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NATURE AND STRUCTURE OF HARVESTED PRODUCTS

How plants and plant products are handled after harvest and the changes that occur within them during the postharvest period are strongly influenced by their basic structure. For example, plant parts that function in nature as storage organs behave after harvest in many ways that are distinctively different than structurally dissimilar parts such as leaves or flowers. Consequently, it is desirable to be familiar with the structure not only of the general product but with the tissues and cells that comprise it. This chapter describes general morphological groupings of harvested products, the tissues that are aggregated to form these products, and the structure of the cells that make up these tissues.

One extremely important concept of plant morphology is that structure, whether at the organ, tissue or the cellular or subcellular level, is not fixed, but is in a state of transition. Changes in structure are especially important during the postharvest period. A structural unit once formed is eventually destined to be degraded and recycled back to carbon dioxide. Marked changes in structure occur with eventual use of the product (e.g., consumption of a food product) or loss due to pathogen invasion. Although less dramatic, distinct and important structural alterations occur in plant products during storage and marketing. Formation of fiber cells, loss of epicuticular waxes during handling, and chloroplast degradation or transformation are but a few of many changes that can occur. At the cellular and subcellular level, very pronounced changes occur and these intensify as the product approaches senescence, or as in the case with seeds and intact plants, during the beginning of renewed growth. It is of paramount importance, therefore, that we view organs, tissues, cells and subcellular bodies of harvested products as structural units in a state of change. Decreasing this rate of change is in most cases an essential requisite for successful extended storage of the product.

1. GROUPING OF HARVESTED PRODUCTS BASED ON MORPHOLOGY

The range of plant products that are harvested and used by mankind is vast and the characteristic responses after harvest are so varied that some system of grouping or classification is necessary. Our interest in postharvest biology stems from the practical requirement of getting perishable plant products from producers to consumers and maintaining the desired supply and quality throughout the year. The classification most useful for this purpose is one which brings together products with similar environmental requirements after harvest for maintenance of quality or those that are susceptible to chilling or other types of injury. Although this system is extremely useful to the practical operator, it does not help us to understand the na-

ture of the harvested produce. Likewise, classification according to the product's use, that is, fruits, vegetables, florist items, nursery products, agricultural seed products, does not aid in understanding those products and there is often considerable overlap of the categories. For example, foliage is not only used as a florist item but also as vegetative cuttings and edible vegetables. Their characteristic postharvest behavior is very similar, irrespective of the end use. Fruits such as tomato are used as vegetables but still ripen like other fruits. Understanding the nature of the product, rather than for what it is to be used, is more useful and allows prediction of the likely response of harvested products.

Botanical classification into family, genus, and species is of only limited value with regard to postharvest handling.* Whole plants or any of the separate organs from that plant may have vastly different characteristics and behavior, yet all are from the same botanical specimen.

A classification according to plant part and stage of development is a satisfactory alternative. It allows an understanding of the nature of the harvested product, and therefore a means of predicting behavior. Both physical and physiological characteristics are indicated. It should be recognized that classifications are systems devised by scientists and applied to the subject of their choice to serve a particular purpose. In this case, the intent is to classify harvested plant products in order to reduce their number for easy management and to be able to predict the behavior and handling requirements of products for which there is no specific information available. Because of the very nature of biological systems and the inherent variation both within and among species, as well as the wide range of uses of plant products, no classification system can be perfect. For example, the storage temperature requirements for sweetpotato and beetroot, both root crops, differ substantially. As a consequence, scientists must be prepared to allow for the exceptions and to refine or alter the classification for specific purposes.

Classifying according to plant part and knowing the characteristics of those parts makes it easier to understand the current and potential processes that may be operative during the postharvest period.

1.1. Intact Plants

Whole plants are considered to be harvested when they are removed from the production environment. They retain both the shoot and root system which may or may not still be associated with soil or growing media. Whole plants should have little or no harvest injury and maximum capacity to continue or to recommence growth and development. They commonly have access to all the normal requirements for plant growth, that is, water, mineral nutrients, oxygen, carbon dioxide and light (energy) and are susceptible to all the influences on plant growth: physical, chemical and biological.

Germinated seed such as bean or alfalfa sprouts have the endosperm as an energy source and do not require light. They have a very high metabolic rate and release a substantial amount of heat. In the juvenile shoot, there has been little development of the cuticle and the roots are exposed. The seedlings are therefore very susceptible to water loss and to mechanical damage.

Bare root seedlings and rooted cuttings are physiologically more developed than germinated seeds, but are also very subject to water loss and mechanical damage. These young plants do not have stored reserves, as do germinated seeds, so are dependent on either continued photosynthesis or minimized metabolic rate for maintenance of quality. More mature whole plants can tolerate harsher conditions as they are in general less brittle, have a better-developed cuticle and have accumulated some stored reserves. The extreme is seen in dormant

*Botanical classification can, however, be useful in tracing the evolution of certain traits.

woody plants where metabolic rate is suppressed and leaves and active feeder roots are absent, so susceptibility to water loss, mechanical damage and microbial infection is greatly reduced.

It is easier to maintain the quality of intact plants marketed in containers. The root systems are not exposed and as a consequence, are less subject to stress and mechanical damage. The medium around the plant roots provides a reservoir of mineral nutrients and water, increasing the amount of water available to the plant. Water, however, will be depleted unless it is periodically replenished or the plant is kept in an environment where water loss does not occur. Very often during retail sales, containerized plants are subjected to water stresses of sufficient magnitude to result in quality losses.

Tissue cultured plants are a special type of containerized intact plants. Due to the special environment under which they are produced, they are particularly delicate, but at the same time, they are relatively well protected within the microenvironment of their containers. Their compact size and controlled environment often enables them to be shipped through normal mail and parcel delivery systems that are not accustomed to handling live material. Special precautions, however, are necessary to maintain orientation, to protect from temperature extremes and to avoid prolonged delays.

1.2. Detached Plant Parts

Plant organs utilized by humans come from virtually every portion of the plant. This fact is perhaps best illustrated by vegetables (Figure 2.1), which range from immature flowers to storage roots.

1.2.1. Aboveground Structures

a. Leaves

Leaves, widely consumed as foods, are also utilized for ornamental purposes. In some cases, they may also represent propagules for asexually reproducing plants. Morphologically the leaves of most dicotyledonous plants are comprised of a leaf blade, the thin flattened portion of the leaf, and a petiole which attaches the blade to the stem. Many of our leafy crops have intermediate-to-large petioles (e.g., spinach, collards, Ceylon spinach), while others have only sessile (having the blade attached directly to the stem) or very much reduced petioles (e.g., Chinese cabbage, lettuce, cabbage). Several species have been developed in which the leaf petiole is the product of interest (e.g., celery, rhubarb). However, these tend to have significantly different postharvest responses and as a consequence are covered separately.

While attached to the plant, the primary function of a leaf blade is the acquisition of carbon through photosynthesis. Leaves also control, to a large extent, transpiration by the plant, which helps to regulate their temperature. After harvest, these functions are seldom operative. The leaf loses its potential to acquire additional carbon (energy) and is cut off from its supply of transpirational water. Hence the energy required by the cells of the leaf for the maintenance of life processes must now come from recycled carbon found within. Leaves of most species do not act as long-term carbon storage sites. This lack of energy reserves decreases their potential postharvest life expectancy. As a consequence, leaves are stored under conditions that will minimize the rate of utilization of these limited energy reserves.

Water loss from harvested leaves is an additional limitation to long-term storage. With detachment from the plant, the leaves can no longer replenish water lost through transpiration. The leaf responds with closure of the stomata, the primary avenue of water loss. Closure greatly decreases the rate of water loss, but does not eliminate it.

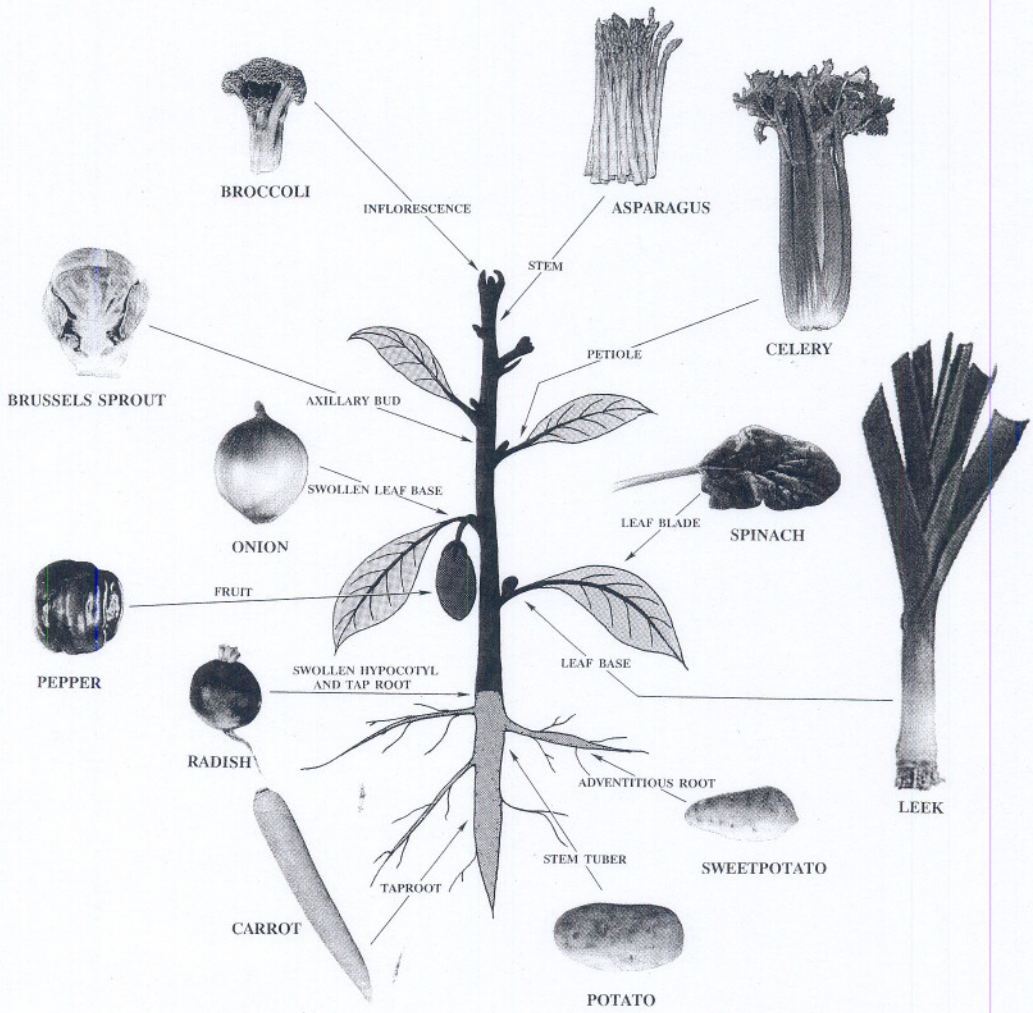


Figure 2.1. Plant organs utilized by man are derived from virtually every portion of the plant. The diagram illustrates examples of various plant organs used as vegetables.

The exterior surface of leaves of some species (e.g., cabbage and collards) is covered with a relatively thick waxy cuticle that helps to decrease water loss. The rate of water loss, therefore, is modulated by both the nature of the product and the environmental conditions in which it is stored. Thus leafy products are usually stored under conditions of high relative humidity and a reduced temperature to minimize the loss of water.

Another method that is used to help increase the longevity of leafy products is harvesting the leaves and stem intact. Although the stem may not be consumed, it acts as a reservoir for both water and carbon, helping to increase the life expectancy of the leaves.

b. Petioles

With intact plants, petioles of dicotyledonous leaves function as conduits for the transport of photosynthates from the leaf to sites of utilization and for the transport of water and nutrients

from the root system to the leaf. The petiole also provides support and positioning for the leaf within the aerial canopy of the plant. In a few cases, the petiole acts as a site for the storage of photosynthetic carbon.

Several plants have well-developed fleshy petioles which are the primary morphological component. Celery, rhubarb and pak-choi are utilized either exclusively or largely for their edible petioles.[27] These petioles tend to have more stored energy reserves than the leaf blades. They also lose water less readily due to a smaller surface-to-volume ratio and fewer disruptions in the continuity of the surface. Thus products such as celery and rhubarb have a considerably greater potential storage duration than whole leaves. Nevertheless, losses of water and carbon remain of critical importance and storage conditions very similar to those for whole leaves are utilized for petioles.

c. *Stems, shoots and spikes*

Postharvest products in which the stem is a primary or essential component can be separated into two general classes. (1) Products such as asparagus, coba, sugarcane, celtuce, kohlrabi, tsatsai and bamboo shoots are utilized almost exclusively for their stem tissue even though rudimentary leaves may be present. (2) With many ornamental foliages and floral spikes, the stem represents an essential part of the product although it is generally considered as secondary to the leaves and/or flowers present. Common examples would be gladiolus spikes or any one of many species used for cut foliage. The former class tends to be largely meristematic or composed of very young tissues and is metabolically highly active. They typically can continue to take up water and elongate if placed on moist pads or in shallow pans of water. Exceptions to this would be kohlrabi and tsatsai which are formed at the base of the stem and are more mature and metabolically less active. Products such as ornamental asparagus and floral spikes have developed leaves and/or flowers. These also have relatively high metabolic rates and can continue to take up water if handled properly.

Several stem products (e.g., gladiolus and flowering ginger spikes or asparagus spears) exhibit strong gravitropic responses after harvest. If stored horizontally, the apical portion of the stem will elongate upward, producing a bent product of diminished quality.

Optimum storage conditions vary in this relatively diverse group; however, moist cool conditions predominate. Holding the cut base of the stem in water is either desirable or essential for many stem crops.

d. *Flowers*

Flowers are compressed shoots made up of specialized foliar parts that are adapted for reproduction. A significant number of harvested plant products are, in fact, flowers. Flowers represent a diverse group varying in size, structure, longevity and use. Uses range from aesthetic appeal to articles of food (e.g., cauliflower, broccoli, lily blossoms).

Flowers are made up of young, diverse, metabolically active tissues, typically with little stored carbon. There are distinct limits on potential longevity when detached from the parent plant, even when held under optimal conditions. In fact, while attached to the parent plant, many of the flowers structural components display only a brief functional existence. Anthesis or flower opening represents a very short period in the overall sequence from flower initiation to seed maturation. Almost invariably, floral products are highly perishable, seldom lasting more than a few weeks after harvest.

From a handling and storage perspective, flowers can be separated into two primary groups: those that are detached from the parent plant at harvest and those that remain attached. Most floral products fall into the former classification. As with other detached plant

parts, after harvest they are unable to fix additional carbon through photosynthesis* nor are they able to import photosynthate from adjacent leaves on the parent plant. With many floral products, attached stems represent a reserve of carbon and water that can in part be utilized by the flower. In many cases, this reserve greatly extends the potential longevity of the individual flowers. Thus flower crops are typically made up of much more than just the floral tissues. Attached stems and leaves represent important components and these structures often strongly influence the postharvest behavior of the flower.

Some flowers are marketed attached to the parent plant (e.g., potted chrysanthemum or azalea). The flower or flowers may represent the sole reason for purchase or their presence may simply enhance the attractiveness of the plant, which is the article of primary interest. Both advantages and disadvantages are realized during the postharvest period by having the flowers attached to the parent plant. While the flowers benefit from a continued supply of photosynthate, water and minerals, storage conditions are generally dictated by what is best for the entire plant and not for the flowers alone. Optimal storage temperature for the plant may not necessarily coincide with the optimal storage temperature of the flower.

Individual flowers are borne on a stem or flower stalk, the structure and arrangement of which varies widely between species. They may be found as a solitary flower or on spikes, umbels, panicles and other variations. Structurally a complete flower is made up of sepals, petals, stamens, and pistil borne on a receptacle. Incomplete flowers lack one or more of these floral parts.

The sepals, from the Greek word for covering, are often leaf-like scales that make up the outermost part of the flower. Although leaf-like, the sepals are structurally not as complex as leaves. Usually they are green, although on some species they may have the same coloration as the petals. Collectively, the sepals of a single flower are called the calyx.

The petals (the Greek word for flower leaves) are also modified leaves, and as with the sepals, they are of greater structural simplicity than an actual leaf. The petals of the flower, especially those utilized for their ornamental appeal, are generally brightly colored and showy. Collectively the petals are called the corolla and the petals and sepals the perianth.

Interior to the petals are the pollen bearing parts of the flower, the stamens. The upper portion of a stamen, which produces the pollen, is the anther. This is supported on a slender stalk called the filament. While this male floral part is occasionally found singly, usually there are multiple stamen within a flower. Together, the stamens within a single flower make up the androecium.

The female portion of the flower is the pistil. Structurally it is comprised of three major parts: the stigma, which is the apical tip of the pistil that acts as the receptive surface for the pollen; the style, which is an elongated column of tissue connecting the stigma with the ovary; and the ovary, which is at the base and is the reproductive organ of the flower. Within the ovary are individual ovules attached to the placenta that develop into seeds when fertilized. The pistil may be composed of a single carpel or several carpels fused together. Collectively the carpels make up the gynoecium.

e. Fruits

A fruit is a matured ovary plus associated parts; this includes both the fleshy fruits of commerce such as banana and apple—products normally associated with the term "fruit"—and dry fruits such as nuts, legumes, and siliques. Many of the vegetables we utilize are, in fact, botanically fruits (e.g., tomato, squash, melons, snapbean). It is evident, therefore, that the

*Photosynthesis can occur under the appropriate conditions; however, the rate is exceedingly low.

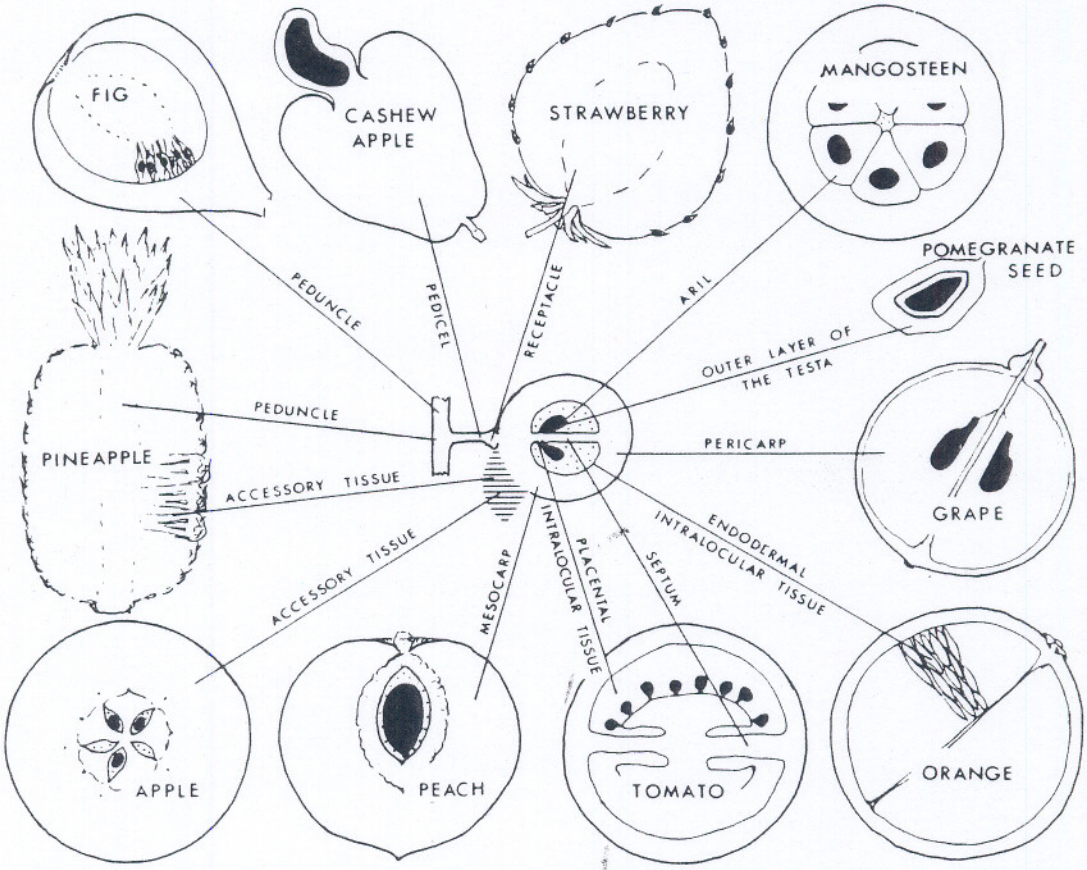


Figure 2.2. A wide range of inflorescence structures can become fleshy and make-up the edible portion of fruits. The diagram illustrates the origin of the fleshy portion of a number of common fruits (*from Coombe*[13]).

term "fruit" encompasses a very broad range in morphological, biochemical and physiological variation.

i. Fleshy Fruits

The actual morphological part of fleshy fruits that is consumed varies widely (Figure 2.2). The fleshy portion can be derived from either the pistil or from parts other than the pistil (accessory parts). The ovary wall, which matures into the pericarp, can be substantial in some fruits. It is subdivided into three regions: the exocarp, mesocarp, and endocarp (from the outside inward). Practically all parts of the floral structure can develop, in various species, into the fleshy part of the fruit. In the peach, the edible portion is principally mesocarp tissue. In many species the accessory tissues of the fruit dominate over the carpellary tissue, making up a majority of the fruit's volume. For example, with the apple the edible portion is perianth tissue, whereas in the strawberry it is largely receptacle tissue. Because of this diversity in morphological makeup of various fruits, an equally wide range in chemical composition between various types of fruits and in biochemical changes within these tissues after harvest should be anticipated.

