The Maternal to Zygotic Transition in Animals and Plants

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In the animal kingdom, maternal control of early development is a common feature. The onset of zygotic control over early development, defined as the maternal to zygotic transition (MZT), follows fertilization with a delay of a variable number of cell divisions, depending on the species. The MZT has been well defined in animals, but investigations remain in their infancy in plants. Recent evidence suggests, however, that in plants as in animals, the MZT also occurs several division cycles after fertilization. The likely convergent evolution of the MZT in the animal and plant kingdoms is fascinating and raises major questions regarding its biological significance, particularly with regard to its importance in genome reprogramming and the acquisition of totipotency by the embryo.

Plants and animals have each evolved different reproductive strategies that determine the extent to which the parents, usually the female, exert control over the developing offspring. Fertilization can be external or internal. In the latter case, the fertilized egg can be laid on a nutritive substrate (e.g., insects) or it develops within a protective and nurturing matrix (the placenta of mammals, the egg of birds and reptiles, the seed of seed plants). The MZT marks the end of maternal control and the onset of zygotic control over embryo development. It is characterized by the simultaneous degradation of stored maternal products and zygotic genome activation (Andéol 1994; Schultz 2002; Tadros et al. 2003; Stitzel and Seydoux 2007). In animals, the MZT occurs several cell cycles after fertilization. As a consequence, the first stages of embryonic development essentially rely on maternally deposited products. Despite divergent reproductive strategies and differences in the parental provisioning for offspring development, current evidence indicates that plants and animals share a marked maternal control of early postfertilization development. We review this evidence and our knowledge regarding the mechanisms controlling the onset of the MZT in both animals and plants. We hypothesize that shared biological constraints on early embryo development explain the existence of convergent mechanisms for maintaining maternal predominance.

EARLY EMBRYOGENESIS IN ANIMALS AND HIGHER PLANTS

Embryogenesis in flowering plants and animals has in common the union of a male and a female gamete that produces the zygote and the sequential events of cell proliferation, morphogenesis, and organogenesis that follow (Fig. 1). In animals, a single female gamete, the oocyte, fuses with a motile sperm to produce the zygote. Cell proliferation generates a multicellular morula of 16–32 cells

in mammals, a blastula of approximately 30,000 cells in *Xenopus*, and a syncytial blastoderm of about 6000 nuclei in *Drosophila*. Cellularization (for the syncytial blastoderm of insects) and asymmetric divisions define the onset of morphogenesis, and cellular migration marks the beginning of gastrulation and organogenesis (Browder et al. 1991).

In flowering plants, two pairs of gametes fuse, a process termed double fertilization. The two female gametes, the egg and central cell, are each fertilized by a sperm to produce the embryo and the endosperm, respectively. The endosperm is a protective and nurturing tissue that has a role similar to that of the placenta in eutherian mammals (Harper et al. 1970). The female gametes are produced together with “accessory” cells (the synergids and antipodals) within the female gametophyte (embryo sac), which is enclosed in the ovule that, after fertilization, forms the seed. Ovule and seed development occurs in the gynoecium in the center of the flower. The two sperms are produced by the male gametophyte (pollen), which germinates and grows through tissues of the gynoecium to deliver the sperm cells to the embryo sac. In plants, the early events of embryo development and pattern formation have been best described in the model plant *Arabidopsis thaliana*. In contrast to the situation in animals, the first division of the zygote is asymmetric and produces an apical cell, giving rise to the embryo proper, and a basal cell, forming the embryonic suspensor and the hypophysis, which will contribute to the root meristem of the embryo (Park and Harada 2008). The apical and basal cells are distinguished not only by their shape, but also by the differential expression of key regulatory genes (Breuninger et al. 2008). The apical cell then divides symmetrically until the fourth, asymmetric cleavage, which establishes the protoderm, the precursor of the epidermis. Further asymmetrical divisions will set up the apical-basal and radial polarity of the globular-stage embryo that contains about 100 cells. The transition from radial to bilateral symmetry occurs later with the formation of the early heart-stage embryo (Jürgens 1992; Park and Harada 2008). The embryo and endosperm of flowering

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Figure 1. Early development in animals and plants using the mouse and *Arabidopsis* as models. Sexual reproduction involves dimorphic gametes in both animals and plants, which are highly differentiated. The products of fertilization will undergo several cleavage cycles before morphogenesis. These stages of early development are largely under maternal control. In mammals (e.g., the mouse) symmetrical cleavages form a morula, whereas further asymmetrical cleavages and positioning of daughter cells separate the inner cell mass (icm) from the peripheral trophectoderm (tp), being precursors of the embryo and the placenta, respectively. In flowering plants (e.g., *Arabidopsis*), double fertilization takes place. It involves two sperm cells (sp) delivered by the pollen to the female gametophyte. The latter consists of seven cells, two of which are the female gametes (the egg [ec] and the central cell [cc]) and the others (synergids [syn] and antipodals [a]) are accessory cells. Double fertilization produces the zygote (z) and the primary endosperm nucleus (e), precursors of the embryo (green) and the endosperm (orange), respectively. Seed stages are defined according to the embryo stage (protoderm, globular, and heart stages only are represented here). The endosperm develops initially as a syncytium. Three mitotic domains are established at the globular stage and are positioned along the anteroposterior axis (chalazal endosperm [cze], peripheral endosperm [pen], micropylar endosperm [mce]). The peripheral endosperm becomes cellularized when the embryo reaches the early heart stage.

plants develop simultaneously and in coordination but along distinct developmental pathways. In *Arabidopsis*, the endosperm undergoes about ten nuclear division cycles within a syncytium before cellularization occurs and three endosperm domains differentiate along the anteroposterior axis (Brown et al. 1999; Boissard-Lorig et al. 2001).

