Plant Cell Structure and Ultrastructure

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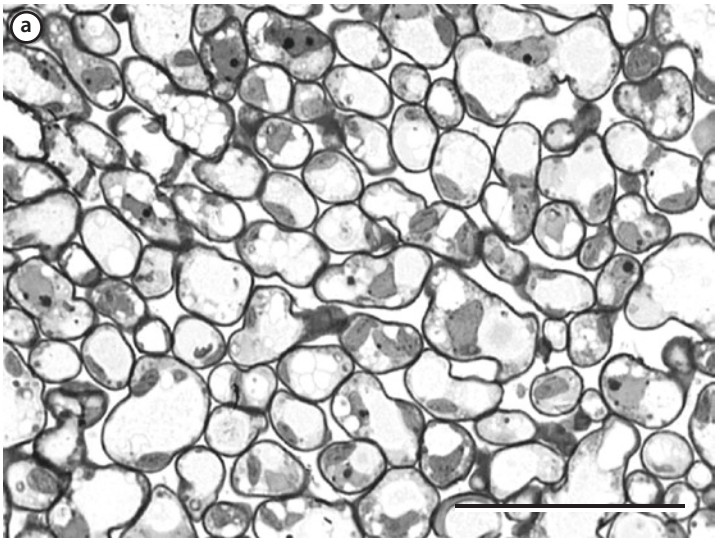
Introduction

Plants typically contain millions of cells and a wide variety of cell types (cells are discussed in ► Chap. 6: Parenchyma, Collenchyma, and Sclerenchyma). Plant cells are composed of cell walls (► Chap. 5), a cytoplasm, and vacuoles, which are primarily water sacs that contain storage and waste products of metabolism and which provide turgor pressure for the cell. While the vacuole physically takes up the most space in the cell, the cell contains many **organelles** within the protoplasm that are pushed up against the cell wall. Protoplasmic organization includes nuclear structure and the cytoplasmic contents of the cell. The most basic to the organization of cells are membranes which represent the limiting boundary of the living components, being organized into various unique functional bodies called organelles. Such organelles are usually thought of as membrane-bound bodies that have a specific function and identifiable structural organization. The exceptions are certain elements of the cytoskeleton, which are considered to be organelles but are not limited by a membrane.

3.1 Plant Cells Are Complex Structures

With the development of the transmission electron microscope in the mid-twentieth century, plant biologists were able to visualize for the first time the organization of cells at a level much finer than that seen with the light microscope (◘ Fig. 3.1a, b). Hence, the terms *ultrastructure* and *fine structure* came about in reference to



◘ **Fig. 3.1** **a** Light microscopy (LM) showing a **paradermal** section (i.e., cut parallel with the surface) of a leaf from the lyre-leaved sand cress (*Arabidopsis lyrata*). Scale bar = 50 μm (RR Wise)

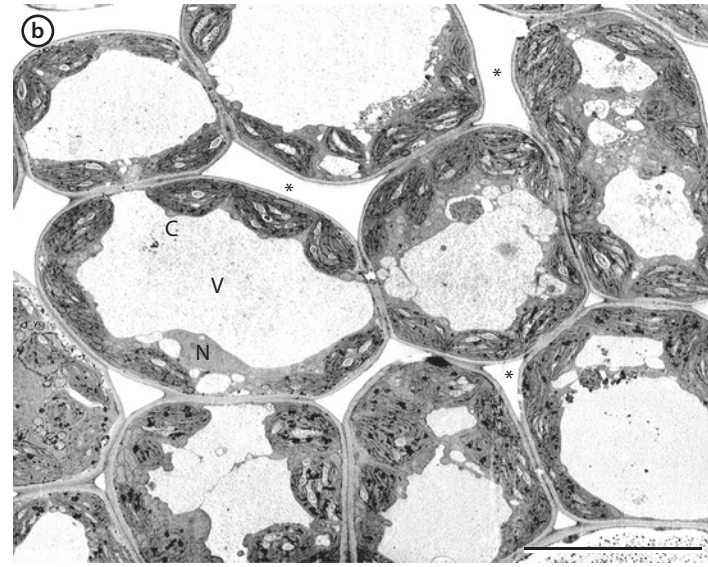


Fig. 3.1 **b** TEM of several leaf cells from *Arabidopsis thaliana*. Each cell contains a large central vacuole (V), nucleus (N), and numerous chloroplasts (C). Note the intercellular air spaces (*). Other organelles are too small to be seen at this magnification. Scale bar = 10 μm (RR Wise)

the detailed cellular structure shown with the electron microscope. The information learned from the use of the electron microscope in plant anatomy has revealed that cells are primarily composed of membrane-bound organelles associated with specific functions. Here, we consider the major structural entities and their functions. In recent years, a variety of techniques have been developed which enable investigators to identify elemental composition, localize functional (usually enzyme) activities, and quantify cellular structure. These techniques extend our observations beyond merely descriptive ones.

3.2 Plant Cells Synthesize an External Wall and Contain a Variety of Internal Compartments

Plant cells vary greatly in the numbers and types of organelles they contain. That is why textbooks usually show a drawing and not a micrograph of a "typical plant cell"—there is no such thing in real life. Figure 3.2 is, therefore, a "convenient fiction" showing all the organelles neatly arranged in a prototypical plant parenchyma cell. The four basic components are (from the outside in) cell wall (a primary wall in this case), plasma membrane, cytoplasm (which contains many and varied organelles), and vacuole.

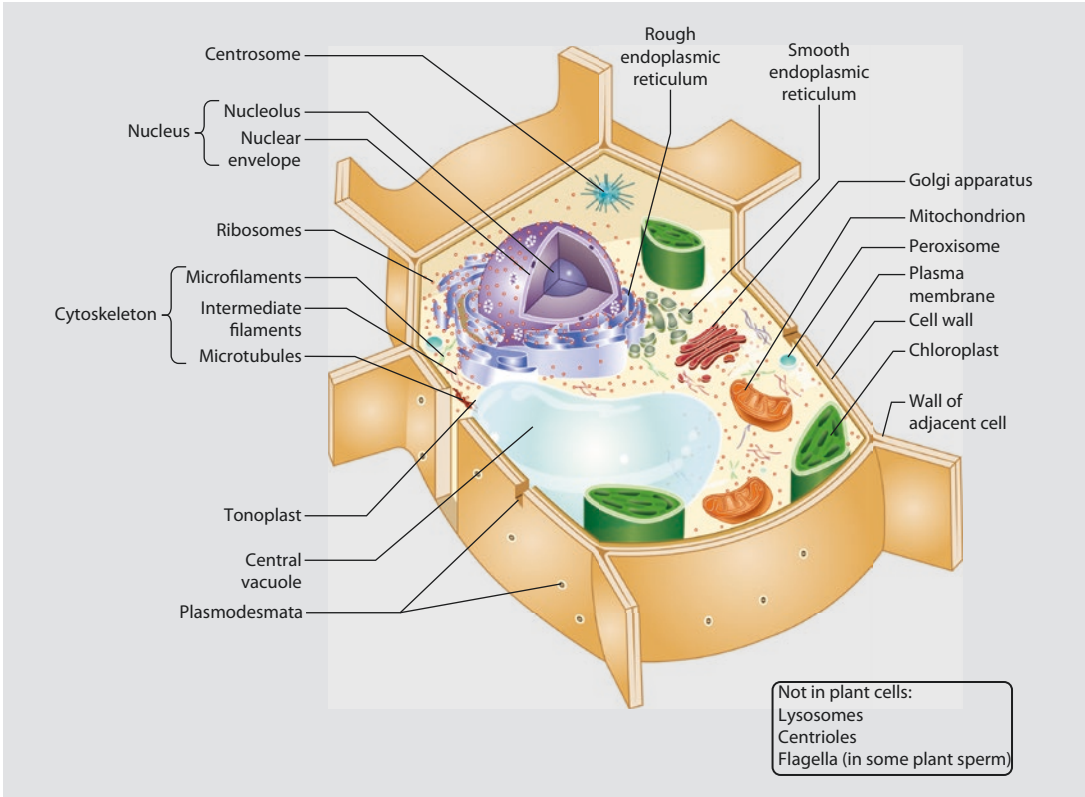


Fig. 3.2 Basic components of a plant cell. The individual organelles are discussed throughout this chapter (Redrawn from Wikipedia)

3.3 Cells and Cell Organelles Are Typically Bound by Lipid Bilayer Membranes

The biological **membrane** is a ubiquitous and remarkable boundary of all living cells and most cell organelles. All membranes share a common structure and function (Fig. 3.3a, b), although the individual components and the precise roles played by membranes can vary greatly. The cell membrane (a.k.a. **plasma membrane**) will be discussed in this section. Membranes of organelles such as those in the chloroplast, nucleus, or Golgi apparatus share many of the same basic characteristics.

Observed with very high-resolution transmission electron microscopy, membranes often appear as two tracks or dense lines when observed in a distinct cross-sectional plane (Fig. 3.3a). That phenomenon occurs because of the deposition of osmium and associated stains (all contain heavy metals that do not transmit the electron beam of the microscope). The density appears to take place primarily towards each side of the membrane, leaving a somewhat translucent region in the center where the hydrophobic "tails" of lipids are in contact from the two layers. Some investigators have designated this type of pattern as a "unit membrane" image.

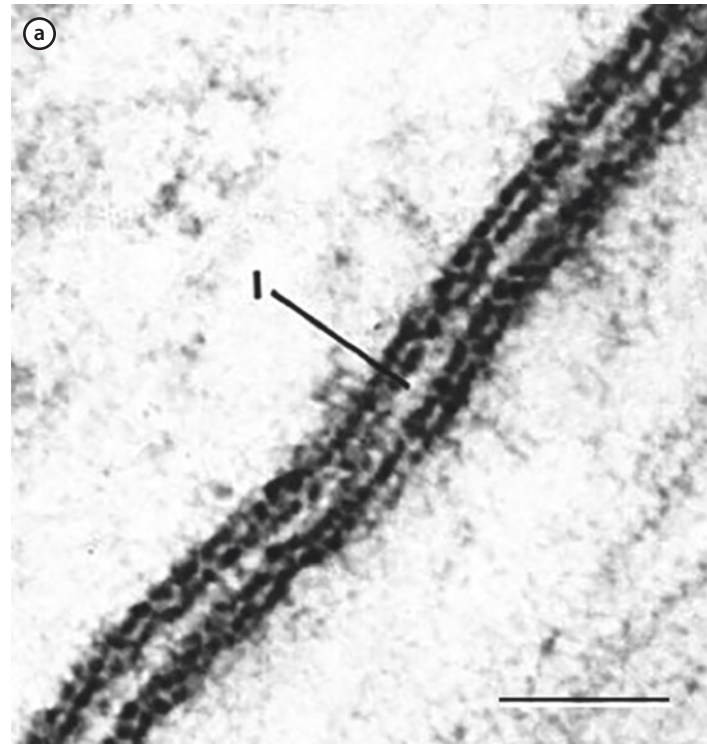


Fig. 3.3 **a** Unit membrane structure of **nuclear envelope** observed with very high-resolution transmission electron microscopy. Two unit membranes are found closely opposed to each other, with an intervening space (I), which is similar to the nuclear envelope or outer double membrane of chloroplasts. The magnification of this micrograph is close to 350,000×, and the thickness of each membrane is approximately 10 nm (i.e., 100 Å). Scale bar = 50 nm. (Image from Macleod (1973) Cytology: The Cell and Its Nucleus, The Upjohn Co, with permission)

Biological membranes are called a "fluid mosaic lipid bilayer." The latter term, "lipid bilayer," obviously means that the membrane is composed of two layers of lipids (Fig. 3.3b). The individual lipid molecules are amphipathic, meaning they have a hydrophilic head group and (usually two) hydrophobic tails. In the bilayer structure, the hydrophilic head groups are oriented towards the outsides of the membrane, exposed to the aqueous milieu on either side of the membrane, while the hydrophobic tails face each other in the membrane's interior. Individual lipid molecules are free to rotate or diffuse sideways within the plane of the membrane, hence the modifier "fluid." Phospholipids are a common membrane lipid, although many other molecular species contribute to the diversity of membrane structure and function across the plant and animal kingdoms. Cholesterol, when present, helps maintain membrane structure and fluidity. Cholesterol is common in animal membranes but relatively scarce in plant membranes. Membranes may also contain other lipids such as chlorophyll, carotenoids, and the lipid-soluble, redox-active quinones of the chloroplast and mitochondrion (plastoquinone and ubiquinone).

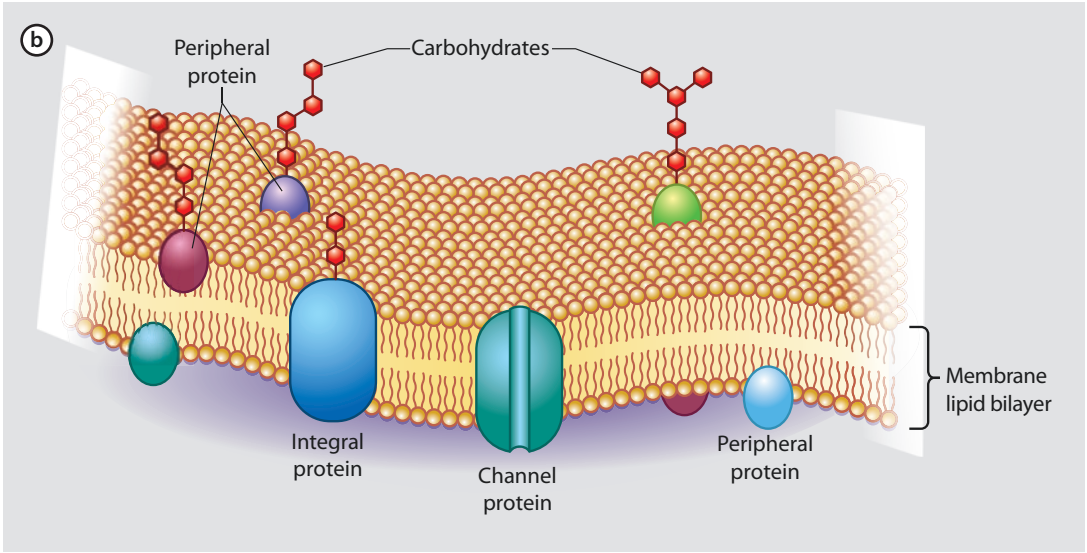


Fig. 3.3 **b** Basic components of a plant cell membrane. The amphipathic lipids face each other creating two hydrophilic surfaces and a hydrophobic interior. Different proteins may be on the surface of, or embedded within, the membrane (Redrawn from Crang and Vassilyev 2003)

The term "mosaic" refers to the fact that membranes are a mixture of lipids and proteins occurring in varying proportions, depending on the role that the membrane plays in the plant cell. Proteins can make up a significant portion of the membrane and play key roles in membrane functions. In fact, the energy-transducing membranes in chloroplasts and mitochondria are approximately 85% protein by weight and only 15% lipid. Proteins may be associated with the surface of the membrane (peripheral proteins) or embedded within and even span the membrane from one side to the other (integral protein). Many membrane proteins are free to diffuse throughout the membrane (like lipids), while others, particularly proteins in the limiting cell membrane, are anchored to cytoskeletal elements lying close to the cytoplasmic (inside) surface of the cell. The cellulose-synthesizing protein complex is actually dragged through the plane of the membrane by the cytoplasmic cytoskeleton during cell wall synthesis (► Chap. 5). Short chains of carbohydrates may be covalently attached to proteins (glycoproteins) or lipids (glycolipids) and facing the outer surface of the plasma lemma. By facing the exterior, the sugars, their number and subunit structure, carry important information for neighboring cells.

Biological membranes are selectively permeable, implying that some substances cross the membrane more easily and rapidly than others. Membranes can fuse one with another, and they also can grow by adding new molecules. They can form bubble-like **vesicles**, which segregate certain products that are moved to different sites in the cytoplasm.

