Genetic Control and Phytohormonal Regulation of Plant Embryogenesis

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Abstract

The review is devoted to genetic mechanisms of regulation of plant embryonic development. Numerous families of genes identified to date that control this phase of plant ontogenesis are presented in detail; their key role in the formation and development of plant seed is described. Data concerning important role of different classes of phytohormones such as auxins, cytokinins, gibberellic acid, brassinosteroids, abscisic acid, ethylene and jasmonic acid in the regulation of plant growth and development during embryogenesis are presented.

Keywords: Plant Seed; Plant Embryonic Genes; Differentiation and Specialization of Embryonic Cells; Seed Growth and Development; Plant Hormones; Auxins; Cytokinins; Gibberellic Acid; Brassinosteroids; Abscisic Acid; Ethylene; Jasmonic Acid; Developmental and Phytohormonal Regulation of Plant Embryonic Genes.

Introduction

It is known that in the early stages of seed embryogenesis dual pollination is followed by formation of diploid embryo and triploid endosperm (i.e. angiosperm or gymnosperm) [1,2]. In Arabidopsis and many mono- and dicotyledonous plants, the development of a seed occurs through the initial phase of active proliferation, during which elongation of endosperm and integument of seed occurs. This phase is followed by the mitotic division of endosperm cells with subsequent formation of multi-nucleated cells with highly specialized functions. As a result the mature embryo, which is much greater by its size than endosperm, is formed [1,3]. A thin layer of integument is formed around the embryo and endosperm through differentiation of ovule in the nucellus and aleurone cells in the endosperm [4]. Thus, at the early stages of embryogenesis the seed size is regulated coordinately by development of triploid endosperm, maternal diploid ovule and diploid embryo. Many studies were devoted to identifying of key genes differentially expressing during plant embryogenesis [1,5,6]. The data presented in this review testify about existing clearly coordinated genetic program of plant embryonic development, in the regulation of which natural growth regulators - phytohormones play an important part.

Genes Controlling Flowering, Formation of Seed and Embryonic Development of Plants

Genes controlling flower development

It is found that MADS-box transcription factors encoded by floral homeotic genes play leading role in the control of plant flowering and formation of seed and fruit. MADS-box gene family of Arabidopsis plants is divided into five functional classes, to the first class belongs AG (AGAMOUS) gene that controls homeotic transformation of floral organs [1,7-9]. Detailed studies carried out in the yeast two-hybrid system have shown that proteins of the MADS-box family regulate expression of embryonic genes through formation of specific heterodimeric and monodimeric AGL61 (DIANA)/FEM111/AGL80 (AGAMOUS-LIKE80) and AGL62/AGL80 complexes in the central cells of the endosperm with gradual formation of differentiated cells [9-12]. Phenotype of fem111 and agl61 mutant plants is similar to fem111/agl80 mutants, in which the premature degradation of the central cell occurs before the pollination period, while nucleus in the central cells of agl62 mutant plants is reduced and these cells prematurely enter into mitotic phase. As a result seed structure is completely destroyed [1,10].

The leading role of AP1, AP2 и AP3 (APETALA 1, 2 and 3) genes in the regulation of flower, embryo and endosperm de-
development has been confirmed [1,7-9,13]. It is found that the MADS-domain protein AP1 (which is highly homologous to the CAULIFLOWER protein) controls specialization of floral meristem and initiation of perianth [8,14]. Now over 2,000 genes responsible for initiation of meristem of floral organs at early stages were identified. It is shown that expression of these genes is activated or repressed by trans-factor protein AP1 in the later stages of development. Some genes, identified among repressed target genes such as FD gene (which belongs to bZIP trans-factor family), SQUAMOSA PROMOTER BINDING PROTEIN-LIKE 9 gene, SOC1 (SUPPRESSOR OF OVEREXPRESSION OF CONSTANS 1) and AGL24 (AGAMOUS-LIKE 24) floral integrator genes, can activate in turn expression of AP1 gene [8]. Gene family activated by AP1 includes: LFY (LEAFY) gene participating in the control of specification and initiation of floral organs, SEP3 (SEPALALLATA3) gene which encodes a MADS-box protein that belongs to the family of DNA-binding transcription factors, PI (PISTILLATA) gene as well as SVP (SHORT VEGETATIVE PHASE) gene [1,8,9,12,13,15]. It is found that the LFY (LEAFY) trans-factor controls the differentiation of inflorescence meristem to floral meristem in different ways. One way occurs through the direct activation of AP1 expression by LFY trans-factor. Other ways occur indirectly through the activation of expression of several genes, namely, UFO (UNUSUAL FLORAL ORGANS1) gene, which encodes the F-box protein - member of SCAF complex, AP3 and PI (PISTILLATA) genes, or through the direct interaction of trans-factor LFY with promoter elements of AG gene [12,13,16]. Transcription factor WUS (WUSCHEL) belonging to homeobox transcription factor family acts as cofactor of this process, its high level expression is observed in the central meristem [8,13,17].

AP2 trans-factor (that has a DNA-binding domain consisting of 68 amino acids) activates expression of WUS (WUSCHEL) gene and is responsible for the specialization of sepals and petals and differentiation of the stem cells [1,7,8]. Now more than 2000 AP2-binding sites of genes whose expression is repressed in the transition from vegetative to flowering stage either directly by AP2 trans-factor, or indirectly through activation of other repressor genes with participation of miRNAs, were identified [8]. These include, for example, floral homeotic AG (AGAMOUS) gene, which repression by AP2 trans-factor occurs in young meristem of petals and sepals [18]. It is found that PKI (PICKIE), ULTRAPETALAIA 1, PAN (PERIANTHIALA), WUS and LFY trans-factors on the contrary activate the expression of AG gene [8,19]. It should be noted that expression of floral homeotic AG (AGAMOUS) gene is repressed by PRC1-like groups and PRC2-like groups of PeG (Polycomb) protein complexes during flower, embryo and endosperm development. Proteins of PRC1-like groups of PeG protein complexes are encoded by LHP1 (HETEROCROMATIN PROTEIN 1) and EMF1 (EMBRYONIC FLOWER 1) genes, while proteins of PRC2-like groups of PeG protein complexes (which participate in the trimethylation of histone H3 at lysine 27 residue of the AG locus) are encoded by CLF (CURLY LEAF), FIE (FERTILIZATION INDEPENDENT ENDOSPERM), FIS2 (FERTILIZATION INDEPENDENT SEED2), EMF2 (EMBRYONIC FLOWER 2) and MSH1 (MULTICOPY SUPPRESSOR OF IRA1) genes [20,21].

