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A leaf cell consists of several metabolic compartments

In higher plants photosynthesis occurs mainly in the **mesophyll,** the chloroplast-rich tissue of leaves. Figure 1.1 shows an electron micrograph of a mesophyll cell and Figure 1.2 shows a schematic presentation of the cell structure. The cellular contents are surrounded by a **plasma membrane**

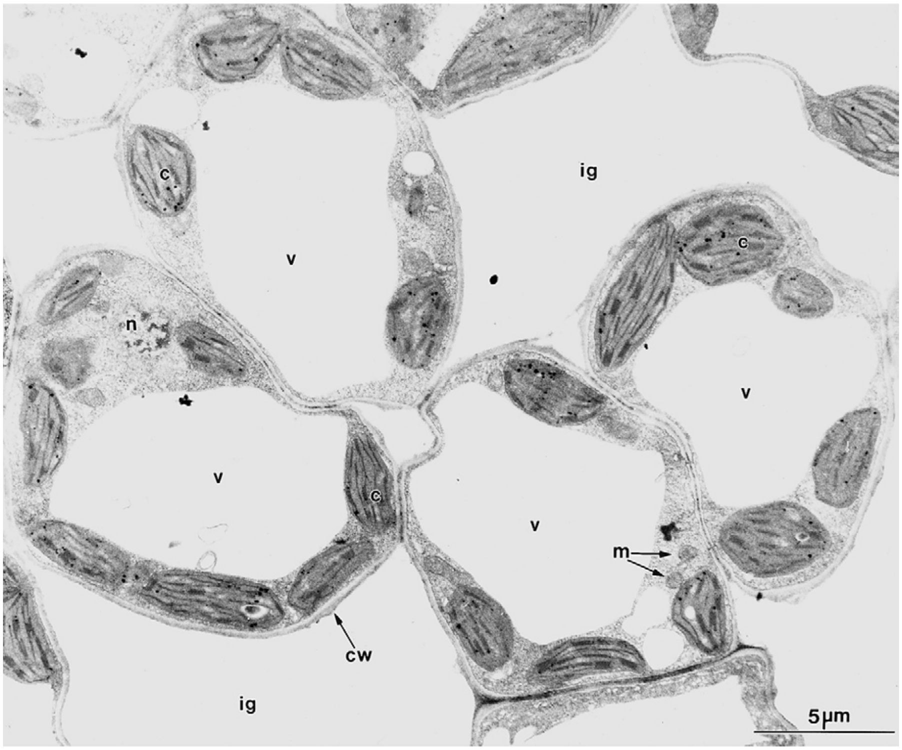

Figure 1.1 Electron micrograph of mesophyll tissue from tobacco. In most cells the large central vacuole is to be seen (v). Between the cells are the intercellular gas spaces (ig), which are somewhat enlarged by the fixation process. c: chloroplast; cw: cell wall; n: nucleus; m: mitochondrion. (By D. G. Robinson, Heidelberg.)