Fleshy fruits may be divided into several subclasses based on their morphology.

Berry—A pulpy fruit from a single pistil with one or more carpels with several-to-many seeds (e.g., tomato, papaya).

Hesperidium—Fruits of several carpels with a leathery rind and inner pulp juice sacs or vesicles [e.g., orange, lime, grapefruit, lemon).

Pepo—Fruits derived from an inferior ovary that develops from multiple carpels bearing many seeds (e.g., squash, cucumber, melons).

Drupe—A simple fruit where the mesocarp tissue becomes thick and fleshy and the endocarp stony (peach, plum, cherry, olive).

Pome—A simple fruit comprised of several carpels, the edible portion of which is made up of accessory tissue (e.g., apple, pear).

Thus mesocarp, aril, peduncle, pedicel, receptacle, testa, placental, endodermal and other tissues may, in respective fruits, represent all or a major portion of the fleshy edible part of the crop (Figure 2.2). As a consequence, classification of fruits on a strict morphological basis is not overly useful after harvest in that handling and storage requirements do not follow the same classification.

From a postharvest viewpoint, it is more useful to separate fleshy fruits into those that have the potential to ripen after harvest (climacteric fruits) and those that must be ripe when gathered (nonclimacteric fruits). Climacteric fruits such as apples, tomatoes, pears and bananas typically have much more flexibility in the rate at which they may be marketed. For example, it is possible to store mature, unripe apples for as long as 9 months before eventual ripening. This flexibility greatly alters how we approach the postharvest handling, storage and marketing of these products. Most nonclimacteric fruits are ripe at harvest and, although there are notable exceptions to their potential storage duration (e.g., dates and citrus), many have relatively short storage lives. As a consequence, these fruits tend to be marketed relatively quickly.

ii. Dried Fruits

With dried fruits, the fruit wall is sclerenchymatous and dry at maturity. Seldom is the entire fruit utilized; in food crops, typically only the seed represents the article of commerce. Crops such as wheat, rice and soybeans or seeds of many other species are examples of species in which a portion of the dried fruit is used. In contrast to the fleshy parenchymatous tissue of succulent fleshy fruits, the fruit wall of these species is dry at maturity. In a number of dried fruit species, the integuments are completely fused to the ovary wall such that the fruit and seed are one entity (grains, grasses). Likewise, they may also have accessory parts such as bracts that remain attached. Many dried fruits are dehiscent with the fruit wall splitting open at maturity. Most dehiscent fruits contain multiple ovules. Thus dehiscence represents a means for dispersal of the individual seeds. Dried fruits, both dehiscent and indehiscent, can be divided into several subclasses based on fruit morphology. The following are subclasses of dehiscent fruits.

Capsule—The fruit is formed from two or more united carpels each of which contains one-to-many seeds. Common examples of capsules would be the fruits of the poppy, iris and Brazil nut.

Follicle—The fruit is formed from a single carpel that splits open only along the front suture at maturity. Follicles are found widely in floral crops such as the peony, delphinium and columbine.

Silique—The fruit is formed from two united carpels splitting two long halves that are separated longitudinally with the seeds attached. Examples would be fruits in the Brassicaceae family such as those of the radish or mustard.

Legume—The fruit is formed from a single carpel which splits along two sides when mature. Examples would be soybean and the common bean.

Indehiscent fruits often contain a single seed and do not split open upon reaching maturity. The following are subclasses of dehiscent fruits.

Achene—It is a thin-walled fruit containing one seed and in which the seed coat is free, attached to the pericarp at only one point. Examples of species having achenes are the strawberry, sunflower and *Clematis* spp. Although the fruit of the strawberry is botanically a dried fruit, the crop is treated after harvest as a fleshy fruit because the fleshy receptacle is the edible portion of interest.

Caryopsis—It is a one seeded fruit in which the thin pericarp and the seed coat are adherent in the fruit. Rice, wheat and barley are plants with a caryopsis fruit.

Nut—With nuts, the single seed is enclosed within a thick, hardened pericarp. Examples of species having nuts are the filbert, pecan and acorn.

Samara—They are one- or two-seeded fruits which possess a wing-like appendage formed from the ovary wall. The winged propagules of dispersal of the ash, maple and elm are examples of plants with this type of fruit.

Schizocarp—The fruit is formed from two or more carpels that split upon reaching maturity, yielding usually one seeded carpels. The fruits of many of the Apiaceae (e.g., carrot, parsley) are schizocarps.

Mature ovules or seeds contained within the ripened dried fruit represent the primary article of interest for agriculturists. In most instances the seeds are removed from the fruit during harvest or before storage. Seeds are comprised of an embryo, endosperm and testa.

The embryo consists of an axis that at one end is the root meristem and at the other the cotyledon(s) and shoot meristem. The level of structural complexity varies widely; for example, lateral shoot or adventitious root primordia may be present. The endosperm represents the storage tissue of the seed. Not all seeds have endosperms, although those utilized in agriculture almost exclusively have well-developed endosperms. Endosperm structure varies widely, for example, cell wall thickness and amount and nature of stored materials. The principal storage component in most seeds is starch with lower amounts of protein and lipids. In oil seed crops and some nuts, lipids are the primary storage component. In many seeds (e.g., Poaceae), the outer layer of the endosperm (the aleurone layer) is an important site for the synthesis of the enzymes required for the remobilization of the stored material during germination. The testa or seed coat represents a protective barrier for the seed. Its structure (e.g., thickness), composition and physical properties vary considerably.

Like fleshy fruits, dried fruits and seeds begin a progressive, irreversible series of deteriorative changes after maturation and harvest. While it is not possible to stop the process of deterioration, we can, through proper storage conditions, greatly decrease the rate. One important postharvest consideration influencing the way in which the product is handled is the eventual use of the dried fruit or individual seed. Seeds that are to be used for reproduction typically have more stringent storage requirements than seeds that are to be processed into foods or other products. Deteriorative processes in seed stocks result in losses of seedling vigor and subsequently in the ability of the seed to germinate. In most tests, seeds that will no longer germinate due to deterioration are considered dead. In many cases, however, the majority of the cells may be alive. While no longer useful for reproduction, these seeds remain, in many cases, useful for processing. It is also possible for seed to lose its functional utility as a raw product for processing (due to postharvest deterioration) without the complete loss in the ability to germinate. An example would be when low levels of lipid-peroxidation cause sufficient rancidity in an oil seed crop destined for human consumption causing the quality to be impaired (e.g., pecans). Postharvest peroxidation of seed lipids, however, normally is thought to be a primary factor in storage deterioration of seed germination potential.[40,52]

In general there are four critical factors that affect the rate of postharvest losses of dried

fruits and seeds. These are the nature of the fruit or seed, its moisture content and the temperature and oxygen concentration of the storage environment. Therefore, proper handling and storage can greatly extend the functional utility of these products.

f. Other structures

Mushrooms, members of the Ascomycetes and Basidiomycetes, represent another form of detached aboveground structures. Some, such as truffles, may be formed belowground. Unlike seed-producing Angiosperms, mushrooms reproduce from spores. The actual mushroom of commerce is the fruiting body of the organism. It is comprised of three distinct parts: the pileus or umbrella-like cap; the lamellae or delicate spore forming gills at the base of the pileus; and the stipe, the stalk on which the pileus is held. The fruiting body may also be thin, ear-shaped and gelatinous or various other structural variations.

Mushrooms sold undried as a fresh product have a relatively short storage and marketing potential. After harvest, the fruiting body continues to develop with the pileus, initially in the form of a tight button or closed cap, opening exposing the gills. With spore shed, the fruiting body begins to deteriorate with development of off-odors. Mushrooms are also subject to quality losses after harvest due to breakage, bruising and discoloration. As the pileus opens, the mushroom becomes much more susceptible to mechanical damage.

1.2.2. Belowground Structures

Subterranean storage organs are specialized structures in which products of photosynthesis accumulate and serve to maintain the plant during periods of environmental stress such as winter or drought. These underground structures do not normally contain chlorophyll but derive the energy necessary for a continued low rate of metabolism from their stored reserves. Commonly buds in these storage organs or in parent tissue associated with them are dormant when harvested and therefore have a suppressed rate of metabolism. While it is desirable for this dormancy to be maintained, it is not always possible. If suitable environmental conditions prevail, active growth commences at the expense of the storage reserves.

a. Roots

Roots are modified to form storage organs in several crops. They are characteristically swollen structures which may contain reserves, primarily of starch and sugars.

The edible radish is partly root and partly hypocotyl tissue. The secondary xylem parenchyma continues to grow and divide and forms the bulk of the radish. There is relatively little stored reserve in the radish; it is mainly cellulose and water. Small amounts of glucose, fructose and starch may accumulate under different cultural conditions. Similarly, the carrot storage root is actually formed from hypocotyl and taproot tissue. The cortex sloughs off and secondary growth results in a central xylem core surrounded by phloem and pericycle tissue. In all these tissues, there is extensive development of parenchyma in which starch is stored. The fleshy root of beet is also of hypocotyl-root origin, but in this case, secondary development is different. A series of cambia develop outside the primary vascular core, each producing strands of xylem and phloem embedded in parenchyma. This structure results in the concentric ring pattern characteristic of cross-sections of beet roots. Starch and sugars accumulate in the parenchyma cells.

The sweetpotato storage organ is an adventitious root in which an anomalous secondary

growth occurs. There is a large proportion of parenchyma in the primary xylem and cambia develop in this tissue. These produce xylem, phloem and many storage parenchyma cells in the tissue that was originally xylem. The normal phloem surrounds this unusual development of the xylem, as does the periderm which originates in the pericycle. During secondary growth of these storage roots the cortex and epidermis do not continue to grow but are split by the expanding secondary vascular tissue and eventually slough off. Periderm arises in the pericycle during secondary growth and forms a protective tissue to replace the epidermis. Its protective capacity is due to the accumulation of layers of suberin, a fatty acid substance, and wax in the cell walls.

The capacity to form a protective periderm is not only important in the normal development of storage roots but also in wound healing of roots, particularly sweetpotato, and of modified stems such as the potato tuber. The exposed cells are first sealed with suberin and other fatty materials. High humidity, proper temperature, and adequate aeration are necessary for sealing of the wound, providing an environment that stimulates cell division and formation of a periderm. If excessive moisture is present, suberization may be inhibited and callus tissue formed instead.

b. Rhizomes and tubers

While rhizomes and tubers are underground structures with the superficial appearance of roots, they are anatomically stems. They arise from lateral buds near the base of the main stem and grow predominately horizontally through the soil. They have nodes and internodes with leaves, sometimes reduced to scale leaves, at the nodes. Buds, often referred to as eyes, form in the axil of leaves. These buds may elongate into shoots and adventitious roots may develop from the stem tissue. Rhizomes may be somewhat enlarged and function as storage organs. In some species, they are used for vegetative propagation of the plant, for example many of the members of the *Iris* genus. For others, the rhizomes may be utilized for both propagation and consumption as in ginger and lotus.

Potato tubers form as swelling at the end of short rhizomes. In potatoes, the swelling begins by division of the parenchyma cells in the pith followed by division in the cortex and vascular regions. Vascular elements become separated by parenchyma tissue. Starch begins to accumulate in the cortex and later in the deeper tissues of the vascular region and the pith. The epidermis is replaced by a suberized periderm derived from the subepidermal layer. Numerous lenticels are formed by the production of loose masses of cells under the stomates of the original epidermis. Under favorable conditions the lenticels proliferate and rupture the epidermis and are evident as small white dots on the surface of the tuber. Tissues of the tuber retain their capacity to form periderm even after harvest, provided satisfactory humidity and temperature conditions are maintained. This capacity to heal periderm that is damaged during harvest and handling or even to heal cuts across the tuber in preparation of sets (seed pieces) for propagation is a very important characteristic. Without the formation of this protective layer, the damaged tuber would be subject to excessive water loss and microbial infection.

Yams are another very important food crop usually regarded as tubers. However, Onwueme[38] points out some important differences, particularly the lack of scale leaves, nodes or buds. These so-called tubers do not arise from stem tissue but rather as outgrowths of the hypocotyl. While the tubers do not have preformed buds, they are able to form buds from a layer of meristematic tissue just below the surface. Once dormancy is broken, these buds grow and can be the cause of major postharvest losses. The tubers are covered by several layers of cork (phellem) which arise from successive cork cambia (phellogen). Periderm formation may continue after harvest and is essential for wound healing.

c. Bulbs

Bulbs, as occur in onion, tulip and hyacinth, are underground buds in which the stem is reduced to a plate with very short internodes and the sheathing leaf bases are swollen to form a storage organ. At horticultural maturity, the aboveground parts of leaves shrivel and die but the swollen leaf bases remain alive. There is no anatomical distinction between these two parts and therefore no formation of a protective layer such as occurs in abscission zones or periderms. Therefore, adequate curing or drying of the neck and outer leaf bases is needed if quality is to be maintained during the postharvest period.

Bulbs, as storage organs, have a dormant period during which their metabolic rate is low and keeping quality is good. However, they contain intact shoots and are therefore capable of growth if dormancy is broken and suitable environmental conditions exist.

d. Corms

Corms are short, thickened, underground stems. When dormancy is broken the terminal bud or lateral buds grow into new plants with adventitious roots arising from the base of parent corms and from the new shoots. The dry leaf bases and hollow flower stem of *Gladiolus* spp. tend to remain more or less attached to the corm and afford protection from water loss and mechanical damage.

Taro, on the other hand, does not retain its leaf bases but has a well developed periderm on the corm. Secondary corms or cormels arise from lateral buds on the corm. The Chinese water chestnut forms corms at the end of slender rhizomes. These corms have a scaly, brown periderm.

e. Non-storage organs

Products included in this category are primarily used as propagation material. To be effective as such, they must contain some stored reserves to supply energy and nutrients for the early development of the new plant.

i. Root Cuttings

While a number of species can be propagated from root cuttings (e.g. peony and bramble fruits are occasionally marketed commercially), there is relatively little use of this technique, since other propagation systems are generally less labor intensive and are quicker.

Root cuttings are commonly taken during the dormant stage so they do not display a high level of metabolic activity. Typically, root cuttings are thickened secondary roots with a well-developed periderm. There are often no obvious anatomical features that can be used to determine the orientation of root cuttings, but polarity is maintained, with shoots being produced from the proximal end and roots from the distal. It is, therefore, important to use a handling system that identifies the ends. One such system is to cut the proximal end straight and the distal end slanted.

ii. Crowns

Crown is a general term referring to the junction of shoot and root system of a plant. Those marketed in the horticultural trade are most commonly herbaceous perennials and consist of numerous branches from which adventitious roots arise. Crowns are divided by cutting,

preferably during the dormant period, and are marketed before or soon after the onset of active growth. Some plants like asparagus develop thick storage roots as well.

Crowns with young shoots and active roots are susceptible to mechanical damage, and the cut surfaces are subject to microbial infection and water loss. Stored reserves are present in the mature stems and roots and the metabolic rate is comparatively low.

2. TISSUE TYPES

The structure of harvested products can be further subdivided into four general tissue types of which the products are composed. These include the dermal, ground, vascular and meristematic tissues. Dermal tissues form the interface between the harvested product and its external environment and as a consequence, are extremely important after harvest. They often have a dominant influence on gas exchange (e.g., water vapor, oxygen, carbon dioxide) and the resistance of the product to physical and pathological damage during handling and storage. With some postharvest products, the dermal tissues are also important components of the products visual appeal. The luster imparted by the epicuticular waxes on an apple or the presence of desirable pigmentation in the surface cells are examples of this.

Ground tissues make up the bulk of many edible products, especially fleshy products such as roots, tubers, seeds and many fruits. These often act as storage sites for carbon; however, they have many other functions. Maintenance of their characteristic texture, composition, flavor and other properties after harvest is especially important. Vascular tissues are responsible for movement of water, minerals and organic compounds throughout the plant. Their function is especially critical during growth; however, in detached plant parts their primary role is diminished in importance. With some products, for example, carrots, the vascular tissues make up a significant portion of the edible product. Within the vascular and ground tissue systems are found support tissues such as collenchyma and sclerenchyma that give structural support to the plant. Collenchyma tissues are found widely within plants, whereas sclerenchyma tissues, being much more lignified and rigid, are less common in most edible products. Lastly, meristematic tissues are comprised of cells that have the capacity for active cell division. As a consequence, they are of particular importance during growth.

2.1. Dermal Tissue

Dermal tissue covers the outer surface of the plant or plant part and constitute its interface with the surrounding environment. The two principal types of dermal tissues are the epidermis and the periderm.

2.1.1. Epidermis

Epidermal cells covering the surface of the plant are quite variable in size, shape and function. Most are relatively unspecialized, although scattered throughout these unspecialized cells are often highly specialized cells or groups of cells such as stomates, trichomes, nectaries, hydathodes and various other glands.

The epidermis is typically only one layer of cells in thickness, although with some species, parts of the plant may have a multilayered epidermis. Epidermal cells are typically tabular in shape and vary in thickness with species and location on the plant. The cells are alive, metabolically active and may contain specialized organelles and pigments within the vacuoles. Cu-

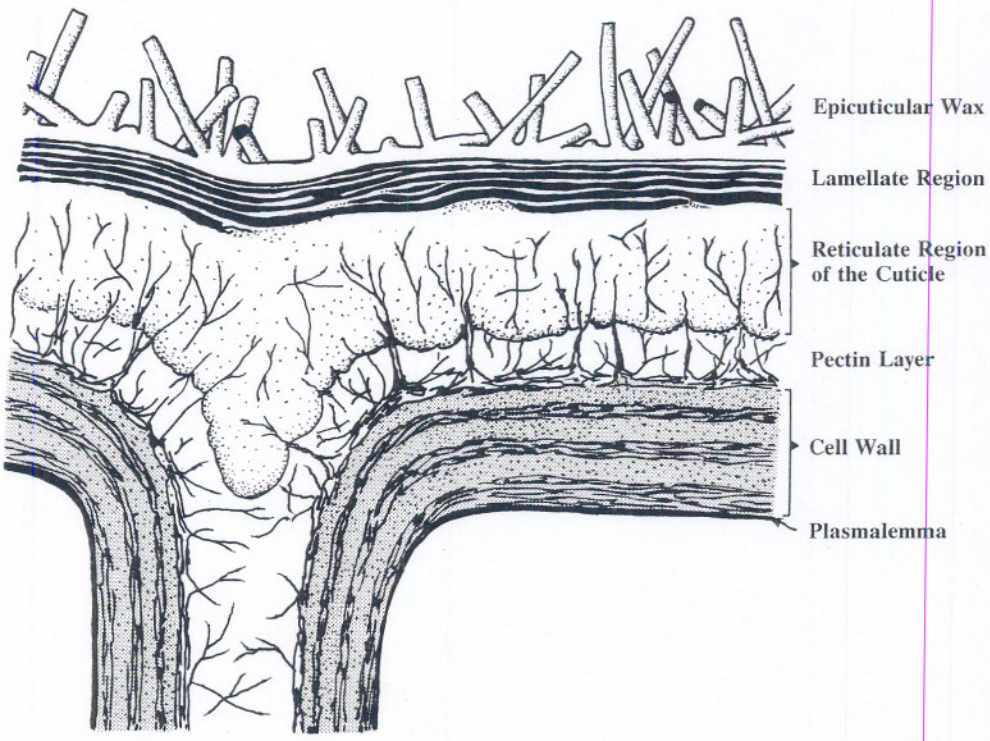


Figure 2.3. Diagrammatic representation of a plant cuticle. Successive layers from the plasmalemma of the surface cell outward are the cell wall, pectin layer and the pectin layer of the middle lamella, the reticulate region of the cuticle in which cutin and waxes are traversed by cellulose fibrils, the lamellate region where there are separate layers of cutin and wax, and the exterior epicuticular wax (*after Juniper and Jeffree*[26]).

ticle is found on the outer surface of epidermal cells of all aboveground plant parts (e.g., leaves, flowers, stems, fruits, seeds) and often on significant portions of the root system. The cuticle functions as a barrier to water loss and protection against pathogens and minor mechanical damage. It also affects the wetability of the surface, requiring the use of wetting agents (surfactants) for many agricultural chemicals, and the surface optical properties of the product. Cutin, comprised of complex fatty substances found intermeshed within the outer cell wall and on the outer surface of the epidermis, is a primary component of the cuticle, as are waxes (Figure 2.3). Surface cuticular waxes may be seen as flat plates or as rods or filaments protruding outward from the surface (Figure 2.4).

a. Stomata

Stomata are specialized openings in the epidermis which facilitate the bidirectional exchange of gases (water vapor, carbon dioxide, oxygen, etc.).[50] Although varying widely in appearance (Figure 2.5), stomata are comprised of a pair of specialized cells, called the guard cells, which through changes in their internal pressure alter the size of the stomatal opening (Figure 2.6).[20] Below the guard cells is the substomatal chamber (Figure 2.7).