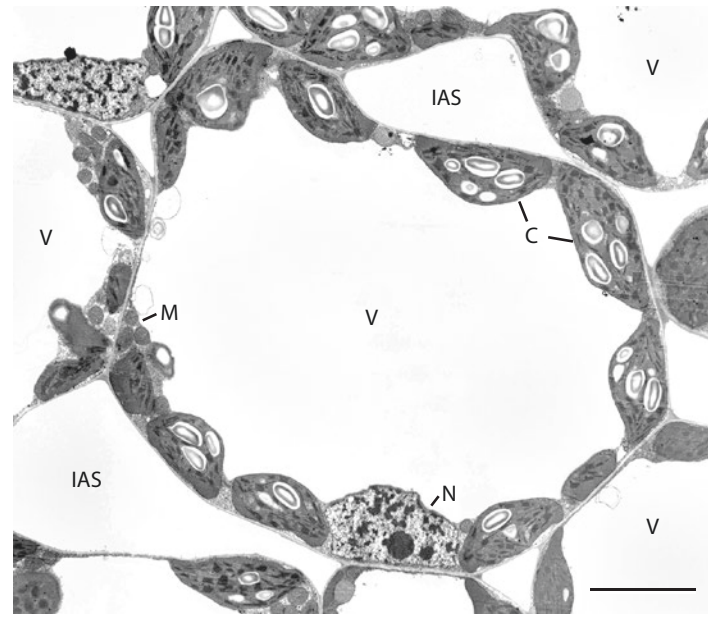
Membranes play many important roles. First, and foremost, they create a boundary between the inside and outside of a cell or organelle, which allows for the compartmentalization of metabolism. Catabolic processes can take place in the mitochondrion,

while anabolism may simultaneously proceed in the chloroplast or endoplasmic reticulum. Second, membranes, specifically the membrane proteins, control the transport of water, ions, and molecules into and out of the cell or organelle. Third, because membranes are basically two-dimensional, the proteins involved in metabolic or electron transport pathways can be arranged side-by-side, thus allowing metabolites or electrons to be passed directly from one protein molecule to the next.

3.4 Vacuoles Play a Role in Water and Ion Balance

A large central **vacuole** as seen in ◘ Fig. 3.4 is a key characteristic of almost every mature plant cell. Once thought of as merely empty space fillers ("vac" is Latin root for "empty"), vacuoles are now seen as fully functional cellular organelles that play crucial roles in cell homeostasis, water balance, metabolite, ion and pigment storage, and detoxification and lysis of unwanted compounds.

The vacuole is bounded by a single membrane called the **tonoplast**, which at 10 nm (0.01 μm) in thickness is too thin to be visible in ◘ Fig. 3.4. The tonoplast contains **transport proteins** that control the movement of water and molecules into and out of the vacuole, which is critical to controlling the movement of water throughout the plant and the maintenance of turgor (refer to ► Sect. 1.2). Water-soluble pigments such as anthocyanins accumulate in vacuoles in epidermal cells and impart the purple, red, and blue colors



◘ **Fig. 3.4** TEM of a **mesophyll** cell from a pea (*Pisum sativum*) leaf with a large central vacuole (V) and a thin rim of cytoplasm. Organelles such as a nucleus (N, with nucleolus), chloroplasts (C), and mitochondria (M) occupy the majority of the cytoplasm volume. Intercellular air spaces (IAS) are situated between the cells. Scale bar = 10 μm (RR Wise)

of many flower petals and leaves, whereas seed vacuoles are adapted for protein storage. Vacuoles are also sometimes used to store the end products of catabolism.

3.5 Plastids Are a Diverse Family of Anabolic Organelles

Chloroplasts are photosynthetic organelles found in plant cells. Indeed, the very definition of what it means to be a plant is largely predicated on their photoautotrophic abilities, which reside exclusively in the chloroplast. However, chloroplasts are only one member of the **plastid** family, a large, closely related and diverse group of organelles (Kirk and Tilney-Bassett 1967). Depending on the breadth of the definition, there are as many as 20 distinctly different types of plastids found in both plants and (in a few surprising cases) animals (Wise 2006, ◘ Table 3.1).

Plastids are sometimes categorized based on their color. In such a scheme, the nonpigmented plastids such as proplastids, etioplasts, amyloplasts, and elaioplasts are called leucoplasts. Red and orange plastids (chromoplasts and gerontoplasts) are grouped together as chromoplasts. Green plastids (C_3, dimorphic C_4, and guard cell) are

◘ **Table 3.1** Summary of plastid forms and functions

Plastid type	Function(s)	Distinctive features
Proplastid	Source of other plastids	Found in egg, meristematic and embryonic cells; source of all other plastids in the plant
Etioplast	Transitionary stage	Develops in dark-grown tissue; site of gibberellin synthesis; converts to chloroplast in light
Amyloplast	Starch synthesis and storage	Also functions in gravisensing
Elaioplast	Oil synthesis and storage	Supplies lipids and oils to exine upon pollen grain maturation
Chromoplast	Fruit and flower coloration	Rich in carotenoids; used to attract pollinators and seed/fruit-dispersing animals
Gerontoplast	Catabolism	Controls the dismantling of the photosynthetic apparatus during senescence
Chloroplasts		
C_3	Photosynthesis, etc.	Also functions in fatty acid, lipid, amino acid and protein synthesis, N and S assimilation
C_4	Photosynthesis, etc.	**Dimorphic chloroplasts** provide a CO_2-rich, O_2-poor environment for enhanced Rubisco activity (enzyme for early carbon fixation)
Sun/shade	Photosynthesis, etc.	Dimorphic forms develop under different light conditions in order to optimize photosynthesis
Guard cell	Stomatal functioning	Senses light and CO_2; signals and metabolically drives opening and closing of stomata

called chloroplasts. Because this system merely focuses on common color, and not distinct structure or function, it is not relied upon in this text.

Substantial evidence exists to support an **endosymbiotic** origin for plastids, with the original endosymbiont being a photosynthetic cyanobacterium. Two processes took place during the ensuing 1.6 billion years of evolution: (1) approximately 90% of the plastid genome was transferred to the nucleus and (2) the proto-chloroplast radiated and evolved into the other plastid types. Thus, all plastids share the same basic characters of a double-membrane envelope; a separate and third internal membrane system of greater (chromoplast, chloroplast) or lesser (proplastid, amyloplast) complexity; a complete prokaryotic-like genetic machinery consisting of organellar DNA, transcription factors, and ribosomes (► Sect. 3.9); and division by fission (again, very prokaryotic-like). Unlike mitochondria, which were also derived endosymbiotically, plastids did not surrender the anabolic abilities of their free-living ancestors. In fact, the power to manufacture all the biomolecules needed for complete growth and development has enabled plants to use plastids as the central organelle for anabolism, catabolism, energy regulation, and environmental sensing. The seven main plastid types found in green plants are described as follows.

3.5.1 Proplastid

Plants begin with an egg cell, and the egg cell is the primary source of organelles for the zygote that eventually leads to an adult plant (► Chap. 18). Egg cell plastids, of which there may be 50–100 per egg, are called "**proplastids**" and are the progenitors of all the other plastids (regardless of type) found in the mature plant. Subsequent mitosis and the generation of new tissues in plants take place in meristems (► Chap. 4), and meristematic plant cells also contain proplastids. Most plants continue to grow throughout their entire life to support shoot and root expansion. Therefore, they may have hundreds to thousands of meristems at any given time and thus a large population of proplastids.

Unlike the other plastid types, proplastids as a group are defined by their appearance and location, and not by any specific metabolic function. Characteristically, they are small, relatively non-differentiated with few internal membranes and only found in young, undifferentiated cells (◘ Fig. 3.5a, b).

3.5.2 Etioplast

Etioplasts develop in complete darkness in shoot tissue and are a transitional stage between the proplastid and the chloroplast during the process of greening (◘ Fig. 3.5c, d). The reverse process—degreening (chloroplast to etioplast)—is also possible as evidenced by the pale color that results under any light barrier laid on a green lawn (board, tarp, garden hose, etc.). In this process, the green grass undergoes chlorosis (the controlled, enzymatic loss

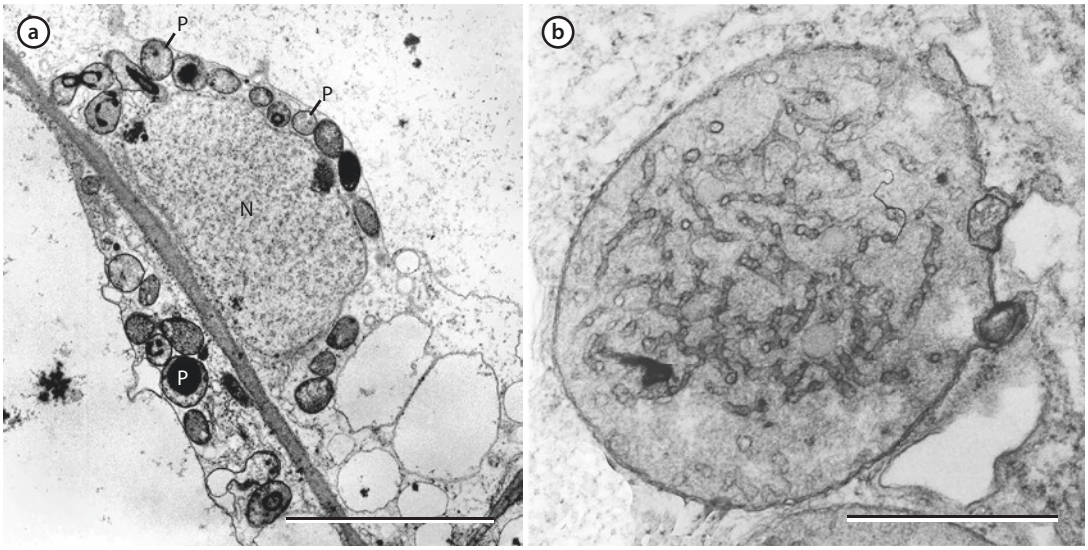


Fig. 3.5 **a** Proplastids (P) surrounding the nucleus (N) in a cell from a mangrove (*Rhizophora mangle*) embryo. Scale bar = 10 µm (RR Wise). **b** A single proplastid from sweet potato (*Ipomea batatas*) root tip. Scale bar = 0.5 µm (**a**, **b** RR Wise)

of chlorophyll) and becomes pale green upon the imposition of darkness. Removing the obstruction allows the greening process to resume. Thus, the etioplast-to-chloroplast-to-etioplast transition is quite dynamic and under strict genetic control in response to environmental conditions.

Etioplast ultrastructure is dominated by the prolamellar body (PLB), a large, ordered lattice of membranes (Fig. 3.5e). While the exact function of the PLB remains obscure, it probably represents a "holding pattern" for the large amount of membrane and protein that will ultimately be utilized in formation of the thylakoid system (see chloroplast below). Interestingly, etioplasts only form in dark-grown cells of the leaves and stems, tissues that under normal conditions will eventually be exposed to light. They never form in roots or tissues that are insensitive to light. The plant growth regulator **gibberellic acid** (GA) is synthesized in the etioplast. Because GA helps direct many early developmental processes, such as those in an expanding and greening leaf, the etioplast probably contributes directly to the light-to-dark transition.

3.5.3 Elaioplast

Lipid synthesis in animal cells is localized to the smooth endoplasmic reticulum (refer to ► Sect. 3.9). However, SER is rarely seen in plant cells because most plant lipids are made in the proplastid, chloroplast, or elaioplast. **Elaioplasts** (Fig. 3.5f) are plastids that specialize in oil synthesis and storage and are found primarily in the layer of cells in the anther that surrounds developing pollen grains (called the tapetum or tapetal layer; refer to ► Chap. 17). After meiosis and just prior to pollen release, the tapetal layer degrades and releases the elaioplasts, which contribute their oils to the exine, the outermost, waterproof pollen wall (Fig. 3.5g).

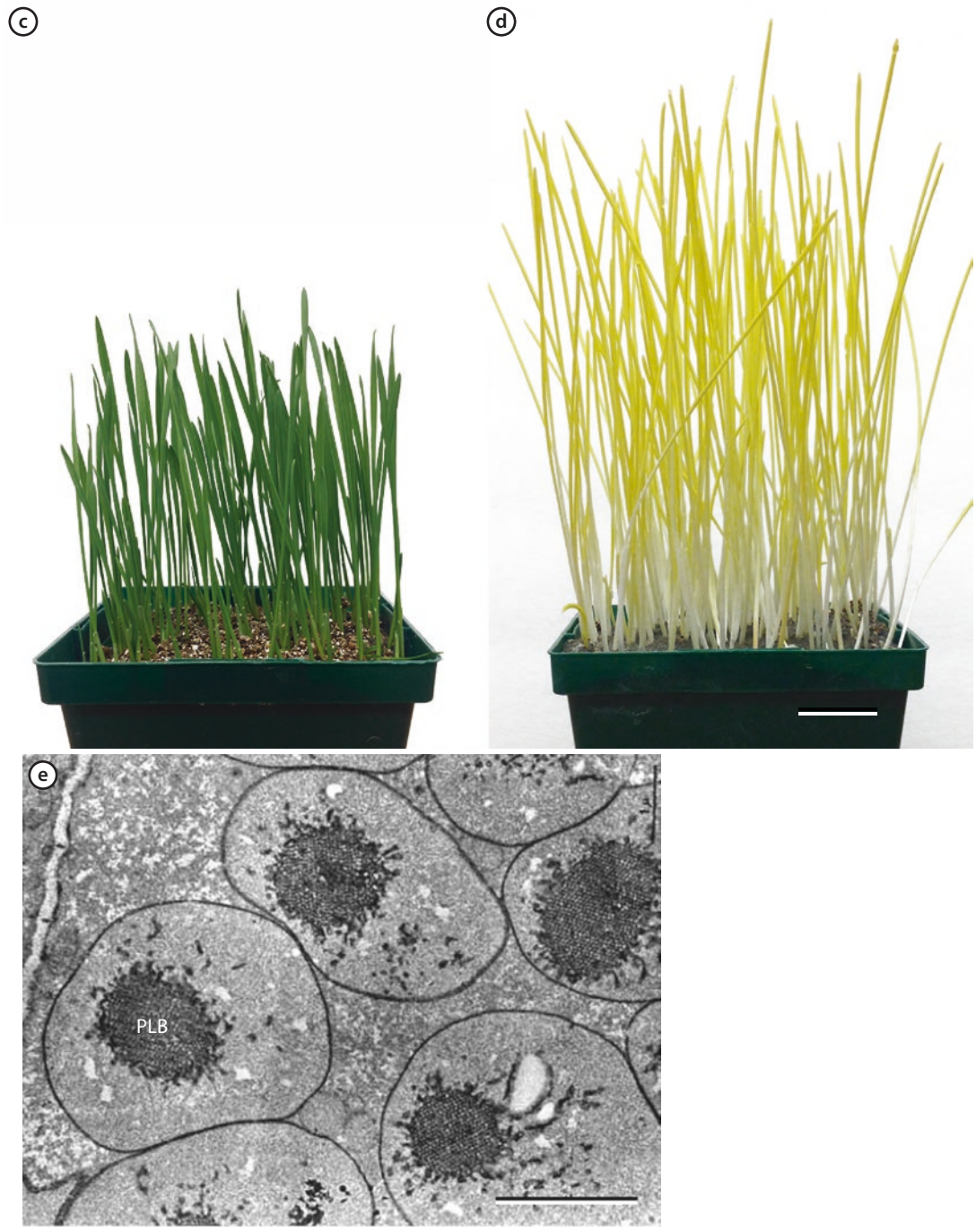


Fig. 3.5 **c**–**e** Wheat (*Triticum aestivum*) seedlings grown either in the light **c** or dark **d**. Note how etiolated growth results in pale, long, weak plants. Scale bar = 2 cm (RR Wise). **e** TEM of four etioplasts from the dark-grown plants similar to those seen in **d**. Note large prolamellar bodies (PLB) inside each etioplast. Scale bar = 0.5 μm (**c**, **d** RR Wise, **e** Crang and Vassilyev 2003)

3.5.4 Amyloplast

Starch is a macropolymer of several thousand repeating glucose units. All starch synthesis occurs inside a plastid, and large starch granules can be found in proplastids, chloroplasts, and amyloplasts.

