Developmental and genomic architecture of plant embryogenesis: from model plant to crops

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ABSTRACT

Embryonic development represents an important reproductive phase of sexually reproducing plant species. 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 eudicot Arabidopsis thaliana with monocot crops, focusing on genome activation, paternal and maternal regulation of early zygote development, and key organizers of patterning, such as auxin and WOX transcription factors. While the early stages of embryo development are apparently 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 genomics in plant embryo studies.

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

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INTRODUCTION

Previously, we have discussed the genetic and metabolic pathways that regulate seed size and seed nutritional value in important crops, as well as strategies for the genetic improvement of oilseeds and grains (Venglat et al., 2014). 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, are 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.

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 (Reiser and Fischer, 1993).

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

After fertilization in *A. thaliana*, the nucleus of the zygote moves to the apical pole and the zygote divides asymmetrically to produce a small apical cell that will generate the entire embryo, with the exception of the suspensor, hypophysis, and root cap, which are derived from the larger basal cell. Cell division in these two lineages produces the 2- to 4-cell-stage embryo at ~48 h after pollination (HAP), the 8-cell embryo at ~60 HAP, the 16-cell dermatogen embryo at ~66 HPA, the 32-cell globular embryo at ~72 HAP, and the ~500-cell heart-stage embryo ~120 HAP (Jürgens and Mayer, 1994). 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 (Figure 1). 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).
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After pattern formation and morphogenesis, embryos of *Arabidopsis* and closely related oilseed crop species undergo maturation, culminating in the desiccated seed (Goldberg et al., 1994). Maturation stages include the mid-heart, torpedo, bent cotyledon, 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 (Baud and Lepiniec 2010). Late maturation also involves the loss of water (desiccation) and the establishment of seed dormancy (Leprince et al., 2017).

Coincident with the development of the embryo, the endosperm is initially a coenocyte formed by nuclear division and migration 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 embryogenesis (approximately 5 days after pollination [DAP]), the endosperm cellularizes. As in many dicots, the *Arabidopsis* endosperm is consumed during seed maturation, leaving only a peripheral aleurone-like cell layer next to the seed coat, surrounding the mature embryo (Olsen, 2004).

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 (Lepiniec et al., 2006). 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 the outer integument layers accumulate starch-containing amyloplasts during growth. The epidermal layer of the outer integument synthesizes and secretes mucilage (a pectinaceous carbohydrate) 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 (Haughn and Chaudhury, 2005).

**Embyrogenesis 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; Xiang et al., 2019). 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 dermatogen stages (known as proembryo stages), followed by the transition-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) (Itoh et al., 2005, 2016; Vernoud et al., 2005).

**Principal differences in embryo development between monocots and eudicots**

In *Arabidopsis* and related dicots, such as *Capsella bursa-pastoris*, the first division of the zygote is asymmetrical, and the following divisions are stereotypical, meaning that cell identities can be followed 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 (Nardmann et al., 2007; Sarkar et al., 2007). 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., 2020a) (Figure 1).

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 phyloptic stage of embryogenesis (Xiang et al., 2019). This is earlier than the phyloptic stage in *Arabidopsis*, which occurs at the torpedo stage when the transition from morphogenesis to the maturation phase occurs (Quint et al., 2012). The difference in the timing of primordium initiation and organ differentiation in monocots and eudicots may explain this shift in the phyloptic stage.

In contrast to monocots, where the endosperm persists in the mature seed and serves as a nutrient source during seedling growth, the endosperm is mostly absent in mature seeds of eudicots as it is consumed by the embryo during seed development. Thus, the eudicot embryo itself must contain oils, carbohydrates, and proteins necessary for seedling development. For example, seeds of soybean (*Glycine max*), linseed (*Linum usitatissimum*), and rapeseed (*Brassica napus*) contain large amounts of...
oils, and up to 90% FAs of the seed of *B. napus* are synthesized within the embryonic cotyledons. Despite the transient nature of the endosperm in *A. thaliana*, the development of the endosperm has been shown to influence the embryo, and vice versa. A two-way molecular dialogue between embryo and endosperm has recently been shown to be required for embryonic cuticle formation. This interaction requires GSO-RLK receptors that depend on the sulfated peptide precursor TWS1 as a ligand. TWS1 is produced in the embryo and diffuses to the endosperm, where it is cleaved and activated by the ALE1 subtilase before diffusing back to the embryo to trigger GSO1/2-dependent cuticle deposition (Doll et al., 2020b).