Stomata are found on most aerial portions of the plant including fruit; however, they are most abundant on leaves. The number of stomata per unit surface area of leaf varies widely among species, cultivar and the environmental conditions under which the plants are grown.

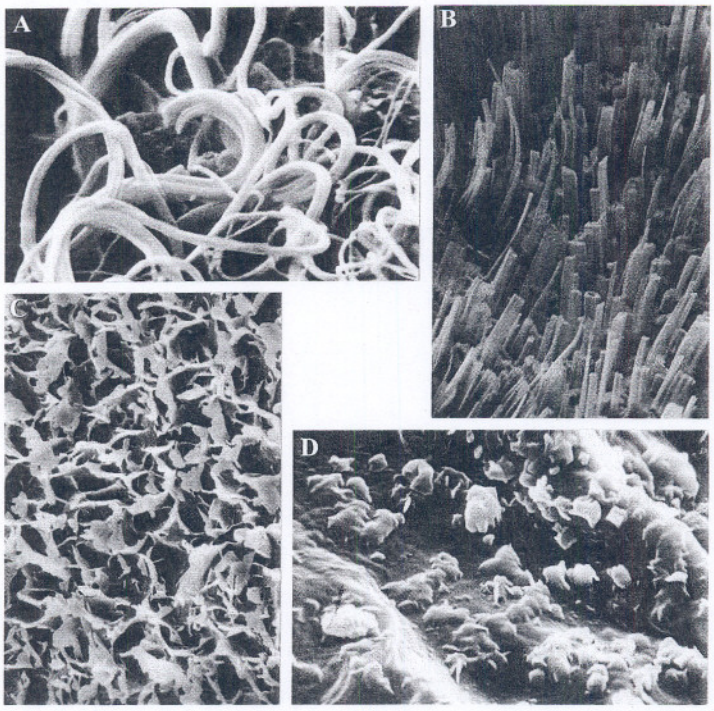


Figure 2.4. The surface of many aerial plant parts is covered with a layer of epicuticular wax. The deposition and continuity of these waxes varies widely from long coiled cylindrical rods (A), long tubules (B), fringed plates (C), to irregularly shaped plates (D) (*from Baker*[3]).

Typically the lower surface of the leaf has the greatest number of stomata; in some cases, they are found only on the lower surfaces, in others (e.g., waterlily) only on the upper surface, and in submerged aquatics generally absent. A density of approximately 100 stomata per mm^2 is common; however, greater than 2,200 per mm^2 are found on *Veronica cookiana* Colenso.[44] In young apple fruit (cv. Golden Delicious) stomatal function is similar to that in leaves, the density of which (25 mm^{-2}) decreases markedly as the fruit increases to its final size (<1 mm^{-2}).[7]

Stomatal opening is altered by light, carbon dioxide concentration and plant water status. The mechanics of opening and closing of the stomatal aperture appears to be largely controlled by the movement of potassium ions between the guard cells and their adjacent neighboring cells. When the potassium ion concentration in the guard cells is high, the stomate is open, when it is low, closure occurs.

Stomatal closure represents a means of conserving water within the tissue. When plant parts are severed at harvest from the parent plant, the supply of water from the root system is eliminated and the stomata typically decrease their aperture markedly. During the postharvest period, stomata also represent potential sites for entry of pathogenic fungi. This allows the fungi to bypass the plants' surface defense mechanisms (chiefly the cuticle and epicuticular waxes) and gain rapid entry into the interior.

b. Trichomes

Trichomes represent another type of specialized epidermal cells that may be found on virtually every part of the plant.[21] These extend outward from the surface, greatly expanding the

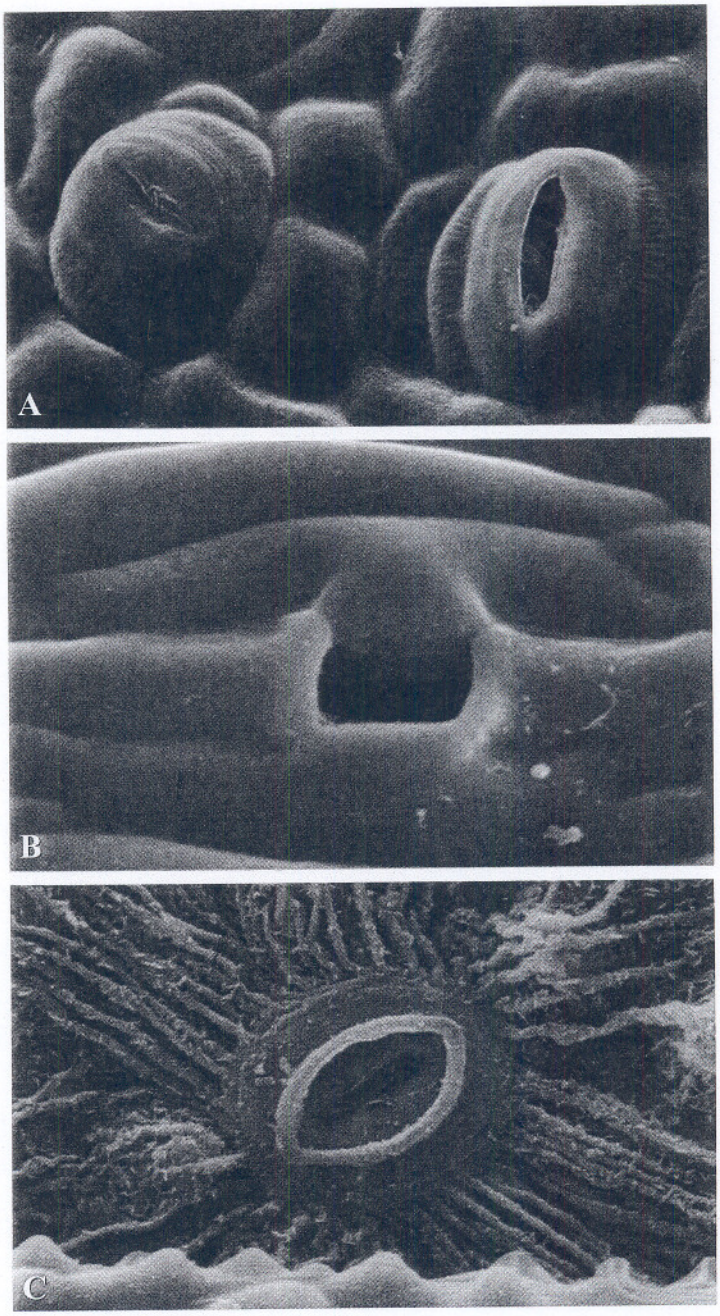


Figure 2.5. Stomata seen from the surface of: (A) *Liquidambar styraciflua* L.; (B) a *Pinus caribaea* Morelet. × *P. palustris* Mill. hybrid; and (C) *Cornus florida* L. illustrate variations in morphology (*Photographs courtesy of H. Y. Weitzstein*).

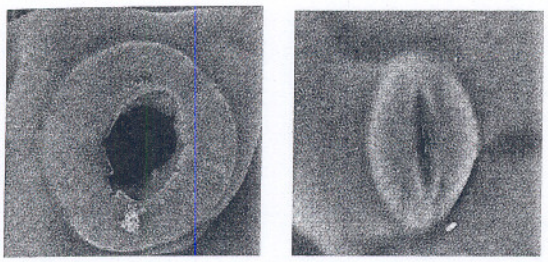
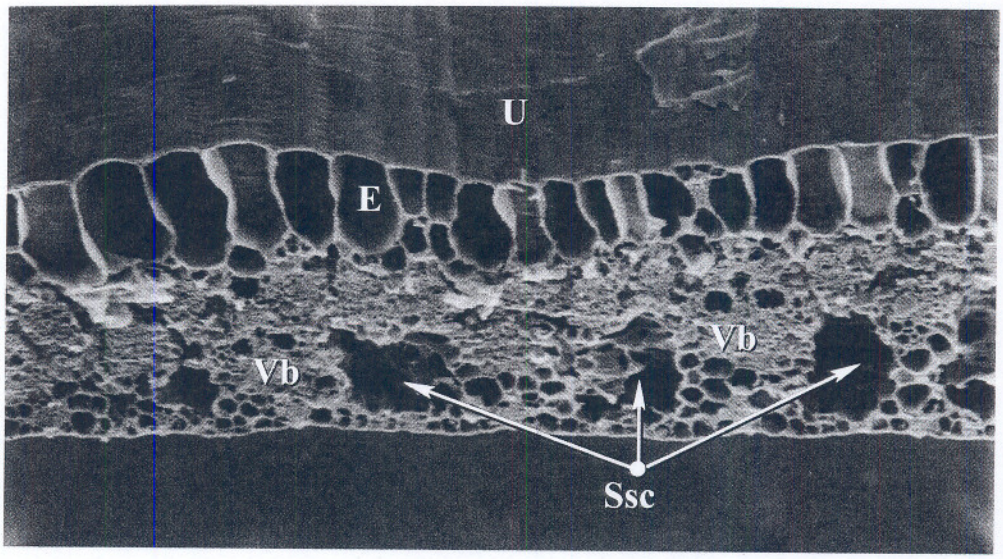


Figure 2.6. Open and closed stomata of *Arabidopsis thaliana* (L.) Heynh., the opening of which is caused by the transport of potassium into the guard cells mediating an increasing turgor pressure and their outward swelling (*Scanning electron micrographs courtesy of E. Grill and H. Ziegler*[20]).



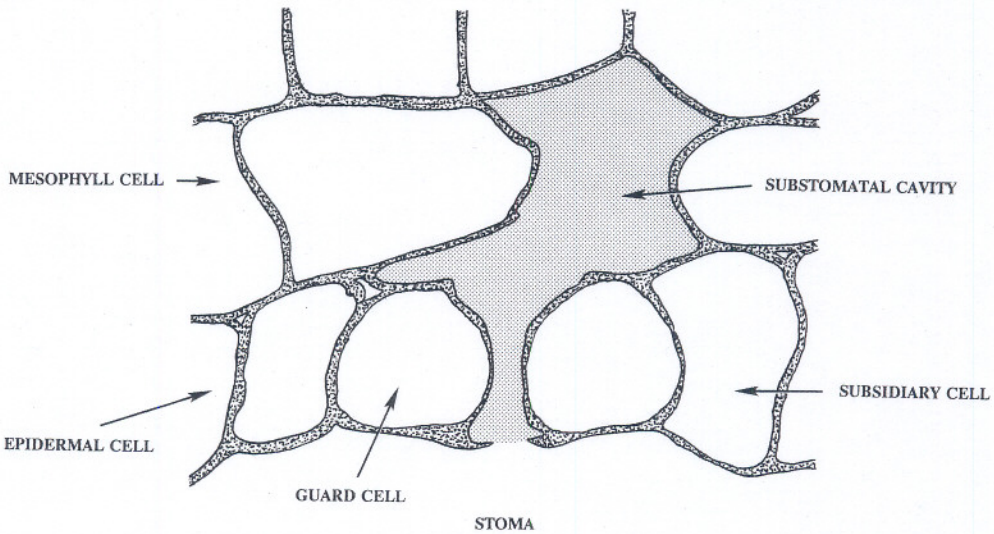


Figure 2.7. (A). An electron micrograph of a *Cyperus* spp. leaf displaying stomata with large substomatal cavities (Ssc) on the lower surface (U—upper surface of the leaf; E—epidermal cell; Vb—vascular bundle). (B). Diagrammatic representation of a lemon leaf stomata in cross-section. (*Scanning electron micrograph courtesy of H. Y. Wetzstein*).

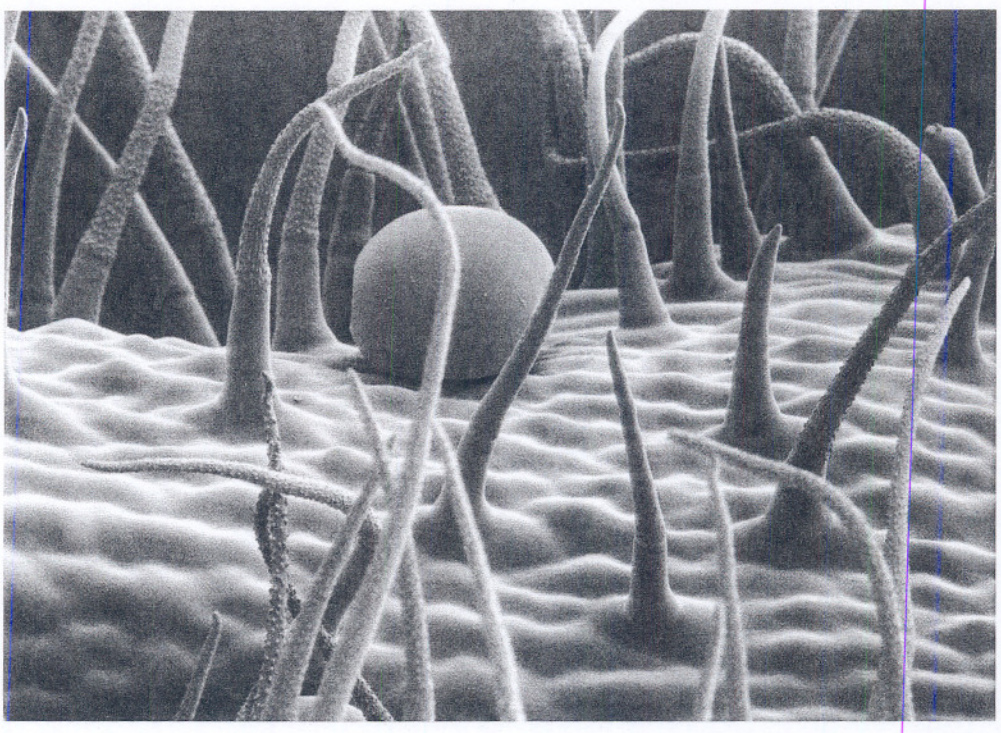


Figure 2.8. Surface trichomes are found in various shapes, sizes, and densities, depending upon species and position on the plant. The cyro scanning electron micrograph displays simple multicellular hairs and a peltate gland on the surface of a *Nepeta racemosa* Lam. leaf (*Micrograph courtesy of R.J. Howard, DuPont Co.*).

surface area (Figure 2.8). As a class, trichomes are highly variable in structure, ranging from glandular to nonglandular, single celled to multicelled. The tremendous diversity makes classification into precise groups difficult,[39] as a consequence, they are often separated into three very general groups: glandular, nonglanular and root hairs. The surface fuzz on peach and okra fruit is an example of trichomes.

Root hairs greatly expand the water and nutrient absorbing surface of the root system as well as anchoring the elongating root from which they are borne. With aerial trichomes, the role is less well defined. In some species, they represent one means by which the plant combats insect predation. The specialized hooked trichomes of some species trap insects, thus providing a physical barrier (Figure 2.9). Trichomes may contain a number of chemicals which attract or repel specific insects. In addition, some trichomes function as sites for the sequestering and/or secreting of certain chemicals. Excess salts taken up by some species are removed *via* the trichomes. Trichomes are also known to exert a pronounced effect on the boundary layer of air around the organ, affecting the exchange of gases.

During the postharvest period, trichomes which are broken during harvesting or handling provide primary entry sites for pathogens. Operations such as defuzing peaches (trichome removal), as a consequence, can greatly decrease the life expectancy of the product if appropriate treatments are not utilized.

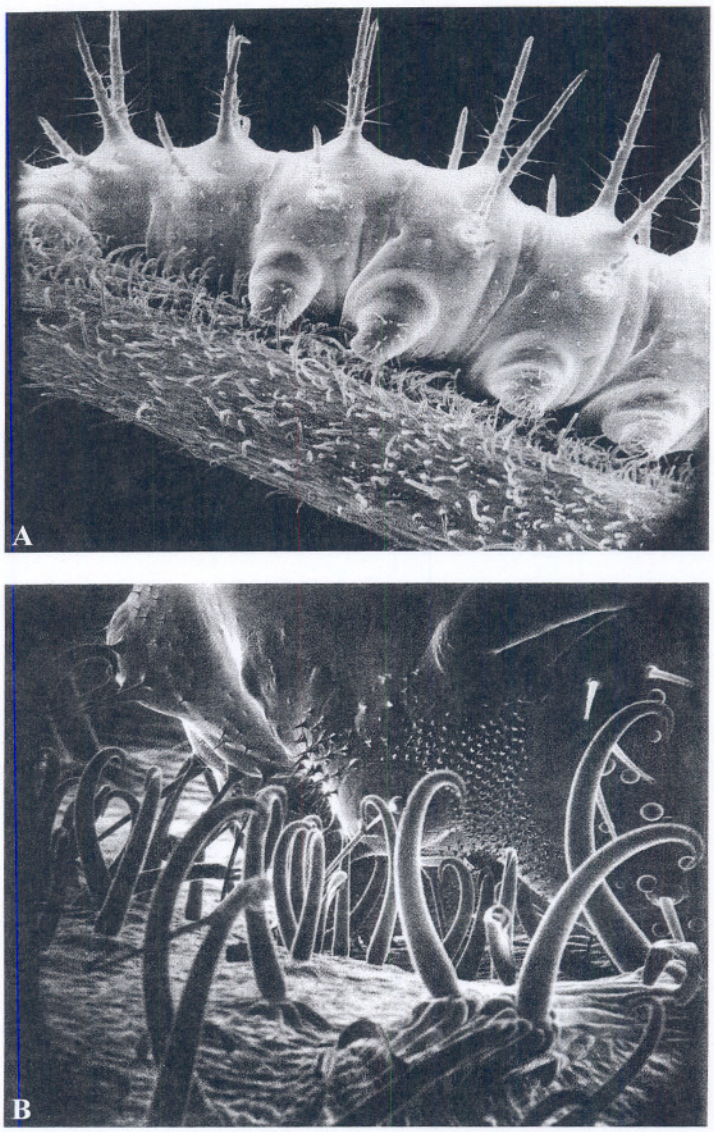


Figure 2.9. Trichomes may in some species function as defense structures discouraging insect herbivores. The photographs show the trapping of second (top) and third (bottom) instar larvae of *Heliconius melpomene* by the hooked trichomes on the leaves and petioles of *Passiflora adenopod* (*from Gilbert*[18]). Damage to trichomes during or after harvest, however, provides entry sites for postharvest pathogens.

c. Nectaries

Nectaries are multicellular surface glands found on flowers and other aerial plant parts that secrete sugars and certain other organic compounds (Figure 2.10). Their position on flowers, the most common site, varies with species; they may be found on the petals, sepals, stamens, ovaries or receptacle. Nectaries may be flush with adjacent surface cells or be found as out-

