

## Introduction

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MUCH OF THE BEAUTY of plants stems from their intricate spacing patterns of organs, tissues and specialized cells, the results of developmental programs that generate the adult plant from the zygote. To cope with changes in the environment without the ability to move around, plant development displays a remarkable plasticity that is evident at the organismal and at the cellular level. As organisms, plants redirect development in response to environmental cues such as light and nutrient availability. Individual cells are able to change fate when position within the organism is changed or when various stresses have to be counteracted. Perhaps it is not an overstatement that plants 'behave' by integrating these cues into developmental pathways. Accordingly, perception and interpretation of signals must be extremely important to allow the integration of internal and external developmental cues.

The plant and animal kingdoms do not appear to share a common multi-cellular ancestor. The evolutionary history of their developmental mechanisms is therefore entirely different. Furthermore, plants display cellular properties such as the cell wall that prevents extensive cell movement and may impose other strategies for cell–cell communication. Can one thus conclude that all developmental mechanisms are different in plants? Answering this fundamental question represents an important test case for the generality of our concepts of development. The growing body of knowledge on transcription factors involved in flower development certainly shows that at the level of nuclear gene expression, parallels exist between pattern formation in plants and animals. The five essays in this issue of *Seminars in Cell and*

*Developmental Biology* probe different signalling events during plant development and clarify that such similarities extend beyond the nucleus.

It is intriguing to note not only a difference in the history of the major multicellular kingdoms, but also in the history of the scientific discoveries regarding their development. A burst of insight in animal development was obtained by the revelation of a cascade of early genetic activities leading from zygote to segmented larva in *Drosophila*. In contrast, the understanding of plant development appears to move in an opposite direction. While the molecular action of several signals that govern later aspects of plant development is beginning to be understood in increasing detail, early phases of plant development such as axis formation and early patterning, still hide many secrets. Accordingly, this issue starts off with essays that focus on signalling events that are crucial for later steps in development, to conclude with a dispatch on the earliest signalling events in zygote and embryo.

One can hardly be surprised that light, the energy source of plants, is an important signal for the modification of development (Deng and Quail, this issue). In their strive for optimal utilization, plants cannot walk to the source but have to develop towards it. Dramatic programmed changes catch the eye when comparing light- and dark-grown juvenile plants. Mutants that confer dark-grown development in the light and vice versa have been starting points to obtain insights into the signalling network that links light of various wavelengths to development. On the perception side, it appears that proteins with capacity for photoregulated phosphorylation trigger signalling cascades. Two protein classes are identified, in one case derived from cyanobacterial photoregulated kinases and in the other from eukaryotic serine kinases. Further downstream in the light signalling cascade, a large protein complex has been implicated in regulation of gene expression. It is striking that

this complex resembles both the regulatory component of a yeast proteasome, suggesting a role for selective protein degradation, and a human complex of which subunits have been implicated in diverse functions such as transcription factor activation and cell cycle progression.

Another signal of overall importance in plant development, and contributing to a flexible response on changing conditions, is the plant hormone auxin. The list of molecular players directing the action of this small molecule with its extreme range of effects is increasingly growing (Leyser and Berleth, this issue). Again genetic screens based on signal response, but also developmental screens and molecular studies on auxin target genes have been pivotal. The importance of a protein degradation pathway resembling the ubiquitination pathway in yeast has been established. Two transcription factors specifically involved in auxin-responsive gene expression have now been described, and one of them was also identified as the gene associated with mutations that confer embryonic as well as post-embryonic developmental defects. Auxin sensitivity has recently been shown to be influenced by 'early auxin response genes' that do not have DNA binding domains but share several domains with the above-mentioned transcription factors. Good candidates for auxin importers and exporters with the capacity to mediate auxin distribution have been identified. Lastly, a connection between auxin signalling and a MAPK pathway has been demonstrated, and this pathway may mediate cross-talk between auxin and other phytohormone pathways. Clearly, despite the fact that receptors remain to be unequivocally identified, the stage is now set for the dissection of the diverse roles of auxin in plant development.

