Does Early Embryogenesis in Eudicots and Monocots Involve the Same Mechanism and Molecular Players?[1][OPEN]

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The flowering plant life cycle alternates between a diploid sporophytic and a haploid gametophytic generation. The sporophytic generation is initiated with the double fertilization event that results in the formation of a diploid zygote and a triploid endosperm. The unique zygote or fertilized egg cell represents the starting point of a new generation and undergoes an asymmetrical division, giving rise to a smaller apical and a larger basal cell with distinct developmental fates. Subsequently, apical and basal cells will collaborate to complete the whole process of embryogenesis and generate a multitude of different cell types (ten Hove et al., 2015). In most eudicots, the smaller apical cell will contribute to the major compartments of a mature embryo, establishing an apical-basal axis and a radial pattern through several elaborate developmental processes. The larger basal cell usually undergoes limited division to form a suspensor composed of a few cells. The uppermost suspensor cell in eudicots differentiates into the hypophysis and eventually becomes part of the primary root meristem. In monocots, apical and basal cell lineages are usually incorporated into a pear-shaped proembryo and are difficult to distinguish from each other. Over the last two decades, great efforts have been made to elucidate the molecular mechanisms underlying the early events of embryogenesis (for review, see Jenik et al., 2007; Lau et al., 2012; ten Hove et al., 2015). Despite the well-described morphological dynamics occurring during early embryogenesis and many advances in the identification of molecular players regulating embryo pattern formation in the eudicot model Arabidopsis (*Arabidopsis thaliana*; see Advances), there still exists a lack of knowledge about the gene regulatory network in other plant species, especially in the monocots. Moreover, there are still numerous open questions, such as the regulation of egg cell activation, establishment of zygote polarity, asymmetric zygote division, apical and basal cell fate determination, etc., which are summarized in

ADVANCES

- It has been widely recognized that both paternal and maternal inherited genetic information are involved in early embryogenesis, and zygotic genome activation is initiated before the first zygotic cell division.
- Genetic information delivered from both parental genomes and *de novo* factors generated from the zygotic genome are required for zygotic cell division.
- Accurate orientation of the zygotic division plane is essential for the differentiation of basal cell lineages and subsequent embryo pattern formation.
- The basal cell lineage before globular stage has the potential to develop into an embryo, which is suppressed by the apical cell lineage during normal embryogenesis.
- An apical-basal auxin gradient and cell-type-specific auxin response machineries are required for the establishment of the apical-basal axis of the proembryo additionally controlling cell fates in early embryos.
- Cell-to-cell communication plays a crucial role in cell fate determination during early embryogenesis.

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Outstanding Questions. By comparing eudicot and monocot model plants, we will focus in this *Update* article on recent advances and open questions on gene regulatory networks during zygote development, parental influences on early embryogenesis, zygotic genome activation, and cell fate determination (Box 1; Rademacher et al., 2012; Zhao et al., 2011; Del Toro-De Leon et al., 2014).

TIMING OF ZYGOTIC GENOME ACTIVATION

The zygote is the starting point for embryogenesis (Fig. 1) and will develop into a mature embryo upon a series of elaborate developmental events. In animals, early embryogenesis is regulated by maternal genetic information deposited before fertilization in the egg cell and later by de novo-synthesized zygotic factors, a process known as maternal-to-zygotic transition (Tadros and Lipshitz, 2009; T. Lee et al., 2014; Baroux and Grossniklaus, 2015; Zhao and Sun, 2015). This process combines two interrelated events: (1) degradation of maternal factors and (2) onset of zygotic genome transcription, a process known as zygotic genome activation (ZGA; Tadros and Lipshitz, 2009). In plants, these processes are still poorly understood mainly because of technical limitations (Zhao and Sun, 2015).

Although a clear picture about the contribution of de novo zygotic transcripts to early embryogenesis could not be drawn at the present stage, after more than a decade of intense research, a common perspective in both eudicots and monocots is that de novo transcription already occurs at the zygote stage. In the eudicot model plant tobacco (*Nicotiana tabacum*), several de novo transcripts lacking in sperm and egg cells were detected through reverse transcription PCR in zygotes, indicating that the zygotic genome is not quiescent and instead has started to transcribe and generate novel transcripts (Ning et al., 2006). Moreover, zygotic division and elongation were strongly affected by transcription inhibitors actinomycin D and cordycepin, which could efficiently block de novo transcription, suggesting that de novo zygotic transcripts are likely required for elongation and division of the zygote (Zhao et al., 2011). In zygotes of the monocot model maize (*Zea mays*), de novo transcripts of three different cyclin genes, *ZmCycA1;1*, *ZmCycB1;2*, and *ZmCycB2*, were already detected during early zygote formation. Notably, *CycA1;1* transcripts were degraded within the first 3 h after in vitro fertilization and reaccumulated 17 h after fertilization, indicating de novo transcription (Sauter et al., 1998). Comparative transcript analysis of egg cells and zygotes in maize revealed the presence of de novo transcripts for ribosomal proteins (S21A, L39) and MCM DNA replication factors in the zygote shortly after fertilization (Dresselhaus et al., 1999, 2006). Furthermore, using a paternal mRNA reporter line, translation activity was observed in early zygotes 6 h after in vitro fertilization, indicating that decondensation of the male chromatin already occurs during the initial stages of embryogenesis, allowing accessibility to the

