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PLANT EMBRYOGENESIS: DEVELOPMENTAL AND GENOMIC PERSPECTIVES FROM MODEL TO CROP PLANTS

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ABSTRACT

Embryonic development represents an important reproductive phase of sexually reproducing plant spe cies. The fusion of egg and sperm produces the plant zygote, a totipotent cell that, through cell division and cell identity specification in early embryogenesis, establishes the major cell lineages and tissues of the adult plant. The subsequent morphogenesis phase produces the full-sized embryo, while the late embryogenesis maturation process prepares the seed for dormancy and subsequent germination, ensuring continuation of the plant life cycle. In this review on embryogenesis, we compare the model eudi cot Arabidopsis thaliana with monocot crops, focusing on genome activation, paternal and maternal regu lation of early zygote development, and key organizers of patterning, such as auxin and WOX transcription factors. While the early stages of embryo development areapparently conserved among plant species, embryo maturation programs have diversified between eudicots and monocots. This diversification in crop species reflects the likely effects of domestication on seed quality traits that are determined during embryo maturation, and also assures seed germination in different environmental conditions. This review describes the most important features of embryonic development in plants, and the scope and applications of geno mics in plant embryo studies.

Keywords: embryogenesis, embryo patterning, zygote genome activation, transcription factors, genomics, transcriptomics

a. introduction

In this review, we focus on advances made using genomics to investigate plant embryogenesis. We address how efforts with Arabidopsis have uncovered key aspects of early embryo development and highlight which mechanisms might be conserved in other eudicots and monocots. Recent genomic studies in monocots, such as rice, maize, and wheat, have advanced our understanding of the molecular aspects of monocot embryogenesis. Besides developmental insights, the application of genomics technologies using transcriptome analysis of eudicot crops, such as oilseeds and legumes, revealing the flexibilities that exist in carbohydrate, protein, fatty acid (FA), and secondary metabolite and storage product synthesis during the maturation phase of embryo development. Integration of developmental biology and genomics will create new opportunities to engineer crop seed embryos with desirable composition and yield traits.

B. Research Method

This study uses a literature review method with a descriptive qualitative approach that focuses on tracing, analyzing, and synthesizing various research findings related to plant embryogenesis. The review is focused on research published during the period 2019–2025, with priority given to primary sources from reputable scientific journals such as *Frontiers in Plant Science, Plant, Cell* & *Environment, Current Opinion in Plant Biology, and BMC Plant Biology.*

The analysis results are presented in an analytical descriptive form by relating the latest research findings to produce a conceptual synthesis on the development and genomics of plant embryogenesis: from model plants to cultivated plants.

C. Result And Discussion

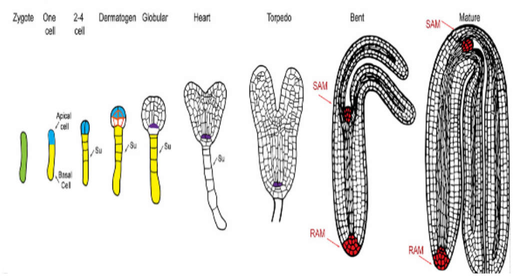
1. Embryo Development in Plants

Angiosperm seeds are a combination of genotypes and tissue types. Gametes are produced by meiosis, and then segregate into the male and female gametophytes. Each pollen grain has two haploid sperm cells, while the ovule has a haploid egg cell and a diploid central cell that is derived from the fusion of two identical haploid polar nuclei. The seed is produced by a double fertilization event, where one sperm cell fuses with the diploid central cell to create the triploid endosperm, and the second sperm cell fuses with the egg cell to produce the diploid zygote. The resulting embryo and endosperm continue to develop within the seed coat, which is derived from the maternal tissues of the ovule. The diploid embryo has one maternal and one paternal genome, the triploid endosperm has two maternal genomes and one paternal genome, and the diploid seed coat is derived entirely from diploid maternal tissue, without undergoing meiosis (Alaniz et al., 2020).

2. Arabidopsis *thaliana*: a model for embryogenesis in eudicots

After fertilization in A. *thaliana*, the nucleus of the zygote moves to the apical cell that will generate the entire embryo, with the exception of the suspensor, the 8-cell embryo at 60 HAP, the 16 cell dermatogen embryoat 66 HPA, 72HAP, andthe 500-cell heart-stage embryo at 120 HAP (Zheng et al., 2019). The epidermal lineage is specified at the dermatogen stage, while the ground and vascular tissue lineages, as well as shoot apical meristem (SAM) and root apical meristem (RAM), are produced at the globular stage. Cotyledons (embryonic leaves, the first lateral organs) are produced at the heart stage, when all major pattern elements of the Arabidopsis embryo have been established. After pattern formation, the embryo undergoes a period of morphogenesis where growth of the organs that were established by the heart stage lead to an embryo with fully organized SAM and RAM, hypocotyl (embryonic stem), and elongated cotyledons which fold over as the embryo grows inside the seed coat (Figure 1).