Genes controlling endosperm, embryo and cotyledon development

It is found that AP2 trans-factor plays key role in controlling of endosperm and embryo size [1,7,8]. Seed size of ap2 mutant plants is increased significantly as a result of the manifold extension of the central vacuole of the epidermis cells of the endosperm and the integument, and as a result of growing size and number of embryo cells [1]. At the same time synthesis and accumulation of unsaturated fatty acids and proteins are increased in seeds of ap2 mutant plants; in these seeds the redistribution of carbohydrates leading to increased content of hexose and reduced sucrose content occurs as a result of their over-consumption by enlarged seeds [7]. The MINI3 gene, which belongs to the WRKY trans-factor family, plays an important role in the regulation of endosperm development [22]. Expression of the MINI3 gene is observed only after fertilization and does not occur in the unfertilized ovule. It is shown that cells’ mitosis at mini3 mutant plants begins prematurely without a preliminary extension phase; the period of embryo development is reduced, resulting in formation of seeds with reduced size [4].

Leucine-rich repeat (LRR) kinases encoded by HAUKU2 (IKU2) and EXS/EMS1 (EXTRA SPOROGENOUS CELLS/EXCESS MICROSPOROCYTES1) genes play a major role in the control of proliferation phase and mitotic cycle of the endosperm. The main function of these genes is regulation of the endosperm size and seed weight [1,23]. Phenotype haiku (iku) mutant plants is similar to mini3 mutant plants with decreased expression of IKU2 gene [4,22]. Arabidopsis exs mutant plants have a greater number of sporogenous cells in stamens. In wild type plants the high level expression of EXS gene is observed in globular embryos and endosperm at the early stages of embryogenesis. At the same time expression of EXS gene is increased in meristematic active cells of young shoots and roots at the later stages. It is found that seeds of exs mutant plants are reduced in size; moreover the development of endosperm and embryo is inhibited in these plants [1].

It is found that the SHB1 (SHORT HYPOCOTYL UNDER BLUE) gene together with IKU2 and MINI3 genes belonging to WRKY family of transcription factors, are involved in regulating the development of endosperm and embryo. Function of the SHB1 gene was originally studied in shb1-D mutant plants with increased expression of the SHB1 gene. Phenotype of these mutant plants is characterised by long hypocotyls in the conditions of red, near-red and blue light [24]. Embryo development of shb1-D mutant plants begins earlier - at the 4th day after pollination, embryo and seed size is greatly increased, while the phase of mitotic cell cycle of endosperm starts later. In contrast, mutant alleles with reduced expression shb1 gene have significantly reduced embryo and seed size [1]. There are also data on the interaction of SHB1, IKU2 and MINI3 genes in common signaling pathways controlling embryogenesis and in the seed germination early stages [1]. Using chromatin immunoprecipitation method it is shown that proteins encoded by SHB1 gene in association with other regulatory proteins comprehensively regulate endosperm development through interaction with promoter regions of MINI3 and IKU2 genes [24].

Key role Dek1 gene in the endosperm growth was investigated. In the seeds of ded (defective kernel) mutant corn plants mitotic activity is decreased and DNA replication process occurs in the absence of cell division, as a result weight of seeds is reduced. Dek1 gene (encoding a membrane protein that is similar to animal calpain) and CRINKLY4 gene (encoding a receptor kinase that is similar to tumor necrosis factor) play major role in concentration of aleurone cells in the outer layer of the epidermis [23,25]. Mutant
for another allele *rgf1* (*reduced grain filling*) plants have irregularities in the transport and localization of aleurone, resulting in a final significant reduction of seed weight by 30% relative to control plants [23,26].

The important role of *LEC1* and *LEC2* (*LEAFY COTYLEDON 1, 2*) genes in the development of seed cotyledons was shown [23,27]. In early period of embryogenesis *LEC* gene family controls specialization and formation of cotyledon tissues, whereas in later period these genes control seed maturation and prevent premature seed germination. The premature synthesis of storage proteins 1S and 2S and oleosin [28] as well as induction of somatic embryogenesis from vegetative cells were observed in mutant plants with ectopic expression *LEC1, LEC2* and *FUS3* (*FUSCA 3*) genes, that confirms key role of these genes in the control of early period of embryogenesis. It is found that all *LEC* genes encode regulatory proteins. *LEC1* gene encodes HAP3 subunit of CCAAT-binding transcription factor CBF; *LEC2* and *FUS3* genes encode B3 DNA-binding domain proteins which are similar to the domain-containing proteins - transcription factors VP1 (VIVIPAROUS 1) of maize and ABI3 (ABA INSENSITIVE 3) identified in Arabidopsis [23,27,29-31]. The important role of *PID* (PINOID), *ENP* (ENHANCER OF PINOID) and *CUC1/2/3* (CUP-SHAPED COTYLEDON 1/2/3) genes in the cotyledon initiation and development was found [32,33].

The defects in plastid genes that encode stress proteins - chaperones, such as chaperonin Hsp60s, are observed in small-sized cotyledons of *Arabidopsis* plants with another embryolethal *sfp* (*schlepper*) mutations [23,34,35]. Plants with mutation in *bio* allele have premature termination of cotyledon development, which leads to defects in the synthesis of biotin synthetase, whereas plants with *twu2* (*twu2*) mutation have embryos defective in the synthesis of valil-tRNA synthetase [34].

Genes of transcription factors that are homologous to genes of *Arabidopsis* and involved in embryo and endosperm development are also found in *Oryza sativa* seeds [36]. Expression of *FUS3, BBM, RBR1, CH2, HB, HHL1, WRI1, RGE1, KZP, GBE, SBF, AP2/EERE/BP* genes in the embryo is associated with expression of genes that regulate the processes of DNA replication, cell proliferation and cell cycle, whereas expression of these genes in the endosperm is associated with genes that regulate synthesis and storage of nutrients [36].

The major role of *PeG* (Polycomb group) proteins in the epigenetic regulation of endosperm development and inheritance of parental traits in the next generation of *Arabidopsis* plants was revealed. Many genes, which are involved in the regulation of endosperm in female gametophyte in the absence of fertilization, encode these proteins, namely: *FIS2* (*FERTILIZATION INDEPENDENT SEED 2*), *FIE* (*FERTILIZATION INDEPENDENT ENDOSPERM*)/FIS3, *MEA* (*MEDEA*)/FIS1, *MSI1* (*MULTICOPY SUPRESSOR OF IRA*), *SWN* (*SWINGER*), *BGA* (*BORGIA*), *RBR1* (*RETINOBASTOMA RELATED PROTEIN 1*), *PHE1* (*PHRESIS1*) and *FWA* genes [1,11,21,37-39]. *PeG* proteins encoded by these genes control gene expression in seeds through the formation of repressive complexes that carry out methylation histones. As a result of overexpression of these genes in the female gametophyte of mutant plants a rapid increase of the endosperm begins before fertilization process and at the same time, there is no mitotic cell division in endosperm. In these plants as a result of significant infringement of cell proliferation and morphogenesis, the embryo development does not occur after fertilization [1].

