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Genetic Control and Phytohormonal Regulation of Plant Embryogenesis

Review Article

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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 resulted.

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.

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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* mutant plants, 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* та *AP3* (*APETALA 1, 2* and *3*) genes in the regulation of flower, embryo and endosperm de-

velopment 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 (SEPALLATA3)* gene which encodes a MADS-box protein that belongs to the family of DNA-binding transcription factors, *PI (PISTILATA)* 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 ORGANS171)* gene, which encodes the F-box protein - member of SCF^{UFO} 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 PKl (PICKlE), ULTRAPETAlA 1, PAN (PERIANTHIA), 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 PcG (Polycomb) protein complexes during flower, embryo and endosperm development. Proteins of PRC1-like groups of PcG protein complexes are encoded by *LHP1 (HETEROCHROMATIN PROTEIN 1)* and *EMF1 (EMBRYONIC FLOWER 1)* genes, while proteins of PRC2-like groups of PcG 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 (FERTILISATION INDEPENDENT ENDOSPERM), FIS2 (FERTILISATION INDEPENDENT SEED2), EMF2 (EMBRYONIC FLOWER 2)* and *MSI1 (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 *HAIKU2 (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 expession 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 1)* 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, far-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 *dek (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 of seed maturation and prevent premature seed germination. The premature synthesis of storage proteins 12S 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 (FUSCA3)* 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 shaperonin Hsp60α, are observed in small-sized cotyledons of *Arabidopsis* plants with another embyolethal *slp (schlepperless)* 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 *twn2 (twin2)* 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, C2H2, HB, bHLH, WRI1, RGE1, bZIP, GRF, SBP* and *AP2/EREBP* 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 PcG (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 (RETINOBLASTOMA RELATED PROTEIN 1), PHE1 (PHERES1)* and *FWA* genes [1,11,21,37-39]. PcG 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 PcG, 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 *fis* 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 (PHERES1)* 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 hipomethylation 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 hipomethylation DNA of parental genome leads to acceleration of the process of mitotic division of endosperm cells without previous phase of cell elongation. At the same time DNA hipomethylation 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-bound 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, *Mn1 (Maize 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

activity is observed in the endosperm of *mn1* mutant plants. In contrast, more storage proteins and lipids are accumulated in *ap2* mutants of *Arabidopsis* (due to increased activity of the *CwbINV* gene and lengthening of the period of cell division). Seeds largest in size are produced, although their total number is reduced, because of the negative effect of these mutations, which reduce fertilization ability due to morphological defects of flowers [23].

Sterols play an important role in the formation of cellular structures of embryo cotyledons. Their biosynthesis is controlled by *FCK/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/paternal 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/ap-2* alleles 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 enlarged anther and ovule. Besides that, it is possible to obtain transgenic plant lines with a moderate level of expression of the *ANT* gene by artificial pollination to get seeds with larger embryos due to prolonged proliferation of embryo cells. Other genes that play an important role in the control of ovule such as *HLL (HUELLENLOS), INO (INNER NO OUTER), UCN (UNICORN), SUB (STRUBBELIG), BAG (BLASIG), MOG (MOLLIG), LAL (LAELLI)* and *LUG (LUENIG*) were identified. Their mutations lead to reduction of ovule size, to a stop its cell division, to absence of gametogenesis and the lack of subsequent formation of inner cover and integument around them [39].

It is shown that *TTN6 (TITAN6)* 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 (RETARDED GROWTH OF EMBRYO1)* gene in the control of embryo development is found. *RGE1* gene belongs to *bHLH* 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 gene families [2,6,8,13,17,23,25,27,29,33-35,39,46-61]: *STM (SHOOT MERISTEMLESS), BP (BREVIPEDICELLUS), LOB (LATERAL ORGAN BOUNDARIES), RML1 (ROOT MERISTEMLESS 1), RHD6 (ROOT HAIR DEFECTIVE6), TTG (TRANSPARENT TESTA GLABRA), GL2 (GLABRA2), WER (WERWOLF), SCM (SCRAMBLED), HBT (HOBBIT), KNOX (Knotted1-like homeobox), WUS (WUSCHEL), CLV (CLAVATA), KNAT (Homeobox protein knotted-1 like)* and *KNAT1, SHL2 (SHOOTLESS2), SHO1,2 (SHL4/SHOOT ORGANIZATION 1,2), CUC (CUP-SHAPED COTYLEDON), ZLL (ZWILLE), ANT (AINTEGUMENTA), GK (GURKE), PAS (PASTICCINO), BDL (BODENLOS), AXR6 (AUXIN RESISTANT 6), GNOM/EMB30 (GNOM/ EMBRYO DEFECTIVE30), GK (GURKE), HAN (HANABA TARANU), KAN (KANADI), YAB (YABBY), FIL (FILAMENTOUS FLOWER), AMP1 (ALTERED MERISTEM PROGRAM 1), MP (MONOPTEROS), BBM (BABYBOOM), PHB (PHABULOSA), PHV (PHAVOLUTA), REV (REVOLUTA), SYD (SPLAYED), TPL (TOPLESS), TPR (TOPLESS-RELATED), PLT1-2 (PLETHORA 1-2), FK (FACKEL), ULT1 (ULTRAPETALA1), WOX2 (WUS-RELATED HOMEOBOX 2), WOX5, STIMPY-LIKE (STPL)/WOX8, PIO (PINOCCHIO), WOL (WOODEN LEG), WRKY2 (WRKY DNA-BINDING PROTEIN 2), REV (REVOLUTA), PHB (PHABULOSA), PHV (PHAVOLUTA), YDA (YODA), YUC1/4/10/11 (YUCCA 1/4/10/11), WAG1/2, DRN/ESR (DORNRÖSCHEN/ENHANCER of SHOOT REGENERATION), CLF (CURLY LEAF), TPl (TOPlESS), HD-ZIP (homeobox-LEUCINE ZIPPER), PHD-FINGER, ATHB1 (ARABIDOPSIS THALIANA HOMEOBOX 1), ATHB8, CNA (CORONA)/ATHB15, ARF17,* 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 (GLABRA 2)* genes to which belong *ATML1 (ARABIDOPSIS THALIANA MERISTEM LAYER 1)* and *PDF2 (PROTODERMAL FACTOR 2)* genes of Myb homeodomain-like transcription factors, *ZLL (ZWILLE), AGO10 (ARGONAUTE 10), SHR, RPK1 (RECEPTOR-LIKE PROTEIN KINASE 1), TOAD2 (TOADSTOOL 2), CLE (CLV3/ESR-RELATED)* and *AS1 (ASYMMETRIC LEAVES1)* genes; *ACR4 (ARABIDOPSIS CRINKLY4)* and *ALE2 (ABNORMAL LEAF-SHAPE 2)* genes that encode leucine-rich receptor-like protein kinases (LRR-RLKs); *WER (WEREWOLF)* gene - a positive regulator of trihoblast growth; *CPC (CAPRICE)* and *TRY (TRYPTYCHON)* genes that encode Myb transcription factors - negative regulators of trichoblast epidermis growth; *PIR (PIROGI), GIRL (GNARLED)* and *BRK1*

