Cell biology
From molecules to cells to organisms

Editorial overview
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Abbreviation
PPB pre-prophase band

Cell biology provides an important insight into biological systems at the level of a fundamental unit of biological organisation — the cell. At the same time it interfaces with other levels of analysis: downwards in scale to molecular biology and macromolecular organisation and activity; and upwards to intercellular interactions, developmental biology and physiology. We have taken an inclusive, but eclectic, view of plant cell biology in this issue and hope that we have created a stimulating diversity. The first six reviews describe intracellular processes, while the next two reviews examine single cell signalling events. A contribution on the origin of multicellular plants is followed by two reviews and a commentary on cell–cell signalling and developmental processes. The final review discusses the evolution of chloroplasts.

In the first article, Huntley and Murray (pp 440–446) describe the recent molecular characterisation of plant cell cycle components. A major aim of plant cell cycle research is to understand the role of the cell cycle in plant development, in the response to intrinsic factors (hormones) and environmental cues (light, temperature, water status, etc). The discovery of the Retinoblastoma protein (Rb) and E2F in plants has further emphasised the conservation of the mechanisms that regulate the cell cycle in plants and animals. Cell cycle components that are regulated by cytokinin and abscisic acid (ABA) have been identified, providing a mechanism of action for these plant hormones. The isolation and characterisation of cell cycle genes need to be followed by in vitro biochemical experiments that address mechanistic issues (e.g. the identification of the site(s) of regulatory phosphorylation and interacting partners). Knowledge from such experiments will provide a rational basis for the construction of appropriate transgenes to be tested in vivo.

In a complementary article, Smith (pp 447–453) reviews recent developments in cytokinesis, and the intriguing, but still poorly understood, connection between the pre-prophase band (PPB) of microtubules and the subsequent positioning of the phragmoplast. Although we are still some way from a clear picture of these processes, several major protein players and mutants have been recently identified. These include phragmoplastin — a dynamin-like protein which may be involved in formation of membrane tubules from vesicles — and the KNOLLE protein, which is perhaps involved in membrane fusion. KNOLLE is related to the syntaxins, which have been implicated in cellularisation in Drosophila embryo development and in cytokinesis in Caenorhabditis elegans embryos. Several interesting mutants have been identified in Arabidopsis and in maize in which either the link between PPB and phragmoplast location is disrupted (TON/FASS in Arabidopsis) or the PPB itself fails to form (maize tangled1 [tan1] and dicordia [did]). Although actin has been implicated in the link between the PPB and the phragmoplast for many years, there are still no clear molecular candidates for whatever ‘landmark’ is set up by the PPB to subsequently target the phragmoplast.

Recently, the availability of green fluorescent protein fusion markers localised to specific subcellular compartments in plant cells has fuelled the reinvestigation, by optical imaging of living plants, of many problems in plant cell biology hitherto inaccessible to traditional methodology. In their review, Hawes, Brandizzi and Andreeva (pp 454–461) demonstrate how the new technology allows the visualisation of endomembrane and organelle dynamics in vivo, the identification of the molecular mechanisms that govern organelle fission and fusion and the establishment of links between membrane trafficking and signal transduction. These investigations have also shown that results obtained from mammalian and yeast cells may not necessarily apply to plant cells and that there are indeed plant-specific phenomena (e.g. endoplasmic reticulum/Golgi membrane relationships) yet to be discovered.

More generally, regulated secretion is an important process in plant cells whose significance deserves a better appreciation. Polarised secretion is clearly at work in cytokinesis, where vesicles are directed primarily to the phragmoplast (see review above by Smith) and during the tip growth of elongating pollen tubes and root hair cells. There is little change in the cell width as hypocotyls elongate; thus wall materials must be deposited preferentially to the longitudinal sides of the cells. The situation of a maturing trichome with three branches is even more complex, since to make a spire-like structure (a trichome branch) we have to postulate that wall materials are delivered symmetrically to all sides, but with a gradient going from the base to
the tip. All of these growth phenomena require highly regulated vesicular trafficking. At present only a few components of the secretary pathway have been identified and there is a need to identify additional players. It would be very useful, and may be possible using green fluorescent protein technology, to make markers to distinguish new growth in the plasma membrane from existing plasma membrane, and thus describe the type of growth (localised or diffuse) in each cell type and the mechanisms that regulate it. In an interesting recent study, Steinmann et al. [1] have shown that GNOM, a membrane-associated guanine-nucleotide exchange factor on ADP-ribosylation factor G protein, is involved in the establishment of polarity during Arabidopsis embryogenesis. In mutants defective in GNOM, PIN1, thought to be an auxin efflux carrier, fails to be localised correctly. This suggests that GNOM-dependent vesicle trafficking may establish cell polarity and result in polar auxin transport.

