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Organs, cells and tissues

1.1 Organs

Plants consist of several organs, which in their turn are composed of tissues. Broadly, vegetative organs support plant growth, and reproductive organs enable sexual reproduction. The three main types of vegetative organ are the root, stem and leaf. Roots typically occur underground, and extract moisture and nutrients from the soil, though there are many examples of plants with aerial roots. The stem and leaves together comprise the shoot (Fig. 1.1). Stems occur both above and below ground. Some stems are modified into underground perennating or storage organs such as corms or rhizomes. Leaves typically occur above ground level, though some underground stems possess reduced scale leaves, and underground bulbs possess swollen leaves or leaf bases.

Primary organs and tissues develop initially from the shoot and root apical meristems and from cell divisions in meristems closely adjacent to them, such as the primary thickening meristem. Secondary tissues such as secondary xylem (wood) develop from lateral meristems such as the vascular cambium. Organs such as adventitious roots develop from differentiated cells that have retained meristematic capacity. At the onset of flowering, the shoot apical meristem undergoes structural modification from a vegetative to a reproductive apex and subsequently produces flowers (chapter 5). Flowers are borne on an inflorescence, either in groups or as solitary structures. A group of inflorescences borne on a single plant is termed a synflorescence[121] (Fig. 1.2).

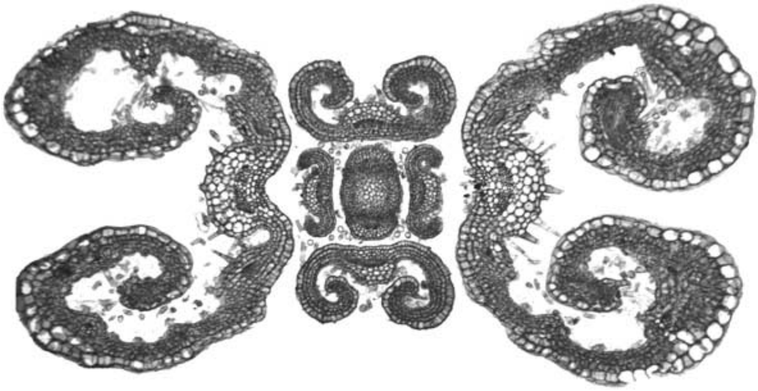

Figure 1.1 *Hyptis ditassoides* (Lamiaceae), transverse section of vegetative bud near apex, showing three successive pairs of leaf primordia surrounding central stem. Scale = 100 μm.

1.2 Cells

Plant cells typically have a cell wall containing a living protoplast (Fig. 1.3). The layer that contacts the walls of adjacent cells is termed the middle lamella. Following cessation of growth, many cells develop a secondary cell wall which is deposited on the inside surface of the primary wall. Both primary and secondary walls consist of cellulose microfibrils embedded in a matrix and oriented in different directions. Secondary cell walls consist mostly of cellulose, but primary walls commonly contain a high proportion of hemicelluloses in the gel-like matrix, affording a greater degree of plasticity to the wall of the growing cell. The secondary wall can also contain deposits of lignin (in sclerenchymatous cells) or suberin (in many periderm cells), and often appears lamellated.

Thin areas of the primary wall, which usually correspond with thin areas of the walls of neighbouring cells, are primary pit fields, and usually have protoplasmic strands (plasmodesmata) passing through them, connecting the protoplasts of neighbouring cells[36]. The connected living protoplasts are collectively termed the symplast. Primary pit fields often remain as thin areas of the wall even after a secondary wall has been deposited, and are then termed