The important role of *MEA* gene (encoding the SET (Su(var) 3-9, Enhancer-of-zeste, Trithorax)-domain protein PeG, which is highly homologous to MET1 methyltransferase) in the chromatin repression was found [37]. *FIE* protein with sequences that are specific to WD40 protein family and similar to sequences of EXTRA SEX COMBS proteins in *Drosophila* interacts with *MEA* protein [23,37]. *FIS2* gene encodes zinc-finger transcription factor that interacts with promoters of genes in endosperm. Growth and development of seeds stops in the *fs* mutant plants. MSI1 protein belonging to the WD40 protein family interacts with FIE protein to form a repressive Polycomb complex [23,37]. AGL62 protein mediates action of FIS protein, its expression is significantly reduced during mitosis of endosperm cells [23]. *PHE1* (*PHRESIS1*) gene encodes protein (a member of MADS-box gene family) that is involved in joint functioning with a complex of FIS and MEA proteins [40]. *PHE1* gene plays key role in repression of target genes in complex with Polycomb proteins. Expression of the *PHE1* gene is observed in embryo and endosperm after fertilization and during seed development. It is shown that in the *mea* mutant plants stable level of *PHE1* gene expression prevents of the negative effects of mutations - abortion [1].

*MET1* (*METHYLTRANSFERASE 1*) gene *Arabidopsis* encodes metylase which controls endosperm size and seed weight through DNA methylation at CpG dinucleotides and takes part in the repressor pathways with *MEA* and *FIS2* genes [37]. The reduced expression of this gene leads to DNA hemimethylation of maternal genome; as a result seed size is increased in *met1* mutant plants. In contrast, smaller-sized seeds are formed in case of *met1* mutations in paternal genome. This can be explained by the fact that hemimethylation DNA of paternal genome leads to acceleration of the process of mitotic division of endosperm cells without previous phase of cell elongation. At the same time DNA hemimethylation of maternal genome postpones the phase of mitotic division of endosperm cells and prolongs the phase of elongation of endosperm cell leading to increase of endosperm and seed size [1].

Differentiated activity of protein kinase genes that control mitotic cycle in the embryo and endosperm cells is observed during seed development. Protein kinase SnRK (Sucrose Nonfermenting-1-Related Protein Kinase), regulating the carbohydrate metabolism in the endosperm, plays an important role among them [41]. Different genes that encode other receptor-like protein kinases (RLKs), calcium-dependent and casein-dependent protein kinases regulating the development of endosperm and interacting with a network of transcription factors during seed embryogenesis were identified [2,38].

A key role of *SuSy* gene of sucrose synthetase in control of transport and metabolism of carbohydrates, which are necessary for the development and differentiation of the embryo seed, such as sucrose that is hydrolyzed by *CwBINV* enzyme (cell wall-bounded acid invertases) to hexose, glucose and fructose, was found. Different classes of *CwBINV* enzymes are identified to be located in cell walls of *Arabidopsis, Brassica napus*, and *Vicia faba* plants [34,42]. Functional relationship between *CwBINV* gene, *Mst1* (*Matz miniature1*) gene, which encodes the endosperm-specific invertase, and floral homeotic *AP2* gene [1,23], was revealed in maize plants. Reduced activity of the *CwBINV* gene, resulting in decreased mitotic
Sterols play an important role in the formation of cellular structures of embryo cotyledons. Their biosynthesis is controlled by FKCI/HYD2 (FACKEL/HYDRA2), SMT1/CPH (STEROL METHYL TRANSFERASE1/CEPHALOPOD) and HYDRA1 genes. Mutations of these genes are appear in violation of cells’ division and elongation, in abnormal forms of cotyledons (with reduced central and basal zones) and defects in the in polar transport of auxin with participation of PIN1 and PIN3 proteins in the root cells [13,43].

Now key genes that control the development of the seed embryo were identified using T-DNA insertional and chemical mutagenesis. Multifamily of EMB genes, 1,000 members of which were identified in recent years in Arabidopsis, plays a leading role among them [1,25,44,45]. It is shown that process of initiation and formation of the embryo is disrupted in the emb (embryo-defective) mutant plants. Most of the EMB genes control gametogenesis, but in mutant for these alleles plants have no lethal phenotype of gametophytes, because of the presence of heterozygous for these alleles maternal/maternal gametophytes.

ANT (AINTEGUMENTA) gene similar to AP2 gene plays a leading role in the proliferation of seed embryo of Arabidopsis [1,33,39]. Like AP2 gene expression, ANT gene expression is observed in floral and vegetative organs. Mutant for ant in Arabidopsis plants with reduced expression of AP2 and ANT genes have significant abnormalities in the formation and development of floral organs, manifested in the lack of integument and female gametophyte [1]. In contrast, overexpression of ANT gene leads to irregularly large ovule size of flowers, pods and leaves [1]. Most mutant plant lines that overexpress ANT gene are sterile due to abnormally elongated anther and ovule. Besides that, it is possible to obtain transgenic plant lines with a moderate level of expression in floral and vegetative organs. Mutant for these alleles plants have no lethal phenotype of gametophytes, because of the presence of heterozygous for these alleles maternal/maternal gametophytes.

It is shown that TTN6 (TT456) gene, which encodes isopeptidase T, that belongs to the family of enzymes participating in deubiquitination of polyubiquitinated proteins with subsequent degradation of these proteins in proteasomes, plays major role in the control of embryo in the early stages of embryogenesis. Mutations of this gene lead to lethality of embryos [34]. Important role RGE1 (RETERAD GROWTH OF EMBRYO1) gene in the control of embryo development is found. RGE1 gene belongs to hHIL1 gene family, which encodes helix-loop-helix type proteins - transcription factors [1]. The slow embryo growth, resulting in the formation of dried seeds with reduced size and with developed endosperm, is observed in mutant plants with reduced RGE1 gene expression [1]. Major role of ARP7 gene (encoding actin-like proteins) in controlling dynamics of chromatin and transcription regulation during embryo development was shown [34].

