1

Organs, cells and tissues

1.1 Organs

Plants are essentially modular organisms; each individual plant consists of distinct but connected organs. In their turn, the organs are composed of cells, which are mostly grouped into tissues. Vegetative organs support photosynthesis and plant growth, and reproductive organs enable sexual reproduction. In seed plants, the primary vegetative organs are the root, stem and leaf (Figure 1.1). Roots and stems have well-defined growing points at their apices, but the leaves are determinate lateral organs that stop growing when they reach a particular size and shape. When a seed germinates, the seed coat (testa) is ruptured and the embryonic structures emerge from opposite poles of the embryo: a seedling root (radicle) grows downwards from the root apex and a seedling axis (hypocotyl) bears the first leaves (cotyledons) and the shoot apex, which ultimately develops new foliage leaves.

1.2 Cells and cell walls

Plant cells consist of a living protoplast contained within a protein-rich plasma membrane, which is itself enclosed by a cell wall. During the cell-division cycle, cells undergo a series of phases that are broadly grouped as interphase, nuclear division (mitosis or meiosis) and cytokinesis (cleavage of the cytoplasm and cell-wall formation). During mitosis, nuclear division occurs first, followed by progressive deposition of membranes in the cytoplasm into a cell plate that is

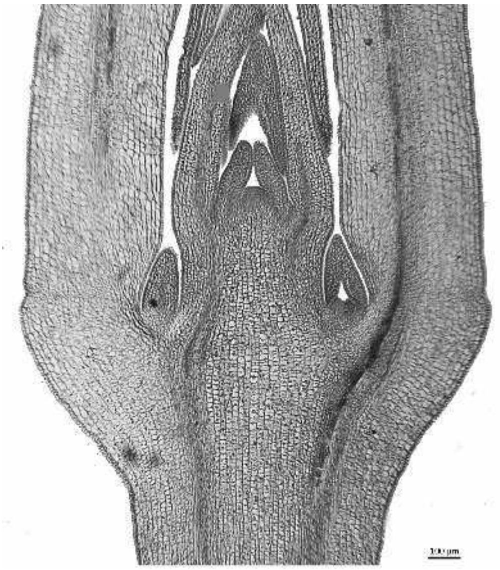

Figure 1.1 *Ligustrum vulgare* (eudicot: Oleaceae), longitudinal section of vegetative shoot apex. Scale = 100 µm

located in the equatorial zone between the two daughter nuclei[138]. The cell plate extends to join the cell wall, thus depositing a new wall.

The primary cell wall consists mostly of carbohydrates: microfibrils of cellulose and hemicelluloses embedded in a matrix of pectins (Figure 1.2). Cell walls of adjacent cells are linked together by a pectin-rich middle lamella[37, 39]. Following cell enlargement and elongation, a secondary cell wall is deposited on the inside surface of the primary wall. Secondary cell walls often appear layered and can contain deposits of complex organic polymers such as cutin, lignin and suberin. Cutin is the primary component of the plant cuticle, which covers the aerial epidermis (Section 1.8). Lignin provides strengthening and rigidity to sclerenchyma cells, especially in the secondary xylem, but also in fibres close to the vascular bundles in the stem and leaf. Suberin is a complex hydrophobic lipid that provides a protective water-resistant lipophilic barrier in periderm cells.

