Plant Cell: Overview

Fiona Doris, *University College, Dublin, Ireland*

Martin Steer, *University College, Dublin, Ireland*

Although plant cells share the same eukaryotic ancestor cells as animal cells, and hence bear strong resemblance to one another, there are many differences between the two. These differences reflect the distinct structural, developmental and environmental pressures which plant cells experience and include the presence of cell walls, differences in membrane structure and changes to the endomembrane system and structures associated with cell division.

Introduction

Plants evolved from the same eukaryotic ancestor cells as animals, so it is not surprising that the cell and molecular biology of plants bears a strong resemblance to that of animals. However, there are differences. Some may just have evolved with the passage of time, while others are directed to optimizing the efficiency of a rather different mode of nutrition and life form. A major difference is that plants exhibit indeterminate growth, generated by shoot and root meristems. Also, cells from almost any part of the plant body can be induced to undergo divisions to form new meristems, which can give rise to new plants. This 'totipotency', the ability to summon up the entire nuclear genome programme of a differentiated cell, is in marked contrast to the terminal differentiation of animal body cells.

The evolution of a stable, more or less permanent, cell wall marked a significant step in the development of plants. Cell walls may have arisen as the result of the ready availability of carbohydrate monomers, resulting from the photosynthetic activity of chloroplasts. The cell wall imposed a physical barrier on the access of everything except solutes and the smallest particles (< 10 000 Da) to the outer face of the plasma membrane. The evolution of multicellular forms means that cells of these individuals live in boxes of carbohydrate that are protective in providing an essential external water phase, but restrictive in what they allow to pass from cell to cell.

An additional advantage of the cell wall is that it releases the organism from a requirement for active water regulation to cope with the osmotic uptake of water. The osmotic potential gradient drawing water into the cell is matched by an internal hydrostatic pressure generated by the resistance of the cell wall to expansion. The large cell vacuole acts as a sink for solutes and serves to spread the cytoplasm in a thin layer against the plasma membrane. This overcomes the major limitation on cell size, the need to maintain a constant surface area-to-volume ratio.

A generalized cell is shown in **Figure 1**. The functions of the main components and the differences between them in animals and plants are discussed below.

Plasma Membrane

As with animal cells, research on plant plasma membranes has identified specific features associated with ion transport, glycoprotein insertion and cytoskeletal attachment. Aspects of the plasma membrane that are unique to plants include cell wall synthesis, the cell-to-cell transport channels, plasmodesmata and lipid composition.

Evidence for the crosslinking of the plasma membrane to the cell wall comes from observations during plasmolysis. First, the solute concentration required to cause plasmolysis is higher than predicted on the basis of the internal cell solute concentration, suggesting that some additional resistance must be overcome. Second, microscope observations reveal the presence of connecting strands (Hechtian strands) between the plasma membrane and the detached cell wall of partially plasmolysed cells.

On the cytoplasmic side, microtubules are found crosslinked to the plasma membrane. Antimicrotubule agents cause changes in the plasma membrane, disrupting cell wall formation. Antiactin drugs do disrupt some key processes such as cell extension and tip growth, but the molecular interactions have yet to be characterized.

Cell Walls

Plant cell walls serve two functions: they provide mechanical support and maintain an aqueous phase at the extracellular leaflet of the plasma membrane.