**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* embryogenesis, with 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 (Haecker et al., 2004). The elongation of the zygote and its first asymmetric division are regulated through the YODA (YDA) mitogen-activated protein kinase kinase kinase (MAPKKK), which acts through the MAP kinase kinases, MPK3/MPK6, to phosphorylate and activate the WRKY2 TF (Ueda et al., 2017). Thereafter, WRKY2 promotes WOX8 transcription in the zygote (Ueda et al., 2017). The YODA-MAP signaling cascade in the zygote is initially activated by paternal SHORT SUSPENSOR (SSP) (Bayer et al., 2009), a membrane-associated pseudo-kinase delivered from the sperm cell. A maternal contribution is also required for the YODA-MAPK cascade, as reciprocal crosses between wild-type and MAPKKK mutants showed only a maternal effect on asymmetric division and cell elongation (Zhang et al., 2017) (Figure 2).

Early embryo patterning in *Arabidopsis* also requires the accumulation of the hormone auxin in the apical cell, driven by polar transport from the suspensor. 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 (Frimer et al., 2003). Auxin regulates pattern formation in embryos, and thus defects in auxin response, auxin biosynthesis, and auxin transport affect embryonic development (Robert et al., 2018). Inhibition 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 embryonic development from the suspensor (Radoeva et al., 2019). Recently, the SOSEKI family of polarly localized proteins was found in a transcriptome experiment with arf5 mutants. SOK1-YFP is first detected in the apical side of lower-tier inner cells at the early globular stage. The unique corner localization pattern of SOSEKI proteins suggests that they might influence cell division orientation in embryos (Yoshida et al., 2019). soseki single mutants do not show any embryo defects (Yoshida et al., 2019), demonstrating the utility of transcriptomics in identifying new key players in embryogenesis that would be difficult to find in genetic screens due to redundancy in gene families (Figure 2).

To identify the molecular components of the genetic program of embryonic development, studies of embryo gene expression have been carried out using microarrays or RNA sequencing (RNA-seq) (Xiang et al., 2011; Gao et al., 2019; Hofmann et al., 2019). Furthermore, some of these studies focused on specific cell types within the embryo (Belmonte et al., 2013; Slane et al., 2014; Palovaara et al., 2017; Zhou et al., 2020). Genomics approaches were also applied for understanding microRNA (miRNA) regulation of embryo patterning and maturation programs (Nodine and Bartel, 2010; Willmann et al., 2011; Armenta-Medina et al., 2017; Lepe-Soltero et al., 2017; Plotnikova et al., 2019). Despite the ongoing debate about the contribution of paternal and maternal genomes to zygotic genome activation in Arabidopsis (Del Toro-De León et al., 2016; Armenta-Medina and Gillmor, 2019), 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 (Pilotti et al., 2010; Kao and Nodine, 2019; Zhao et al., 2019). *De novo* transcripts are detectable in the zygote after fertilization (Zhao et al., 2019), yet it is also true that the majority of transcripts found in the plant zygote are already present in the egg cell (Xiang et al., 2011; Zhao et al., 2019), which suggests transcript carryover representing maternal origin from the egg cell to the zygote.

Xiang et al. (2011) used microarrays for one of the first genome-wide gene expression studies of embryogenesis in plants, profiling the zygote through mature-stage Arabidopsis embryos. This study revealed that auxin stimulus, response, and signaling events are more prominent in early embryogenesis. Once the body plan is established, meristem and morphogenesis genes are more active, while at later phases, carbohydrate, FA, and storage protein synthesis activities occur, reflecting deposition of storage reserves. At the mature phases, genes associated with abscisic acid response and dehydration are more highly expressed, while the embryo undergoes desiccation to become a dormant and fully mature embryo. Subsequent studies used RNA-seq to profile transcripts in whole embryos throughout development. Gao et al. (2019) used this approach to identify methylation, initiation of photosynthesis, and storage/energy-related protein activation as three signature gene activities associated with early/middle, late, and mature stages of embryo development, respectively. They found GO terms, including DNA replication, RNA methylation, and histone 3 lysine 9 (H3-K9) methylation, enriched for transcripts expressed from zygote to torpedo stages of embryo development, supporting the role of significant epigenetic programming during early and middle stages of embryo development (Gao et al., 2019). 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.