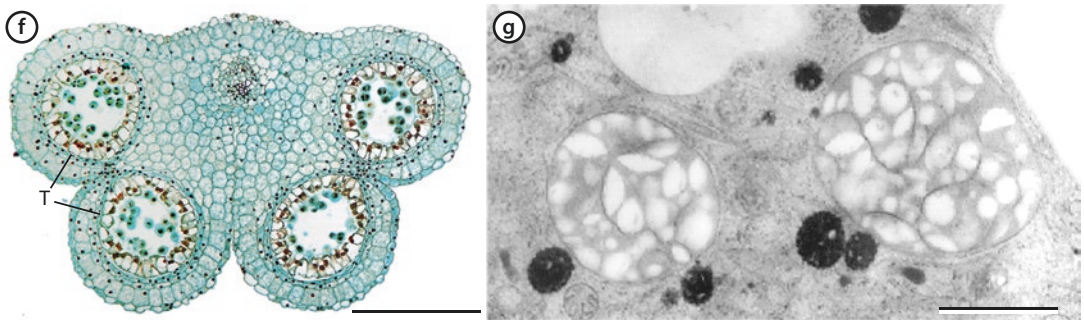


Fig. 3.5 **f** LM of lily (*Lilium* sp.) anther in cross-section. The tapetum (T) lines the cavity (loculus) in which the pollen grains develop. Cells of the tapetum contain dense bodies of oil-rich elaioplasts. Scale bar = 0.5 mm (RR Wise). **g** TEM of two elaioplasts in *Arabidopsis thaliana* anther, showing light oil inclusions. Scale bar = 1 μm. (Image courtesy of Dr. Denis Murphy, University of South Wales)

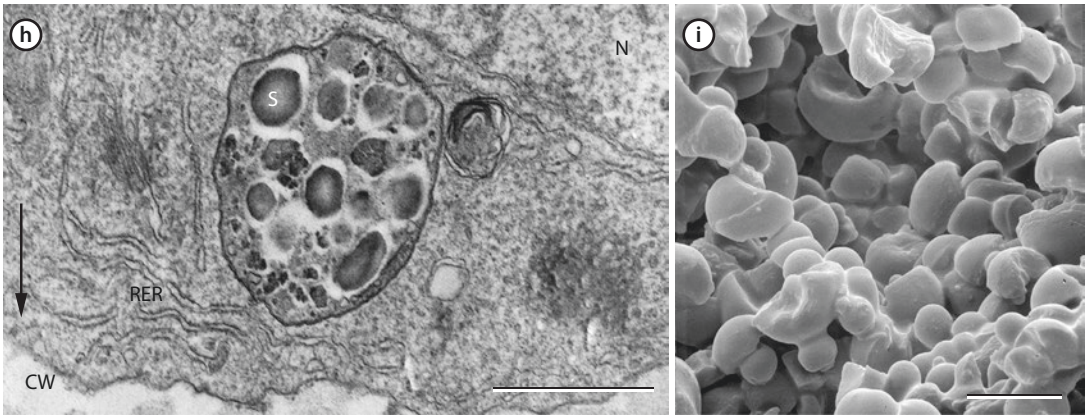


Fig. 3.5 **h** TEM of an amyloplast from root tip (columella) of mung bean (*Vicia faba*). Note starch granules (S) in the amyloplast, nucleus (N), rough endoplasmic reticulum (RER), and cell wall (CW). The direction of the gravitational field is indicated by the arrow. Scale bar = 1 μm (Image courtesy of Dr. Denis Murphy, University of South Wales). **i** SEM of storage starch granules isolated from pea (*Pisum sativum*) amyloplasts. These starch grains are considerably larger than those shown in Fig. 3.5h. Scale bar = 5 μm (**h**, **i** RR Wise)

Chloroplasts make short-term transitory starch with the entire pool being synthesized during the day and degraded and exported at night. Proplastids and, in particular, amyloplasts make long-term storage starch that may persist for weeks, months, or even years.

While most plastid types can contain starch, **amyloplasts** are unique because of the copious amounts of starch they synthesize in the form of large grains (Fig. 3.5h, i). In another example of plastid versatility, amyloplasts play two uniquely different roles. The function of amyloplasts in starch storage has already been noted. A second, separate function is in **gravisensing** (a positive response to the force of gravity). Starch is heavy, and starch-filled amyloplasts settle toward the pull of gravity on a minute time scale, even within plant cells. Amyloplasts in special tissues in the stem (the endodermis—refer to ► Sects. 10.4 and 11.5) and the root (the columella— ► Sect. 10.4) perform a mechanical, not a metabolic, function as they sink to the bottom of the cell, contact the **rough endoplasmic reticulum** (RER), and signal an upper/lower cell polarity that initiates a gravitropic growth response through a plant

growth regulator **indoleacetic acid** (IAA). Shoots therefore exhibit negative gravitropism and grow away from the signal, or up, while roots exhibit positive gravitropism and grow towards the signal, or down.

3.5.5 Chromoplast

Chromoplasts (◘ Fig. 3.5j) contribute the bright red, orange, and yellow colors to many fruits that serve to attract and conscript animals to act as seed dispersers. They originate as chloroplasts, and the chloroplast-to-chromoplast transition (refer to ◘ Fig. 3.6) is tightly coordinated with the complex process of fruit ripening. In developing tobacco (*Nicotiana tabacum*) nectaries, an amyloplast-to-chromoplast transition is the source of the carbohydrate used for nectar production (Horner et al. 2007).

The colors of chromoplasts come from large accumulations of carotenoid pigments of which there are two types: carotenes (carbon and hydrogen only) and xanthophylls (C, H plus oxygen). In addition to functioning as animal visual attractants, the carotenoids are also precursors for vitamin A biosynthesis in animals, thus rewarding seed dispersers with an essential nutrient. During the chloroplast-to-chromoplast transition, the chlorophyll-containing thylakoid membranes of the chloroplast are degraded and replaced with outsized pigment-protein droplets called **plastoglobuli** (◘ Fig. 3.5k). The protein, fibrillin, which has many other functions in plant cells, helps maintain plastoglobus structure.

3.5.6 Gerontoplast

Leaf cells each may have up to a hundred individual chloroplasts, and each chloroplast is rich in the proteins needed for photosynthesis. **Autumnal senescence** ("fall colors") is a genetically programmed, step-by-step dismantling of the chloroplast with the sole purpose of recovering that leaf protein (◘ Fig. 3.5l). Cell walls and chloroplast lipids, including the lipid chlorophyll, are not recovered and remain in the leaves that are eventually shed. As senescence proceeds, thylakoid membranes are degraded, lipids and pigments form large droplets, and the chloroplast is slowly converted to a **gerontoplast** (◘ Fig. 3.5m). Gerontoplasts have few internal membranes and many plastoglobuli—lipid accumulations that represent the catabolic end product of resource recovery.

3.5.7 Chloroplast

These common chlorophyll-containing organelles are found in leaves and stems of eukaryotic plants and in algae. They utilize carbon dioxide and water in the presence of sunlight to initially produce simple sugars that build up food for the plant.

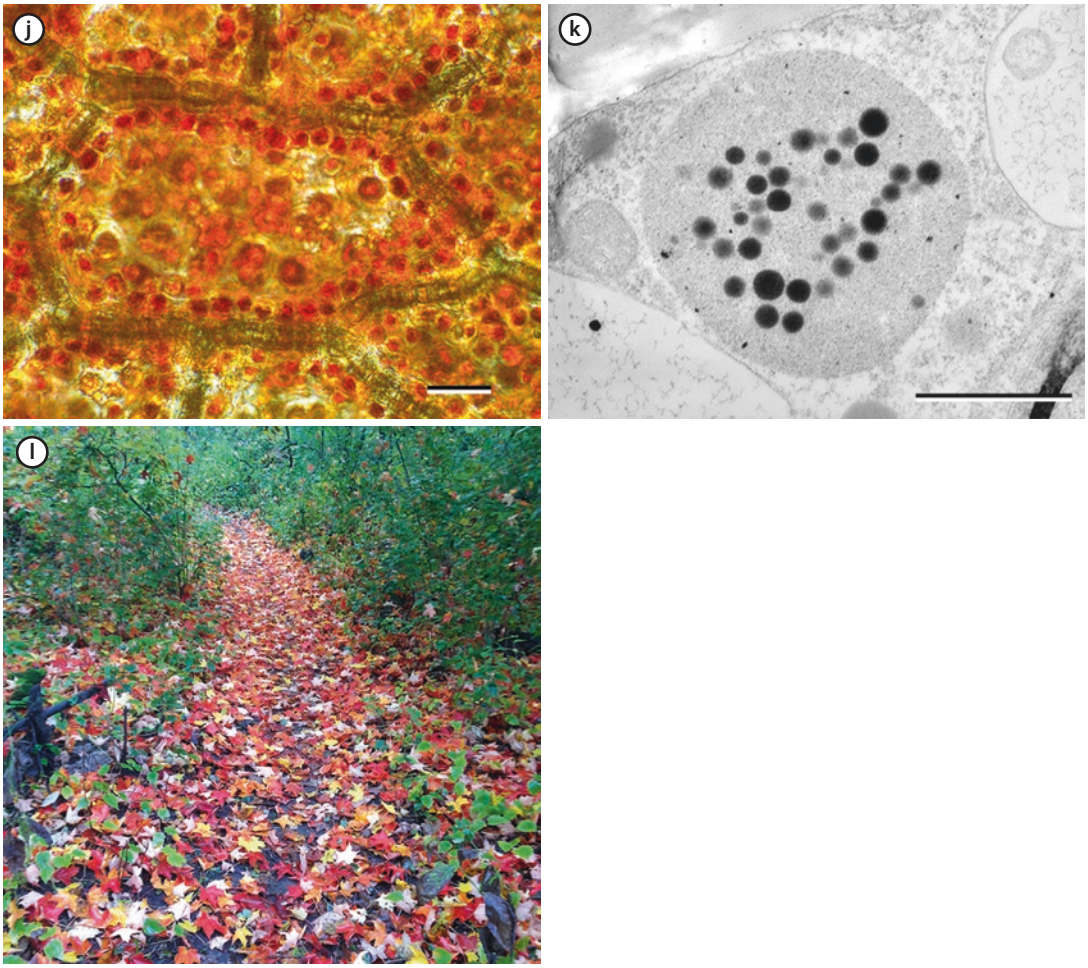


Fig. 3.5 **j** Cells of a red bell pepper (*Capsicum annuum*) fruit containing many chromoplasts. **k** A single chromoplast from tomato (*Solanum lycopersicum*) fruit containing numerous dark, carotenoid-containing plastoglobuli. Scale bars = 10 μm in **j** and 1 μm in **k**. **l** Maple leaves at the final stage of autumnal senescence (**j–l** RR Wise)

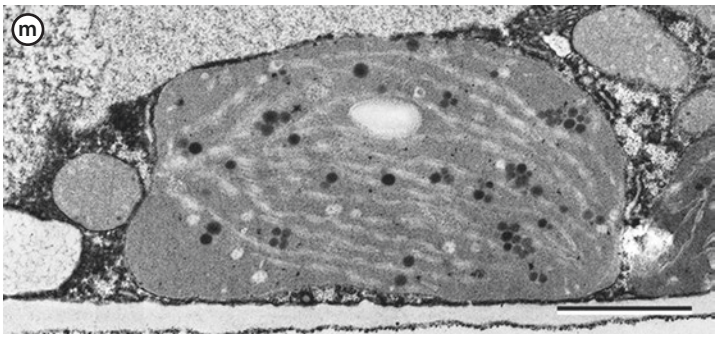


Fig. 3.5 **m** TEM of a gerontoplast from a senescing leaf of hydrangea (*Hydrangea* sp.). Note the numerous, small dark plastoglobuli (refer to ► Sect. 3.5.5), which result from the breakdown of the photosynthetic membranes. Scale bar = 1 μm (RR Wise)

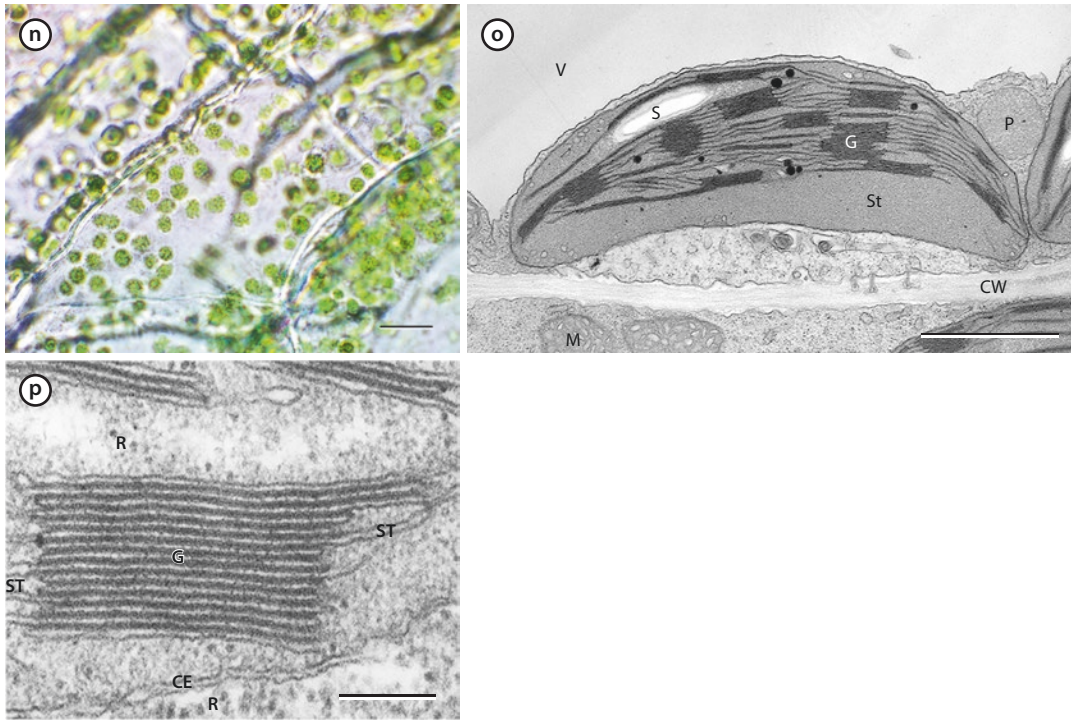


Fig. 3.5 **n** LM of chloroplasts from the outer layer of a green bell pepper (*Capsicum annuum*) fruit. The dark specks inside the chloroplasts are grana. Scale bar = 10 μm. **o** TEM of spinach (*Spinacia oleracea*) chloroplast situated between the vacuole (V) and cell wall (CW). Internally, chloroplasts have stacks of granal thylakoid (G) and starch grains (S) suspended in the stroma (St). Scale bar = 3 μm. **p** This single granum (G) from a spinach (*Spinacia oleracea*) chloroplast is composed of 15 thylakoid membranes stacked (appressed) on top of each other. Stromal thylakoids (ST) are unstacked (unappressed) and extend from the edges of the granum. Note the two membranes of the chloroplast envelope (CE) and ribosomes (R). Cytoplasm, also with many ribosomes (R), is to the bottom of the image. Scale bar = 0.5 μm (**n**–**p** RR Wise)

The typical **C_3 chloroplast** is a round, plano-convex organelle approximately 5 to 10 μm in length (Fig. 3.5n; see below for definition of the C_3 photosynthetic pathway). They have a double-membrane envelope and a third, internal system of membranes, **thylakoids**, that is suspended in a protein-rich fluid, the stroma (Fig. 3.5o). In a functional chloroplast, thylakoids form a closed, flattened volume, with the stroma to the outside and the lumen to the inside. Two categories of thylakoids are recognized: (1) Granal thylakoids are pressed together in stacks called grana in which an individual granum may contain 2–30 or more thylakoids. (2) Intergranal thylakoids (a.k.a. stromal thylakoids) are unappressed and span the stroma to interconnect grana (Fig. 3.5p).

3.5.8 Chloroplast Functions

Because chloroplasts have a constant supply of reduced carbon, NADPH, and ATP and originated from free-living prokaryotic endosymbionts, they have evolved over time to be capable of

performing a large array of anabolic functions in a plant cell. Some of those functions are given here.

Chloroplasts use photosynthesis to manufacture low-molecular-weight, reduced carbon compounds, commonly called sugars. In brief, photosynthesis can be divided into two distinct sets of reactions:

1. The light-dependent reactions harvest light energy and use that energy to transport electrons through an electron transport chain embedded in the thylakoid membrane. Chlorophyll is the primary photosynthetic pigment; hence, thylakoid membranes are deep green in color. The light-dependent reactions synthesize ATP and the reductant NADPH.
2. The light-independent reactions subsequently use that NADPH and ATP to reduce and phosphorylate oxidized atmospheric carbon to the level of a sugar phosphate. The light-independent reaction occurs in the liquid stroma of the chloroplast and converts CO_2 and other compounds to glucose.

Nitrogen and sulfur are two of the 20 essential elements plants need for growth and development. Both are rather scarce in the environment, at least in bioavailable forms. While different pathways are responsible for the uptake of nitrogen and sulfur (and will not be discussed here), once in the plant, both elements must be assimilated into safe, transportable, and usable forms such as amino acids.