(BRICK 1) genes that control the localization of actin filaments in epidermal cells [2,8,17,25,30,62,63]. The leading role of *HD-ZIPIII (III HOMEODOMAIN-LEUCINE ZIPPER), ATHB8, ATHB15, bZIP, CCAAT, PDH (FIDDLEHEAD), AP2/ER-EBP* and *bHLH* genes, which encode transcription factors, in the initiation and formation of SAM and RAM and in the regulation of endosperm and embryo development is showed [13,34,46,56].

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 [1,5,25]. 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 proanthocyanidin 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. 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 *ttg2/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 fragmoplast), *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 preprophase band and reorientation of microtubule arrays with formation of cytoskeleton), *KIS (KIESEL)* 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, Linaceae* 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 (BANYULS)* 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 dihidroflavonol reductase, *LDOX* gene of leucoanthocyanidin dioxygenase, *GT* gene of glycosyltransferase, *FLS1* 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)* 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), *TT2, TT8, 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 proanthocyanides 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), brassinosteroids (BR), abscisic acid (ABA), ethylene (ET), and jasmonic

acid (JA) 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/CULLIN 1) and RUB (RELATED-TO-UBIQUITIN) proteins; proteins that are subunits of heterodimeric RUB-activating complex: AXR1, AXL, 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 [1,25,38,48,79,80,83]: AUX1 protein - auxin importer, PIN1-PIN7 family of proteins - auxin exporters in *Arabidopsis* (PIN1 protein is also named by EIR1, AGR1/AtPIN2 or WAV6X); GH3 family of IAA-amido synthetases that regulate auxin homeostasis and conjugation of excess auxin with amino acids [27,48,79]; as well as *SAUR (SMALL AUXIN-UP RNAs)* gene family that encodes regulated by auxin small RNAs [48,79,84,85].

A significant role of auxin-regulated *GNOM/EMB30 (GNOM/EMBRYO DEFECTIVE30)* gene is also found. This gene encodes a small-sized GN proteins of class Arf-GEF (ADP ribosylation factor-GDP/GTP exchange factor) involved in the control: 1) of PIN1-dependent transport of auxin through the plasmatic membranes; 2) of Arf-GTP-regulated intercellular transport of vesicles and 3) in the regulation of polarity of apical-basal embryo axis and mitotic cell cycle [17,25,57,82]. Polar localization of PIN proteins and processes of their circulation, degradation and reverse phosphorylation are important to maintain appropriate auxin gradients. A variety of proteins-enzymes are involved in the regulation of these processes, to them belong proteins: ARA7/RAB-F2B proteins (Rab5-binding GTPase), VPS9A (Rab-GEF VACUOLAR PROTEIN SORTING 9A) and VPS29 proteins, serine/threonine protein phosphatase PP2A, protein kinase PID, and endosomal sorting complex of 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 SCF^{TIR1} complex, whose components are CDC53/AtCULLIN1 (encoded by *AXR6* gene) [1], SKIP 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)/ARF5* 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 HYPOCOTYL4)/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 TMO7 (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 hypophysis development is under control of genes: *SCR (SCARECROW), PLT1, PLT2, PLT3 (PLETHORA3), BABYBOOM (BBM)/PLT4*, whose expression is regulated by *BDL-MP* genes and by close homologue of *MP* gene - *NPH4 (NONPHOTOTROPIC HYPOCOTYL 4)/ARF7* gene, whereas *WOX5 (WUSCHEL RELATED HOMEOBOX 5)* and *PLETHORA* 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 (ETTIN)/ARF3* gene of auxin-responsive factor; *GH3.3* gene of auxin-conjugating enzyme, which through formation of complex with protein encoded by *SEP3 (SEPALLATA3)* gene 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: *ARGOS (AUXIN-REGULATED GENE INVOLVED IN ORGAN SIZE)* gene, *AIL/PLT (AINTEGUMENTA-LIKE/PLETHORA)* genes that are members of *AP2/ERF (APETALA2/ETHYLENE RESPONSE FACTOR)* gene family, and *AXR1 (AUXIN-RESISTANT 1)* gene; as well as genes of transcription factors regulating auxin biosynthesis during carpel and gynoecium development: *STY1 (STYLISH1), NGA1* and *SHI/STY (SHORTINTERNODES/STYLISH)* 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-