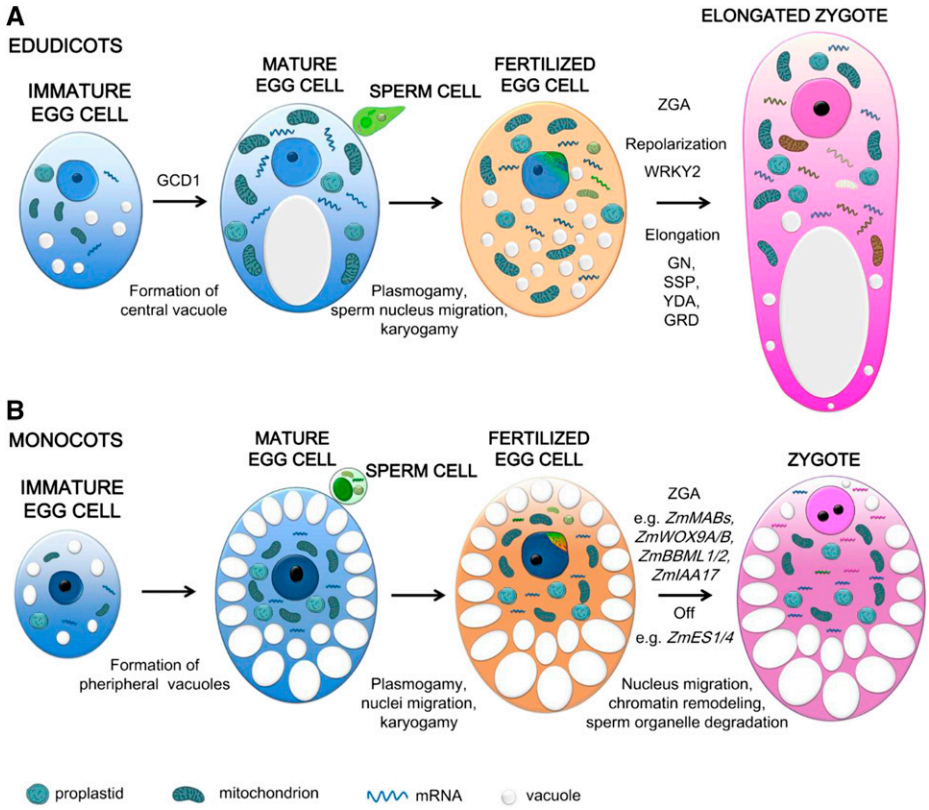

Figure 1. Egg cell maturation and zygote development in flowering plants. A, Egg cell maturation in the eudicot model Arabidopsis. The smaller immature egg cell will develop into a larger mature egg cell for fertilization and subsequent embryogenesis, which requires GCD1 deposited in the egg cell. After gamete fusion, the fertilized egg cell or zygote elongates rapidly along its apical-basal axis, during which zygotic polarity is established and the zygotic genome commence to transcribe. A number of genes required for zygote development and morphological changes are indicated. B, In grasses as monocot models, immature egg cells experience an evident increase in size, characterized by the formation of a high number of vacuoles distributed in the mature egg cell periphery. After gamete fusion, egg cell nucleus migration takes place, culminating in karyogamy and further movement toward the chalazal pole. In contrast to Arabidopsis, zygote elongation and increase in cell size do not take place. De novo expression of genes associated to ZGA and down-regulation of a few example genes are indicated.

transcriptional machinery of at least a part of the male genome (Scholten et al., 2002).

Based on transcriptome analysis of sperm cells, egg cells, and zygotes, several fertilization-induced genes were identified in the zygote of rice (*Oryza sativa*). These include *OsMAPK5*, *OsMET1*, *OsWRKY*, and *histone H2A*, which are up-regulated after fertilization (Abiko et al., 2013). These genes have already been reported in Arabidopsis and other species as key regulators of polarity establishment and elongation. Three putative *H2A.Z* genes were reported being parentally expressed (Anderson et al., 2013). The transcripts of two genes (*Os03g06670* and *Os03g53190*) are enriched in egg cells, while the third gene (*Os10g28230*) showed sperm cell enrichment, suggesting that at least a subset of paternal genes are poised for expression in the zygote. Similarly in wheat (*Triticum aestivum*), transcriptome analyses indicated that transcriptional changes take place considerably and soon after fertilization (Sprunck et al., 2005), as shown by comparative analyses of expressed sequence tags from egg cells and in vitro-developed two-celled proembryos. Novel transcripts, including those for histone H2A and ribosomal proteins, were highly represented, suggesting that similar genes are likely activated soon after fertilization in both monocots and eudicots. Furthermore, two additional genes (*TaTDL1* and *TaMAB2*) were shown to be de novo induced after fertilization. The former encodes a Cys-rich protein and was only detected in two-celled proembryos. The latter encodes an E3-ligase component polarity protein and is likely involved in asymmetric cell divisions like its maize homolog ZmMAB1 (Juranič et al., 2012). *TaMAB2* is specifically expressed in wheat zygotes and proembryos, indicating early ZGA also in this species (Leljak-Levanić et al., 2013). Related studies in Arabidopsis also support the idea that ZGA occurs at the zygote stage. Transcript comparisons between gametes and zygotes as performed in monocots have not yet been done in Arabidopsis, possibly due to the difficulties of manipulating small gametic cells and zygotes. However, genetic experiments of zygote-arrest mutants (Xu et al., 2005; Ronceret et al., 2008; Guo et al., 2016) and transcription activity analyses in zygotes using a LhG4/pOp transactivation system (Nodine and Bartel, 2012) suggested that the zygotic genome of Arabidopsis is not silenced and both paternal and maternal alleles are active in the zygote and required for zygote development and embryogenesis, respectively.

In summary, our current knowledge indicates that genome integration from male and female gametic cells commence to transcribe before zygote division, or in other words, the onset of ZGA already occurs shortly after fertilization. De novo-transcribed genetic information is likely required for zygote division and early development of embryos, although more detailed studies are urgently needed. Genome-wide transcriptional studies of zygotic genomes at different stages and functional analysis of de novo transcripts during zygote polarity, zygotic division, and apical/basal cell fate determination are now required and would allow more precise conclusions about ZGA in higher plants.

ESTABLISHMENT OF ZYGOTE POLARITY

Cellular polarity is a key aspect during plant development. Before fertilization, egg cells of eudicots such as Arabidopsis display evident polarity with the nucleus located toward its chalazal pole and a large vacuole located toward its micropylar end (Fig. 1A). After fertilization and karyogamy, the zygote elongates and the large vacuole divides into many small vacuoles, giving rise to a transiently symmetric appearance of the elongated cell lacking obvious visible polarity. Thereafter, it will undergo a series of further elaborated cytological changes, including nucleus migration toward the chalazal pole and formation of a large vacuole at the

BOX I: Glossary of Terms

1. Zygotic genome activation (ZGA): onset of the transcription of the zygotic genome, which gives rise to the generation of de novo-synthesized transcripts.

2. Maternal-to-zygotic transition: transition of embryonic developmental from maternal control to zygotic genome control, beginning with clearance of maternal transcripts, followed by de novo transcription in the zygote.

3. Zygotic polarity: mainly refers to a spatial uneven distribution of cellular organelles, transcripts, and proteins in a zygote.

4. Asymmetrical cell division (ACD): a specific cell division pattern that produces two daughter cells with different sizes, intrinsic cellular components, and usually different developmental fates.

5. Genomic imprinting: an epigenetic phenomenon by which certain genes are expressed in a parent-of-origin-specific manner.

6. Apical cell: the apical daughter cell of a zygote after an asymmetrical cell division, which will develop into the major part of the embryo proper.

7. Basal cell: the basal daughter cell of a zygote after an asymmetrical cell division, which will develop into the suspensor through limited cell divisions. In some eudicot plants, like Arabidopsis and tobacco, it also contributes to hypophysis formation.

8. Cell fate determination: refers to a process involved in cell fate commitment during which a cell differentiates into an irreversible final cell type or organism regardless of its environment.

micropylar pole to rebuild cell polarity during further zygote development (Souter and Lindsey, 2000), which could be visualized by the relative position of nucleus and vacuole in the zygote.