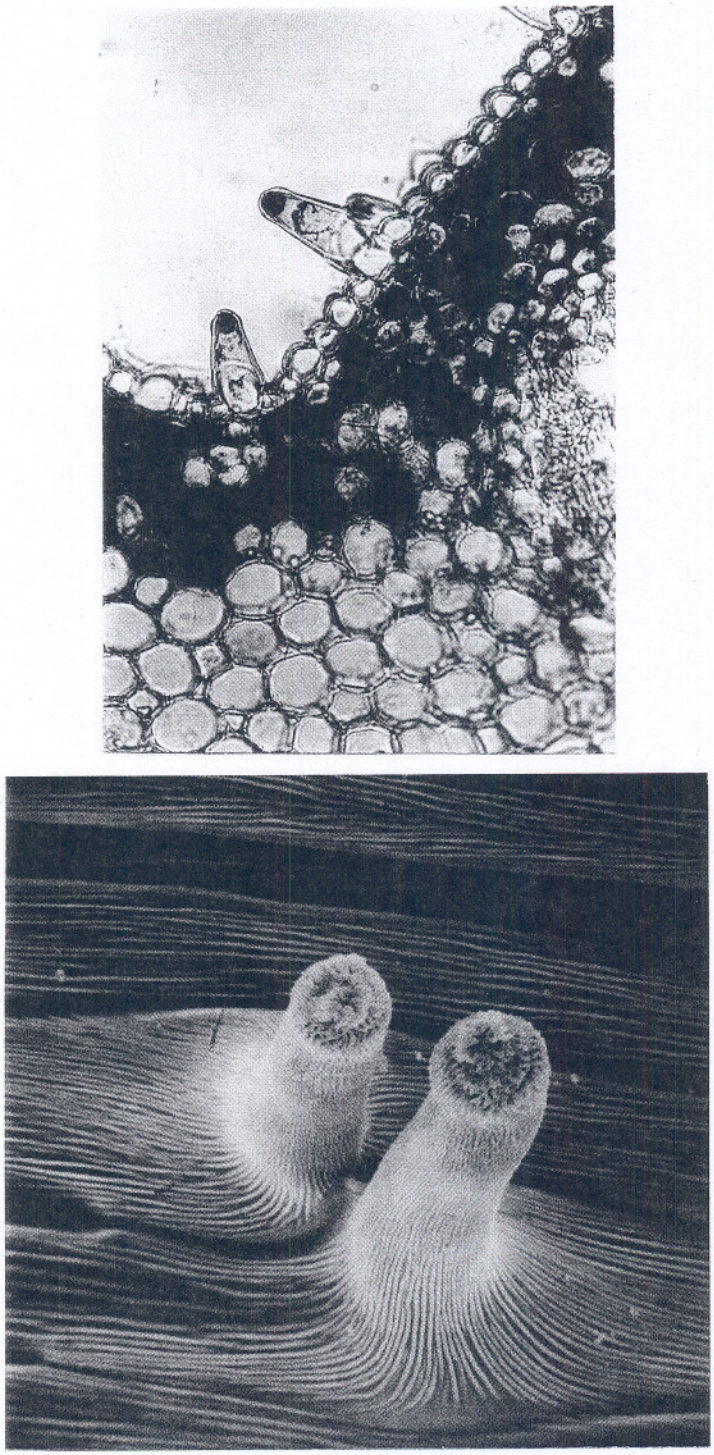


Figure 2.10. Micrographs of nectaries from the flower of *Tropaeolum majus* L. (*left*—cross-section; *right*—scanning micrograph). On some species nectaries may be found on other organs (e.g., leaves, bracts, sepals). Their postharvest importance lies largely in their potential role as sites for the entry of pathogens (*Micrographs courtesy of Rachmilevitz and Fahn*[41]).

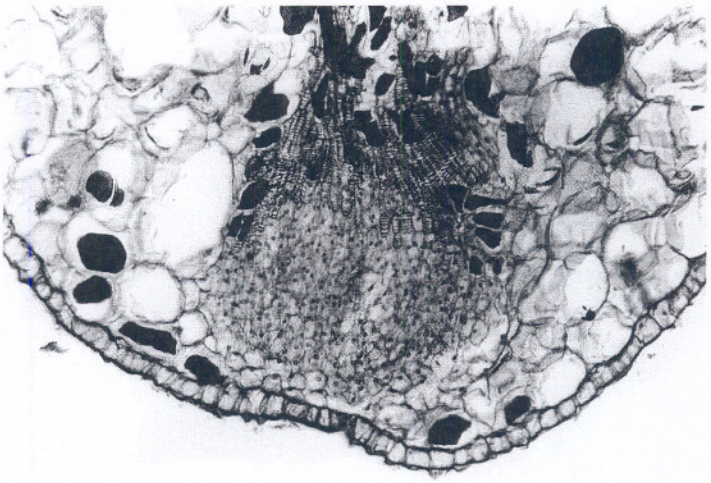


Figure 2.11. Light micrograph of a hydrothode. Hydrathodes represent one of several types of specialized secretory structures. They secrete water which is brought to the leaf periphery by tracheids. The water then moves through an area of loosely packed parenchyma cells called the epithem, exiting through modified stomata (pores), no longer capable of closing. Secretion of water, called guttation, results in the formation of droplets along the border of the leaf (*Micrograph courtesy A. Fahn*[17]).

growths or sunken. They consist of an epidermis, with or without trichomes, and specialized parenchyma.[15] Sugars are the primary group of organic compounds secreted, which exude from either modified epidermal cells or trichomes of the nectary. The primary function of nectaries is the facilitation of flower pollination by insects.[47]

d. Hydathodes

Hydathodes are much more complex than just modified epidermal cells; however, their function is in many ways similar. They represent a modification of both the vascular and ground tissues along the margins of leaves, that permits the passive release of water through surface pores that remain permanently open[45] (Figure 2.11). Guttation, the discharge of water in the liquid state, results in small droplets forming on the leaf margins or tip and occurs through the hydathodes. Guttation is most noticeable when transpiration is suppressed, such as when the relative humidity is high during the night. The surface pore or opening is of stomatal origin; however, unlike stomates, a hydathode is not capable of altering its aperture. Hydathodes represent potential sites for water loss and pathogen entry in harvested leafy products.

2.1.2. Periderm

On plant parts such as roots and stems that increase in thickness due to secondary growth, the epidermis is replaced by a protective tissue called the periderm. Periderm is also formed in response to wounding in most species. When roots are damaged during harvesting, wound periderm forms over the wound surfaces, decreasing the risk of pathogen entry.

The periderm is composed of three tissue types: (1) the phellogen or cork cambium from

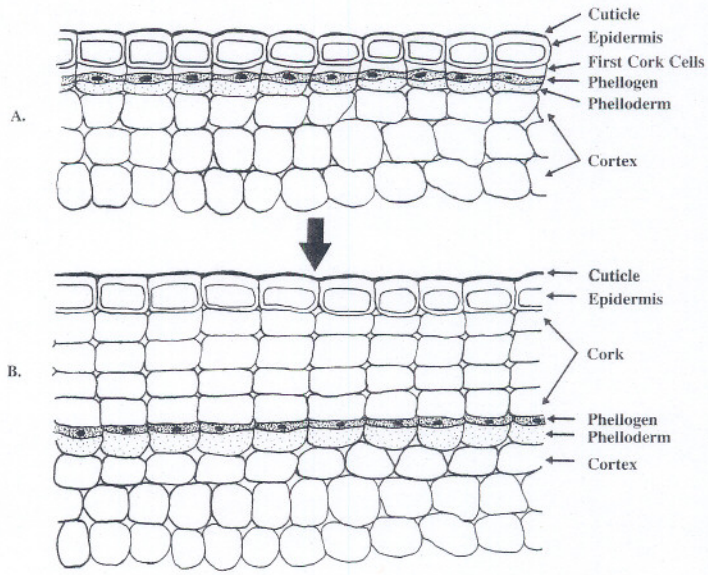


Figure 2.12. When plant parts increase in thickness due to secondary growth, the epidermis is replaced by periderm (A) which is composed of the phellogen, the phellem or cork and the phelloderm. The phellogen divides (B) forming successive layers of cork cells which act as a protective barrier (*redrawn from Kramer and Kozlawski*[28]).

which the other cells of the periderm arise; (2) the phellem or cork, which is the protective tissue or the exterior surface; and (3) the phelloderm, which is tissue found interior to the cambium (Figure 2.12). The phellem or cork cells are not alive when mature and typically have suberized cell walls. They are tightly arranged, having virtually no intercellular space between adjacent cells, and are found in layers of varying cell number in thickness.

Some harvested products such as sweetpotato roots or white potato tubers must be held under conditions favorable for wound periderm formation prior to storage. Warm temperature and high relative humidity (i.e., 5–7 days at 29°C, 90–95% RH for sweetpotato roots) favor rapid wound periderm formation, thus decreasing water loss and pathogen invasion during storage.

Interspersed on the periderm of many species are lenticels comprised of groups of loosely packed cells having substantial intercellular space (Figure 2.13). These appear to be present to facilitate the diffusion of gases into and out of the plant. Unlike stomata, lenticels are not capable of closure and as a consequence, their presence enhances the potential for water loss from the product after harvest.

Lenticels range in size from extremely small to up to 1 cm in diameter depending on the species and location on the plant. They are often seen as groups of cells with a more vertical orientation, protruding above the surface of the periderm (Figure 2.13).

2.2. Ground Tissue

2.2.1. Parenchyma

Parenchyma cells form the ground tissue of most postharvest products. In fleshy fruits and roots and in seeds they act as storage sites for carbohydrates, lipids or proteins and make up

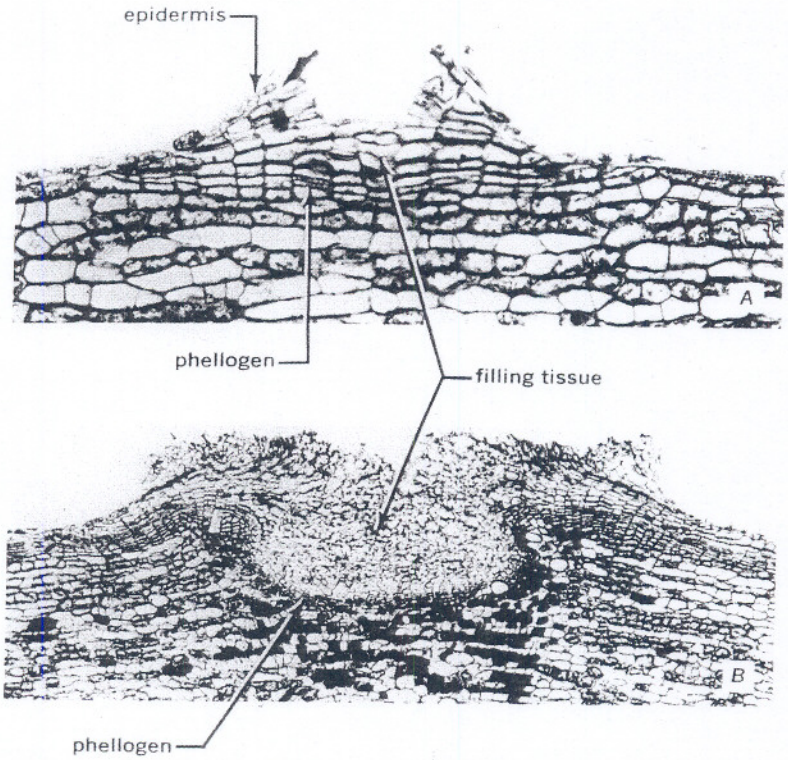


Figure 2.13. Cross-sections of a young (A) and old (B) lenticels from *Persea americana* Mill. stems. Note the phellogen at the base of the lenticels and the extensive filling of the older lenticel (B) (*from Esau*[15]).

the bulk of the edible portion. In leaf tissue, parenchyma cells have numerous chloroplasts and have a photosynthetic function. Parenchyma cells may also act as secretory cells and can resume meristematic activity in response to wounding.

Parenchyma cells have numerous sides or facets and are highly variable in shape. The number of sides ranges from approximately 9 to 20 or more. Within a single mass of relatively homogenous parenchyma cells, both the number of sides and the actual size of the individual cells often vary. In fruit, roots and tubers there is considerable intercellular space, whereas in seeds the parenchyma cells are much more compacted. In some aquatic species, the parenchyma cells are very loosely packed forming a tissue called aerenchyma, facilitating diffusion of gases.

The characteristics of individual parenchyma cells are to a large extent dependent on the function of the tissue and its composition. Photosynthetic parenchyma in the mesophyll of leaves forms chlorenchyma due to the abundance of chlorophyll. Storage parenchyma cells exhibit characteristics that are in part dependent on the organic compounds sequestered within their specialized plastids. Parenchyma cells of tubers, roots and some fruits contain amyloplasts that store starch. The parenchyma cells in flowers contain chromoplasts or vacuoles with various colorful pigments.

Parenchyma cells typically have relatively thin primary cell walls, although in some seeds these walls may be rather thick. This general lack of structural rigidity of the wall makes the parenchyma cells rapidly loose their shape and textural properties when water is lost. In many

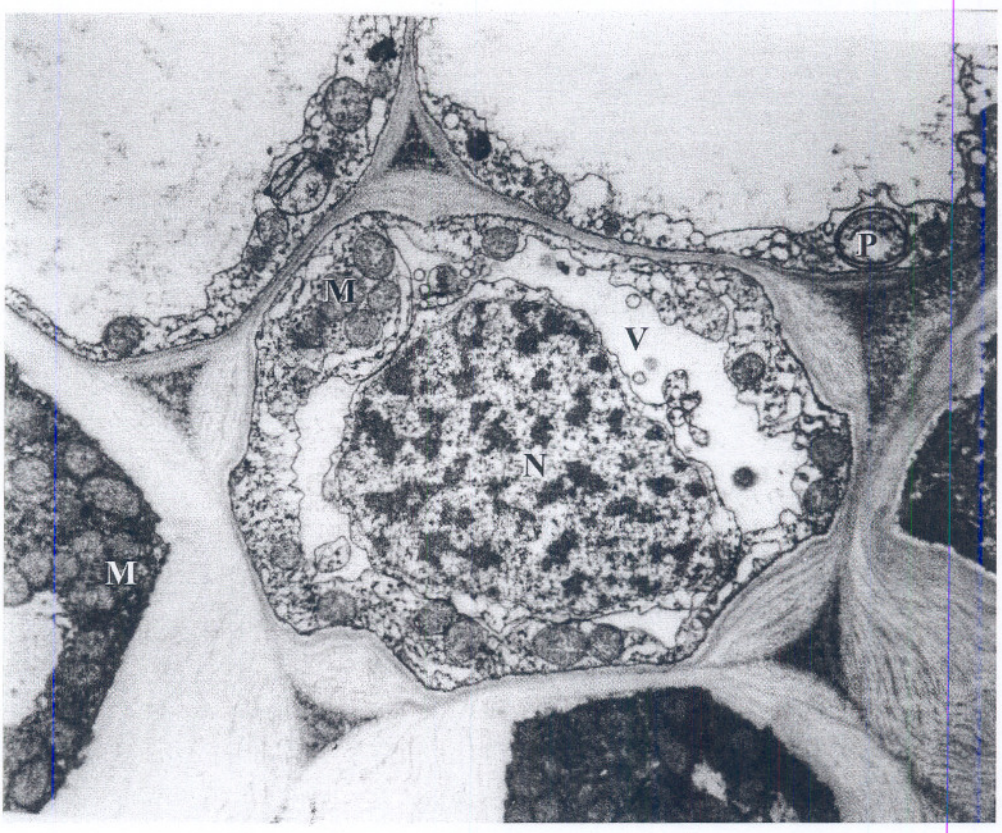


Figure 2.14. Electron micrograph of collenchyma. Particularly noticeable are the much thickened primary cell walls which lend structural support to the tissue and the presence of protoplasm containing a central nucleus (N), vacuole (V) and a number of mitochondria (M). The cell wall is nonlignified, containing large amounts of pectin and water (*Electron micrograph ×16,500 from Ledbetter and Porter*[30]).

postharvest products, the actual percentage of the total water present that must be lost before significant alterations occur in the tissues' physical properties is often relatively small.

2.2.2. Collenchyma

Collenchyma is in many ways similar to parenchyma; however, collenchyma cells have thickened cell walls that provide structural support for the plant (Figure 2.14). The cells are strong and flexible with nonlignified cell walls. The walls are primary in nature but considerably thicker than those found surrounding parenchyma cells. In addition, collenchyma cells tend to be more elongated in shape than parenchyma cells. The walls of collenchyma are much more pliable than their structural counterparts, sclerenchyma (Figure 2.15). In addition, they remain metabolically active and have the ability to degrade much of the wall if induced to resume meristematic activity.

The walls are composed primarily of cellulose, pectins and hemicelluloses but are not lignified. Thickening of the wall occurs as the cell grows. Mechanical stress caused by wind in-

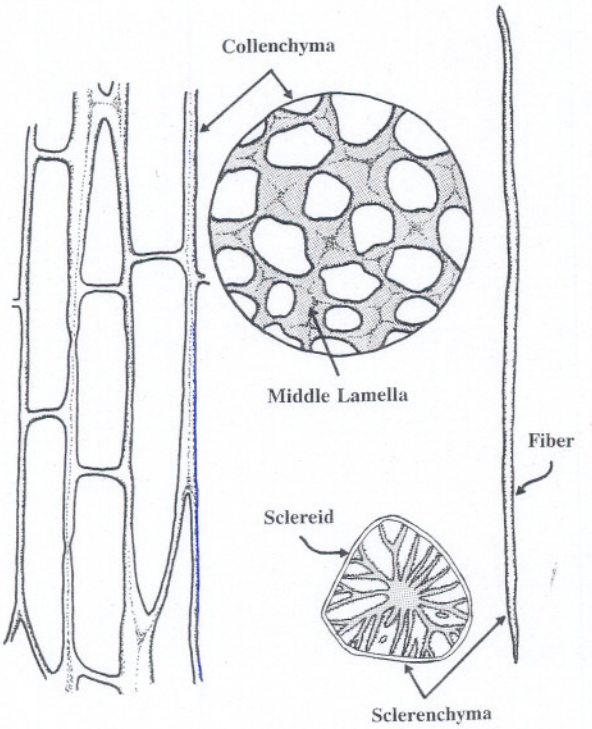


Figure 2.15. Supporting cells of collenchyma (left) and sclerenchyma (right) tissues are often elongated. Sclereids, one form of sclerenchyma, tend to be shorter and compact. Collenchyma cells have irregularly thickened primary cell walls and differ from sclerenchyma in that the latter usually have well developed secondary cell walls (*after Esau*[15]).

creases the extent to which the walls thicken. In older parts of the plant, collenchyma cells may form secondary cell walls, becoming sclerenchyma.

As a support tissue, collenchyma is found in the aerial parts of the plant and not in the roots. The cells generally are located just below the surface of leaves, petioles, and herbaceous stems. The strands of cells found in the edible petioles of celery are collenchyma cells and vascular tissue.

2.2.3. Sclerenchyma

Sclerenchyma lends hardness and structural rigidity to plants and plant parts. Cells of this tissue have lignified secondary cell walls which are formed after the completion of expansion (Figure 2.15). At maturity most are nonliving and no longer contain protoplasts. Sclerenchyma is found throughout the plant but seldom in the extensive homogenous masses in which parenchyma and collenchyma are found. Rather, sclerenchyma is usually found as individual cells or in small clusters interspersed among other cell types. Two general cell types may be distinguished based primarily on shape. Sclereids tend to be shorter and more compact than fibers which typically are quite elongated. Sclereids are highly variable in shape; some are compact and more-or-less regular, while others may be highly branched. They are often found in layers or clusters in epidermal, ground and vascular tissues of stems, leaves, seeds and some fruits. The stone cells in pears are an example of sclereids (Figure 2.16).

Fibers are elongated cells (Figure 2.17) varying from quite short to as long as 250 mm in the ramie fibers of commerce. They function as support elements in non-elongating plant parts, especially stems and the leaves and fruit of some species. The formation of fiber can oc-

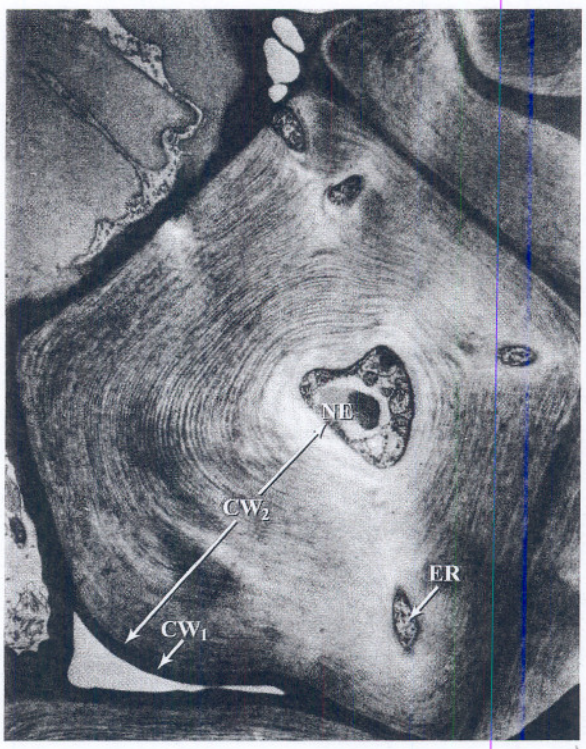


Figure 2.16. Stone cells such as those found in pear fruit represent an example of a sclereid. Extensive secondary cell wall (CW_2) surrounds the cytoplasm which contains mitochondria, plastids and nuclear envelope (NE). The primary cell wall (CW_1), is found external to the outer layers of the secondary wall (ER—endoplasmic reticulum), (*Electron micrograph ×12,000 courtesy of Ledbetter and Porter*[30]).

