



# New cues for body axis formation in plant embryos

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Plant embryogenesis initiates with the fusion of sperm and egg cell, and completes the generation of the basic outline of the future plant. Here, we summarize the recent findings about the signaling cascade triggering the zygotic transcription, and the intracellular events and regulatory factors involved in the formation of the two major body axes. We highlight the lack of systematic *de novo* transcriptional activation in the zygote, and emphasize the importance of cytoskeletal reorganization to polarize the zygote and control the first asymmetric division that establishes the apical–basal axis. Finally, the limited knowledge of mechanisms that control the cell divisions separating the inner and outer cell layers is summarized and we propose approaches to enhance our understanding of basic principles of plant embryogenesis.

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## Introduction

In both animals and plants, sexual reproduction produces male and female gametes, which are fused to generate the zygote. In plants, zygotic development marks the transition from the gametophytic haploid life phase to the sporophytic diploid life phase. Therefore, the gametophytic state is reprogrammed to a new sporophytic state that initiates the series of transcriptional events directing embryogenesis. Thereafter, the zygote and the embryo generate the body axes as the basis of subsequent pattern formation. In *Arabidopsis thaliana*, the apical–basal axis is defined by the asymmetric division of the zygote, which generates a small apical daughter cell and a large vacuolated basal daughter cell (Figure 1) [1]. The apical daughter cell gives rise to the spherical proembryo by

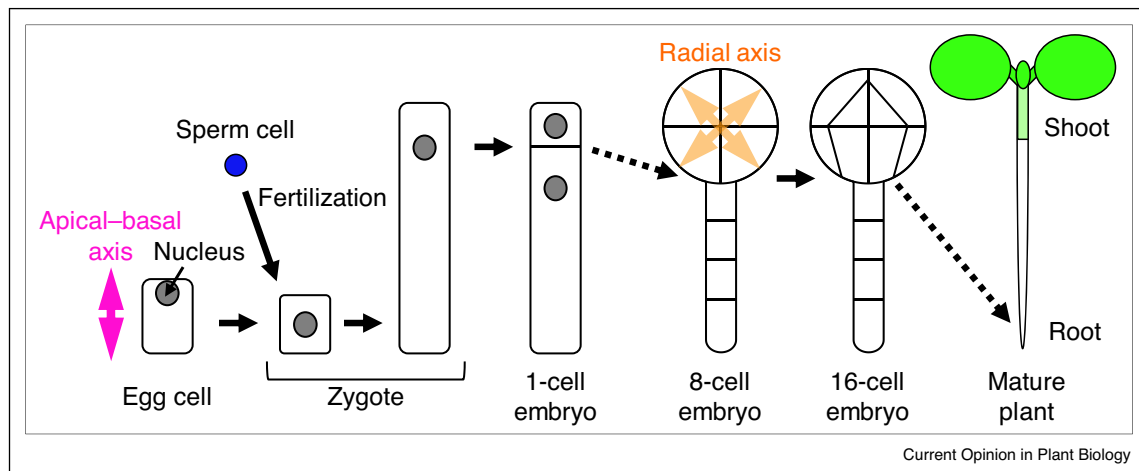
divisions in different orientations. In contrast, the basal daughter cell continues to divide horizontally to produce a filamentous suspensor that connects the proembryo to maternal tissues [1,2]. Each cell in the 8-cell stage proembryo performs an asymmetric (periclinal) division that separates an outer protoderm layer from a mass of inner cells. These divisions generate the radial axis in the 16-cell embryo (Figure 1). The protoderm differentiates as the epidermis, and the stem cell niche of the shoot meristem arises from the inner lineage [3–5], showing that the basic body plan is already generated at such an early stage although patterning of organs takes place post-embryonically.

## Onset of zygotic/embryonic transcriptional program

In animals, early embryogenesis depends on maternal RNAs deposited in the unfertilized egg cell, and the transcription of the zygotic genome is activated only after several cycles of embryonic cell division [6,7]. In plants, *de novo* transcription takes place in the zygote and the contribution of parental genomes have been analyzed using transcriptomes from hybrids between different accessions and mutants [8–10]. Several contradictory results were reported, possibly due to differing degrees of contaminating maternal tissues [11,12]. A consensus emerges that in angiosperms, there is no concerted maternal to zygotic transition, and the zygotic transcriptional machinery is active after completion of fertilization. This was shown for genes that are transcribed *de novo* immediately after fertilization [11]. Yet other genes are gradually activated transcriptionally or silenced during early stages of embryogenesis [13]. This progressive activation of zygotic genes was recently confirmed by the RNA sequencing of isolated zygotes in rice and maize [14,15]. By comparing the transcripts in sequential stages of zygote development, it was shown that the maternal transcripts are abundant at early stages, but *de novo* transcripts become gradually predominant during the first zygotic cell cycle.