In monocots such as the grasses, egg cell polarity is visually less distinguishable. However, due to the larger number of peripheral vacuoles at the micropylar pole, the nucleus appears to be slightly shifted toward the chalazal pole (Fig. 1B). After fertilization, the egg nucleus is surrounded by endoplasmic reticulum and other organelles and moves toward the chalazal pole where karyogamy is executed. Further movement determines the future asymmetric cell division plane. Compared with many eudicots, zygote elongation or growth does not take place (Mol et al., 1994; Sato et al., 2010), indicating that polarity establishment of egg cells and zygotes in eudicots and monocots is differentially regulated.

For Arabidopsis, it was suggested that regulatory mechanisms underlying zygote polarity establishment may be independent to that in the egg cell. This notion could be drawn, for example, from studies on the zinc-finger transcription factor WRKY2 (Ueda et al.., 2011). Expression pattern analysis revealed that *WRKY2* is expressed both in the egg cell and zygote. However, in homozygous *wrky2* mutants, egg cells display normal polarity but the process of zygote repolarization from the transient symmetric state failed, resulting in dispersed nucleus and vacuoles throughout the zygote. As a consequence, cell division occurred symmetrically (Ueda et al., 2011). This excellent example points out the idea that polarity establishment in egg cell and zygote is

Table I. *Genes involved in early embryogenesis regulation in eudicots*

Abbreviation	Full Name	Organism	AGI No.	Protein Family/ Conserved Domains	Function	Reference(s)
BDL	Bodenlos	Arabidopsis	At1g04550	AUX/IAA family (IAA12)	Apical-basal embryonic pattern formation	Hamann et al. (1999, 2002)
FAC1	Embryonic Factor 1	Arabidopsis	At2g38280	AMP deaminase	Initiation of zygotic division	Xu et al. (2005)
FAC19	Embryonic Factor 19	Arabidopsis	At1g13800	Pentatricopeptide repeat protein	Initiation of zygotic division	Yu et al. (2012)
FS	FASS	Arabidopsis	At5g18580	Ser/Thr-protein phosphatase 2A regulatory subunit B	Cell division plane and morphogenesis	Torres-Ruiz and Jürgens (1994)
GCD1	Gamete Cell Defective 1	Arabidopsis	At5g62270	Unknown	Gamete maturation and initiation of zygote division	Wu et al. (2012)
GN	GNOM	Arabidopsis	At1g13980	GDP/GTP exchange factor	Zygote elongation and asymmetric division	Mayer et al. (1993)
GRD	Grounded	Arabidopsis	At5g53040	RWP-RK family	Zygote elongation and basal cell fate determination	Jeong et al. (2011)
MP	Monopteros	Arabidopsis	At1g19850	Auxin response factor	Apical-basal embryonic pattern formation	Hardtke and Berleth (1998); Hamann et al. (2002)
NtCYS	Cystatin	*Nicotiana tabacum*	KF113570	Cystatin	Prevention of precious cell death of basal cell lineage	Zhao et al. (2013)
PIN7	Pin-Formed 7	Arabidopsis	At1g23080	Auxin transporter	Establishment of apical-basal auxin gradients	Friml et al. (2003)
SSP	Short Suspensor	Arabidopsis	At2g17090	IL-1 receptor-associated kinase	Zygote elongation/zygote asymmetric division	Bayer et al. (2009)
WRKY2	WRKY DNA-Binding Protein 2	Arabidopsis	At5g56270	Zinc-finger domain transcription factor	Zygote polarization	Ueda et al. (2011)
WOX2	Wuschel Related Homeobox Protein 2	Arabidopsis	At5g59340	WUSCHEL-related homeobox protein	Apical-basal axis formation	Breuninger et al. (2008)
WOX8	Wuschel Related Homeobox Protein 8	Arabidopsis	At5g45980	WUSCHEL-related homeobox protein	Apical-basal axis formation	Breuninger et al. (2008)
YDA	YODA	Arabidopsis	At1g63700	MAPKK kinase	Basal cell fate determination	Lukowitz et al. (2004)
ZYG1	Zygote Arrest 1	Arabidopsis	At3g05870	Anaphase-promoting complex/cyclosome subunit 11	Initiation of zygotic division	Guo et al. (2016)
ZEU1	Zygote Stage Zeus 1	Arabidopsis	At5g59440	Thymidylate kinase	Initiation of zygotic division	Ronceret et al. (2008)
ESF1	Embryo Surrounding Factor 1	Arabidopsis	At1g10747, At1g10745, At1g10717	Cys-rich peptide	Embryonic pattern and suspensor formation	Costa et al. (2014)

independent, and not intimately linked together. Very interestingly, zygote repolarization defects in homozygous *wrky2* mutants could be restored either by paternal- or maternal-derived WRKY2 in the reciprocal crosses (Ueda et al., 2011). It is not clear yet whether *WRKY2* expression in zygotes is driven by gametic cells during fertilization or de novo produced from the zygotic genome. However, the findings revealed that either male or female WRKY2 is sufficient for zygote repolarization, suggesting that both paternal- and maternal-derived WRKY2 are involved in zygote polarity establishment.

Zygote elongation occurs rapidly in eudicots along its apical-basal axis during the processes of zygote polarization. In Arabidopsis, zygote elongation and asymmetric division are regulated by the GDP/GTP exchange factor for small G-proteins of the ARF class (ARF-GEF) GNOM (GN). In GN knock-out plants, zygote elongation and asymmetric division were compromised (Mayer et al., 1993). The involvement of *mitogen-activated protein kinases* (*MPK3* and *MPK6*), *short suspensor* (*SSP*), and *Yoda* (*YDA*) as regulators of zygote polarity and elongation was also reported (Wang et al., 2007; Bayer et al., 2009), but the exact mechanism remained unclear. See Table I for an overview of zygote polarity factors. It will remain a difficult task for future studies to elucidate the molecular mechanisms regulating egg cell and zygote polarity in more detail, but the identification of additional players will also help to understand the establishment of cell polarity during other developmental processes in both eudicots and monocots.