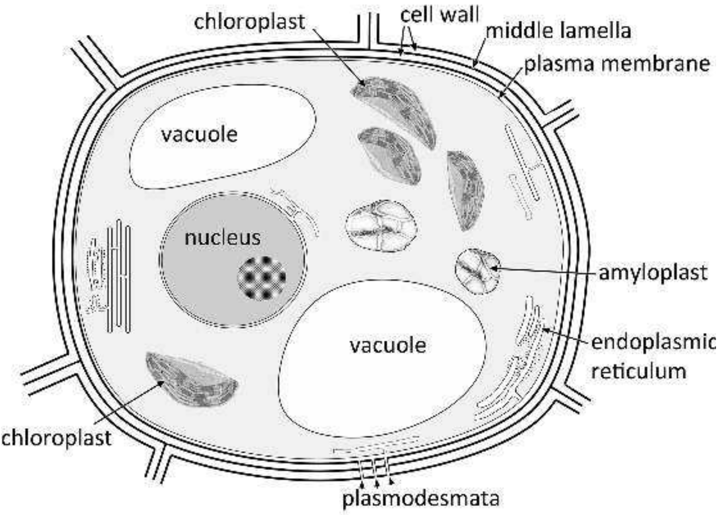

Figure 1.2 Diagram of a generalized plant cell

Primary pit fields are thin regions of the primary cell wall that correspond with similar regions in the walls of neighbouring cells. Pits have protoplasmic strands (plasmodesmata) passing through them, connecting the protoplasts of adjacent cells. The connected living protoplasts are collectively termed the symplast. Primary pit fields often persist as thin areas of the wall even after a secondary wall has been deposited. In simple pits, which occur on relatively non-specialized cells such as parenchyma, the pit cavity is of more or less uniform width. In bordered pits, which are present in tracheary elements, the secondary wall arches over the pit cavity so that the opening to the cavity is narrow and the outer rim of the primary pit field appears as a border around the pit opening when viewed through a light microscope[18].

1.3 Cytoplasm, plastids and photosynthesis

The living cell protoplast consists of cytoplasm that encloses a complex range of membrane-bound internal structures termed

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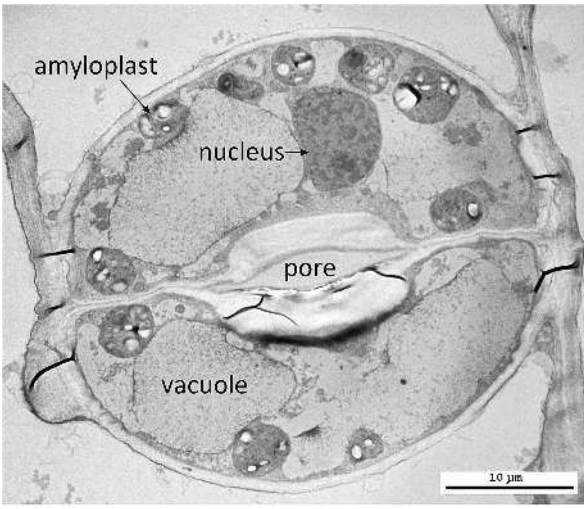

Figure 1.3 *Lapageria rosea* (monocot: Philesiaceae), stomatal pore and guard cells (TEM). Scale = 10 μm

organelles; they include mitochondria, the nucleus, plastids and vacuoles, as well as small particles termed ribosomes and sometimes inorganic contents such as oil, starch grains or crystals (Figure 1.3).

Most plant cells possess a single nucleus that is bounded by a pair of membranes; the outer membrane is continuous with the endoplasmic reticulum. At interphase, one or more nucleoli can sometimes be distinguished, together with the uncondensed chromatin within the nuclear sap. During nuclear division, the chromatin becomes condensed into chromosomes that bear the hereditary information. Vacuoles are membrane-bound structures that contain a watery sap; they can vary considerably in size and shape during the life history of a cell. They can accumulate storage products and soluble pigments such as anthocyanins.

Plastids are large cell organelles that develop from proplastids. They each contain their own genome, which is much smaller than the nuclear genome and normally heritable via the maternal parent. Each plastid is bounded by a pair of membranes, and many contain a system of membranes termed thylakoids. Plastids such as amyloplasts, chloroplasts and chromoplasts play specialized roles within the cell. Amyloplasts are the source of starch grain production. Chromoplasts contain carotenoid pigments that produce some of the colours found in some plant organs, such as flower petals. Mitochondria – the sites of respiration within the cell – are smaller than plastids; they also contain their own heritable genetic material and are enclosed within a double-membrane system. Both plastids and mitochondria originated via endosymbiotic events at an early unicellular stage in plant evolution[50].

