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Editorial Overview: Growth and development

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Gwyneth Ingram's group is interested in understanding how both molecular and physical interactions coordinate the development of the three major compartments of the developing angiosperm seed. Her group uses a wide range of approaches, from biophysics and modelling through histology and molecular genetics to address this question.

Ari Pekka Mähönen's laboratory studies the development of vascular cambium by using *Arabidopsis thaliana* root as a model. Combination of lineage tracing, imaging and molecular genetics are utilized in his studies. The roles of phytohormones auxin and cytokinins, and their downstream factors, are assessed in the vascular cambium development.

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This exciting issue brings together a suite of topical reviews addressing key aspects of cell and tissue level communication events controlling plant morphogenesis and cell fate and behaviour transitions during development.

No collection of reviews on plant growth and development would be complete without an update on the role of auxin, one of the major hormones regulating plant development. Auxin not only mediates endogenous developmental programmes, but is also considered to act as a hub to integrate environmental cues into developmental programmes. In this issue [Manh Linh *et al.*](#) review the central role of auxin and its polar transport in the coordination of cell polarity during patterning of leaf vein networks. Despite the central role of auxin, recent findings also indicate as yet unidentified auxin-independent components in vein patterning ([Manh Linh *et al.*](#)). The role of auxin in tropic growth responses to environmental cues is addressed by [Harmer and Brooks](#). Interestingly, the dominant role of auxins is challenged by new data revealing that although most tropic responses involve changes in polar auxin transport, hydrotropism and autostraightening occur without changes in auxin distribution. These tropisms are mediated by abscisic acid signalling and mechanosensing, respectively ([Harmer and Brooks](#)).

In addition to auxin, cytokinins also regulate plant morphogenesis. Intimate interactions between cytokinins and auxin are the key driving force in many developmental processes. During gynoecium formation, PIN auxin efflux carriers pattern auxin distribution to establish tissue domains in the gynoecium ([Deb *et al.*](#)). In root meristems, PIN mediated auxin accumulation in the xylem domain coordinates vascular patterning ([Vaughan-Hirsch *et al.*](#)). Interestingly, in both the gynoecium and root vasculature, cytokinins affect auxin distribution by regulating PIN expression or polarity, and this interaction is important in generating boundaries between tissue types. Moreover, in both developmental contexts auxin inhibits cytokinin signalling by locally promoting the production of the repressive AHP6 protein, thus forming a feedback loop between the two hormones ([Deb *et al.*](#), [Vaughan-Hirsch *et al.*](#)). Furthermore AHP6, produced in response to auxin accumulation, also delimits cytokinin signalling in the shoot apex by moving from organ primordia towards the meristem ([Truskina and Vernoux](#)). Thus, a common regulatory feedback loop between cytokinins and auxin seems to have been deployed to facilitate patterning in diverse plant tissues.

As the Shoot Apical Meristem (SAM) produces leaves during the vegetative phase of development, axillary meristems (AM) are formed between the flanks of newly formed leaves and the SAM. AMs give rise to new, dormant, shoot meristems called axillary buds ([Truskina and Vernoux](#), [Wang and](#)

Jiao). Recent studies have demonstrated that the AMs originate from the stem cell pool of the SAM during the leaf initiation process. Auxin minima, and resulting cytokinin accumulation are required for AM activation, revealing another developmental process in which these two hormones cooperate (Wang and Jiao). Since new branches arise from the activated buds, shoot architecture is largely determined by regulating their dormancy. Transcript profiling of axillary buds entering dormancy have identified a common set of responses that resemble a Low Energy Syndrome. This response is conserved between several distantly related species suggesting that it is a central player in bud quiescence (Sánchez Martín-Fontecha *et al.*).

New root meristems can be regenerated from the base of cut leaves without external hormone applications (Xu). This *de novo* root regeneration process is likely initiated by wounding and environmental signals, followed by auxin accumulation and consequent induction of the expression of two genes encoding members of WUSCHEL RELATED HOMEODOMAIN (WOX) transcription factor family. These WOX proteins in turn promote the expression of key root stem cell factors to initiate adventitious root organogenesis (Xu). Cytokinin induced *de novo* shoot regeneration from calli or from lateral root primordia also proceeds in a stepwise manner: regardless of the starting material, the regeneration process involves a gradual replacement of root stem cell determinants with shoot stem cell factors (Radhakrishnan *et al.*). Members of the AINTEGUMENTA-LIKE/PLETHORA (AIL/PLT) transcription factor family confer pluripotency and competence to make shoot progenitors during regeneration (Radhakrishnan *et al.*). Interestingly these transcription factors seem to have a general function in promoting cell division and inhibiting cell differentiation both in root and shoot meristems, although their target genes appear to be somewhat different in these two meristem types (Scheres and Krizek).