Mechanical support can be exerted through turgor pressure of the protoplast pushing out on the cell wall, like a balloon skin. In nonwoody stems and leaves the outer walls of the epidermal cells are specially thickened to resist the stretching forces of the tissue cells within, holding the structure semirigid. Wilting is due to loss of turgor pressure and collapse of the inflation pressure.
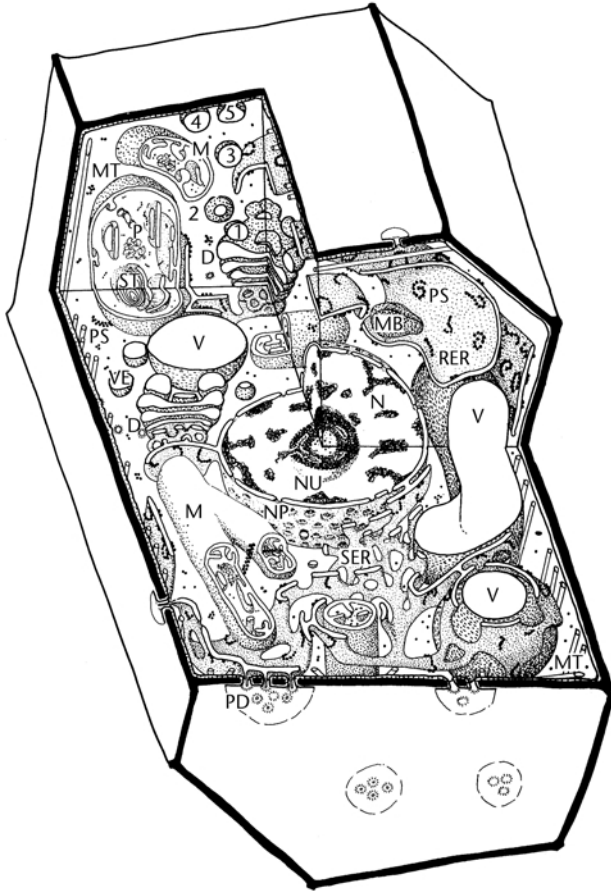
Figure 1 Diagram of a generalized cell cut open to show the three-dimensional structure of the main components. These are not drawn to scale, nor are their relative numbers representative of a plant cell. D, dictyosome, with numbered sequence of vesicles undergoing exocytosis (1–5); RER, rough endoplasmic reticulum; SER, smooth endoplasmic reticulum; M, mitochondria; MB, microbody; MT, microtubule; N, nucleus; NP, nuclear pore; NU, nucleolus; PD, plasmodesmata; P, plastid; PS, polysome; ST, starch; V, vacuole; VE, vesicle. Reproduced with permission from Gunning and Steer (1996).

Alternatively, walls can be modified to provide innate mechanical strength, as with wood and timber. Usually the cell contents die after the wall has been formed.

Primary walls, of dividing cells and parenchyma cells, contain microfibrils of cellulose embedded in a matrix of branched-chain hemicelluloses and acidic pectins. These components are noncovalently crosslinked to each other, so that they can deform in response to the pressures of cell expansion. Growth is accompanied by thinning of the original wall and addition of new material to the inner wall face.

New microfibrils are formed by rosettes, each consisting of six plasma membrane particles arranged in a hexagon. These cellulose synthases span the plasma membrane, polymerizing UDP-glucose units from the cytoplasm to form linear antiparallel chains that crystallize to form the microfibril. The act of polymerization pushes the synthase complex along in the plane of the plasma membrane, through the lipid bilayer. It is probable that cytoplasmic microtubules stabilize lipids in the plasma membrane, so restricting the directions that the synthases can take to tracts between adjacent pairs of microtubules. Since microfibril direction affects the local wall strength, growth occurs preferentially at weaker wall sites due to osmotic swelling. Hence microfibrils, laid down in response to the arrangement of microtubules, control cell shape.

Matrix components are synthesized within the Golgi apparatus and delivered to the plasma membrane surface by secretory vesicles. These components diffuse into the growing wall, establishing crosslinks with existing and new microfibrils.

Secondary walls, formed after the cell has ceased to expand, can be of the same structure as primary walls. More often they are further modified by the addition of different molecules, such as lignin or suberin. Lignin binds the microfibrils together in a rigid framework, giving mechanical strength, as in the walls of xylem cells that are the main component of wood. Suberin serves to water-proof the wall, preventing migration of water and solutes along that particular segment of wall. Such walls are found protecting the root stele from direct exposure to the soil solution, and underlying some salt and nectary glands preventing water loss onto the plant surface.

Transport of solutes from cell-to-cell across the intervening wall depends on diffusion down concentration gradients established by ion pumps and channels in the opposing plasma membranes. This is a relatively inefficient route. Plasmodesmata obviate the need for solutes to cross a lipid bilayer by providing direct cytoplasmic communication channels. Each plasma membrane-lined channel, 50 nm in diameter, contains an endoplasmic reticulum tubule that limits the size of molecules able to pass through to about 1.5 nm across, equivalent to about 1000 Da. Plant viruses are able to spread from cell to cell because they encode a 30 kDa movement protein that opens the plasmodesmata pores to about 10 nm. This protein also binds and unwinds viral nucleic acids so that they can be transported from cell to cell. There can be vast numbers of these channels interconnecting adjacent cells.