Genes controlling shoot apical meristem and root apical meristem development

The key genes controlling formation, differentiation and growth of shoot apical meristem (SAM) and root apical meristem (RAM) of seed embryos of Arabidopsis, Oryza sativa and soybean plants are identified and characterized. These include numerous homologous genes [2,6,8,13,17,23,25,27,29,33-35,39,46-61]: STM (ROOT MERISTEMLESS), BP (BREPEDIDEL-LUS), LOB (LATERAL ORGAN BOUNDARIES), RML1 (ROOT MERISTEMLESS 1), RHD6 (ROOT HAIR DEFEC-TIVE), TTY (TRANSPARENT TESTA 1 GLABRA1), GL2 (GLABRA2), WER (WERFEL), SGM (SCRAMMED), HBT (HOBBIT), KNOX (Knotted-like homeobox), WUS (WUSCHEL), CLV (CLAVATA), KNAT (Homeobox protein knotted-1 like) and KNAT1, SHI2 (SHOOTLESS2), SHO1,2 (SHOOT ORGANIZATION 1,2), CUC (CUP-SHAPED COTYLEDON), ZLL (ZWILLE), ANT (AINTEGUMENTA), GKR (GURKE), PAS (PASTICCINO), BDL (BODENLOS), AXR6 (AXIN RESISTANT6), GNO (GNO1), EMB (EMBRYO DEFECTIVE330), GKR (GURKE), HAN (HANABABA TANALI), KAN (KANADI), YAB (YABBY), FIL (FILAMENTOUS FLOWER), AMP1 (ALTERED MERISTEM PROGRAM 1), MP (MONOP-TEROS), BBM (BABYBOOM), PHB (PHABULOSA), PHV (PHA0_VOLUTA), REV (REVOLUTA), SYP (SPLAYED), TPL (TOLLSLESS), TPR (TOPLESS-RELATED), PLT (PLETHY-ORA 1-2), FK (FACKEL), ULT1 (ULTRAPETALAL1), WOX2 (WOX2-RELATED HOMEOBOX 2), WOX5, STIMPY-LIKE (STL)/ WOX8, PIO (PINOCCHIO), WOL (WOODEN LEG), WF (WFK2), WRFY (WRFY DNA-BINDING PROTEIN 2), REV (REVOLUTA), PHB (PHABUOSA), PHV (PHA0_VOLUTA), YDA (YODA), YUC1/4/10/11 (YUCCA1/4/10/11), WAG1/2, DRN/ERV (DORNROSCHEL/ENHANCER OF SHOOT REGEN-ERATION), CLF (CURLY LEAF), TIP (TOPLESS), HD-ZIP (homeobox-LIKE LEUCINE ZIPPER), PHD-FINGER, ATHB1 (ARABIDOPSIS THALLIANA, HOMEOBOX 1), ATHB8, CNA (CORONA)/ATHB15, AREF1, as well as SHR–SCR (SHORT ROOT–SCARECROW) genes encoding transcription factors of GRAS family. Mutations in these genes result in violation of the differentiation and growth of the apical meristem of shoots and roots in embryo.

A gene families that regulate differentiation of epidermal and protodermal cells of shoot apical meristem (SAM) of embryos are identified. These include: GL2 (GLABRA2) genes to which belong ATML1 (ARABIDOPSIS THALLIANA A MERISTEM LAYER 1) and PDF2 (PROTODERMAL FACTOR 2) genes of Myb homeodomain-like transcription factors, ZLL (ZWILLE), AG010 (ARGONAUTE 10), SHR, RPK1 (RECEPTOR-LIKE PROTEIN KINASE 1), T0AD2 (TOADSTOOL 2), CLE (CLV3/ESR-RELATED) and ASI1 (ASYMMETRIC LEAVES1) genes; ACR4 (ARABIDOPSIS CRINKLY4) and ALE2 (ABNORMAL LEAF-SHAPE 2) genes that encode leucine-rich receptor-like protein kinases (LRR-RKs); WER (WERFEL) gene - a positive regulator of trichoblast growth; CPC (CAPRICE) and TRY (TRYPTYCHON) genes that encode Myb transcription factors - negative regulators of trichoblast epi- dermis growth; PRR (PIRROGI), GIRL (GN-ARLED) and BRK1
Genes controlling seed integument development

Central role of MADS-box and WRKY gene families of transcription factors in the regulation of the development and formation of the seed integument is revealed [1,5,23]. 16 groups of MADS-box proteins that have common name TT16/ABS (TRANSPARENT TESTA 16/ARABIDOPSIS BSISTER) are identified in Arabidopsis [1,23]. Violation in the synthesis and accumulation of proanthocyanin pigment precursor in the seed integument and its specific localization in endothelial cells are found in mutant for tt16/abs locus plants. Mutations of other MADS-box transcription factor GORDITA/AGL63 are manifested in abnormally increased size of seeds in Arabidopsis [1]. Constitutive expression of GORDITA gene in normal plants is observed in the integument of seed during its growth and development [64]. Thus, transcription factors - MADS-box proteins are involved in the regulation of seed size by controlling the seed integument development.

An important role of another TTG2 (TRANSPARENT TESTA GLABRA2) gene, which also belongs to family of transcription factors WRKY, in the control of development of endosperm and seed integument is found [1,23]. The main function of this gene is direct control of elongation of seed integument and, consequently, the control of growth and size of the endosperm [1,23]. IKU2 gene takes part in this process as well. A cumulative effect, which results in reducing the endosperm and seed size, is observed in double ttk2/iku2 mutant plants [65].

The important role of numerous gene families in the synthesis of cell wall of embryo integument that occurs during cytokinesis in fragmoplast – complex structure, which includes microtubules, microfilaments and vesicles, is found. To these families belong genes: HINKEL/NACK1 gene (encoding protein homologous to kinesin that controls the reorganization of microtubules of microfilaments and vesicles), KN (KNOLLE) and KEU (KEULE) genes (encoding complex of v-SNARE and t-SNARE proteins syntaxines - carriers of vesicles to membranes), TONNEAU2/FASS (TON2) gene (encoding a protein phosphatase type 2A, the main function of which is creation of prephosphate band and reorientation of microtubule arrays with formation of cytoskeleton), KIS (KIESSEL) gene (encoding TFCs (Tubilin-Folding Cofactors) proteins that control the balance of monomeric α/β-tubulines, which are important for microtubule biogenesis) and ANP1/NPK1 gene, which belongs to the MAPKKK (MITOGEN-ACTIVATED PROTEIN KINASE KINASE KINASE) family that is involved in cell plate expansion [13,66-71].