MATERNAL CONTROL OF EARLY DEVELOPMENT AND THE MATERNAL TO ZYGOTIC TRANSITION

Defining the Maternal to Zygotic Transition

Early development in animals is under maternal control. This was dramatically illustrated by enucleation experiments first conducted on sea urchins by Harvey in 1936. When induced by seawater, enucleated eggs are able to undergo normal cleavages and form plutei, their free swimming larval form (Harvey 1936). Thus, the cleavage stage of the sea urchin relies solely on maternally stored products and does not require the expression of the zygotic genome until the larvae metamorphose into the adult form.

Since Harvey's experiments, it has been found that early development of many animal species—evolutionarily as divergent as echinoderms, amphibians, fishes, worms, insects, birds, and mammals—also relies on maternally deposited products (Andéol 1994). The stage at which maternal reliance ends and control of embryo development is transferred to the zygotic genome is referred to as the MZT. The MZT, under this definition, is distinct from the stage of zygotic genome activation (ZGA), which corresponds to the onset of de novo transcription from the zygotic genome. ZGA and MZT can coincide, but this is not always the case (Table 1). The MZT is also distinct from the midblastula transition (MBT), a developmental transition in amphibians and fishes associated with cell cycle lengthening, asynchronous cleavage, and the acquisition of cell motility, which, however, does not require zygotic transcription (Newport and Kirschner 1982a). The distinction is not always clear in the literature, and the MBT and ZGA are often referred to as marking the MZT, although this is clearly not true in all organisms. In this review, we adhere to a strict distinction as defined above.

Importantly, ZGA is not sufficient to ensure control by

Table 1. Maternal to zygotic transition and zygotic gene activation in plants and animals

Organism	ZGA		MZT	References
	first detection	major ZGA		
Animals				
Sea urchin	zygote, paternal pronucleus	zygote	pluteus (larvae)	Harvey (1936); Poccia et al. (1985)
<i>C. elegans</i>	four cells	90–125 cells	gastrulation (~28 cells)	Schauer and Wood (1990); Edgar et al. (1994); Seydoux and Fire (1994)
<i>Xenopus</i>	pre-MBT (~256 cells)	MBT (~4000 cells)	blastula (~30,000 cells)	Newport and Kirschner (1982b); Yang et al. (2002)
<i>Drosophila</i>	cleavage 8	cleavage 14 (~6000 cells)	blastoderm	Robbins (1980); Pritchard and Schubiger (1996)
Zebra fish	pre-MBT (~64/128 cells)	MBT	at epiboly	Kane et al. (1996); Mathavan et al. (2005)
Mouse	zygote, paternal pronucleus	two-cell embryo	two-cell embryo	Schultz (2002); Zeng et al. (2004)
Plants				
<i>Arabidopsis</i>	two-cell embryo	globular embryo	globular embryo?	Vielle-Calzada et al. (2000); Baroux et al. (2001); Weijers et al. (2001)
Maize	zygote	globular embryo	n.d.	Grimanelli et al. (2005); Meyer and Scholten (2007)
Maize IVF	zygote	n.d.	n.d.	Dresselhaus et al. (1996, 1999); Leduc et al. (1996) Scholten et al. (2002)
Wheat	two-cell proembryo	n.d.	n.d.	Sprunck et al. (2005)
Tobacco	zygote	n.d.	n.d.	Ning et al. (2006)

ZGA is gradual in animals and plants and can occur concomitantly or earlier than the MZT, as assessed by enucleation experiments (sea urchin), pharmacological treatments (inhibition of RNA pol II with α -amanitin), mutant analyses, or both (other organisms). n.d. indicates not determined; IVF, in vitro fertilization.

the zygotic genome. Although ZGA is a necessary condition, it is not sufficient because the MZT also requires that the maternally stored products no longer influence the further development of the embryo. Regulation of the MZT must thus depend on an appropriate balance between maternal mRNA clearance and ZGA.

Timing of the Maternal to Zygotic Transition in Plants and Animals

The MZT was originally defined using α -amanitin, an inhibitor of RNA polymerase II and III. Application on fertilized eggs or later stages blocks zygotic transcription and the induced developmental arrest marks the MZT. In worms, echinoderms, amphibians, fishes, and insects, the MZT takes place after the entire cleavage period is completed. In particular, in amphibians and fishes, the MZT occurs after the MBT, only at the onset of the first morphogenetic event (Newport and Kirschner 1982a; Stroband et al. 1992; Kane et al. 1996). In contrast, mammalian embryos require zygotic transcription already at the two-cell stage (Andol 1994). The MZT can take place after as few as one cycle (two-cell mouse embryo) or about 15 cell cycles (*Xenopus* blastula). On an absolute timescale, the MZT occurs between 2 hours (*Drosophila* nuclear blastoderm) and 2 days (four- to eight-cell human embryo) after fertilization. Thus, the extent of maternal control and the timing of the MZT vary greatly among species.

