsis thaliana. Annu. Rev Cell Dev. Biol. 23: 207–236.
[40]. Kammen, A., and De Vries, S. C. 1994. Description of somatic-embryo forming single cells in carrot suspension cultures employing video cell tracking. Planta 194: 565–572.
[41]. Kanabus J, Pikaard CS, Cherry JH. Heat shock proteins in tobacco cell suspension during growth cycle. Plant Physiol 1984; 75:639-44.
[42]. Kragh KM, Hendriks T, De Jong AJ, Lo Shiavo F, Bucherna N, Hojrup P,Mikkelsen JD,de Vries SC.1996. characterization of chitinases able to rescue somatic embryo of the temperature-sensitive carrot variant ts11. Plant molecular biology 31, 631-645.
[43]. Kreuger M, van Holst GJ. Arabinogalactan proteins are essential in somatic embryogenesis of Daucus carota L.Planta 1993; 189:243-8.
[44]. Koltunow AM, Hidaka T, Robinson SP. Polyembryony in citrus. Accumulation of seed storage proteins in seeds and in embryos cultured in vitro. Plant Physiol 1996; 110:599-609.
[45]. Komamine, A., Kawahara, R., Matsumoto, M., Sunabori, S., Toya, T., Fujiwara,A., Tsukuhara, M., Smith, J., Ito, M., Fukuda, H., Nomura, K., and Fujimura, T. 1992. Mechanisms of somatic embryogenesis in cell cultures: physiology, biochemistry, and molecular biology. In Vitro Cell Dev. Biol. Plant 28:6-14.
[46]. Komamine, A., Murata, N., and Nomura, K. 2005. Mechanisms of somatic embryogenesis in carrot suspension cultures - morphology, physiology, biochemistry and molecular biology. In Vitro Cell Dev. Biol. Plant41:6-14.
[47]. Lane BG, Dunwell JM, Ray JA, Schmitt MR, Cuming AC. Germin, a protein marker of early plant development, is an oxalate oxidase. J Biol Chem 1993; 268:12239-42.
[48]. Lane, B. G. 2000. Oxalate oxidases and differentiating surface structure in wheat: germins. Biochem. J. 349: 309–321.
[49]. Lane, B. G. 2002. Oxalate, germins, and higher plant-pathogens. IUBMB Life 53: 67–75.
[50]. Lane, B. G., Dunwell, J. M., Ray, J. A., Schmitt, M. R., and Cuming, A. C. 1993.Germin, a protein marker of early plant development, is an oxalate oxidase.J. Biol. Chem. 268: 12239–12242.
[51]. Legrand S, Hendriks T, Hilbert JL, Quillet MC. Characterization of expressed sequence tags obtained by SSH during somatic embryogenesis in Cichorium intybus L. BMC Plant Biol 2007;7:27.
[52]. Letarte J, Simion E, Miner M, Kasha KJ. Arabinogalactans and arabinogalactan-proteins induce embryogenesis in wheat (Triticum aestivum L.) microspore culture. Plant Cell Rep 2006; 24:691-8.
[53]. Lippert, D., Zhuang, J., Ralph, S., Ellis, D. E., Gilbert, M., Olafson, R., Ritland,K., Ellis, B., Douglas, C. J., and Bohlmann, J. 2005. Proteome analysis ofearly somatic embryogenesis in Picea glauca. Proteomics 5: 461–473l.
[54]. Li, Z. and Srivastava, P. (2003), Heat Shock Proteins. Current Protocols in Immunology, 58: A.1T.1-A.1T.6. doi:10.1002/0471142735.ima01ts58.
[55]. Majewska-Sawka A & Nothnagel EA 2000. The multiple roles of arabinogalactan proteins in plant development. Plant Physiol.122: 3-9.
[56]. Mathieu, M., Neutelings, G., Hawkins, S., Grenier, E., and David, H. 2003. Cloning of a pine germin- like proteins (GLP) gene promoter and analysis of its activity in transgenic tobacco Bright Yellow 2 cells. Physiol. Plant. 117:425-434.