The role of the numerous genes responsible for the mucus synthesis in the cell wall of the integument that protects plants of many families such as Brassicaceae, Solanaceae, Linaeace and Plantaginaceae from dehydration in the arid period is defined. In Arabidopsis to these families belong genes: AP2 and TTG1 genes, EGL3 (ENHANCER OF GLABRA 3) and TT8 genes (which encode proteins similar to bHLH transcription factor family), and MYB gene family that encodes tissue-specific transcription factors [72]. Three signaling pathways through which this complex regulates the mucus synthesis are identified. The first way - the complex activates TTG2 gene, which regulates biosynthesis and accumulation of mucus; the second way - the complex activates GL2 gene, which in turn activates MUM4 (MUCILAGE MODIFIED 4) gene that controls pectin biosynthesis; the third way - the complex activates MYB61 gene which controls synthesis and accumulation of mucus regardless of AP2 and TTG1 genes [72].

Genes controlling biosynthesis of flower and seed pigments

Genes that control the synthesis of anthocyanin pigments (which cause coloring of petals and protect flowers and seeds from the UV spectrum of solar radiation) and proanthocyanidines (that cause discoloration of petals), to which belong: dissolved tannins and flavonoids accumulated in the flowers and leaves of plants and in the seed integument, are identified. In Arabidopsis plants BAN (B4NYULS) gene encodes anthocyanidin reductase that regulates the conversion of anthocyanidin (common anthocyanidin and proanthocyanidin predecessor) into proanthocyanidin [23]. Specific expression of BAN gene is observed in endothelium after fertilization process during proglobular seed stage. More than 12 genes, from which 9 genes encode enzymes of flavonoid biosynthesis, are involved in controlling metabolism of functionally important for the seed flavonoids, which besides proanthocyanidines and anthocyanidines also include catechin, epicatechin (which together with phenolic acids and lignin prevent premature seed germination and protect them from infection by enhancing the thickness and mechanical elasticity of the cell wall of seed integument) [73-75]. To these belong key genes: CHS gene of chalcone synthase, CHI gene of chalcone isomerase, F3H gene of flavanone 3′-hydroxylase, DFR gene of dihydroflavonol reductase, LDOX gene of leucoanthocyanidin dioxygenase, GT gene of glycosyltransferase, FLT gene of flavonol synthase, ANR gene of anthocyanidin reductase and LAC15 gene of enzyme modification - lactase 15, group of 5 FLS genes (FLS2 - FLS6 genes) of flavonol synthase, TT (TRANSPARENT TESTA GLABRA) gene family (which members - TT1, TT2, TT8, TT10 and TT16 genes are identified in Arabidopsis), and TTG1 and TTG2 (TRANSPARENT TESTA GLABRA) genes [73-75]. It is found that TT10 (TRANSPARENT TESTA 10) gene encodes laccase-like polyphenol oxidase (member of multifamily of genes which consists of 17 members), TT8, TT18, TTG1 and TTG2 genes that encode R2R3-MYB, bHLH, WD40 and WRKY proteins belonging to the family of transcription factors respectively [73]. The expression of the TTG2 gene is regulated by TTG1, TT12, AHA10 (AUTOINHIBITED H'-ATPase) and TT19 genes. It is shown that expression of TT12 (MATE secondary transporter), BAN (ANR), TT3 (DFR - DIHYDROFLAVONOL-4-REDUCTASE) and TT18 (LDOX) genes is not observed in mutant plants with defects in expression of TT2 (MYB), TT8 (bHLH) and TTG1 (WD40) genes, indicating a regulatory role of these transcription factors in the induction of biosynthesis of proanthocyanidines and their transport enzymes [38,73-75].

Role of Phytohormones in the Regulation of Plant Embryogenesis

There are numerous data confirming the leading role of natural growth regulators such as phytohormones: auxin - indolyl-3-acetic acid (IAA), cytokinins (CK), gibberellic acid (GA), brassinosides (BR), abscisic acid (ABA), ethylene (ET), and jasmionic
acid (IAA) in regulation of gene expression during plant embryogenesis [1,76-79].

Auxins

Investigations of auxin signaling pathway indicate its important role in the regulation of the embryo development [48,77,80,81]. Deficiency or absence of IAA during embryogenesis causes embryo death. Mutations in key genes regulated by auxin lead to violation of the mitotic cycle and cell differentiation, resulting in the abnormalities in the embryo and endosperm development. To these genes belong numerous gene families that encode various types of proteins: auxin receptor - protein APB1 (AUXIN BINDING PROTEIN 1); proteins that interact with negative regulators of auxin signal transduction - Aux / IAA proteins and are involved in their ubiquitination and subsequent degradation in the proteasome - a complex of proteolytic enzymes: F-box protein TIR1 (transport inhibitor response), SKP1, CUL1 (AXR6/CUL-LIN 1) and RUB (RELATED-TO-UBIQUITIN) proteins; proteins that are subunits of heterodimeric RUB-activating complex: AXR1, AXI, ECR1 (E1 C-TERMINAL RELATED 1), ASK1 (ARABIDOPSIS SKP1 HOMOLOGUE 1)/ASK2 proteins and ubiquitin-specific protease UBP14 (UBIQUITIN-SPECIFIC PROTEASE 14) [1,48,70,80,82]; proteins that are involved in polar transport of auxin and its homeostasis [1,25,38,48,80,83]: AUX1 protein - auxin importer, PIN1-PIN7 family of proteins - auxin exporters in Arabidopsis (PIN1 protein is also named by EIR1, AGRI/ ApPIN2 or WAV6X); GH3 family of IAA-amido conjugating enzyme, which through formation of complex with protein encoded by IAA4 gene is also found. This gene encodes a serine/threonine protein phosphatase PP2A, which dephosphorylates IAA/AXR3 proteins controlling the transport of ESCRT-binding proteins: CHMP1A and CHMP1B (CHARGED MULTIVESICULAR BODY PROTEIN/CHROMATIN MODIFYING PROTEIN1A) [17]. Data about auxin-mediated regulatory role of APB1 receptor protein in control of mitotic cell cycle of embryo during embryogenesis are obtained [48,86].

It is found that gene families of proteins - transcription factors control the initiation and formation of the shoot apical meristem (SAM) and root apical meristem (RAM) of embryo, to them belong proteins: ARFs (AUXIN RESPONSE FACTOR) interacting with the III and IV domains of Aux/IAA proteins (the repressors of early auxin-responsive genes), which have a short life period and nuclear localization [13,82,87]. Aux/IAA proteins interact with E3 ubiquitin ligase SCFTIRI complex, whose components are CDC53/ArCULLIN1 (encoded by AXR6 gene) [1], SKIPI and F-box proteins. The main function of SCF complex is ubiquitination of target Aux/IAA proteins followed by their degradation in the 26S proteasome (complex of proteolytic enzymes) [48,79,80,87]. An important part in the degradation of IAA/AXR3 proteins is also played by HBT (HOBBIT) protein - homologue of CDC27 subunit of APC complex (anaphase-promoting/cyclosome complex) controlling cell differentiation and embryonic mitotic cycle [58].