ducted 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 *ahk2,3,4* 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 doesn'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 *cki* 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 (PICKLE)* 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 phytohormonal ways [99]. A family of *ARR* 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 hypocotyls 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 isopentenyl transferase gene (which catalyzes cytokinin biosynthesis) and *KNOXI* gene family - *STM (SHOOTMERISTEMLESS) and BP (BREVIPEDICELLUS)* genes, which encode proteins that regulate shoot meristem development , and *WUS (WUSCHEL)* gene of transfactor, 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 occures through interaction between the receptor protein GID1 (gibberellin insensitive dwarf1) 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: *GA20ox (Gibberellin 20 oxidase)* - a key gene of gibberellin biosynthesis, *GA2OX1* (*gibberellin 2-β-dioxygenase 1)* gene responsible for the metabolism of gibberellin, and *GASR6* gene that encodes protein - the predecessor of the GASA/GAST/Snakin family of proteins involved in responses to gibberellin 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 oxidase 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]. *GASA* gene family belongs to a specific group of genes whose expression is enhanced by gibberellic acid [1]. *GASA 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 *gasa4* 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 (BRI1 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 BKI1/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]. BKI1 protein 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 monooxygenases [1]. Overexpression of this gene in *shk1-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 *BAS1* gene of *Arabidopsis*, which is involved in hydroxylation and inactivation of BR phytohormones, consequently *shk1-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 biosynthesis: *BRASSINOSTEROID-DEFICIENT DWARF2* and *DWARF11* (orthologous of *BRASSINOSTEROID INSENSITIVE1* gene that encodes BR receptor-protein). The reduced seed length is observed in these plants due to the absence of the brassinosteroid signals that promote cell elongation and regulate seed size by stimulating transport of nutrients to zones of growth and development [105]. Mutations of other members of P450 monooxygenase family - cytochrome P450 encoded by *KLUH (KLU)/CYP78A5* gene and its homologous *CYP78A9* gene lead to decrease of leaves and flowers size due to cessation of cells' proliferation in the inner layer of ovule membrane in *klu* plants [1]. In turn, contrast seed size increase is observed in mutant plants overexpressing *KLU* gene. Other signaling components of BR are identified - *BIM1 (BES INTERACTING MYC-LIKE PROTEIN 1)* and *AP2* genes, *DRN (DORNROËSCHEN)* and *DRNL (DORNROËSCHEN-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-epoxycarotenoid dioxygenase that participates in ABA biosynthesis from precursor 9-cis-neoxantin into xantoxin and *CYP707A* gene that encodes enzyme ABA 8-hydrolase, 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.

ABI 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 *ABI* 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 *Em (EARLY METHIONINE LABELED)* 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 maturation phase [23,27,29,31,41,51]. *Arabidopsis* plants with mutations in *abi3, lec1 (leafy cotyledon1), lec2* 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-contaning 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 families 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-Responsive 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 INSENSITIVE)* gene [2,74]. It is found that expression of *EIN2* gene is regulated by ETP (EIN2 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 E*BF (EIN3 BINDING F-BOX PROTEINS/2)* gene, whose expression is controlled by a complex proteins encoded by *AIN/EIN5/XRN (ACC INSENSITIVE1/EIN5/ EXORIBONUCLEASE4)* genes [108]. During embryogenesis the activity of gene that encodes key enzyme of ethylene biosynthesis - aminocyclopropane-1-carboxylate oxydase1 is inhibited by a complex of proteins CBFs/DREBs (C-repeat (CRT)-binding factors /dehydration responsive-element-binding proteins), which belong to the AP2/ERF (APETALA2/ 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 transfactors 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 SCF^{COI1} 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 *Vsps* and *AtVsp* 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 *AtVsp* 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]. *VSPs* gene family encodes two proteins (Vspa and Vspb), which function as a phosphatase with low acid activity, and as lipoxygenase 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].

Conclulsions

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 adaptation to biotic and abiotic stresses with use of natural or synthetic growth regulators and genetic engineering methods.

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References

[1]. Sun X Shantharaj D, Kang X, Ni M (2010) Transcriptional and hormonal signaling control of Arabidopsis seed development. Current Opinion in Plant Biology. 13: 611–620.

[2]. Kucera B, Cohn M. A, Leubner-Metzger G (2005) Plant hormone interactions during seed dormancy release and germination. Seed Science Research. 15: 281–307.

[3]. Sundaresan V (2005) Control of seed size in plants. Proc. Natl. Acad. Sci. USA. 102: 17887–17888.

[4]. Garcia D, Saingery V, Chambrier P, Mayer U, Jürgens G, et al. (2003) Arabidopsis haiku mutants reveal new controls of seed size by Endosperm. Plant Physiol. 131:1661–1670.

[5]. Belmontea M.F, Kirkbridea R.C, Stonea S.L, Pelletiera J.M, Buib A.Q, et al. (2012) Comprehensive developmental profiles of gene activity in regions and subregions of the Arabidopsis seed. Proc Natl Acad Sci USA. 1–10.

[6]. Howell S.H (1998) Embryogenesis. In: Molecular Genetics of Plant Development. Cambridge University Press. 55 - 82. http://www.amazon.com/Molecular-Genetics-Development-Stephen-Howell/dp/ 0521587840

[7]. Ohto M. A, Floyd S.K, Fischer R.L, Goldberg R. B, Harada J.J (2009) Effects of APETALA2 on embryo, endosperm, and seed coat development determine seed size in Arabidopsis. Sex. Plant Reprod. 22: 277–289.