In the next review, Kost, Mathur and Chua et al. (pp 462–470) discuss the cytoskeletal dynamics that underpin many developmental processes such as cell division, cell expansion, elongation of specialised cell types, trichome morphogenesis, cell differentiation, cell-to-cell communication and organogenesis. Actin- and microtubule-associated proteins are being characterised and cloned from plants and some of these have been shown to regulate cytoskeletal dynamics in vitro. On the basis of work in yeast and animals, cytoskeletal proteins are expected to play an important role in cell morphogenesis, and indeed such mutants (e.g. zwiebel) are beginning to be characterised from plants. Future work will focus on the elucidation of signal transduction pathways linking a particular stimulus, such as a hormone, to changes and remodelling of the cytoskeleton in plant cells.

One of the defining features of plants is, of course, that they possess chloroplasts and other plastids. In the first of two reviews in this issue relating to chloroplasts, Keegstra and Froehlich (pp 471–476) look at protein targeting to the chloroplast. Work in the last few years has led to the identification of the membrane-associated components and chaperones required for the translocation of precursor proteins across the outer and the inner chloroplast envelope membranes. A unique feature of chloroplast import is its requirement for GTP which binds to two outer membrane components, TOC34 and TOC159. Surprisingly, many chloroplast translocation components are encoded by a multigenic family, whose significance requires further elucidation. Sequence comparison suggests that components of the chloroplast import machinery were derived from protein components used for secretion in cyanobacteria (see also McFadden — pp 513–519).

In the second contribution on chloroplasts, McFadden discusses the evolution of plastids through the incorporation of cyanobacterial-like symbionts to form the first plant cells. Although this hypothesis has been accepted for many years, it is only with the recent availability of entire cyanobacterial genome sequences and the coming availability of entire plant genome sequences that the tools are in place for a thorough analysis of this crucial symbiosis. Even determining which proteins are destined for the plastids will be a major task. Of the several thousand genes in a cyanobacterium many must have been lost altogether and all but a hundred or so have been transferred to the nuclear chromosomes. Understanding the mechanisms that allowed this transfer and the forces that drove it will be fascinating, as will understanding how the host cell regulates and controls its semi-autonomous partners.

Ion channels are important in controlling membrane potential and for signal transduction in plant cells. With the prospect of a complete catalogue of ion channel proteins, which will become available once we can interpret the Arabidopsis genome sequence, Zimmermann and Sentenac (pp 477–482) review the current knowledge of plant ion channels. Among the seven families of ion channels identified in plants the best characterised ones are K+ channels of the Shaker family in which some structure–function analyses have been carried out. Future research on ion channels will include identification of their interacting proteins and analysis of their regulation by phosphorylation and by binding to cyclic nucleotides.

From ion channels in general, we move neatly on to signalling in nodulation (Downie and Walker, pp 483–489). The synthesis, structure and function of Nod factors have been well investigated in the past several years. Recent focus has shifted to the issue of how Nod factors induce responses in plants leading to productive nodulation. In this case, ion channels are clearly involved in signal transduction since following Nod factor interaction with root hairs there are ion fluxes across membranes followed by the establishment of an intracellular Ca2+ wave. Pharmacological studies suggest the involvement of G-protein-mediated signalling leading to the generation of inositol triphosphate (IP3) and concomitant increases in intracellular Ca2+. Although some progress has been made with respect to the characterisation of Nod-binding proteins, none of those isolated thus far have the expected properties of a Nod receptor. Isolation of the latter could be complicated if the receptor is a hetero-oligomeric protein. Genetic approaches have been initiated to isolate plant mutants defective in nodulation. We can expect that the use of transposon tagging in Medicago and Lotus will lead to the identification of genes important for this process.

In a second example of single cell signalling, Franklin-Tong (pp 490–495) discusses signalling in pollination. The germinating pollen tube has been used as a model system to investigate polarised cell growth, cell-to-cell communication, and intracellular and intercellular signalling. Like root hairs, pollen tubes are tip-growing cells. Although it was first thought that Ca2+ influx might regulate pollen tube growth directly, recent evidence suggests a
more complex relation between changes in intracellular 
Ca^{2+} concentration and changes in the rate and direction of 
tube growth. The source of the increase in intracellular 
Ca^{2+} has not yet been identified; Ca^{2+} influxes from the tip 
region could contribute to this increase, or Ca^{2+} might be 
released from internal stores by IP_{3} through a functional 
phosphoinositide pathway. Polarised tube growth has been 
shown to be mediated by the GTP-binding proteins Rac 
and Rop, members of the family of Rho-GTPases, which 
may integrate signalling from several pathways. Future 
research will include the identification of the mechanism 
by which Rac/Rop regulate the actin cytoskeleton.

