

STRUCTURE & FUNCTION of PLANTS

JENNIFER W. MacADAM



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Dedication

This book is dedicated to scientists in the fields of plant physiology and plant anatomy who continue to uncover how plants work, particularly my colleagues and mentors who communicate their unflagging enthusiasm for these subjects through their own excellence in teaching and research.

Contents

Preface

This book is written for anyone who is curious about plants and wants to better understand the plants we use in our fields and gardens for food, and the plants we love for the beauty they add to our lives. It addresses not only what plants do, but why, to provide insight for our interactions with the plants we cultivate, struggle with, and depend on in the natural environments that are our heritage and our future.

This book is intended for casual readers who want to know how plants actually work, not just how to care for a particular plant in a particular climate, and for students of plant science seeking an understanding of plant structure and function. It is hoped that both groups will be well-served by a simple but accurate overview of the subjects of plant anatomy and plant physiology.

The early chapters of the book are descriptive of roots, stems, leaves, and flowers, and the cells and tissues from which these structures are built. Such organs have much in common from plant to plant, but observing their differences helps us understand plants' adaptations to the often challenging environments in which they developed. The balance of the book describes how plants work: how they extract water and nutrients from the soil, how they use sunlight to create the carbohydrates that are the first link in the food chain, and how they manage to survive and reproduce literally rooted in one spot.

The emphasis of this book is on inclusive explanations, and concepts are illustrated with examples from agricultural and horticultural plants. When used as a text, this material should be supplemented with a hands-on lab where students can observe the anatomical features and physiological processes introduced here. The book is arranged in 14 chapters, a useful length for a one-semester introductory course in plant anatomy and physiology.

Acknowledgments

I thank the many colleagues who generously allowed me to use their drawings and photographs, and the publishers who facilitated my sharing of research figures from the work of numerous other scientists with readers of this book. Adam Black turned sketches of concepts and mechanisms into the illustrations used in this book, and I thank him for his talent and patience.

Structure and Function of Plants

Chapter 1

The plant cell

We appreciate plants for their beauty and usefulness, and on a different level, for the ability of plant species to adapt to an amazing diversity of climates and soils (two of many abiotic influences) as well as their ability to interact with microbes, animals, and other plants (biotic influences). The differences in characteristics such as stem, leaf, and flower structure that result from these and other adaptations were the original basis for classification of plants into different taxonomic groups. However, for all their differences in overall appearance (morphology), plants have the same basic structures at the cellular level, so we begin by looking at the cellular structures of plants. Figure 1.1 is a simplified illustration of a plant cell, and the structures labeled in Figure 1.1 are discussed in more detail in this and other chapters.

Protoplast

The **protoplast** is a collective term that includes the plasma membrane and the cellular objects it contains. It is filled with liquid, the cytosol, that bathes the cellular organelles including the nucleus. The protoplast includes all the "living" parts of the cell, so the cell wall to its outside is not included. The protoplast is composed of 60–75% proteins by dry weight.

Cytoplasm

The **cytoplasm** is the protoplast minus the nucleus. The nucleus directs the work that goes on in the cytoplasm.

Cytosol

The **cytosol** is the liquid portion (matrix) of the cytoplasm, which surrounds organelles and in which a number of proteins, salts (including nutrient ions),

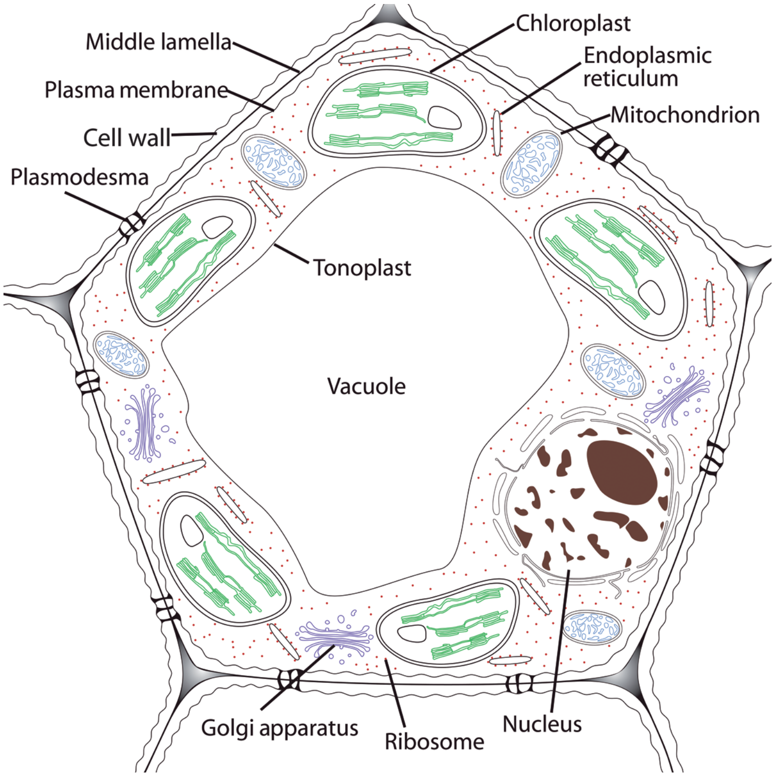

Figure 1.1 Components of a plant cell.

and sugars are dissolved. The cytosol has the thickened consistency of a gel. The cytosol of adjacent cells is continuous, by way of plasmodesmata.