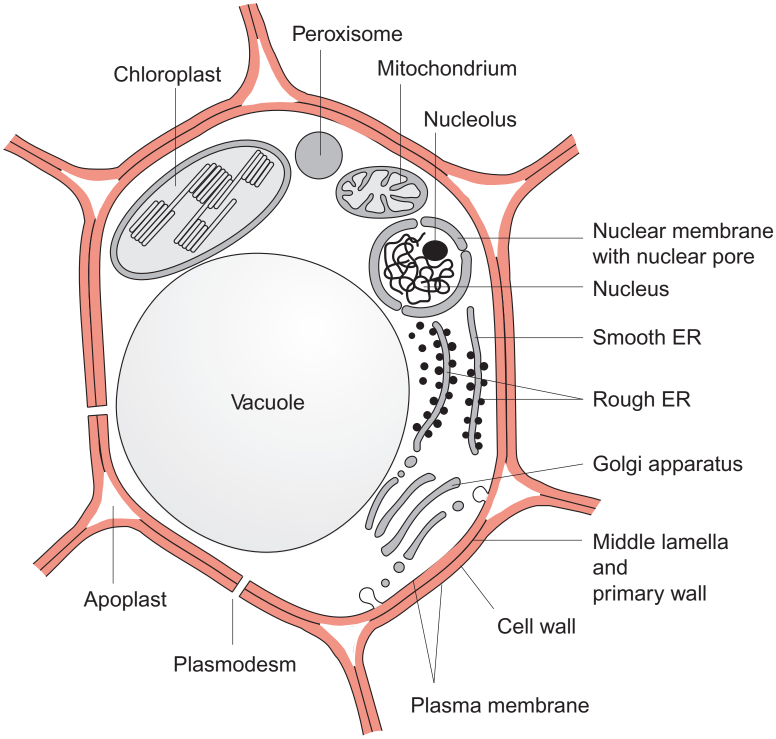

Figure 1.2 Schematic presentation of a mesophyll cell. The black lines between the red cell walls represent the regions where adjacent cell walls are glued together by pectins.

called the plasmalemma and are enclosed by a **cell wall**. The cell contains organelles, each with its own characteristic shape, which divide the cell into various compartments (subcellular compartments). Each compartment has specialized metabolic functions, which will be discussed in detail in the following chapters (Table 1.1). The largest organelle, the vacuole, usually fills about 80% of the total cell volume. Chloroplasts represent the next largest compartment, and the rest of the cell volume is filled with mitochondria, peroxisomes, the nucleus, the endoplasmic reticulum, the Golgi bodies, and, outside these organelles, the cell plasma, called **cytosol**. In addition, there are oil bodies derived from the endoplasmic reticulum. These oil bodies, which occur in seeds and some other tissues (e.g., root nodules), are storage organelles for triglycerides (see Chapter 15).

The **nucleus** is surrounded by the **nuclear envelope**, which consists of the two membranes of the endoplasmic reticulum. The space between the two membranes is known as the **perinuclear space**. The nuclear envelope is interrupted by **nuclear pores** with a diameter of about 50 nm. The nucleus contains **chromatin**, consisting of DNA double strands that are stabilized

Table 1.1: Subcellular compartments in a mesophyll cell* and some of their functions

	Percent of the total cell volume	Functions (incomplete)
Vacuole	79	Maintenance of cell turgor.
		Store of, e.g., nitrate, glucose and storage proteins, intermediary store for secretory proteins, reaction site of lytic enzymes and waste depository
Chloroplasts	16	Photosynthesis, synthesis of starch and lipids
Cytosol	3	General metabolic compartment, synthesis of sucrose
Mitochondria	0.5	Cell respiration
Nucleus	0.3	Contains the genome of the cell. Reaction site of replication and transcription
Peroxisomes		Reaction site for processes in which toxic intermediates, such as H_2O_2 and glyoxylate, are formed and eliminated
Endoplasmic reticulum		Storage of Ca^{++} ions, participation in the export of proteins from the cell and in the transport of newly synthesized proteins into the vacuole and their secretion from the cell
Oil bodies (oleosomes)		Storage of triacylglycerols
Golgi bodies		Processing and sorting of proteins destined for export from the cells or transport into the vacuole

* Mesophyll cells of spinach; data by Winter, Robinson, and Heldt (1994).

by being bound to basic proteins (**histones**). The genes of the nucleus are collectively referred to as the **nuclear genome**. Within the nucleus, usually off-center, lies the nucleolus, where ribosomal subunits are formed. These ribosomal subunits and the messenger RNA formed by transcription of the DNA in the nucleus migrate through the nuclear pores to the ribosomes in the cytosol, the site of protein biosynthesis. The synthesized proteins are distributed between the different cell compartments according to their final destination.

The cell contains in its interior the **cytoskeleton**, which is a three-dimensional network of fiber proteins. Important elements of the cytoskeleton are the **microtubuli** and the **microfilaments**, both macromolecules formed by the aggregation of soluble (globular) proteins. Microtubuli are tubular structures composed of α and β **tubuline** monomers. The microtubuli are connected to a large number of different motor proteins that transport bound organelles along the microtubuli at the expense of ATP. Microfilaments are chains of polymerized **actin** that interact with **myosin** to achieve movement.

