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KEY CONCEPTS

1. Fruits are ripened ovaries that are the end products of sexual reproduction in angiosperms and are a major vehicle for the dispersal of their enclosed seeds.
2. Protected by a tough outer coat, seeds are ripened ovules that contain an embryonic plant plus some nutritive tissue and are the starting point for the next generation.
3. Edible fruits of various types play a major role in the human diet.

CHAPTER

Plant Life Cycle: Fruits and Seeds

Pineapple, a multiple fruit, forms from the fusion of the ripened ovaries of each flower in the spike.
Fruits, as are flowers, are unique aspects of sexual reproduction in angiosperms; they protect the enclosed seeds and aid in their dispersal. Not only are fruits essential in the angiosperm life cycle; they also are widely utilized as significant food sources.

FRUIT TYPES
The fruit wall that develops from the ovary wall is known as the pericarp and is composed of three layers: the outer exocarp, the middle mesocarp, and the inner endocarp. The thickness and distinctiveness of these three layers vary among different fruit types.

Simple Fleshy Fruits
Simple fruits are derived from the ovary of a single carpel or several fused carpels and are described as fleshy or dry. When ripe, the pericarp of fleshy fruits is often soft and juicy. Seed dispersal in the fleshy fruits is accomplished when animals eat the fruits. The following describes the most common types of fleshy fruits (fig. 6.1):

A berry has a thin exocarp, a soft fleshy mesocarp, and an endocarp enclosing one to many seeds. Tomatoes, grapes, and blueberries are familiar berries.

A hesperidium is a berry with a tough leathery rind such as oranges, lemons, and other citrus berries.

A pepo is a specialized berry with a tough outer rind (consisting of both receptacle tissue and exocarp); the mesocarp and endocarp are fleshy. All members of the squash family, including pumpkins, melons, and cucumbers, form pepos.

A drupe has a thin exocarp, a fleshy mesocarp, and a hard stony endocarp that encases the seed; cherries, peaches, and plums are examples. Apples and pears are pomes; most of the fleshy part of pomes develops from the enlarged base of the perianth that has fused to the ovary wall.

As described for the pepo and pome, some fruits develop from flower parts other than the ovary; fruits of these types are termed accessory fruits.

Dry Dehiscent Fruits
The pericarp of dry fruits may be tough and woody or thin and papery; dry fruits fall into two categories, dehiscent and indehiscent. Dehiscent fruits split open at maturity and so release their seeds. Dehiscent fruits usually contain more than one seed and often many seeds. When the fruit wall opens, the seeds can be dispersed individually rather than en masse. Wind often aids the dispersal of seeds from dehiscent fruits.

Three common types of dehiscent fruit—follicles, legumes, and capsules—are characterized by the way in which they open. Follicles, as found in magnolia and milkweed, split open along one seam while legumes such as bean pods and pea pods split along two seams (fig. 6.1). The most common dehiscent fruit is a capsule that may open along many pores or slits; cotton and poppy are representative capsules.

Dry Indehiscent Fruits
Indehiscent fruits do not split open. Instead, they use other means of dispersing the seeds. Achenes, samaras, grains, and nuts are examples of indehiscent fruits. Sunflower “seeds” are, in fact, achenes, one-seeded fruits in which the pericarp is free from the seed (fig. 6.1). Carried by the wind, the winged fruits of maple, elm, and ash trees are familiar types of samaras. Samaras are usually described as modified achenes. The fruits of all our cereal grasses are grains, single-seeded fruits in which the pericarp is fused to the seed coat. Also called a caryopsis, this type of fruit is found in wheat, rice, corn, and barley. Botanically, nuts are one-seeded fruits with hard stony pericarps such as hazelnuts, chestnuts, and acorns. In common usage, however, the term nut has also been applied to seeds of other plants; peanuts, cashews, and almonds are actually seeds, not nuts.