Cell walls

The plant cell protoplast is enclosed by a fibrous wall that grows as the cell expands to its mature size, but which becomes cross-linked and eventually limits the growth of the cell, defining and supporting the cell and collectively providing support for stems and leaves. Some cells, like photosynthetic and storage cells, only have a thin **primary cell wall**, and other cells have both a primary wall and a thick, lignified and therefore rigid **secondary cell wall**, either to retain the cell's shape against the tension of water movement through the plant, as in xylem cells, or to provide concentrated regions of support or protection as in fiber cells or sclerids. The trunk of a tree is made up of concentric layers of water-transporting (xylem) cells with secondary walls that serve both water-carrying and support functions.

Components of the cell wall

Cellulose

The fundamental component of cell walls is **cellulose**, which in turn is made up of long chains of glucose molecules, from thousands to tens of thousands of glucose units per molecule of cellulose. The chemical structure of glucose is illustrated in Figure 1.2, with each of the six carbon atoms (C) numbered. α- and β-Glucose differ in the orientation of the bonds at C-1. Starch and cellulose are both long chains of glucose, but starch is easily digested by monogastrics, like humans, while the bonds between glucose molecules in cellulose are most commonly broken by enzymes produced by microbes inhabiting the guts of ruminants, such as cattle and sheep (and termites). The difference in these chains of glucose is illustrated in Figure 1.3. Bonds in both starch and cellulose are between the 1- and 4-carbons of successive glucose molecules, but while in starch the orientation of each α-glucose molecule in the chain is the same, in cellulose every other β-glucose molecule is flipped on its horizontal axis.

Cellulose is the "fiber" in paper. Cellulose molecules are grouped together into microfibrils consisting of 50–60 cellulose molecules held together by hydrogen bonds, which are relatively loose bonds but effective in large numbers, as in cellulose (Figure 1.4). Cellulose is such a big molecule that it is synthesized at the plasma membrane rather than inside the protoplasm. Microfibrils are extruded into the extracellular matrix, like toothpaste from a

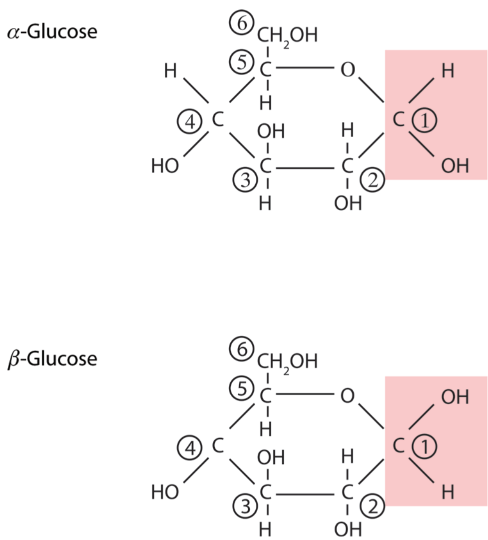

Figure 1.2 The structures of α- and β-glucose, demonstrating the difference in orientation of the –OH at Carbon 1.

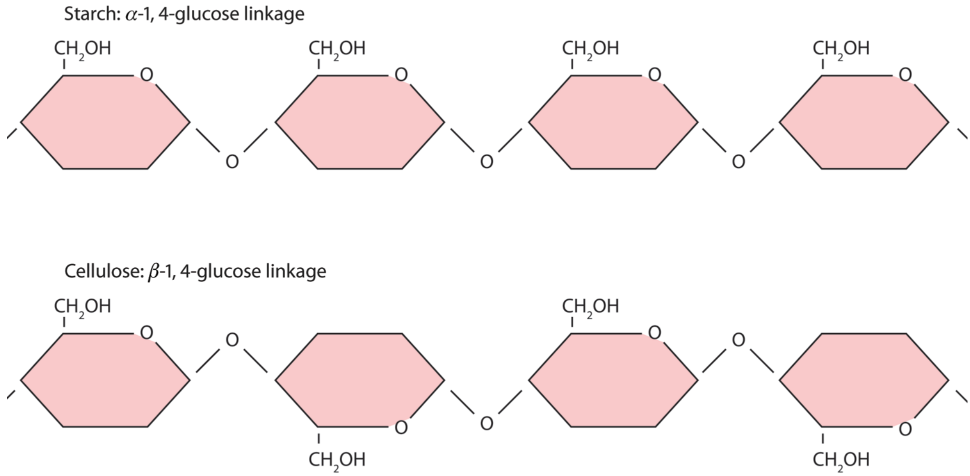

Figure 1.3 The structure of starch and cellulose molecules, demonstrating the difference in bonds between the 1- and 4-carbons of α-glucose molecules in starch and the 1- and 4-carbons of β-glucose molecules in cellulose.

tube (Figure 1.5). Other cell wall components are secreted into the cell wall by way of Golgi vesicles, and assemble around the cellulose microfibrils.