The first to describe tissue-specific transcriptomes from embryo and seed compartments were Belmonte et al. (2013). Using laser-capture microdissection and microarray analysis, they isolated and profiled gene expression in the embryo proper and suspensor; micropylar, peripheral, and chalazal subregions of the endosperm; and chalazal and distal seed coat regions, at preglobular, globular, heart, torpedo, and mature green stages. The embryo proper showed transcripts enriched for GO terms associated with patterning events, while the globular-stage suspensor was enriched for auxin-related genes, such as YUC3, the auxin efflux carrier PIN7, and the auxin-responsive TF ARF16. Surprisingly, genes encoding all the enzymes required for starch biosynthesis were detected in the suspensor. Belmonte et al. (2013) also identified seed maturation processes, such as storage protein and oil body synthesis, in the embryo and all three endosperm subregions, involving many of the same genes, suggesting that processes that regulate seed size and filling are coordinated across several subregions and seed compartments.

As an alternative to laser-capture microdissection to look at specific tissues, Slane et al. (2014) used fluorescence-activated nuclear sorting to isolate early stages of the whole embryo, the proembryo, and the suspensor, and profiled these stages using microarray analysis. Isolation of specific embryo tissues has also been explored using INTACT (isolation of nuclei tagged in specific cell types), a two-component transgenic labeling system where biotin ligase (BirA) biotinylates a nuclear envelope GFP protein (nuclear targeting fusion) when co-expressed in the same cell. Thus, biotin-tagged nuclei from crude nuclear preparations are separated using streptavidin beads and can then be used for transcriptome analysis (Deal and Henikoff, 2011). Using tissue-specific promoters, Palovaara et al. (2017) adapted the INTACT system to purify cell-type-specific nuclear RNA and generate a transcriptome atlas of whole embryos and specific cell types at the 16-cell, early, and late globular stages, creating a resource to understand how gene activity shapes the formation of the root stem cell niche. Zhou et al. (2020) also used RNA-seq to study the transcriptomes of apical and basal cell lineages of early embryos at the 1- and 32-cell embryo stages. They reported the expression of 990 long non-coding RNAs (lncRNAs), as well as 320 apical cell-specific and 231 basal cell-specific transcript isoforms, suggesting that alternative splicing may also contribute to lineage specification during early development.
embryo development. Allele-specific transcriptomes of the apical cell and basal cell lineages in reciprocal crosses between *Arabidopsis* Columbia-0 (Col-0) and Landsberg erecta (Ler) 1- and 32-cell embryos, revealed that parent-of-origin genes display developmental stage-dependent and cell lineage-dependent allelic expression patterns, with a more active role in basal cell development than in apical cell development (Zhao et al., 2020). These studies provide insights into gene activities associated with apical and basal specifications that define the tissue patterning.

Phenotypes of mutants affecting miRNA biogenesis demonstrate that embryo patterning processes as well as embryo maturation programs are promoted by miRNAs (Schwartz et al., 1994; Grigg et al., 2009; Nodine and Bartel, 2010; Willmann et al., 2011; Seefried et al., 2014; Armenta-Medina et al., 2017). Functional analysis of miRNAs, such as miR165/166, demonstrated their role during embryogenesis by restricting homeobox-leucine zipper family TFs (McConnell et al., 2001; Liu et al., 2009; Smith and Long, 2010; Miyashima et al., 2013), and miR156/157 by repressing SQUAMOUS PROMOTER BINDING PROTEIN-LIKE (SPL) TF genes, both of which are required for proper divisions of root meristem precursor cells (Nodine and Bartel, 2010).

