Growth and development
Plants from genes: towards the information network
Editorial overview

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Abbreviations

BR	brassinosteroid
CCA	*CIRCADIAN CLOCK ASSOCIATED*
FLC	*FLOWERING LOCUS C*
LHY	*LATE ELONGATED HYPOCOTYL*

This third growth and development issue of *Current Opinion in Plant Biology* marks the turn of the millennium, which naturally makes one muse about the wider significance of plant development. At this point, our planetary ecosystem has reached a critical stage, in which a man-made environment changed by mankind is imposed on all living species. Against this background, it will become utterly necessary to understand the biology of plants because they, crops and wild species alike, are being forced to develop under changing conditions. Increasing knowledge of development can help to monitor the state of affairs in the plant kingdom and deliver unmistakable warning signs when the potential to cope with change approaches its limits. If we can apply developmental information in this environmental context, their utility may extend well beyond the agricultural or industrial progress often taken to be the only measure of the success of plant science.

The first section of this issue focuses on the growth and development of the shoot and on processes that require the coordinated development of tissues and organs. The starting point in characterizing almost all of these processes has been the isolation of a mutant, followed by the increasingly rapid molecular identification and study of the gene and its product. The increased ease with which this happens relies to no small extent on the increasing availability of genomic data in these last years of the century.

Three reviews (Bowman [pp 17–22], Fletcher and Meyerowitz [pp 23–30] and Scanlon [pp 31–36]) summarize the progress made in understanding the development of the shoot apical meristem and its immediate products, the leaves. Here we find the classical botanical concepts of the central zone (home of the self-renewing initial cells) and the peripheral zone (leaf-generating zone of the meristem) revisited with new tools. The central and peripheral zones of the shoot apical meristem have long been recognized as distinct regions. For instance, the cells in the central zone divide more slowly and stain less intensely with histological dyes than do the peripheral zone cells. More recently, dye injection studies have indicated that the central and peripheral zones are separate, symplasmic domains. Understanding how plant cells modulate plasmodesmatal connections with their neighbors and how this modulation is used in plant development represents an important challenge to cell and developmental biologists.

We are also beginning to recognize a finer grain of pattern in the cells of the shoot apical meristem (reviewed by Fletcher and Meyerowitz). Many gene products are restricted to specific meristem subdomains. If the particular combination of gene products that a cell expresses is taken into account, we see that the shoot apical meristem actually encompasses more cell types than were apparent just a few years ago.

The CLAVATA1 and CLAVATA3 gene products are among those that are localized to specific subdomains in the apical meristem. *CLAVATA1* and *CLAVATA3* transcripts are found in the basal and apical regions of the central zone, respectively. Both genes act to limit the size of the central zone: if either gene is mutated the central zone becomes greatly enlarged. The *CLAVATA1* gene encodes a predicted receptor kinase, whereas the *CLAVATA3* gene product, a rather small protein, is currently the best candidate for its associated ligand. Although the CLAVATA1 and CLAVATA3 gene products have yet to be shown to physically interact, if the receptor–ligand model holds up this system will become a paradigm for short range cell signalling in the plant.

The list of genes required to make a meristem has grown yet longer this year (Fletcher and Meyerowitz). Some of these genes contain motifs that indicate they are likely to encode transcription factors (e.g. *WUSCHEL*), the role of others is tenuously linked to translation initiation (e.g. *PINHEAD/ZWILLE*), whereas the function of further genes remains unknown (e.g. *CUP-SHAPED COTYLEDON).*

A major function of the shoot meristem is to make leaves. Scanlon summarizes new developments in our understanding of early events in leaf development. For instance, the problem of phyllotaxis (or how the plant decides where to put the next leaf) has occupied mathematicians and botanists alike. The *terminal ear* and *abphyll*

mutations of maize both cause changes in leaf placement. *TERMINAL EAR* encodes a predicted RNA-binding molecule indicating that posttranscriptional events may have a role in leaf placement.

Scanlon also considers the early events involved in specifying the cluster of cells that are destined to become leaf tissue. One of these early events is the 'downregulation' of *KNOX* gene expression in the presumptive leaf primordium. *KNOX* gene expression is closely correlated with meristem cell fate, and ectopic *KNOX* gene expression interferes with normal leaf development. The ROUGHSHEATH2 gene product of maize, is required for this negative regulation to occur: in *roughsheath 2* mutants, *KNOX* genes are inappropriately expressed in the leaf primordium. Whether the *ROUGHSHEATH2* gene is involved in initiating *KNOX* downregulation as well as in maintaining this state in the leaf is currently unknown.