Aggregate and Multiple Fruits
Aggregate fruits develop from a single flower with many separate carpels, all of which ripen at the same time as in raspberries and blackberries. Strawberries, another aggregate fruit, also contain accessory tissue. The brownish yellow spots on the surface are actually achenes inserted on the enlarged, fleshy, red receptacle (fig. 6.1).

Multiple fruits result from the fusion of ovaries from many separate flowers on an inflorescence. Figs and pineapples are examples of multiple fruits (fig. 6.1).

SEED STRUCTURE AND GERMINATION
A seed contains the next generation and so completes the life cycle of a flowering plant. The seed develops from the fertilized ovule and includes an embryonic plant and some form of nutritive tissue within a seed coat. Differences between dicots and monocots are apparent within seeds. The very names, dicot and monocot, refer to the number of seed leaves, or cotyledons, present in the seed. Dicot seeds usually have two cotyledons that are attached to and enclose the embryonic plant. The cotyledons, which are often large and fleshy, occupy the greatest part of the dicot seed and have absorbed the nutrients from the endosperm. Thus, the endosperm in many dicot seeds either is lacking entirely or is very much reduced. Monocots have a single thin cotyledon that functions to transfer food from the endosperm to the embryo. In several monocot families, large amounts of endosperm are apparent. Because of these stored nutrient reserves (either in the cotyledons or the endosperm), many seeds, like many fruits, are valuable foods for humans and other animals.

Dicot Seeds
The garden bean, because of its large size, is a good example of a dicot seed (fig. 6.2a). A thin membranous seed coat, also
Figure 6.1 The berry, hesperidium, pepo, and pome are fruits in which at least part of the pericarp is soft and juicy. Fruits such as the follicle, legume, and capsule are characterized by the way in which they open. Achenes, grains, and nuts are dry fruits that do not split open to disperse the seed. A samara (as in elm or maple) is a winged fruit that uses wind as the dispersal agent. Blackberries and strawberries are collections of fruits that develop from the many separate carpels of a single flower. The pineapple is a multiple fruit that forms when the ovaries of individual flowers in a flower cluster fuse.
Figure 6.2  Seed structure and germination of (a) a dicot, the garden bean, and (b) a monocot, corn.
known as the testa, encloses the seed. A hilum and micropyle are visible on the surface of the testa. The hilum is a scar that results from the separation of the seed from the ovary wall. Recall that the micropyle, seen as a small pore, is the opening in the integument through which the pollen tube enters the ovule. If the seed coat is removed, the two large food-storing cotyledons are easily seen and separated. Sheltered between the cotyledons is the embryo axis consisting of the epicotyl, the hypocotyl, and the radicle. The epicotyl develops into the shoot (stems and leaves) of the seedling and typically bears embryonic leaves within the seed. The hypocotyl is the portion of the embryo axis between the cotyledon attachment and the radicle, the embryonic root.

Monocot Seeds

The corn kernel is a familiar grain that can be used to illustrate the composition of a monocot seed (fig. 6.2b). It is important to remember that a grain is a fruit in which the testa of the single seed is fused to the pericarp. One major difference from the garden bean is the presence of extensive endosperm that occupies much of the volume of the seed. The small embryo has only a single cotyledon called a scutellum. Seeds in the grass family (such as corn) have other differences, including the presence of a coleoptile (a protective sheath that surrounds the epicotyl) and a coleorhiza (a protective covering around the radicle).

Concept Quiz

Monocot seeds have a single, thin cotyledon whereas dicot seeds usually contain two prominent cotyledons. How does nourishment of the embryonic plant differ between monocots and dicots?