The timing of the MZT can also be defined genetically. Because the MZT occurs a certain number of division cycles after fertilization, mutations affecting early develop-

ment in animals often display maternal effects. Mutations showing a maternal effect can affect a gene product stored in the egg whose function is required between fertilization and the MZT. Alternatively, maternal effects can result from genomic imprinting, as is the case for genes that are zygotically expressed but with only the maternal allele being active and the paternal allele remaining silent. Genetic characterization coupled with parental allele-specific expression analyses is thus required to distinguish the different mechanisms underlying maternal effects. Maternal-effect mutants with a developmental defect before the MZT are informative for the role of maternal factors in early embryo development, for example, in chromatin remodeling and pronuclear congression (Loppin et al. 2001; Dekens et al. 2003) or the definition of body axes (Moody et al. 1996; Pelegri 2003; Mtango et al. 2008). The mutant class informative for zygotic gene contribution after the MZT consists of zygotic maternal mutants, which display a maternal phenotype that is either rescuable by the wild-type paternal allele (recessive mutant) or is enhanced by a mutant paternal allele (dominant mutant). In zebra fish, zygotic maternal mutants have been isolated that show a developmental arrest or delay of epiboly, the first morphogenetic event and the stage of the MZT (Kane et al. 1996), or they affect cell-fate determination processes at later stages of development (Pelegri 2003). Similarly in *Drosophila*, cell division and patterning genes acting maternally and zygotically have been uncovered in genetic screens (Garcia-Bellido and Robbins 1983; Perrimon et al. 1989, 1996).

Because of their inaccessibility, the plant embryo and

endosperm are not amenable to pharmacological experiments, such as inhibition of transcription by α -amanitin. Thus, genetic approaches have been used to investigate the MZT. However, the analysis of maternal-effect mutants in plants is complicated by the fact that maternal influences on seed development can stem from several possible sources (for review, see Grossniklaus and Schneitz 1998; Chaudhury et al. 2001; Baroux et al. 2002): (1) the intimate relationship of the fertilization products with the surrounding maternal tissues (sporophytic effects), (2) the dominant cytoplasmic contribution of female versus male gametes (gametophytic effects), (3) non-cell-autonomous effects of the endosperm on embryo development, and (4) genomic imprinting as observed in mammals. Thus, genetic characterization, together with thorough expression analyses, has to dissect the contribution of each effect to the observed mutant phenotype.

In plants, very few maternal-effect mutations are informative for the MZT, mostly because relatively few experiments have been conducted to specifically target maternal effects. Thus, very little is known about the nature and role of maternal factors stored in the female gametes. PROLIFERA, an MCM7 protein, is encoded by a maternal-effect gene important for the cell divisions following fertilization (Springer et al. 1995, 2000), but the low penetrance of the mutation suggests a redundant function with other factors. Interestingly, mutations in ORC2, a subunit of the origin recognition complex that, like MCM7, participates in the formation of the prereplicative complex, are suppressed by the maternal-effect mutation *medea*, further illustrating the interplay of maternal and zygotic factors early in development (Collinge et al. 2004). *Arabidopsis* MSI1 (MULTISUPPRESSOR of IRA1), which, among others, interacts with the RETINOBLASTOMA-RELATED (RBR) protein regulating the initiation of replication (Ach et al. 1997), is required in the female gametophyte, and not zygotically, to maternally control embryo and endosperm proliferation (Leroy et al. 2007).

Two genetic screens aimed at the isolation of gametophytic mutations identified a number of maternal-effect mutants affecting embryo development at various, often early, stages (Moore 2002; Pagnussat et al. 2005). As outlined above, it is not easy to determine the underlying mechanisms of a maternal effect in plants, and the mode of action of the genes affected in these mutants is currently not known. Large numbers of recessive mutations with zygotic effects have also been isolated, with the embryo phenotype only observed when both parental alleles are defective (Tzafrir et al. 2004). Some of them can affect embryo development at very early stages, including the zygote (Weijers et al. 2001; Lukowitz et al. 2004; Wu et al. 2007; Ronceret et al. 2008). This observation indicates that the paternal genome can complement for a deficient maternal contribution. Although it is generally assumed that such a paternal rescue stems from transcription of the paternally contributed genome, it could also be contributed by the sperm's cytoplasm. In fact, *Arabidopsis* sperm cells were recently shown to contain a distinct and diverse transcript profile (Borges et al. 2008). Moreover, zygotically acting mutants provide limited information regarding the MZT, because the timing of the paternal rescue is generally unknown. This has rarely been investigated but is illustrated by the mutants *gnom/emb30* and *vacuoleless1 (vcl1)*, which were both classified as recessive zygotic embryo lethals. Both heterozygous mutants produce approximately 25% aborted seeds when screened at a late stage of fruit development (Mayer et al. 1993; Rojo et al. 2001). However, at early stages of embryo development (e.g., two- to four-cell stage), mutant phenotypes are observed at similar frequencies whether self-fertilized or crossed to wild-type pollen (Table 2) (Vielle-Calzada et al. 2000). This indicates that at the two- to four-cell stage, a paternally inherited wild-type allele cannot provide enough activity to rescue the mutant phenotype. Thus, paternal rescue of the maternal mutation occurs later during embryo development. The time course analysis performed for the *vcl1*