As a class of chemical compounds, there are about 500 amino acids, of which only 20 are used to make proteins. These are the so-called proteinogenic (or proteinaceous) amino acids. Humans can only make 11 of the 20 proteinogenic amino acids. In contrast, plants can synthesize all 20 proteinogenic amino acids (as well as hundreds of others), and plastids are the site for the synthesis for the 9 essential amino acids that humans need. Lacking plastids, humans must acquire these nine "essential" amino acids via their diet, by eating plants or other animals that feed on plants.

Glyphosate (Roundup©) is a potent inhibitor of a key plastid enzyme in the aromatic amino acid pathway (phenylalanine, tyrosine, and tryptophan), and, thus, it is a powerful and specific herbicide. Synthesis of the branched-chain amino acids (isoleucine, leucine, and valine) is also plastid localized and can be the subject of specific herbicide inhibition.

Plastids, in one form or another, synthesize chlorophylls, carotenoids, fatty acids, phospholipids, sulfolipids and galactolipids, tocopherols, and quinone lipids. Plant cells only rarely possess smooth endoplasmic reticulum, the site of most lipid synthesis in animals.

Box 3.1 Where Are Tannins Made?

Tannins are a type of polyphenol that serve many purposes for plants, including protection from predators (due to a bitter taste), regulating plant growth, and protecting plants from ultraviolet radiation. They are what give things like tea, pomegranates, and under-ripe raspberries their "dry" effect.

Tannins form bonds with proteins, cellulose, starches, and even minerals to create substances that resist decomposition. In fact, tannins from trees like oak, maple, and mangrove were used by ancient and indigenous cultures to preserve animal skins for clothing and blankets. Hence the terms "tanned leather" and "suntan."

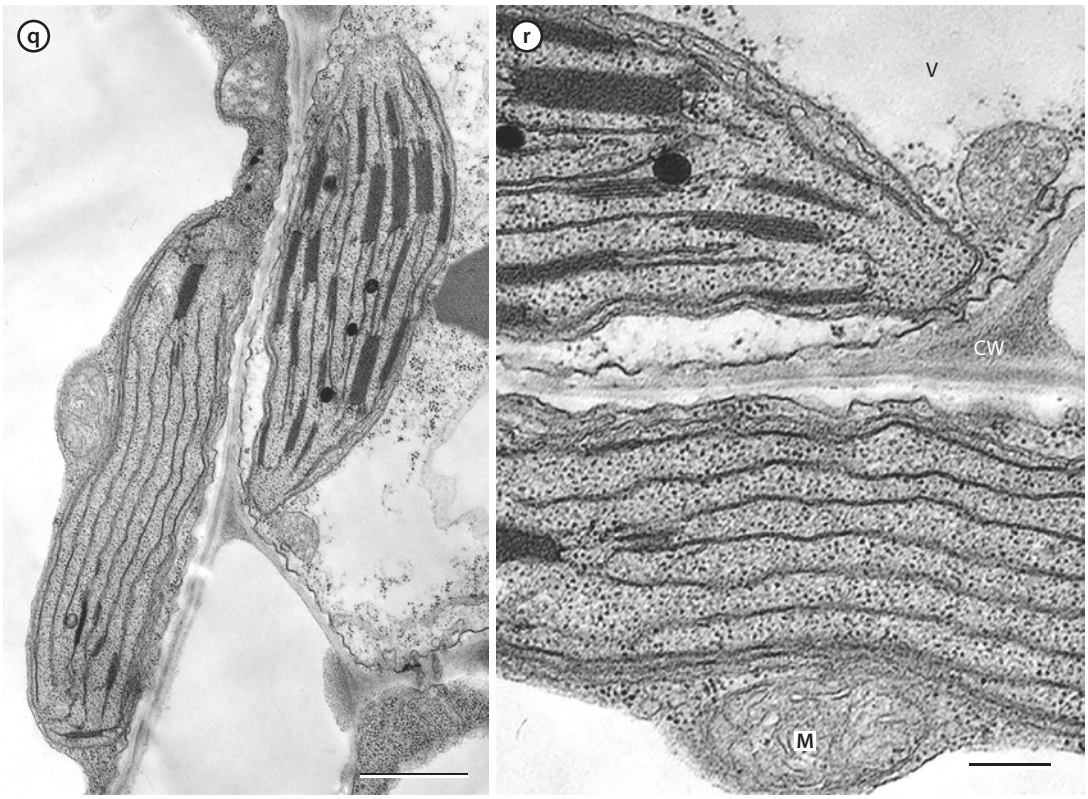
When you drink green tea, beer, wine, or even fruit juices, the bitter taste in your mouth results from the presence of condensed tannins. Condensed tannins are substances that are produced in a wide variety of plants and are located within leaves, fruits, and bark. Tannins provide plants with protection against herbivores and even from the UV rays of the sun. People utilize tannins for their antioxidant properties, often consuming them for anticancer, anti-inflammatory, and anti-allergenic benefits (Frazier et al. 2010). But how and where are tannins produced within plant cells?

Light, epifluorescence, and confocal microscopy have elucidated that tannins accumulate in **tannosomes**, small bodies found within the central vacuole. Tannosomes contain both tannins and chlorophyll, linking the tannosomes with chloroplasts. By employing TEM, Brillouet et al. (2013) further identified that tannins, and the tannosomes, are produced within differentiated chloroplasts. These specialized chloroplasts are larger than normal chloroplasts and contain unstacked grana that generate small, membrane-bound structures in a process the authors called "pearling." The pearls thus produced are filled with tannins, concentrate together at the chloroplast membrane, and are encapsulated in a membrane. This structure and the tannosomes within are shuttled from the chloroplast, through the cytoplasm and to the central vacuole.

3.5.9 The Dimorphic Chloroplasts of C_4 Photosynthesis

The photosynthetic pathway described above results in the generation of a three-carbon compound, glyceraldehyde-3-phosphate. Hence, plants that use this pathway are called **C_3 plants**. Other plants, most notably grasses such as maize and sugar cane, produce a four-carbon acid as the first stable product of photosynthesis. That form of photosynthesis is called the **C_4 pathway**.

C_4 plants differ from C_3 plants on biochemical, physiological, anatomical (refer to ► Sect. 12.5), and ultrastructural bases. In C_4 photosynthesis, carbon dioxide is initially fixed in chloroplasts in the mesophyll cells of the leaf. Mesophyll cell chloroplasts contain grana stacks and are termed "granal." A four-carbon compound is transported to the bundle sheath cells where it is decarboxylated to a three-carbon molecule and CO_2. The released CO_2 is then fixed again in the **bundle sheath chloroplast**, which lacks grana ("agranal") (◘ Fig. 3.5 q, r). Different ultrastructures arise because the enzyme responsible for the secondary fixation in the bundle sheath chloroplast, ribulose-*bis*phosphate carboxylase/oxygenase (a.k.a. Rubisco, an acronym for the enzyme ribulose *bis*phosphate carboxylase/oxygenase), is inhibited in the presence of oxygen. Unlike C_3 chloroplasts and C_4 mesophyll cell chloroplasts, the C_4 agranal bundle sheath chloroplasts are non-oxygenic; thus, the O_2 inhibition of Rubisco is alleviated.



◘ **Fig. 3.5** **q** TEM of portions of a maize (*Zea mays*) mesophyll cell (*left side*) containing an agranal chloroplast and a bundle sheath cell (*right side*) with a granal chloroplast. Scale bar = 2 µm. **r** Higher magnification of the two plastids in **q** showing granal (*top*) and agranal chloroplast (*bottom*) structure in more detail. V = vacuole, CW = cell wall, M = mitochondrion. Scale bar = 1 µm (**q**, **r** RR Wise)

3.5.10 Guard Cell Chloroplasts

Stomata (stoma = sing.) are minute, adjustable pores on the leaf surface that allow for CO_2, H_2O, and O_2 gas exchange between the leaf and the atmosphere. Specialized pairs of epidermal cells, called **guard cells**, inflate with water and then bend and open the stomatal pore. Subsequent loss of water causes the guard cells to deflate and close the pore. In most plants stomata are closed at night (when photosynthesis cannot operate) and open during the day. The signals to open and close come from environmental cues and an internal circadian clock. The energy to drive the opening and closing comes from guard cell chloroplasts that respond to osmotically driven water movements.

Guard cell chloroplasts (GCC) are, in all respects, the same as C_3 chloroplasts. They contain thylakoids, grana, chlorophyll, and all the components needed to perform both the light-dependent and the light-independent reactions of photosynthesis. They fix carbon and make starch. What sets GCCs apart from other chloroplasts is that they contribute nothing to the carbon economy of the leaf. GCCs function solely to provide the energy and osmotic pressure changes needed to drive stomatal opening and closing (◘ Fig. 3.5s–u).

Guard cell chloroplasts are an impressive example of the evolutionary flexibility of plastids. Plants evolved from green algal ancestors and began land colonization during the Silurian period (approximately 440 million years ago). One of the many adaptations needed for a terrestrial life was a waxy, water impervious outer cuticle, which drove the need for stomatal openings in that cuticle. As guard cells evolved, plastids were enlisted to serve as the power plant for stomatal functioning. They are sensitive to light (and light is a major signal for stomatal opening) and can generate the ATP and the low-molecular-weight ions needed to support osmotically driven stomatal opening and closing.

3.5.11 Sun Versus Shade Chloroplasts

Chloroplast development is light-dependent, and different ultrastructures and physiologies can result as a consequence of the light environment during development. Because light is limiting in the shade, chloroplasts in leaves that develop in the interior of a tree canopy develop to favor the light-dependent reactions over the light-independent reactions. **Shade-type chloroplasts** are optimized for light capture with larger grana, more thylakoids per granum and more chlorophyll per antenna (or light-harvesting) complex. Stromal volume is concomitantly reduced. **Sun-type chloroplasts**, which develop at the exterior of the canopy where light is not limiting, have smaller grana, less chlorophyll (reduced capacity for the light-dependent reactions), and more stromal volume (increased capacity for the light-independent reactions). Both chloroplast types can be found on the same plant; thus, these two different developmental outcomes are driven solely by the light environment experienced during leaf expansion (◘ Fig. 3.5v, w).

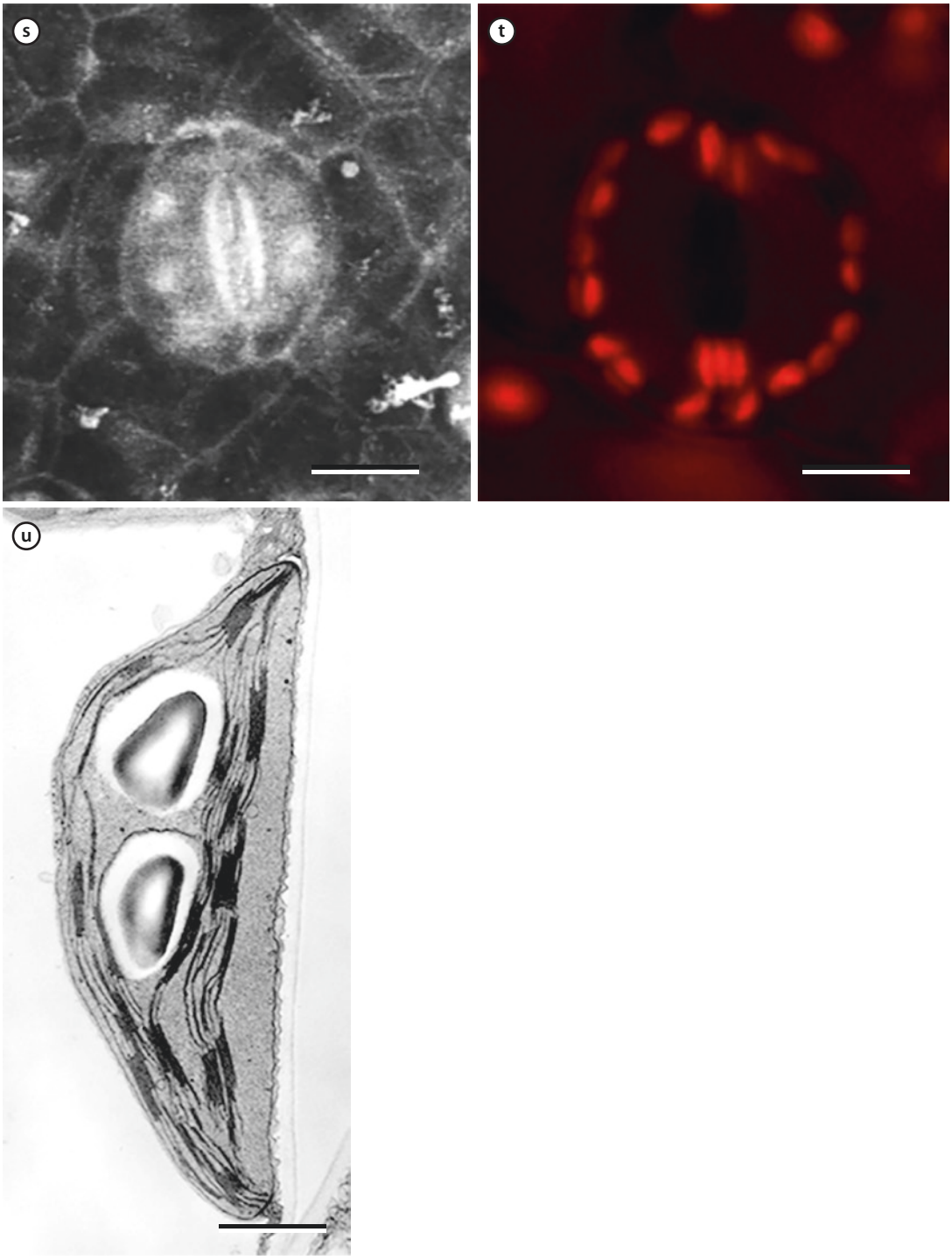


Fig. 3.5 **s** SEM image of an upland cotton (*Gossypium hirsutum*) guard cell pair. Chloroplasts appear as white spots within the guard cells. **t** Confocal laser scanning microscopy (CLSM) fluorescence image of a *Nicotiana benthamiana* guard cell pair. Chloroplasts appear as red spots in guard cells due to chlorophyll fluorescence. **u** TEM of guard cell chloroplast of spinach (*Spinacia oleracea*). Scale bars = 10 μm in **s** and **t**, 1 μm in **u** (**s**–**u** RR Wise)

Box 3.2 Can Plants Absorb Green Light?

Chloroplasts of most land plants capture blue and red wavelengths of light for photosynthesis and reflect green wavelengths, giving plants a green color. However, species that grow in deep shade are challenged in their ability to capture sufficient light as the intensity and quality of light have been filtered by canopy leaves. Jacobs et al. (2016) have discovered that some species of understory *Begonia* have evolved a unique light-capturing adaptation, specifically the iridoplast, which results in blue iridescent leaves.

Iridoplasts are plastids located within the epidermal cells of some tropical *Begonias*; these plastids are unique in two ways. First, most plants lack epidermal chloroplasts. Second, iridoplasts enable plants to utilize green and red wavelengths for photosynthesis, contrasting with most terrestrial plants that utilize blue and red. This feat is accomplished by having highly structured, multilayered thylakoid membranes within the iridoplasts. The multilayered structure greatly increases the absorption of green light, which is enriched in the understory because the canopy plants depleted the incoming light of the red and blue wavelengths. This allows the plant to increase the quantum yield when in the deep shade of the tropical forests. Thus, by utilizing green light and increasing quantum yield, iridoplasts are important structures in the evolution of understory tropical begonias.