ASYMMETRIC ZYGOTE DIVISION AND ITS INFLUENCE ON EMBRYOGENESIS

Zygotic division is the first and likely the most critical cell division event during the process of early embryogenesis. The zygote usually divides transversely and asymmetrically, giving rise to an apical and a basal cell with different division patterns and distinct developmental fates. The small apical cell develops into the main body of the embryo proper, whereas the larger basal vacuolated cell continues to expand longitudinally in eudicots and divides transversely to form a

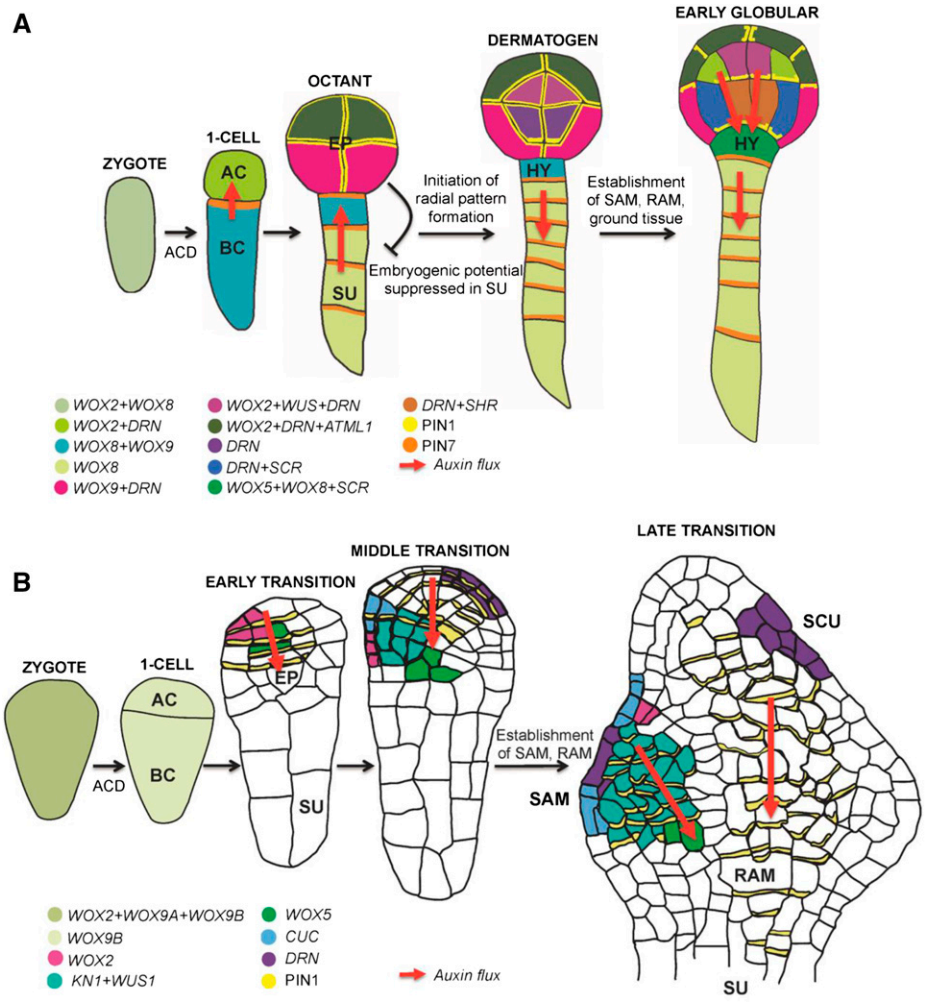

Figure 2. A comparison of gene expression pattern and auxin fluxes regulating cell fate determination during early embryogenesis in Arabidopsis (A) and maize (B), respectively. Colors represent expression of different genes as indicated in the legends. Auxin fluxes are shown by red arrows. Transcripts are written in italic and proteins in normal letter code. Stages and major differentiation mechanisms are indicated. Abbreviations: AC, apical cell; ACD, asymmetric cell division; BC, basal cell; EP, embryo proper; HY, hypophysis; RAM, root apical meristem; SAM, shoot apical meristem; SCU, scutellum; SU, suspensor.

suspensor composed of a single file of cells (Fig. 2A). In the grasses, the basal cell inherits most vacuoles of the zygote and divides less regularly, resulting in the formation of a basal cell lineage containing transverse, longitudinal, and intermediate cell division planes (Fig. 2B). But how does the zygote initiate its first division and how does the asymmetrical division influence apical and basal cell fate determination and embryo pattern formation?

Over the past decade, first insights about these essential questions have been obtained. Zygote-lethal phenotypes of Arabidopsis mutants have been identified as valuable tools to understand the mechanisms regulating the initiation of the zygotic division. *EMBRYONIC FACTOR1* (*FAC1*), encoding an AMP deaminase, was identified through a screening of ethyl methanesulfonate-mutagenized plants. Homozygous *fac1* mutants are arrested at the zygote elongation stage, resulting in the failure of onset of asymmetric cell division. In addition, either maternal or paternal FAC1 could restore the zygote-lethal phenotype through reciprocal crosses with wild-type plants, suggesting that independent of the parental origin, FAC1 could support the initiation of zygote division (Xu et al., 2005). Several additional recessive mutants with the zygote-lethal phenotype include the genes *FAC19*, *AtZYG1*, and *ZEU1* (Ronceret et al., 2008; Yu et al., 2012; Guo et al., 2016). *AtZYG1* encodes an anaphase-promoting complex (APC) subunit 11 (APC11) protein, a ubiquitin E3 ligase that is known to target cyclins (Peters, 2006). Protein sequence analysis revealed high similarity to APC11 proteins from rice (OsAPC11) and maize (ZmAPC11; Guo et al., 2016). It needs to be shown whether knock-out of *APC11* from monocots also leads to zygote lethality that could suggest a conserved pathway in both monocots and eudicots. Another example of zygote lethality was shown in the *gcd1* mutant. *GCD1* encodes a mitochondria-located protein, and its enrichment in female gametophytes is essential for final maturation of female gametes. *GCD1* mutation leads to immature egg cells, which could fuse with sperm cells and develop into an elongated zygote, but could not initiate zygote division. Expression pattern analysis revealed that both paternal and maternal *GCD1* transcript could be detected in the zygote, but paternal *GCD1* could not rescue the phenotype attributed by the female *gcd1* mutation, suggesting that egg-deposited GCD1 is required for the onset of zygotic division (Wu et al., 2012). Thus, its role in embryogenesis could not be replaced by its paternal counterpart. Taken together, it now becomes clear that both maternal and paternal genetic information are involved in the initiation of zygote division in plants, and parental factors may have specific roles in triggering zygote division. Moreover, rapid elongation of the zygote seems to be independent of the initiation of zygote division but appears associated with asymmetric division.