Table 2. Delayed paternal rescue of *vacuoleless1* and *gnom/emb30*

	Two-four cells (2 dap)	Globular (3 dap)	Heart (4 dap)	Late heart (5 dap)	Mature seed
<i>vacuoleless1/vcl1</i>					
<i>vcl1/VCL1</i> selfed	53% (<i>n</i> = 243)	25% (<i>n</i> = 271)	16% (<i>n</i> = 290)	20% (<i>n</i> = 287)	25% (<i>n</i> = 999)
<i>vcl1/VCL1</i> × <i>VCL1/VCL1</i>	38% (<i>n</i> = 258)	12% (<i>n</i> = 232)	1% (<i>n</i> = 210)	0% (<i>n</i> = 318)	
<i>VCL1/VCL1</i> × <i>vcl1/VCL1</i>	3% (<i>n</i> = 137)	1% (<i>n</i> = 171)	1% (<i>n</i> = 119)	0% (<i>n</i> = 137)	
<i>gnom/emb30</i>					
<i>emb30/EMB30</i> selfed	12% (<i>n</i> = 131)				25% (<i>n</i> = ?)*
<i>emb30/EMB30</i> × <i>EMB30/EMB30</i>	13% (<i>n</i> = 116)				0% (<i>n</i> = 157)
<i>EMB30/EMB30</i> × <i>emb30/EMB30</i>	0% (<i>n</i> = 53)				

vcl1 and wild-type plants were pollinated 2 days after emasculation, and embryos were scored at 2, 3, 4, and 5 days after pollination (dap); seeds were cleared as described previously (Rojo et al. 2001). The frequency of *emb30-3* mutant embryos is cited from Vielle-Calzada et al. (2000) except for (*), which is cited from www.arabidopsis.org (lethal phenotype curated by ABRC). The percentage of mutant embryos is shown, with the total number examined in parentheses. For each cross, the female genotype is listed first.

mutation (Table 2) suggests that the maternally driven mutant phenotype is gradually rescued by the paternal allele and that the MZT in *Arabidopsis* takes place between the two- to four-cell stage and the globular stage. Additional reassessments of existing recessive embryo lethal mutants arrested at late stages would allow defining the MZT with more precision.

ZYGOTIC GENE ACTIVATION

Zygotic Genome Activation Precedes the Maternal to Zygotic Transition and Is Gradual

ZGA was initially defined as the stage where a large increase in de novo RNA synthesis could be measured, for instance, following the incorporation of radioactive-labeled uridine or adenosine (Zalokar 1976; Clegg and Piko 1977). However, it was early recognized that specific transcripts such as α -histone mRNA, selective species of rRNA or tRNA could be synthesized de novo before the major ZGA (Anderson and Lengyel 1980). Furthermore, microinjection of reporter genes, as done in *Xenopus* and mouse embryos (Newport and Kirschner 1982b; Telford et al. 1990), elegantly demonstrated the developmental acquisition of transcriptional capacity before the major ZGA. Since then, additional examples of zygotic genes expressed before the major ZGA in *Drosophila*, but also in *Xenopus*, zebra fish, mouse, and *Caenorhabditis elegans*, established that ZGA is a gradual process (see Table 1). Recent profiling experiments comparing α -amanitin-sensitive and α -amanitin-insensitive genes (differentiating de novo from maternally deposited transcripts) confirmed that a large number of zygotic genes are already active at the one-cell stage in the mouse embryo with a selective, although abundant, activation of genes involved in transcription and RNA processing at the two-cell stage (Zeng et al. 2004). Such early expressed genes are likely to have a specific role in the MZT itself. This view is supported by the observation that in *Drosophila*, but also in *Xenopus* and *C. elegans*, early inhibition of zygotic gene transcription (using α -amanitin) prolongs maternally driven embryonic development in comparison to blocking the major ZGA by a treatment just before the MZT (for review, see Andol 1994). It was suggested that early expressed genes, such as the *Drosophila string* gene, may also have an important role in controlling the degradation of maternally stored transcripts (Edgar and Lehner 1996). The recent identification of the zinc finger protein Zelda, a regulator of ZGA in *Drosophila*, confirms this scenario (Liang et al. 2008).

ZGA coincides with the MZT in mouse and *Drosophila* embryos (Andol 1994). However, ZGA precedes the MZT in amphibians or fishes by several cell cycles (Table 1). In the sea urchin, where the zygote has no transcriptional quiescence, this difference is even more dramatic. Importantly, even in these animal species, ZGA is a gradual process with a subset of genes being activated early before the dramatic increase in transcription at the major ZGA.

Similar experiments of ZGA have not been performed in plants, where the developing embryo is deeply embedded in maternal tissues that act as a barrier for pharmacological treatments. It is also difficult, as in animals, to discriminate

maternally stored from de-novo-synthesized zygotic transcripts in fertilization products. This could be done by looking at nascent transcripts performing RNA-FISH (fluorescence in situ hybridization) on developing embryos, as was done in *Drosophila*, for instance (Ronshaugen and Levine 2004). To date, similar techniques have only been applied to the *Arabidopsis* endosperm, where the maternally expressed, imprinted *MEDEA* locus was found to be actively transcribed immediately following fertilization (Vielle-Calzada et al. 1999). One route around this problem is to analyze the activation of paternally inherited alleles as a substitute for zygotic gene expression, albeit with provisions regarding the synchronous activation of both parental genomes (see later in the text). In *Arabidopsis* and maize, the activation of paternal genes has been followed using reporter transgenes, allele-specific reverse transcriptase-polymerase chain reaction (RT-PCR), or both, for a discrete number of loci. It was found that most paternal loci remained silent or were expressed at very low levels until the globular embryo stage (Vielle-Calzada et al. 2000; Baroux et al. 2001; Grimanelli et al. 2005). Importantly, the verification of paternal activation of endogenous genes using allele-specific RT-PCR excluded transgene-specific paternal silencing effects. This finding was corroborated in maize, where transcript profiles from sexually produced seeds were compared with profiles from seeds of exclusively maternal origin (generated through asexual reproduction) (Grimanelli et al. 2005). The results indicate major changes in the transcript profile only around the globular stage of embryogenesis. A ZGA only after several division cycles was confirmed in *Arabidopsis* by the observation of delayed expression for several other paternally inherited transgenes, or endogenous genes, in unrelated reports (Table 3). Importantly, a delay in paternal gene expression is observed in both the embryo and endosperm.