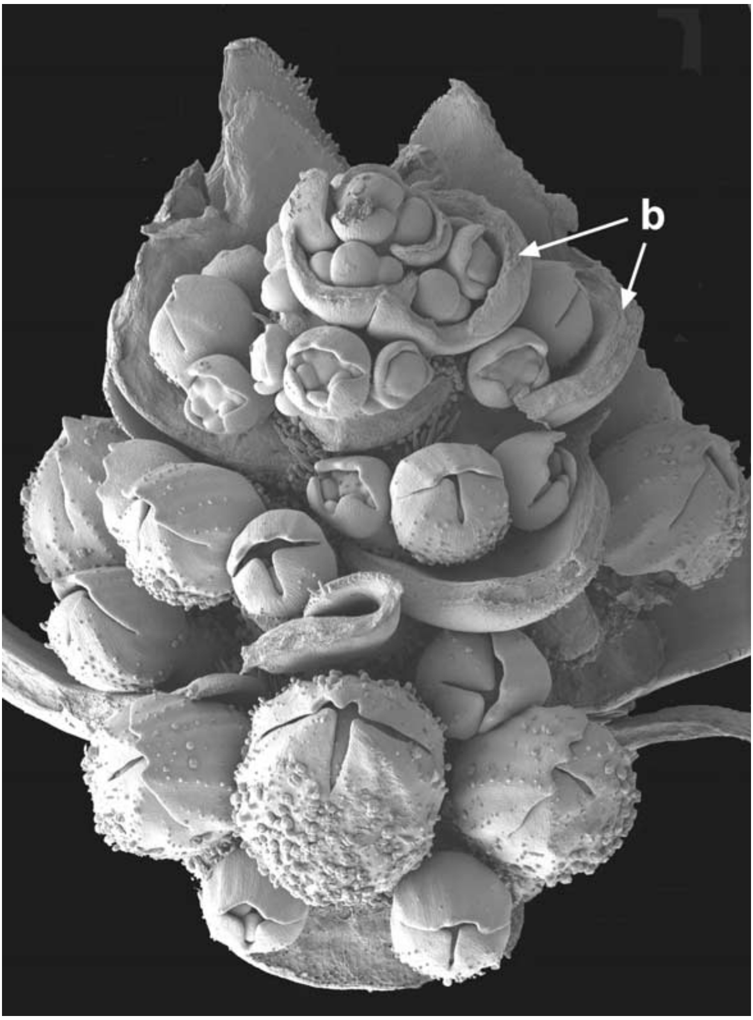

Figure 1.2 *Salvia involucrata* (Lamiaceae), dissected developing synflorescence showing flower clusters, each consisting of three flowers enclosed within a bract; younger stages towards apex. b = bract. Scale = 500 μm.

pits, or pit-pairs if there are two pits connecting adjacent cells. Pits may be simple, as in most parenchyma cells, or bordered, as in tracheary elements. In simple pits the pit cavity is of more or less uniform width, whereas in bordered pits the secondary wall

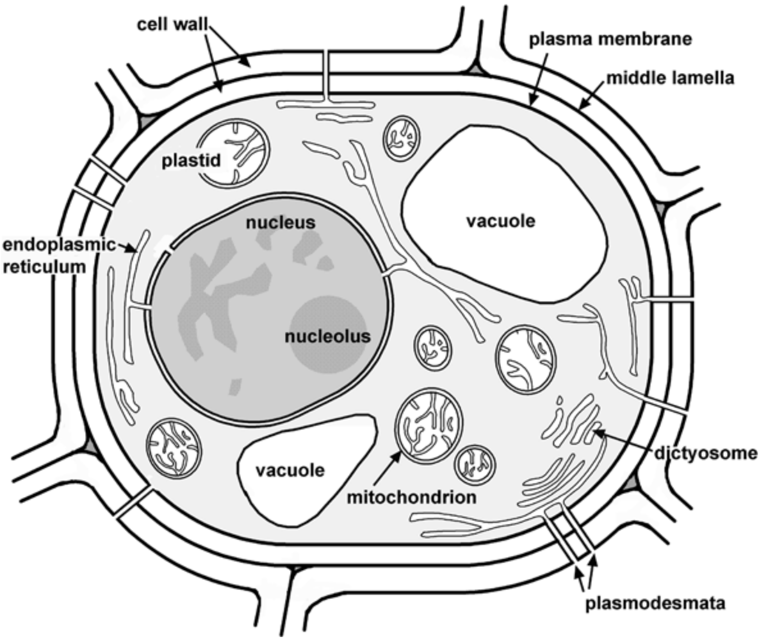

Figure 1.3 Diagram of a generalised plant cell illustrating details of protoplasmic contents.

arches over the pit cavity so that the opening to the cavity is relatively narrow. Through a light microscope the outer rim of the primary pit field appears as a border around the pit opening.