Hemicellulose

Hemicellulose also consists of chains of sugars, but the sugars are much more diverse than in cellulose, which contains only glucose. Hemicelluloses are highly branched because of the bonds that form among the sugars that make them up, and they form a network that coats the much larger cellulose microfibrils. Hemicelluloses adhere to cellulose by way of hydrogen bonds. Hemicellulose molecules coating individual cellulose microfibrils become cross-linked or bound together by covalent bonds, which limits cell wall expansion because the cellulose microfibrils can no longer slide past each other and allow the cell wall to grow. In Figure 1.6, the components of the cell wall are illustrated to show hemicelluloses forming cross-linkages between cellulose microfibrils.

Pectin

The **middle lamella** is the outermost layer of a plant cell and has a high concentration of pectins, which consist of uronic acids, the acidic (and therefore charged) forms of glucose and galactose, and other sugars. The middle lamella is the first boundary formed between what will become adjacent

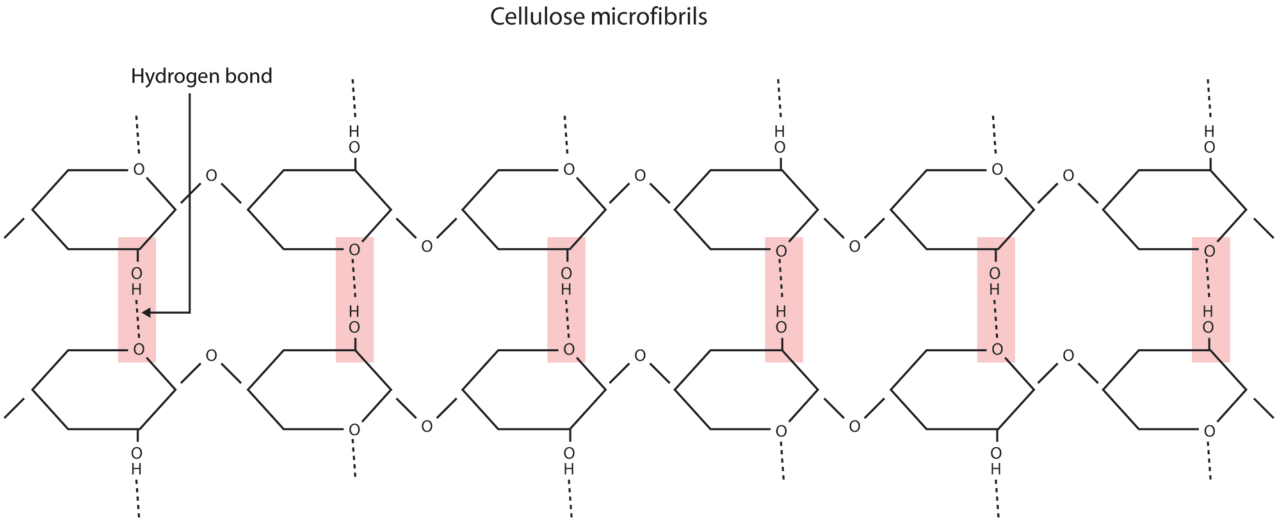

Figure 1.4 Hydrogen bonds between cellulose molecules that result in cellulose microfibrils.