Interestingly, as in animals, several genes are zygotically active before the major stage of paternal genome activation as defined above. A few paternally inherited alleles were found to be expressed already in two-cell *Arabidopsis* embryos (Weijers et al. 2001), albeit at low levels (Baroux et al. 2001). Early activation is more prominent in maize. Embryo-expressed genes were shown to be expressed biallelically in the zygote using allele-specific assays on manually dissected maize zygotes and embryos (Meyer and Scholten 2007). Although for 13 of the 25 genes tested, there was no significant difference in the levels of maternally and paternally derived transcripts in the zygote, paternal activation is not complete at this stage for other loci. At the zygote stage, 10 of 25 genes showed predominantly maternal expression, decreasing to 8 of 25 loci at 3 days after pollination and to 5 of 25 loci at 6 days after pollination (Meyer and Scholten 2007). Thus, maternal predominance decreases gradually because either paternal alleles are increasingly more transcribed or maternal transcripts are degraded, or both.

Therefore, as in animals, ZGA seems to be a gradual process in higher plants. Differences between maize and *Arabidopsis* seem to exist, however, up to the earliest stage at which zygotic genes can be detected. This discrepancy may relate to different reproductive strategies. Out-crossing plants, such as maize, may benefit significantly from heterosis effects related

Table 3. Reported examples of predominant maternal expression in the early embryo and/or endosperm of higher plants

Locus (gene or transgene)	Method of investigation	Reference
<i>Arabidopsis</i>		
<i>AGP18</i>	allele-specific RT-PCR/ enhancer detector	our unpublished observations
<i>AtLPT1:GUS</i> , <i>AtLTP1:LhG4</i>)	reporter expression	Baroux et al. (2001)
<i>AtSUC5</i>	allele-specific RT-PCR/ reporter expression	our unpublished observations
<i>CYCB1;1:GUS</i> , <i>CBCB1;1:LhG4</i>	reporter expression	Baroux et al. (2001)
<i>DCL1:GUS</i>	reporter expression	Golden et al. (2002)
DD36	reporter expression	our unpublished observations
ET346	enhancer detector	Vielle-Calzada et al. (2000)
ET552	enhancer detector	Vielle-Calzada et al. (2000)
ET1041	enhancer detector	Vielle-Calzada et al. (2000)
ET1051	enhancer detector	Vielle-Calzada et al. (2000)
ET1119	enhancer detector	Vielle-Calzada et al. (2000)
ET1275	enhancer detector	Vielle-Calzada et al. (2000)
ET1278	enhancer detector	Vielle-Calzada et al. (2000)
ET1811	enhancer detector	Vielle-Calzada et al. (2000)
ET1849	enhancer detector	Vielle-Calzada et al. (2000)
ET2209	enhancer detector	Vielle-Calzada et al. (2000)
ET2567	enhancer detector	Vielle-Calzada et al. (2000)
ET2612	enhancer detector	Vielle-Calzada et al. (2000)
ET2634	enhancer detector	Vielle-Calzada et al. (2000)
ET3536	enhancer detector	Vielle-Calzada et al. (2000)
ET3757	enhancer detector	Vielle-Calzada et al. (2000)
ET3988	enhancer detector	Vielle-Calzada et al. (2000)
ET3992	enhancer detector	Vielle-Calzada et al. (2000)
ET4320	enhancer detector	Vielle-Calzada et al. (2000)
ET4336	enhancer detector	Vielle-Calzada et al. (2000)
ET4563	enhancer detector	Vielle-Calzada et al. (2000)
<i>FIE:GUS</i> , <i>FIE:GFP</i>	reporter expression	Yadegari et al. (2000)
<i>GNOM/EMB30</i>	allele-specific RT-PCR	Vielle-Calzada et al. (2000)
KS117	reporter expression	Sørensen et al. (2001)
<i>LACHESIS:GUS</i>	reporter expression	our unpublished observations
<i>MSI</i>	allele-specific RT-PCR	Leroy et al. (2007)
<i>pOp/LhG4</i> components	reporter expression	Baroux et al. (2001)
<i>PROLIFERA</i>	allele-specific RT-PCR/ enhancer detector/gene trap	Springer et al. (2000); Vielle-Calzada et al. (2000)
<i>Zea mays</i>		
AB073081	allele-specific RT-PCR	Grimanelli et al. (2005)
AF371278	allele-specific RT-PCR	Grimanelli et al. (2005)
AI670662	allele-specific RT-PCR	Grimanelli et al. (2005)
AI677212	allele-specific RT-PCR	Grimanelli et al. (2005)
AI677270	allele-specific RT-PCR	Grimanelli et al. (2005)
AI745997	allele-specific RT-PCR	Grimanelli et al. (2005)
AI746088	allele-specific RT-PCR	Grimanelli et al. (2005)
AI746192	allele-specific RT-PCR	Grimanelli et al. (2005)
AI833700	allele-specific RT-PCR	Grimanelli et al. (2005)
AI854929	allele-specific RT-PCR	Grimanelli et al. (2005)
AW066244	allele-specific RT-PCR	Grimanelli et al. (2005)
AW066927	allele-specific RT-PCR	Grimanelli et al. (2005)
AW091461	allele-specific RT-PCR	Grimanelli et al. (2005)
AW181192	allele-specific RT-PCR	Grimanelli et al. (2005)
AW216004	allele-specific RT-PCR	Grimanelli et al. (2005)
AW216025	allele-specific RT-PCR	Grimanelli et al. (2005)
AW216194	allele-specific RT-PCR	Grimanelli et al. (2005)
DW475554	MS on RT-PCR products	Meyer and Scholten (2007)
EH038205	MS on RT-PCR products	Meyer and Scholten (2007)
EH038208	MS on RT-PCR products	Meyer and Scholten (2007)
EH038209	MS on RT-PCR products	Meyer and Scholten (2007)
EH038210	MS on RT-PCR products	Meyer and Scholten (2007)
EH038211	MS on RT-PCR products	Meyer and Scholten (2007)
EH038212	MS on RT-PCR products	Meyer and Scholten (2007)
EH038213	MS on RT-PCR products	Meyer and Scholten (2007)
EH038215	MS on RT-PCR products	Meyer and Scholten (2007)
EH038218	MS on RT-PCR products	Meyer and Scholten (2007)
<i>Fie2</i>	allele-specific RT-PCR	Danilevskaya et al. (2003)
<i>Meg1</i>	allele-specific RT-PCR	Gutiérrez-Marcos et al. (2004)