To understand the role of miRNAs in embryogenesis, transcriptomes were generated using mutants defective in the miRNA processing enzymes, DICER LIKE 1 (DCL1) and SERRATE (SE) (Nodine and Bartel, 2010; Willmann et al., 2011; Armenta-Medina et al., 2017). Functional analyses suggested that the miR156, miR159, miR160, miR166, miR171, and miR319 families are among the most highly expressed miRNAs in early embryos. Transcriptomes of *dcf7* embryos showed an increase of seed storage protein and late embryogenesis genes, and subsequent analyses showed that much of this misregulation is due to the absence of miR156 (Nodine and Bartel, 2010; Willmann et al., 2011). Recently, Plotnikova et al. (2019) took a more direct approach to identify miRNAs and other small RNAs in the embryo, by direct profiling of small RNA libraries from embryos at eight embryo developmental stages from preglobular to mature green. Three hundred and forty-nine miRNAs belonging to 259 families were identified in at least one embryonic stage. Analyses of small RNA and mRNA transcriptomes indicated that miRNA:target interactions primarily repress TFs belonging to the ARF, GRAS, HD-ZIP, MADS-box, MYB, NAC, SBP, and TCP domain families.

Now that a wealth of genomic data exists for miRNA, IncRNAs, and small RNA populations in embryos, additional functional analysis is needed to understand the role of TFs, splicing variants, miRNAs, small RNAs, and IncRNAs in the regulation of the developmental and genetic programs that promote cell-type specification during embryogenesis in *Arabidopsis*.

**GENOMIC STUDIES OF EMBRYOGENESIS IN CROP PLANTS**

With the increasing availability of advanced genomics tools and crop genomes, embryo transcriptomes have been produced for species of agronomical importance, such as canola, flax, soy-, bean, rice, wheat, and maize. Although embryo development in several eudicot crops shares developmental and morphological similarities with *Arabidopsis*, seeds of these species have varying compositions of carbohydrates, proteins, and FAs as well as diverse pathways for important secondary metabolites, such as glucosinolate, mucilage, and phytic acid. Monocot seeds have been domesticated for grain filling, resulting in a large domestication effect on seed/grain development and composition. Monocot crops, such as rice, maize, and wheat, have embryos that are morphologically different from dicots, with specialized structures whose functions have not been well defined and understood.

**Embryo transcriptomes in eudicot crops**

*B. napus* is an allopolyploid (A\(^{n}\)A\(^{c}\)C\(^{n}\)C\(^{n}\)) derived from hybridization between *B. rapa* (A\(^{n}\)A\(^{n}\)) and *B. oleracea* (C\(^{n}\)C\(^{n}\)). These oilseeds contain over 35% oil, with triacylglycerols (TAGs) being the main nutritious lipid components of canola oil (Dawidowicz-Grzegorzewska and Podstolski, 1992). Because of canola oil’s economic importance, many transcriptome studies have focused on late stages of embryo development, when the majority of the FA metabolism and the deposition occurs. A study of *B. napus* used a combination of metabolome and transcriptome profiling of developing embryos to focus on lipid biosynthesis, finding that the expression of genes associated with TAG and FA synthesis and elongation substantially increased during late seed development (from 21 to 35 DAP) (Tan et al., 2019). The expression of the FA desaturase, *FAD3*, was closely correlated with the abundance of palmitic acid, oleic acid, linoleic acid, and arachidic acid content in seed embryos. Differentially expressed TFs included *Leafy Cotyledon 2* (LEC2) and *Wrinkled 1* (WR1), two TFs that are known to be key regulators of gene expression during oil biosynthesis (Baud et al., 2007; Tan et al., 2011).

A more recent transcriptome study profiled subregions of *B. napus* seeds at early (globular, heart) and late (mature green, dry seed) stages, revealing that the smaller A\(^{n}\) subgenome derived from *B. rapa* is preferentially expressed, perhaps because the A\(^{n}\) subgenome is less densely populated with transposable elements than the C\(^{n}\) subgenome (Khan et al., 2020). Homologs of *MYB17*, *MYB32*, *MYB61*, and *MYB95* TFs from both A\(^{n}\) and C\(^{n}\) subgenomes are expressed in early seed development, suggesting that transcriptional regulation of early stages is conserved in *Brassica*. Interestingly, TFs encoded by the A\(^{n}\) subgenome were expressed primarily in the seed coat, whereas those encoded by the C\(^{n}\) subgenome were expressed primarily in the embryo. Network analysis of late stage-enriched transcripts derived from the A\(^{n}\) and C\(^{n}\) subgenomes yielded dramatically different predictions of TF regulatory circuits in seed maturation: the A\(^{n}\) subgenome network contained numerous MYB and bHLH interactions, while the C\(^{n}\) subgenome network involved only FUS3 and WOX12 (Khan et al., 2020).