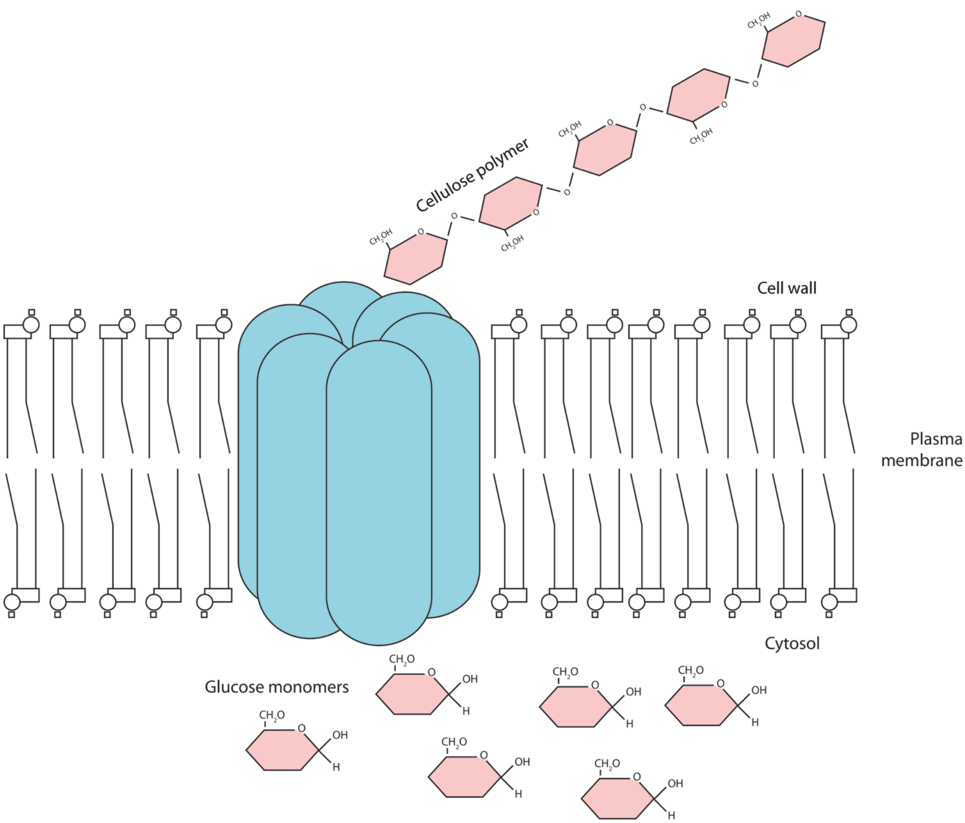

Figure 1.5 Cellulose is formed from glucose by a protein complex, cellulose synthase, at the plasma membrane.

cells during cell division. In cell division, the genetic material of the cell is duplicated and the two groups of chromosomes move to opposite ends of the cell. In Figure 1.7, the middle lamella (yellow) is beginning to form as the boundary between the two new cells. The phragmoplast, a remnant of the organizing structure needed to divide the genetic material, which is shown as groups of white cylinders, is oriented between the daughter nuclei and the developing middle lamella.

After cell division, the primary cell wall forms to the *inside* of the middle lamella, and also has a relatively high content of pectin (up to 35%). The secondary cell wall, when present, then forms to the *inside* of the primary cell wall. The components of both walls are formed in the protoplast and secreted via the Golgi apparatus across the plasma membrane.

Extensin

A structural protein (in contrast to enzymes, which are soluble in the cytoplasm or the matrices of the cellular organelles), extensin, forms a network

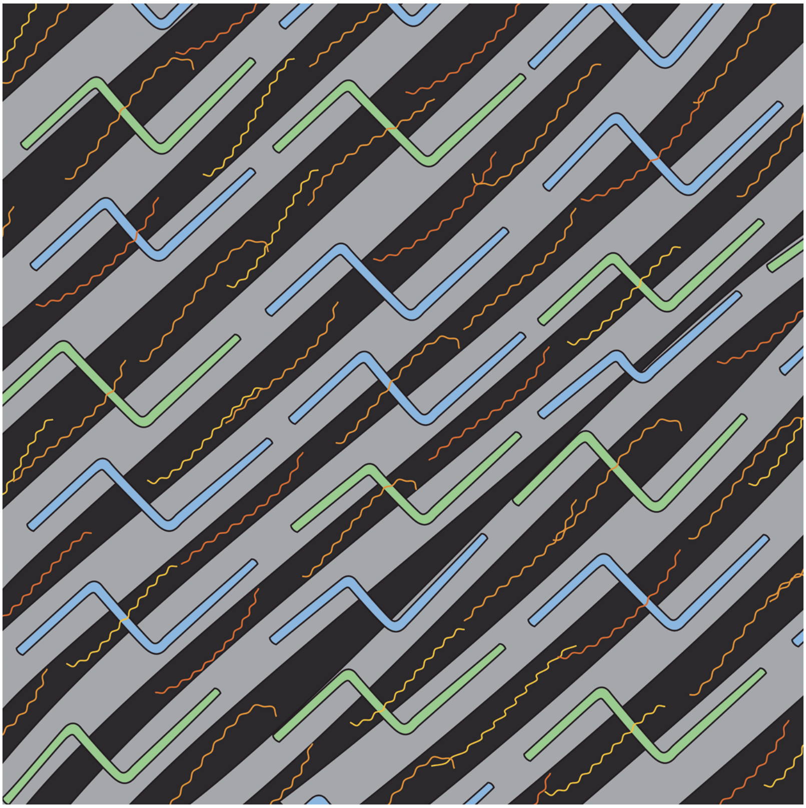

Figure 1.6 Components of the primary cell wall include cellulose microfibrils (gray), hemicelluloses (blue and green), and pectins (orange). In cells such as fibers with secondary cell walls, the space between cellulose and other molecules (black) becomes filled with lignin in both the primary and secondary walls.

within the cell wall that can become cross-linked, like the hemicellulose network. Extensins make up, at most, about 10% of the cell wall, and were first identified in broadleaf plants (dicots), but proteins with similar functions are found in the grasses (monocots).