Genes or transgenes (enhancer detectors, reporter gene fusions, components of gene *trans*-activation systems) are listed, together with methods used to discriminate the expression of parental alleles for the two species *Arabidopsis* and maize. Putative or known functions assigned to these genes do not suggest any common trend with respect to their cellular functions. (MS) Mass spectrometry.

to early paternal genome activation (Meyer and Scholten 2007), but no heterosis effects are observed in embryos of self-fertilizing species, such as *Arabidopsis*, at this early stage.

Mechanisms of Zygotic Genome Activation

Establishment of a permissive chromatin state. Following fertilization in mammals, reprogramming of chromatin occurs on a large scale by rapid and active demethylation of the paternal genome, whereas the maternal genome is progressively and passively demethylated (Santos et al. 2002). Imprinted genes, however, escape these demethylation processes (Branco et al. 2008). Genome-wide demethylation reflects the release of a global, silent chromatin state, a prerequisite for transcriptional activation. Furthermore, the apparent increase in histone acetylation at the one- to two-cell transition in the mouse may provide the basis for a permissive transcription state (Sarmiento et al. 2004). In favor of this argument, depletion of maternal BRG1, a catalytic subunit of SWI/SNF-related chromatin remodeling complexes, does not affect global levels of histone acetylation, but affects levels of H3K4me₂, a mark of active chromatin (Bultman et al. 2006). Maternal depletion of BRG1 causes embryos to arrest at the MZT (two-cell arrest) and results in down-regulation of 30% of the genes that are normally expressed at this stage. Maternal mutations in the mouse homolog of *Xenopus* nucleoplasmin 2 (NPM2), which induces sperm DNA decondensation in vitro, lead to a loss of heterochromatin and deacetylated histone H3 associated with nucleoli (Burns et al. 2003). However, the exact role of maternal NPM2 in regulating zygotic gene expression levels is not known.

During this reprogramming process, repressive mechanisms also act to ensure relative embryonic quiescence. The role of transcriptional repressors has been uncovered by conditional inhibition of protein synthesis during embryo development. This is the case for the *Xenopus* homolog of the mammalian DNA-methyltransferase Dnmt1 (xDnmt1), where embryos deficient in xDnmt1 exhibit premature gene expression at least two cell cycles earlier than normal (Stancheva and Meehan 2000; Stancheva et al. 2002). Repression by xDnmt1 is independent of its catalytic activity, and it may act as a general DNA-binding transcriptional repressor (Duncan et al. 2008). Similarly, the methyl-CpG-binding protein KAISO was identified as a global transcriptional repressor of early transcription in *Xenopus* (Ruzov et al. 2004). In KAISO-depleted embryos, 35S-UTP incorporation was detected two cell cycles earlier than in mock injected embryos, which was associated with a developmental arrest similar to that observed in embryos depleted for xDnmt1.

The timing of ZGA results, therefore, from a fine-tuned balance between chromatin-based repressive mechanisms and the establishment of a chromatin state permissive for transcription. Silencing and activating epigenetic pathways acting at the genome-wide scale are well described in plants (for review, see Vaillant and Paszkowski 2007). In *Arabidopsis*, these include DNA methylation at symmetric CG sites controlled by the maintenance of methyltransferase MET1, DNA methylation at non-CG sites (a plant-specific

modification) controlled by CMT3 (CHROMOMETHYLASE3), which involves RNA-dependent DNA methylation linking the chromatin small interfering RNA (siRNA)-dependent pathway with DNA methylation, and histone H3 methylation on lysine 9 (H3K9me₂). The potential role of these pathways in early zygote transcriptional silencing and the MZT remains to be determined.