Seed Germination and Development

With appropriate environmental conditions (adequate moisture and oxygen and appropriate temperature) seeds germinate (fig. 6.2). The first structure to emerge from the seed is the radicle, which continues to grow and produces the primary root. In corn, the radicle first breaks through the coleorhiza. This early establishment of the root system enables the developing seedling to absorb water for continued growth. Next, the shoot emerges. In garden beans, the hypocotyl elongates and breaks through the soil in a characteristic arch that protects the epicotyl tip with its embryonic leaves. In most dicots the cotyledons are carried aboveground with the expanding hypocotyl while in others the cotyledons remain belowground. Soon after the tissues of the seedling emerge from underground and are exposed to sunlight, they develop chlorophyll and begin to photosynthesize. The exposure to sunlight also triggers the hypocotyl to straighten into an erect position. The coleoptile of corn emerges from the soil; the epicotyl soon breaks through the coleoptile, and the embryonic leaves begin expanding. Establishment of the seedling is the most critical phase in the life of a plant, and high mortality is common. Seedlings are sensitive to environmental stress and vulnerable to attack by pathogens and predators; established plants have a greater array of defenses.

REPRESENTATIVE EDIBLE FRUITS

Of the more than 250,000 known species of angiosperm, only a small percentage produce fruits that have been utilized by humans; however, these have made a significant impact on our diet and economics. Fruits are packed with nutrients and are particularly excellent sources of vitamin C, potassium, and fiber. As this chapter describes, a fruit is a mature or ripened ovary, but this botanical definition has been ignored in the marketplace. Even the U.S. Supreme Court has debated the question, What is a fruit?

It all started in the late nineteenth century when an enterprising New Jersey importer, John Nix, refused to pay the vegetable import tariff on a shipment of tomatoes from the West Indies. He argued that the 10% duty placed on vegetables by the Tariff Act of 1883 was not applicable to tomatoes since botanically they are fruits, not vegetables. This fruit-vegetable debate eventually reached the U.S. Supreme Court in 1893 (fig. 6.3). Justice Horace Gray wrote the decision, stating,

Botanically speaking, tomatoes are the fruits of the vine, just as are cucumbers, squashes, beans and peas. But in the common language of the people, whether sellers or consumers of provisions, all these are vegetables which are grown in kitchen garden, and which, whether eaten cooked or raw, are, like potatoes, carrots, parsnips, turnips, beets, cauliflower, cabbage, celery, and lettuce, usually served at dinner, in, with, or after the soup, fish, or meats, which constitute the principal part of the repast, and not, like fruits, generally as dessert.

Tomatoes were legally declared vegetables and Nix paid the tariff. Despite the legal definition, botanists still consider tomatoes to be berries.

Tomatoes

Tomatoes, *Solanum lycopersicum*, (formerly *Lycopersicon esculentum*) are native to Central and South America, in the Andes region of Chile, Colombia, Ecuador, Bolivia, and Peru and are believed to have been first domesticated in Mexico. The Spanish conquistadors introduced the tomato to Europe,
decided that the tomato was legally a vegetable.

Figure 6.3 The most familiar varieties of tomatoes are interested in the salt tolerance of Solanum lycopersicum, which is native to the Galápagos Islands. This species, unlike S. lycopersicum, is able to survive in seawater, with its high salt concentration. Developing salt tolerance in crop plants is one of the aims of plant-breeding programs since salt-tolerant crops will allow agriculture to expand into areas with saline soils.

Tomatoes are one of the most common plants grown in the home garden. Even in large metropolitan areas, many apartment dwellers will grow patio varieties in containers. Home gardeners have all watched the stages of growth, flowering, and fruit ripening as they wait for the first harvest. Tomato fruits require 40 to 60 days from flowering to reach maturity. Once fertilization has occurred, the fruit rapidly increases in size, reaching its mature size in 20 to 30 days. In the latter half of fruit development, color changes reflect internal changes in the acidity, sweetness, and vitamin C content of the fruit. The first hint of ripening is seen when the green fruit lightens as a result of chlorophyll breakdown. As the chlorophyll content continues to decrease, additional carotenoids are synthesized. The carotenoids, beta-carotene (orange) and especially lycopene (red), give the mature fruit its characteristic color. As the red color deepens, the acidity decreases, the sugars and vitamin C increase, the flavor develops, and the fruit softens. These changes coincide with increases in ethylene and a sudden peak in respiration in the fruit. Ethylene is a gaseous plant hormone that is involved in several developmental stages but is best known for its involvement with fruit ripening. (See A Closer Look 6.1—The Influence of Hormones on Plant Reproductive Cycles.) When tomatoes are picked green and ripened in storage, they have lower vitamin C and sugar content and poorer flavor; this explains why most people prefer a vine-ripened tomato.