Groups of cells interconnected by plasmodesmata constitute a symplast, a collection of cells all sharing the same cytoplasmic milieu. Conversely, the interconnected cell wall spaces provide a nonliving pathway for solute flow, termed the apoplast. Symplastic domains in different parts of the plant are interconnected by the living sieve tubes of the phloem, providing long-distance pathways, especially for sugars. Xylem vessels and tracheids provide the equivalent long-distance route for substances moving in the apoplast.

In parts of some plants, intensive exchange of solutes between the symplast and apoplast is assisted by a local

increase of plasma membrane area. This is accomplished by the formation of finger-like wall ingrowths into the cell, each bounded by plasma membrane. This can lead to a four-fold increase in the surface area of the cell. Such cells are called transfer cells. They are often found at sporophyte–gametophyte junctions in mosses and in higher plants, at phloem and xylem solute exchange points and in the walls of epidermal cells of water plants, where they increase the area of membrane for uptake of nutrients from the surrounding water.

Endomembrane System

Superficially the endomembrane system of plant cells is very similar to that of animal cells, with endoplasmic reticulum providing precursors for the Golgi apparatus. However, there are major differences arising from the rather different forms and functions of these two cell types. While animal cells are relatively small, and have endomembrane systems that are concerned with exporting proteins to the cell surface and to lysosomes, plant cells are much larger and secrete mainly polysaccharides. These differences mean that plant cell endomembranes contain a widely dispersed Golgi, in the form of many small discrete stacks or dictyosomes, but lack a clear association between endoplasmic reticulum and the *cis*-Golgi cisternae, as found in animal cells.

Endoplasmic reticulum

As in animal cells, the endoplasmic reticulum in plants can be found in a variety of morphological shapes and cellular positions, reflecting a multiplicity of functional activities. Branched tubules of smooth endoplasmic reticulum produce long-chain carbon compounds and are most prevalent in oil glands. Flat cisternae of endoplasmic reticulum are formed in response to the docking of polyribosomes with their associated mRNA, forming rough endoplasmic reticulum. These occur in all plant cells, but unusually extensive arrays of cisternae are found in some gland cells and in developing seeds laying down storage protein. These are very similar to the stacks of rough endoplasmic reticulum found in some animal cells, such as pancreatic acinar cells.

Some plant cells contain pleated cisternae, for example in sieve tubes. These appear to originate from rough endoplasmic reticulum, but become smooth as the intercisternal spaces become narrower.

Bifacial endoplasmic reticulum, with ribosomes on only one side of the cisterna, has the smooth face adjacent to another membrane system. This is usually the plasma membrane, but can be another organelle such as a mitochondrion or plastid. These probably represent areas of exchange between the cisternae and the other compart-

ment. Associations with the plasma membrane reflect ion exchange and morphogenesis functions, such as in the patterning of xylem vessel walls and the architecture of pollen grain surfaces.

At mitosis, the nuclear envelope disperses at the end of prophase, with the loss of nuclear pores, as in animal cells. After anaphase cisternae of rough endoplasmic reticulum surround the dispersing chromosomes, forming a new nuclear envelope, complete with pores.

During cell division the endoplasmic reticulum plays a crucial role in cell plate and plasmodesmata formation. At telophase opposing arrays of microtubules position endoplasmic reticulum and secretory vesicles in the plane of the spindle equator. The endoplasmic reticulum is in the form of a branched tubular network, within which the Golgi vesicles are enmeshed. The vesicles expand and coalesce to form the new cell wall and plasma membrane. The trapped tubules of endoplasmic reticulum form plasmodesmata.

Golgi apparatus

In plant cells the Golgi apparatus consists of many individual stacks of cisternae, sometimes called dictyosomes. The multiple stacks of Golgi membranes in plant cells exhibit great variability, both between species, within single plants of the same species and through the developmental life of a single cell. The number of cisternae is usually 4–8, but can be much higher, up to 20–30. In some cells that have a secretory phase, the number of cisternae increases prior to the onset of secretion and then steadily declines during the active secretion phase.