Transcriptional activation of zygotic genes. Genome-wide studies identified *cis*-regulatory elements in the 5' region of zygotically transcribed genes in *Drosophila*, which may prime them for expression during early cleavage stages (ten Bosch et al. 2006; De Renzis et al. 2007). The genes possessing the heptamer motif "CAGGTAG" in their 5'-regulatory regions are referred to as "TAG genes" and suggest a collective control of their expression during ZGA by a sequence-specific transcriptional activator(s). This motif was used as an entry point to identify the Zelda (Zld) transcription factor, in a one-hybrid screen (Liang et al. 2008). Zld is maternally stored in the zygote and is required for normal cell division and patterning of the embryo. The broad range of phenotypes observed in *zld* mutants indicates that *zld* embryos fail to express genes essential for cellular blastoderm formation. This was confirmed for several patterning genes by in situ hybridization, and microarray analyses detected at least 279 genes controlled by Zld. Among these, 82% were zygotically active genes. Surprisingly, an equal amount of genes are up-regulated in *zld* mutants and correspond to maternal genes. This effect can be explained by a lack of maternal transcript turnover due to the expression of miR309, a target of Zld that is derepressed in mutant *zld* embryos. Zld therefore provides a mechanistic link between ZGA and maternal transcript degradation (see below and Fig. 2).

Parent-specific mechanisms. Differences in parental genome activation have been observed and can be related to the distinct epigenetic control of maternal and paternal chromosomes. In the mouse, the paternal pronucleus shows transcriptional activity as early as the one-cell stage, before the maternal pronucleus, based on BrUTP incorporation (Aoki et al. 1997). Differential DNA methylation profiles have been found between the two parental genomes in mammals: The maternal genome undergoes a stepwise passive demethylation (see above), whereas the paternal genome is rapidly demethylated before the first cell division (Reik 2007). Moreover, genome-wide analysis of DNA methylation in promoters using mouse embryonic stem cells, embryonic germ cells, and sperm cells shows that their DNA methylation patterns are surprisingly similar. This suggests that although the sperm is a highly specialized and differentiated cell type, its epigenome is already largely reprogrammed before fertilization, resembling that of a pluripotent state (Farthing et al. 2008). Moreover, in contrast to the female genome, the male genome must undergo drastic chromatin remodeling after fertilization. The protamines, which are required for tight chromatin packaging in the sperm, have to be replaced by histones, including H3.3 variants. These histone variants have been associated with transcriptionally active chromatin in animals. The distinct chromatin composition of male and female genomes at

Figure 2. Mechanisms of zygotic genome activation and maternal transcript degradation in *Drosophila*. Early development is driven by maternal transcripts deposited in the egg. *Zelda* transcripts are inherited maternally and encode a global transcription factor that recognizes a specific regulatory motif called “TAG.” Genes containing the TAG motif in their regulatory regions are transcribed actively in the early embryo after fertilization. Several hundred TAG genes have been identified. Among these, the precursor of microRNA-miR309 (pre-miR309) allows the coupling of zygotic transcriptional activation to the large-scale degradation of maternal transcripts. miR309 targets hundreds of maternally deposited transcripts, inducing their translational inhibition and destabilization. This coupling results in the coordinated decrease and increase in levels of maternal and zygotic transcripts, respectively.

fertilization may provide a mechanistic basis for parentally distinct transcriptional activation mechanisms.

As in animals, the plant sperm chromatin is highly compacted at fertilization. Sperm-specific histone variants have been identified that may package plant sperm genomes similar to the animal protamins (Okada et al. 2005). In *Arabidopsis*, karyogamy is quickly followed by the removal of at least one of these histones, an H3.3 variant (Ingouff et al. 2007). Interestingly, this removal follows distinct dynamics in the two fertilization products, with a rapid elimination in the zygote and a progressive dilution through successive replication rounds in the endosperm (Ingouff et al. 2007). These findings suggest that changes in core nucleosome composition occur in plants after fertilization, indicating a converging role in plants and animals for histone H3 and its variants in enabling transcription from paternally inherited chromatin.

OVERCOMING MATERNAL DOMINANCE: DEGRADATION OF MATERNAL FACTORS DURING THE MATERNAL TO ZYGOTIC TRANSITION

The establishment of the zygotic transcriptional program requires the degradation of maternally contributed RNAs. Although some of the maternal mRNAs are stable and continue to contribute to development long after ZGA, degradation mechanisms start to act early after fertilization, creating a mixed maternal/zygotic gene expression profile in the young embryo. Genome-wide profiling in *Drosophila* showed that 33% of the maternally

deposited transcripts are degraded in the embryo (De Renzis et al. 2007). Two RNA degradation pathways are used to promote turnover of maternal transcripts during the MZT, and both target 3'UTR (untranslated region) sequence motifs (for review, see Stitzel and Seydoux 2007; Tadros et al. 2007a). The first pathway is driven by maternally encoded factors, whereas the second coincides with the onset of zygotic transcription.