One complexity of phytohormone signalling is that the diversity of target cells and their responses is immense. Studies are also being performed on very defined cell signalling events, relying on specific gene sets. A signal that represents developmental communication between two defined cell types is the one that governs self-incompatibility during fertilization: the rejection of 'self' pollen by the female stigma cells (Gaude and McCormick, this issue). In many plants studied, the compatibility appears to be regulated by a single multigenic locus, the S-locus—obviously promoting this system as one in which to study cell–cell communication. Rejection occurs when similar alleles of the locus are present in pollen and stigma. Several S-locus products active in stigmatic tissue have been identified. In some plants these

encode specific RNases with hypervariable and conserved regions—reminiscent to our own immunoglobulins, in other plants they encode other glycoproteins of unknown function, and in yet others they encode Ser–Thr receptor kinases with resemblance to animal receptors. Curiously, no pollen-expressed S-locus genes that determine allele specificity are identified yet, despite intense efforts. Is there a mechanistic surprise waiting for us?

It is evident that cell signalling in development is not restricted to special cases such as communicating pollen and stigma. Cell type specification in plants is position-dependent upon perturbation, implying extensive cellular communication (Dolan and Okada, this issue). Plant cells are specified during two phases. Although transcription factor networks with members of various well-known classes (homeodomain; myb) are involved in the specification of a few cell types, the molecular nature of the signalling events that manifest themselves during experimental interference remains unknown. New approaches, which circumvent potential problems like genetic redundancy and lethality, will be required to identify the components involved. Signalling events regarding a special kind of cell specification, that of 'meristem stem cell', form an exception in that the identification of receptors and signals seems to be close at hand. In the shoot meristem, a receptor kinase with potential ligand-binding extracellular leucine-rich-repeats (LRRs) has been shown to be required for the progression of cell differentiation of a stem cell. An interacting gene potentially encoding a peptide ligand has been identified. Interestingly, many LRR transmembrane kinases are present in the plant genome, and a fair amount of them are involved in pathogen recognition. Thus, this class of receptors has diverse roles in the plant life cycle, reminiscent to one *Drosophila* receptor involved in both patterning and pathogen response.

Evidently, the pattern of diverse cell types in defined axes of the plant needs to be set up during embryogenesis. In the embryo, the three major-epidermal, ground, and vascular-tissues form concentric layers perpendicular to the main axis, and they diversify in the organs that are formed along this axis—leaves at the apical and a root at the basal end. Furthermore, two populations of stem cells are formed, the shoot and root meristems. These cells will continue to give rise to progeny post-embryonically, leading to a second phase of (continuous) cell specification. The deeply buried plant embryo has been reluctant to reveal its patterning secrets. To overcome this prob-

lem, studies on zygotic embryogenesis are being complemented with studies on other systems: developing algae and somatic embryos (Vroeman, De Vries and Quatrano, this issue). In algae, axis formation can be brought about by various cues, and is correlated with re-distribution of  $\text{Ca}^{2+}$  channels. Interestingly, the subsequent step of axis fixation requires Golgi-based secretion in algae. A gene implicated in fixation of the main axis in higher plants encodes a protein with high similarity to a nucleotide exchange factor involved in vesicle docking during secretion. It will be interesting to see whether the polarization of the higher plant zygote involves a similar mechanism when compared to algae. Genetic analysis of early embryo patterning events that follow axis specification in higher plants, suggest that early regions are defined in the embryo, and that subsequent signalling between regions diversifies the pattern. Somatic embryogenesis, where embryos are formed from somatic body cells in culture, is a system that can be used in parallel to identify molecules involved in the early steps of embryogenesis. Studies in this system have revealed several molecules with potential roles in axis formation/fixation, among which glycosylated cell wall proteins, although a role for these

proteins in zygotic embryogenesis remains to be established. Two potentially important messages have emerged. First, mutant phenotypes suggest that cell regions in the early embryo signal extensively during pattern formation. Second, at least one gene involved in interpretation of auxin amount or flux mutates to an early patterning phenotype, and several specific patterning defects can be provoked in embryos by manipulating auxin distribution. Would auxin, which has been known for decades, be one of the elusive signals that helps to pattern the plant embryo?

It is hoped that the reader enjoys these essays on a selection of currently studied signalling pathways in plant development. It is expected that he/she arrives at two almost inescapable conclusions. First, plants contain complex and interesting signalling networks. Second, at least parts of these networks appear to be variants of those in bacteria, yeast and animals. Is the same true for the as yet undiscovered components? Getting to the answer of this question may resolve whether plants just use novel combinations of a similar repertoire of building blocks, or whether additional molecular tools are required to create the highly dynamic signalling system that allows them to tune development to the environment.