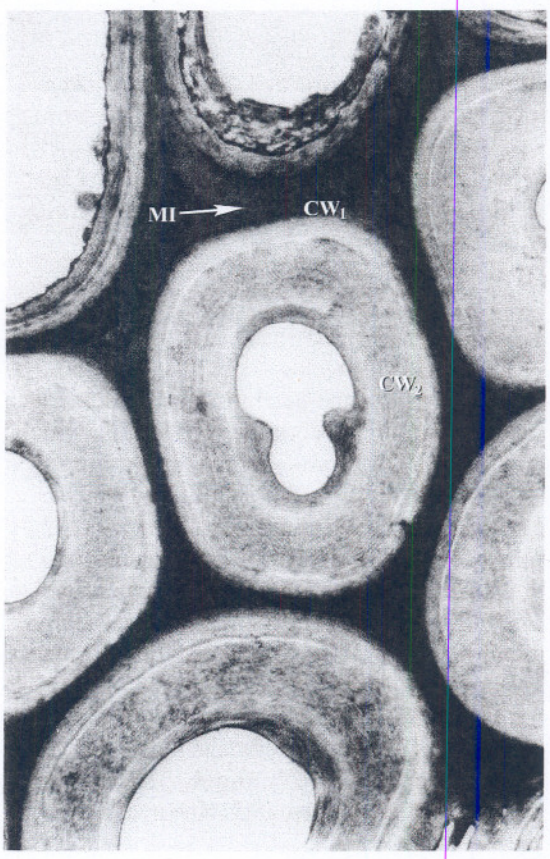


Figure 2.17. Fibers seen in cross section. The central fiber has an empty central cavity which is surrounded by a thick secondary cell wall (CW_2) composed of three layers. Adjacent to the exterior layer of the secondary cell wall is the primary cell wall (CW_1), followed by the middle lamella (MI), (*Electron micrograph ×17,000 courtesy of Ledbetter and Porter*[30]).

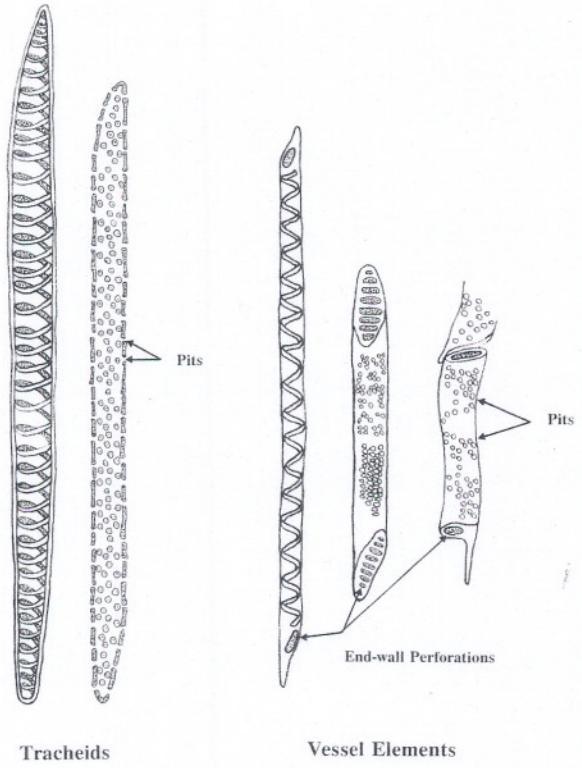


Figure 2.18. Water and minerals are moved throughout the plant in specialized xylem cells, tracheids and vessel elements. Tracheids have tapered end walls and represent a more primitive form of xylem than vessel elements. The geometry of the secondary cell wall varies from spiral to extensive. When there is an extensive secondary wall, numerous pits are generally present through which water moves from tracheid to tracheid. Vessel elements are found end to end, with water moving through their perforated end walls (*redrawn from I.P. Ting*[46]).

cur after harvest in some products, decreasing their acceptability. This is often a problem, for example, in asparagus and okra.

2.3. Vascular Tissue

Vascular tissues provide the conduits for the movement of water and nutrients throughout the plant. Of the tissues found in the plant, vascular tissue is the most complex, being composed of several types of cells. The xylem and phloem are the two types of vascular tissues. Within the xylem, water, minerals and some organic compounds from the root system move upward throughout the plant. Carbohydrates (chiefly sucrose) and to a much lesser extent other organic compounds formed in the leaves or apical meristem are transported both acropetally and basipetally in the phloem.

2.3.1. Xylem

The xylem functions primarily as a tissue for the conduction of water, but it also has storage and support functions. This diversity in roles is in part due to the occurrence of several types of cells making up the xylem. Tracheids and vessel members are the water-conducting cells (Figure 2.18). Tracheids are elongated cells, tapering toward the ends, with secondary cell walls that impart structural support to the plant. At maturity they are nonliving. Water moves through openings, called pits, in the sides of the cells into adjacent pits of neighboring tracheids.

Vessel elements, also elongated cells but often with flattened porous ends, are joined end-

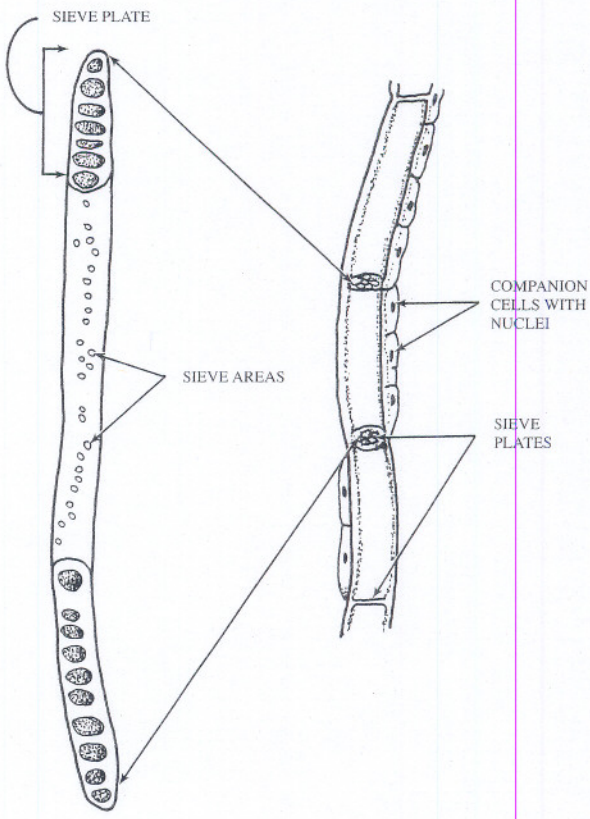


Figure 2.19. Photosynthates and other organic constituents move through the cells of the phloem. Illustrated at the left is an elongated sieve-tube element with sieve plates on the end walls formed from groups of sieve areas. Sieve areas are also found on the side walls through which some lateral transport takes place. At the right are three sieve-tube cells attached end to end forming an elongated conduit (*adapted from Wilson and Loomis*[51]).

to-end, forming vessels. These may be as much as a meter or greater in length in some species. Vessels are a more complex form of water-conducting cells found in angiosperms. They appear to have evolved from tracheids during the evolutionary development of the angiosperms.

Associated with tracheids and vessel elements are parenchyma cells which act as storage sites. These cells may contain starch, lipids, tannins or other material and are particularly important in the secondary xylem of woody perennials. Fibers are also part of the xylem, providing further structural support.

The xylem may be of either primary or secondary origin. Primary xylem is formed during the initial development of the plant, arising from the procambium. Secondary xylem develops during the secondary thickening of stems and roots, and is derived from the vascular cambium.

2.3.2. Phloem

The phloem is the photosynthate-conducting tissue of vascular plants. Carbohydrates formed in the leaves are transported both acropetally to the growing tip of the plant and basipetally toward the root system. The directional allocation depends on the position and strength of competing sinks within the plant for photosynthate, the position of the individual leaf on the plant, its stage of development, time of day and other factors. In plant parts that are detached from the parent plant at harvest, phloem transport is essentially eliminated.

Phloem, like the xylem, is composed of several types of cells; however, phloem tends to be less sclerified. Photosynthate and other organic compounds are transported through specialized elongated cells called sieve elements (Figure 2.19). While sieve elements are much like

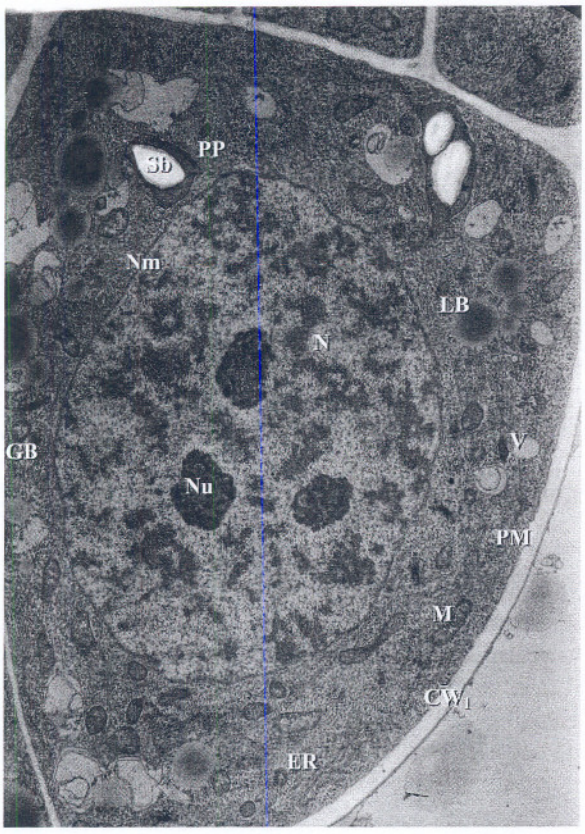


Figure 2.20. Meristematic cells are characteristically small, have only a few small vacuoles (V) and a relatively thin primary cell wall (CW_1), (N—nucleus; Nu—nucleoli; NM—nuclear membrane; PM—plasma membrane; PP—protoplastid; ER—endoplasmic reticulum; LB—lipid body; M—mitochondrion; Sb—starch body; GB—Golgi bodies) (*Electron micrograph courtesy of H. Ammerson*).

the tracheids of the xylem, they differ in being alive at maturity, although they do not contain a nucleus or vacuole. Individual cells are joined end to end, forming sieve tubes. At the ends of each cell is a porous plate called the sieve area or sieve plate which allows, and may in part control, the movement of material from one cell to the next. The remainder of the cell wall is variable in thickness and may also have perforated regions.

Associated with a sieve element are one or more parenchymatous companion cells. These appear to partially control the enucleate sieve element and are joined by an interconnecting membrane system. Companion cells also function during the loading of photosynthate into the phloem and the subsequently unloading upon arrival at the sink site. These parenchyma cells may also act as storage sites for an array of organic compounds.

Fibers are also associated with the phloem. These provide structural support and rigidity to the system.

Phloem, like the xylem, can be divided into two general classes based on origin. The primary phloem is derived from the procambium while the secondary phloem arises from the vascular cambium during secondary thickening.

2.4. Meristems

Meristems are comprised of groups of cells that retain the ability for cell division. Their primary function is in protoplasmic synthesis and the formation of new cells. Meristematic cells are typically small with a thin primary wall and few vacuoles (Figure 2.20). Certain of these

cells undergo division, forming new cells. Using *Arabidopsis* as a model, the mechanisms controlling turning on the cell division process in meristematic cells and switching them from vegetative to reproductive growth[48] are beginning to be elucidated.

An apical meristem is found in the growing tip of shoots and roots. It gives rise to the primary growth and structure of the plant. Lateral meristems give rise to the secondary growth of tubers, storage roots and woody stems. A third type of meristematic tissue is the intercalary meristem found in the growing stems of many monocots, such as grasses.

When plant parts are decapitated at harvest, there is generally little meristematic activity. Some tissues, however, can and do recycle nutrients and water into these cells resulting in growth. After extended cold storage, the apical portion of the stem of cabbage will resume growth. With intact plants during storage, conditions are generally selected to minimize growth, and as a consequence, meristematic activity is also repressed. Maintenance of meristems in a healthy condition in intact plants, however, is essential. With improper storage, the apical meristems can readily die, decreasing both the quality of the product and the rate of which it recovers upon subsequent planting.

3. CELLULAR STRUCTURE

Cells are the structural units of living organisms, aggregations of which form tissues. Plant cells vary widely in size, organization, function and response after harvest. They differ from

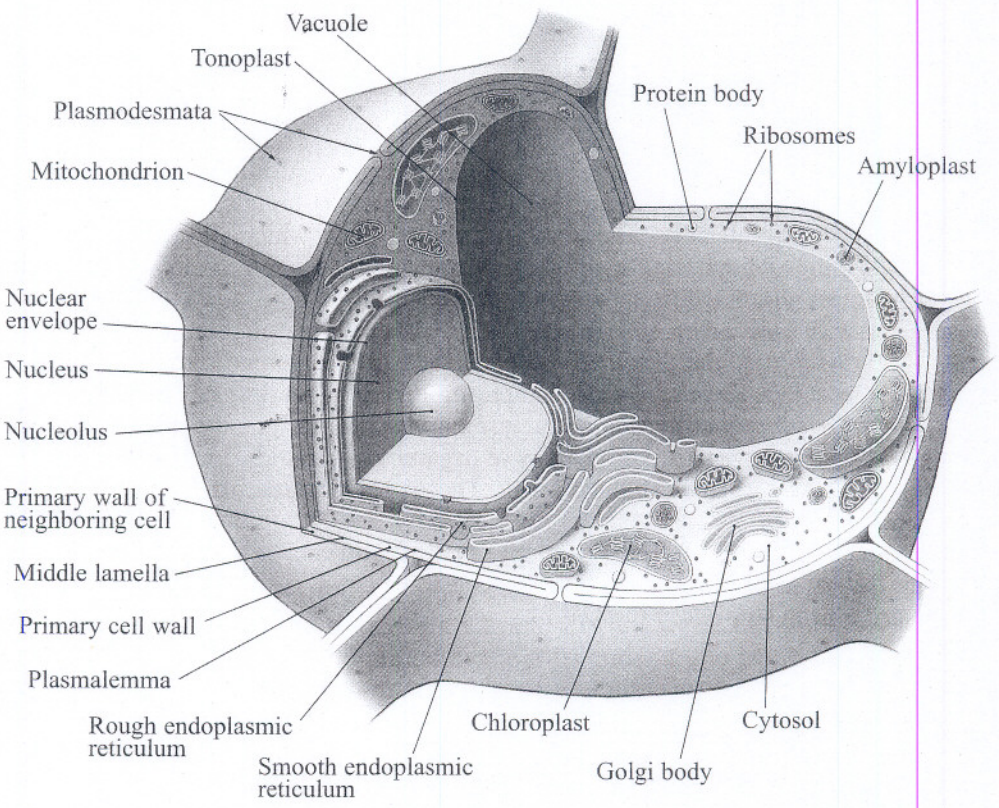


Figure 2.21. A diagrammatic representation on the 3-dimentional structure of a plant cell.

Table 2.1. Comparison of the Size and Number of Subcellular Structures.

Constituent	*Size (diameter)*	*Number per cell**
Vacuole	up to 95% of cell volume	1–several
Nucleus	5–15 μm	1
Chloroplasts	5–10 × 2–4 μm	0–200†
Chromoplasts	3–10 μm × 2–4 μ	0–200
Amyloplasts	7–25 μm × 7–45 μm	0–30
Nucleolus	3–5 μm (dia)	1
Mitochondria	1–4 × 0.5–1.0 μm	500–2,000
Primary cell wall	1–3 μm (thick)	1
Microbodies	0.5–1.5 μm (dia)	few–>1000
Peroxisomes	0.5–1.0 μm (dia)	highly variable
Glyoxysomes	1.0–1.5 μm (dia)	highly variable
Golgi apparatus	0.5–2.0 μm (dia)	few–>100
Ribosomes	0.015–0.025 μm (dia)	5–50 × 10^5

*The specific number of many organelles can be highly variable depending upon cell type, age, condition and other factors.
†Beet leaf parenchyma cells contain 40–50 chloroplasts.[6]

animal cells in the presence of a rigid cell wall and a large central vacuole. Interior to the cell wall is the plasma membrane or plasmalemma, which separates the interior of the cell and its contents, the protoplasm, from the cell's external environment. Much of the cell's energy transfer and synthetic and catabolic reactions occur within the cytoplasm, as does information storage, processing and transfer systems. Within the cytoplasm of eukaryotic cells (organisms other than bacteria and blue-green algae) are numerous organelles and cytoplasmic structures. These provide a means of compartmentalization of areas within the cell that have specific functions. Organelles such as the nucleus, mitochondria, plastids, microbodies and Golgi bodies and cytoplasmic structures such as microtubules, ribosomes and the endoplasmic reticulum are found within the cytoplasm (Figure 2.21). While the number of various organelles varies with cell type, age, and location within the plant, a general example of the relative number per cell is presented in Table 2.1.

The response of plant products after harvest is a function of the collective responses of these subcellular organelles. An understanding of the structure and function of cells and their individual components provides the basis for a more thorough understanding of postharvest alterations occurring in the product.

3.1. Cell Wall

The cell wall has long been known to act as a cytoskeleton, providing mechanical support for plants and harvested products, but only recently has it been established that the wall plays a much more dynamic role.[10] For example the wall appears to be involved in instigating certain pathogen defense mechanisms. Likewise, postharvest structural changes in the cell walls of some products are of tremendous importance in that they can result in alterations in texture and quality. There are two types of walls, primary (Figure 2.22) and secondary, the latter being much more rigid and formed interior to the primary wall (Figure 2.16). While all cells have primary wall, not all have secondary. Typically very few of the cells in edible products contain secondary walls.

The cell wall varies widely in composition and appearance among cell types, species, location and other factors. The wall can vary in thickness, number of plasmodesmata (small,

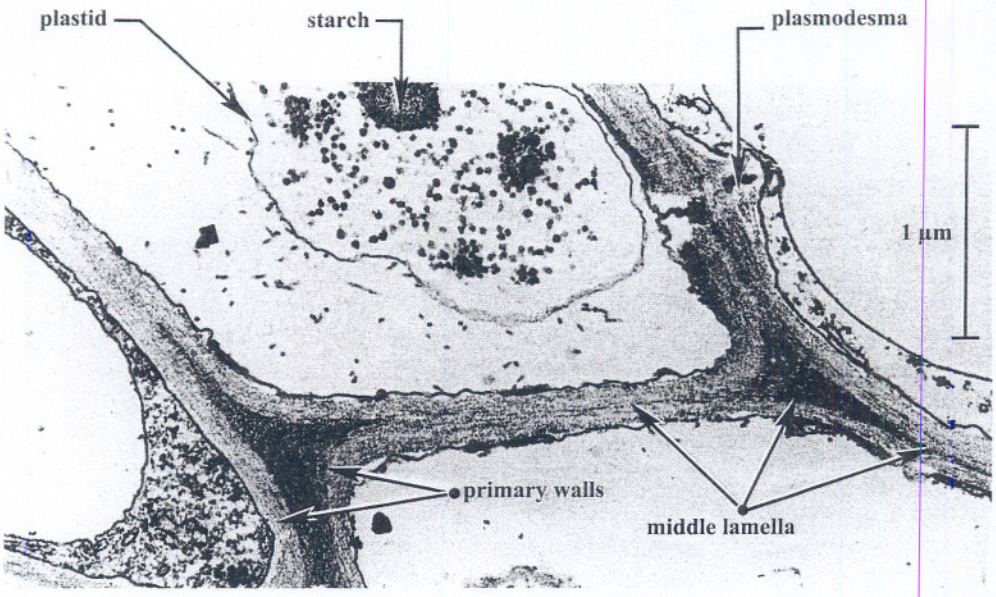


Figure 2.22. The primary cell walls of phloem tissue from *Nelumbo nucifera* Gaertin. Note the middle lamella, found externally to the primary cell wall, and the absence of a secondary cell wall (*from Esau*[15]).

membrane-lined channels transversing the wall and connecting neighboring cells through which constituents are transported and communication occurs), and other factors depending upon the location of the cell. Epidermal cells, for example, typically have substantially thinner interior than the exterior walls, the latter being embedded with cutin and waxes. The primary cell walls of onion are only about 0.1 μm thick; however, the wall can range up to 3 μm in thickness in the cells of some species.