Many home gardeners have noticed the role that temperature plays in tomato development and ripening. Most varieties do best when air temperatures are between 18° and 27°C (65°–80°F). When temperatures are either too hot or too cold, fruit set is inhibited. Also, temperatures above 29°C (85°F) inhibit the development of the red pigments.

Some species of wild tomatoes in South America produce purple fruits, but the tomatoes are small and often poisonous. Seeds of purple tomatoes were collected in the 1960s
Many phases of the plant life cycle, including flowering and fruit development, are influenced by hormones, which act as chemical messengers that are effective at very low concentrations. Hormones are produced in one part of an organism and have their effects on another part of that organism. The major types of plant hormones are auxins, gibberellins, cytokinins, abscisic acid, and ethylene. In addition, some other hormones have recently been described.

Auxins are the best known of the plant hormones and were the first to be discovered. The research done by Charles Darwin and his son Francis in the late 1870s led to the discovery of this hormone several decades later. The Darwins studied phototropism (growth toward the light) and suggested that this response was due to an “influence” produced in the tip of a coleoptile that then moved to the growing area. Experiments by Dutch physiologist Frits Went in the 1920s demonstrated that the “influence” was actually a chemical compound, which Went named auxin. Auxins are produced in apical meristems and other actively growing plant parts including young leaves, flowers, fruits, and pollen tubes.

In addition to phototropism, auxins are involved in many stages of growth and development. Auxins promote elongation of young stems and coleoptiles by stimulating cell elongation. They inhibit lateral bud development and thus promote apical dominance, producing a plant with a main stem and limited branching. Auxins stimulate adventitious root initiation and are also involved in growth responses to gravity (gravitropism).

Auxins regulate fruit development. They are produced by the pollen tube as it grows through the style and by the embryo and endosperm in developing seeds. Fruit growth depends on these sources of auxin. The application of auxins to the flowers of some plants, such as tomato and cucumber, before the pollen is mature can promote parthenocarpy, leading to the development of seedless fruits (see Chapter 5).

Synthetic auxins have auxinlike activity but do not occur naturally in plants. Often they are more effective than natural auxins in stimulating plant responses. There are many agricultural and horticultural uses for both naturally occurring and synthetic auxins. In general, auxins have no effect on flowering; the exception is pineapple. Auxins can be applied to pineapple plants to promote uniform flowering; however, this is a secondary effect because the auxins stimulate ethylene formation, and ethylene is the hormone that actually promotes flowering in pineapple.

Gibberellins were isolated and chemically identified in 1939 by Japanese botanists. Like auxins, gibberellins are involved in many aspects of plant growth and development. Gibberellins promote stem elongation of dwarf plants by stimulating internode elongation. Dwarf varieties of many species will grow to normal size if supplied with gibberellins. Gibberellins promote seed germination of some plants by substituting for an environmental (cold or light) trigger.

Gibberellins can stimulate flowering in biennials during the first year. Biennials typically produce a tight cluster of leaves (called a rosette) in their first year. This rosette occurs on stems with very short internodes. In the second year, internodes expand greatly and the plants flower; this expansion and flowering is called bolting. The application of gibberellins to the rosette will promote bolting during the first year. This hormone-induced bolting allows growers to harvest seeds after one year instead of two. Commercially, gibberellins are also used to increase the size of seedless grapes and to stimulate germination of barley seeds for beer production.

Cytokinins stimulate cell division and differentiation of plant organs. This hormone, along with auxins, is necessary as an ingredient in media for tissue culture of plant
cells (see Chapter 15). Cytokinins also delay senescence in detached plant parts. Treated areas remain green and healthy while the surrounding tissues age and die. For this reason, cytokinins are sometimes used commercially to maintain the freshness of cut flowers.