[8]. Kaufmann K, Pajoro A, Angenent G.C. (2010) Regulation of transcription in plants: mechanisms controlling developmental switches. NATURE REVIEWS Genetics. 11: 830–842.

[9]. Alvarez-Buylla E.R, Adriana Corvera-Poiré A, García-Ponce A.G.B, Jaimes-Miranda F, Pérez-Ruiz R.V (2011) A MADS view of plant development and evolution. In: Chimal-Monroy J. (Ed.) Topics in Animal and Plant Development: From Cell Differentiation to Morphogenesis. 181–220. https://www.researchgate.net/publication/235225764_Topics_in_Animal_and_Plant_Development_From_Cell_Differentiation_to_Morphogenesis

[10]. Steffen J.G, Kang I.H, Portereiko M.F, Lloyd A, Drews G.N (2008) AGL61 interacts with AGL80 and is required for central cell development in Arabidopsis. Plant Physiol. 148: 259–268.

[11]. Day R.C, Herridge R.P, Ambrose B.A, Macknight R.C. (2008) Transcriptome Analysis of Proliferating Arabidopsis Endosperm Reveals Biological Implications for the Control of Syncytial Division, Cytokinin Signaling, and Gene Expression Regulation. Plant Physiology. 148: 1964–1984.

[12]. Wuest S.E, O'Maoileidigh D.S, Rae L., Kwasniewska K, Raganelli A, et al. (2012) Molecular basis for the specification of floral organs by APETALA3 and PISTILLATA. PNAS. 109 (33): 13452–13457.

[13]. Willemsen V, Scheres B (2004) MECHANISMS OF PATTERN FORMATION IN PLANT EMBRYOGENESIS. Annu. Rev. Genet. 38: 587–614.

[14]. Kaufmann K, Wellmer F, Muiño J.M, Ferrier T, Wuest S.E, et al. (2010). Orchestration of floral initiation by APETALA1. Science. 328: 85–89.

[15]. Theissen G, Melzer R (2007) Molecular Mechanisms Underlying Origin and Diversification of the Angiosperm Flower. Ann Bot. 100 (3): 603–619.

[16]. Chae E, Tan Q.K, Hill T.A, Irish V.F (2008) An Arabidopsis F-box protein acts as a transcriptional co-factor to regulate floral development. Development. 135: 1235–1245.

[17]. Smet I.D, Lau S, Mayer U, Ju¨rgens G (2010) Embryogenesis – the humble beginnings of plant life. The Plant Journal. 61: 959–970.