The number of stacks is usually several hundred per cell, although some unicellular algae resemble animal cells in possessing only a single stack per cell. Golgi stacks replicate by vertical division, starting from the *cis*-face, so maintaining numbers across cell division cycles.

In animal cells, microtubule-depolymerizing agents disrupt stack structure. This does not happen in plant cells. However, in plants disruption of microfilaments causes local clustering of stacks.

Functionally the plant Golgi is similar to that of animals. There is a distinct polarity from *cis*- to *trans*-face, most easily recognized following pre-embedding staining with osmium–zinc salts. The mechanism of forward movement of cargo molecules from *cis*- to *trans*-face is as unknown in plants as it is in animals. Observations on dynamic changes in the number of cisternae and on the formation of algal scales, which are as large as a single cisterna, have been especially cited by plant cell biologists who support the original cisternal progression model. In this model the cargo remains in the cisterna, and the complete cisterna is matured and used up in secretory vesicle formation. While work on animal cells displaced this model in favour of

transport of cargo by vesicle shuttles between adjacent cisternae, there is now a revival of interest in the original model.

The molecular mechanisms directing vesicle trafficking in plants are probably very similar to those found in animals and yeasts. Homologues of genes for the proteins involved have been found in searches of DNA sequences from plants.

There are functional differences in the protein glycosylation steps in plants compared with animals. While the early stages of *N*-glycosylation are similar, there are differences in the terminal residues. *N*-Acetyl-neuraminic acid is not found, but the presence of β-1,2 xylose is unique to plants. Plants use β-1,3-linked fucose instead of β-1,6-linked fucose, found in animals. *O*-Glycans of plants have different sugars from animals and hydroxyproline is frequently glycosylated, as well as the serine and threonine residues.

Plant cells undertake complex carbohydrate synthesis in making cell wall polysaccharides, with a variety of sugar transferases being localized in the Golgi. Matrix components are assembled in the *trans*-Golgi cisternae and packaged into secretory vesicles destined for the plasma membrane.

The plasma membrane is the default pathway for secretory vesicles, as in animal cells. Targeting to plant vacuoles requires the intervention of specific routing signals. These mechanisms are relatively well understood in yeasts, and comparison of yeast with plant cDNA sequences suggest that similar proteins are present in plants. However, these sequences are present as multiple homologues in plants, possibly reflecting greater functional diversity. Evidence for both v- and t-SNARE proteins has been found in plants.

The mechanism for separating proteins destined for vacuoles from plasma membrane-destined proteins in plants is quite different from that in mammals and yeasts. In mammals, mannose 6-phosphate glycans target lysosomal proteins to receptors in vesicle buds that are destined for lysosomes. In plants, there is a vacuole-targeting motif NPIR (asparagine, proline, isoleucine, arginine), which can be at any location in the polypeptide chain. This motif can also redirect other proteins to the vacuole if included in a transgenic product.

The NPIR sequence appears to bind to a 80 kDa membrane-bound receptor in the *trans*-Golgi membranes. This is a Type 1 membrane protein with its large N-terminal domain in the cisternal lumen. The terminal 400 bases are unique to plants, but these are followed by EGF repeats (epidermal growth factor, animal). Such repeats are usually associated with protein–protein interactions mediated by calcium ions.

The 80 kDa receptor does not target to the tonoplast, but rather to a prevacuolar compartment. It is possible that this allows a membrane-bound ATPase to acidify the compartment, releasing the NPIR–80 kDa conjugates.

The released vacuolar protein continues to the vacuole and the 80 kDa protein is recycled to the *trans*-Golgi.

Nucleus and Cell Division

Although the nucleus of plants is very similar to that of animals, the nucleolus often lacks the distinctive demarcation into granular and fibrillar layers. Also there is no distinctive nuclear laminar on the inner face of the nuclear envelope.

Mitosis and cytokinesis are processes that do show considerable differences from those in animal cells. Multicellular plants lack centrioles, so these are not a feature of the spindle poles, and the plant cell wall renders the plasma membrane relatively immobile, so that it cannot assist in cell separation.

