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# Growth and development

## The diversity of plant development

Editorial overview

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The reviews on plant development presented here cover a wide range of subjects that seem only loosely connected. In a sense, this is a departure from the direction of the field over the past 15 years with its increasing focus on *Arabidopsis* as a model system. It is legitimate to ask whether we have lost something by narrowing our attention on a single species. Will *Arabidopsis* be like the *Escherichia coli* of the 1980s? Is it a powerful model system soon to be abandoned because it has made more complex systems accessible? Or to put it positively: does the remarkable progress made in *Arabidopsis*, combined with the ever increasing power of brute-force genomics, allow us to broaden our horizons again, revisit classical problems and perhaps identify novel avenues for research? While there is no sign at all of *Arabidopsis* losing its attractiveness, it is also true that alternative model species and comparative analyses are beginning to regain popularity. In this issue of *Current Opinion in Plant Biology*, we have attempted to provide examples of this new trend. In plant developmental biology, progress has been made on three fronts: comparative studies at the molecular and genetic level are illuminating the history of morphogenesis in plants; the evolution of key molecular players in developmental regulation is also being elucidated; and finally, developmental principles are being elucidated in the context of the whole organ or organism by utilizing real-time analyses and computer modeling.

Zimmerman's telome theory has long been the guiding principle for understanding the evolution of vascular plant morphology. Beerling and Fleming provide a timely recapitulation of this theory in the context of the evolution of megaphylls, or leaves as we know them. Recent molecular and developmental insights are used to determine if there is evidence for the hypothetical series of three transformations leading to the evolution of leaves: the formation of determinate lateral branches (overtopping), followed by the development of 'flattened' branch systems (planation), and culminating in the fusion of planated branches with lateral outgrowths to form the leaf blade (webbing). Beerling and Fleming suggest that although there are plausible genetic, cellular and physiological mechanisms in extant higher plants for overtopping and planation, there is only limited evidence for the process of webbing. This review also highlights outstanding questions in our understanding of morphological innovations in leaves.

Kidner and Timmermans provide an in-depth overview of leaf polarity. At least three overlapping pathways are involved in specifying the upper and lower surfaces of a leaf. The contribution of each of these pathways varies strongly between plant species, as exemplified by the role of the *ARP* genes

(*PHANTASTICA*, *ROUGH SHEATH2* and *ASI*, in historical order). The analysis of maize mutants is providing unique evidence for a cascade of mutually antagonizing regulatory small RNAs. A surprising level of variation is also observed in the action of downstream polarity targets. For example, the YABBY transcription factors are localized at opposite faces of the leaf primordium in *Arabidopsis* and maize, but they direct the outgrowth of the leaf margin in both species. These are illuminating examples of how comparative analyses can broaden our perspective on a process as fundamental as leaf polarity.

Comparative studies across several monocot and dicot models suggest that different genes might have been selected to regulate plant architecture during crop domestication. The spikelet in grass inflorescences directly affects grain production, whereas growth habit and architecture impact planting density. The environment and gene regulation both have important consequences for growth habit and plant architecture. Architectural variation is seen in both vegetative and reproductive growth, and the genes that regulate architecture during both of these phases are beginning to be identified. Doust reviews branching in grasses, and compares the genes and mechanisms in this group with those in dicot models. Analyses of quantitative trait loci (QTL) have been used to identify *TEOSINTE BRANCHED1* as a major regulator of branching in maize but not in rice. In rice, the *MORE AXILLARY BRANCHING (MAX)*-like genes (which regulate branching in *Arabidopsis*, *Petunia* and pea) appear to have a greater role than *Tb1*-like genes in regulating vegetative branching. Inflorescence architecture in the grasses is reviewed by Kellogg, who outlines some major concepts; for example, the grasses had long been considered to be a single genetic system. This concept is now being realized as genetic synteny is used in conjunction with the sequenced rice genome to identify genes that regulate economically important traits, such as spikelet number and grain shattering. It is also clear that extrapolation from *Arabidopsis* will not lead to a sufficient understanding of inflorescence development in the grasses. A comparative approach also helps underline the variation in inflorescence architecture within the grasses, and suggests the same trends as seen for vegetative architecture. During the evolution of inflorescence architecture, some common elements were utilized, but clade-specific unique features were also selected.

The classical genetic screens in *Arabidopsis* and other species have yielded a wide array of developmental mutants. Naturally, the most attractive mutants are those with clearly defined, specific, phenotypes. In a typical regulatory pathway consisting of signal, receptor, transducers, transcription factors and downstream target genes, mutations in genes that encode transcription factors are most likely to yield non-pleiotropic phenotypes (for an authoritative early review see [1]). It is perhaps not

surprising, therefore, that homeobox-, MADS-box-, bZIP- and GRAS-type transcription factors are so prominently represented among the genes that were isolated from genetic screens for developmental mutants. The MADS-box gene family has undergone extensive expansion in number of members and diversification of function in higher plants. Rijpkema and co-authors take a fresh look at the MADS-box family and suggest that although orthologs can be determined by phylogenetic analyses, functional conservation between these orthologs is not the rule. Sub-functionalization and neo-functionalization events are both seen in recently duplicated genes. Because the *MADS* genes often function in autoregulatory loops and often encode proteins that form higher-order complexes, Rijpkema *et al.* suggest that analyzing each MADS-box gene in isolation may not be fruitful. In addition to the use of homologous promoters, the organismal context of gene expression is crucial if transgenic analyses are to decipher the correct role(s) for these genes in generating plant morphology.