The importance of epigenetic reprogramming during early embryo development has recently been shown for *B. rapa*, in which the RNA-dependent DNA methylation pathway (RdDM) is required in the maternal sporophyte for successful seed development (Grover et al., 2018). The RdDM pathway promotes transcriptional gene silencing of transposons through the action
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of 24-nt small interfering RNAs that establish DNA methylation at thousands of genomic loci. Loss of maternal RdDM causes severe developmental defects and high rates of seed abortion. During B. rapa seed development, 90% of 24-nt siRNAs are produced from fewer than 200 loci that are highly expressed in the ovule and seed coat, accumulate in the endosperm, and at low levels in embryos. These siRNAs remain expressed throughout embryogenesis, indicating that they are likely involved in regulating their target genes throughout seed development (Grover et al., 2020).

Flax (Linum usitatissimum) is prized for its high omega-3 FA oil content (50% of the total seed FAs consist of alpha-linolenic acid), as well as certain seed coat lignans that are present in flax seeds at levels 75–800 times greater than any other crops. To better understand the transcriptomic basis of these characteristics, Venglat et al. (2011) produced flaxseed EST libraries from embryo, endosperm, and seed coat tissues at early, mid, and late developmental stages. Of the enzymes that participate in the four key steps of FA synthesis, transcripts encoding acyl-chain elongation and termination peaked at the torpedo stage, while transcripts for desaturation and TAG synthesis appeared at the cotyledon and mature stages (Venglat et al., 2011). The transcript encoding the enzyme pinoresinol-lariciresinol reductase, which acts late in the lignan pathway to convert coniferyl alcohol to the antioxidant phytoestrogen, secosolariciresinol di-glucoside (SDG), is expressed in the seed coat at the torpedo stage (Venglat et al., 2011). These findings provide new avenues to modulate the quantity and quality of some TAGs; for example, by increasing omega-3 by fine-tuning the expression of a specific FA desaturase in late stages of embryo development. The insights gained may also offer new strategic opportunities for engineering an SDG enzymatic pathway and the possibility of producing increased SDG levels by increasing or modifying the enzymes involved in the synthesis.

Transcriptome studies in monocots

In recent years, embryo transcriptomes have been produced for the globally staple crops maize, rice, and wheat (Itoh et al., 2016; Anderson et al., 2017; Chen et al., 2017; Xiang et al., 2019; Yi et al., 2019). In rice and maize, the majority of transcripts found in the zygote were also present in the egg cell; nonetheless, transcripts for several thousand genes are upregulated in the zygote compared with the egg cell, presumably due to de novo transcriptional activation after fertilization (Anderson et al., 2017; Chen et al., 2017). Parent-of-origin profiling in rice indicates that more than 99% of transcripts are of maternal origin; paternal transcripts in rice zygotes are restricted to a small number of genes encoding putative pluripotency factors, among them three rice orthologs of the Arabidopsis PLETHORA (PLT)/BABYBOOM (BBM) TFs (Anderson et al., 2017; Khanday et al., 2019).

Auxin is essential for early embryo patterning in both Arabidopsis and maize, but key players are likely differently expressed in maize and other grasses compared with Arabidopsis. For example, PIN1, PIN3, PIN4, and PIN7 are required to establish apical-basal polarity via directional auxin transport during Arabidopsis embryogenesis (Friml et al., 2003). In maize, the earliest ZmPIN1 localization was observed at 6 DAP on the adaxial side of the embryo proper (Chen et al., 2014). Moreover, transcripts encoding homologs of key players in auxin-regulated early embryo patterning in Arabidopsis, such as ARFS (MP), IAA12 (BDL), and PIN7, were absent in zygotes and their daughter cells in maize (Chen et al., 2017). In rice, PIN-like genes showed polarized expression along the adaxial-abaxial axis; however, the rice PIN-like genes exhibiting the most polarized expression were homologous to PIN2, PIN5, and PIN8, which do not have important functions in embryogenesis in Arabidopsis (Wang et al., 2009). In maize, ZmWOX9A and ZmWOX9B likely represent the homologs of AtWOX8 and AtWOX9, respectively. Both ZmWOX9A and ZmWOX9B are induced shortly after fertilization and expressed at higher levels in basal cells than in apical cells, like their counterparts in Arabidopsis (Chen et al., 2017). In rice, the orthologs of WOX8/9 (LOC_Os01g47710) show de novo expression at 2.5 h and WOX2 (LOC_Os01g62310) at 5 h after fertilization (Anderson et al., 2017).