From intracellular or cell autonomous processes, we move 
on to processes that are fundamentally multicellular. Kirk 
(pp 496–501) describes progress in understanding how a 
multicellular system might have evolved, using the algae 
related to Volvox as a model. The first step probably 
involved incomplete cytokinesis which delayed the separa-
tion of sister cells until cell wall deposition. The 
evolution from colonies to multicellular organisms (e.g. in 
Volvox carteri) would entail a division of labour. Volvox car-
teri contains ~2,000 somatic cells and 16 gonidia. The 
germ-soma differentiation is thought to occur by an asym-
metric cell division which sets apart large ‘gonial initials’ 
from small ‘somatic initials’. Kirk postulates three types of 
genetic programs: first, gls which governs asymmetric cell 
division, second, RegA, which acts in somatic cells to nega-
tively regulate reproductive development, and third, Lag 
which acts in gonidia cells to repress somatic development. 
So far, gls and RegA have been cloned. gls encodes a 
J domain protein which in association with HSP70 is 
localised to the mitotic spindle in dividing cells. How 
these molecules bring about asymmetric cell division is 
being investigated. RegA is a transcriptional repressor 
which probably prevents the expression of a large number 
of genes encoding chloroplast components in somatic cells, 
restricting the number of chloroplasts in these cells and 
preventing them from growing large enough to divide.

A highly distinctive feature of higher plants is the cell wall. 
The orthodox view of plant biologists in the past was that 
the cell wall was inert and simply served as a physical bar-
rier to encase and protect plant cells. However, Braam 
(pp 521–524) reviews evidence suggesting that proteogly-
can and cell wall polysaccharide fragments may act in 
cell-to-cell signalling. With the discovery of putative trans-
membrane receptors in plants it has become apparent that 
ligand–receptor interaction is a likely to be a major theme 
in plant signalling and that the cell wall has to be suffi-
ciently porous to allow the passage of such ligands. Cell 
wall proteins (e.g. arabino-galactan proteins [AGPs]) may 
also serve as ligands. For example, AGPs have been found 
to enhance or suppress the embryogenic potential of cells. 
Cell wall fragments (oligogalacturans, xyloglucans) have 
been implicated in pathogen attack and, in some spe-
cialised cases such as thin cell layer tissue cultures, in 
growth and development. Receptors for these fragments 
have not yet been found. The mechanical properties of the 
cell wall may also influence the pattern of cell division and 
subsequent morphogenesis.

As has been clear for some time in animals, the multicellu-
lar growth and development of plants often involves, and 
perhaps requires, the controlled death of individual cells. 
Lam et al. (pp 502–507) review the current state of knowl-
dge of programmed cell death (PCD) in plants, which, 
although lagging behind the animal field, is now making 
rapid progress. In plant development, tracheary element 
differentiation and tapetal cell and endosperm degenera-
tion are examples of programmed cell death; the 
hypersensitive response to pathogen attack has also 
received much attention. Many of the usual suspects have 
been identified in signalling pathways leading to cell 
deat — Ca^{2+}, heterotrimeric G proteins, reactive oxygen 
Species and NO. In animals, PCD is modulated by serum 
proteases called caspases; in plants there is good evidence 
for protease involvement and growing circumstantial evi-
dence for caspase-like proteases, but as yet no definitive 
proof. As is becoming apparent in animals, the mitochon-
dria have important roles in both the signalling and in 
the execution of the death programmes.

The recent huge interest in Dolly — a sheep produced by 
somatic cloning — may have left many plant biologists won-
dering what all the fuss was about, as the regeneration of 
plants from single somatic cells has been commonplace for 
many years. This development shows, however, that pluripotency is not restricted to plant cells. In their contri-
bution, Schnittger, Schellmann and Hülskamp (pp 508–512) 
examine our current knowledge of the control of differenti-
ation in plants. A fundamental question is the extent to 
which differentiation is maintained by extrinsic (i.e. signals 
from other cells) and intrinsic factors (e.g. chromatin-depen-
dent gene silencing). It is becoming clear that both types of 
mechanism have roles, both in plants and in animals. 
Furthermore, the more both types of organisms are studied, 
the more similarities become apparent at the molecular 
level. However, it seems that cell fate is less tightly con-
trolled in plants than in animals. This presumably explains 
the relative ease with which plants can be regenerated.

Reference
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