The primary wall is formed from the cytoplasm during cell division and contains cellulose, hemicellulose, pectin, both structural and non-structural proteins,[12] water, and other organic and inorganic substances. A substantial amount of metabolic energy is invested in the synthesis of these components at precise times and in appropriate amounts during development when the actual size of the cell increases from 10 to 1000 fold. The wall also has a diverse mosaic of specialized carbohydrates and proteins that interact with molecules both inside and outside of the cell. This interaction is especially important during development, when the fate of a cell depends on the neighboring wall(s) it is touching. The wall's role in turning undifferentiated cells into specific organs has established it as far more than simply a rigid enclosure for the protoplasm.

In the primary cell wall, cellulose molecules, composed of long chains of glucose subunits, occur in orderly strands arranged into microfibrils. Microfibrils make up the cellulose framework of the wall, which is embedded with a hydrated complex of polysaccharides. The microfibrils are aligned and cross-linked with other constituents to give a very stable, rigid structure (Figure 2.23). The cellulose component is quite stable, and as a consequence, there is little alteration after harvest in the cellulosic structure of the cell wall, exceptions being in abscission zone cells and during senescence. As a consequence, alterations in the wall leading to softening do not involve alters in microfibril composition.

Hemicelluloses are flexible polysaccharides that are attached to the surface of the mi-

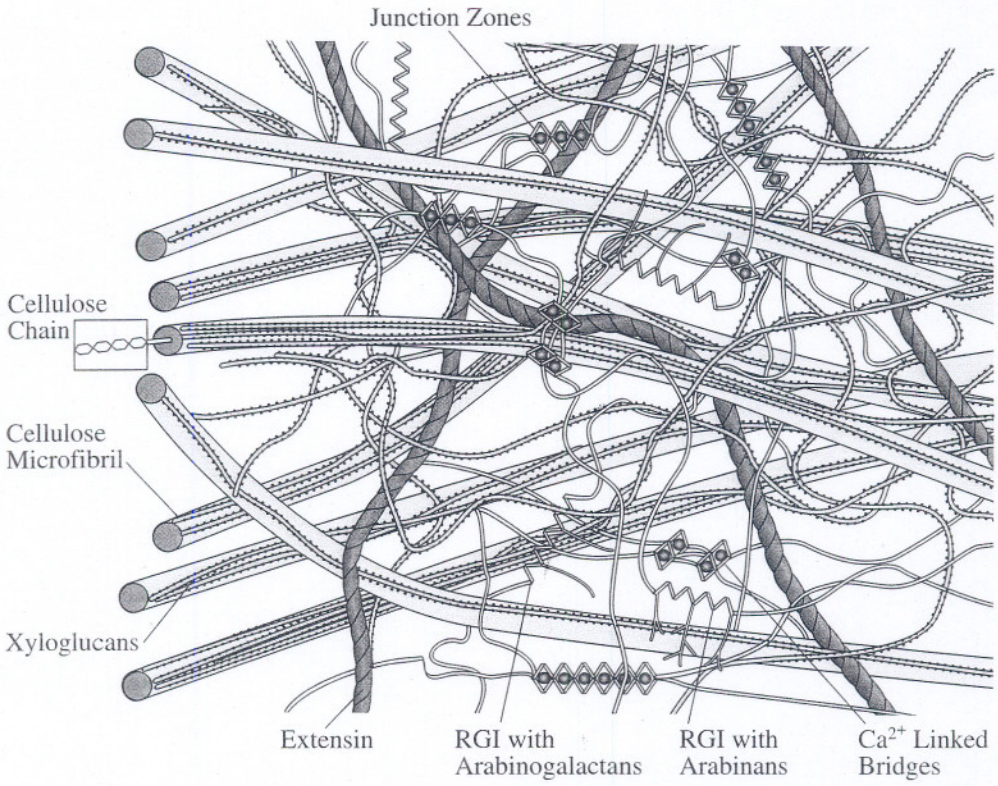


Figure 2.23. Schematic of the primary cell wall's structure. Cellulose microfibrils, comprised of straight chains of glucose molecules, are coated and cross-linked by xyloglucans. In addition, rhamnogalacturonans (RGI) with arabinogalactans or arabinans attached, protein strands (extensin), cross-linkages *via* Ca^{2+} bridges and junction zones collectively form a three-dimensional framework. Interspersed within the structure are enzymes that facilitate structural alterations in the rigidity of the wall, for example, during fruit ripening (*after Buchanan, et al., Carpita and Gibeart,*[11] *and Rose and Bennett*[42]).

crofibrils, tethering them together. Embedded within this structure is a watery gel of pectin molecules and structural proteins. Pectins are found in the middle lamella, the area between neighboring cell walls, and act as a cementing gel holding adjacent walls together. They are also interspersed in the cellulose microfibrils along with hemicellulose and structural proteins. The ratio of these components on a dry weight basis in cell walls varies from approximately 25% cellulose, 25% hemicellulose, 35% pectin and >8% protein in many cells to 60–70% hemicellulose, 20–25% cellulose, and 10% pectin in grass coleoptiles. Tomato fruit cell walls, for example, have relatively high levels of hemicellulose. Water also represents a major component of the walls, comprising 75–80% of the total fresh weight.

Secondary cell walls, formed interior to the primary cell wall, provide much greater rigidity to the cell due to the presence of lignin. The secondary cell walls also contain cellulose and hemicelluloses, but very little pectin. Most edible plant products do not have a large number of cells with secondary cell walls.

After harvest or during ripening pectin and hemicellulose molecules in the primary cell walls of many fruit are enzymatically altered, leading to significant changes in cell-to-cell bonding and the rigidity of the structural framework of the tissue. Therefore postharvest al-

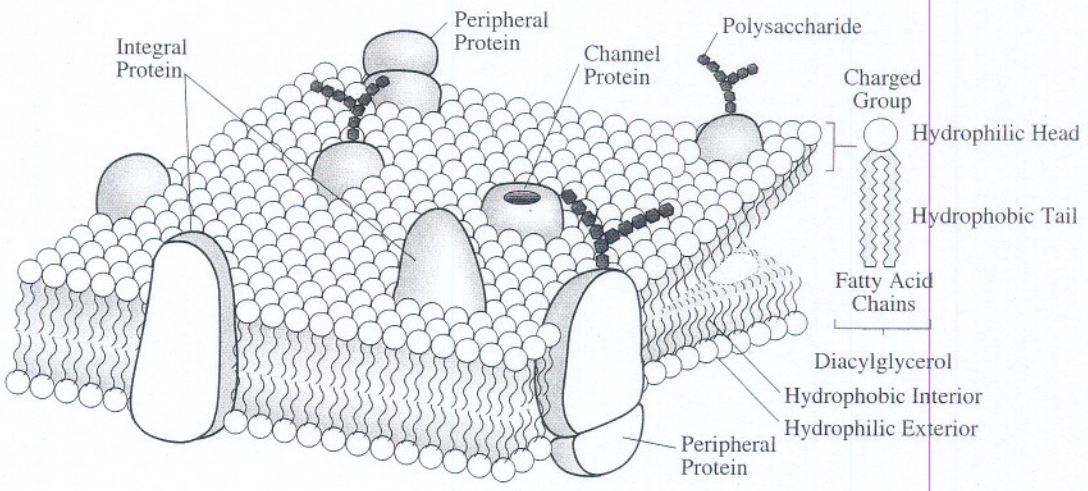


Figure 2.24. Diagrammatic representation of a plant membrane bilayer separated in one corner as would be visualized using freeze fracture preparation. Present is the lipid bilayer with hydrophobic head groups and hydrophobic tails, transport proteins and glycoproteins. The structure of a common membrane phospholipid, illustrates the hydrophilic head group and the hydrophobic tail (*after Wolfe*[53]).

terations in the wall play an important role in textural changes in products, such as softening in apple and pear fruit.

3.2. Cellular Membranes

Diverse membranes are integral components of the cell. Cellular membranes are no longer viewed as separate, autonomous entities, but rather as part of a dynamic and interaction system which plays a major role in controlling the movement of molecules within and secretion outside of the cell, as a site for the biosynthesis of compounds, and in the production of certain cytoplasmic organelles. Postharvest disruption of the membrane system due to low temperature, mechanical or other stresses can have a disastrous impact on the cell.

Cellular membranes are comprised of a lipid bilayer where two layers of polar lipids (predominately diacylglycerols) are oriented with their hydrophobic tails toward the interior of the membrane (Figure 2.24) and their hydrophilic end facing the aqueous exterior. Phospholipids or glycolipids, depending upon the particular membrane, make up the bulk of the membrane structure; however, proteins, both lipoproteins and non-conjugated proteins, are critical components that have transport, catalytic and other functions. The lipid composition of the membrane imparts a flexible, fluid-like structure under ambient conditions that is essential for its proper function. At low temperatures fluidity can be greatly reduced, especially in certain areas of the membrane. This reduction in fluidity can impair membrane function, leading to physiological disorders (chilling injury) in certain crops.

The cell's membrane system is often separated into several very general segments—the **plasmalemma** (or plasma membrane) which surrounds the cell, the **endomembrane system** (endoplasmic reticulum, nuclear envelope, tonoplast, Golgi apparatus, microtubules, etc.), and the mitochondrial and plastid membranes, the latter being self-reproducing and as a consequence, more independent of the endomembrane system.

The cell is separated from its surrounding environment by the plasmalemma, a thin membrane (approximately 7.5 nm wide) found just interior to the cell wall. The plasmalemma is composed of a viscous lipid bilayer (Figure 2.24). Interspersed on the surface and within the

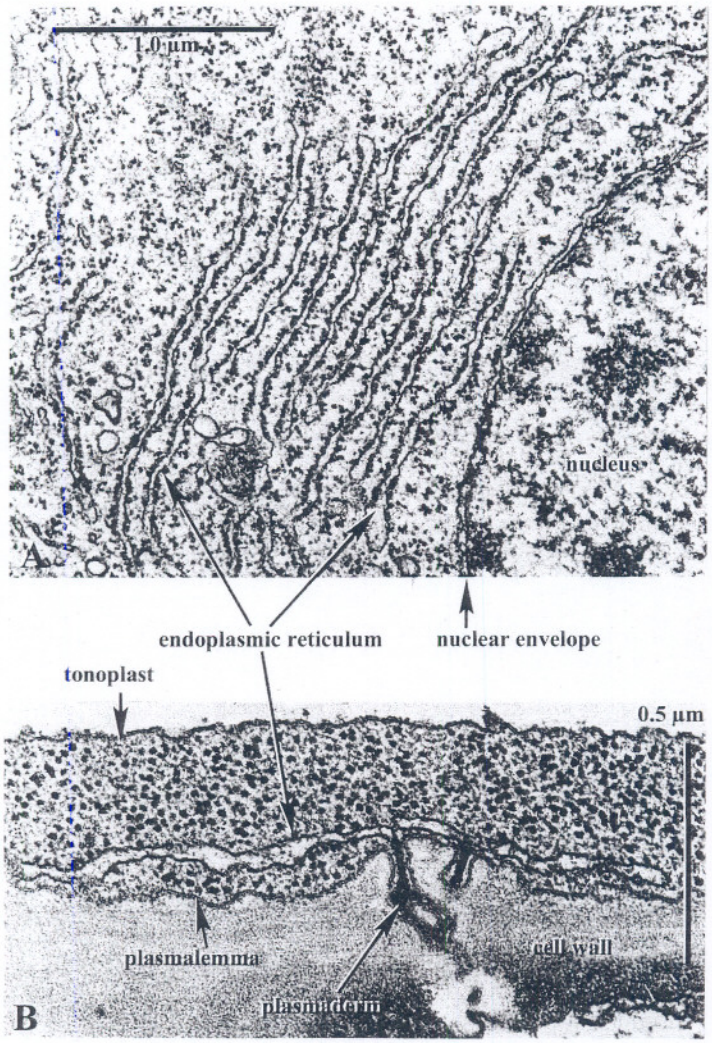


Figure 2.25. Transmission electron micrograph of leaf cells of *Nicotiana tabacum* L. (A) and *Beta vulgaris* L. (B) displaying the endoplasmic reticulum (ER), plasmalemma, nuclear envelope and tonoplast membrane (*from Esau*[15]).

membrane are a number of other molecules (e.g., proteins) which carry out an array of critical functions. For example, some sites on the membrane control the specificity of transport of molecules across the membrane into and outside of the cell, while others catalyze specific reactions. Interspersed along the plasmalemma are plasmodesmata[34], narrow cylindrical strands of cytoplasm bound by the plasmalemma that penetrate through the cell walls and into the neighboring cell, transforming the plant from a collection of individual isolated cells into a interconnection network of protoplasts. Molecules that due to their size or charge can not readily cross the plasmalemma can move between cells by way of the plasmodesmata. For example, transcription factors that instigate gene expression can move from cell to cell *via* plasmodesmata.[37]

A number of other membranes are found within the cell (Figure 2.25). Organelles such as the nucleus, mitochondria, and plastids are bound by two membranes. The vacuole and mi-

crobodies, on the other hand, are enclosed by a single membrane. Also found throughout the cytoplasm is the endoplasmic reticulum. It forms a continuous membrane system that functions as a reactive surface for many biochemical reactions and in compartmentalization of certain compounds. Ribosomes, which carry out the assembly of new proteins, are often attached to the endoplasmic reticulum (called the rough endoplasmic reticulum). The smooth endoplasmic reticulum (areas without ribosomes) is believed to be involved in transporting and secreting sugars and lipids.

3.3. Cytoplasm

The cytoplasm is the viscous matrix which envelops all of the more differentiated parts and organelles of the protoplasm. It is the cellular mass interior to the plasma membrane and exterior to the vacuolar membrane, the tonoplast. Individual organelles (e.g., nucleus, mitochondria, plastids) while found in the cytoplasm, are not considered part of it. The cytoplasm contains proteins, carbohydrates, amino acids, lipids, nucleic acids, and other substances that are water soluble. Generally, nonorganelle structures such as microtubules, ribosomes, and the endoplasmic reticulum are also considered as part of the cytoplasm. Although under certain conditions the cytoplasm can assume a gel-like structure, typically it is viscous and can move within the cell. This movement, called protoplasmic streaming, is quite substantial in some types of cells.

3.4. Nucleus

Nearly all living cells of agricultural plant products are uninucleate. Exceptions would be mature sieve tube cells which no longer contain a nucleus and certain specialized cells which are multinucleate. The nucleus represents the primary repository of genetic information within the cell and thus functions in the replication of this information during cell division, and more importantly from a postharvest context, as the cell's command center, controlling protein synthesis. Specific enzymes essential for ripening and other postharvest changes are assembled in the cytoplasm. The nucleus is delimited by two porous membranes separated by a perinuclear space (Figure 2.26).

Interior to the nuclear membrane is the nuclear matrix or nucleoplasm which contains deoxyribonucleic acid (DNA), ribonucleic acid (RNA), nucleic acids, proteins, lipids, and other substances. Also found in the nuclear matrix is a dark spherical body, the **nucleolus.** It functions in the storage of RNA and the synthesis of ribosomal RNA. The chromosomes are also found here; however, with the exception of during cell division, they are not in a tightly coiled state, but are found as a matrix of DNA and protein called **chromatin.** These associated proteins, a significant number of which are histones, act as repressors and activators of transcription, impart a three dimensional structure, aid in protection and have various other functions.

As the primary control center, a critical question in plant and animal biology has been how does the nucleus communicate with the rest of the cell? What chemical signals move into the nucleus to activate the expression of specific genes* and since enclosed in a double membrane that excludes molecules of any size, how do these chemical signals enter and RNA exit to instigate protein synthesis in the cytoplasm? Recent work has begun to identify the molecular structure and control of a series of pores that transverse the membrane, facilitating the

*The control of gene expression is discussed in Chapter 5.

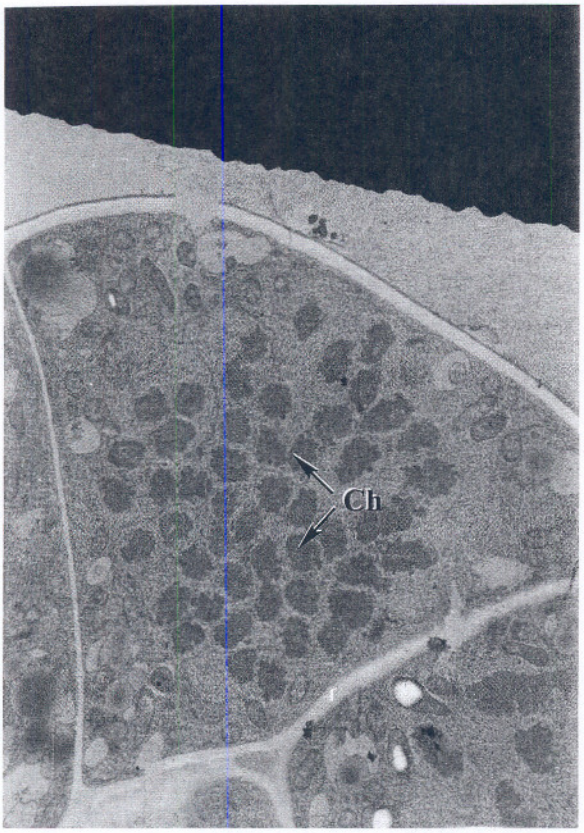


Figure 2.26. As meristematic cells begin to divide, the nuclear membrane disappears and the chromatin becomes organized into chromosomes (Ch) (dark masses in the center of the above *Pinus taeda* L. cell) (*Electron micrograph courtesy of H. Ammerman*).

movement of large molecules across. With the assistance of transport proteins and proteins that control loading and unloading of the cargo from the transport proteins,[35] the flow of large molecules is very precisely regulated.

3.5. Mitochondria

Mitochondria are small, elongate, occasionally spherical structures, 1 μm to 5 μm long. The number of mitochondria per cell varies with cell type, age and species, ranging from a few hundred to several thousand. Their primary function is in cellular respiration. Within the mitochondria occur the energy conversion processes of the tricarboxylic acid cycle and the electron transport system. As a consequence, mitochondria are of critical importance in the recycling of stored energy after harvest.