Chloroplasts are highly specialized plastids containing green chlorophyll proteins that absorb energy from sunlight. During photosynthesis, plants convert light energy into chemical energy in energy-storage molecules such as adenosine triphosphate (ATP), which they use to make carbohydrates from carbon dioxide (CO_2) and water, releasing oxygen as a by-product. Chloroplasts occur in all green cells but are most abundant in the leaf mesophyll. In most plants, photosynthetic carbon reduction is achieved via a three-carbon compound (C_3 cycle), but some plants capture inorganic carbon more effectively using CO_2-concentrating mechanisms via a C_4 cycle or Crassulacean acid metabolism (CAM)[31]. Some C_4 plants possess a distinctive leaf anatomy, termed Kranz anatomy (Section 4.9).

1.4 Inorganic cell inclusions

Many cells possess non-protoplasmic contents such as mucilage, oils, tannins, starch granules, calcium oxalate crystals and silica bodies. Both oil and mucilage are produced in isolated specialized secretory cells (idioblasts). Tannins are phenol derivatives that are widely distributed in plant cells; they are amorphous and appear yellow, red or brown in cells of sectioned material due to oxidation.

Starch is also widespread in plant tissues but especially common in storage tissues such as endosperm or in parenchyma adjacent to a nectary. Starch granules are formed in specialized plastids

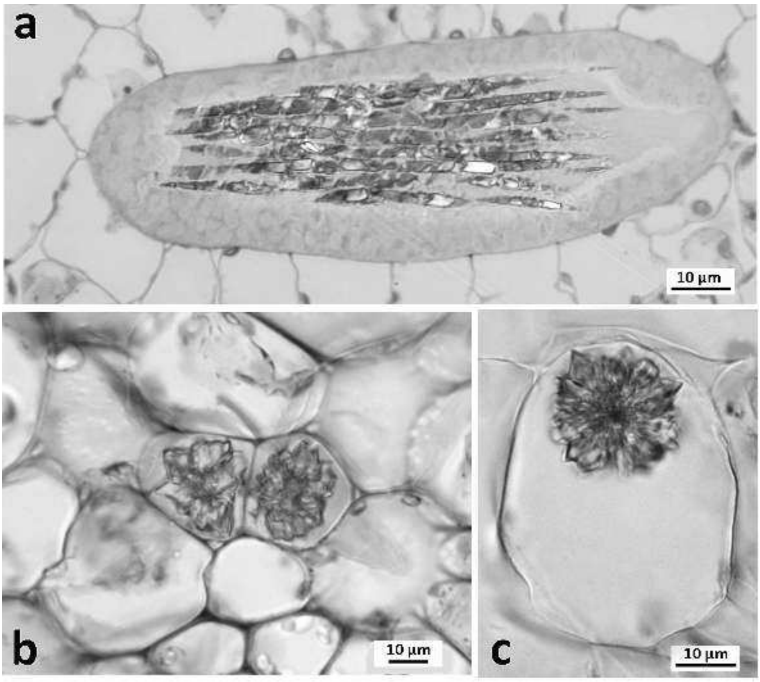

Figure 1.4 Idioblastic cells containing crystals of calcium oxalate. (a) *Dioscorea sosa* (monocot: Dioscoreaceae), raphide crystals in a mucilage sheath. (b) *Cissus rhombifolia* (eudicot: Vitaceae), druse (cluster crystal). (c) *Atriplex hymenelytra* (eudicot: Amaranthaceae), druse. Scale = 10 µm

(amyloplasts). They often appear layered due to the successive deposition of concentric rings and possess characteristic shapes. The unusual and specialized starch grains present in laticifers in some species of *Euphorbia* possess highly characteristic elongated rod- or bone-like shapes compared with the more rounded starch grains of neighbouring parenchyma cells[85].