The cell protoplast is contained within a plasma membrane. It consists of cytoplasm that encloses bodies such as the nucleus, plastids and mitochondria, and also non-protoplasmic contents such as oil, starch or crystals. The nucleus, which is bounded by a nuclear membrane, often contains one or more recognizable bodies (nucleoli) together with the chromatin in the nuclear sap. During cell division the chromatin becomes organized into chromosomes. Most cells possess a single nucleus, but examples of multinucleate cells (coenocytes) include the non-articulated laticifers found in many plant families (chapter 1.4). Such cells elongate and penetrate established tissues by intrusive tip growth, in which the cell apices secrete enzymes that dissolve the middle lamellae of neighbouring cells; bifurcation occurs when they encounter an obstacle[36].

Mitochondria and plastids are surrounded by double membranes. Plastids are larger than mitochondria, and are classified into different types depending on their specialized role. For example, chloroplasts are plastids that contain chlorophyll within a system of lamellae that are stacked to form grana; this is the site of photosynthesis. Chloroplasts occur in all green cells, but are most abundant in the leaf mesophyll, which is the primary photosynthetic tissue (chapter 4.5). Membranes occur widely throughout the cytoplasm, sometimes bounding a series of cavities. For example, the endoplasmic reticulum is a continuous membrane-bound system of flattened sacs and tubules, sometimes coated with ribosomal particles. Dictyosomes are systems of sacs associated with secretory activity. Vacuoles are cavities in the cytoplasm; they are usually colourless and contain a watery fluid. Their size and shape varies in different cell types, and also changes during the life of a cell.

1.3 Cell Inclusions

Many cells possess non-protoplasmic contents such as oils, mucilage (slime), tannins, starch granules, calcium oxalate crystals and silica bodies. Both oil and mucilage are produced in secretory idioblasts which are often larger than adjacent parenchymatous cells. Tannins are phenol derivatives which are common in plant cells; they are amorphous, and appear yellow, red or brown in colour in cells of sectioned material. Cystoliths are cellulose bodies encrusted with calcium carbonate that occur in epidermal cells in some species (Fig. 4.4); the body is attached to the cell wall by a silicified stalk[36].

Starch is especially common in storage tissues such as endosperm or in parenchyma adjacent to a nectary. Starch granules

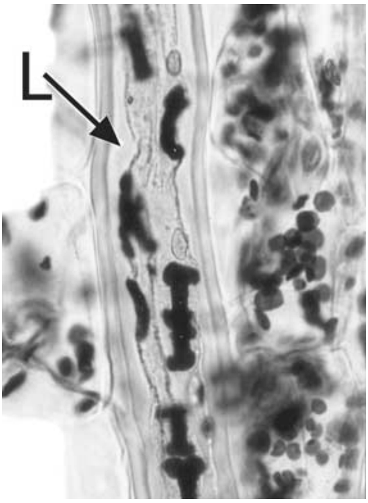

Figure 1.4 *Monadenium ellenbeckii* (Euphorbiaceae). Elongated I-shaped starch grains in laticifer (L); ovoid starch grains present in adjacent parenchyma cells. Scale = 20 μm.

are formed in plastids (amyloplasts). They often appear layered due to the successive deposition of concentric rings, and may possess characteristic shapes. For example, in species of *Euphorbia*, starch grains in laticifers are elongated and sometimes rod-shaped or bone-shaped compared with the more rounded starch grains of neighbouring parenchyma cells (Fig. 1.4)[70].