[18]. Yant L, Mathieu J, Dinh T. T, Ott F, Lanz C,et al. (2010). Orchestration

of the floral transition and floral development in Arabidopsis by the bifunctional transcription factor APETALA2. Plant Cell. 22: 2156–2170.
[19]. Das P, Ito T, Wellmer F, Vernoux T, Dedieu A, et al. (2009). Floral stem cell termination involves the direct regulation of AGAMOUS by PERIANTHIA. Development. 136: 1605–1611.
[20]. Schubert D, Primavesi L, Bishopp A, Roberts G, Doonan J, et al. (2006) Silencing by plant Polycomb-group genes requires dispersed trimethylation of histone H3 at lysine 27. EMBO J. 25: 4638–4649.
[21]. Guitton A-E, Page D.R, Chambrier P, Lionnet C, Faure J.-E, et al. (2004). Identification of new members of FERTILIZATION INDEPENDENT SEED polycomb group pathway involved in the control of seed development in Arabidopsis thaliana. Development. 131: 2971–2981.
[22]. Luo M, Dennis E.S, Berger F, Peacock W.J, Chaudhury A (2005) MINISEED3 (MINI3), a WRKY family gene, and HAIKU2 (IKU2), a leucine-rich repeat (LRR) KINASE gene, are regulators of seed size in Arabidopsis. Proc. Natl. Acad. Sci. USA. 102: 17531–17536.
[23]. Ohto M, Sandra L. Stone S.L, Harada J.J (2007) Genetic control of seed development and seed mass. In: Bradford K.J., Nonogaki H. (Eds.), Annual Plant Reviews Volume 27: Seed Development, Dormancy and Germination. Blackwell Publishing Ltd., Oxford, U.K. 1-24. http://www.slideshare.net/Hariezt24/annual-plant-reviews-seed-development-dormancy-and-germination
[24]. Kang X, Ni M (2006) Arabidopsis SHORT HYPOCOTYL UNDER BLUE1 contains SPX and EXS domains and acts in cryptochrome signaling. Plant Cell. 18: 921–934.
[25]. Lau S, Slane D, Herud O, Kong J, Jürgens G. (2012) Early Embryogenesis in Flowering Plants: Setting Up the Basic Body Pattern. Annu. Rev. Plant Biol. 63: 483–506.
[26]. Lid E, Gruis D, Jung R, Lorentzen J.A, Ananiev E, et al. (2002). The defective kernel 1 (dek1) gene required for aleurone cell development in the endosperm of maize grains encodes a membrane protein of the calpain gene superfamily. Proc. Nat. Acad. Sci. USA. 99 (7): 5460–5465.
[27]. Umehara M, Ikeda M, Kamada H (2007) Endogenous Factors that Regulate Plant Embryogenesis: Recent Advances. Japanese Journal of Plant Science. 1(1): 1-6.
[28]. Gazzarrini S, Tsuchiya Y, Lumba S, Okamoto M, McCourt P (2004) The transcription factor FUSCA3 controls developmental timing in Arabidopsis through the hormones gibberellin and abscisic acid. Developmental Cell. 7: 373–385.
[29]. Feurtado J.A, Kermode A.R (2007) A merging of paths: abscisic acid and hormonal cross-talk in the control of seed dormancy maintenance and alleviation. In: Bradford K.J., Nonogaki H. (Eds.), Annual Plant Reviews Volume 27: Seed Development, Dormancy and Germination. Blackwell Publishing Ltd., Oxford, U.K. 176–223. http://www.slideshare.net/Hariezt24/annual-plant-reviews-seed-development-dormancy-and-germination
[30]. Ogawa M, Hanada A, Yamauchi Y, Kuwahara A, Kamiya Y, et al. (2003) Gibberellin biosynthesis and response during Arabidopsis seed germination. The Plant Cell. 15: 1591–1604.
[31]. Rock C.D (2000) Pathways to abscisic acid-regulated gene expression. New Phytol. 148: 357–396.
[32]. Treml B. S, Winderl S, Radykewicz R, Herz M, Schweizer G, et al. (2005). The gene ENHANCER OF PINOID controls cotyledon development in the Arabidopsis embryo. Development. 132: 4063–4074.
[33]. Nonogaki H, Chen F, Bradford K.J (2007) Mechanisms and genes involved in germination sensu stricto. In: Bradford K.J., Nonogaki H. (Eds.), Annual Plant Reviews Volume 27: Seed Development, Dormancy and Germination, eds.. Blackwell Publishing Ltd., Oxford, U.K. 264–304 . http://www.slideshare.net/Hariezt24/annual-plant-reviews-seed-development-dormancy-and-germination
[34]. Abid G, Jacquemin J, Sassi K, MUHOVSKI Y, TOUSSAINT A, et al. (2010) Gene expression and genetic analysis during higher plants Embryogenesis. Biotechnol. Agron. Soc. Environ. 14(4): 667–680.
[35]. Galun E (2007) Regulation of gene expression. In: Plant Patterning. Structural and Molecular Genetic Aspects. Copyright by World Scientific Publishing Co. Pte. Ltd. 127–143. http://www.worldscientific.com/worldscibooks/10.1142/6326
[36]. Xue L-J, Zhang J-J, Xue H-W (2012) Genome-Wide Analysis of the Complex Transcriptional Networks of Rice Developing Seeds. PLOS ONE. 7 (2): 31081.
[37]. Luo M, Bilodeau P, Dennis E.S, Peacock W.J, Chaudhury A (2000) Expression and parent-of-origin effects for FIS2, MEA, and FIE in the endosperm and embryo of developing Arabidopsis seeds. Proc. Natl. Acad. Sci. USA. 97: 10637–10642.
[38]. Holdsworth M.J, Bentsink L, Soppe W.J.J (2008) Molecular networks regulating Arabidopsis seed maturation, after ripening, dormancy and germination. New Phytologist. 179: 33–54.
[39]. Chaudhury A.M, Craig S, Dennis E.S, Peacock W.J (1998) Ovule and embryo development, apomixis and fertilization. Current Opinion in Plant Biology. 1: 26–31.