Abscisic acid is an inhibitor hormone that promotes dormancy in seeds and buds. It is also involved in regulating water balance in plants by causing stomata to close. This last response is the one that is understood best. In well-watered plants, abscisic acid concentrations in leaves are very low, but levels increase rapidly if plants are exposed to severe drought. The buildup of abscisic acid results in stomatal closure, which causes transpiration rates to decrease dramatically.

Ethylene is an unusual plant hormone because it is a gas. This gas can be produced in all parts of the plant but is especially prominent in roots, the shoot apical meristem, senescing (aging) flowers, and ripening fruit. In addition, high levels of auxin stimulate ethylene production. Ethylene is sometimes considered a stress hormone because it is produced in wounded or infected tissues and flooded plants. These stressed plants exhibit leaf epinasty (downward curling), swollen stems, or leaf abscission, responses all induced by ethylene.

Ethylene promotes flowering in a few species such as pineapple. As described, synthetic auxins have been used to trigger flowering in pineapple plantations. The auxins stimulate ethylene formation, which induces uniform flowering. Today, many growers take a direct approach and spray their plants with ethephon, a compound that breaks down to release ethylene.

Possibly the most dramatic effects of ethylene are on fruit ripening. Ethylene stimulates fruit softening, the conversion of starch to sugars, and the production of volatile compounds that impart aromas and flavor in many types of fruit, especially apples, oranges, tomatoes, and bananas. These changes are generally accompanied by a peak in cellular respiration of the fruit (box fig. 6.1). Commercially, ethylene can be used to produce ripe fruits throughout the winter. Apples and other fruits are picked green and stored under conditions that inhibit ethylene synthesis. When fruits are required for sale, they are exposed to small amounts of ethylene, which induce ripening. As the fruits begin to ripen they produce their own ethylene, which further accelerates the maturing process and provides table-ready fruit throughout the year.

**Box Figure 6.1** Researchers measure the respiration and ethylene production of tomatoes in experiments aimed at maintaining the quality of fresh produce.

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**Concept Quiz**

Plant hormones influence many phases of plant growth and development, from seed germination to flowering and fruit formation.

Which of the plant hormones can be utilized commercially because of their effects on fruit development or maturation?

Rutgers California Supreme tomato seeds were aboard LDEF for almost 6 years, experiencing weightlessness and exposure to cosmic radiation for longer than any previous NASA experiment involving biological tissue. The satellite was recovered by the Space Shuttle Columbia and returned to Earth on January 20, 1990. The first germination test began in late February and continued throughout the spring as seed packages were mailed to teachers and students. The
first conclusion reached was that after nearly 6 years in space, the tomato seeds were still viable. In fact, they consistently exhibited an 18%–30% faster germination rate than their Earth-based counterparts. Growth rates of the space seedlings were also accelerated for the first three or four weeks; after that the Earth-based seedlings caught up and no significant differences between the Earth and space tomato plants or their fruits were observed (table 6.1). Researchers also observed a greater number of mutant individuals such as albino plants, stunted individuals, and one plant with no leaves at all, in the space-exposed group. Interestingly, plants of space-exposed seeds had greater levels of chlorophylls and carotenes than did those of the Earth group. Perhaps the most significant conclusion of the SEEDS project is the proof that seeds can survive relatively undamaged in space for long periods of time.

Apples

Apples, *Malus pumila*, have a long history of human use; they were among the first tree fruits to be domesticated in temperate regions. Most of today’s cultivated varieties are descendants of apples native to central and western Asia, where the apple has been domesticated for thousands of years. Near Almaty, formerly Alma-Ata in Kazakhstan, there are forests of 50-foot (17-meter) wild apple trees, some 350 years old. Alma-Ata, in fact, means “father of the apple.” Because of its long history, the apple also has a place in the imagery and folklore of many cultures. The following expressions reveal the apple as more than a tasty fruit in American culture: the “Big Apple,” “American as apple pie,” “apple of your eye,” “apple polishing,” “apple pie order,” and “an apple a day keeps the doctor away.”