In eudicots, such as canola, epigenetic programming has been shown to possibly be important in early embryo development. Arrangement of epigenetic marks is also part of the monocot embryo developmental program. In rice zygotes, transcripts for replication-associated genes, such as the replication-dependent canonical histones H3.1 and the MCM2–7 factors, exhibit a substantial increase in expression with increases of 4- to 163-fold at 9 h in rice zygotes. The transition from G1 through S phases into G2 in rice is characterized by increased expression of a number of epigenetic-associated genes, including rice E2F TF, licensing factors MCM 2–7, CDC45, 14 histones, 6 putative helicases, 3 BRCA family genes, 2 RAD51 orthologs, and CDC6, which are all induced in the zygote (Anderson et al., 2017). Also, in maize at the coenocYTE formation stage (20–44 HAP), 12 H3 histones genes were expressed; canonical H3 deposition is coupled to DNA synthesis during replication and repair (Chen et al., 2017).

Other monocot transcriptome studies have focused on TFs of essentially unknown biological functions with specific expression patterns during seed development. RNA-seq studies of maize B73 seeds from 0 to 144 HAP uncovered expression of differential seed-specific TFs (Yi et al., 2019). In wheat, transcriptome analysis of seeds identified TF families with embryo-specific enrichment, although the transcript contributions from different subgenomes of the polyploid wheat genome varied between individual TFs (Xiang et al., 2019). Functional understanding of these shared and distinct expression patterns of signaling, transcriptional, and epigenetic factors will help to address how embryonic development shapes the divergence of seed development in dicots and monocots.

EMBRYO AND SEED DEVELOPMENT STUDIES ARE IMPORTANT FOR FOOD SECURITY

The introduction and continuous improvement of hybrid seed technologies have significantly improved crop productivity in the last 100 years. In maize hybrids, maternal and paternal contributions play an essential role in heterosis and kernel development (Meyer et al., 2007). In Arabidopsis, the effects of hybridization of different ecotypes have been proposed to at least partly explain the differences seen in parent-of-origin.
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Gene expression between different hybrid combinations (Autran et al., 2011; Nodine and Bartel, 2012; Del Toro-De León et al., 2014; Del Toro-De León et al., 2016; Zhao et al., 2019; Alaniz-Fabían et al., 2020). The effect of maternal and paternal gene contributions at early stages of embryo development on hybrid vigor has not been critically evaluated and might be of great importance for seed yield.

Knowledge from embryo studies in rice (Ohnishi et al., 2014; Anderson et al., 2017) has allowed the engineering of artificial apomixis (an asexual type of reproduction that produces clonal seeds). To do this, Khanday et al. (2019) bypassed both meiosis and fertilization, generating clonal seeds identical to the maternal parent (apomixis) in rice. The strategy used in this study avoided meiotic recombination in the germline using the MiMe system (mitosis instead of meiosis), a triple knockout of the meiotic genes REC8, PAIR1, and OSD1 (d’Erfulth et al., 2009). To induce parthenogenesis (embryogenesis without fertilization), they took advantage of the AP2 family pluripotency factor BABY BOOM1 (BBM1), which is normally paternally expressed in rice zygotes and serves as an important trigger to induce division of the zygote. Using an Arabidopsis egg cell-specific promoter, they ectopically expressed BBM1 from the maternal genome, inducing parthenogenesis in unreduced egg cells, achieving apomixis. The induction of apomixis (clonal seeds) in rice is a major agricultural breakthrough that could enable the maintenance of hybrid traits by seed propagation, reducing the time and labor required to generate F1 hybrid seeds every year.