[57]. Mathieu, M., Lelu-Walter, M. A., Blervacq, A. S., David, H., Hawkins, S.,and Neutelings, G. 2006. Germin-like genes are expressed during somatic embryogenesis and early development of conifers. Plant Mol. Biol. 61: 615–627.
[58]. Malinowski, R., and Filipecki, M. 2002. The role of cell wall in plant embryogenesis. Cell Mol.Biol. Lett.7: 1137–1151.
[59]. Neutelings G, Domon JM, Membre N, Bernier F, Meyer Y, David A, et al. Characterization of a germin-like protein gene expressed insomatic and zygotic embryos of pine (Pinus caribaea Morelet). PlantMol Biol 1998; 38:1179-90.
[60]. Norhnagel, E.A., Int. Rev. Cytol., 1997, 174, 195-291.
[61]. Park, S., and Harada, J. J. 2008. Arabidopsis embryogenesis. Methods in Mol.Biol. 427: 3-16.
[62]. Patnaik, D.and Khurana,p., Indian J. Exp. Biol., 2001, 39, 191-200.
[63]. Pedrosa M.C and Pais M.S., Plant Cell Tissue Org. Cult., 1995, 43, 147-154.
[64]. Rajavel , M., Kulkarni, N.N., and Gopal, B. 2008. Conformational studies suggest that the double stranded beta helix scaffold provides an optimal balance between protein stability and function. Protein peptide let. 15: 244-249.
[65]. Reinert,J., planta 1959, 53, 318-333.
[66]. Rensing, S. A., Lang, D., Schumann, E., Reski, R., and Hohe, A. 2005. EST sequencing from embryogenic Cyclamen persicum cell cultures identifies a high proportion of transcripts homologous to plant genes involved in somaticembryogenesis. J. Plant Growth Regul. 24: 102–115
[67]. Rocha DI, Dornelas MC. Molecular overview on plant somatic embryogenesis. CAB Rev 2013; 8:1-17. Available from: http://www.cabi.org/cabreviews. [Last accessed on 2013 Feb].
[68]. Saare-Surminskia K, Preilb W, Knoxc JP, Liebereia R. Arabinogalactan proteins in embryogenic and non-embryogenic callus cultures of Euphorbia pulcherrima. Physiol Plant 2000; 108:180-7.
[69]. Samaj J, Baluska F, Bobak M & Volkmann D 1999. Extracellular matrix surface network of embryogenic units of friable maize callus contains arabinogalactan-proteins recognized by monoclonal antibody JIM4. Plant Cell Rep. 18: 369-374.
[70]. Schweizer, P., Christoffel, A., and Dudler, R. 1999. Transient expression of members of the germin-like gene family in epidermal cells of wheat confers disease. Plant J. 20: 541–552.
[71]. Sharon, N. and Goldstein, I.J., Science, 1998, 282, 1049.
[72]. Smertenko A, Bozhkov PV. Somatic embryogenesis: Life and death processes during apical–basal patterning. J Exp Bot 2014;12:1-18
[73]. Sossoutzov, L et al., Plant Cell 1991, 3, 923-933.
[74]. Stacey N, Roberts K, Knox JP. Patterns of expression of the JIM4 arabinogalactan-protein epitope in cell cultures and during somatic embryogenesis in Daucus carota L. Planta 1990; 180:285-92.
[75]. Sterk P, Booij H, Schellekens G, Van Kammen A, De Vries S. Cellspecific Expression of the carrot EP2 lipid transfer protein gene. Plant Cell 1991; 3:907-21.
[76]. Steward, F.C., Mapes,M.O. and Mears,K. Am.J.Bot., 1958, 45, 705-708.
[77]. Tchorbadjieva, M., Kalmukova, R., Pantchev, I., and Kyurkchiev, S. 2005. Monoclonal antibody against a cell wall marker protein for embryogenic potential of Dactylis glomerata L. suspension cultures. Planta 222: 811–819.

