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Editorial overview: Growth and development: Signals and communication in plant pluripotency, differentiation and growth

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Doris Wagner — The lab of Doris Wagner studies how reprogramming of cellular identity and function is orchestrated during developmental transitions or in response to the environment. Her lab focusses on formation of flowers, plant structures critical for reproductive success. The reprogramming to floral fate relies on altered transcriptional programs, chromatin state changes and is guided by hormonal cues.

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Dolf Weijers' lab uses the early plant embryo as a model to understand how plant cells acquire different identity, and how cell-specific genetic programs instruct cell division orientation. As much in plant development is controlled by the plant hormone auxin, an important focus is to understand the molecular basis of diverse yet specific auxin action during development.

Multicellular plant development by definition involves more than a single cell, and usually more than a single cell type. We have focused this issue of Current Opinion in Plant Biology on the challenges that multicellularity poses: a number of reviews discuss how unique gene expression programs are established, while others focus on the internal and environmental signals and communication mechanisms that coordinate development. Much of the recent progress in plant developmental biology relies on facilitating technologies. Hence, several reviews focus on such technologies.

Transcription, noncoding RNA and epigenetics

Multicellular organism development is largely driven by differential gene expression, and several reviews in this issue focus on regulation of cell-specific and stage-specific gene expression programs. At the very beginning of a new organism, the gene expression program is dependent on the parent of origin. As Del Torro-de Leon *et al.* point out, biased expression of the two parental alleles occurs in the first days of development during zygotic gene activation, at selective loci due to imprinting (mainly in the endosperm) and when two different genomes are combined in hybrids. Monoallelic gene expression during zygotic genome activation and at imprinted loci relies in large part on epigenetic silencing of one of the two alleles. Likewise, heterosis in hybrids has been linked to altered RNA-dependent DNA methylation.

Lewis and Hake tackle the question how the identity of the ligule, a small region that separated the sheath and blade of leaves in the grasses, is established. The ligule arises through periclinal cell divisions in the adaxial epidermis. Genetic studies have shown that the transcription factors that specify initiation, maintenance and identity of the shoot meristem also play a role in ligule development. These include KNOX homeodomain transcription factor (*liguleless 3*; *lg3*), SBP family transcription factors *lg1* and a mobile bZIP transcription factor *lg2*. The phenotype of *lg2* suggests that proximal/distal and medial/lateral leaf patterning are linked.

Leaves are the major site of photosynthesis, which requires uptake of CO_2 trough specialized openings in the leaf epidermis called stomata. Simmons and Bergmann review the pivotal role of bHLH transcription factors in the development of stomata. These transcriptional regulators control entry into and exit from the stomatal lineage as well as the number of stomates formed and their relative position to one another. Signaling pathways, involving the ERECTA family of receptor-like kinases and their ligands, modulate accumulation of the SPEECHLESS bHLH proteins. SPCH controls entry into the stomatal lineage and recent studies have begun to elucidate the transcriptional changes triggered by this factor to enable this event.

The Retinoblastoma protein is important for exit from the stomatal lineage and differentiation and is also more generally linked to cell proliferation and differentiation as discussed by Harashima and Sugimoto. RBR1, the Retinoblastoma protein from Arabidopsis partners with transcription factors that contain 3 MYB repeat domains to activate G2/M specific genes during G2/M phase of the cell cycle and to repress these genes at other phases of the mitotic cycle or during the endocycle. The multiple roles of RBR1 in cell proliferation and differentiation can be explained through different activities of diverse RBR1-containing protein complexes. Further studies are needed to determine how the association of RBR1 with other proteins in these complexes is controlled.

Noncoding RNAs (ncRNA) also play important roles in plant development, this topic is the subject of the review by Fouracre and Poethig. In particular, microRNAs and trans-acting siRNAs have been linked to timing of developmental phase transitions, tissue identity and patterning, differentiation and senescence, as well as hormonal responses. Many small ncRNAs target transcription factors, restricting their expression to the correct developmental stages or tissue. Whether small noncoding RNAs act through a dose-dependent or threshold mechanism remains to be determined. While it was originally thought that plant microRNAs primarily direct transcript cleavage, recent investigations have revealed that they also trigger translational repression.

The shoot apex with its central stem cell pool is important for plant form, function and adaptation to the environment. Soyars *et al.* discuss recent advances in our understanding of stem cell pool self-renewal in the shoot apex. The CLV3-WUS regulatory loop for maintenance of the stem cell population is tightly evolutionarily conserved and exquisitely regulated. Recent additions to the model include the posttranslational modification of the CLV3 peptide by arabinose to enhance its activity, movement WUS transcription factor into the stem cell niche and perception of the CLV3 ligand by an overlapping set of receptor-like kinases (similar to those that act in stomatal development, see above). These signals converge on GRAS family transcriptional regulators.

GRAS family transcription factors also play important role in formation of the root apical meristem (see review by Fischer and Sozzani below). A third meristem important in both annual and perennial plants is the vascular cambium required for secondary growth. Lehmann and Hardtke report that secondary growth is coupled to upstream regulators of the onset of flowering, but not the floral transition per se, via the phytohormone gibberellin. Auxin and strigolactone, acting through receptor like kinases that perceive peptide signal similar to CLV3, also contribute. Downstream of these signals, modules known to promote meristem activity and organ polarity in the shoot are redeployed, but with slightly different roles. STM and related transcription factors promote differentiation (xylem formation), while GRAP family transcription factors limit cambial activity.

The MADS-box transcription factor family, discussed by Yan *et al.*, control floral organ identity and flowering time. Three classes of MADS box genes (A–C) determine the identity of the floral organs in each of the four concentric whorls. A fourth class (E, the SEPALLATA genes) are required for formation of all floral organs as essential components of hetero-tetrameric complexes with the class A-C proteins. The resulting MADS complexes can have unique functions, both at the level of recruitment to unique target loci (by specific *cis* motif sequences or spacing) and with respect to activation or repression of transcription. The latter is at least in part controlled by the type of co-regulator recruited.

How it the transcriptional program set up in each cell type by these sequence specific binding proteins and noncoding RNAs remembered? Förderer *et al.* discuss the role of Polycomb proteins that act in two general types of complexes, Polycomb Repressive Complex1 (PRC1) or PRC2. Mutants in components of the PRC2 complex were first identified because they triggered embryo lethality due to endosperm overproliferation; a similar defect is observed when PRC1 function is impaired. Subsequent to germination, both PRC1 and PRC2 are required for differentiation, defects in either PRC1 or PRC2 triggers formation of undifferentiated callus-like tissues. PRC2 complexes comprised of different paralogous subunits affect expression of different subsets of genes and the mutant phenotypes can vary dramatically. In addition, the different PRC1 can have unique biochemical activities.

Developmental signals from within

Signals that control growth and development are plentiful. Plant hormones can act either locally or at a distance, and the same is true for small peptides, or even proteins. In addition, it has emerged that reactive oxygen species and redox regulation contribute to development by locally altering growth.

Smet and De Rybel review the interplay of signaling molecules and regulatory pathways that drive growth and patterning in the vascular tissue. Starting from a small number of founder cells in the early embryo, vascular tissue grow in width, driven by oriented periclinal divisions. These divisions are subject to tight control with