Actin and myosin are the main constituents of the animal muscle. The cytoskeleton has many important cellular functions. It is involved in the spatial organization of the organelles within the cell, enables thermal stability, plays an important role in cell division, and has a function in cell-to-cell communication.

1.1 The cell wall gives the plant cell mechanical stability

The difference between plant cells and animal cells is that plant cells have a cell wall. This wall limits the volume of the plant cell. The water taken up into the cell by osmosis presses the plasma membrane against the inside of the cell wall, thus giving the cell mechanical stability. The cell walls are very complex structures; in *Arabidopsis* about 1,000 genes were found to be involved in its synthesis. Cell walls also protect against infections.

The cell wall consists mainly of carbohydrates and proteins

The cell wall of a higher plant is made up of about 90% carbohydrates and 10% proteins. The main carbohydrate constituent is **cellulose**. Cellulose is an unbranched polymer consisting of D-glucose molecules, which are connected to each other by β-1,4 glycosidic linkages (Fig. 1.3A). Each glucose unit is rotated by 180° from its neighbor, so that very long straight chains can be formed with a chain length of 2,000 to 25,000 glucose residues. About 36 cellulose chains are associated by interchain hydrogen bonds to a crystalline lattice structure known as a **microfibril**. These crystalline regions are impermeable to water. The microfibrils have an unusually high tensile strength, are very resistant to chemical and biological degradations, and are in fact so stable that they are very difficult to hydrolyze. However, many bacteria and fungi have cellulose-hydrolyzing enzymes (cellulases). These bacteria can be found in the digestive tract of some animals (e.g., ruminants), thus enabling them to digest grass and straw. It is interesting to note that cellulose is the most abundant organic substance on earth, representing about half of the total organically bound carbon.

Hemicelluloses are also important constituents of the cell wall. They are defined as those polysaccharides that can be extracted by alkaline solutions. The name is derived from an initial belief, which later turned out to be incorrect, that hemicelluloses are precursors of cellulose. Hemicelluloses consist of a variety of polysaccharides that contain, in addition to D-glucose,