During prophase the spindle develops in a clear zone around the nucleus. Breakdown of the nuclear envelope is followed by completion of the spindle. This has an overall barrel-shape, with relatively diffuse poles formed by bundles of microtubules running into the equator. Plant chromosomes are often much larger than their animal counterparts. They attach to the spindle normally, by their centromeres, but the chromosome arms usually lie up and down the spindle at metaphase, rather than radiating out from it.

Anaphase and telophase lead to the formation of daughter nuclei in the usual way, leaving the remnant spindle. This now serves in the formation of the new cell wall, or phragmoplast, so the spindle fibres are now renamed phragmoplast fibres. These guide secretory vesicles from the Golgi apparatus to the spindle equator. The Golgi persists in plant cells through mitosis, unlike in animal cells, in which it degenerates at prophase and reforms at telophase.

The vesicles form a flat disc in the centre of the cell at the equator, with endoplasmic reticulum tubules between them. As more vesicles arrive at the edge of this centrifugally expanding disc, the ones in the centre fuse together. Their contents are new wall polysaccharides and the fused membranes form a *de novo* plasma membrane. This disc of new wall extends out towards the side walls of the parent cell, as more vesicles fuse with its margins. Trapped elements of the endoplasmic reticulum form new plasmodesmata in the new cross wall.

While cytokinesis most often divides a cell into identical daughters, there are situations where a smaller cell is split off from a larger one. The plane of these divisions is determined before prophase by a circumferential ring of microfilaments and microtubules located just beneath the plasma membrane, at the point of eventual fusion of the cell plate with the side walls. These preprophase bands disappear during spindle formation, but some molecular memory must exist at their original location, because the

cell always divides at this predetermined point. In extreme cases, as in the formation of stomatal guard cell mother cells, the ring can lie entirely on one side wall, so that a hemispherical cell plate is formed enclosing one daughter nucleus with only a small fraction of the parental cell cytoplasm.

Vacuoles

As one of the major distinguishing features of plant cells, the vacuoles, and their bounding membranes, the tonoplast, have been extensively studied. On the purely physical level of size and location, the vacuole allows a plant cell to expand in size while maintaining a constant ratio of plasma membrane surface to cytoplasmic volume. This is in marked contrast to animal cells, where increasing size is limited by capacity of the plasma membrane transport systems to maintain an ever-increasing volume of cytoplasm.

As part of the osmoregulatory system, the enclosed solutes provide the osmotically driven turgor pressure, maintaining tissue and organ shape and position. Cell expansion, and hence plant growth, is regulated, by the rate of accumulation of vacuolar solutes.

Sequestration of solutes into the vacuole can lead to the formation of crystals, often of organic and inorganic salts of calcium (e.g. oxalate, silicate, carbonate, phosphate).

Ion transport studies on plant tissues, especially with respect to the uptake of nutrients, have located specific ion pumps on the vacuolar membranes. There is also an important membrane-bound vacuolar ATPase that pumps protons from the cytoplasm into the vacuole, lowering its pH.

Most obviously, to a microscopist, vacuoles serve as storage compartments for pigments (water-soluble pigments of leaves, stems and flowers) and proteins, especially storage proteins of seeds, but also protease inhibitors that inactivate gut enzymes of phytophagous insects.

Less well understood are the roles of vacuoles in autophagy. There is some evidence that they serve as a lysosomal equivalent in plant cells, but the control of sequestration into the vacuole and digestion is not clearly understood.

Not surprisingly, these multiple roles of vacuoles are not reconciled readily with the existence of a single structure. In some cells there is evidence for the existence of more than one type of vacuole, with lytic functions separated from storage functions. It has yet to be shown how universal this is.

Microbodies

This general term is used to describe single-membrane bound organelles that carry out a variety of oxidase functions in the cell. In leaf cells, they are involved in recycling the carbon from glycollate, a product of photorespiration in chloroplasts. The complete biochemical pathway involves enzymes in chloroplasts, microbodies and mitochondria, so these three organelles are often found lying in close proximity to each other. In the microbody, reactions lead to the formation of highly toxic peroxides. These are very rapidly broken down to water and oxygen by the high levels of catalase enzyme present. The presence of this set of enzymes in these organelles has led to them also being called peroxisomes. The high levels of catalase frequently lead to the formation of crystals, a useful distinguishing characteristic in micrographs.