Molecular processes, such as gene expression, and the diffusion of hormones and other signalling molecules, are inherently stochastic. Additionally, cell and tissue properties, such as growth rate and mechanical properties, are heterogeneous by nature. Understanding the importance of this molecular-level stochasticity and tissue level heterogeneity underlies an increasingly active research field across all biological systems, and has recently exploded as a key topic in plant developmental biology. In their review Radhakrishnan *et al.* highlight heterogeneity in gene expression and regeneration competence during early shoot regeneration from callus and associated apparent stochasticity in the formation of regenerating foci. Several recent studies have focused on understanding how stochasticity at the molecular and/or cellular level (for example at the

level of gene expression or cell growth rate) can either be harnessed either to promote differences between individual cells or groups of cells (for example during *de novo* organ initiation in regenerating shoots, or during cell patterning in developing organs), or can conversely undergo spatio-temporal averaging to ensure the robustness of developmental programmes and ensure uniformity of organ shape. In her review Adrienne Roeder highlights both these roles by examining specific examples in the recent literature. Mutants showing abnormally high levels of variation in organ growth, have revealed genes and proteins involved in the spatio-temporal averaging of “noise”, although the underlying molecular mechanisms remain relatively poorly understood. In contrast, by varying responsiveness to apparently stochastic variations in the concentration of regulatory proteins, for example during different phases of the cell cycle, differences can be fixed in a subpopulation of cells to generate two distinct cell types within a field of cells.

Changes in cell identity and/or behaviour, although in some cases dependent upon apparently stochastic events in individual cells, are often established through cell to cell signalling-based mechanisms which are becoming increasingly well understood in plants. In addition to hormone-mediated signalling addressed above, reviews in this issue highlight the importance of regulated intercellular movement of other key signals for plant development. For example, Nakajima highlights the importance of the intracellular movement of siRNAs in reproductive development. Plant germ cells are generated through successive patterning events during gametogenesis and sporogenesis. Coordinated cell cycle regulation and several short RNA pathways restrict specification of spore mother cells to a single cell. Egg cell differentiation in turn involves plant-specific RKD transcription factors that are evolutionarily conserved between liverworts and vascular plants (Nakajima). The intercellular movement of peptides and proteins is also of critical importance for a wide range of patterning events, as illustrated in the case of AHP6 (Truskina and Vernoux). Cell signalling during stomatal development has proved a particularly rich source of information about such signaling events, and in this issue Hepworth and colleagues provide a fascinating overview of recent advances in our understanding of the cell-signalling events underlying the formation of stomatal complexes in grasses. In their review both cytoplasmic movement of transcription factors during the specification of subsidiary cells in grasses, and peptide based signalling are addressed. Their review brings into sharp focus the types of molecular innovations that could underlie evolutionary differences in key signalling pathways between major plant groups, identifying some potentially novel players and highlighting unresolved issues.

Peptide based apoplastic signalling is also addressed by the reviews of [Muschiatti and Wengier](#), and of [Nakamura and Grebe](#). [Muschiatti and Wengier](#), rather than addressing cell specification, address the question of the role of Receptor-kinases in pollen tube biology, using a variety of *in silico* resources to uncover potential novel receptors and downstream signalling components involved in pollen tube growth regulation and in the complex dialogue between growing pollen tubes and the tissues of the gynoecium and ovule. In contrast, [Nakamura and Grebe](#), address how the polar localisation of the components of a well characterised apoplastic signalling pathway active in the endodermis, allows the monitoring and closure of a tightly spatially regulated apoplastic barrier, the Casparian strip. This fascinating example of how apoplastic signalling can both control, and be controlled by, apoplastic modification forms part of a comprehensive review of recent advances of the molecular players underlying the establishment of both ‘inside-outside’ and ‘apical-basal’ cell polarity in the developing root, encompassing lipid microdomain establishment, the regulation of the actin cytoskeleton and the role of endocytosis.

Apoplastic barriers, including the Casparian strip, also feature prominently in an original review contributed by [Do *et al.*](#), addressing the multiple and surprisingly diverse functions of ABC transporters in plant growth and development, which range from the polar secretion of hydrophobic cutin, suberin and lignin monomers, to the

transport of a wide range of plant hormones both within and between plant cells. [Do *et al.*](#) highlight the key role likely to have been played by these remarkably polyvalent transporters in the evolution of land plants. Finally a prominent role for the Casparian strip (an essentially inextensible barrier), and the endodermis more generally during lateral root emergence is highlighted by [Stöckle and colleagues](#), who illustrate very clearly the importance of the controlled alteration of the biophysical properties of specific plant cells and tissues in allowing proper morphogenesis. Their review studies the integration of chemical (hormonal) and mechanical factors in permitting the unimpeded movement of lateral roots move through overlying cell layers.

Finally, over and above molecular signaling events involving hormone, RNA and protein movement, it is interesting to note the evocation of the potential role of mechanical feedbacks in regulating morphogenesis in several of the reviews in this issue ([Roeder](#), [Radhakrishnan *et al.*](#), [Nakamura and Grebe](#), [Stöckle *et al.*](#), [Truskina and Vernoux](#) and [Harmer and Brooks](#)). This underlines a growing awareness of the importance of taking biophysical parameters, and plant cell responses to mechanical cues, into account when studying plant development. The molecular basis for the perception of mechanical cues remains a hot topic in plant developmental biology, which will doubtless form the subject of future reviews in this field.