[40]. Villar C.B.R, Erilova A, Makarevich G, Trösch R, Köhler C (2009) Control of PHERES1 Imprinting in Arabidopsis by Direct Tandem Repeats. Molecular Plant. 2 (4): 654–660.
[41]. Marion-Poll A, Leung J (2006) Abscisic acid synthesis, metabolism and signal transduction. In: Hedden P., Thomas S.G. (Eds.), Plant Hormone Signaling. Blackwell Publishing Ltd. 1–35. http://samples.sainsburysebooks.co.uk/9781405173063_sample_387254.pdf
[42]. Borisjuk L, Rolletschek H, Radchuk R, Weschke W, Wobus U, Weber H (2004) Seed development and differentiation: a role for metabolic regulation. Plant Biology. 6: 375–386.
[43]. Ross J.J, Symons G.M, Abas L, Reid J.B, Luschnig C (2006) Hormone distribution and transport. In: Hedden P., Thomas S.G. (Eds.), Plant Hormone Signaling. Blackwell Publishing Ltd. 257–292 pp. http://samples.sainsburysebooks.co.uk/9781405173063_sample_387254.pdf
[44]. Meinke D, Sweeney C, Muralla R (2009) Integrating the Genetic and Physical Maps of Arabidopsis thaliana: Identification of Mapped Alleles of Cloned Essential (EMB) Genes. PLOS ONE. 4(10): 7386.
[45]. Meinke D, Muralla R, Sweeney C, Dickerman A (2008) Identifying essential genes in Arabidopsis thaliana. Trends in Plant Science. 13 (9): 483–491.
[46]. Che P, Lall S, Nettleton D, Howell S.H (2006) Gene Expression Programs during Shoot, Root, and Callus Development in Arabidopsis Tissue Culture. Plant Physiology. 141: 620–637.
[47]. Smith Z.R, Long J.A (2010) Control of Arabidopsis apical–basal embryo polarity by antagonistic transcription factors. Nature. 464: 423–121.
[48]. Cohen J.D, Gray W.M, (2006) Auxin metabolism and signaling Plant Hormone Signaling. Blackwell Publishing Ltd, 37–66. http://samples.sainsburysebooks.co.uk/9781405173063_sample_387254.pdf
[49]. Thomas S. G, Hedden P (2006) Gibberellin metabolism and signal transduction Plant Hormone Signaling. Blackwell Publishing Ltd. 147–184. http://samples.sainsburysebooks.co.uk/9781405173063_sample_387254.pdf
[50]. Chen Y.F., Etheridge N., Schaller G.E. (2005). Ethylene signal transduction. Annals of Botany. 95: 901–915.
[51]. Lea B.H, Cheng C, Bui A.Q, Wagmaister J.A, Henry K.F, et al. (2010). Global analysis of gene activity during Arabidopsis seed development and identification of seed-specific transcription factors. Proc Natl Acad Sci. 107 (18): 8063 –8070.
[52]. Galun E (2007) The shoot apical meristem. In: Plant Patterning. Structural and Molecular Genetic Aspects. Copyright by World Scientific Publishing Co. Pte. Ltd., 181–221. http://www.worldscientific.com/worldscibooks/10.1142/6326
[53]. Galun E (2007) Patterning of roots. In: Plant Patterning. Structural and Molecular Genetic Aspects. Copyright by World Scientific Publishing Co. Pte. Ltd. 223–273. http://www.worldscientific.com/worldscibooks/10.1142/6326
[54]. Veit B (2009) Hormone mediated regulation of the shoot apical meristem. Plant Mol. Biol. 69: 397–408.
[55]. Yadav R.K, Girke T, Pasala S, Xie M, Reddy G.V (2009) Gene expression map of the Arabidopsis shoot apical meristem stem cell niche. PNAS. 106 (12): 4941–4946.
[56]. Haerizadeh F, Wong C.E, Singh M.B, Bhalla P.L (2009) Genome-wide analysis of gene expression in soybean shoot apical meristem. Plant Mol. Biol. 69: 711–727.
[57]. Okumura K, Goh T, Toyokura K, Kasahara H, Takebayashi Y, et al. (2013). GNOM/FEWER ROOTS is Required for the Establishment of an Auxin Response Maximum for Arabidopsis Lateral Root Initiation. Plant Cell Physiol. 54 (3): 406–417.
[58]. Serralbo O, Pérez-Pérez J.M, Heidstra R, Scheres B (2006) Non-cell-autonomous rescue of anaphase-promoting complex function revealed by mosaic analysis of HOBBIT, an Arabidopsis CDC27 homolog. Proc Natl Acad Sci USA. 103 (35): 13250–13255.
[59]. Galinha C, Hofhuis H, Luijten M, Willemsen V, Blilou I, et al. (2007). PLETHORA proteins as dose-dependent master regulators of Arabidopsis root development. Nature. 449: 1053-1057.
[60]. Kieffer M, Stern Y, Cook H, Clerici E, Maulbetsch C, et al. (2006). Analysis of the transcription factor WUSCHEL and its functional homologue in Antirrhinum reveals a potential mechanism for their roles in meristem maintenance. Plant Cell. 18: 560-573.
[61]. Capron A, Chatfield S, Provart N, Berleth T (2009) Embryogenesis: Pattern Formation from a Single Cell. The Arabidopsis book. 7:0126 http://www.ncbi.nlm.nih.gov/pmc/articles/PMC3243344/
[62]. Li L, Yu X, Thompson A, Guo M, Yoshida S, et al. (2009) Arabidopsis MYB30 is a Direct Target of BES1 and Cooperates with BES1 to Regulate Brassinosteroid-Induced Gene Expression. Plant J. 58 (2): 275–286.
[63]. Guo H-S, Xie Q, Fei J-F, Chua N-H (2005) MicroRNA Directs mRNA Cleavage of the Transcription Factor NAC1 to Down regulate Auxin Signals for Arabidopsis Lateral Root Development. The Plant Cell. 17: 1376–1386.