Calcium oxalate crystals (Figs 1.5, 1.13) are borne in crystal idioblasts that can occur in almost every part of the plant, including both vegetative and reproductive organs[82]. They are often present near veins, possibly due to transport of calcium through the xylem, and are sometimes associated with air space formation; some aquatic plants possess calcium oxalate crystals projecting into air spaces. Crystals form within vacuoles of actively growing cells and are usually associated with membrane chambers, lamellae, mucilage and fibrillar material. Crystal sand is relatively amorphous and represents fragmented non-nucleated crystalline particles. Druses (cluster crystals) are aggregated crystalline structures that have precipitated around a nucleation site. Raphides are bundles of needle-like crystals that are borne in the same cell; they occur commonly in monocots. In the monocot family Araceae,

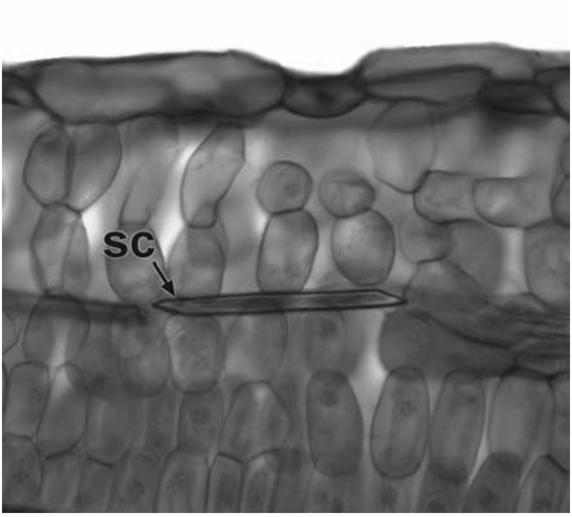

Figure 1.5 *Crocus cancellatus* (Iridaceae), longitudinal section of leaf showing crystal idioblast containing styloid crystal (sc). Scale = 50 μm.

raphides are characteristically grooved and sometimes barbed. Styloid crystals are typically solitary, larger and needle-like or rhomboidal; they are highly characteristic of some families, such as Iridaceae[91].

Opaline silica bodies are also a characteristic feature of some plant groups[83]. They occur in all plant parts, often associated with sclerenchyma, though they are rare in roots. In many dicot species they occur in the ray or axial parenchyma cells in secondary xylem. Some families, such as grasses (Poaceae), sedges (Cyperaceae), orchids (Orchidaceae) and palms (Arecaceae), possess characteristic silica bodies contained in well-defined cells, either in the epidermis (e.g. in grasses: Fig. 4.3B) or in vascular bundle sheath cells (e.g. in palms and orchids).

1.4 Secretory Ducts and Laticifers

In many plants, substances such as oils, resins and mucilage are secreted internally, often into specialized ducts formed either by

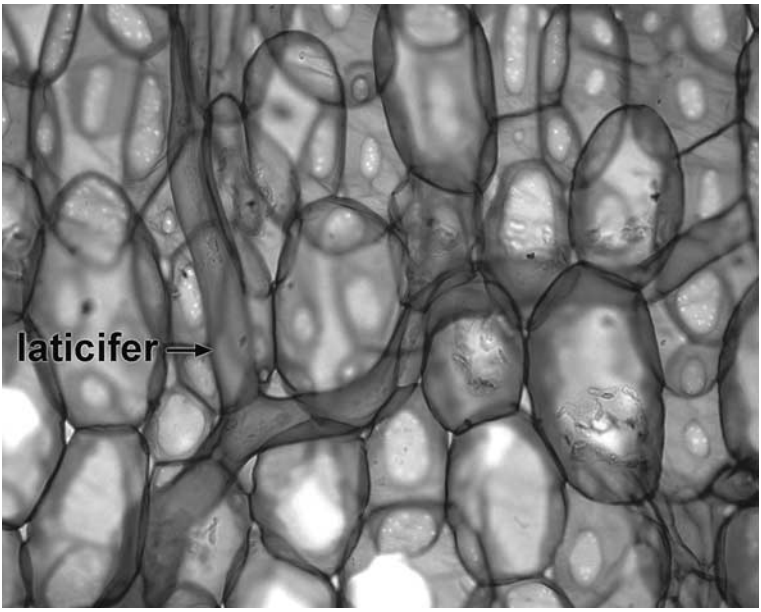

Figure 1.6 *Euphorbia eyassiana* (Euphorbiaceae), longitudinal section of stem showing branched non-articulated laticifers in parenchyma. Scale = 50 μm.