a. Arabidopsis embryo



b. Gramineous embryo

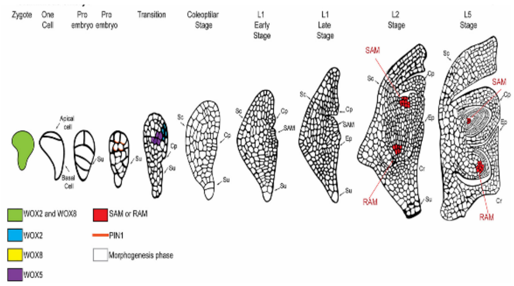


Figure 1. Embryo development in dicot Arabidopsis and monocot Graminae

3. Developmental Genomics of Plant Embryogenesis

After pattern formation and morphogenesis, embryos of Arabidopsis and closely related oilseed crop species undergo maturation, culminating in the desiccated seed (Zhou et al., 2020). Maturation stages include the mid-heart, torpedo, bent coty ledon, mature green, and dry seed. During early maturation, also known as ‘‘seed filling,’’ embryos experience rapid cellular division and expansion, turning green starting at the mid-heart stage, and also produce and accumulate seed storage proteins (cruciferins/12S globulins and arabins/2S albumins). Starting at the early torpedo stage, the oils and waxes that form the cuticle of the epidermis are produced. Storage of lipids, carbohydrates, and FAs during late embryogenesis is critical for supporting the subsequent energy demands of germination. Late maturation also involves the loss of water (desiccation) and the establishment of seed dormancy (Yoshida et al., 2019).

Coincident with the development of the embryo, the endosperm is initially a coenocyte formed bynuclear division andmigration of the nuclei from the micropylar region (surrounding the embryo) toward the opposite (chalazal) end of the seed. The endosperm of Arabidopsis has three regions that become distinct as the seed grows: the micropylar endosperm that surrounds the embryo, the peripheral endosperm in the central region, and the chalazal endosperm. Beginning at the heart stage of embryo genesis the endospermcellularizes (Radoeva et al., 2019).

The seed coat (or testa), the outermost compartment of the seed that protects the embryo, is a maternal tissue and consists of five cell layers: the innermost endothelial layer, followed by two cell layers of inner integument and two more cell layers of the outer integument (Grover et al., 2020). During the first week after fertilization in Arabidopsis, the endothelium cells synthesize proanthocyanin flavonoid compounds that subsequently oxidize, giving a brown color to the seed coat. The inner integument layers do not appear to differentiate further, while theouterintegumentlayersaccumulate starch-containingamylo plasts during growth. The epidermal layer ofthe outerintegument synthesizes and secretes mucilage (a pectinaceous carbohy drate) and also develops a thick secondary cell wall. During the later stages of seed development, the cells of all seed coat layers die except for the epidermis. Epidermal cells develop secondary cell walls that are assumed to provide support, protection, and impermeability to water and oxygen (Doll et al., 2020).

4. Embryogenesis in monocot model species

Zygotes of grasses, such as maize, rice, and wheat, are also polarized, with the nucleus at the apical pole. Unlike Arabidopsis, the zygote does not elongate after fertilization (Chen et al., 2017). In rice, maize, and wheat the first transverse division of the zygote forms a two-cell embryo, where the basal cell transforms into a large vesicular cell and continued division of the apical cell gives rise to the quadrant, octant, and dermat ogen stages (known as proembryo stages), followed by the tran sition-stage embryos (Xiang et al., 2019). At the transition stage, corresponding to about 8 DAP in maize and 4 DAP in rice, the adaxial–abaxial axis of the embryo becomes obvious, as the coleoptile primordium begins to protrude from the adaxial region of the embryo, while the scutellum arises from the abaxial side. The coleoptile protects the developing SAM, while the scutellum is equivalent to the dicot cotyledon (Figure 1). The SAM develops on the adaxial side and will produce several embryonic leaves during seed development, while differentiation of the RAM defines the basal pole of the embryo. In rice, the embryo reaches its mature shape when organ differentiation is complete at 7–8 DAP, although morphogenesis continues as the embryo enlarges and shoot and root meristems are completely surrounded by the protective coleoptile and coleorhiza, respectively. In grasses, the early vegetative stages of the embryonic seedling are incorporated into the embryo before dormancy (Figure 1) (Zhao et al., 2020).

In Arabidopsis and related dicots, such as Capsella bursa-pasto ris, the first division of the zygote is asymmetric, and the following divisions are stereotypical, meaning that cell identities can be fol lowed based on similar division orientation and cell morphology. This is not the case in grasses, where the first division is asymmetric in terms of cell size, and subsequent divisions do not follow any set pattern. In grasses, root specification occurs in the center of the embryo, while in Arabidopsis the root meristem differentiates from the hypophysis, which is located at the interface between the suspensor and the embryo. In agreement with this difference between monocots and dicots, WOX5, a molecular marker for the RAM, shows expression in the hypophysis of Arabidopsis and at the center of the embryo in maize (Rolletschek et al., 2020).