Reference: Jacobs et al. (2016)

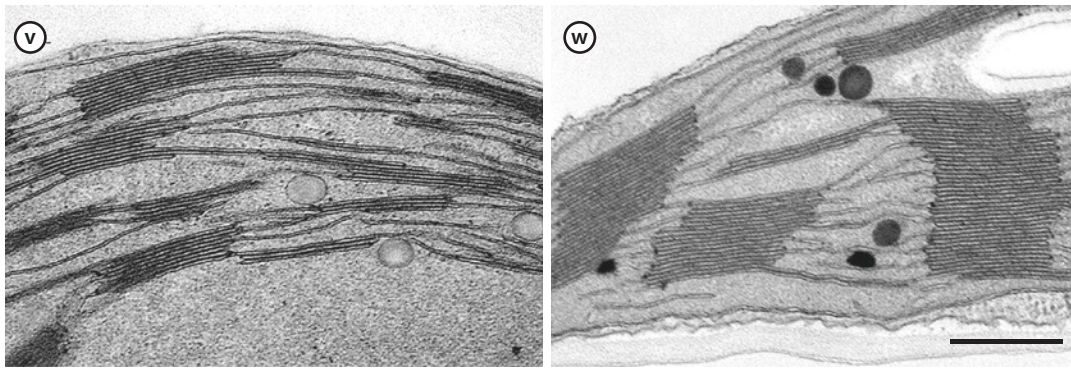
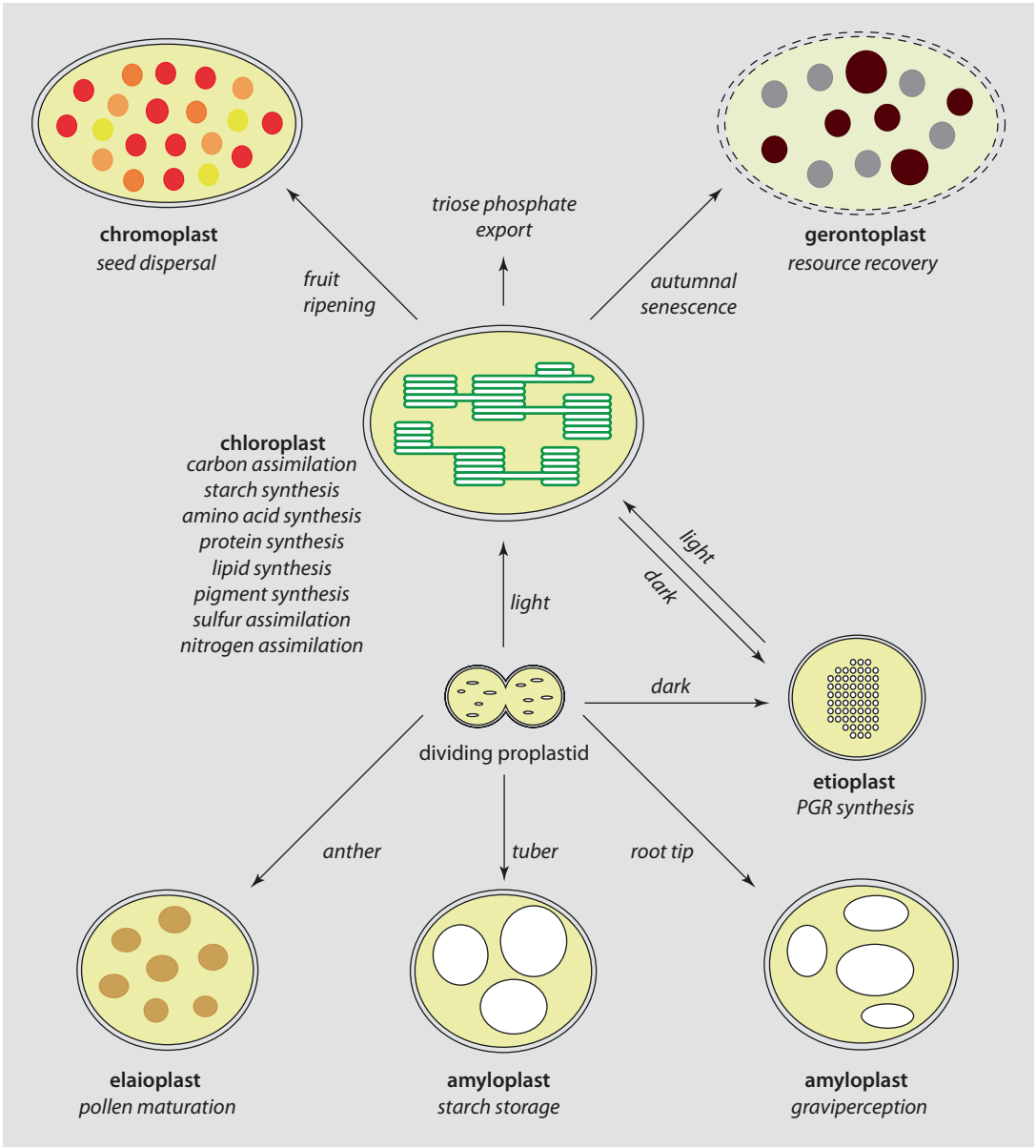


Fig. 3.5 TEM of **v** high-light and **w** low-light chloroplasts from spinach (*Spinacia oleracea*) leaves. **v** The high-light leaves were treated with 1000 μmol photons m^{-2} s^{-1} irradiance for 4 h prior to sampling. **w** The low-light chloroplast is from a leaf on the same plant that received 4 h of high light and then 10 min of 50 μmol photons m^{-2} s^{-1}. Scale bar in w = 0.5 μm and applies to both panels. (**v**, **w** Philip Rozak)

3.6 All Plastids Are Developmentally Related

All plastids in a plant are descendants of the hundred or so proplastids provided by the egg cell in angiosperms. ◘ Figure 3.6 shows the development of the various plastid types starting with the proplastid in the center of the figure. Plastids in anthers, roots, and etiolated tissues develop in the dark (or near dark) and do not turn green. Those plastids become elaioplasts in the tapetum, starch storage or gravisensing amyloplasts in the root, or etioplasts if shoot tissue develops in the dark. Once tissues are exposed to



◘ **Fig. 3.6** The different pathways of plastid development depicted in the drawing are both light- and tissue-dependent. The function(s) of each plastid type is given in italics (RR Wise)

the light, either through leaf development or by placing the plant in the light, etioplasts convert to chloroplasts. C_3, C_4, guard cell, and sun/shade chloroplasts follow different developmental pathways depending on their host tissue. Chloroplasts in leaves typically go through the gerontoplast stage as leaves proceed through the senescence process. Chloroplasts in developing fruit, such as those in a green tomato, convert to chromoplasts during ripening.

3.7 Mitochondria Synthesize ATP and Small Carbon Skeletons

Mitochondria are the sites of two of the three phases of respiration: the citric acid cycle and oxidative phosphorylation. Those two stages are preceded by glycolysis, which takes place in the cytoplasm. Respiration takes the low-molecular-weight, reduced carbon compounds produced by photosynthesis, extracts the high-energy electrons (some during glycolysis, most during the citric acid cycle), and feeds those electrons into the mitochondrial electron transport chain to drive ATP synthesis (phosphorylation). In addition to ATP production, mitochondria also export two- to five-carbon skeletons for use by many other metabolic pathways in the cytoplasm.

Mitochondria have two membranes. The outer membrane serves as a barrier between the cytoplasm and the mitochondrial interior. In composition, it is more like the other native cell membranes, i.e., plasmalemma, vacuolar membrane, and many membrane-limited vesicles. The inner membrane has numerous folds called **cristae** that are the site of the mitochondrial electron transport chain, which culminates with ATP synthesis via chemiosmosis. The enzymes of the citric acid cycle reside in the fluid-filled interior, the matrix. The number of mitochondria per cell can vary from only a few to fifty or a hundred, depending on cell type and activity level (◘ Fig. 3.7a–c). However, recent research has demonstrated that mitochondria and the endoplasmic reticulum interact in strikingly dynamic ways in response to light and oxygen deprivation, fusing and splitting on a short time scale (Jaipargas et al. 2015).

Like plastids (refer to ► Sect. 3.5), mitochondria were derived endosymbiotically and have retained the machinery needed to code for and manufacture some of their own proteins.

3.8 Microbodies Are the Site of Specific Biochemical Pathways

In contrast to plastids and mitochondria, **microbodies** are bounded by a single membrane, have no internal membrane structure, lack DNA, and are amorphous internally or, in some cases, may have internal protein crystals, which represent enzymes such as catalase. Like plastids and mitochondria, microbodies multiply by a type of fission division.

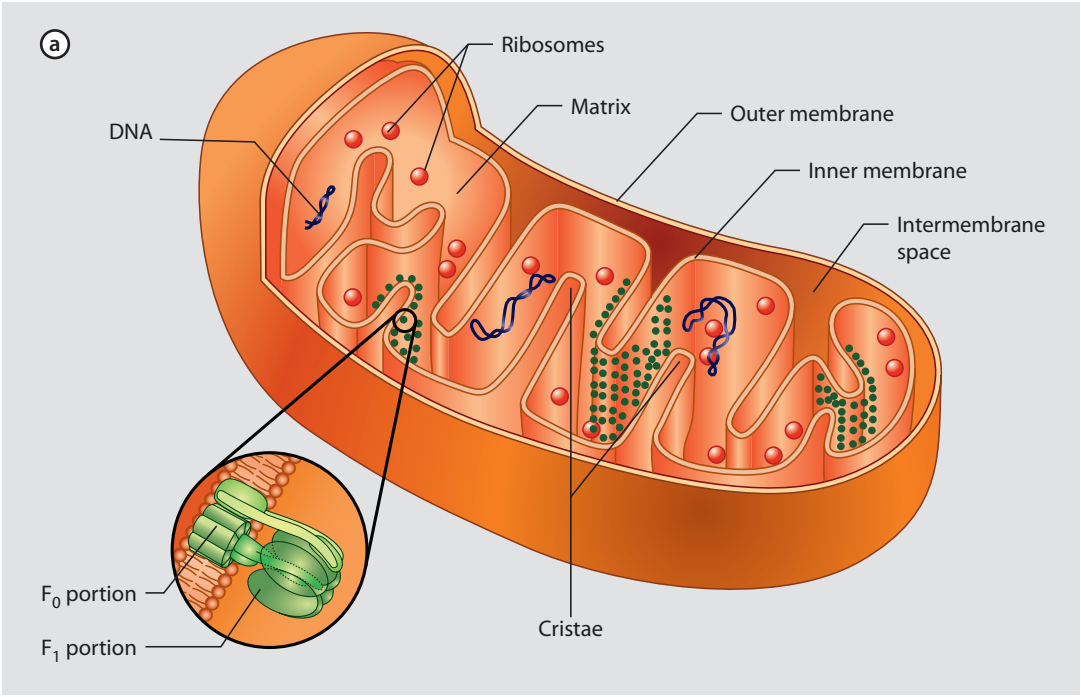


Fig. 3.7 **a** Drawing of a typical plant mitochondrion (Redrawn from Crang and Vassilyev 2003)

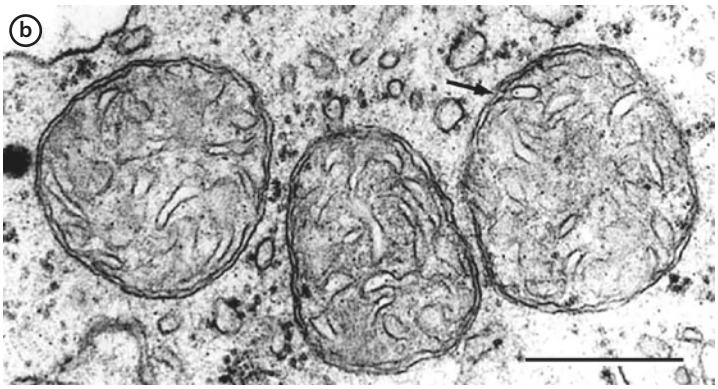


Fig. 3.7 **b** TEM of three mitochondria from a secretory cell in the digestive gland of *Drosophyllum lusitanicum*, a carnivorous plant. Note the continuity of cristae with the inner mitochondrial membrane (*arrow*). Scale bar = 1 μm (RR Wise)

There are two types of microbodies, and both received their name due to their small size and simple structure. Microbodies in leaf cells are called **peroxisomes**, and they participate in the oxidation of glycolate to glyoxylate that produces H_2O_2 (hydrogen peroxide), which in turn is destroyed by the enzyme catalase (Fig. 3.8a). This process is called photorespiration because it consumes oxygen, generates CO_2, and occurs only in the light. It represents an inefficiency of **Rubisco**, which accepts oxygen instead of the normal substrate CO_2 when O_2 accumulates to high concentrations. The oxygen-rich Rubisco is tricked into releasing CO_2.

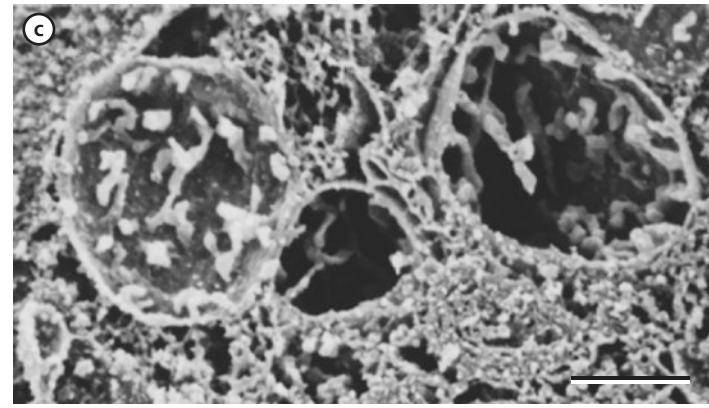


Fig. 3.7 **c** Scanning electron microscopy (SEM) of mitochondria from a spinach (*Spinacia oleracea*) leaf using a frozen and fractured surface. Cristae are visible as outgrowths of the inner membrane. Scale bar = 1 μm (RR Wise)

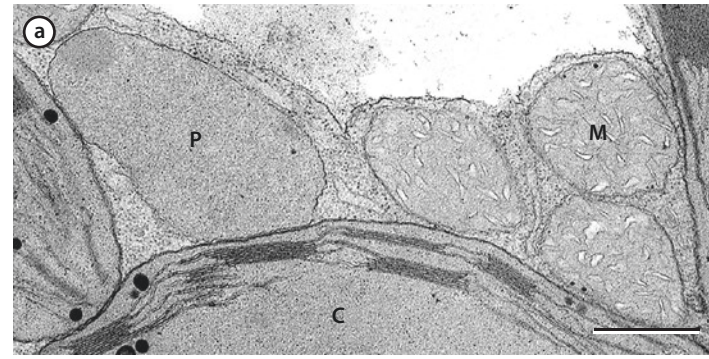


Fig. 3.8 **a** This TEM image shows one peroxisome (P) and several mitochondrion (M) tightly appressed to a chloroplast (C) in a spinach (*Spinacia oleracea*) leaf mesophyll cell. The image reflects the metabolic cooperation of these three organelles. Scale bar = 1 μm (RR Wise)

Glyoxysomes, the second type of microbody, are key organelles in oil-storing cells of seeds where they work together with mitochondria to catabolize the long carbon chains on storage oils and lipids into smaller carbon skeletons for respiration and growth (Fig. 3.8b).

3.9 The Endoplasmic Reticulum Synthesizes Proteins and Some Lipids

Plant cells are capable of synthesizing every biomolecule needed for complete growth, development, and reproduction; proteins and lipids are two major cellular components, and the endoplasmic reticulum (ER) plays a role in the synthesis of both. The ER is an interconnected series of tubules and sacs that lie in the cytoplasm and comes in two forms, smooth and rough. Rough endoplasmic reticulum (RER) is studded with ribosomes (refer to RER in Fig. 3.9c). Ribosomes are composed of a large and a small subunit (Fig. 3.9a), and there may be thousands of individual ribosomes in a cell that are actively producing proteins.