In oil- and fat-storing seeds microbodies participate in the mobilization of these reserves via the glyoxylate cycle, hence the term glyoxysomes. Again peroxide is a byproduct that is rapidly removed by catalase. In some germinating seeds (e.g. sunflower, cucumber) the oil-storing cotyledons emerge above the soil, expand and become green and photosynthetic. The glyoxysomes formed at germination have their enzyme complement gradually modified until they are transformed into peroxisomes. Catalase is common to both, and so is retained throughout the transition.

Other types of microbody have been discovered, all sharing the same general function of providing an oxidase capability.

Microbodies arise as buds from the endoplasmic reticulum, but their enzymes are translated on free cytoplasmic ribosomes and targeted to specific peptide receptors on the outside of the membrane. Many are imported as apoproteins that are modified in the microbody before final assembly into a multimeric enzyme unit.

Plastids

The defining difference between plants and animals is the presence of plastids in plant cells. While they may have originated as photosynthetic endosymbionts, providing autotrophic nutrition for the host cells, they are now an integral part of the genetic and biochemical machinery of plant cells. They contain genetic information in the form of circular DNA chromosomes, along with a protein-translation machinery based on bacterial-type ribosomes. Within plant cells plastids serve a wide variety of functions; some, such as chloroplasts, are well understood, while little is known of the functions and activities of others.

Plastids divide by binary fission, so that each daughter has at least one chromosome. Division occurs throughout the cell cycle to maintain a population of 50–200 plastids per cell.

Chloroplasts

These contain the familiar green pigment, chlorophyll, and are found in all the green parts of plants: leaves, stems, flower buds and unripe fruits. One of the main functions of chloroplasts is photosynthesis. The very extensive membrane system carries the chlorophyll–protein molecules that trap light energy. The membranes are organized into a series of stacks (grana) of discs (thylakoids) that are interconnected by stroma lamellae or frets. Each thylakoid disc is a closed membrane cisternum that separates the outer, stromal, phase from the inner lumen. The lumen has connections with the lumen of the stroma lamellae and thence to all other thylakoids in all the grana stacks in the chloroplast.

There are two photosystems – specific complexes of chlorophyll–proteins with other proteins – that are responsible for the two photochemical steps. Other light-harvesting chlorophyll proteins serve to trap energy from photons and channel it into the photosystems. Photosystem I and photosystem II act in concert to reduce water. ATP and NADPH are produced and oxygen is released as a waste product. These products provide the energy for carbon dioxide fixation reactions in the stroma. Chloroplasts are inherited from one generation to the next, but usually only through the maternal side of the fertilization process. So chloroplast-derived phenotypic features are inherited on the female line. Loss of chloroplast mutants can lead to all white phenotypes, usually lethal, or to variegated mutants if the loss has been confined to one of the three cell layers that make up plants.

Photosynthetic enzymes can be coded for by either plastid or nuclear DNA, which affects their pattern of inheritance. Some, such as the carbon dioxide-fixing enzyme, ribulose biphosphate carboxylase, have subunits from both DNA sources. Cytoplasmically made proteins are imported across the chloroplast envelope.

Etioplasts

These plastids are found in photosynthetic organs that have developed in the dark. The familiar yellow patches formed on lawns after the grass has been covered for a few days are due to the presence of yellow etioplasts in the leaf cells. These contain the yellow pigment, protochlorophyll, associated with a convoluted tubular membrane system that resembles a crystal structure when sectioned. Exposure to light converts the protochlorophyll to chlorophyll by a photochemical reaction and initiates the transformation of tubular membranes into flat lamellar sheets on which the thylakoid discs are assembled. The etioplast is converted into a photosynthetic chloroplast.

Proplastids and leucoplasts

'Proplastids' is a loose term for structurally undifferentiated plastids in meristematic cells. In stems these develop into chloroplasts of stem and leaf. In roots, they develop into leucoplasts which may contain one or more starch grains, oil droplets and proteinaceous crystals. The specific biochemical properties of these organelles are largely unexplored. It is known that plastids are a major site of fatty acid synthesis in the cell, so the lack of a specialized ultrastructure should not be taken to mean that proplastids are insignificant cellular components.