Grasses also have embryo-specific organs, such as the scutellum, coleoptile, and epiblast, that are not present in dicots. In many cases, the function of these grass-specific embryonic organs has not been extensively studied. For example, the functional role of the scutellum in maize seeds has only recently been explored by genetic assays (Doll et al., 2020).

There are also differences in the developmental timing of the embryo between Arabidopsis and grasses. For example, in wheat the middle embryo developmental stages (transition and early leaf stages) represent the phylotypic stage of embryogenesis (Xiang et al., 2019). The difference in the timing of primordium initiation and organ differentiation in monocots and eudicots may explain this shift in the phylotypic stage.

5. Genomic Studies of Embryo Development in A. *thaliana*

Many years of systematic developmental and genetic studies have resulted in identification of more than 500 for embryo defective (emb) mutants. EMB genes are broadly defined as essential genes whose function is required during embryogenesis, including cell-type differentiation mutants, transformation of suspensor cell mutants, meristem differentiation mutants, maturation program mutants, and genes required for basic cellular functions whose loss results in embryo or seedling lethality (Meinke, 2019). These findings provided a framework for processes that play critical functions during Arabidopsis implications for other plant species.

Functional and molecular studies have identified signaling pathways and transcription factors (TFs) that regulate the first divisions of the zygote, leading to the first cell fate differentiation events in the embryo. For example, the WOX TF family genes WOX2 and WOX8 are co-expressed in the zygote. After the first asymmetric division, WOX2 is expressed in the apical daughter cell and WOX8 is specifically expressed in the basal daughter cells of the zygote (Khan et al., 2020).

This polar auxin transport is mediated by the auxin efflux transporter PIN7, which is expressed in the basal cell lineage. Later in embryo development, other auxin transporters, such as PIN1, are expressed in the apical proembryo (Hofmann et al., 2019). Auxin regulates pattern formation in embryos, and thus defects in auxin response, auxin biosynthesis, and auxin transport affect embryonic development of auxin responses in embryos results in cellular reprogramming of suspensor cells into extraembryonic cells. Transcriptional analysis of these suspensor cells revealed a helix-loop-helix TF network suppressing embryo development from the suspensor (Radoeva et al., 2019).

To identify the molecular components of the genetic program of embryo development, studies of embryo gene expression have been carried out using microarrays or RNA sequencing (RNA seq) (Hofmann et al., 2019). Furthermore, some of these studies focused on specific cell types within the embryo (Zhou et al., 2020). Despite the ongoing debate about the contribution of paternal and maternal genomes to zygotic genome activation in Arabidopsis there is a consensus for the importance of early zygotic transcriptional activity, because inhibition of RNA polymerase II in the zygote caused a delay or arrest of cell divisions of Arabidopsis zygotes. Denovo transcripts are detectable in the zygote after fertilization, yet it is also true that the majority of transcripts found in the plant zygote are already present in the egg cell (Zhao et al., 2019), which suggests transcript carryover representing maternal origin from the egg cell to the zygote.

Hofmann et al. (2019) took a similar approach, profiling embryos from preglobular to mature green stages. In addition to identifying known TF markers for early embryogenesis, such as WOX2, WOX8, and DRN, they also identified new markers for many later stages of development, concluding that there are four overall transcriptome phases in Arabidopsis embryogenesis: preglobular–heart stage, torpedo stage, bent cotyledon stage, and mature green stage. Their analysis suggests that the Arabidopsis embryonic transcriptome undergoes radical global changes after both the globular and bent cotyledon stages.

Analysis of epigenome marks by chromatin immunoprecipitation sequencing data combined with single-cell expression using either INTACT or other single-cell technologies will give us a more complete picture of how regulatory gene activities of chromosomes organize during embryogenesis. It will also help determine if parental chromatin states can be inherited in the newly formed embryos and how these might relate to allele-specific gene expression in hybrids and their impact on hybrid vigor. The use of emerging technolo gies for probing the relationship between three-dimensional chromatin structure and gene expression will allow us to under stand the genomic contribution of different subgenomes in em bryos of polyploid crops, and will also provide information about the evolution of gene expression in polyploids and the selective pressures placed on seed and grain production in crop species during domestication and breeding.

D. Concluding Remarks

Although structural differences in embryo development between dicots and monocots have been reported, we have only understand the underpinning molecular similarities and differences with embryogenesis in the model plant Arabidopsis and in agriculturally important dicots, such as soybean, flax, and canola, and monocot species, such as corn, wheat, and rice. These advances are providing increased understanding of the develop mental and molecular differences and the particularities specific to dicots versus monocots.

Detailed studies of embryo maturation programs have generated insights into the synthesis and deposition of the economically important major storage product sespecially carbohydrates, lipids, and storage proteins. However, significant knowledge gaps still exist in the biochemical and molecular understanding of several important seed secondary metabolites and their synthesis in both monocot and dicot crops of commercial interest. With the availability of genome sequences for all major crops, it is possible to apply recent advances in genomics technologies (fluorescence-activated cell sorting, INTACT, ATAC-seq) to elucidate the fundamental functional characteristics of embryo developmental programs, facilitating the pros pects to design crop seeds with desirable nutritional composition and yields.

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