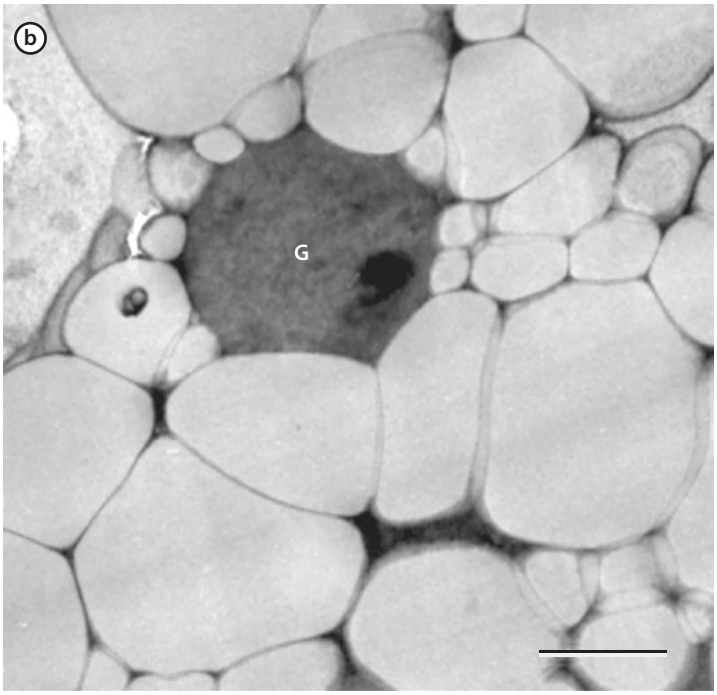


Fig. 3.8 **b** TEM of glyoxysome (G) in the endosperm of a lyre-leaved sand cress (*Arabidopsis lyrata*) seed surrounded by lighter lipid bodies. Scale bar = 1 μm (RR Wise)

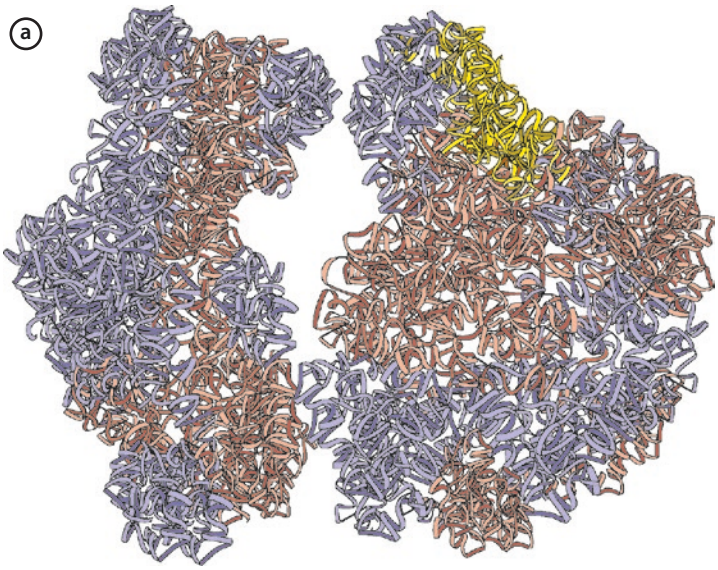


Fig. 3.9 **a** The two ribosome subunits showing rRNA (*brown and yellow*) and protein (*blue*) molecules. Scale bar = 10 nm (Protein data base, public domain)

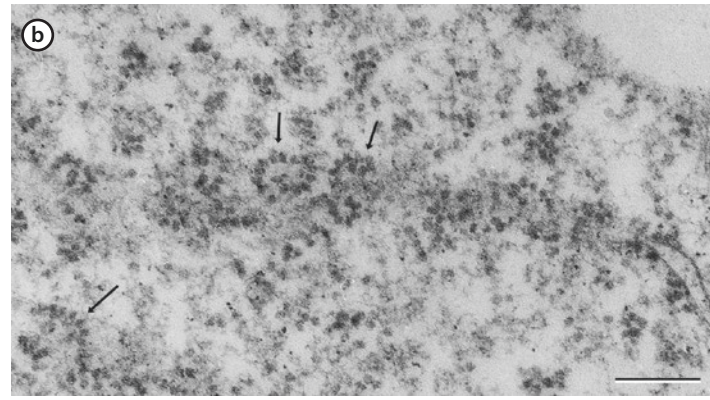


Fig. 3.9 **b** Polysomes (*arrows*) in the cytoplasm of a thale cress (*Arabidopsis thaliana*) root. Scale bar = 0.5 µm. (Image courtesy of Dr. Harry Horner)

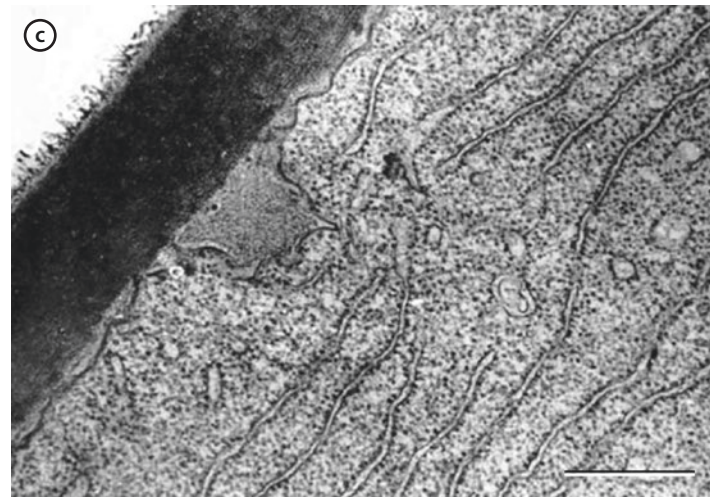


Fig. 3.9 **c** TEM image of rough endoplasmic reticulum in a rhizodermal cell of the water plant, *Limnobium bogotense* (a member of the grass family). Scale bar = 0.2 µm (Image courtesy of Dr. Harry Horner)

Plant cells have three sets of ribosomes. Those in the cytoplasm may be attached to the endoplasmic reticulum, forming rough ER (Fig. 3.9b), or they may be free-floating and not attached to any membrane. A single molecule of mRNA may be bound by multiple ribosomes, each at different position along the message, in a structure called a polysome. When seen in the TEM, polysomes appear as strings of beads (Fig. 3.9b). The other two sets of ribosomes are found in the chloroplast stroma (► Sect. 3.5) and the mitochondrial matrix (► Sect. 3.7).

Proteins synthesized by the ribosomes attached to the RER are inserted into the RER membrane or injected into the interior space (lumen). In ultrathin sections for transmission electron microscopy, RER appears as double-membrane profiles covered with bumps (Fig. 3.9c). The RER is involved in the synthesis and storage of

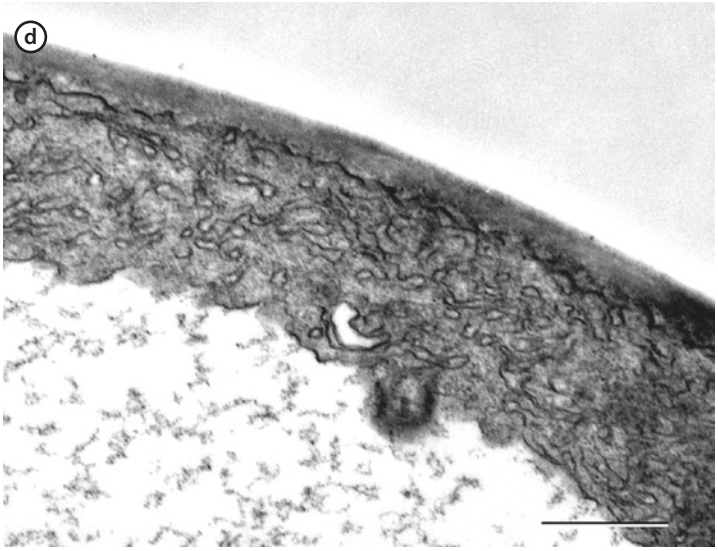


Fig. 3.9 **d** TEM of a portion of a leaf mesophyll cell from the thale cress (*Arabidopsis thaliana*) experiencing a bacterial infection. As a response to the infection, the cells are induced producing callose, via the tubules shown. Scale bar = 1 μm (RR Wise)

specific proteins (hydrolytic enzymes, membrane, storage, and secretory proteins). **Smooth ER** is more vesicular and tubular than the thinner and flatter RER. In animal cells, SER plays a large role in lipid synthesis, a function that plants mainly perform using plastids. In plants, the SER is active in the synthesis and secretion of specific lipophilic substances such as oils and terpenes. Therefore, SER is rarely seen in plant cells and usually is only prominent in plant secretory structures such as oil seed tissues, nectaries, and leaf glands. Smooth ER is also seen in leaf cells that have been infected by bacteria. Such cells often synthesize and secrete copious amounts of callose via the SER (Fig. 3.9d).

3.10 The Golgi Apparatus Processes and Packages Polysaccharides and Proteins for Secretion

The **Golgi apparatus** is the sum of all of the dictyosomes with common function in a plant cell. The dictyosomes are membranous organelles in the cell cytoplasm engaged in the processing and export of materials to the cell exterior. In animal cells, glycosylated proteins are the major export product. However, in plant cells, the Golgi system is primarily used to manufacture and export the non-cellulose polysaccharides used in cell wall synthesis or root cap slime (Rose and Lee 2010). Only in rare instances, such as the digestive traps of carnivorous plants, does the plant Golgi apparatus secrete proteins.

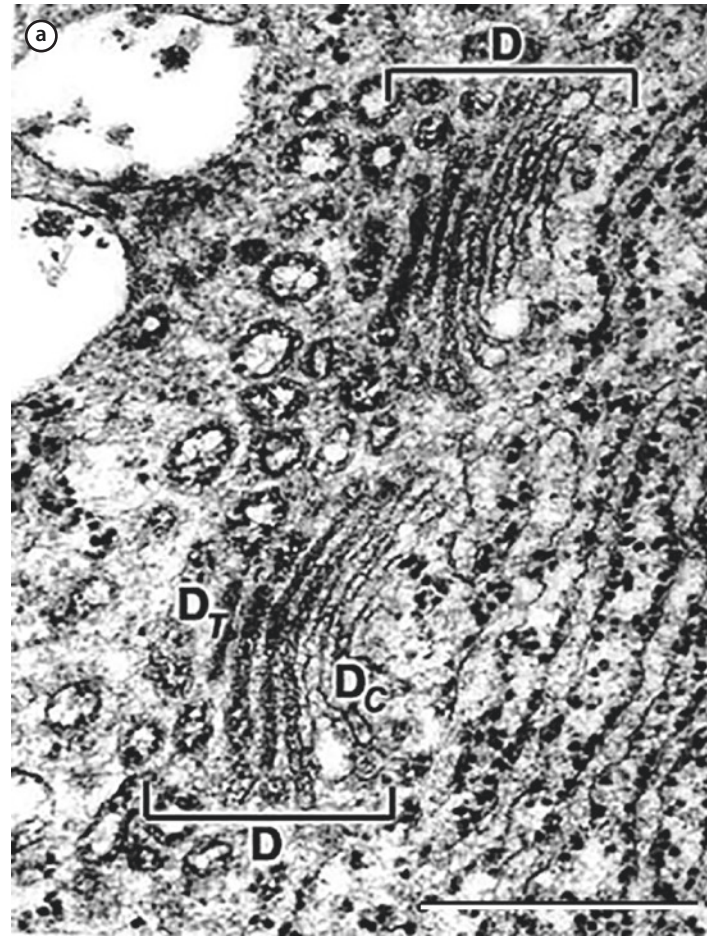


Fig. 3.10 **a** The plant Golgi apparatus consists of an array of dictyosomes (D), two of which are shown here using TEM from a secretory cell of poplar (*Populus* sp.) leaf gland. Note the *cis* (D_C) and *trans* (D_T) faces of a dictyosome. Scale bar = 0.5 µm (Crang and Vassilyev 2003)

The Golgi apparatus consists of dictyosomes and vesicles (Fig. 3.10a, b). Dictyosomes are stacks of (usually) 5–7 membrane cisternae, which exhibit polarity. Membrane vesicles containing proteins and carbohydrate precursors are trafficked from the ER to the ***cis* face** (or regenerative pole). Those materials are enzymatically modified as they travel through the dictyosome and then are eventually secreted in vesicles from the ***trans* face** (or secretory pole). In micrographs, the polarity is generally obvious inasmuch as the thickness and contents of the cisternae change from the *cis* (D_C) to the *trans* (D_T) side of the stack. Dictyosomes represent functional units of a Golgi apparatus, so that all dictyosomes in a given cell that have similar functionality represent a single Golgi system. Thus, there may be one or more Golgi systems per cell.

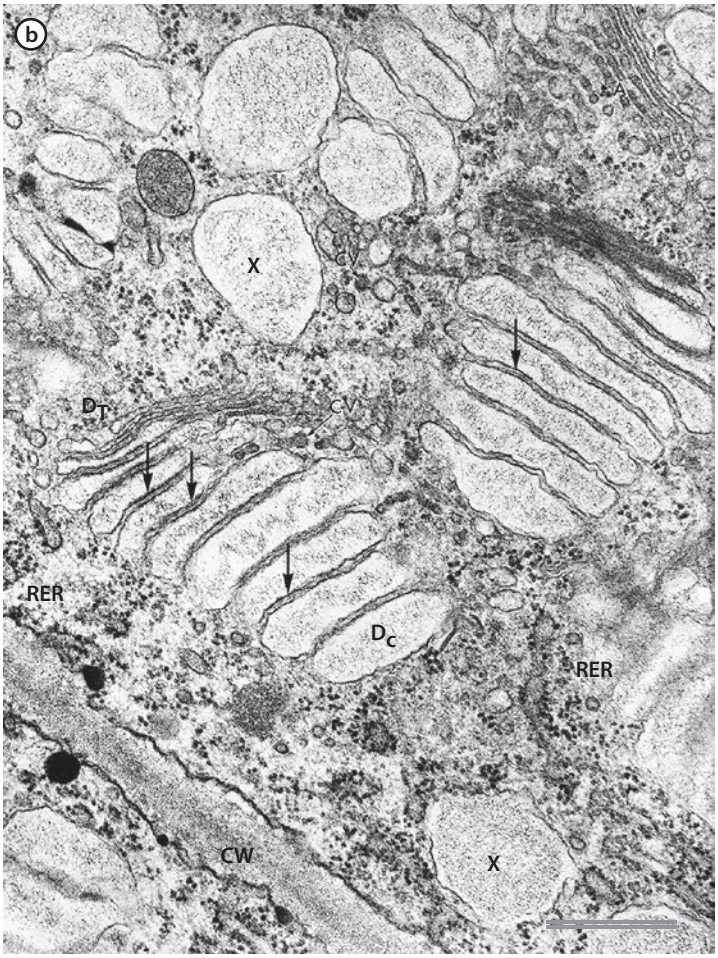


Fig. 3.10 **b** Root cap cell of timothy grass (*Phleum pratense*) observed with transmission electron microscopy. Dictyosome cisternae mature from *cis* (DC) to *trans* (DT) face where they become large secretory vesicles (X) which move polysaccharides to the cell periphery where they fuse with the plasma membrane and discharge their contents into the periplasmic space. Small protein-coated vesicles are also shown. *Arrows* indicate the sites of intercisternal fibrils. CW = cell wall, RER = rough endoplasmic reticulum. Scale bar = 1 μm. (Image from Ledbetter and Porter (1970), with permission)

Carnivorous plants typically occupy ecological niches with low nutrient availability such as bogs and swamps. As such, these plants acquire much of their nitrogen and phosphorous by capturing and digesting insects in tubular traps (pitcher plants), sticky pads (sundew), or closable claws (Venus flytrap). The plant then secretes enzymes into the trap, which digest the prey and releases the nutrient from absorption through the trap surface. In such plants, enzyme secretion is meditated by the Golgi apparatus. Refer to ► Chap. 13 for more information on secretory structures.

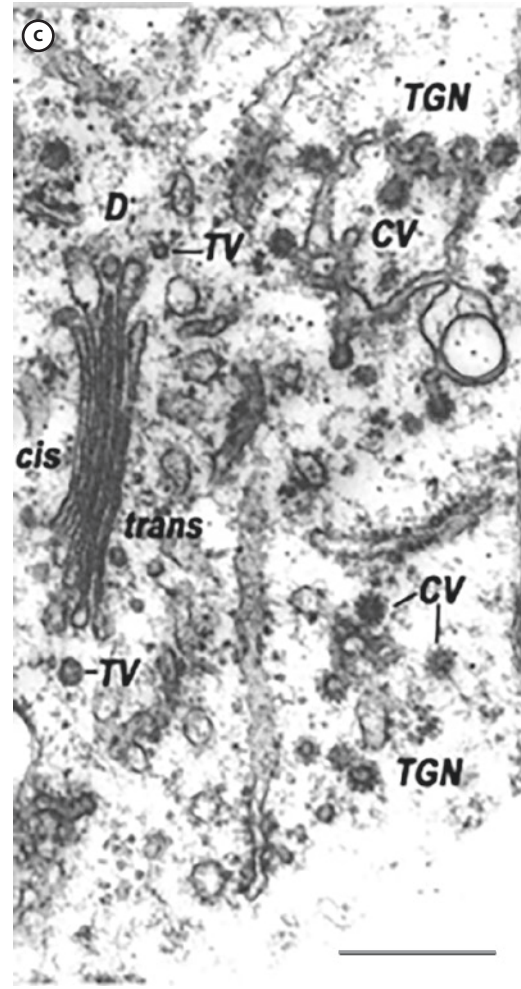


Fig. 3.10 **c** Shown here are a dictyosome (D) and *trans*-Golgi network (TGN), (a.k.a. *trans*-Golgi reticulum) which is the site of protein sorting. Note the clathrin-coated vesicles (CV) and the transport vesicles (TV). Such cells synthesize and secrete digestive enzymes involved in the digestion of captured insects. TEM. Scale bar = 0.5 μm (Crang and Vassilyev 2003)

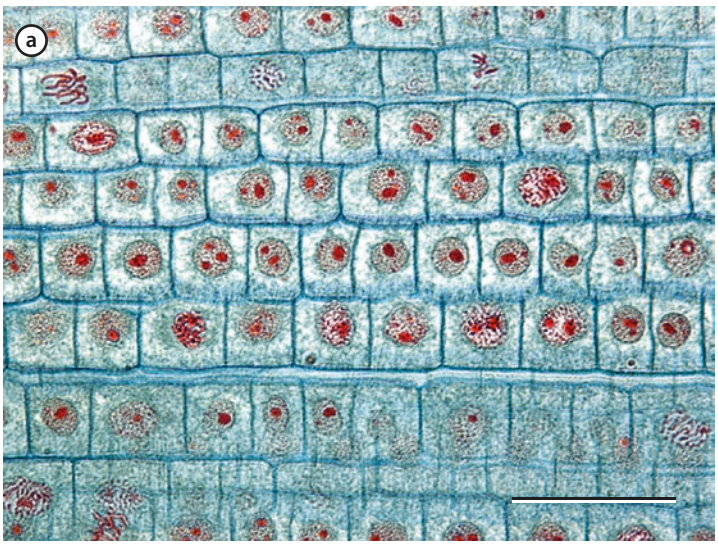
Figure 3.10c shows details of a cell from a secretory cell of the digestive gland of *Drosophyllum lusitanicum*, a carnivorous plant. Unlike cells secreting polysaccharides, in cells producing proteins, there is no shifting of cisternae in the dictyosomal stack from *cis* to *trans* sides. On the contrary, cisternae in the stack remain stationary, and the exchange of the maturing protein among them occurs through small transport vesicles (TV) that successively pinch off and fuse with neighboring cisternae in the trans-direction. Finally, the transport vesicles fuse with the trans-Golgi network (TGN), an irregular body, where sorting of different proteins and

their packing in different secretory vesicles occurs. The digestive enzymes are packed in clathrin-coated vesicles (CV). The name of these vesicles is derived from a spiny coat made of a specific type of protein called clathrin. The coated vesicles bud off the TGN, lose their coat, and move to the plasmalemma. After the fusion of their membrane with the plasma lemma, their cargos, hydrolases, are then released from the cell.