cell wall separation (schizogenous ducts) or cell wall degradation (lysigenous ducts), or a combination of the two processes (schizo-lysigenous ducts)[13]. Some angiosperms, especially eudicots such as *Euphorbia* and *Ficus*, produce latex from specialized cells (laticifers) that permeate their tissues (Figs 1.4, 1.6). In *Euphorbia*, the laticifers are derived from a small group of initial cells in the cotyledonary node of the embryo; these cells are coenocytes, since they undergo repeated nuclear divisions without corresponding wall formation. They grow intrusively between cells of surrounding tissues, and often branch and eventually ramify throughout the entire plant[31,71,87,90]. Coenocytic laticifers are termed non-articulated laticifers. By contrast, laticifers of a few species (e.g. *Hevea brasiliensis*, the source of commercial rubber) undergo cell-wall formation, and thus consist of linked chains of cells; these are termed articulated laticifers. Laticifers of the opium poppy

(*Papaver somniferum*) are always associated with vascular bundles[122]; the alkaloids produced in the latex of these cells are the source of narcotic analgesics such as morphine.

1.5 Transfer Cells

Transfer cells occur at the interface between tissues; they are specialized cells that facilitate transport (absorption or secretion) of soluble substances across tissue boundaries. For example, they can occur at the junction of the megagametophyte and megasporophyte, in companion cells in phloem tissue (especially at the node of a stem), in root nodules, in the haustoria of parasitic plants, and in the epidermis of water plants[80]. Several cells of the embryo sac and seed, including synergids, antipodals and specialized endosperm cells, have been identified as transfer cells in different species. Transfer cells are typically characterized by numerous cell-wall ingrowths protruding into their protoplasts or those of adjacent cells; these ingrowths are sometimes visible using light microscopy. Secretory cells, such as those of glandular hairs and nectaries, also frequently possess wall ingrowths. The plasma membrane of the transfer cell follows the contour of the wall ingrowths, thus increasing the surface area.

1.6 Tissues

Simple tissues, such as parenchyma, collenchyma and sclerenchyma, consist of a single cell type, though they may be interspersed with other, isolated, cell types (idioblasts). Complex tissues consist of multiple cell types, and can be divided into three main groups: dermal tissue (epidermis), ground tissue and vascular (conducting) tissue, each distributed throughout the plant body, and often continuous between the various organs. Complex tissues often include elements of several different simple tissue types; for example, secondary xylem includes not only vascular tissue, but also parenchyma and sclerenchyma.

1.6.1 Parenchyma

Parenchyma cells are typically thin-walled and often polyhedral or otherwise variously shaped, sometimes lobed. Cells with living contents that do not fit readily into other categories are often termed parenchyma cells. They are the least specialized cells of the mature plant body and often resemble enlarged meristematic cells. Parenchyma cells may occur in primary or secondary tissues. Relatively specialized types of parenchyma include certain secretory tissues and chlorenchyma, which contains chloroplasts for photosynthesis. Parenchymatous cells may be tightly packed or may be interspersed with intercellular air spaces.

Callus tissue is a cellular proliferation that is often produced at the site of a wound by divisions in parenchyma cells that have retained the ability to divide at maturity. A single isolated callus cell can be used to artificially grow a new plant using tissue culture methods.

1.6.2 Aerenchyma

Aerenchyma is a specialized parenchymatous tissue that often occurs in aquatic plants (hydrophytes). It possesses a regular, well-developed system of large intercellular air spaces (Fig. 1.7) that facilitates internal diffusion of gases. In leaves, stems and roots of some water plants (e.g. *Hydrocharis*), aerenchyma is associated with a system of transverse septa or diaphragms that provide mechanical resistance to compression. These septa are uniseriate layers of parenchyma cells that are thicker-walled than neighbouring aerenchyma cells.

1.6.3 Collenchyma

Collenchyma consists of groups of axially elongated, tightly-packed cells with unevenly thickened walls. This tissue has a strengthening function and often occurs in the angles of young stems, or in the midribs of leaves, normally in primary ground tissue. Collenchyma cells differ from fibres in that they often retain