During zygote division, the control of the position and orientation of the cell division plane is a critical issue for early embryogenesis. Recently, the receptor kinase ZAR1 was found to regulate the proper position of zygote division in Arabidopsis. Homozygous *zar1* leads to embryo abortion, but does not affect male or female gametogenesis. Phenotype analysis revealed that *zar1* zygote elongation is normal, but its division becomes symmetrical, resulting in the failure of embryogenesis (Yu et al., 2016). *NtDRP*, encoding a dynamin-related protein, was found to control zygote division orientation in tobacco. Down-regulation of *NtDRP* caused zygotic cell division to occur in an incorrect orientation, resulting in the formation of an embryo-like structure without a typical suspensor (Zhao et al., 2016). This observation suggests that *NtDRP*-dependent zygotic division plane orientation is essential for the differentiation of both apical and basal cell lineages, especially for suspensor formation. In conclusion, asymmetrical cell division of the zygote appears critical for the establishment of the future embryonic pattern. However, more solid evidence in other plant species is still required to draw a final conclusion.

In rice, transcript for DNA methyltransferase 1 (OsMET1), which functions in maintaining CG DNA methylation (Kankel et al., 2003), was identified among a number of highly up-regulated genes in cultured zygotes (Abiko et al., 2013). Inhibition of *OsMET1* expression slightly enhances asymmetric zygote division; however, normal globular embryos were observed during subsequent embryo culture. This finding suggests that asymmetric cell division could be partly affected by the inhibition of OsMET1. As reported, the redundancy of DNA methylation pathways (Xiao et al., 2006; Mathieu et al., 2007; Jullien et al., 2012) may explain the developmental recovery during early embryogenesis after the interruption of asymmetric zygote division in rice. However, it could also be due to the in vitro system limitations. In wheat, for instance, disturbance of or lack of initial polarity was observed in cultured zygotes compared with zygotes generated in planta (Bakos et al., 2009). Interestingly, a similar phenotype was observed in zygotes of *met1* mutants in Arabidopsis, where about 13% of two-celled embryos had abnormal cell division patterns, suggesting a similar role for MET1 in eudicot zygote division (Xiao et al., 2006). Thus, epigenetic control likely also represents a key mechanism for early embryogenesis, but more detailed studies need to be conducted involving the studies of many more genes.

INFLUENCES OF THE PARENTAL GENOMES ON EARLY EMBRYOGENESIS

During fertilization, one sperm cell fuses with the egg cell to produce a zygote, and thus the parental genetic information integrates to form the diploid zygotic genome. In animals, early genetic and molecular studies have shown that maternal inherited information deposited in egg cells is usually sufficient to support early embryogenesis toward the midblastula transition stage (Tadros and Lipshitz, 2009). However, recent evidences

indicated that different epigenetic mechanisms in sperm cells could also regulate offspring metabolism and health. One of the proposed mechanisms involves the influence of transfer RNAs of sperm cells as paternal epigenetic factors controlling offspring metabolism (Chen et al., 2016; Sharma et al., 2016). Another proposed mechanism suggests the involvement of the histone H3 Lys 4 demethylase KDM1A. Expression of KDM1A in developing sperm cells was shown to be essential for the survivability and development of offspring (Siklenka et al., 2015). These new findings imply that both sperm- and egg cell-delivered information are critical for the development of offspring in animals.

In plants, the influences of parent-inherited genetic information on early embryogenesis are still largely unknown, especially regarding the specific developmental events of early embryogenesis. Although the extent of parental contribution to embryogenesis has been differently elucidated, a common perspective in plants is that both paternal and maternal inherited information are involved in early embryogenesis (Luo et al., 2014). Based on high-throughput sequencing, it was concluded that early embryogenesis is maternally controlled in Arabidopsis (Autran et al., 2011). Down-regulation of the paternal alleles by the maternal chromatin small interfering RNA pathway has been suggested as a controlling mechanism, whereas the activation of the paternal alleles during the course of embryogenesis is thought to be mediated by the maternal histone chaperone complex CAF1 (Autran et al., 2011). Nonetheless, a similar approach concluded that the majority of genes expressed during early embryogenesis were equally derived from both parental genomes (Nodine and Bartel, 2012). In monocots, parental influence during embryogenesis have been less studied; in maize, an equivalent parental contribution in the zygote during early embryo development was observed by studying a limited number of genes (Meyer and Scholten, 2007). More global studies are necessary to elucidate to which extent both parental genomes contribute to early embryogenesis.

The contribution of parental information toward the zygote and thus early embryogenesis is also reflected by the delivery of parental organelles and cytoplasmic factors. Generally, it is thought that mitochondria and plastids are delivered maternally by the egg cell, while sperm organelles degenerate. However, early ultrastructure observations implied that mitochondria could also be transmitted from sperm to the egg cell in tobacco (Yu and Russell, 1994; Fig. 1A). Studies focusing on cytoplasmic factors are limited due to the difficulties associated with distinguishing gamete-delivered from zygote-de novo-synthesized factors. Nonetheless, the first example of a sperm-delivered transcript exerting a known function during early embryogenesis is *SSP*. Although *SSP* transcripts could be detected in mature pollen, yellow fluorescent protein (YFP)-tagged SSP protein was not observed in mature sperm cells. Only transient YFP-tagged SSP fluorescence was visible after fertilization in the zygote (Bayer et al., 2009). After transmission to the zygote, *SSP* transcripts appear to be translated and transiently accumulate to regulate asymmetric zygotic division by activating the downstream YDA signaling pathway (Bayer et al., 2009). In rice, transposon silencing mediated by microRNA and small interfering RNA pathways was found to be more active in egg cells compared with sperm cells, suggesting that the regulation by small RNAs in the zygote is inherited from the egg cells (Anderson et al., 2013). Another example of maternal control was observed in the *GAMETE CELL DEFECTIVE1* (*GCD1*) gene in Arabidopsis. Its mutation leads to the formation of a small and immature egg cell, which is capable of fusing with a sperm cell during fertilization, but subsequent zygotic division was arrested. Expression pattern analysis revealed that both paternal and maternal GCD1 could be detected in the zygote (Fig. 1A), but paternal GCD1 could not rescue the phenotype attributed by the female *gcd1* mutation, suggesting that a *gcd1* mutant egg is not able to sustain zygote development and initiate embryogenesis after the egg cell fused with a normal sperm cell (Wu et al., 2012). Another way parents exert influences on their offspring is through genomic imprinting, which results in monoallelic gene expression in early embryos dependent on their parent of origin. In plants, genomic imprinting has been primarily characterized in the endosperm. In Arabidopsis, the endosperm is a transient tissue consumed by the embryo during seed development, while in monocots, the endosperm is persistent and nourishes the germinating seedling. The first maternally expressed imprinted gene in the embryo, *MEE1*, was identified in maize. Allele-specific expression of *MEE1* was correlated with differences in allelic methylation levels (Jahnke and Scholten, 2009). Genome-wide approaches using embryos of monocots and eudicots have later identified several additional candidate imprinted genes (Gehring et al., 2011; Hsieh et al., 2011; Luo et al., 2011; Waters et al., 2011; Zhang et al., 2011). In Arabidopsis, analysis of reciprocal F1 embryos identified more than 100 potentially imprinted genes (Autran et al., 2011; Nodine and Bartel, 2012). Most of the imprinted genes confirmed by allele-specific expression and reporter gene assays were of maternal origin, while only one was paternally derived (Raissig et al., 2013). Despite these new findings, the effects of imprinted genes on embryo development are largely unknown. Thus, the role of imprinted genes and the parental control of early embryogenesis in plants still need to be elucidated in more detail in the future. Furthermore, whether epigenetic regulation is one of the major molecular mechanisms in plant embryogenesis is still a remaining question to be explored.