Key genes of embryogenesis belong to numerous ARF families, which include: MP (MONOPTEROS)/ARF3 gene participating with PID (PINOID) gene that encodes serine/threonine kinase in the regulation of expression of PIN-FORMED7 (PIN7) gene (that encodes receptor-protein, which participates in the transport of auxin) and in the phosphorylation of protein encoded by PIN7 gene; NPH4 (NON-PHOTOTROPIC HYCOTYL4)/ARF7 gene with highly homology to the MP gene; proteins that are encoded by these genes regulate auxin signaling pathway through formation of heterodimeric complex [13,17,25,79,81-83,88-90].

Auxin signaling pathway are also controlled by BDL/IAA12 (BODENLOS/INDOLE-3-ACETIC-ACID12) gene, which inhibits expression of MP gene [17,48,91]. It is found that MP and BDL genes control expression gene of transcription factor TM07 (TARGET OF MONOPTEROS 7) in hypophysis cells (i.e., adjacent to embryo cells that are involved in the formation of the root pole) [25]. The process of hyposis development is under control of genes: SCR (SC/ARECROW), PLT1, PLT2, PLT3 (PLETHOR-A3), BABYBOOM (BBM)/PLT4, whose expression is regulated by BDL-AMP genes and by close homologue of MP gene - NPH4 (NONPHOTOTROPIC HYCOTYL 4)/ARF7 gene, whereas WOX5 (WUSCHEL RELATED HOME- OBOX 5) and PLETHOR-A genes control development of root and stem cells [13,17,25,27,83].

Important data witnessing about participation of numerous gene families in the control of formation and development of floral organs were obtained. To these families belong genes: ETT (ETTI- TIN)/ARF3 gene of auxin-responsive factor; GH3.3 gene of auxin-conjugating enzyme, which through formation of complex with protein encoded by SYP33 (SEPALLATA-LIKE 3) genes takes an important part in controlling the expression of many genes of floral organs; PID and PIN4 genes of auxin-transporter proteins; ETT, ARF6, ARF8 and IAA4 genes of proteins which conduct auxin signals; auxin-inducible gene families that control flower size and growth of lateral meristems of floral organs: ARGO3 (AUXIN-REGULATED GENE INVOLVED IN ORGAN SIZE) gene, AIL/PLT (INTEGUMENTA-LIKE/PLETHOR- A4) genes that are members of AEP2/EIR (APELTAL2/ETHYLENE RESPONSE FACTOR) gene family, and AXR1 (AUXIN-RESISTANT 1) gene; as well as genes of transcription factors regulating auxin biosynthesis during carpel and gynoe- cium development: STY1 (STYLISH), NGA1 and SHI/STY (SHORTINTERNODES/STYISH) genes [88,90,92].

Cytokinins

Phytohormones cytokinins positively affect the differentiation and specialization of embryo and endosperm cells of seeds and filling of cotyledons by nutrients that are essential for the further development of seedlings [77,80,93]. Transcriptome analysis con-
duced on the early stages of Arabidopsis endosperm development identified about 800 genes, which specific expression was observed in the endosperm of immature seeds [1]. Histidine kinases (AHKs) of Arabidopsis function as cytokinins’ receptors which exercise phosphorylation of histidine transporter proteins (AHPs) after perception of cytokinins’ signal [11,94,95]. AHPs proteins functioning in the nucleus carry phosphate groups to ARRs proteins regulating responsive to cytokinin reactions, resulting in activation of gene transcription processes [1,93,96,97].

Major regulatory function among this group AHKs is performed by cytokinin receptor-protein CRE1/AHK4 that regulates size of seed and its germination, primary root formation and regeneration of shoots, and by AHK3 protein that is involved in photomorphogenesis and together with AHK2 protein controls the formation of leaves and roots [52,80,93,94,96-99]. It is shown that the triple abk2,3,4 plants with mutations in genes of cytokinin receptor-proteins have embryos that are increased in size by 30% compared to wild type of plants [1]. It is found that the WOL (WOODEN LEG) gene that is allelic to AHK4 gene encodes a cytokinin receptor protein participating in the formation of radial vascular tissues during embryogenesis [29]. The functions of cytokinin-regulated CKI1 (CYTOKININ INDEPENDENT 1) gene were identified. This gene encodes histidine kinase, which don’t have cytokinin perception domain, while this domain is found in AHK2,3,4 proteins [93,96,97]. Overexpression of CKI1 gene leads to appropriate physiological responses observed in the plant cells and tissues culture without the use of exogenous cytokinin [1]. On the contrary, plants with mutant ski allele reveal insensitivity to cytokinin and produce fewer seeds, but their sizes are significantly increased [100].

Cytokinin-regulated CYTOKININ-HYPERSENSITIVE 2 (CKH 2) gene was identified. This gene is allelic to PKL (PICLE) gene, which encodes the transcription factors controlling the expression of gibberellin-regulated genes, that testifies about integrated role of this gene in the controlling the different phytormonal ways [99]. A family of ARRs genes that encode transcription factors (regulating cytokinin signaling pathway) was identified. It is found that ARR1 - ARR15 and ARR18 - ARR21 genes are involved in the control of elongation of hypocotyl and meristems of roots, shoots, leaves, stems, stamens, pistils, sepals and flowers). It is shown that trans-factors ARR7 (ARABIDOPSIS RESPONSE REGULATOR) and ARR15, which inhibit cytokinin signaling, are involved in hypophysis development [17,25,52,94-96,98]. The expression of these genes is regulated by auxin together with MP-BDL genes.

The numerous gene families that display major impact on cytokinin synthesis and transduction their signals are identified, to them belong genes: CKX3 (CYTOKININ OXIDASE-3) gene, KNOX gene of transcription factor activating isopentenylation transferase gene (which catalyzes cytokinin biosynthesis) and KNOX1 gene family - STM (SHOOTMERISTEMLESS) and BP (BREVIPEDICELLUS) genes, which encode proteins that regulate shoot meristem development, and WUS (WUSCHEL) gene of trans-factor, which activates cytokinin-dependent cell division in the meristems of shoots [49,52,54,80,101].