Secondary cell walls

In structural cells like fibers and in the water-carrying xylem cells, additional cell wall layers are laid down inside the primary cell wall after cell growth stops. These secondary cell walls have a higher cellulose content than primary walls, and may be distinctly layered. In Figure 1.8, which is an electron micrograph of fiber cells, the middle lamella (ML), primary cell wall (CW_1), and distinct layers of the secondary cell wall (S_1, S_2, and S_3) can be seen. The walls of these cells also become lignified, a process in which small **lignin** precursor molecules are secreted into the cell wall and assemble into large,

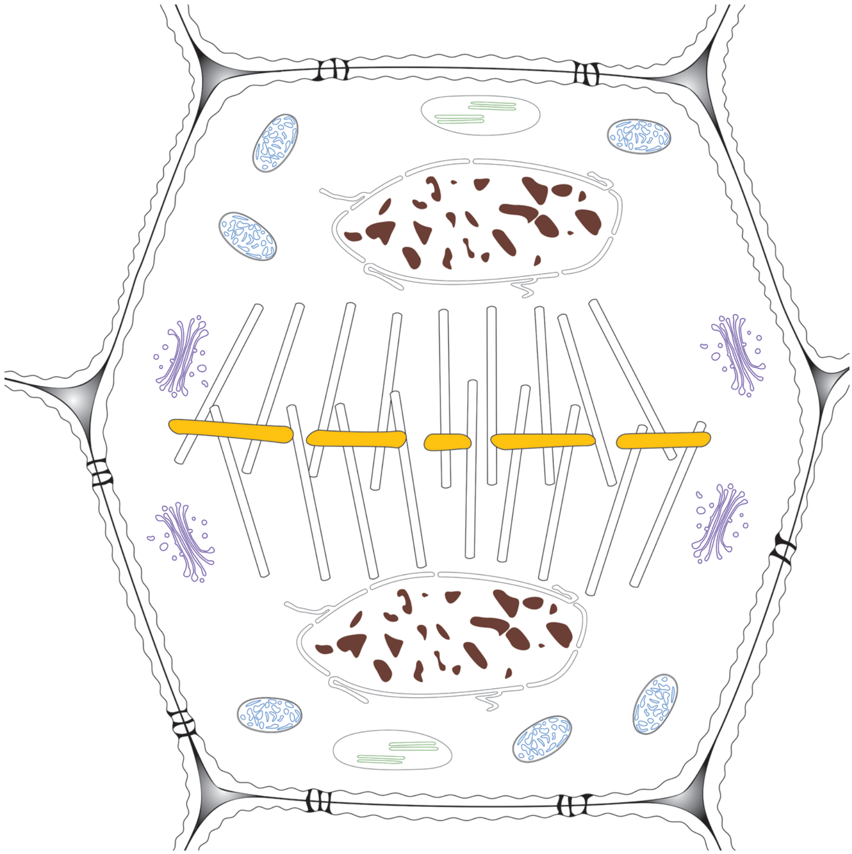

Figure 1.7 Cell division following the duplication of genetic material begins with the formation of a cell plate that develops into the new middle lamella, plasma membranes, and cell walls.

unorganized molecules that displace water (see Chapter 14). The function of lignin is to waterproof xylem vessels and to make cell walls resistant to degradation by invading pathogens. Lignin also greatly increases the rigidity of the cell wall, and is therefore an important component of wood. However, lignin must be extracted for the production of paper, and greatly reduces the digestibility of the fiber cells in plants such as the grasses used as animal feed. Xylem cells, which are the water-carrying cells in roots and shoots, and fiber cells do not contain a protoplasm at maturity and therefore are nonliving cells.

Plasma membrane/cytoplasmic membrane/plasmalemma

The **plasma membrane, cytoplasmic membrane,** and **plasmalemma** are all accepted names for the selectively permeable membrane that encloses the