[64]. Prasad K, Zhang X, Tobo´n E, Ambrose B.A (2010) The Arabidopsis Bsister MADS-box protein, GORDITA, represses fruit growth and contributes to integument development. Plant J. 63 (6): 914–924.
[65]. Zhou Y, Zhang X, Kang X, Zhao X, Zhang X, et al. (2009) SHORT HYPOCOTYL UNDER BLUE1 associates with MINISEED3 and HAIKU2 promoters in vivo to regulate Arabidopsis seed development. Plant Cell. 21: 106–117.
[66]. Lukowitz W.W, Assaad F, Schwarz H, Jürgens G, Mayer U (2000) The Arabidopsis KNOLLE and KEULE genes interact to promote vesicle fusion during cytokinesis. Current Biology. 10 (21): 1371–1374.
[67]. Kirik A, Ehrhardt D.W, Kirik V (2012) TONNEAU2/FASS Regulates the Geometry of Microtubule Nucleation and Cortical Array Organization in Interphase Arabidopsis Cells. The Plant Cell. 24: 1158–1170.
[68]. Tanaka H, Ishikawa M, Kitamura S, Takahashi Y, Soyano T, et al. (2004). The AtNACK1/HINKEL and STUD/TETRASPORE/ AtNACK2 genes, which encode functionally redundant kinesins, are essential for cytokinesis in Arabidopsis. Genes Cells. 9 (12): 1199–1211.
[69]. Assaad F.F. Huet Y. Mayer U. Jurgen G (2001) The cytokinesis gene KEULE encodes a Sec1 protein that binds the syntaxin KNOLLE. J. Cell. Biol. 152: 531-543.
[70]. Strompen G, Elkasmi F, Richters S, Lukowitz W, Asaad F, et al. (2002). The Arabidopsis HINKEL gene encodes a kinesin-related protein involved in cytokinesis and is expressed in a cell cycle-dependent manner. Curr. Biol. 12: 153-158.
[71]. Kirik V, Grini P.E, Mathur J, Klinkhammer I, Adler K, et al. (2002). The Arabidopsis TUBULIN-FOLDING COFACTOR gene is involved in the control of the α/α-tubulin monomer balance. The Plant Cell. 14: 2265-2276.
[72]. Western T.L, Young D.S, Dean G.H, Tan W.L, Haughn A.L (2004) MUCILAGE MODIFIED4 encodes a putative pectin biosynthetic enzyme developmentally regulated by APETALA2, TRANSPARENT TESTA GLABRA 1, and GLABRA 2 in the Arabidopsis seed coat. Plant Physiology. 134: 296–306.
[73]. Debeaujon I, Lepiniec L, Pourcel L, Routaboul J.M (2007) Seed coat development and dormancy. Annual Plant Reviews Volume 27: Seed Development, Dormancy and Germination. Blackwell Publishing Ltd. Oxford, U.K. 25–49. http://www.slideshare.net/Hariezt24/annual-plant-reviews-seed-development-dormancy-and-germination
[74]. Bentsink L, Soppe W, Koornneef M (2007) Genetic aspects of seed dormancy. Annual Plant Reviews Volume 27: Seed Development, Dormancy and Germination. Blackwell Publishing Ltd. Oxford, U.K. 113–132. http://www.slideshare.net/Hariezt24/annual-plant-reviews-seed-development-dormancy-and-germination
[75]. Pourcel L, Routaboul J-M, Lucien Kerhoas L, Caboche M, Lepiniec L, et al. (2005). TRANSPARENT TESTA10 Encodes a Laccase-Like Enzyme Involved in Oxidative Polymerization of Flavonoids in Arabidopsis Seed Coat. The Plant Cell. 17: 2966–2980. www.plantcell.org/cgi/doi/10.1105/tpc.105.035154
[76]. Hilhorst H.W.M (2007) Definitions and hypotheses of seed dormancy. Annual Plant Reviews Volume 27: Seed Development, Dormancy and Germination. Blackwell Publishing Ltd. Oxford, U.K. 50–71. http://www.slideshare.net/Hariezt24/annual-plant-reviews-seed-development-dormancy-and-germination
[77]. Yamaguchi S, Nambara E (2006) Seed development and germination. In: Hedden P., Thomas S.G. (Eds.), Plant Hormone Signaling. Blackwell Publishing Ltd. 311–338. http://samples.sainsburysebooks.co.uk/9781405173063_sample_387254.pdf
[78]. Richards D.E, King K.E, Ait-Ali T, Harberd N.P (2001) How gibberellin regulates plant growth and development: a molecular genetic analysis of gibberellin signaling. Annu Rev. Plant Physiol. Plant Mol. Biol. 67–88.
[79]. Chapman E.J, Estelle M (2009) Mechanism of Auxin-Regulated Gene Expression in Plants. Annu. Rev. Genet. 43: 265–285.
[80]. Galun E (2007) Plant Hormones. In: Plant Patterning. Structural and Molecular Genetic Aspects. Copyright by World Scientific Publishing Co. Pte. Ltd. 29–85. http://www.worldscientific.com/worldscibooks/10.1142/6326
[81]. Berleth T, Krogan N.T, Enrico Scarpella E (2004) Auxin signals – turning genes on and turning cells around. Curr. Opin. in Plant Biol. 7: 553-563.
[82]. Spartz A.K, Gray W.M (2008) Plant hormone receptors: new perceptions. Genes & Development. 22: 2139–2148.
[83]. Galun E (2007) Patterning of the angiosperm embryo. In: Plant Patterning. Structural and Molecular Genetic Aspects. Copyright by World Scientific Publishing Co. Pte. Ltd. 159–179. http://www.worldscientific.com/worldscibooks/10.1142/6326
[84]. Halliday K.J (2004) Plant Hormones: The Interplay of Brassinosteroids and Auxin. Current Biology. 14:1008–1010.
[85]. Kant S, Bi Y.-M, Zhu T, Rothstein S.J (2009) SAUR39, a Small Auxin-Up RNA Gene, Acts as a Negative Regulator of Auxin Synthesis and Transport in Rice. Plant Physiology. 151: 691–701.
[86]. Teale W.D, Papanov I.A, Palme K (2006) Auxin in action: signalling, transport and the control of plant growth and development. Mol. Cell. Biol. 7: 847–859.
[87]. Tsygankova V.A,Galkina L.A, Musatenko L.I, Sytnik K.M (2005) GENETIC AND EPIGENETIC CONTROL OF PLANT GROWTH AND DEVELOPMENT. MOLECULAR-GENETIC CONTROL OF AUXIN SIGNALS: TRANSMISSION AND REALIZATION. Biopolymers and cell. 21(1): 187–219. https://www.academia.edu/4565635/Signalling_Pathways_of_auxin
[88]. Krizek B.A (2011) Auxin regulation of Arabidopsis flower development involves members of the AINTEGUMENTA-LIKE/PLETHORA (AIL/PLT) family. J. Exp. Bot. 62: 3311- 3319.
[89]. Michniewic Z.M, Zago M.K, Abas L, Weijens D, Schweighofer A, et al. (2007). Antagonistic regulation of PIN phosphorylation by PPA2 and PINOID directs auxin flux. Cell. 130: 1044-1056.
[90]. Wellmer F, Bowman J.L, Davies B, Ferrándiz C, Fletcher J.C, et al. (2014). Flower development: open questions and future directions. Methods Mol Biol. 1110: 103 - 124.
[91]. Hamann T, Benkova E, Baurle I, Keintz M, Jurgens G (2002) The Arabidopsis BODENLOS gene encodes an auxin response protein inhibiting MONOPTEROS-mediated embryo patterning. Genes Dev. 16: 1610-1615.
[92]. Krizek B.A, Anderson J.T (2013) Control of flower size. J. Exp. Bot. 64 (6): 1427–1437.
[93]. Brenner W.G, Romanov G.A, Kollmer I, Bürkle L, Schmülling T (2005) Immediate-early and delayed cytokinin response genes of Arabidopsis thaliana identified by genome-wide expression profiling reveal novel cytokinin-sensitive processes and suggest cytokinin action through transcriptional cascades. The Plant Journal. 44: 314–333.
[94]. Heyl A, Werner T, Schmülling T (2006) Cytokinin metabolism and signal transduction. In: Hedden P., Thomas S.G. (Eds.), Plant Hormone Signaling. Blackwell Publishing Ltd. 93–124 pp. http://samples.sainsburysebooks.co.uk/9781405173063_sample_387254.pdf
[95]. Müller B, Sheen J (2007) Arabidopsis cytokinin signaling pathway. Sci. STKE. 407: cm5.
[96]. Lee D.J, Park J-Y, Su-Jin Ku S-J, Ha Y-M, Kim S, et al. (2007). Genome-wide expression profiling of ARABIDOPSIS RESPONSE REGULATOR 7 (ARR7) overexpression in cytokinin response. Mol. Genet. Genomics. 277: 115–137.
[97]. Che P, Gingerich D.J, Lall S, Howell S.H (2002) Global and Hormone-Induced Gene Expression Changes during Shoot Development in Arabidopsis. The Plant Cell. 14: 2771–2785.
[98]. Rashotte A. M, Carson S. D. B, To J. P. C, Kieber J. J (2003) Expression Profiling of Cytokinin Action in Arabidopsis. Plant Physiology. 132: 1998–2011.
[99]. Kakimoto T (2003) Perception and signal transduction of cytokinins. Annu. Rev. Plant Biol. 54: 605–627.
[100]. Deng Y, Dong H, Mu J, Ren B, Zheng B, et al. (2010). Arabidopsis histidine kinase CKI1 acts upstream of HISTIDINE PHOSPHOTRANSFER PROTEINS to regulate female gametophyte development and vegetative growth. Plant Cell. 22 (4): 1232–1248.
[101]. Khodakovskaya M, Zhao D, Smith W, Li Y, McAvoy R (2006) Expression of ipt gene controlled by an ethylene and auxin responsive fragment of the LEACO1 promoter increases flower number in transgenic Nicotiana tabacum. Plant Cell Rep. 25: 1181–1192.
[102]. Dill A, Thomas S.G, Hu J, Steber C.M, Sun T.P (2004) The Arabidopsis F-box protein SLEEPEY1 targets gibberilin signaling repressors for gibberillin-induced degradation. The Plant Cell. 16: 1392-1405.
[103]. Marti E, Carrera E, Ruiz-Rivero O, Garcia-Martinez J.L (2010) Hormonal regulation of tomato gibberellin 20-oxidase expressed in Arabidopsis. Journal of Plant Physiology. 167: 1188–1196.
[104]. Szekeres M, Bishop G.J (2006) Integration of brassinosteroid biosynthesis and signaling. In: Hedden P., Thomas S.G. (Eds.), Plant Hormone Signaling. Blackwell Publishing Ltd. 67–92. http://samples.sainsburysebooks.co.uk/9781405173063_sample_387254.pdf
[105]. Tanabe S, Ashikari M, Fujioka S, Takatsuto S, Yoshida S, et al. (2005) A novel cytochrome P450 is implicated in brassinosteroid biosynthesis via the characterization of a rice dwarf mutant, dwarf11, with reduced seed length. Plant Cell. 17: 776–790.
[106]. Graeber K, Linkies A, Muller K, Wunchova A, Rott A, et al. (2010) Cross-species approaches to seed dormancy and germination: conservation and biodiversity of ABA-regulated mechanisms and the Brassicaceae DOG1 genes. Plant Mol. Biol. 73: 67–87.
[107]. Shinozaki F.K, Yamaguchi-Shinozaki K (2000) Molecular responses to dehydration and low temperature: differences and cross-talk between two stress signaling pathways. Current Opinion in Plant Biology. 3: 217–223.
[108]. Vandenbussche F, Vaseva I, Vissenberg K, Straeten D.V.D (2012) Ethylene in vegetative development: a tale with a riddle. New Phytologist. 194 (4):