Calcium oxalate crystals (Figure 1.4) occur within crystal idioblasts; they can be distributed in almost every part of both vegetative and reproductive organs and are often located near veins, possibly reflecting transport of calcium through the xylem. They form within the vacuoles of actively growing cells and are usually associated with membrane chambers, lamellae, mucilage and fibrillar material. Contrasting crystal shapes can be highly characteristic of different plant families; for example, styloid crystals characterize the *Iris* family (Iridaceae). Common crystal types include solitary needle-like or rhomboidal crystals (styloids), bundles of needle-like crystals borne together in the same cell (raphides), aggregate crystalline structures that have precipitated around a nucleation site (druses) and numerous fine particles of crystal sand. In some woody eudicot species, crystals occur in the secondary phloem or secondary xylem; for example, crystal cells are common in the ray parenchyma of some woods (Chapter 2). Cystoliths are calcareous bodies that are mostly located in leaf epidermal cells (Figure 4.4).

Most plants deposit silica in at least some of their tissues[101]. Some species accumulate silica in large quantities and deposit it as discrete bodies of solid silicon dioxide in the lumina of specific plant cells. Opaline silica bodies, commonly termed 'phytoliths', are

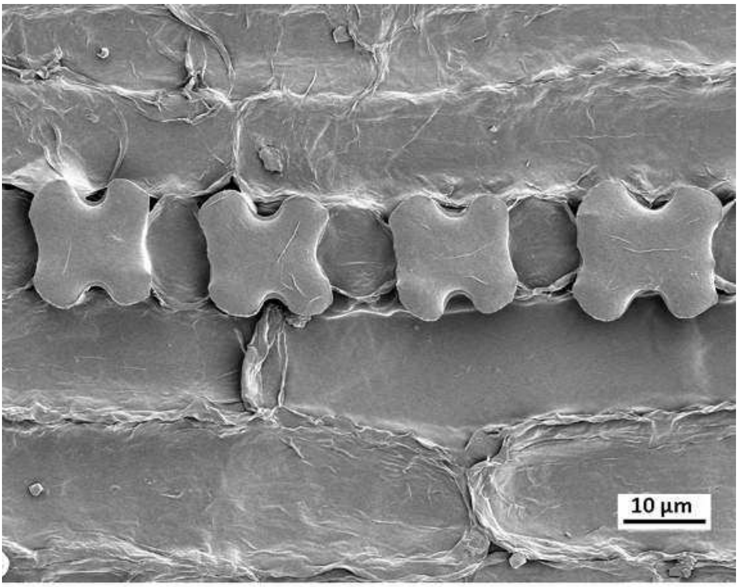

Figure 1.5 *Oryza sativa*, rice (monocot: Poaceae), H-shaped silica bodies (phytoliths) in a leaf epidermis (SEM). Scale = 10 µm

a characteristic feature of some flowering plant groups. These groups include several commelinid monocots, notably the grass family Poaceae[118], in which silica bodies are almost exclusively restricted to the epidermis, and the palm family Arecaeae, in which they are primarily restricted to the vascular bundle sheath cells. Grass phytoliths occur in various shapes that can characterize different species, so they can have immense significance as diagnostic markers in studies of grassland palaeoecology (Figure 1.5). Silica bodies are often associated with sclerenchyma. In some woody eudicot species they can occur in the secondary xylem.

1.5 Meristems

Meristems are the growing points of the plant. They represent localized regions of thin-walled, tightly packed living cells that undergo frequent mitoses and often continue to divide indefinitely. Most of the plant body is differentiated at the meristems, though cells in other regions may also occasionally divide.

Apical meristems are located at the shoot apex (Figures 1.1, 2.1), where the primary stem, leaves and flowers differentiate, and at the root apex (Figures 3.1, 3.2), where primary root tissue is produced. In flowering plants, the shoot and root apical meristems are highly organized but differ from each other in many respects. Both shoot and root apical meristems contribute to extension growth and are self-renewing. The shoot apical meristem also initiates lateral organs (leaves) at its flanks in a regular nodal arrangement, each node bearing a single leaf, a pair of leaves or a whorl of leaves. Subsequent elongation of the shoot axis occurs at the stem internodes, either by diffuse cell divisions and growth throughout the youngest internodes (uninterrupted meristem) or in a restricted region, often at the base of the internode (intercalary meristem). Both intercalary and uninterrupted meristems represent growth in regions of differentiated tissues.