A small explosion of publications describing the findings of experiments in the area of leaf polarity has occurred recently. The goal of these studies is to understand how the top of the leaf becomes different from the bottom of the leaf, and how the leaf blade develops. The seminal paper in this active field of research was written by Waites and Hudson in 1995 [1]. In that paper, a model was presented in which the juxtaposition of the adaxial (i.e. top) and abaxial (i.e. bottom) domains of the young leaf primordium generates a novel domain which permits blade outgrowth. In accordance with this model, mutants in which the adaxial domain is transformed to an abaxial domain (or *vice versa*) lack blade growth and develop radially symmetrical leaves. The model itself was, in fact, formulated to explain the snapdragon *phantastica* mutant, which has radially symmetrical leaves with abaxial characters around their circumference. The *PHANTASTICA* gene was recently [2] found to encode a gene product with a MYB domain indicating that PHAN probably promotes adaxial fate by regulating transcription.

The Waites–Hudson model [1] thus provides a conceptual framework upon which to hang the functions of an ever-growing number of leaf-polarity mutants. Among these are the YABBY family of genes (reviewed by Bowman). The YABBY genes encode proteins with a predicted zinc-finger domain juxtaposed with an HMG-like domain. This arrangement of domains has thus far been found only in plants and indicates that YABBY genes may regulate transcription. YABBY gene family members are expressed in the abaxial domain of leaves and appear to confer abaxial fates when overexpressed. In the appropriate double mutant combinations, mutations of these genes result in the development of adaxialized primordia.

Nevertheless, the interpretation of the *phantastica* mutant is not without controversy; the maize *ROUGHSHEATH2* gene described above and the snapdragon *PHANTASTICA* genes are in fact highly similar in sequence. One possibility is that these genes perform different functions in maize and snapdragon leaf development. Another possibility is that the leaf phenotypes have been misinterpreted. Consistent with the latter line of reasoning, Scanlon provides the reader with an alternative interpretation of the *phantastica* leaf phenotype which brings *PHANTASTICA* function in line with maize *ROUGHSHEATH2* function.

The next two reviews emphasize the plant's response to its environment, especially to stimuli, such as vernalisation (i.e. cold treatment), that induce flowering (reviewed by Reeves and Coupland, pp 37–42). The *FLOWERING LOCUS C* (*FLC*) locus, which encodes a MADS-box containing protein, appears to be a critical regulator of flowering in response to vernalization. *FLC* RNA concentrations are initially high in genotypes with a vernalization requirement and decreased in response to cold treatment. Moreover, in *vernalization* mutants, which fail to respond to cold treatments, *FLC* levels remain high. The mechanism through which cold temperatures influence *FLC* mRNA concentrations is still a black box.

Both Murtas and Millar (pp 43–46) and Reeves and Coupland discuss the connections between the circadian clock and time of flowering. Several mutants have been found that affect the clock and render the plant insensitive to daylength. One gene, the *LATE ELONGATED HYPOCOTYL* (*LHY*) may be closely connected to the central oscillator. The related *CIRCADIAN CLOCK ASSOCIATED* (*CCA*) gene (both gene products contain MYB domains) also appears to function close to the central oscillator. The role of *CCA* in controlling flowering time is unknown and its determination is somewhat complicated by the similarity of *CCA* and *LHY*, which may reflect redundancy in gene action.

Murtas and Millar summarize additional information indicating that we may be significantly closer to an answer to the question of how plants tell time. In addition to describing experiments that implicate the phosphorylation of CCA1 in the regulation of its DNA-binding capabilities, they also describe new evidence indicating that both CRYPTOCHROME and PHYTOCHROME photoreceptors sense daylength and thus provide inputs into the clock. A new output of the clock, hypocotyl growth, has been added to the list of circadian-regulated processes.

Once conditions conducive to flowering are present, how do floral induction signals bring about the actual changes in development at the meristem? The *LEAFY* gene regulates both flowering time and the development of organ identity in the flower. Ng and Yanofsky (pp 47–52) review experiments in which these two roles of *LEAFY* have been dissected. During floral differentiation, *LEAFY* is shown to directly regulate the so-called "ABC" genes, which are the immediate regulators of floral organ identity.

In the second section of this issue, attention is focused on the role of intracellular processes in plant development. Descriptive accounts of plant development almost invariably emphasize the roles of the two most readily observable cellular phenomena that are associated with morphogenesis: rates and planes of cell division, and the orientation and extent of cell expansion. Ever since the first descriptions, plant scientists have wondered whether cellular behavior (in terms of division and expansion) dictates the development and morphogenesis of the whole plant or *vice versa*. Are these opposing viewpoints resolved by recent research on regulated cell division and cell expansion?