Mitochondria, like the nucleus, are enclosed within a double membrane. The outer membrane is relatively porous while the inner membrane contains numerous tubular folds or extensions called cristae (Figure 2.27). The energy transfer proteins of the electron transport system are situated on the surface of cristae. Found free within the mitochondrial matrix are many of the enzymes of the tricarboxylic cycle (some, e.g., succinic dehydrogenase, are located in the inner membrane). Also located in this aqueous portion of the mitochondria are RNA and DNA that control the synthesis of certain mitochondrial enzymes.[32] The presence of genetic information within the mitochondria has led to the belief that they were originally au-

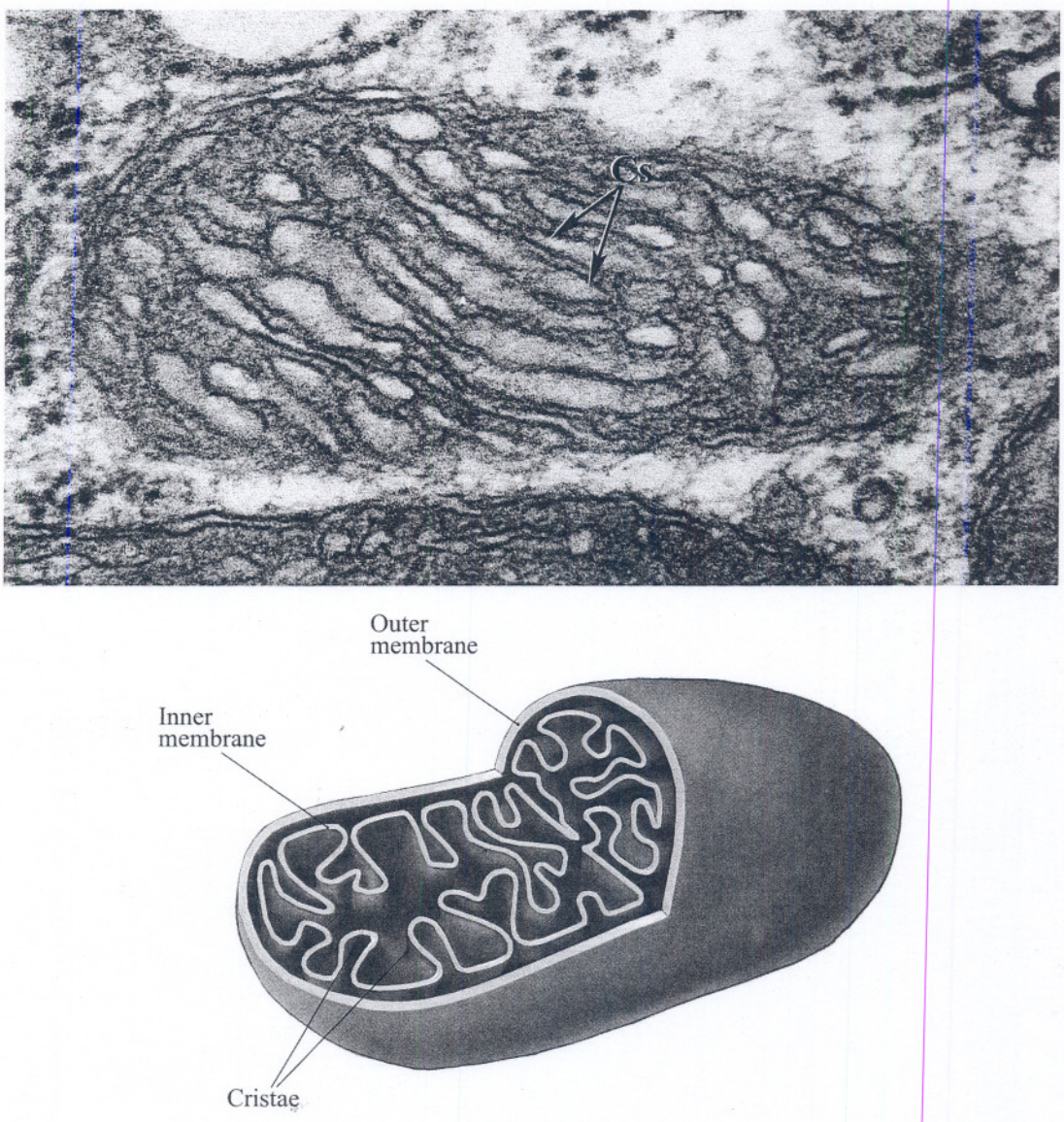


Figure 2.27. Electron micrograph of a mitochondrion showing the outer membrane and cristae (Cs) and diagrammatic illustration of what is thought to be the arrangement of the double membrane forming the outer membrane, inner membrane and cristae (*Electron micrograph ×250,000 courtesy of W.W. Thomson; drawing after Ting*[46]).

tonomous organisms that became associated with eukaryotic cells early in the evolution of life.[19]

Increases in the number of mitochondria within a cell appear to begin initially with an increase in their size, which is followed by division into two separate organelles. An interesting facet of the mitochondria story is that mitochondrial DNA (mtDNA) comes entirely from the female parent, hence the mtDNA in the progeny of crosses between two plants does not change through the input of genes from the male parent, as with nuclear DNA. Changes in the mtDNA arise from mutations, seen as nucleotide substitutions in the mtDNA. As a conse-

quence, mtDNA has be used as a "molecular clock": the fewer the number of substitutions, the older the organism. Utilizing this approach, researchers have estimated that our common female ancestor or "mitochondrial Eve" lived about 200,000 years ago in Africa. The critical assumption of the mitochondrial clock is that the rate of insertion of mutations is relatively constant over time; however, recent evidence suggests that this is not always the case.

An important additional role for mitochondria that is beginning to be elucidated is in the regulation of programmed cell death or **apoptosis.** In animals, and to a much lesser extent in plants, there is a continual turnover in certain cells; old cells die and new cells are formed. A central question has been, "What controls programmed cellular death?" Since mitochondria are essential for energy metabolism, shutting down the mitochondria would lead to rapid death.[9] It now appears there are several means by which mitochondria can affect apoptosis (e.g., disruption of energy metabolism; release of proteins that mediate death). Deterioration in the mitochondria also appears to be closely associated with the aging of organs and organisms.

3.6. Plastids

Plant cells contain a distinct group of organelles called plastids. As with the nucleus and mitochondria, these organelles are enclosed within a double membrane. Plastids are found with differing form, size, and function. The three principal types are **chloroplasts** (chlorophyll containing plastids in which photosynthesis occurs), **chromoplasts** (plastids containing other pigments such as carotene or lycopene in red tomato fruit), and the non-pigmented **leucoplasts.** One type of leucoplast (i.e., amyloplasts) acts as a storage site for starch and is prevalent in a wide range of harvested products. Much of the research on plastids has focused on chloroplasts, however, the structure, physiology and biochemistry of leucoplasts is of considerable interest in postharvest biology in that they represent sites of stored energy, e.g., amyloplasts (Figure 2.28).

Plastids arise from proplastids inherited with the cytoplasm in newly formed cells. These proplastids appear to divide and differentiate into the various types of plastids (Figure 2.29), depending upon the nature of the cell in which they exist. Their final form is not static, however, in that there is often considerable interconversion between types of plastids (Figure 2.30). In many cases, pronounced changes are associated with major physiological events such as fruit ripening or senescence.

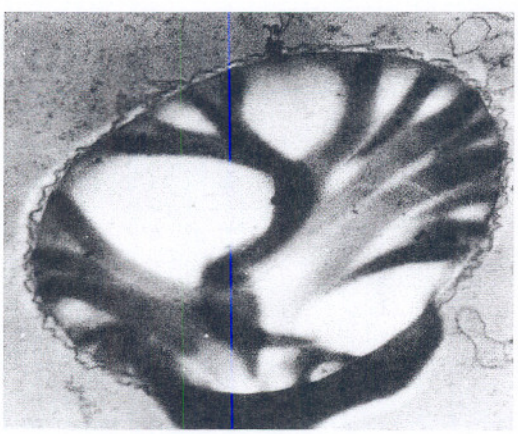


Figure 2.28. Electron micrograph of a potato tuber amyloplast containing a single starch grain (*Electron micrograph ×74,000 courtesy of H.Y. Wetzstein*).[49]

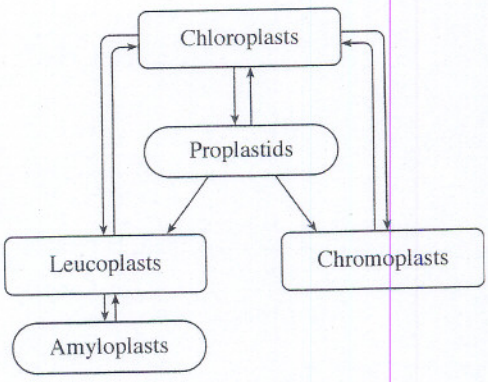


Figure 2.29. Schematic of the formation of various types of plastids.

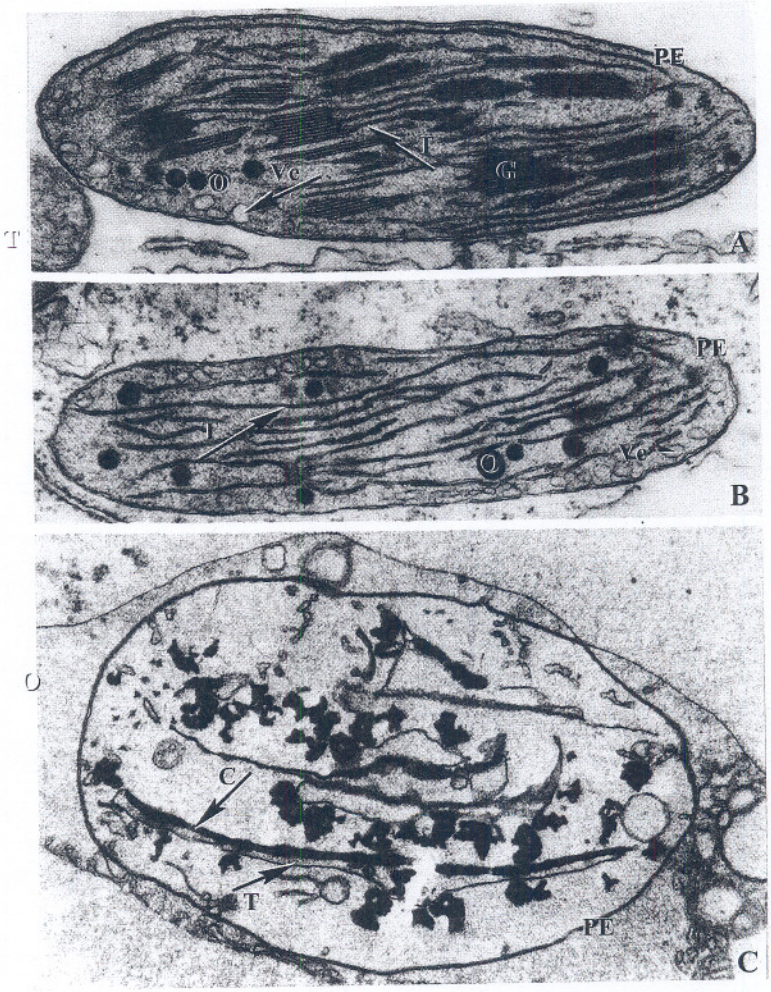


Figure 2.30. The transition during ripening of an elongated chloroplast (A) from tomato fruit with distinct granal and stromal thylakoids, to a metamorphosing chloroplast (B) with only a few vestiges of granal thylakoids remaining and finally a chromoplast (C) containing lycopene crystals (C—crystal; G—granum; O—osmiophilic globule; PE—plastid envelope; T—thylakoid; Ve—vesicle) (*Electron micrographs: (a) ×46,800, (b) ×43,700 and (c) ×23,900 courtesy of Rosso*[43]).

Contained within a plastid such as a chloroplast are proteins, lipids, starch grains, DNA, RNA, and various organic compounds. Chloroplasts have a complex inner lamellar membrane system of varying levels of complexity and an embedding matrix called the stroma. The membrane system is composed of grana, seen as flattened thylakoids stacked in the shape of a cylinder, and frets, an inner-connecting membrane system transversing the stroma between individual grana (Figure 2.31). In the stroma the photosynthetic CO_2 fixation reactions occur, while the photosynthetic photosystems are found on the thylakoid membranes.

Like mitochondria, chloroplasts contain their own DNA and synthesize a portion of the proteins required there. It is estimated, however, that greater than 80% of their protein is encoded by the nucleus and assembled outside of the chloroplast. An area of research interest has been how proteins formed in the cytosol are targeted to and transported across the chloroplast's outer membrane. Transmembrane trafficking of proteins is now known to be controlled by an import apparatus in the membrane called a translocon.[25] Targeting is accomplished by amino acid sequences at the end of the protein, which are removed once the molecule has arrived at its destination.

3.7. Microbodies

Microbodies are small (0.5–1.5 μm) spherical organelles (Figure 2.32) found in a variety of plant species and types of cells. There may be from 500 to 2000 microbodies in a single cell. They are bound by a single membrane and contain specific enzymes. The enzymes present and the function of the microbody vary depending upon its biochemical type. Microbodies that are associated with chloroplasts and function in glycolate oxidation during photorespiration are called **peroxisomes.** Those present in oil rich seeds and that function in the conversion of lipids to sugars during germination (glyoxylate cycle) are called **glyoxysomes.**

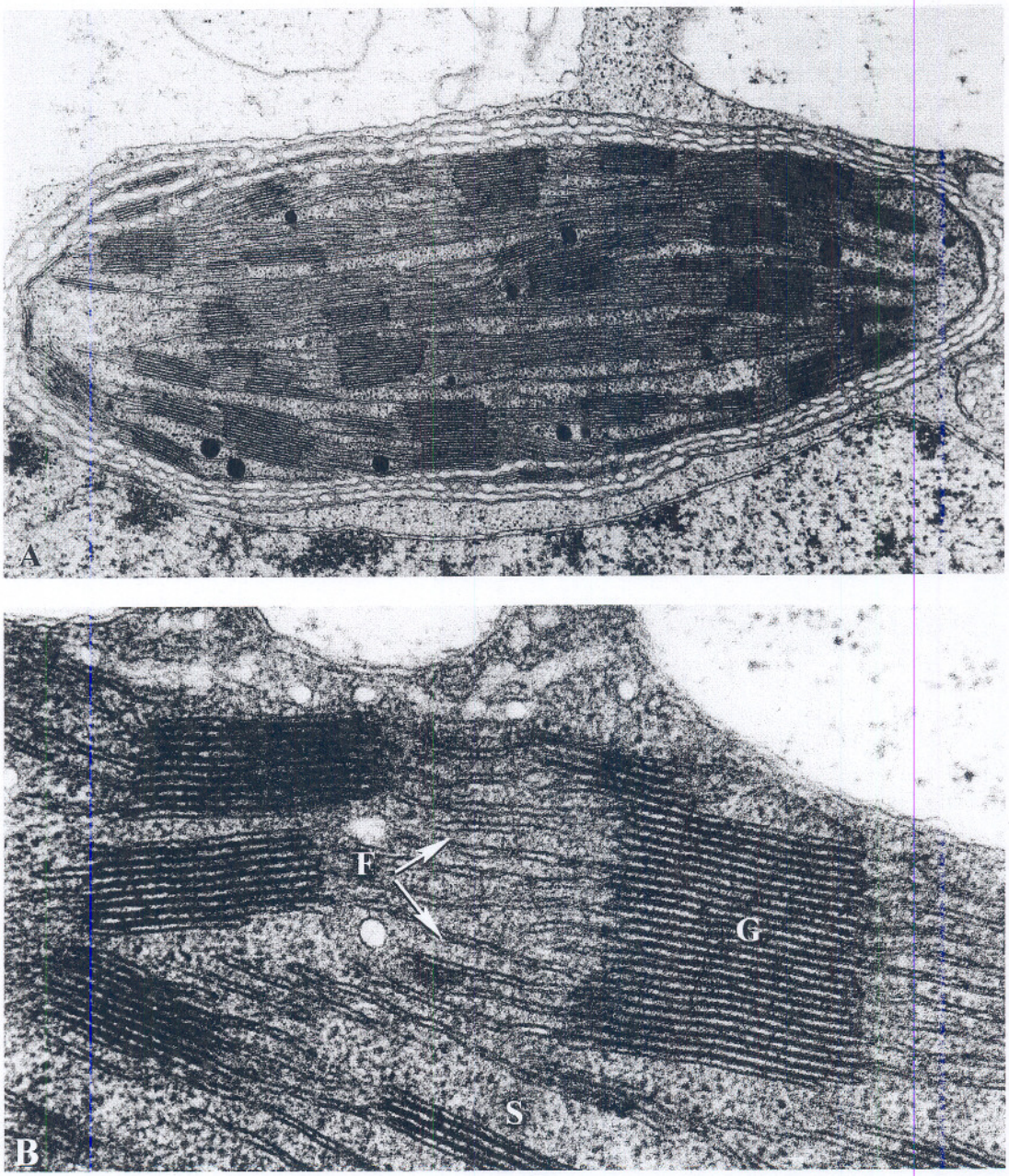
Microbodies appear to be formed from invaginations on the smooth endoplasmic reticulum. Their internal matrix is generally amorphous although crystalline substances may be present.

3.8. Vacuole

In mature cells, the vacuole is seen as the central feature within the cytoplasm (Figure 2.33). Young meristematic cells have numerous small vacuoles, which may with time enlarge and coalesce into the large central vacuole of the mature cell. Structurally, the vacuole is bound by a single membrane, called the tonoplast, which exhibits a differential permeability to various molecules. Thus the movement of many molecules into and out of the vacuole is closely controlled. Contained within the vacuole is a diverse array of possible compounds. For example, the vacuole may contain sugars, organic acids, amino acids, proteins, tannins, calcium oxalate, anthocyanins, phenolics, alkaloids, gums and other compounds. These may be dissolved in the aqueous medium, found as crystals (Figure 2.33), or congealed into distinct bodies.

The vacuole has several critical functions within the cell.[31] It acts as a storage site for a wide range of compounds, including pigments and chemicals that would be harmful to the cytosol (e.g., alkaloids, crystals) if allowed to reside there. Thus the vacuole acts as a disposal site for certain "waste" material from the cytosol. This function is essential since most plant cells can not readily excrete unwanted substances outside of the cell. As a consequence the vacuole acts as repository for these substances.

The cytosolic concentration of hydrogen ions (pH) is modulated by the vacuole, with excess levels being transported there. The concentrating of hydrogen ions accounts for the more



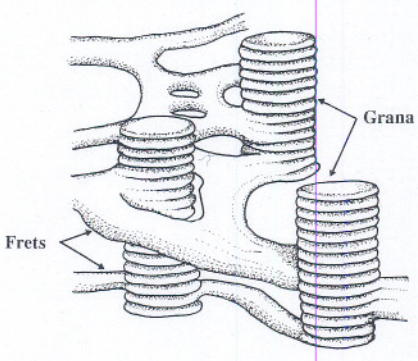


Figure 2.31. Electron micrograph of a chloroplast (A) with enlarged view of a granal region (B) (G—grana; S—stroma; F—fret). Diagramed is the arrangement of the grana and fret structure within the granal region (*Electron micrograph courtesy of W.W. Thompson; drawing after Bidwell*[5]).

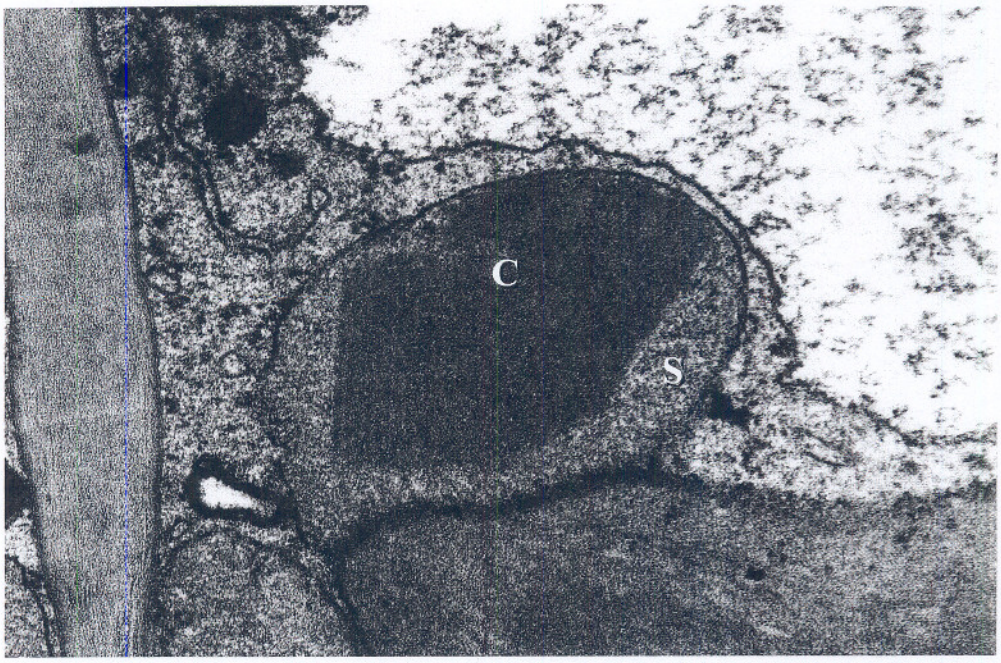


Figure 2.32. Electron micrograph of a microbody from a *Citrus* mesophyll cell (×81,700). S = stroma, C = crystalline inclusion of protein, possibly the enzyme catalase (*Electron micrograph courtesy of W. W. Thompson*).