CELL FATE DETERMINATION OF APICAL AND BASAL CELL LINEAGES

Cell fate determination is one of the most critical developmental events for morphogenesis and pattern formation during early embryogenesis. A number of

recent studies contributed to our understanding of the potential role of the asymmetric cell division and the interaction between apical cell and basal cell lineages on cell fate determination (see also above). In Arabidopsis, a MAPK cascade was shown to regulate zygote elongation and developmental fate determination of the basal cell lineage. The sperm-specific receptor-like cytoplasmic kinase SSP, the MAPKK kinase YDA, and the RWP-RK transcriptional regulator GROUNDED were found to regulate the development of basal cell lineages (Lukowitz et al., 2004; Jeong et al., 2011). Zygotes of *yda* mutants fail to elongate and divide symmetrically into a normal-sized apical cell and a considerably smaller basal cell. The apical cell lineage shows a normal division pattern up to the eight-celled octant stage. In contrast, the small basal cell exhibits a random division pattern and fails to form a functional suspensor. Gain-of-function of *YDA* has an opposite effect on suspensor development, causing exaggerated growth of the suspensor. It is difficult to determine whether these basal cell lineage defects are attributed to the failure of zygote elongation or its symmetrical division since the two events are always coupled in *ssp* and *yda* mutants. However, *ZAR1* encoding like *SSP* a RLK/Pelle kinase in Arabidopsis provides a chance to peep at the contribution of zygote elongation and asymmetrical cell division to daughter cell fate determination. Defective *zar1* does not affect the process of zygote elongation but disrupts the first asymmetric division. Accordingly, both apical and basal cell fates were impaired, suggesting that intrinsic factors are required for asymmetrical division and the division itself is likely involved in daughter cell fate determination (Yu et al., 2016). Moreover, central cell-derived peptide ESF1 was recently shown to be required for basal cell lineage development acting through the YDA MAPK pathway in Arabidopsis. *ESF1* genes are only detected in the central cell and subsequent endosperm, but not in the embryo itself. Down-regulation of *ESF1* expression in the endosperm led to patterning defects in the embryo proper and suspensor formation coupled with abnormal spatial expression of suspensor markers, indicating that extrinsic signals from maternal tissues and the developing endosperm also contribute to development of both apical and basal cell lineages (Costa et al., 2014).

Almost nothing is known about cell fate determination during early embryogenesis in grasses. In maize, two hemoglobin-encoding genes, *ZmHb1* and *ZmHb2* (Table II), were identified as master regulators in determining the developmental fate of specific cells during maize in vitro embryogenesis (Huang et al., 2014b).

Table II. *Genes regulated during early embryogenesis in monocots*

Please note that in monocots (grasses) only expression pattern have been described.

Abbreviation	Full Name	Organism	Gene ID	Reference
MEE1	Maternally expressed in embryo 1	*Zea mays*	GRMZM2G104572	Jahnke and Scholten (2009)
CycA1;1	Cell cycle A1	*Zea mays*	GRMZM2G387227	Sauter et al. (1998)
CycB1	Cell cycle B1	*Zea mays*	GRMZM2G073003	Sauter et al. (1998)
CycB2	Cell cycle B2	*Zea mays*	GRMZM2G138886	Sauter et al. (1998)
RPL39	60S ribosomal protein L39	*Zea mays*	GRMZM2G100467	Dresselhaus et al. (1999)
RPP0	60S acidic ribosomal protein P0	*Zea mays*	GRMZM2G066460	Dresselhaus et al. (1999)
RPS21A/B	40S ribosomal protein S21A	*Zea mays*	GRMZM2G134109	Dresselhaus et al. (1999)
ZmHb1	Plant hemoglobin 1	*Zea mays*	AF236080	Huang et al. (2014b)
ZmHb2	Plant hemoglobin 2	*Zea mays*	DQ171946	Huang et al. (2014b)
WOX2	Wuschel homeobox like 2	*Zea mays*	AM234767	Nardmann et al. (2007)
WOX5	Wuschel related homeobox like 5	*Zea mays*	GRMZM2G116063	Nardmann et al. (2007)
DRN	Dornröschen	*Zea mays*	GRMZM2G120401	Zimmermann and Werr (2007)
Knotted1	KN1	*Zea mays*	GRMZM2G017087	Smith et al. (1995)
CUC	Cup-shaped cotyledon	*Zea mays*	AJ833968	Zimmermann and Werr (2005)
DSUL	Di-SUMO like	*Zea mays*	GRMZM2G006324	Srilunchang et al. (2010)
MAB1	MATH-BTB domain protein 1	*Zea mays*	AC195147	Juranič et al. (2012)
MCM6	Minichromosome maintenance protein 6	*Zea mays*	GRMZM2G021069	Dresselhaus et al. (2006)
MAPK 5	MAPK 5	*Oryza sativa*	Os03g0285800	Abiko et al. (2013)
MET1	Cytosine-5 DNA methyltransferase 1	*Oryza sativa*	Os07g0182900	Abiko et al. (2013)
H2A	Histone H2A	*Oryza sativa*	Os03g0279200	Abiko et al. (2013)
WRK19	WRKY transcription factor 19	*Oryza sativa*	Os05g0571200	Abiko et al. (2013)
WRK42	WRKY transcription factor 42	*Oryza sativa*	Os02g0462800	Abiko et al. (2013)
HTA712	Histone H2A variant 1	*Oryza sativa*	Os03g06670	Anderson et al. (2013)
HTA705	Histone H2A variant 9	*Oryza sativa*	Os10 g28230	Anderson et al. (2013)
HTA713	Histone H2A.Z	*Oryza sativa*	Os03g53190	Anderson et al. (2013)
MPK6	MAPK 6	*Oryza sativa*	Os10g0533600	Yi et al. (2016)
TH254	Histone H2A.4	*Triticum aestivum*	Q43208	Sprunck et al. (2005)
CyP3	Peptidyl-prolyl cis-trans isomerase	*Triticum aestivum*	Q93W25	Sprunck et al. (2005)
MAB2	MATH-BTB domain protein 1	*Triticum aestivum*	ACA64045.1	Leljak-Levanić et al. (2013)
TDL1	TAPETUM DETERMINANT-like 1	*Triticum aestivum*	CA722121	Leljak-Levanić et al. (2013)

A *ZmHb1* and *ZmHb2* proposed model indicates regulation of cell fate by controlling the accumulation of nitric oxide and Zn^{2+}, which triggers a MAPK cascade leading to the accumulation of reactive oxygen species in cells destined to die. Moreover, immunolocalization of ZmPIN1 proteins was affected in immature somatic embryos down-regulating *ZmHb1* or *ZmHb2*, indicating that *ZmHbs* control cell fate by regulating auxin flux via ZmPIN1 (Huang et al., 2014a). However, neither cell death nor *ZmPIN1* expression occurs during early embryogenesis in maize (Chen et al., 2014), indicating that alternative approaches are required to identify genes regulating cell fate determination at the initial stages of embryogenesis.