3.11 The Nucleus Houses the Cell's Genetic Material and Participates in Ribosome Synthesis

The **nucleus** is the site of storage of the cell's genetic information, in the form of chromosomes. Recall that plants have three genomes: the plasmid genome contains approximately 100 genes, the mitochondrial genome has 40 or fewer, while the nuclear genome holds between about 26,000 in the thale cress (*Arabidopsis thaliana*, Arabidopsis Genome Initiative, 2000) to 45,550 in black cottonwood (*Populus trichocarpa*; Tuskan et al. 2006). The nucleus is also where the components of cytoplasmic ribosomes are synthesized and partially assembled.

Just as the vacuole is the dominant structure in leaf mesophyll cells, the nucleus is normally the predominant protoplasmic organelle of the cell and thus is one of the largest cellular organelles. In small meristematic cells, such as those shown in ◘ Fig. 3.11a, the nucleus can easily be visualized with the light



◘ **Fig. 3.11** **a** Light micrograph of dividing cells in an onion (*Allium cepa*) root tip. Each cell has a prominent nucleus. Scale bar = 50 µm (RR Wise)

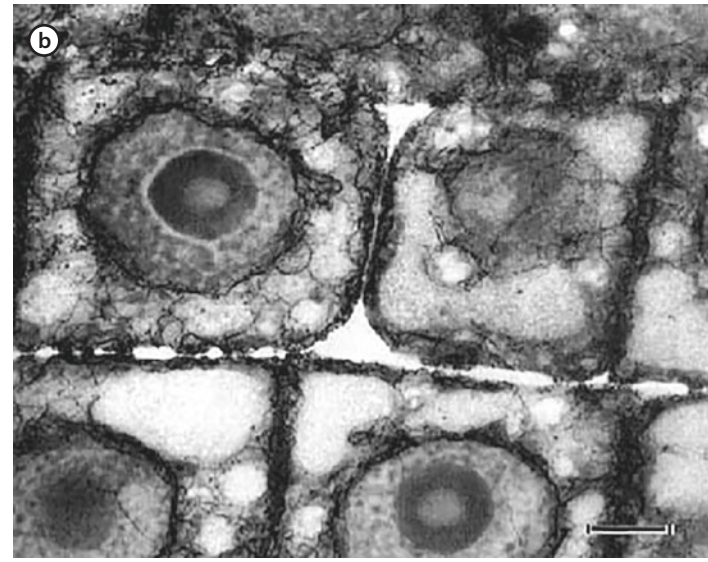


Fig. 3.11 **b** A TEM micrograph showing two rows of cells from a meristematic region of a root with prominent nuclei and their nucleoli and scattered membranes about the cytoplasm with some prominent vacuolated areas. This TEM image is of a thick (one micron) section and therefore shows more cellular structure. Scale bar = 10 μm (Crang and Vassilyev 2003)

microscope and can be seen to occupy a major portion of the cell's volume when viewed in more detail in the electron microscope (Fig. 3.11b).

Nuclei in cells that are actively engaged in protein synthesis typically contain a large **nucleolus**, a substructure within the nucleus that participates in ribosome synthesis. The transmission electron micrograph in Fig. 3.11c illustrates a nucleus from an African violet. The nucleolus is the center of production for ribosome precursors (rRNA and imported proteins), which constitute the granular component. These particles are smaller than ribosomes in the cytoplasm, and only after they pass through the nuclear pores do they acquire the remaining proteins to become full-sized and mature ribosomes.

The nucleus is bounded by a double-membrane envelope that is perforated with numerous nuclear pores (Fig. 3.11d, e). Nuclear pores are gateways, which regulate the exchange of RNA and proteins between the nucleus and cytoplasm. More than merely a hole in the envelope, the pores are actually a complicated protein complex that spans the two membranes and selectively regulates the trafficking of molecules into and out of the nucleus.

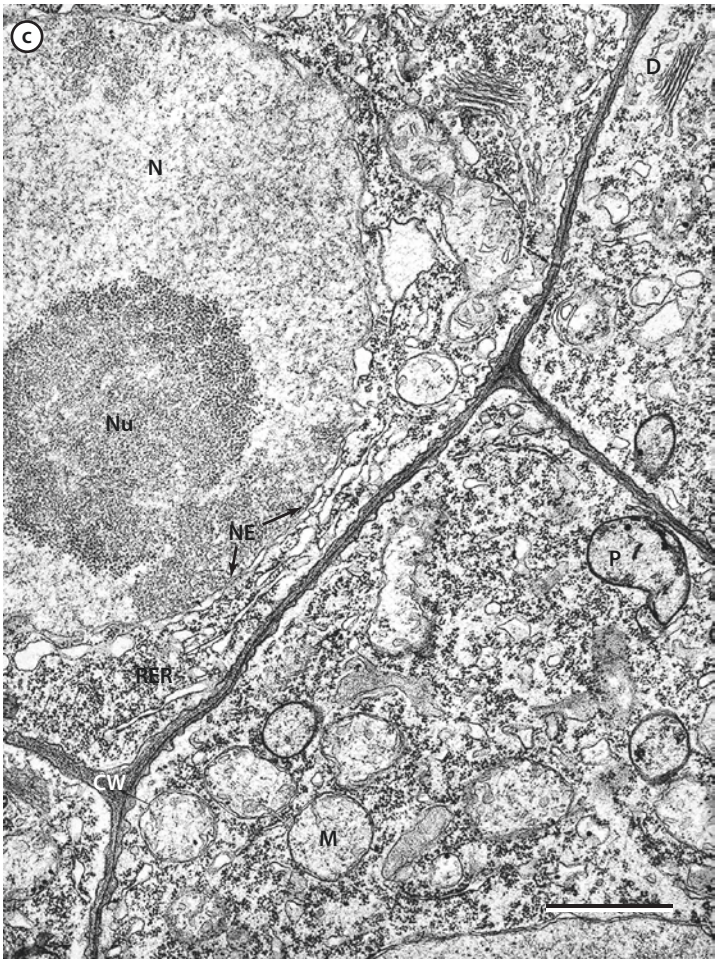


Fig. 3.11 **c** TEM image of a portion of a nucleus from undifferentiated sporogenous tissue of African violet (*Saintpaulia ionantha*). The nucleus (N) occupies a major portion of the cell volume. The genetic material of this interphase nucleus is formed of diffuse (most active) and condensed (least active) chromatin. The large nucleolus (Nu) consists of intermingled granular and fibrillar components which are responsible for assembling ribosomes. NE = nuclear envelope, CW = primary cell wall, D = dictyosome, P = plastid, M = mitochondrion, RER = rough endoplasmic reticulum. Scale bar = 5 µm. (Image from Ledbetter and Porter (1970), Introduction to the Fine Structure of Plant Cells, Springer-Verlag, with permission)

3.12 The Cytoskeleton Organizes the Cell and Helps Traffic Organelles

The **cytoskeleton** is an architectural framework of protein strands found in the cytoplasm of all eukaryotic cells. It is composed of two types of components: structural and force-generating. All eukaryotes have a cytoskeleton, but recent research has shown that there are significant differences between the cytoskeletal proteins of plant and animal cells.

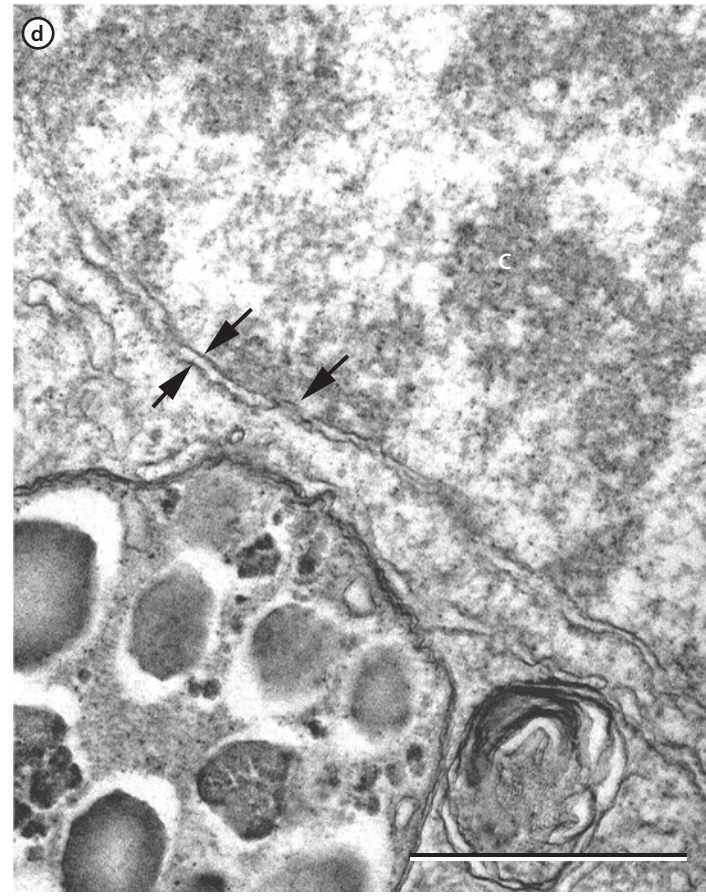


Fig. 3.11 **d** TEM image showing a portion of a nucleus (*top right*) and amyloplast (*bottom left*) in a mung bean (*Vicia faba*) root tip. Note the two membranes of the nuclear envelope (*between the two arrows*), nuclear pore (*single arrow*), and condensed chromatin (C). Scale bar = 5 μm (RR Wise)

In plants, microtubules and microfilaments (Fig. 3.12a) are the two structural fibers that form the scaffolding of the cytoskeleton while individual motor proteins generate force and move vesicles and organelles along the fibrous scaffold. A third class of cytoskeletal proteins which are purely structural, the so-called **intermediate filaments**, are present in animal cells but are not found in plant cells. Intermediate filaments play multiple roles in animals and are a main component of hair, nails, and skin. They also form a supportive network to the interior of the nuclear membrane. While hair, skin, and nails are not found in plants, analogous structural proteins can be found in plant nuclei.

Microtubules (MT) are polymers of the globular protein **tubulin**, which occurs as dimers of α- and β-tubulin subunits. The subunits are packed in a spiral manner with a hollow core. In cross section, the tubule diameter is approximately 25 nm and typically

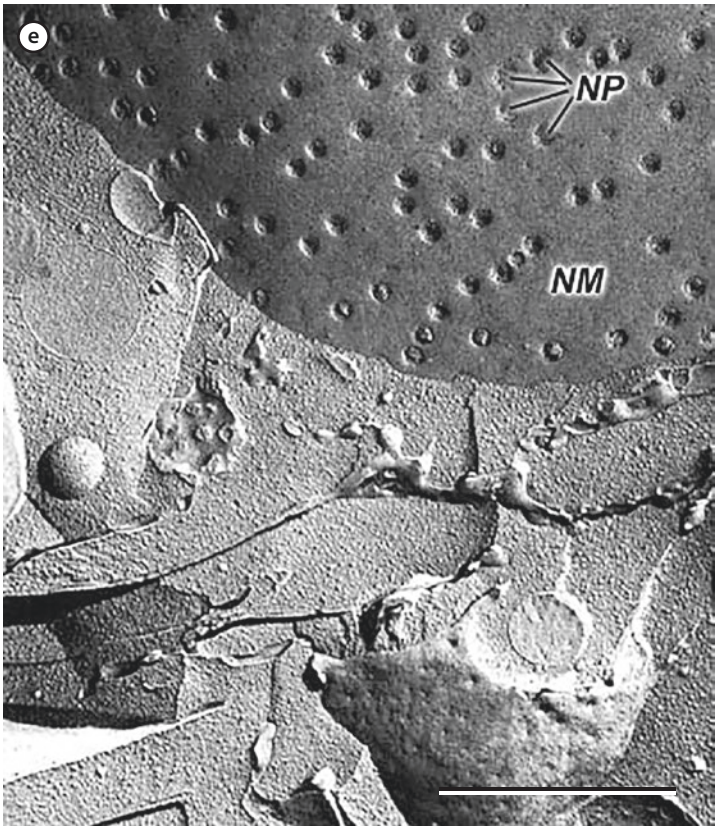


Fig. 3.11 **e** A freeze-fracture TEM image of the surface of a nuclear envelope membrane (NM) in face view with numerous nuclear pores (NP). Scale bar = 5 μm. (Illustration modified from Jensen and Park 1967, Cell Ultrastructure, Wadsworth Publishing Co., Inc.)

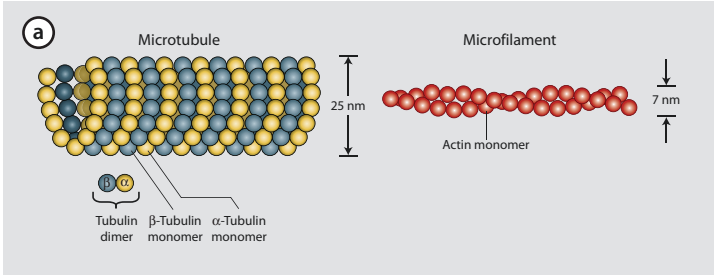


Fig. 3.12 **a** The two classes of structural proteins found in plant cell cytoskeletons (Redrawn from Crang and Vassilyev 2003)

shows 13 subunits (Fig. 3.12b). Microtubules play numerous important roles in the plant cell (refer to Hepler et al. 2013 for a historical perspective). Microtubules are primarily known for their role in the movement of chromosomes during nuclear division and in the formation of the cell plate during cytokinesis, but in interphase cells they are usually confined to the cell periphery. Such cortical microtubules are involved in orienting and depositing

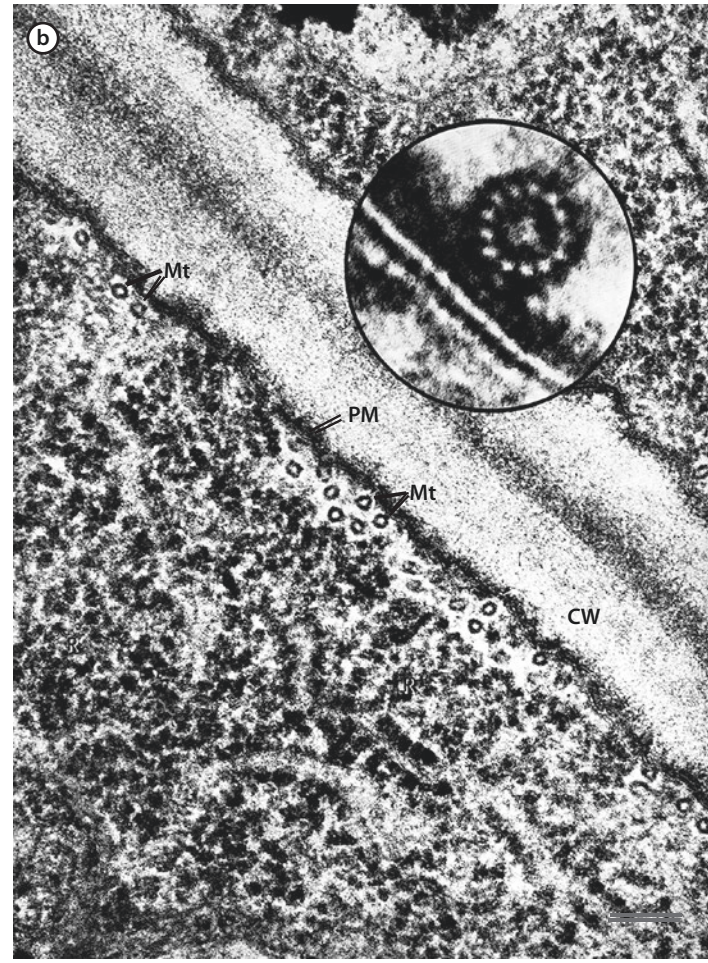


Fig. 3.12 **b** Plant microtubules are shown here in close association with the plasma membrane. The inset demonstrates a very high-resolution TEM image of a single microtubule from a root tip cell of juniper (*Juniperus chinensis*) in cross section revealing 13 subunits of structure around a hollow core. CW = cell wall, Mt = microtubules (in cross section), PM = plasma membrane. Scale bar = 1 μm. (Image from Ledbetter and Porter (1970), Introduction to the Fine Structure of Plant Cells, Springer-Verlag, with permission)

cellulose of plant cell walls, and some give shape to the cell prior to the deposition of the cell wall.