A survey of 1095 genes known to be maternally deposited before the *Drosophila* MZT identified two families of motifs in their 3'UTR, based on sequence similarity (De Renzis et al. 2007). The first family contains a UUGUU core, which resembles the target site for the Pumilio family of RNA-binding proteins, represented by the Pumilio translational regulator (Wharton et al. 1998). Pumilio controls the expression of the maternally encoded SMAUG protein, which recognizes stem-loop structures present in 3'UTR or coding sequences of maternal mRNAs (Tadros et al. 2007a; Semotok et al. 2008). Microarray analysis showed that Smaug is a general activator of RNA degradation (Tadros et al. 2007b). Sequences from the second family match the AU-rich element (AREs, canonically defined as UAUUUUAU), a mediator of mRNA degradation (Shaw and Kamen 1986). The existence of the zygotic degradation pathway was first demonstrated for the maternal mRNAs of the string/Cdc25 and cyclinA1 cell cycle regulators. Inhibition of transcription in the early embryo by α -amanitin treatment inhibited mRNA degradation, thus showing that ZGA and maternal mRNA degradation are coupled during the MZT (Anderson et al. 2001; Audic et al. 2002). It was proposed that a ribonuclease activity

was responsible for this coupling (Andéol 1994). The regulatory pathway became more intricate with the discovery that regulation by microRNAs (miRNAs) is involved in mRNA degradation during early embryogenesis. miRNAs are small noncoding RNAs, produced from precursors by the Dicer ribonuclease. They silence gene expression by repressing translation or promoting mRNA turnover, via 3'UTR sequence-specific recognition of their target mRNAs. Zebra fish *dicer* mutants, which lack mature miRNAs, show a maternal zygotic effect (Mishima et al. 2006). In zebra fish, a single miRNA family (miR430) drives the repression of several hundreds of maternal mRNAs (Giraldez et al. 2006). miR430 is expressed zygotically shortly after fertilization and is required for embryogenesis to be completed, as shown by reversion of the *dicer* embryo phenotype by miR430 injection. miR430 promotes target mRNA clearance by accelerating deadenylation (Giraldez et al. 2006). Use of miRNAs to promote mRNA turnover during the MTZ appears to be a conserved phenomenon because a comparable role of miRNAs was recently reported in *Drosophila* (Bushati et al. 2008). A cluster of zygotically expressed miRNAs (miR309), activated about 2 hours after fertilization, targets maternal mRNAs for turnover as part of the zygotic degradation pathway. Interestingly, it was recently shown that miR309 zygotic expression is driven by the general ZGA activator Zelda (Fig. 2), providing a link between both the genome activating pathway and the mRNA degrading pathway.

In plants, nothing is known about the mechanisms that lead to a reduction of the maternal dominance at the MZT. A genome-wide analysis of maternal transcripts and their dynamic levels following fertilization would be a prerequisite to identify potential motifs and regulators of their degradation, as was done in *Drosophila* (Liang et al. 2008). Such studies are challenging because female gametes and fertilization products are embedded in maternal tissues and are difficult to access. This may, however, be overcome using manual or laser-assisted dissection of eggs and young embryos (Dresselhaus et al. 1996, 1999; Day et al. 2005; Sprunck et al. 2005; Meyer and Scholten 2007) in combination with transcript profiling or deep sequencing approaches.

BIOLOGICAL SIGNIFICANCE

Gametes are highly differentiated cells and perform unique tasks associated with reproduction. At the same time, they can rapidly lose gametic cell fate following fertilization and endow the zygote with a totipotent state. Performing both functions implies a dramatic reprogramming of the zygotic genome in order to erase the marks associated with gametic cell fate and to establish the transcriptional status associated with totipotency. The consensus today is that the potential for totipotency in both animals and plants is maternally controlled, with most of the control over genome structure and function residing in the egg cytoplasm (Stitzel and Seydoux 2007). The most striking evidence is the ability of parthenogenetic plants and animals to develop functional organisms without any paternal contribution. That male contributions to the zygote are fully dispensable in these cases illustrates that

the female genome maintains enough flexibility to compensate for any essential male contribution, whenever missing. Thus, the oocyte probably drives the events required for totipotency, including the reprogramming of the male genome following fertilization. This is well illustrated by the replacement of paternal histone components by maternally provided histone variants immediately following fertilization.

In animals, this model appears to be true whether the germ line is “predetermined” as in *C. elegans* or *Drosophila* (primordial germ cells are formed early through inheritance of maternal germplasm) or formed by inductive signals later during development, such as in mice. In both systems, transcriptional repression in the germ line is apparently decisive to totipotency (Stitzel and Seydoux 2007). In addition, gene regulation is dependent on cytoplasmic posttranscriptional mechanisms in both of these systems. Although the underlying processes are different in *C. elegans*, *Drosophila*, or mice, shared developmental constraints associated with genome reprogramming and the acquisition of totipotency have led to a set of convergent mechanisms. Transcriptional repression and extensive chromatin remodeling in the gametes are followed by the establishment of a totipotent zygotic program after fertilization through another wave of chromatin reprogramming, and finally, at the MZT, the maternally stored gene products are cleared in the developing embryo.

It is tempting to speculate that the transfer of gene expression to the cytoplasm and the maintenance of relative quiescence in the early embryo represent a buffering mechanism that protects the embryo against uncoordinated genic activity during this dramatic phase of reprogramming. Likely, all living organisms share this constraint, and most animals have apparently responded by evolving remarkably similar mechanisms. Plants more resemble mice than flies, in the sense that they differentiate a germ line very late during development in an inductive manner, often many years after the formation of the embryo. Although the life cycles of plants and animals differ in important ways, the requirement for a reprogramming phase after fertilization remains. Although the data currently available remain inconclusive, we anticipate that the coming years will provide ample opportunities for enriching comparisons between the earliest phase of postfertilization development in animals and that in plants.

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