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HIGHLIGHT

Embryogenesis, a process of pattern formation

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Plant embryogenesis is traditionally defined as a developmental process from zygote to mature embryo, which has the potential to form a complete plant (Bhojwani, 1974; Hu, 2005). In dicotyledonous species, the fertilized egg or zygote usually divides according to a stereotyped pattern and gives rise to an embryo that consists of an embryonic shoot, cotyledons, hypocotyls, and an embryonic root. Thus, the basic body plan of the plant is established during the embryogenesis. Interestingly, the shoot-leaf-stem structure, not including the root, is repeatedly photocopied as a basic unit throughout plant vegetative growth (Wolpert et al., 2002). In this case, embryogenesis is a seemingly endless process and the epitome of plant body-building. However, recent studies on the molecular mechanism of embryogenesis revealed that the basic plant body plan is laid down as the establishment of the radial and apical-basal axes. During this process, both the radial concentric tissue layers and the apical-basal sections of the plant body are generated, especially the root and shoot stem cell pools, which are essential for postembryonic growth (De Smet and Jürgens, 2007; De Smet et al., 2010). All further development and morphogenesis are governed or guided by this basic pattern. Thus, embryogenesis is, in fact, a process of pattern formation.

Recent studies have demonstrated that embryo pattern formation is a rather complex process that involves most current hot topics, such as polarity establishment, cell fate determination, parental effects via gene imprinting, cell–cell communication, positional effects in cell differentiation, directional signal transduction, auxin polar distribution, axis selection, and symmetry establishment (Grossniklaus et al., 1998; Jürgens 2001; Scheres, 2001; Weterings et al., 2001; Weijers et al., 2003; Friml et al., 2003; De Smet et al., 2010). Therefore, embryogenesis becomes an ideal model for addressing multidisciplinary questions regarding plant development.

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Although the elucidation of genome sequences and the development of novel technologies have greatly accelerated our understanding of the basic regulatory processes that control embryogenesis, the answers to many questions remain unknown; for example, how the zygote is activated and tuned to embryogenesis; how apical and basal cell fates are determined; how apical cell derivatives are guided to an embryonic destiny; and how the apical-basal axis of an embryo is matched to the zygote or 2-celled proembryo long axis. In addition, embryo pattern formation is a stage- and cell-lineage–dependent process. Timely connection of these stages is exactly programmed, but it remains unclear how the former stage passes the message to the next and, in the signaling cascade, how the different cell lineages are confined from each other. Investigation of the mechanism of hypophysis specification has provided a good example showing how positional cues lead to a cell's developmental fate (Scheres, 2001; Weijers et al., 2006; Schlereth et al., 2010), and suggests that cell–cell communication and compartmental regulation may be basic regulatory approaches during embryo patterning.

Focusing on all these questions, an article by Zhao et al. in this issue of *Frontiers in Biology* entitled "Patterning the embryo in higher plants: Emerging pathways and challenges" summarized recent progress in the research of embryo pattern formation. To make more of an impact, authors generally try to survey these novel findings from different angles. However, unlike most reviews in this field, the authors of this paper attempt to give readers a panoramic view of all valuable novel findings concerning the mechanism of embryo patterning. Some aspects that are usually mentioned less often or neglected, such as the differentiation of cotyledons and the specification and maintenance of stem cell niches in the shoot apex, are discussed in detail in this review paper. Thus, the review lays out related aspects as much as possible for a depiction of the whole field. In addition, the authors emphasized the cellular pathways in the regulation of embryo patterning. They attempt to integrate different molecular pathways and thus give a better picture of the complex regulatory network. In fact, it is much more difficult to analyze the function of single signaling elements during embryo patterning, due to high genetic redundancy in embryogenesis. Consideration of the simultaneous influence of different regulatory pathways may be the appropriate way to further investigate this issue. This is probably the idea that the authors hoped to share with readers. This, notwithstanding, because many aspects of the molecular mechanisms involved in embryo patterning remain inadequately understood for a clear signaling network to emerge, the novel findings summarized in this paper, including the authors' highlights and clues derived from the authors' discussion, will surely benefit researchers in this field.

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