Transcriptome analysis comparing apical and basal cells in tobacco and maize revealed that asymmetric zygotic division likely results in the uneven distribution of several transcripts (Okamoto et al., 2005; Ma et al., 2011). For example, *NtCYS* transcript encoding a Cys protease inhibitor is exclusively located in the basal cell after zygote division. NtCYS exerts its anti-cell death effect by directly inhibiting cathepsin H-like protease NtCP14 to timely control the onset of programmed cell death in the suspensor (Zhao et al., 2013). Comparable transcriptome analysis between apical and basal cells has not been done in Arabidopsis. However, studies on family members of *WOX* genes (WUSCHEL [WUS]-related homeobox transcriptional regulators) also implied that cell fates of apical and basal cell lineages have been established along with the asymmetric zygotic division (Haecker et al., 2004). Transcripts of *WOX* family members linked to apical and basal cell fate determination, *WOX2* and *WOX8*, were expressed in apical and basal daughter cells of the zygote, respectively. *WOX2* appears to be the main regulator of embryonic shoot patterning. Loss of *WOX2* causes failures to properly separate the protoderm layer by periclinal divisions. Concomitant loss of other apical WOX factors in a *wox2* background results in the formation of shootless structures. Mutations in *WOX8* or its relative *WOX9* have no visible effect on embryo development, but embryo pattern of *wox8 wox9* double mutants is severely disrupted (Breuninger et al., 2008). Similarly, orthologs of *WOX* genes have been identified in maize and their expression pattern characterized (Nardmann et al., 2007; J. Chen and T. Dresselhaus, unpublished data; Fig. 2B). Expression of *ZmWOX2* was detected only transiently in the zygote and later up-regulated in the early transition stage. *ZmWOX9A* and *ZmWOX9B* likely encoding the WOX8 and WOX9 homologs are weakly expressed in the zygote, but only *ZmWOX9B* was later detectable at significant levels in the zygotic daughter cells. These expression patterns indicate that apical and basal cell lineages and cell fate determination in grasses may involve different players or occur at a later embryonic stage. *ZmWOX5* expression was detected from the early transition stage in a central basal domain of the embryo proper subtended by vacuolized suspensor cells. According to their Arabidopsis counterparts, *ZmWOX2* and *ZmWOX5* were suggested as indicators of apical-basal polarity (Nardmann et al., 2007) and could therefore be used as markers for studying early embryogenesis in the grasses. Other maize genes that may be involved in cell fate determination and polarity include *Dornröschen* (*DRN*), *Knotted1* (*KN1*), and *Cup-shaped cotyledon* (*CUC*). Expression of the *DRN* homolog was found to begin during the shift of late proembryo to early transition stage, and its function has been linked to auxin signaling during early embryogenesis (Zimmermann and Werr, 2007; Chandler et al., 2008). *KN1* expression begins at early transition stage embryos and is associated with the differentiation of small, cytoplasm-rich cells at the adaxial face of the embryo proper (Smith et al., 1995). *CUC* expression begins in the early transition stage embryo and together with *WUS1*, *WOX5*, and *DRN* homologs (Fig. 2B) may contribute to bilateral symmetry during early embryogenesis (Zimmermann and Werr, 2005). In summary, the above-described gene expression pattern indicates that cell fate determination and patterning occur delayed compared with Arabidopsis and obviously first involve a stage of cell proliferation before embryonic patterns are established. However, this remains to be shown in functional studies.

At least in Arabidopsis, it appears that both zygote elongation and its asymmetric zygote division seem to directly or indirectly depend on cell type-specific transcripts related to cell fate determination of apical and basal cell lineages. However, it remains unclear how and when the apical and basal cell fates are specified. After zygotic division, the basal cell undergoes limited divisions to form a suspensor. Once a suspensor is formed, suspensor cells stop further divisions and display the typical morphology shown in Figure 2A. It seems that cell fate is already determined at this stage. However, several mutants were identified in which suspensor cells do not initiate programmed cell death and start dividing to form embryo-like structures (Schwartz et al., 1994; Vernon and Meinke, 1994; Yadegari et al., 1994; Zhang and Somerville, 1997; Sanmartín et al., 2011). From the phenotype of these mutants, a model was proposed that embryo-proper-like pathways in the suspensor are suppressed by the embryo proper during the process of normal embryo development (Schwartz et al., 1994). More recently, a combination of in vivo living laser cell ablation and microculture techniques allowed to demonstrate that the basal cell lineage has the potential to produce secondary embryos after the embryo proper has been removed (Gooh et al., 2015; Liu et al., 2015), indicating that the embryonic potential of the basal cell lineage has to be suppressed. Interaction between apical cell and basal cell lineage thus plays a critical role in basal cell fate determination, suggesting that there is cell-to-cell communication between apical and basal cell lineage during the process of early embryogenesis.

Almost nothing is known about apical-basal cell (lineage) communication in monocots and thus urgently needs more attention from the research community.

COMMONALITIES AND DIFFERENCES DURING EARLY EMBRYOGENESIS OF EUDICOTS AND MONOCOTS

The diversification of the monocot and eudicot clades occurred approximately 140 to 150 MYA (Chaw et al., 2004). Within the window of evolutionary history, striking variations in embryo development evolved in both classes of flowering plants. Cell division pattern, differentiation and cell fate establishment of apical and basal cell lineages, as well as the number of cotyledons show striking differences between both clades during the process of embryogenesis. The major characters of embryogenesis that distinguish monocots from eudicots include lack of a typical suspensor, less predictable cell division patterns, unclear cell tiers in the embryo proper, usually a bent apical-basal axis, a single cotyledon, and an extra dorsoventral axis. Additional embryonic organs, such as a scutellum, coleoptile, and coleorhiza, add to the morphological variation of embryos in monocots. Whether other structures such as a hypophysis, founder cell of the embryonic root meristem in eudicots (ten Hove et al., 2015), are also formed during embryogenesis in monocots is still unclear. Although these variations already occur at early stages of embryo development, many essential processes are comparable between monocots and eudicots. The first zygote division is usually asymmetric and results in a small apical cell and a larger basal cell as in eudicots, which was also found in *Platanus racemosa*, a basal eudicot (Floyd et al., 1999). This observation indicates a common character in all angiosperms. In addition, both radial and apical-basal patterns are established, and thus the basic embryo architecture is similarly composed of a shoot apical meristem and a root apical meristem connected by a hypocotyl. Additionally, epidermal, ground, and provascular tissues are differentiated during embryogenesis in all angiosperms. These major characteristics of an embryo likely have been inherited from a common embryophyte ancestor.