In animal cells, the motor protein **kinesin** is responsible for force generation and vesicle trafficking along microtubule tracks. However, the motor kinesins of plant play a much reduced role, as compared to animal cells. Instead, vesicle trafficking, organelle orientation, and cytoplasmic streaming are all mediated in plant cells by an actomyosin system. **Microfilaments** (MF) are polymers of the protein actin and are smaller than MTs, typically, solid rods about 7 nm in diameter. Microfilaments provide the tracks along which cytoplasmic streaming and the independent movement of organelles and vesicles occur. The motor protein myosin is attached at one end to a vesicle, mitochondrion, or chloroplast. It uses the energy in ATP molecules to travel along

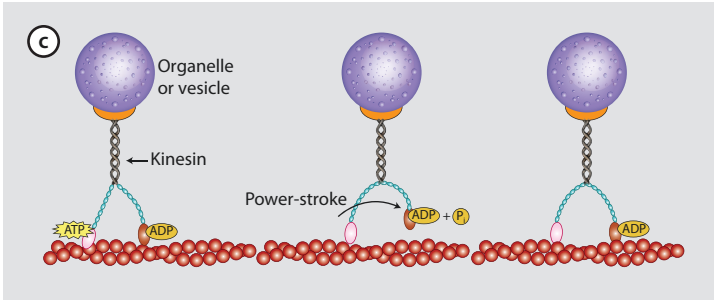


Fig. 3.12 **c** Organelle movement driven by the plant cell actomyosin system (Redrawn from Crang and Vassilyev 2003)

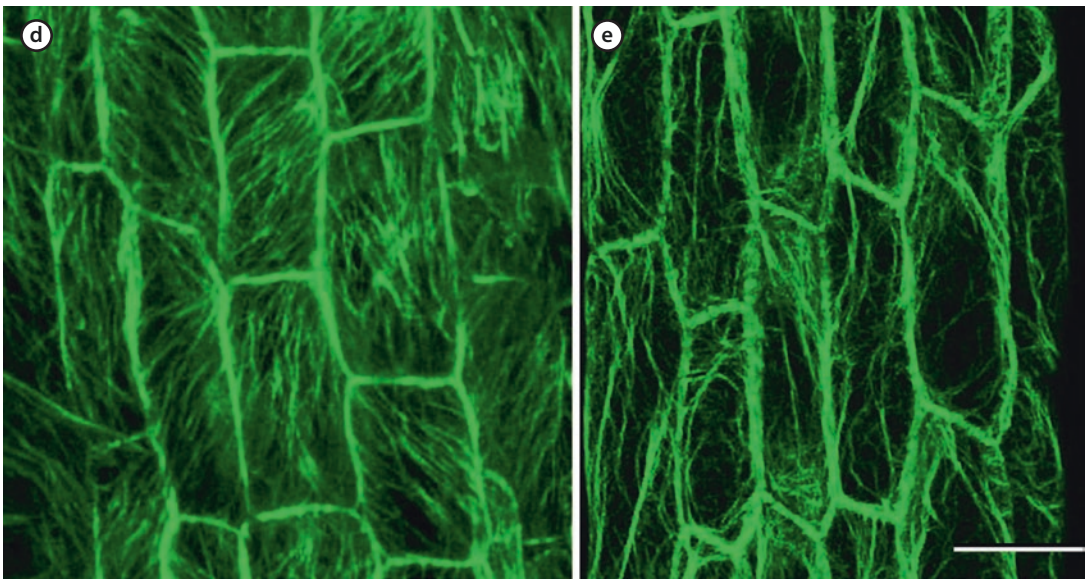


Fig. 3.12 **d** Green fluorescent protein-labeled microtubules in alfalfa (*Medicago sativa*) root cells. The diagonal and diffuse orientation of the MTs probably relates to the direction of primary cell wall synthesis. **e** GFP-labeled microfilaments from Arabidopsis roots. Note that the microfilaments are thinner than the microtubules and arranged at the periphery of the cells. Scale bar in **e** = 50 µm for both panels. (**d**, **e** Images courtesy of Nobel Foundation, Ardmore, OK)

the MFs in a stepwise fashion dragging the cargo vesicle or organelle along with it (Fig. 3.12c). The rate and extent of cytoplasmic streaming can be quite impressive with speeds reaching 10 µm sec^{-1} and the entire cell contents swirling when viewed in the microscope.

Over the life of the cell, the MT and MF networks repeatedly disassemble (depolymerize) and reform (polymerize) to accommodate changes in cell shape or in response to stress. In a mature, nondividing cell, the microtubule system forms a network throughout the cytoplasm that aligns primarily with the orientation of the cellulose synthetic machinery used for primary cell wall production (Fig. 3.12d), as described in ▶ Chap. 5. Microfilaments, on the other hand, are arranged in the cytoplasm where they direct the movement of organelles during cytokinesis (Fig. 3.12e).

3.13 Chapter Review

■ Concept Review

3.1 *Plant cells are complex structures*. Many structural details of plant cells can be revealed through the use of electron microscopy that can employ both descriptive and quantitative information.

3.2 *Plant cells synthesize an external wall and contain a variety of internal compartments*. Surrounded by an external cell wall and an adjacent interior plasma membrane, the cellular cytoplasm contains many varied organelles.

3.3 *Cells and cell organelles are typically bound by phospholipid bilayer membranes*. High-resolution transmission electron microscopy reveals that membranes often appear as two parallel dense lines due to the preparatory stain deposit at the site of hydrophilic phosphate groups from a lipid bilayer. Membranes are designated as being "mosaic" due to various proteins that may be anchored at specific sites or mobile on either side of the lipid bilayer and play a large number of important roles in structural and metabolic functioning.

3.4 *Vacuoles play a role in water and ion balance*. Vacuoles, a major characteristic of plant cells, exchange water and ions with the cytoplasm to help maintain cellular water balance. Toxic substances, pigments, and waste products as well as hydrolytic enzymes may also be stored in the vacuoles of some cells.

3.5 *Plastids are a diverse family of anabolic organelles*. There are approximately a dozen different types of plastids found in various plant tissues and organs. As a group, they function to synthesize all the biomolecules needed for plant life and play additional roles in sensing and responding to the environment.

3.6 *Plastids are developmentally related*. All types of plastids are derived from proplastids and are found in virtually all parts of the plant. Many different developmental patterns are found in the conversion to specific types of plastids at all stages of the plant life.

3.7 *Mitochondria synthesize ATP and small carbon skeletons*. Mitochondria are organelles with two membranes that carry out advanced stages of aerobic respiration. The outer membrane is functionally similar to other cell membranes, whereas the inner membrane functions to produce ATP by means of chemiosmosis on a folded surface. Enzymes of the citric acid cycle are only found in the matrix. Mitochondria assume many three-dimensional forms and may vary from a few to approximately 100 per cell.

3.8 *Microbodies are the site of specific biochemical pathways*. These organelles are bounded by a single membrane and lack internal membranes and DNA. They often contain high levels of enzymes or proteins, sometimes in a crystalline form. In leaves, they are designated as peroxisomes and oxidize glycolate to produce peroxides that in turn is decomposed by catalase, a process termed photorespiration. A second type of microbody designated as glyoxysomes functions with mitochondria to break down long chain oils for respiration and growth.

3.9 *The endoplasmic reticulum synthesizes proteins and some lipids*. Rough endoplasmic reticulum (with ribosomes attached to the membrane) produces, stores, and transports proteins. Smooth endoplasmic reticulum (without attached ribosomes) is relatively rare in plants, but when found in secretory structures, it may synthesize oils or terpenes.

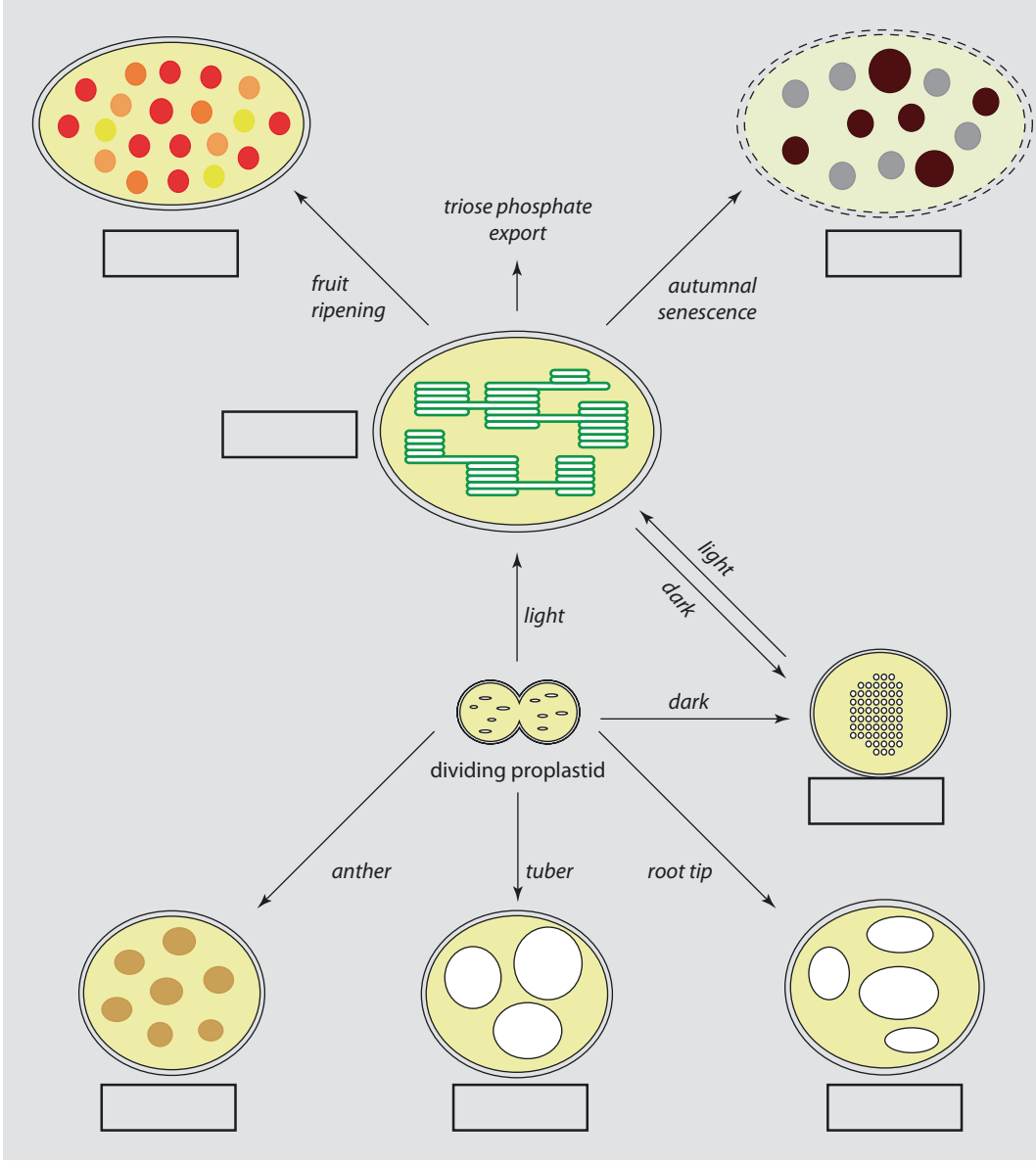
3.10 *The Golgi apparatus processes and packages polysaccharides and proteins for secretion*. The Golgi apparatus is comprised of functionally similar distinctive dictyosomes that transport certain proteins and carbohydrates in vesicles and subsequently to the cell surface for possible discharge. Based on function, there may be one to several Golgi apparatuses per cell. Dictyosomes play a significant role in the secretion of enzymes as found in carnivorous plants.

3.11 *The nucleus houses the cell's genetic material and participates in ribosome synthesis*. In addition to storing the genetic material, the nucleus contains a nucleolus which functions in the synthesis of ribosomes which come to full size after being transported through nuclear pores and into the surrounding cell cytoplasm.

3.12 *The cytoskeleton organizes the cell and helps traffic materials*. A plant cytoskeleton is a framework of protein strands composed of both structural and force-generating components. Microtubules and actin filaments give rise to the shape of the cell and the formation of the cell wall, whereas microtubules direct the movement of chromosomes during mitosis and meiosis. Motor proteins (forms of kinesin) move vesicles from Golgi trans face to cell surface and in other building processes driven by energy from ATP.

■ Concept Connections

? 1. On a separate sheet of paper, identify a name and at least one function for each of the plastid types shown in the figure below.



■ Concept Assessment

? 2. The cytoskeleton of a cell is comprised of
   a. cell wall and membranes.
   b. nucleus and cytoplasm.
   c. intrinsic and extrinsic proteins.
   d. microtubules and microfilaments.
   e. organelles and crystals.

3. Photorespiration is primarily a function of
   a. chloroplasts.
   b. microbodies.
   c. microtubules.
   d. mitochondria.
   e. dictyosomes.

4. In membranes, sugar groups are most likely associated with
   a. inner phospholipid layer.
   b. outer phospholipid layer.
   c. intrinsic proteins.
   d. intercalated cholesterol.
   e. hydrophobic unsaturated lipid chains.

5. The organelle most responsible for cellular water balance is the
   a. nucleus.
   b. chloroplast.
   c. vacuole.
   d. cell wall.
   e. cytoskeleton.

6. If the mitochondrion is the cell's powerhouse, the _____ is the cell's blueprint library.
   a. tannosome.
   b. ribosome.
   c. gerontoplast.
   d. nucleus.
   e. nucleolus.

7. To synthesize a protein and secrete it to the cell wall, a cell would need to use the
   a. nucleus.
   b. ribosomes.
   c. rough endoplasmic reticulum.
   d. golgi apparatus.
   e. all of the above.

8. What is the main anabolic organelle of the plant cell?
   a. nucleus.
   b. golgi apparatus.
   c. rough endoplasmic reticulum.
   d. vacuole.
   e. plastid.

9. What is the function of the cytoskeleton?
   a. organize the cell interior.
   b. synthesize ATP and small carbon skeletons.
   c. traffic vesicles through the cytoplasm.
   d. photosynthesis and photorespiration.
   e. a and c.

10. Ribosomes are found in the
    a. cytoplasm.
    b. chloroplast.
    c. vacuole.
    d. mitochondrion.
    e. a, b, and d.

11. Respiration involves the
    a. glyoxysome.
    b. gerontoplast.
    c. golgi apparatus.
    d. peroxisome.
    e. guard cell chloroplast.

■ **Concept Applications**

12. Plants have the ability to synthesize 100% of the biomolecules and high-energy molecules needed for life. If you were to genetically engineer a cat or a dog to do the same, what processes or organelles would you need to put into your pet?

13. Use the internet to search for the term "kleptoplast." How are kleptoplasts related to other plastid types? How are they different?

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