[78]. Thibaud-Nissen, F., Shealy, R. T., Khanna, A., and Vodkin, L. O. 2003. Clustering of microarray data reveals transcript patterns associated with somatic embryogenesis in soybean. Plant Physiol. 132: 118–136.
[79]. Thoma, S., Hecht, U., Kippers, A., Boletla, J., de Vries, S. C. and Somerville, C., Plant Physiol., 1994, 105, 35-45.
[80]. Thompson HJM & Knox JP 1998. Stage specific responses of embryogenic carrot cell suspension cultures to arabinogalactan protein-binding β-glucosyl Yariv reagent. Planta 205: 32-38.
[81]. Thompson, E.W. and Lane, B.G. 1998. Relation of protein synthesis in imbibing wheat embryos to the cell- free translational capacities of bulk mRNA from dry and imbibing embryos. J. Biol. Chem.255: 5965-5970.
[82]. Toonen, M. A. J., Verhees, J. A., Schmidt, E. D. L., van Kammen, A., and de Vries, S. C. 1997. AtLTP1 luciferase expression during carrot somatic embryogenesis. Plant J. 12: 1213–1221.
[83]. Van Engelen, F.A and de Vries,S.C., trends Genet., 1992, 8. 66-70.
[84]. Van Engelen et al., Plant, Mol, Biol., 1995, 27, 901-910.
[85]. Van Hengel, A. J., Tadesse, Z., Immerzeel, P., Schols, H., van Kammen, A., and De Vries, S. C. 2001. N-acetylglucosamine and glucosamine-containing arabinogalactan proteins control somatic embryogenesis. Plant Physiol. 125: 1880–1890.
[86]. Von Arnold S., Egertsdotter U., Mo L.H. (1995) Importance of Extracellular Proteins for Somatic Embryogenesis in Picea abies. In: Terzi M., Cella R., Falavigna A. (eds) Current Issues in Plant Molecular and Cellular Biology. Current Plant Science and Biotechnology in Agriculture, vol 22. Springer, Dordrecht
[87]. Williates, W. G. T. and Knox, J. P., Plant. J., 1996, 9, 919-925.
[88]. Wojtaszek P, Pislewska M, Bolwell GP, Stobiecki M. Secretion of stress-related proteins by suspension-cultured Lupinus albus cells. Acta Biochim Pol 1998; 45:281-5.
[89]. Wurtele ES, Wang H, Durgerian S, Nikolau BJ, Ulrich TJ.Characterization of a gene expressed early in somatic embryogenesis of Daucus carota. Plant Physiol 1993; 102:303-12.
[90]. Xiyan Yang &Xianlong Zhang (2010) Regulation of Somatic Embryogenesis in Higher Plants, Critical Reviews in Plant Sciences, 29:1, 36-57, DOI: 10.1080/07352680903436291
[91]. Zhang CX, Li Q, Kong L. Induction, development and maturation of somatic embryos in Bunge's pine (Pinus bungeanaZucc. ex Endl.). Plant Cell Tissue Organ Cult 2007; 91:273-80.
[92]. Zeng F, Zhang X, Zhu L, Tu L, Guo X, Nie Y, et al. Isolation and characterization of genes associated to cotton somatic embryogenesis by suppression subtractive hybridization and macroarray. Plant Mol Biol2006; 60:167-83.
[93]. Zeng F, Zhang X, Jin S, Cheng L, Liang S, Hu L, et al. Chromatin reorganization anendogenous auxin/cytokinin dynamic activity during somatic embryogenesis of cultured cotton cell. Plant Cell Tissue Organ Cult2007; 90:63-70.

Rajashree Bordoloi " Expression of Extracellular Proteins in Somatic Embryogenesis of Plants" International Journal of Pharmaceutical Science Invention(IJPSI), vol. 08, no. 01, 2019, pp. 01-07