Gibberellic Acid

It is known that gibberellic acid (GA) performs a various role in seeds’ embryogenesis, namely GA takes part in the growth of the embryo, the absorption of nitrogen, prevents seed abortion and stimulates premature germination of seeds in the late embryogenesis [77,78,80]. The study of GA signaling pathway showed that stimulation of organogenesis and plant growth under the influence of GA occurs through interaction between the receptor protein GID1 (gibberellin insensitive dwarf) and negative regulatory DELLA proteins, with their subsequent ubiquitination and degradation with participation of SCF E3 ubiquitin ligase complex in the 26S proteasome [2,49,80,82,102]. It is shown that during embryogenesis the numerous gene families are expressed in seed embryo, to them belong genes: G+A20ox (Gibberellic 20 oxidase) - a key gene of gibberelin biosynthesis, G+A20X1 (gibberelin 2-β-dioxygenase 1) gene responsible for the metabolism of gibberelin, and G+A/R6 gene that encodes protein - the predecessor of the GASA/GAST/Snakin family of proteins involved in responses to gibberelin in embryo and endosperm [1,103]. However, at later stages of embryo and endosperm development a gradual decrease in expression of ent-kaurene synthase and ent-kaurene oxide genes is observed. Transcription factor KNOX is identified as a key transcriptional suppressor of enzyme involved in GA biosynthesis - GA20ox; the main function of trans-factor KNOX is regulation of the level GA synthesis in the apical meristem and lateral shoots [77]. G+A4 gene family belongs to a specific group of genes whose expression is enhanced by gibberellin acid [1]. G+A+A 4 gene is one of the members of this group, high level of its expression is observed in the apical meristem and floral tissues of embryos during their development. Overexpressing this gene significantly increase size and total weight of seed in mutant Arabidopsis plants. At the same time, although the gaza4 mutant plants with reduced expression of this gene produced smaller seeds, their total number is much higher than in wild type plants. The explanation of this fact can be the assumption that a mutation in this gene has no effect on the expression of a network of other gibberellin-regulated genes.

Brassinosteroids

The study of brassinosteroids (BR) biosynthesis genes and BR signaling pathway genes testify about their important role in embryogenesis of seeds. Numerous gene families are identified, to them belong genes that encode BR receptor proteins: VAK1 kinase (BR1 ASSOCIATED PROTEIN KINASE 1), which is similar to GSK3 (Glycogen Synthase Kinase 3-like) kinase and BIN2 (BRINSENSITIVE 2) kinase and its substrates: BZR1 (BRASSINAZOLE RESISTANT 1) and BES 1 and 2 (BRI1-EMS SUPRESSOR 1, 2) [25,80,104]. Transmission of BR signals is carried out through activation of BR receptor-kinase complex BRI1/VAK1 followed by dissociation of the BRI1/ BKI1 (KINASE INHIBITOR1) complex and formation of a new BK1/VAK1 complex [62,84]. VAK1 kinase participates in phosphorylation of BRI1, thereby increasing the activity of this kinase. Activation of BRI1 leads to phosphorylation of BSKs (BR-SIGNALLING KINASE 1), which activates BSU1 (BRI1 SUPPRESSOR) phosphatase, which in turn inactivates BIN2 kinase through its dephosphorylation; BSU1 phosphatase also inhibits phosphorylation of BZR1 and BES1, which in dephosphorylated state are able to directly bind to DNA and regulate gene expression [104]. BK1 kinase is a negative regulator of BRI1 kinase interaction with BAK1 and other protein substrates. It is a blocker of BR signal transmission from the cytoplasmic membrane [62]. In the absence of BR signals the BIN2 kinase participates in phosphorylation of BZR1 and BES1 substrates in the serine and threonine residues and causes their cleavage
by complex of proteolytic enzymes (proteasome) in the cytosol, thereby blocking their binding to DNA [84,104]. A leading role in brassinosteroid signaling pathway is played by the CYP72C1 gene belonging to the family of P450 monoxygenases [1]. Overexpression of this gene in shbk1-D (shrink1-dominant) mutant plants of Arabidopsis leads to reduced seed organs, including hypocotyls, roots, cotyledons, leaves and pods; seeds become much shorter in length [1]. CYP72C1 gene is highly homologous to the B-A5I gene of Arabidopsis, which is involved in hydroxylation and inactivation of BR phytohormones, consequently shbk1-D mutations reduce the level of endogenous BR [1]. Similar data is obtained in mutant rice plants which have defects in the genes of BR bio-
tivation of BR phytohormones, consequently it is revealed that the expression of this gene in mutant plants belonging to the family of P450 monooxygenases [1]. Overexpression of this gene in mutant plants overexpressing KLH gene. Other signaling components of BR are identified - BMIN (BES INTER-ACTING MYC-LIKE PROTEIN 1) and AP2 genes, DRN (DORNROESCHEN) and DRNL (DORNROESCHEN-LIKE) genes of transcription factors interacting among themselves [8,17,25].

Abscisic Acid

Abscisic acid (ABA) has significant impact on the process of plant embryogenesis. More than 40 genes, differential expression of which is enhanced in response to ABA in endosperm, root, leaves and shoot tissues of embryo, as well as more than 11 genes involved in the biosynthesis and carrying out ABA signals during late embryogenesis at seed maturation phase were identified in Oryza sativa plants [2,41]. Key genes of ABA biosynthesis and metabolism are identified, to them belong genes: NCED gene that encodes a key enzyme 9-cis-epoxy-carotenoid dioxygenase that participates in ABA biosynthesis from precursor 9-cis-neoxanthin into xanthoxin and 8-hydroxylase, which participates in ABK metabolism [30,38,41,74]. It is found in addition that OsVP1 gene that encodes violaxanthin-deepoxygenase, whose high expression is observed during embryo and endosperm development, is also involved in the synthesis of ABA. An important role of this gene in protecting the embryo during embryogenesis from dehydration is defined.

ABI1 gene family belongs to ABA-regulated genes of Arabidopsis plants. This family includes protein kinases, serine/threonine phosphatases (encoded by ABI1 and ABI2 genes) and transcription factors (encoded by ABI3, ABI4 and ABI5 genes) [2,23,31,41,76,106]. Mutations of ABI1 gene family of transcription factors and EEL (Arabidopsis Enhanced Em Level) gene of bZIP trans-factor (that is similar to ABI5) violate cell sensitivity to ABA and reduce of expression of Eim (EARLY METHYNO-cine, L-ABELED) and LEA (LATE EMBRYOGENESIS ABUNDANT) genes that encode proteins of late embryogenesis [23,29]. It is found that LEC1 (LEAFY COTYLEDON1), LEC2 and FUS3 (FUSCA3) genes of transcription factors are involved in controlling the expression of ABI3 genes during seed matura-
tion phase [23,27,29,31,41,51]. Arabidopsis plants with mutations in ab13, le1 (leafy cotyledon1), le2 and fus3 (fusca3) alleles have phenotype similar to the vegetative stage, namely, decreased to drought tolerance, activation of meristem growth, early expression of genes with specific germination stage activity, and simultaneously lack of seed maturation. These results indicate that ABI3, LEC1, LEC2 and FUS3 genes regulate the processes of seed maturation and inhibit premature seed germination [23].