A key target for crop seed breeding is improved nutrient content, which could be achieved by increasing seed protein by optimizing seed maturation programs. Examples of maturation program flexibility in maize include the allocation of α-zein and globulin (GLB) seed proteins: α-zeins accumulate predominantly in the endosperm and globulins in the embryo. When α-zeins are suppressed by RNA interference in the endosperm, more GLB1 is synthesized in the embryo, demonstrating that protein allocation in the embryo can respond to nutritional alterations in the endosperm (Zheng et al., 2019). Protein re-balancing has also been observed when trying to reduce protein production to increase oil storage. In *B. napus*, suppression of napin and cruciferin protein storage genes leads to oleosin protein-containing membrane stacks replacing the normal protein-filled vacuoles, instead of increased lipid accumulation (Rolletschek et al., 2020). A similar effect has been reported in soybean (*Glycine max*) (Schmidt et al., 2011) and maize (Wu and Messing, 2014). Another example of metabolic heterogeneity in embryos comes again from *B. napus*, in which starch levels decline in late embryogenesis, while accumulation of lipids and proteins continues. In mature embryos of both Arabidopsis and *B. napus*, the radicle/hypocotyl and cotyledons accumulate different lipids levels. Photosynthesis in the outer cotyledon is more active than in the inner cotyledon, because the outer cotyledon is more exposed to light, so the inner cotyledon grows heterotrophically. Lipid storage is induced by light, leading to higher lipid content in the outer cotyledon, with implications for the timing of seed harvest for oil production (Ruuska et al., 2004; Goffman et al., 2005). An example of the promise and difficulty of metabolic engineering of seeds is found from efforts to reduce phytic acid. Crops with low phytic acid are desirable because this improves seed mineral bioavailability (especially Fe and Zn) and decreases phosphate pollution when used as feedstock. The first step in the phytic acid biosynthesis pathway is accomplished by myo-inositol phosphate synthase, which converts glucose-6-phosphate to myo-inositol-3-monophosphate. Reducing the expression of myo-inositol phosphate synthase by RNAi in soybean reduced phytic acid content but also leading to defects in seed development (Aghamirzaie et al., 2015; Redekar et al., 2015).

**NEW TECHNOLOGIES TO STUDY EMBRYO AND SEED DEVELOPMENT**

In the future, integrated systems biology approaches to mine data from transcriptomics, proteomics, and metabolomics studies on the embryo, endosperm, and seed coat at different developmental stages will provide advanced understanding and give us a better perspective of metabolic processes that are compartmentalized and coordinated during seed development.

A major challenge for previous studies on embryo development has been the isolation and collection of sufficient specific cell types and tissues. In some cases, this problem can be addressed by isolating nuclei using fluorescence-activated cell sorting or INTACT technologies. To probe regulation of gene expression by chromatin conformation, transposase-accessible chromatin sequencing (ATAC-seq) can be used to delineate open chromatin regions and TF binding sites; ATAC-seq has already been successfully used in vegetative tissues of *A. thaliana*, *Medicago truncatula*, *Solanum lycopersicum*, and *Oryza sativa* (Maher et al., 2018). Analysis of epigenome marks by chromatin immunoprecipitation sequencing data combined with allele-specific 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 technologies for probing the relationship between three-dimensional chromatin structure and gene expression will allow us to understand the genomic contribution of different subgenomes in embryos 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.

**CONCLUDING REMARKS**

Although structural differences in embryo development between dicots and monocots have been reported, we have only begun to understand the underpinning molecular similarities and differences. Genomic studies have revealed gene activities associated 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 developmental and molecular differences and the particularities specific to dicots versus monocots.

During early embryo formation, processes conserved in monocots and dicots determine the genetic program for...
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embryogenesis, including zygotic genome activation, epigenetic reprogramming, and establishment of cell identity by WOX and ARF genes. Auxin synthesis and transport also play pivotal roles in embryogenesis in both monocots and dicots. Despite these advances, a comprehensive understanding of plant embryogenesis still requires critical insights into understanding the functions mediated through various TFs, miRNAs, small RNAs, and IncRNAs in the regulation of genetic and epigenetic programs (Figure 2).

Detailed studies of embryo maturation programs have generated insights into the synthesis and deposition of the economically important major storage products—especially 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 prospects to design crop seeds with desirable nutritional composition and yields.

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