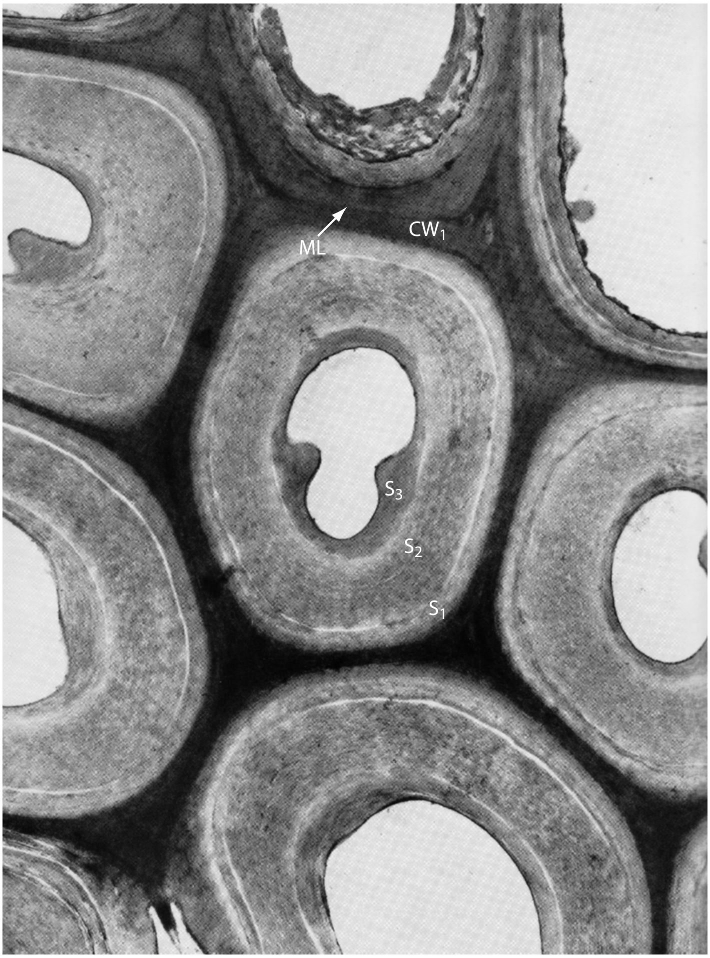

Figure 1.8 Transmission electron micrograph of fiber cells from the stem of Canada yew (*Taxus canadensis*). Fibers provide structure and protection in leaves, stems, and roots. These cells develop secondary wall layers (S_1, S_2, S_3) inside the primary cell wall (CW_1). The middle lamella (ML) can be seen as a dark line between cells (plate 6.1, p. 98, Ledbetter and Porter 1970, used with kind permission of Springer Science and Business Media).

living contents of the cell and controls the movement of materials into and out of the cell.

Membranes

Plant cell membranes are primarily made of lipids (fats and oils) and proteins. Membranes are usually described as consisting of a **lipid bilayer** because of the way the lipid molecules are arranged, but many proteins are embedded

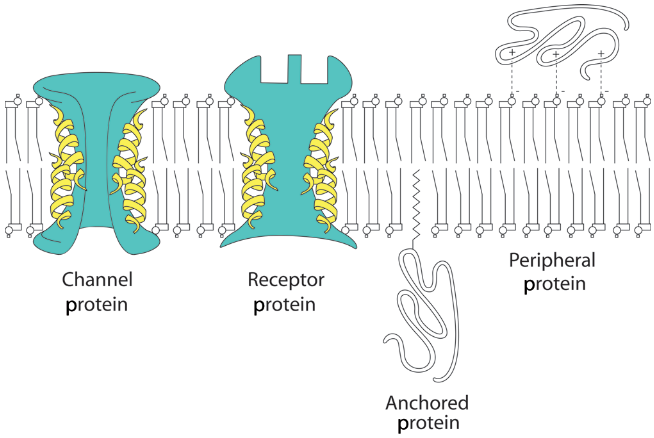

Figure 1.9 The lipid bilayer of the plasma membrane self-assembles from phospholipids, which have hydrophilic, glycerol-containing "heads" oriented outward, and hydrophobic fatty acid "tails" oriented inward. Membrane proteins may extend through the lipid bilayer to act as channels or receptors (green), or they may be bonded to or embedded in the inner or outer surface.

in this bilayer (Figure 1.9). In many cases, these proteins act as gateways for regulation of the contents of the cell.

Membrane lipids

The dominant lipids in the plasma membrane are **phospholipids**, which have a central glycerol molecule with a phosphate molecule attached at one end (the "head") which is water-loving (hydrophilic) and a water-fearing (hydrophobic) "tail" composed of two fatty acids (making these phospholipids diglycerides). The fatty acids are partly unsaturated, making the lipid bilayer fluid, like oils (see Chapter 9).

Phospholipids spontaneously self-assemble into a bilayer in aqueous solutions like a plant cell. They turn their hydrophilic heads outward, some toward the cell wall that encloses the plasma membrane, and some toward the aqueous cell protoplasm, and turn their hydrophobic tails inward to form a double layer. Membranes are fluid—the molecules they contain can easily move past each other in the membrane—but they are also very stable. Membranes can exclude most charged molecules, like nutrient ions, which allows them to control movement of these nutrients into and out of the cell. Water and the gases oxygen and carbon dioxide, however, can cross the lipid bilayer relatively easily.

Other membranes, especially the internal membranes of the chloroplast, contain a large amount of glycolipids, where the head group contains one or two molecules of the sugar galactose instead of a phosphate, and sulfolipids, with a sulfate instead of a phosphate as part of the head group. In these cases, as for phospholipids, the heads are hydrophilic.

Membrane proteins

Proteins make up as much as 50% of the mass of cell membranes. The amino acid composition of proteins determines how the protein is incorporated into the lipid bilayer. If the protein spans the membrane from inside to out, it is an integral protein. If it is bound only to the inside or outside of the bilayer, then it is a peripheral protein. Proteins must have a region that is hydrophobic to be incorporated into the membrane. These membrane proteins can function in the selective transport of solutes across the membrane if they fully span the lipid bilayer (Figure 1.9), or they can act as enzymes like cellulose synthase, or they may form part of an electron transport chain, which are groupings of many different enzymes that are used in photosynthesis and respiration.

Plasmodesmata

The **plasmodesmata** are narrow channels between cells through which dissolved substances but not organelles can pass. Plasmodesmata form during cell division, and allow cell-to-cell communication and transport. One is termed a plasmodesma (Figure 1.10). Plasmodesmata are lined with extensions of the plasma membrane and have an inner structure, the desmotubule, which is continuous with endoplasmic reticulum of the two adjacent cells. Dissolved substances can pass between the plasma membrane and the desmotubule to move between cells. The cytoplasm of adjacent cells connected by plasmodesmata forms a continuous living network among cells called the **symplast**.