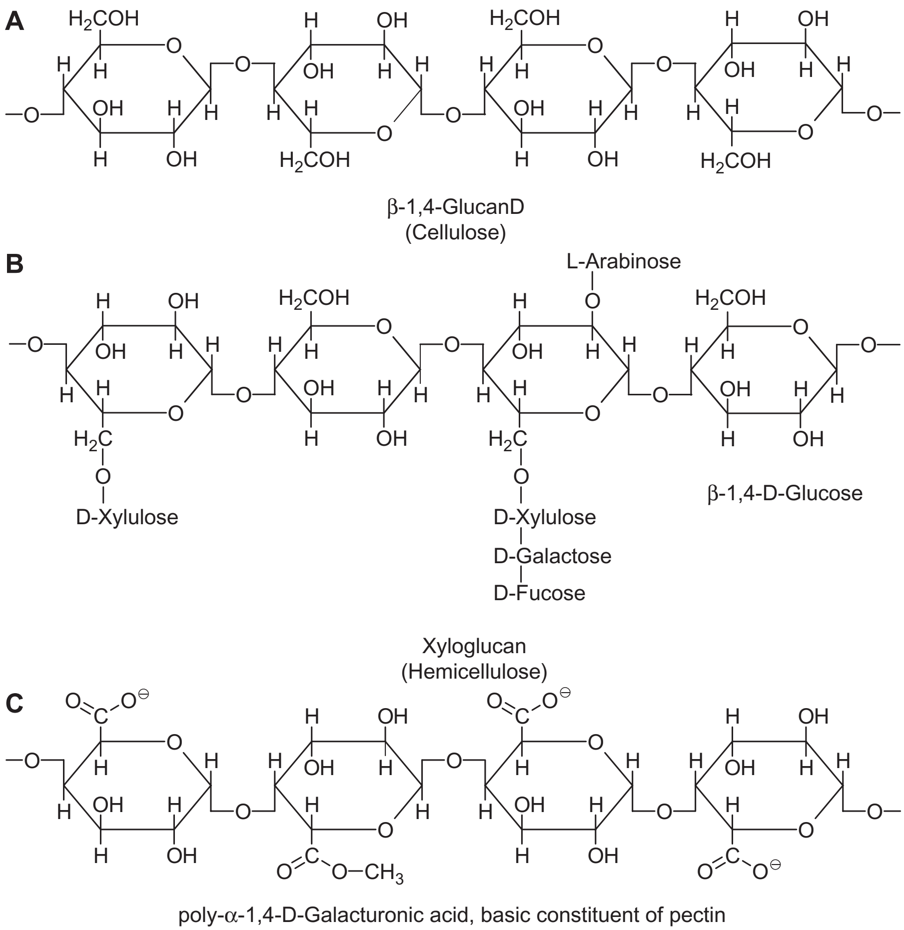

Figure 1.3 Main constituents of the cell wall. A. Cellulose; B. A hemicellulose; C. Constituent of pectin

other carbohydrates such as the hexoses D-mannose, D-galactose, D-fucose, and the pentoses D-xylose and L-arabinose. Figure 1.3B shows xyloglycan as an example of a hemicellulose. The basic structure is a β-1,4-glucan chain to which xylose residues are bound via α-1,6 glycosidic linkages, which in part are linked to D-galactose and D-fucose. In addition to this, L-arabinose residues are linked to the 2′OH group of the glucose.

Another major constituent of the cell wall is **pectin**, a mixture of polymers from sugar acids, such as D-galacturonic acid, which are connected by α-1,4 glycosidic links (Fig. 1.3C). Some of the carboxyl groups are esterified by methyl groups. The free carboxyl groups of adjacent chains are linked by Ca^{++} and Mg^{++} ions (Fig. 1.4). When Mg^{++} and Ca^{++} ions are absent, pectin is a soluble compound. The Ca^{++}/Mg^{++} salt of pectin forms an amorphous, deformable gel that is able to swell. Pectins function like

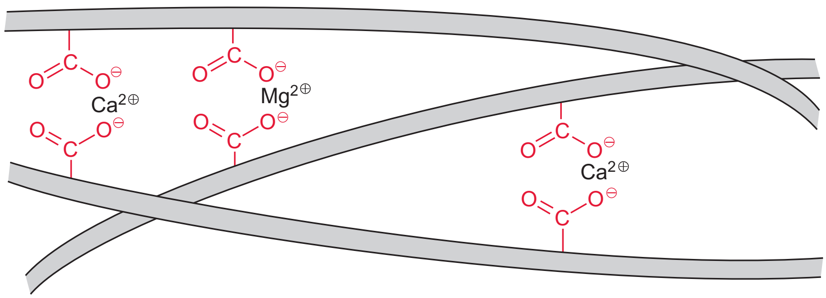

Figure 1.4 Ca^{++} and Mg^{++} ions mediate electrostatic interactions between pectin strands.

glue in sticking neighboring cells together, but these cells can be detached again during plant growth. The food industry makes use of this property of pectin when preparing jellies and jams.

The structural proteins of the cell wall are connected by glycosidic linkages to the branched polysaccharide chains and belong to the class of proteins known as **glycoproteins**. The carbohydrate portion of these glycoproteins varies from 50% to over 90%.

For a plant cell to grow, the very rigid cell wall has to be loosened in a precisely controlled way. This is facilitated by the protein **expansin**, which occurs in growing tissues of all flowering plants. It probably functions by breaking hydrogen bonds between cellulose microfibrils and cross-linking polysaccharides. Cell walls also contain **waxes** (Chapter 15), **cutin**, and **suberin** (Chapter 18).

In a monocot plant, the **primary wall** (i.e., the wall initially formed after the growth of the cell) consists of 20% to 30% cellulose, 25% hemicellulose, 30% pectin, and 5% to 10% glycoprotein. It is permeable for water. Pectin makes the wall elastic and, together with the glycoproteins and the hemicellulose, forms the matrix in which the cellulose microfibrils are embedded. When the cell has reached its final size and shape, another layer, the **secondary wall**, which consists mainly of cellulose, is added to the primary wall. The microfibrils in the secondary wall are arranged in a **layered structure** like plywood (Fig. 1.5).