Lateral meristems are important for stem thickening growth; they include vascular cambium and the primary and secondary thickening meristems (Chapter 2). Lateral meristems occur in localized regions parallel to the long axis of a shoot or root, most commonly in the pericyclic zone, at the junction between vascular tissue and cortex. The phellogen (cork cambium) is a lateral meristem that occurs in the stem or root cortex, where it forms a protective corky layer (Figure 2.10); a phellogen can also develop in the region of a wound or at the point of leaf abscission.

Meristemoids are isolated and densely protoplasmic cells that reactivate embryonic activity to allow tissue differentiation. Typically, a meristemoid either itself undergoes unequal (asymmetric) cell division or is the smaller daughter cell that results from an asymmetric division[16] (Figure 1.6). Asymmetric divisions are caused by cell polarization resulting from organized arrangements of actin filaments in the dense cytoplasm during cell plate alignment[49]. Examples of asymmetric cell divisions include

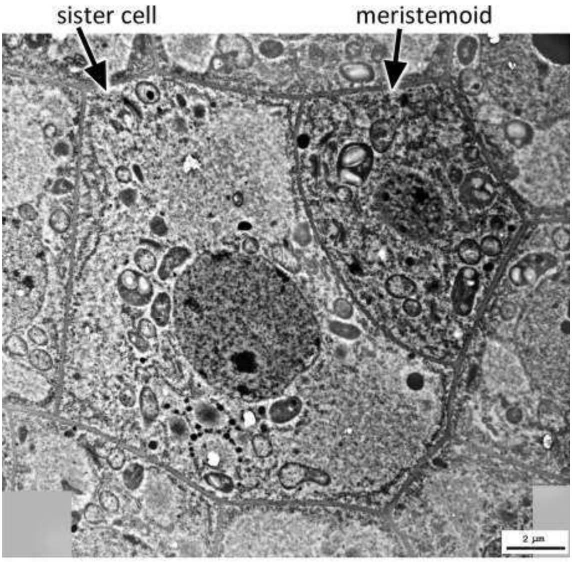

Figure 1.6 *Amborella trichopoda* (ANA-grade: Amborellaceae), developing leaf epidermis, highlighting a pair of cells that have recently undergone asymmetric mitosis to form a dense meristemoid and its larger sister cell (TEM). The meristemoid will form a guard-mother cell and will ultimately divide symmetrically to form a pair of guard cells. Scale = 2 μm

formation of a root hair initial (trichoblast), microspore division into a larger vegetative cell and smaller generative cell, a protophloem mitosis to form a larger sieve tube element and smaller companion cell, and division of a protodermal cell into two cells of unequal sizes, the smaller of which is the guard-mother cell, a meristemoid that will divide symmetrically to form the paired guard cells of a stoma.

Other types of localized meristems occur in some species, in which differentiated plant cells can become de-differentiated and meristematic. One example of such cell-fate plasticity includes localized meristems that occur on the leaf margins of some succulent Crassulaceae; these meristematic cells can give rise to entire plantlets[131]. Plants can also regenerate tissues and organs at the site of a wound by cellular proliferation on callus tissue, a process that is regulated by the plant hormones auxin and cytokinin. Callus cells formed from roots and from some aerial organs resemble the apices of lateral roots derived from the pericycle[81, 137]. Isolated callus tissue can be used in laboratory conditions to artificially grow a new plant using tissue culture methods.

1.6 Cell growth and expansion

Cells develop and expand in different ways depending partly on their location and surrounding tissue and partly on their cell-wall properties. Those in close contact with each other are initially glued together by a pectin-rich middle lamella and hence have a mutual influence on shape during early expansion. Parenchyma cells, which are largely thin walled and isodiametric, typically expand relatively evenly. Different rates of expansion of adjacent cells can result in the formation of lobes and intracellular air spaces, as in the spongy mesophyll of the leaf[5]. Adjacent tissues can also expand at different rates; for example, leaf epidermal cells continue to enlarge after the subepidermal mesophyll cells have ceased growth, influencing development of a substomatal cavity and anticlinal cell-wall undulations in abaxial epidermal cells. Epidermal cells, which