The review by Fiers *et al.* concerns a class of developmental regulators that are not transcription factors, rather they are involved in intercellular communication. The *CLE* family (*CLAVATA3 [CLV3]/ENDOSPERM SURROUNDING REGION* family) of plant-specific genes generate extracellular peptides that are postulated to interact with membrane-bound leucine-rich receptor (LRR) kinases to regulate cell division and differentiation. Limited comparative analyses show some commonalities in the regulation of cell proliferation at the SAM between monocots and dicots. Analysis of the role *CLE* peptides in tracheary element differentiation suggests, however, that whereas some *CLE* peptides promote cell differentiation, others suppress differentiation by some unknown mechanism. The interactions of each *CLE* peptide with a receptor and the functions of these interactions are areas of intense research, and this research should be fruitful in revealing the processes by which meristems make decisions regarding cell division and commitment of cell fates.

Plants possess a diversity of meristems that contain populations of pluripotent cells. Meristems can also be generated *de novo*, as in the case of nodulation in some plants. Beveridge and co-authors provide an overview of diverse meristems and the signaling events that are involved in the generation and maintenance of these structures. The growth hormone auxin, redox potentials and the *CLV* regulatory network appear to have common roles in both *de novo* meristem generation and in meristem maintenance. Recent studies also implicate stress responses, reactive oxygen species and flavonoid and carotenoid signaling in these processes.

Recent work on phyllotaxis has focused on the mechanism of leaf positioning, and has provided evidence that

the active transport of the plant hormone auxin is at the heart of a novel patterning mechanism. [Endress and Doyle](#) concentrate their review on the phyllotactic arrangement of floral organs, which are more difficult to track than leaves but are more interesting from an evolutionary perspective. These authors lucidly discuss the developmental and evolutionary changes that appear to have played a major role in angiosperm evolution. This review also gives food for thought to those of us who are primarily interested in molecular mechanisms.

The controversial theory that developmental decisions might be under the control of physical forces operating in tissues is explored by [Dumais](#). Highly respected scientists have advocated this theory in the past, but modern developmental biologists tend to confront such genetically intractable mechanisms with suspicion. Yet, “Nature has no vested interest in chemistry” and the question of whether physical constraints influence or even dictate developmental decisions is legitimate. Mesophyll cells look like a layer of soap bubbles, suggesting that cell shape is governed by minimization of surface energy. More characteristic patterns of cell division can also be explained using simple physical and geometric rules. An example from the *Drosophila* eye highlights the interaction between physical forces and specific proteins. The characteristic rippling of a grass leaf might be caused by buckling. If the elongation of the lamina exceeds that of the veins, the lamina is forced to buckle out of the plane. Yet, most leaves are flat, indicating that growth and the division of individual cells must be precisely coordinated throughout the leaf.

Related species and even races may have organs of very different shape and size. Such differences can be of substantial adaptive value; for example in the co-evolution of flowers and pollinators. [Anastasiou and Lenhard](#) address the topic of growth and how plant organs reach their characteristic final size and shape from a genetic perspective. Many mutants that affect cell and tissue growth have been isolated and an understanding of their interaction is beginning to emerge. The article ends by describing the links between growth and developmental patterning.

[Martin and Glover](#) discuss the epidermis from different angles but with a clear focus on the function of specialized epidermal cell types. They describe recent progress made in understanding the molecular mechanisms of stomate and trichome development in *Arabidopsis* and ask how general these pathways are, especially in light of the functional divergence between species. The review ends with a brief discussion of the author’s own seminal work on specialized epidermal cells in the flowers. This work highlights the importance of cell shape for the interaction with pollinating insects, and thus is a good example from the budding field of molecular ecology.

Developmental geneticists have traditionally summarized their data in cartoon-style models, in which the interactions between signals, genes and gene products are represented by blocks and arrows. The advances in molecular genetics and genomics make such simple models increasingly inadequate. With networks becoming more and more complex, there is a rising demand for more formal and, importantly, more quantitative approaches. [Alvarez-Buylla et al.](#) discuss gene regulatory network (GRN) models and how they can be applied to plant development. [Heisler and Jönsson](#) provide a few selected examples of quantitative approaches. A particularly gratifying example is the modeling of the WUSCHEL–CLAVATA interaction. For the molecular geneticist, it is not intuitively obvious how an undistinguished group of cells in the center of the shoot meristem can specifically express a gene. Yet, simple rules and assumptions can accurately model the *WUS* expression domain, and even correctly predict the effect of mutations and experimental manipulations.

Some 80% of land plant species live in association with mycorrhizal fungi, which serve to enhance uptake of nutrients. *Arabidopsis* and the other Brassicaceae are among the remaining 20% that is excluded from this world-wide web. Major progress in understanding the mycorrhizal symbiosis has been made in recent years using alternative model systems, such as *Medicago* and *Lotus*. In an entertaining article, [Reinhardt](#) discusses the molecular mechanisms behind the mutual recognition of the partners, attachment penetration and establishment of the symbiosis. It comes as a surprise that so many components of the signaling pathways are shared with nodulation, the highly specific interaction between a legume and nitrogen-fixing bacteria.

The field of plant development began with morphological analyses that focused on understanding developmental diversity. With the advent of new tools in genetics, molecular biology and biochemistry, the analysis of development has progressed in a few model species and reached great heights. The pinnacle of this trend is manifested in the sequencing of whole genomes in *Arabidopsis* and rice. The plant research community has taken on the challenge of understanding the function of all of the genes in a genome. The time is now ripe for plant developmental biology to come full circle and use the information from model organisms to understand the developmental basis for morphological variety, and to set the organismal context for gene function. The set of reviews presented in this issue illustrate the strides that have been made in this direction and also highlight future challenges.

## References

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