Chromoplasts

The ripening of fruits provides a good example of the conversion of green chloroplasts to red/yellow/orange pigment-containing bodies of tomato, lemons and oranges. These colours are due to the formation of globules and crystals of lycopene, xanthophylls and carotenes. The typical chloroplast structure is degraded, as is the chlorophyll. Other plastids can also undergo this transformation: in carrots the proplastids of roots develop into the familiar orange chromoplasts containing crystals of carotene; and in the central trumpet of narcissi, and other flowers, plastids form chromoplasts giving brilliant orange-red colours.

Amyloplasts

These are plastids specialized for starch storage. While chloroplasts and many other plastids may contain one or more small starch grains, these only constitute a minor part of the plastid volume. In amyloplasts, starch grains occupy nearly the whole plastid volume. The starch is laid down in layers of amylose and amylopectin (straight and branched-chain polymers of glucose, respectively). Typically they are common in cells of storage organs such as seeds, underground tubers and in the ray cells of woody stems.

Amyloplasts are of huge economic importance, because of their food value. The physical properties of different starches, which are determined by the relative ratios of amylose to amylopectin, are of major importance in the food industry for making bread, pasta, etc.

Mitochondria

Mitochondria are the cellular centres of respiration, providing ATP for cellular processes. Carbon skeletons from fatty acids and carbohydrates are converted to acetyl–CoA. The carbon skeleton is oxidized to carbon dioxide and the electrons passed to oxygen as the terminal electron acceptor, forming water. Mitochondria are found in all eukaryotic cells, possibly as a result of a symbiotic

association between an amoeboid ancestor and an aerobic bacterium.

Mitochondria possess genetic material, in the form of a single closed circle of DNA, that may be duplicated within each mitochondrion. Plant mitochondria possess a unique genome. For other genomes, knowledge of the DNA gene sequence leads directly to a fairly accurate prediction of the amino acid sequence for the encoded protein. This is not the case for plant mitochondria, where the primary RNA gene transcripts are subject to a series of complex editing steps that rearranges the RNA base sequences. Proteins are made from these highly modified codes, but they are not very different from those found in animal mitochondria. Most mitochondrial proteins are synthesized in the cytoplasm and imported into these organelles.

A further difference in the genome is that each plant mitochondrion contains several different circular DNA molecules, none of which contains all the genes, although collectively there is at least one copy of each present. This is unlike bacteria and chloroplasts, in which all the genes are present on each circular chromosome, which may be present in multiple numbers, all identical to each other.

Mitochondrial ribosomes in plants are larger than their counterparts in animals and larger than those in bacteria and chloroplasts. Although the large and small subunits are similar in size to those of the cytoplasm, they are different in structure, as evidenced by their inability to form functional units when swapping between them.

Mitochondria are formed by binary fission, with the divisions producing several hundred per cell. As with plastids, they are normally inherited through the maternal side of a cross. This maternal inheritance is of crucial importance when considering the effects of mitochondrial genes on the offspring. Of great economic importance are the mitochondrial genes for male sterility, which render the plant incapable of producing pollen. All seeds set on such plants will be hybrids, and so these mitochondria are widely used for the production of F_1 hybrid seeds for agricultural and horticultural use.

There are differences between the proteins of plant and animal mitochondria. Cyanide is a well-known animal poison, because it blocks the terminal cytochrome oxidase inhibiting oxygen uptake. Plants possess an alternative oxidase pathway, which is used in some instances to raise the temperature of particular organs, such as the spadix of arum lily flowers.

As in animal cells, mitochondria are often located close to sites requiring ATP in plant cells, such as adjacent to transfer cell wall ingrowths.

Cytoskeleton

Plant cells contain a cytoskeleton based on actin, forming microfilaments, and tubulin, forming microtubules, as in animal cells. The cytoplasm of many plant cells is spread out as a thin layer over the large central vacuole, and also forms strands running across it. This cytoplasm frequently exhibits vigorous streaming, as evidenced by the flow of numerous small granules around the cell. Specific stains for microfilaments show that the cytoplasm is packed with fine and bundled actin filaments. These appear to promote streaming by interaction between this actin and myosin-like molecules on the surfaces of organelles and membrane systems such as the endoplasmic reticulum.