895–909.
[109]. Wasternack C (2006) Oxylipins: biosynthesis, signal transduction and Action In: Hedden P., Thomas S.G. (Eds.), Plant Hormone Signaling. Blackwell Publishing Ltd, 185–228. http://samples.sainsburysebooks.co.uk/9781405173063_sample_387254.pdf
[110]. Wasternack C, Xie D (2010) The genuine ligand of a jasmonic acid receptor. Improved analysis of jasmonates is now required. Plant Signaling & Behavior. 5 (4): 337–340.
[111]. Turner J. G, Ellis C, Devoto A (2002) The Jasmonate Signal Pathway. The Plant Cell. 14: 153–164.
[112]. Benedetti C.E, Xie D, Turner J.G (1995) COII-Dependent Expression of an Arabidopsis Vegetative Storage Protein in Flowers and Siliques and in Response to Coronatine or Methyl Jasmonate. Plant Physiol. 109: 567–572.
[113]. Kim J, Dotson B, Rey C, Lindsey J, Bleecker A.B, et al. (2013) New Clothes for the Jasmonic Acid Receptor COI1: Delayed Abscission, Meristem Arrest and Apical Dominance. PLOS ONE. 8 (4): 60505.
[114]. Adams E, Turner J.G (2010) COI1, a jasmonate receptor, is involved in ethylene-induced inhibition of Arabidopsis root growth in the light. J. Exp. Bot. 61 (15): 4373–4386.
[115]. Ueda J, Miyamoto K, Aoki M (1994) Jasmonic Acid Inhibits the IAA-Induced Elongation of Oat Coleoptile Segments: a Possible Mechanism Involving the Metabolism of Cell Wall Polysaccharides. Plant Cell Physiol. 35 (7): 1065–1070.