Accordingly, key molecular players regulating early embryo development appear conserved in both monocots and eudicots as illustrated in Figure 2, although only a few embryonic genes have been studied at the functional level in monocots so far. *WOX* family genes, for example, marking cell fates along the apical-basal pattern and PIN-mediated polar auxin transport in eudicots indicate two major conserved molecular mechanisms. In Arabidopsis, *WOX2* and *WOX8* comprise earliest cell fate markers of apical cell and basal cell lineages, respectively (Haecker et al., 2004). *WUS* is critical for shoot meristem activity (Mayer et al., 1998), and *WOX5* is involved in root stem cell organization (Sarkar et al., 2007). As described above, a partly similar expression pattern of several *WOX* family genes was found in monocots, but the expression of candidate orthologous genes appears significantly delayed. While Arabidopsis *AtWOX2* and *AtWOX8* mark apical and basal cell fates after asymmetric zygote division, strong expression of their predicted maize homologs *ZmWOX2A* and *ZmWOX9A/B* could not be detected in the zygote and its daughter cells, but significant expression occurs at the early transition stage when shoot apical meristem and root apical meristem are established (Fig. 2B; J. Chen and T. Dresselhaus, unpublished data; Nardmann et al., 2007). Similarly, the maize predicted orthologs of *WUS* and *WOX5* (*ZmWUS1* and *ZmWOX5*) marking the shoot quiescent center and the root quiescent center in Arabidopsis show expression when the embryo already consists of more than 100 cells. Thus, despite the delayed expression of candidate orthologous genes, this overall similarity of expression patterns of *WOX* family genes implies that a relatively conserved mechanism is likely required for shoot apical meristem and root apical meristem establishment in both monocots and eudicots, which may additionally contribute to the similar apical-basal patterning of the embryo.

However, there also exists some variation in *WOX* family genes between monocots and eudicots: The most striking difference is that no clear homolog of *WOX8* (a marker for suspensor cell fate) has been identified in the genomes of monocots to date. *ZmWOX9A/B* are the closest maize homologs, but their function(s) is not known. This may contribute to the morphological variations of monocot embryos, e.g. that a typical suspensor cell file is not established in early monocot embryos. Auxin-dependent apical-basal axis establishment is another critical event in early embryogenesis. Polar auxin flow mediated by PIN7 and PIN1 was already found very early during embryogenesis (Fig. 2A) in eudicots and contributes to basic embryo architecture establishment at this stage (Friml et al., 2003; Carraro et al., 2006). Again, a significant expression of *ZmPINs* was not found during early embryogenesis in maize until the transition stage, when polarized localization of ZmPIN1 in the apical region of the embryo likely mediated apical-basal auxin flux toward the future root apical meristem region (Fig. 2B; J. Chen and T. Dresselhaus, unpublished data; Chen et al., 2014; Locascio et al., 2014). Based on animal embryogenesis, a molecular embryonic "hourglass" model was also proposed for plants through phylotranscriptomic analysis, suggesting that embryos from various taxa appear different during early stages of development, converge to a similar form during midembryogenesis, and again diverge at later stages (Quint et al., 2012). This model is very interesting but requires extensive functional studies during monocot embryogenesis to be sustained.

OUTSTANDING QUESTIONS

- Which factors keep the gametes in a resting stage and which are the mechanisms that trigger activation of the fertilized egg cell?
- What are the genetic differences between sexual embryogenesis and autonomous embryo development during parthenogenesis?
- How does the fertilized egg cell avoid polyspermy?
- How does the zygote establish its polarity and what is the overall role and importance of polarity in cell fate determination during proembryo development?
- How does the apical-basal axis of a zygote keep in line with polarity of the egg cell and to what extent does the sperm entry site influence zygote polarity?
- What are the exact roles of paternal and maternal genetic information on specific developmental processes during early embryogenesis?
- To which extent does communication with the surrounding maternal tissues and the development of the endosperm influence embryo patterning?

CONCLUSIONS AND PERSPECTIVES

Remarkable progress has been made in understanding the developmental events that regulate early embryogenesis and the molecular mechanisms underlying these processes in the model plant Arabidopsis (see Advances). It is now widely accepted that both paternal and maternal inherited information are involved in early embryo development, although their contributions may differ. The zygotic genome is activated before zygote cell division occurs, and both gamete-deposited and after-fertilization de novo-transcribed genetic factors are required for zygotic cell division. It is also becoming clear that the accurate asymmetrical division of the zygote is critical for daughter cell fate determination. Furthermore, it has been shown that the suspensor cells still have the potential to develop into an embryo, which is suppressed by the embryo proper during normal embryogenesis. This reveals that cell-to-cell communication plays a crucial role in cell fate determination during early embryogenesis.

However, despite the great advances that have been achieved during the last decade many more interesting questions have arisen in this exciting field (see Outstanding Questions). In Arabidopsis, the inaccessibility to egg cells and zygotes was a major barrier to address some of those questions. New sophisticated techniques, including single-cell transcriptome analyses, are now expected to solve some major problems and lead to significant advances in the near future. Among the many open questions, the mechanism(s) of embryogenesis repression in the mature egg cell and the basal cell lineage after fertilization as well as egg cell activation are the most attractive issues to be solved in the future. Understanding the establishment of egg cell and zygote polarity also is expected to contribute to our knowledge of polarity, asymmetric cell division, and cell fate determination in other developmental processes in plants. Information regarding polar distribution of genetic information such as transcripts or proteins has not yet been proven in the zygote, but its pronounced polarity may help to identify such factors.

Cell fate determination strongly depends on communication between apical and basal cell lineages requiring intensive cross talk with the surrounding maternal seed tissues and the developing endosperm. Further studies are needed, especially studies on other model systems such as the grasses, to answer these important questions and to elucidate to which extent early embryogenesis is similar or differentially regulated across different plant species. Novel techniques, including single-cell RNAseq transcriptomics and CRISPR/cas, are now available and could essentially contribute to essentially increase our understanding about early embryogenesis in the near future.

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