Recent work identified a signaling pathway that activates transcription of specific genes after fertilization. *SHORT SUSPENSOR* (*SSP*) encodes a membrane-associated pseudokinase, and its mRNA is inherited from sperm [16]. In the zygote, *SSP* mRNA is translated to activate the mitogen-activated protein (MAP) KK kinase YODA (YDA) (Figure 2a) [16,17]. The downstream MAP kinases MPK3/6 phosphorylates the transcription factor WRKY2, which in turn activates the transcription of *WUSCHEL HOMEODOMAIN* (*WOX8*), by directly binding to its promoter with maternally-derived factors HOMEODOMAIN

Figure 1



Schematic diagram of the Arabidopsis embryogenesis. Egg cell polarity is disrupted by fertilization. Later asymmetry of the zygote is established and determines the apical–basal axis. The radial axis is formed when the inner and outer cells are separated at 8–16 cell stage embryo. Solid and dashed arrows indicate sequential and nonsequential steps, respectively.

GLABROUS11/12 (HDG11/12) [18<sup>•</sup>,19]. *WOX8* and its closest homolog, *WOX9*, redundantly regulate both zygote polarization and embryo patterning, although their direct targets remain unknown [20]. *WOX* genes appear to be plausible targets of zygotic *de novo* expression in Arabidopsis, as shown by the WRKY2-dependent increase of the *WOX8* expression in the zygote, compared to that in the unfertilized egg cell [19]. Also in rice, *de novo* transcription of *WOX2* was suggested, because *WOX2* transcript was not detected in the egg cell but enriched in the zygote [21]. *WOX8* and *WOX9* are derived from an ancestral clade of *WOX* genes represented by *WOX13* in Arabidopsis [22]. This clade contains one gene in the liverwort *Marchantia polymorpha* [23], and three genes in the moss *Physcomitrella patens*, two of these being expressed and required for the first cell division of the zygote [24]. In spite of the deep evolutionary conservation of the role of *WOX* genes in zygotic development, *SSP* is *Brassicaceae*-specific variant of *BSK* gene family [25] and thus it is not likely that the parental cooperation that regulates the activation of the *WOX* cascade in Arabidopsis is widely conserved amongst plant species.

### Apical–basal axis formation: zygote polarization

Although the cell division patterns during embryogenesis are quite diverse amongst plant species [26], the zygotic transverse division that produces the apical and basal cells is common to most species of land plants, including Arabidopsis, rice, mosses and liverworts [24,27–29], implying the fundamental role of zygote polarization during apical–basal axis formation. In Arabidopsis, the unfertilized egg cell shows polar organization, which is marked by the apical position of the nucleus (Figure 1) [30]. At fertilization however, the nucleus becomes

positioned centrally [31]. After the zygote elongation, the nucleus again positions close to the apical apex, and thus the first zygotic division is asymmetric, producing a small apical cell [1]. The living dynamics of the intracellular repolarization were visualized by live-cell imaging of developing Arabidopsis zygotes [32,33<sup>••</sup>]. The preexisting alignment of microtubules (MTs) and actin filaments (F-actins) in the egg cell is disorganized after fertilization, and then MTs organize into a subapical transverse ring to restrict the direction of zygote elongation, whereas F-actin forms an apical cap and longitudinal arrays to move the nucleus to the apical tip (Figure 2b). Similar associations of cytoskeleton features and nuclear migration are observed in tip-growing cells, such as fern protonema and Arabidopsis root hair [34,35], implying that the zygote might utilize the tip growth machinery to polarize. Although it is still possible that maternal polarity determinants are inherited from the egg cell, the dramatic intracellular changes in the elongating zygote imply that egg cell polarity is lost after fertilization, and subsequently the zygote establishes its polarity *de novo* (Figure 2b). Fertilization-triggered loss of polarization might be a general feature of plant zygotes, since dramatic cell shrinkage is reported in various species [33<sup>••</sup>,36–38], and F-actin organization is remodeled during the fusion of gamete nuclei (karyogamy) in rice [39].

The molecular determinants of the apical–basal axis are still unknown. As in most animals, the plant sperm cell could provide a cue to orient the zygote polarity [40,41]. This remains unclear in angiosperms, because of anatomical constraints on the site of sperm fusion with the egg cell *in vivo* and *in vitro* fertilization [42,43]. Some signals might originate from the embryo-surrounding tissue, endosperm, because the cysteine-rich peptide encoded

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