It is revealed that LEC1 gene encodes HAP3 subunit of CCAAT-binding transcription factor CBF, whereas ABI3, LEC2 and FUS3 genes encode B3-domain-containing transcription factors [27,38,41]. Transcription factors encoded by LEC1, LEC2 and FUS3 genes bind to RY motif, which is conserved in the promoter of many seed-specific genes that control seed maturation, whereas transcription factors encoded by ABI3 and ABI5 genes interact with cis-acting promoter elements - ABREs (ABA-responsive elements) [31,38,41]. ABA-regulated gene family of other transcription factors that control embryo development, aleurone and storage protein synthesis in the endosperm, are identified, to them belongs: C2H2, HB, bHLH, bZIP, CCAAT, PHD, NAC, LEC, FUS, AP2/EREBP and AREB3 (ABA-Rsponsive Element Binding protein 3) genes [23]. A larger number of these genes have either ABA-responsive elements (ABREs) or a combination of ABREs with CE - coupling elements, or a combination of ABREs with seed-specific RY/Sph motifs [23,51,76,77].

Ethylene

Phytohormone ethylene (ET) shows antagonistic effect towards ABA during seed embryogenesis [77], modulates the formation and growth of cotyledons during embryo development, participates in programmed endosperm cell death in the final phase of its development [77,107,108]. Study of signaling pathway of ethylene suggests that CTR1 (CONSTITUTIVE TRIPLE RESPONSE 1) gene encodes protein - a negative regulator of ethylene signal, which through interaction with the receptor complex inhibits expression of ethylene responsive EIN2 (ETHYLENE INSensitivity 2) gene [2,74]. It is found that expression of EIN2 gene is regulated by ETP (ETIN2 TARGETING PROTEIN) protein, which prevents the transmission of ethylene signals to EIN3 gene belonging to the family of transcription factors, which activate expression of ERFs (ETHYLENE RESPONSE FACTORS) under presence of ethylene [2,50,108]. Stability of EIN3 protein regulates protein encoded by EBF (EIN3 BINDING F-BOX PROTEIN) gene, whose expression is controlled by a complex of proteins encoded by AIN/EIN3/XRN (ACC INSENSITIVITY/EIN3 EXORIBONUCLEASE/ACEX4) genes [108]. During embryogenesis the activity of gene that encodes key en-
zyme of ethylene biosynthesis - aminoacyclopropane-1-carboxylate oxydase1 is inhibited by a complex of proteins CBFs/DREBs (A-repet (CRT)-binding factors /dehydration responsive-element-binding proteins), which belong to the AP2/ERF (APETAL2/Ethylene Response Factor) family - activators of transcription of numerous genes, which control plant resistance to cold [107,108]: COR (cold regulated), KIN (cold induced), LTI (low-temperature induced) and RD (responsive to dehydration) genes. It is found that tolerance to cold stress factor is positively correlated with increased expression of genes responsible for the metabolism of carbohydrates, amino acids, phospholipids and secondary metabolites in seed.
Jasmonic Acid

Genetic studies of regulatory role of jasmonic acid (JA) showed a significant impact of this phytohormone on the growth of shoot apical meristem, formation of floral reproductive organs, fruits ripening and carotenoid synthesis in them, and embryogenesis of seed [82,109-111]. Major components, which take participation in the JA signals and regulate expression of genes during plants growth and development were identified, their synthesis is encoded by genes: COI1 (coronatine insensitive 1), JAR1 (jasmonate resistant 1) and JIN1/MYC2 (jasmonate insensitive 1/MYC2) genes [109-111]. It is found that JA-regulated COI1 gene encodes protein that is a member of F-box protein family - components of SCF complex of enzymes that are involved in degradation of proteins in the 26S proteasome [82,109-113]. JAR1 gene encodes isoleucine synthetase, which forms a conjugate JA with isoleucine - physiologically active molecule in plants. JIN1/MYC2 gene encodes a transcription factor that regulates the expression of JA-responsive genes. It is found that JAZ gene encodes protein which has JA-binding domain; together with JIN1/MYC2 trans-factors this protein takes part in the repression of JA-responsive genes [110,112,113]. Under impact of JA-isoleucine conjugate complex, the receptor complex of COI1 and COI1-JAZ proteins promotes ubiquitination of JAZ proteins with participation of SCFCOI1 ubiquitin ligase and subsequent degradation of JAZ proteins in the 26S proteasome. As a result MYC2 transcription factor activates expression of JA-responsive genes that control growth and development of plants [82].

VSPs (vegetative storage proteins) genes that encode seed storage proteins belong to the families of genes, the expression of which is increased under the impact of JA during seed development [111,112]. A high level expression of V sp1 and AVip genes of storage proteins (which correlates with increased levels of endogenous JA) in the reproductive organs - flowers and fruits, as well as in the elongating meristems of hypocotyl, stem, root and young leaves during their development and under water deficit conditions is revealed in soybean plants and wild type plants of Arabidopsis [112]. On the contrary, in the insensitive to JA coi1 mutant plants and JA-deficient mutant plants of Arabidopsis expression of AVip gene is not observed, but its activation is observed under the impact of exogenous JA. Violation of viable pollen formation is also observed in these mutant plants [112]. V sp1 gene family encodes two proteins (Vsps and Vspb), which function as a phosphatase with low acid activity, and as lipoxidase that regulates gene expression in the complex with sucrose, phosphate, nitrogen and auxin. The significant role of JA receptor - F-box protein COI (CORONATINE INSENSITIVE 1) in the regulation of floral organ abscission, apical dominance, floral meristem arrest, hypocotyl growth, in the ethylene-induced inhibition of root growth process, as well as in the inhibition of IAA-stimulated elongation of seed coleoptiles through blocking the incorporation of glucose into cell wall polysaccharides is identified [113,115].

Conclusions

Plant embryonic development occurs according to evolutionary genetic program. A great progress in the investigations of molecular-genetic mechanisms regulating embryonic development at the early stages of plant ontogenesis is reached up in recent years. Numerous data prove important role of different classes of phytohormones in the regulation of expression of key genes that play important part in the control of plant embryogenesis. Fundamental knowledge of basic processes of embryonic development of plants is theoretical and practical base for elaboration of new modern biotechnologies for the improvement of plant growth and development, increase of plant productivity and plant adaption toiotic and abiotic stresses with use of natural or synthetic growth regulators and genetic engineering methods.

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