In contrast, the **apoplast** is the nonliving space outside the protoplast and includes the cell wall, the intercellular space, and xylem tissue through which water is transported. The larger spaces between cells in leaves and stems is usually filled with air, although cells are coated with a film of water; in roots, these spaces between cells can contain water being taken up by the plant.

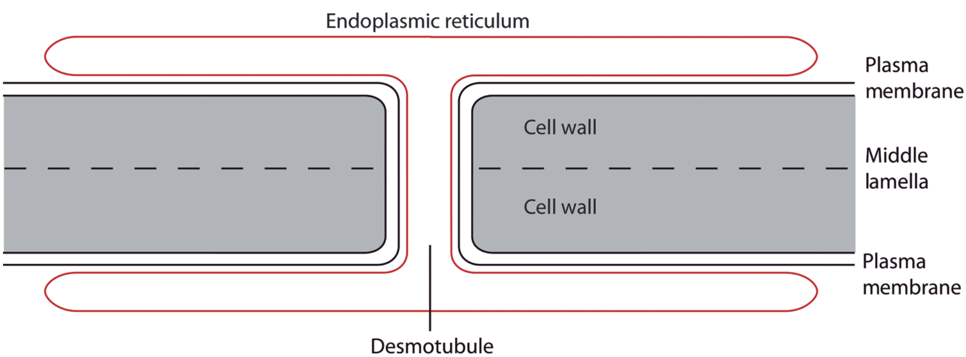

Figure 1.10 Plasmodesmata provide channels between adjacent cells through which dissolved substances can pass.

Cellular organelles

Organelles are membrane-defined compartments inside the cell, each with specific functions. The following are major plant cellular organelles.

Nucleus

The **nucleus** is the location of the genetic material (DNA, deoxyribonucleic acid) contained in almost all cells; the sieve tubes of the phloem are one exception. The nucleus directs the synthesis of the majority of enzyme production and is therefore considered the control center of the cell, since enzymes perform the work (or metabolism) of cells. DNA is organized into chromosomes in plants, and genes are discrete regions of DNA within chromosomes. DNA is the template used to synthesize RNA (ribonucleic acid), which is termed "transcription." RNA is exported from the nucleus to the cytoplasm, where it directs the synthesis of proteins, which is termed "translation." These processes are discussed further in Chapter 9.

Vacuole

Defined by a membrane called the **tonoplast**, the **vacuole** is filled with water, and may comprise 80 or 90% of the volume of a mature plant cell. The vacuole enlarges during growth, and this enlargement occurs by water uptake. The vacuole contains dissolved salts, sugars, organic acids, enzymes, and may contain pigments. Vacuolar transport processes are illustrated in Figure 1.11. The energy of a phosphate bond from ATP (see Chapter 11) is used to pump hydrogen ions (H^+ or protons) into the vacuole; the higher concentration of H^+ in the vacuole reduces the pH of the vacuole compared to the cytosol (for a discussion of pH, see Chapter 7). These H^+ can be exchanged for other positively charged ions such as calcium (Ca^{2+}) and balanced by the

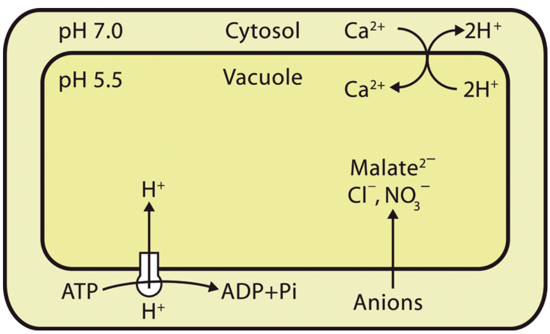

Figure 1.11 The vacuole functions as storage for nutrients, salts, and organic acids, and is active in other transport processes of the cell.

uptake of negatively charged ions such as chloride (Cl^-), nitrate (NO_3^-), or the organic acid malate.

Endoplasmic reticulum

The **endoplasmic reticulum** (**ER**) is a tubular network that is formed from and continuous with the nuclear envelope, and which fills much of the volume of the cytosol. In Figure 1.1, slices through the ER are indicated as ovals covered with red dots that represent ribosomes. Ribosomes may also occur free in the cytosol. The function of the ER is the synthesis of lipids and proteins that are either used to make cellular membranes or exported from the cell. The space enclosed by the membrane layers is called the **lumen** of the ER. The smooth ER, without ribosomes, is involved in lipid synthesis. The rough ER, with **ribosomes**, is the site of protein synthesis. Proteins that will leave the cell are made on the rough ER and passed into the lumen of the ER after synthesis. In the ER lumen, they are altered by posttranslational modifications such as the addition of sugars to form glycoproteins, which help determine the specific function and location of the protein. The modified proteins move through the lumen to the smooth ER and small, enclosed pieces of the smooth ER bud off to form transport vesicles, with the proteins inside. The transport vesicles move to the Golgi apparatus.