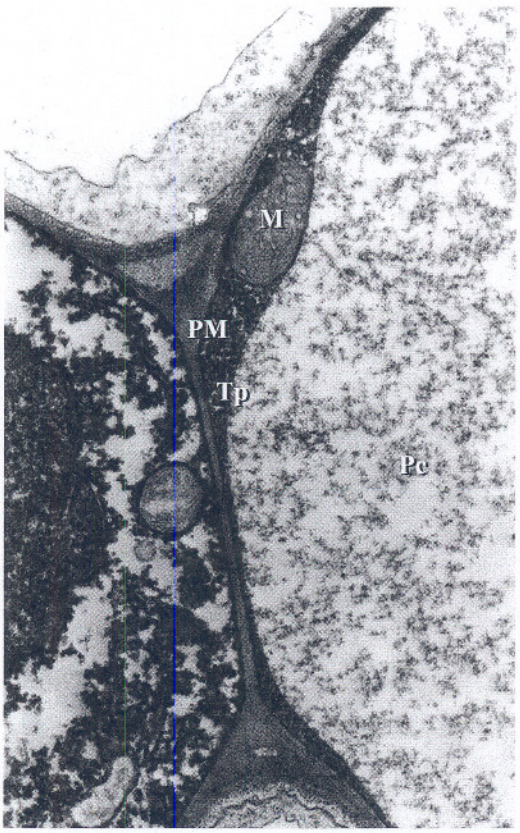


Figure 2.33. Electron micrograph of the central vacuole in a mature *Liquidambar styraciflua* L. cell. Within the vacuole are precipitated components (Pc), (PM—plasma membrane; Tp—tonoplast; M—mitochondria) (*Electron micrograph courtesy of H.Y. Wetzstein*).

acidic pH of the vacuole (as low as 3.0 versus around 7.0 in the cytosol). In certain fruit (lemon, orange) the accumulation of citric or other organic acids in the vacuole contributes to their characteristic tart taste.

The Ca^{2+} and phosphate ion concentrations in the cytosol are also maintained at appropriate levels through their transport across the tonoplast. Due to the lower pH of the vacuole, Ca often forms crystals with oxalate, phosphate or sulfate. Nitrogen is likewise stored in the vacuole, and when its concentration (or phosphate) becomes too low in the cytosol, it can move outward.

The vacuole also functions in the maintenance of the turgor pressure of the cell. The concentrating of solutes within the vacuole alters the osmotic gradient, causing water to move into the vacuole until reaching equilibrium with the cytosol. Absorption of water by the vacuole provides the outward force that contributes to the shape, texture and volume of the cell. Loss of turgor pressure after harvest readily diminishes product quality.

Finally the vacuole contains a large number of hydrolytic enzymes, e.g., proteases, lipases and phosphatases. Under normal conditions these enzymes act in part in the recycling of compounds from the cytosol. However, when the tonoplast is ruptured due to injury or senescence, these hydrolytic enzymes are released into the cytosol. Here they attack a wide range of cellular constituents, accelerating the rate of disorganization and death of the cell. Conversely, certain enzymes are present in the cytosol and their substrates are released with disruption of the vacuole. The discoloration reactions occurring after cells sustain mechanical injury (e.g., bruising) are the result of the action of phenol oxidase on phenols released from the vacuole into the cytosol.

3.9. Oleosomes

Oleosomes, also called oil bodies and spherosomes, are 0.6–2.5 μm diameter bodies (Figure 2.34) bound by a single membrane; they contain an amorphous mass of lipids.[24] Within the cell they may be compressed into irregular shapes; however, when isolated they are spherical. In maize kernels, oleosomes contain 97% neutral lipids and small amounts of protein, phospholipids and free fatty acids. They are formed by vesiculation of the rough endoplasmic reticulum where the lipids are synthesized.[13] Oleosomes in seeds are degraded during germination and growth of the seedling with the constituent lipids converted to carbohydrates for growth.

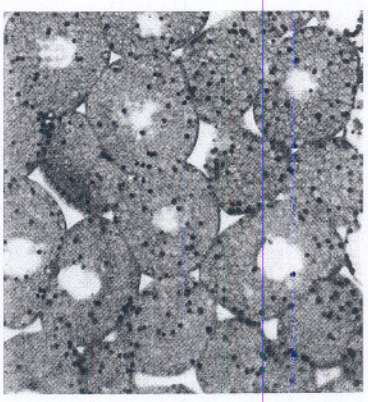


Figure 2.34. Photomicrograph of oleosomes, small dark, oil containing spherical bodies present in cortical nodule parenchyma cells of *Medicago sativa* L. (*courtesy of A.K. Bal*).

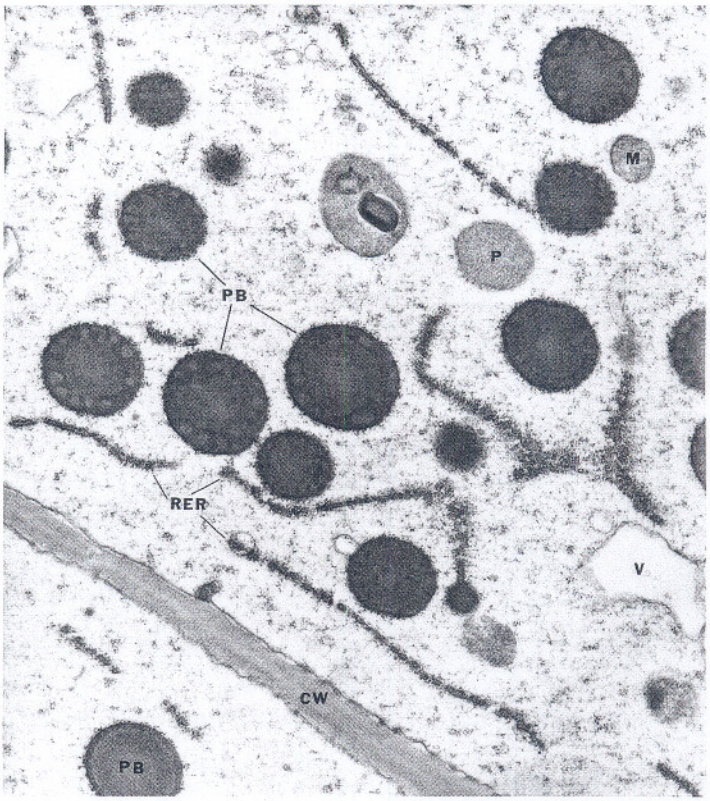


Figure 2.35. Maize endosperm rough endoplasmic reticulum (ER) connected to protein bodies (PB); cell wall (CW) (*courtesy of B.A. Larkins*).[22]

3.10. Protein Bodies

Plants sequester proteins within the cells of certain organs to provide carbon, nitrogen and sulfur for subsequent growth and development (e.g., seeds, certain vegetative tissues). Typically these are storage proteins and accumulate within storage protein vacuoles and protein bodies (Figure 2.35).[22] Protein bodies are 0.1–22 μm diameter spherical, single-membrane organelles. Protein deposits may also be found free within the cytoplasm.[33] Protein bodies differ from protein storage vacuoles in that they arise from the endoplasmic reticulum, the site of protein synthesis. In some seeds, protein bodies are found in aleurone cells located near the seed surface; in legumes they tend to be within cotyledon parenchyma cells. Protein bodies are also found in non-seed tissues (roots, leaves, flowers) but seldom numerically as concentrated as in seeds.

3.11. Golgi Bodies

The interior of the cell is comprised of a maze of compartments, each bound within a lipid membrane. When proteins and polysaccharides are synthesized in the cytoplasm and are des-

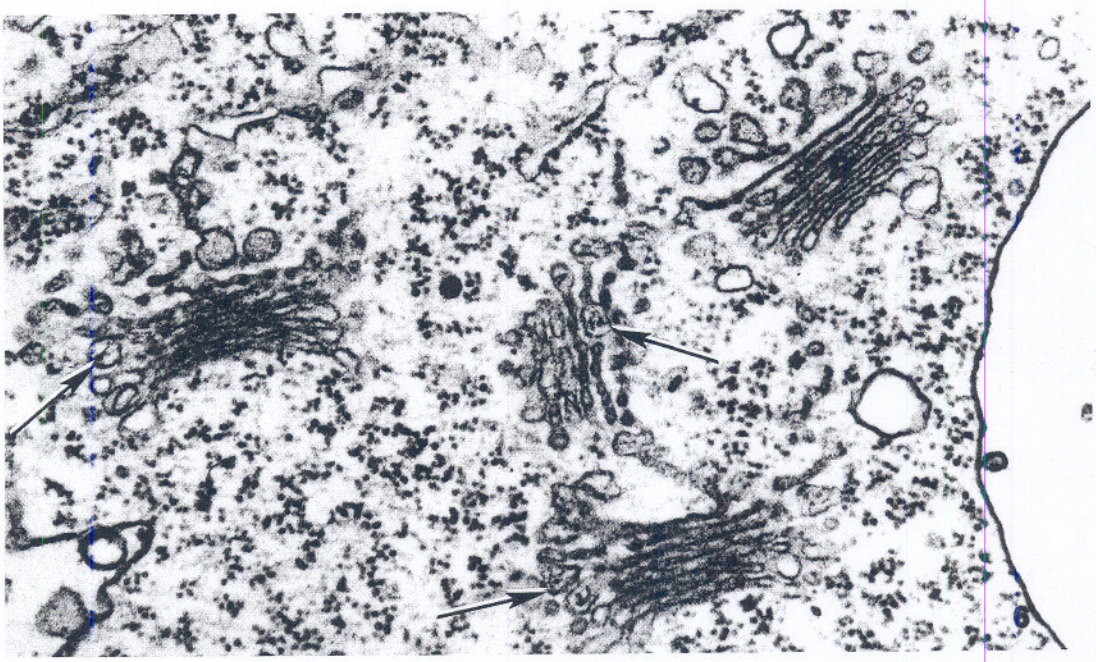


Figure 2.36. Electron micrograph of four Golgi bodies in a young cotton fiber cell. Also present are a large number of ribosomes (*Electron micrograph ×121,000 courtesy of J.D. Berlin*[15]).

tined for a specific organelle or secretion outside of the cell, there must be some orderly way to direct them to the appropriate place. Golgi bodies (named after Camillo Golgi who first identified them in 1898), working in tandem with the endoplasmic reticulum, accomplish this.

Golgi bodies (also known as dictyosomes) are small (1–3 μm in diameter by 0.5 μm thick) subcellular organelles which are composed of stacks of flat circular cisternae, each enclosed by a single membrane (Figure 2.36) and are surrounded by smaller membranous tubules and vesicles. The number of cisternae per Golgi body and number of Golgi bodies per cell varies. There are typically 3 to 10 cisternae in a single Golgi body and from a small number to over 100 Golgi bodies per cell, depending upon cell type, which are dispersed throughout the cytoplasm and are a critical part of the cell wall assembly system. Collectively, the Golgi bodies within a cell are called the Golgi apparatus. Cells that are actively secreting compounds from the cytoplasm, for example, during cell wall development or mucilage from the tips of roots, tend to have an abundance of Golgi bodies. As a consequence, a primary function of Golgi bodies in plant cells is believed to be in the secretion of cellular compounds, chiefly polysaccharides and glycoproteins, exterior to the plasma membrane.

Secretion is accomplished through the formation of small spherical vesicles of polysaccharides or glycoproteins by the cisternae (in animal cells it is primarily proteins). The endoplasmic reticulum participates in the process that now appears to be more complex than originally thought (i.e., protein molecules are enzymatically altered in the Golgi, for example, carbohydrate groups may be attached).[4] Proteins assembled on the endoplasmic reticulum that are destined for secretion are sequestered within membrane-enclosed vesicles that separate from the endoplasmic reticulum and migrate to the Golgi complex. The vesicles fuse with the cisternae and the material progresses, *via* a yet-to-be-ascertained mechanism, from the back cisternae to the most forward. While within the Golgi body, proteins are often structurally modified. Once reaching the most forward cisternae, a second vesicle forms containing

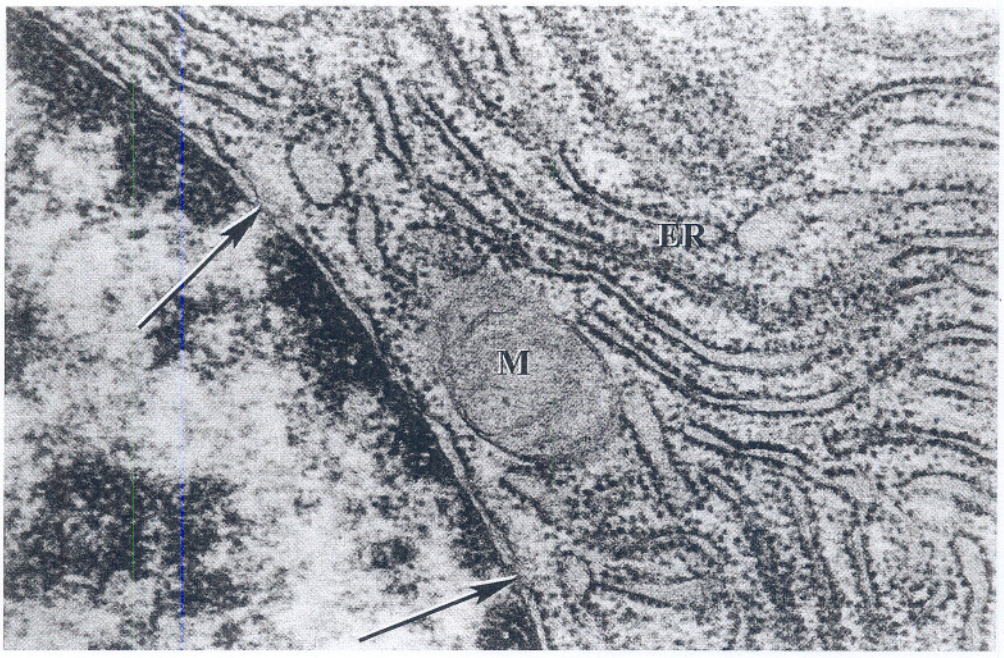


Figure 2.37. Arrangement of ribosomes on the rough endoplasmic reticulum (*Electron micrograph ×59,000 courtesy of Wolfe*[53]). Arrows denote nuclear pores; mitochondria (M).

the molecules for secretion. The vesicle then migrates to the plasma membrane where the vesicle membrane and the plasma membrane fuse, emptying its contents to the exterior for incorporation into the cell wall. Due to the transitory nature of the cisternae, Golgi bodies are constantly changing, with some cisternae growing in size and others disappearing altogether.

3.12. Ribosomes

Ribosomes are small bodies (0.017–0.025 μm in diameter) which are the site of protein synthesis within the cell (Figure 2.37). They are found in the cytoplasm, both associated with the endoplasmic reticulum and free, dispersed singly or in small groups. Ribosomes are also found in nuclei, plastids and mitochondria. These, however, appear to be distinct from those found in the cytoplasm. Because of the relatively short life expectancy of many proteins and the large number required by the cell, many ribosomes are needed. Estimates of the number of ribosomes per cell range from 500,000 to 5,000,000.

When a messenger RNA carrying the code for a specific protein from the nucleus unites with multiple ribosomes, the resulting complex (similar to a string with beads) is called a polysome or polyribosome. Transfer RNAs within the cytoplasm bind to amino acids, bringing these basic building blocks of proteins to the polysome for incorporation into the new protein molecule. By having multiple ribosomes attached to a single messenger RNA, a number of identical proteins can be assembled from the single template. Smaller ribosomes (0.015 μm) are found in the chloroplasts and mitochondria and synthesize a portion of the proteins required in these organelles. The remaining proteins are assembled in the cytoplasm and transported into the chloroplast or mitochondria.

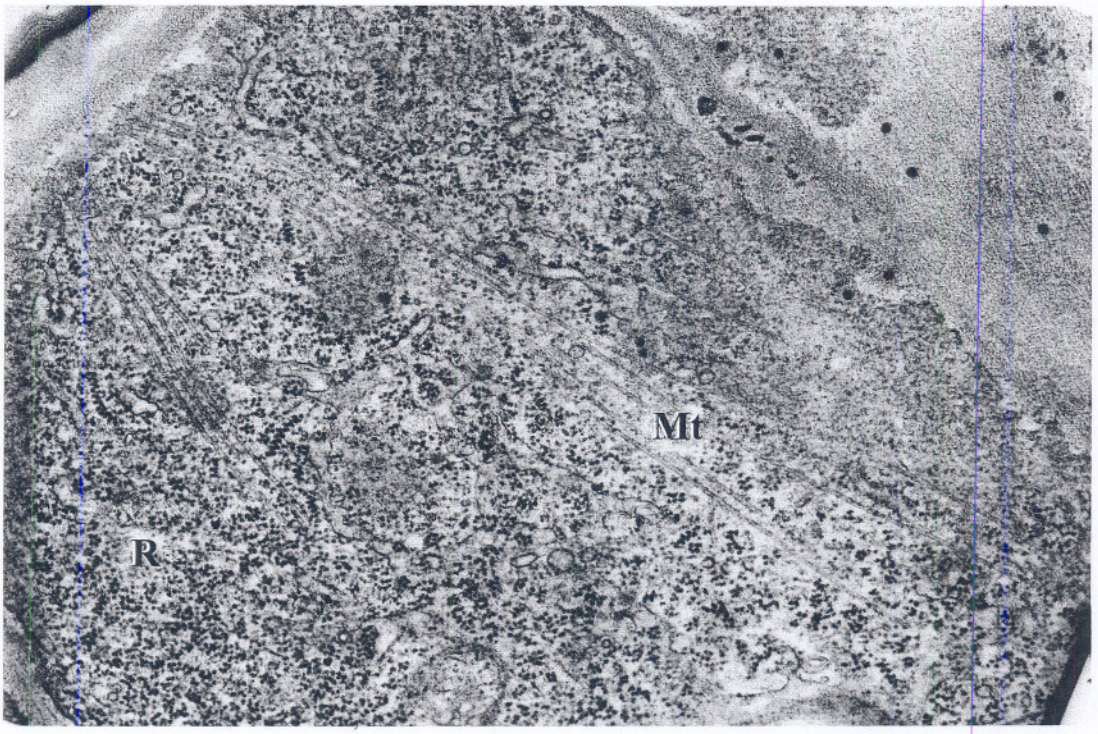
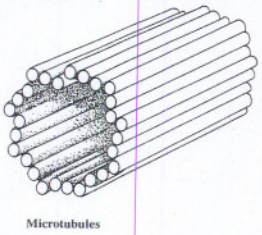


Figure 2.38. Electron micrograph of microtubules (Mt) in a young plant cell. The inset illustrates the arrangement of the fibril making up the elongated tubular nature of the microtubule (*Electron micrograph courtesy of W.W. Thomson; drawing after Ting*[46]).



3.13. Cytoskeleton

While the wall provides the cell a 3-dimensional structure, the interior of the cell also has a structural framework of filamentous proteins called the **cytoskeleton.** The cytoskeleton provides spatial organization for the organelles, scaffolding for movement of organelles and materials within the cell, and is important in cell wall synthesis. It is comprised of three components: microtubules, microfilaments, and intermediate filaments.

3.13.1. Microtubules

Microtubules appear as hollow cylinders approximately 25 nm in diameter and varying from a few nm to several μm in length (Figure 2.38). They are composed of 13 protein fibrils (columns) comprised of hundreds of thousands of subunits of a globular protein called tubulin.

Microtubules appear to have several functions within the cell. During cell division, microtubules form the spindle fibers which control chromosome migration. Colchicine, a chemical used by plant breeders to double the number of chromosomes per cell, binds to tubulin,

preventing chromosome migration during anaphase. Thus the cell retains both sets of chromosomes.

Microtubules also appear to be involved in coordinating the development of the cell wall. They are found in greatest numbers in the peripheral cytoplasm, adjacent to regions with growing cell walls. Disruption of the microtubules with colchicine also appears to alter the orderly arrangement of the new wall. Likewise, exposure to the phytohormone ethylene causes the microtubules to become more elongated, which alters the microfibril structure of the wall. This causes the cell's growth in length to be inhibited and the radial diameter to increase, a classical symptom of ethylene exposure to plants.[2,29] Microtubules are also involved in the transport of proteins and lipids to their appropriate destination within the cell,[23] serving as a rail on which motor proteins convey these components.

3.13.2. Microfilaments

Microfilaments are smaller than microtubules, typically 5 to 7 nm in diameter, and found as two protein chains intertwined in a helical fashion around each other, rather than a tubular structure. They are composed of the protein actin and appear to be responsible for cellular movements such as protoplasmic streaming. Both microtubules and microfilaments can assemble and disassemble, depending upon conditions within the cell; the former being generally more stable.

3.13.3. Intermediate filaments

Intermediate filaments are linear keratin or keratin-like polypeptides aligned in pairs and helically coiled around each other. The double coil then aligns with a similar structure producing a tetramer (4 proteins) which in turn pack together to form a 10 nm diameter filament.[1] Their function in plant cells is not known, but they may act similar to their counterparts in animal cells by providing structure to the interior of the cell. Intermediate filaments have been observed connecting the nucleus surface to the cell periphery[36] and are more stable than microtubules and microfilaments.

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