Components with candidate roles in cell division have mainly been discovered on the basis of their homology with components of non-plant systems. Yang and Sundaresan's review (pp 53–57) of gametophyte formation shows that the analysis of this process also has lead to the identification of genes that are required for specific cell divisions and that have signatures that are implicated in the regulation or execution of cell division. It is possible that a more systematic analysis of gametophytic mutants will provide a doorway to the discovery of many genes involved in controlling the cell cycle. The mutants described so far suggest that a plethora of control mechanisms affect male meiosis, female meiosis [3], female nuclear gametophytic division, and pollen microspore division. It remains to be seen whether this diversity, observed during the ontogeny of the gametophyte, is paralleled by a similar diversity in the control mechanisms involved in sporophytic cell division. It will also be interesting to learn whether the variable cell division controls in the gametophyte (and possibly sporophyte) are ultimately connected to fewer mechanisms for spatial control.

When asking the question of how cell division is oriented, it becomes important to identify the components of the cellular machinery that are involved in cytokinesis. In Sylvester's review (pp 58–66), our knowledge of the spatial regulation of cell division, i.e. how new walls are oriented after nuclear division, is summarized. There has been steady progress in describing cytokinesis and identifying proteins that are involved in this process. Nevertheless, major questions remain. How is the mysterious preprophase band, a transient cortical girdle of microtubules that predicts the orientation of cell division, oriented itself? What is the nature of the cues that guide the expanding cell plate to the peripheral preprophase band? The visualization of the cytoskeleton during cytokinesis using green-fluorescent-protein-tagged proteins and the identification of more genes that are essential for cytokinesis may provide the answers to some of these questions [4].

An important notion revealed by analysis of the brown alga *Fucus* (reviewed by Belanger and Quatrano, pp 67–72) is that the establishment and fixation of cell polarity can underlie both the orientation of cell division and directional expansion. Axis fixation, asymmetrical cell growth and appropriate orientation of cell division in *Fucus* zygotes requires polarized secretion of Golgi-derived vesicles. In the past year, important new evidence has emerged suggesting that vesicular trafficking and the establishment of cell polarity are also intimately involved in the development of higher plants. The GNOM protein, which is required for cellular and organismal polarity in *Arabidopsis* from the zygote stage onward, is a guanine-nucleotide exchange factor located on ADP-ribosylation-factor G-proteins, which are known to be involved in Golgi- vesicle budding. The PIN1 protein, implicated in the cellular auxin efflux machinery, has emerged as a marker for cell polarity because it is asymmetrically distributed in the cell membrane. Interestingly, coordinated polar localization is affected in *gnom* mutants. This finding now begs the question of whether mis-localization of auxin transporters is causally related to the defects in *gnom* mutants (including mis-orientation of cell division and cell expansion), and whether polar auxin distribution that is mediated by coordinated cellular mechanisms plays a general role in patterning. Several recent papers suggest specific roles for auxin in leaf vein, root and embryo patterning, consistent with the idea that a cellular transport mechanism contributes to oriented cell division and oriented cell expansion [5–8]. As with cell division, the basic mechanisms of cell expansion must be investigated in some detail before their spatial controls can be understood.

An important breakthrough in understanding cell expansion has been the identification of a family of proteins mediating cell-wall relaxation (described in the review by Cosgrove, pp 73–78). This gene family displays a high degree of tissue specificity in *Arabidopsis*, providing ample possibilities for differential regulation. Whether spatially restricted activation of expansins contributes to local and oriented cell expansion remains to be investigated. Analyses using localized mis-expression or genetic mosaics should enable critical tests in the near future.

Is expansion regulated globally or locally? A starting point in attempting to answer this question may come from the revival of interest in the brassinosteroids (BRs) as plant hormones, which reviewed and updated by Schumacher and Chory (pp 79–84). The realization that a number of dwarf mutants are defective in BR synthesis or perception indicates that particular aspects of cell size may be regulated non-cell-autonomously by diffusible hormones. Potentially cell-autonomous components, such as the BRI1 receptor, are now available for experimentation and it is feasible to direct BR synthesis to only particular parts of the plant. Thus, it should become possible to determine at least whether this cell elongation control mechanism acts at long or at short range. It will also be interesting to establish a connection between BR signaling and the downstream targets that mediate cell elongation, such as the expansins.

Do the five reviews of this "cellular" section teach us whether the plant makes the cells, or the cells make the

plant? The multiple interactions that are shown or suggested by the reviewed work show us that cells form an interconnected information network where every player has its say in the execution of a developmental program but also responds to its neighbors. The contribution of intra- and extracellular inputs may vary, such that perhaps neither of the two aphorisms above is true. A representation of plant cells and their genetic and physiological state as such an information network may be an interesting challenge to start off the new millennium.

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