Golgi apparatus (formerly dictyosomes)

A **Golgi apparatus** consists of a stack of separate flattened sacs (cisternae) where products of the ER are processed further. Transport vesicles from the ER deliver their contents by fusing with a membrane of the Golgi apparatus. After processing, products of the Golgi are packaged in secretory vesicles that bud off for transport within the cell, or fuse with the plasma membrane to secrete their contents outside the cell (Figure 1.12). Some of the carbohydrates that make up the cell wall are also formed in the Golgi.

Mitochondria

Mitochondria are the site of respiration (Chapter 11), which releases the chemical energy stored in food (most commonly carbohydrates and fats) and transfers this energy to form ATP (adenosine triphosphate), a chemical compound that can be transported to other locations in the cell. The outer membrane of a mitochondrion is readily permeable, and the inner membrane, which has many invaginations called cristae, is very high in protein (70%), and is much more selective. Inside the inner membrane is a matrix that has a high concentration (40–50%) of dissolved protein (enzymes) where key steps in respiration occur (Figure 1.13).

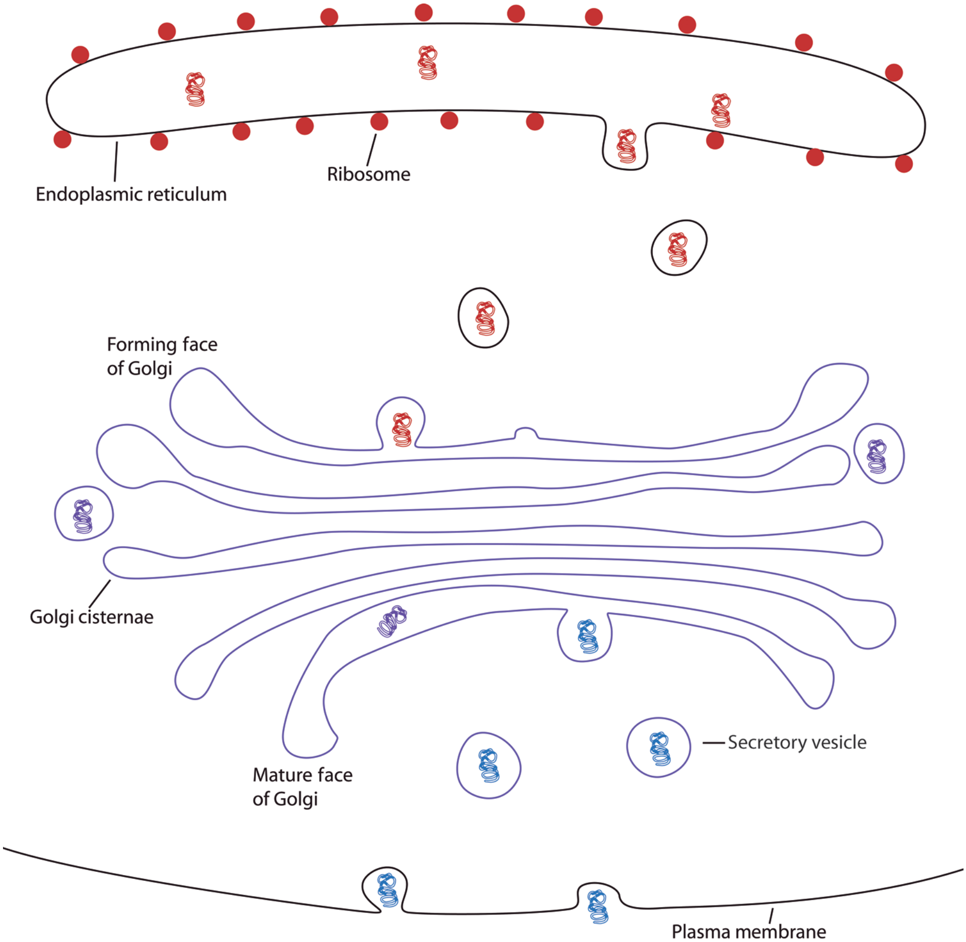

Figure 1.12 The Golgi apparatus functions in the processing and export from the cell of glycoproteins (proteins with sugars attached) synthesized in the endoplasmic reticulum (ER), and in the synthesis and export of some cell wall carbohydrates (hemicelluloses and pectins).

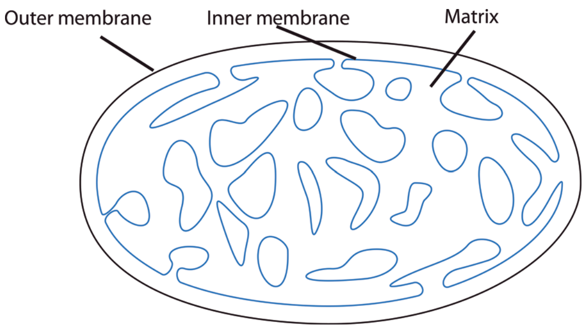

Figure 1.13 Mitochondria are the cellular organelles in which most steps of respiration occur.