Microtubules usually lie in parallel arrays just below the plasma membrane. These cortical arrays often form interlocking helices, unlike the organization in animal cells, where microtubules are straight or gently curving. There is morphological evidence for crosslinks to the plasma membrane, but these have not been characterized. Structural, physiological and developmental studies show that one role for these microtubules is in the determination of cell shape. This is through their probable influence on the organization of the cell wall. As cell surface cellulose synthases polymerize microfibrils, they are propelled through the fluid mosaic lipid bilayer of the plasma membrane. The crosslinks, from the microtubules, stabilize parallel tracks of plasma membrane, restricting the cellulose synthase movements to the bands in between. Thus microfibrils are laid down in parallel bands that mirror the orientation of the microtubules in the cortical cytoplasm. This microfibril orientation determines the physical properties of the wall, such that turgor-driven expansion growth preferentially stretches the walls in the weakest direction, at right angles to the microfibril direction. This results in the formation of every shape, from simple cylinders that grow in length, to stellate cells and cells with concertina walls. Root hair outgrowth is a further example of subtle cell shaping.

Plasma membrane protein–cytoskeleton complexes are an important feature of animal cells. To date these have not been well characterized in plants, although there are indications that equivalent associations do exist at the plant cell surface.

The role of the plant cytoskeleton in cell division has been described above in the section 'Nucleus and cell division'.

Further Reading

Battey NH and Blackbourne HD (1993) The control of exocytosis in plants. *New Phytologist* **125**: 307–338.

Brennicke A and Kück U eds (1993) *Plant Mitochondria*. Weinheim: VCH.

Cassab GI (1998) Plant cell wall proteins. *Annual Review of Plant Physiology and Molecular Biology* **49**: 281–309.

Chrispeels MJ (1991) Sorting of proteins in the secretory system. *Annual Review of Plant Physiology and Molecular Biology* **42**: 21–53.

Fowler JE and Quatrano RS (1997) Plant cell morphogenesis: plasma membrane interactions with the cytoskeleton and cell wall. *Annual Review of Cell and Developmental Biology* **13**: 697–743.

Ghoshroy S, Lartey R, Sheng J and Citovsky V (1997) Transport of proteins and nucleic acids through plasmodesmata. *Annual Review of Plant Physiology and Molecular Biology* **48**: 27–50.

Gunning BES and Steer MW (1996) *Plant Cell Biology: Structure and Function.* Boston: Jones and Bartlett.

Hanmaker B, Barber J and Boekema EJ (1997) Structure and membrane organisation of photosystem II from green plants. *Annual Review of Plant Physiology and Molecular Biology* **48**: 641–671.

Leon P, Arryo A and Mackenzie S (1998) Nuclear control of plastid and mitochondrial development in higher plants. *Annual Review of Plant Physiology and Molecular Biology* **49**: 453–480.

Mauseth JD (1998) *Botany: an Introduction to Plant Biology*, 2nd edn. Boston: Jones and Bartlett.

Moore R, Clark WD and Vodopich DS (1998) *Botany*, 2nd edn. New York: WCB/McGraw-Hill.

Nick P (1998) Signalling to the microtubular cytoskeleton in plants. *International Reviews of Cytology* **184**: 33–80.

Olsen LJ and Harada JJ (1995) Peroxisomes and their assembly in higher plants. *Annual Review of Plant Physiology and Molecular Biology* **48**: 123–146.

Robinson DG, Hinz G and Holstein SHE (1998) The molecular characterisation of transport vesicles. *Plant Molecular Biology* **38**: 49–76.

Schnell DJ (1998) Protein targetting to the thylakoid membrane. *Annual Review of Plant Physiology and Molecular Biology* **49**: 97–126.

Smith AM, Denyer K and Martin C (1997) The synthesis of the starch granule. *Annual Review of Plant Physiology and Molecular Biology* **48**: 67–87.

Staehelin LA and Moore I (1995) The plant golgi apparatus: structure, functional organisation and trafficking mechanism. *Annual Review of Plant Physiology and Molecular Biology* **46**: 261–288.