The incorporation of **lignin** in the secondary wall causes the lignification of plant parts and the corresponding cells die, leaving the dead cells with only a supporting function (e.g., forming the branches and twigs of trees or the stems of herbaceous plants). Lignin is formed by the polymerization of the **phenylpropane derivatives** cumaryl alcohol, coniferyl alcohol, and sinapyl alcohol, resulting in a very solid structure (section 18.3). Dry wood consists of about 30% lignin, 40% cellulose, and 30% hemicellulose. After cellulose, lignin is the most abundant natural compound on earth.

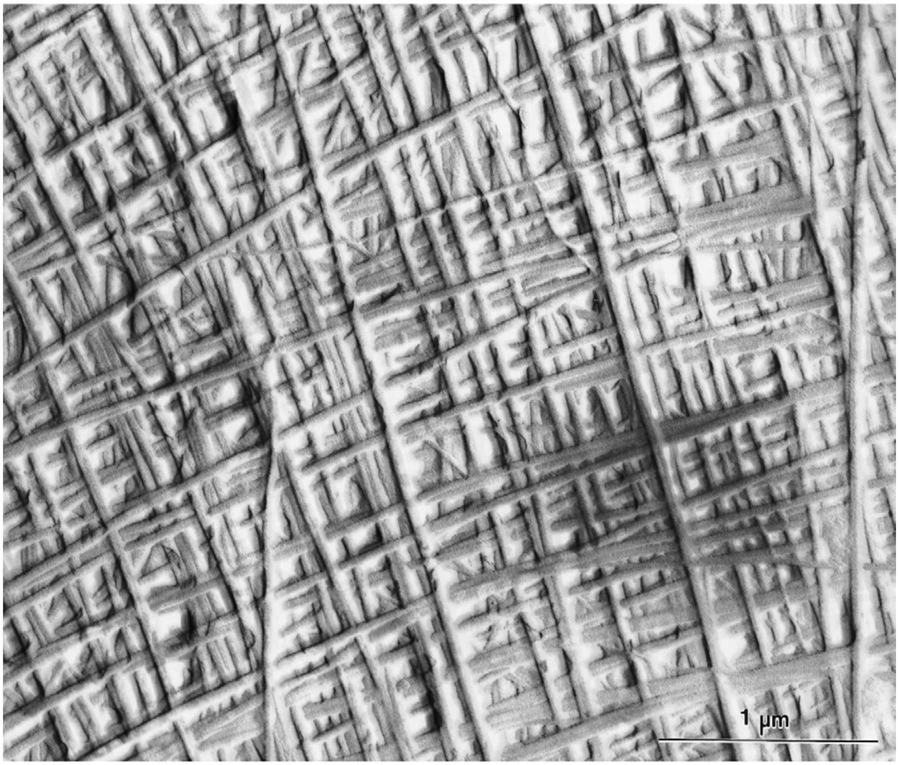

Figure 1.5 Cell wall of the green alga *Oocystis solitaria*. The cellulose microfibrils are arranged in a pattern, in which parallel layers are arranged one above the other. Freeze etching microscopy. (By D. G. Robinson, Heidelberg.)

Plasmodesmata connect neighboring cells

Neighboring cells are normally connected by **plasmodesmata** thrusting through the cell walls. Plant cells often contain 1,000–10,000 plasmodesmata. In its basic structure plasmodesmata allow the passage of molecules up to a molecular mass of 800 to 1,200 Dalton, but, by mechanisms to be discussed in the following, plasmodesmata can be widened to allow the passage of much larger molecules. Plasmodesmata connect many plant cells to form a single large metabolic compartment where the metabolites in the cytosol can move between the various cells by diffusion. This continuous compartment formed by different plant cells (Fig. 1.6) is called the **symplast**. In contrast, the spaces between cells, which are often continuous, are termed the extracellular space or the **apoplast** (Figs. 1.2, 1.6).

Figure 1.7 shows a schematic presentation of a plasmodesm. The tube like opening through the cell wall is lined by the plasma membrane, which is continuous between the neighboring cells. In the interior of this tube there is another tube-like membrane structure, which is part of the endoplasmatic