Most people are familiar with the biblical story of Adam and Eve and the presumed role of the “apple” in the downfall of humankind. In reality, the apple’s only involvement was due to a faulty translation from the Latin version of the Old Testament. The confusion starts with the Latin word *mali*, which could refer to *malum*, meaning evil, or to *malus*, meaning apple tree. In Genesis, Adam and Eve were told not to partake of the fruit of the tree of the knowledge of good and evil. The erroneous association with apple trees began with thirteenth- and fourteenth-century artists, whose Latin was poor; they incorrectly translated the *mali* to mean apple tree.

The legend of Johnny Appleseed is another story familiar to most Americans. There really was a Johnny Appleseed; his name was John Chapman. He was born in Massachusetts in 1774, but we know nothing of his early life. He appeared in 1797 sowing apple seeds in what was the Northwest Territory in frontier America: western Pennsylvania, Ohio, and eastern Indiana. Chapman probably saw more of America than most of his contemporaries; he traveled hundreds of miles by foot, horseback, and canoe. Chapman was an itinerant orchardist who gave away or sold—and even planted with his own hands—apple seeds and seedlings that gave rise to acres of apple trees throughout the region (fig. 6.4). Some of the orchards are still in existence today. He continued his mission until his death in 1845 in Fort Wayne, Indiana, a city that still honors his memory every summer with a Johnny Appleseed Festival.

| Table 6.1 Comparisons of Space-Exposed and Earth-Based Tomato Seeds, SEEDS Project |
|---------------------|---------------------|
| Space-Exposed      | Earth-Based         |
| Percent germination| 66.3                | 64.6                |
| Average height (cm) | 21.2                | 20.9                |
| Percent flowering  | 73.4                | 72.3                |
| Percent fruiting   | 74.6                | 76.1                |

Figure 6.4 John Chapman, known better as Johnny Appleseed, sowed apple seeds on the American frontier from the 1790s to 1845.
Apple trees are medium-sized trees with a broad, rounded crown and a short trunk. They are generally spreading, long-lived trees that can bear fruit for up to a century. In modern commercial orchards, however, dwarf trees have become the norm. Often about 6 feet (almost 2 meters) tall, these trees are easily pruned and mechanically harvested.

The apple blossoms appear in profusion early in the spring before the leaves develop. The fragrant pinkish white blossoms are five-merous flowers (containing five sepals, five petals, numerous stamens, and a five-carpeled ovary) that are usually pollinated by bees (fig. 6.5). The apple tree requires cold winter temperatures in order to flower and, therefore, cannot be grown in tropical and subtropical climates. The leading apple-growing areas in the United States are Washington, Oregon, and northern California in the West and Michigan, New York, and Virginia in the East.

Although Johnny Appleseed distributed thousands of apple seeds, today’s modern orchardist does not grow the trees from seeds. Each seed is a unique combination of traits that are not identical to either parent; in a sense, planting a seed is a genetic experiment. Although some seeds may develop into valuable varieties, most will not. (Interestingly, most of our familiar cultivars did develop as chance or volunteer seedlings from naturally produced seeds.) Also, planting seeds is a long-term experiment, and it would take a number of years to know the results. Today’s apple growers need to ensure uniformity in their orchards, not only to produce apples with the desired flavor and taste but also to maximize efficiency at harvest time. As a result, most apple trees are produced by grafting (a form of asexual reproduction or cloning) in which stem cuttings or buds from a desirable cultivar are joined to the base of a second tree. The cutting or bud, called the scion, will become the upper or top portion of the new tree, while the rootstock, or simply stock, of the second tree is the root system of the graft combination. Grafting can create thousands of identical copies of a variety that will continue to produce apples with the desired characteristics.

As described earlier, the apple is a pome, a simple fleshy fruit with accessory tissue. The core of the apple is a five-carpeled ovary with seeds; the ovary wall is visible as a fine brownish line, and the endocarp is prominent as the parchmentlike material around the seeds (fig. 6.6). The skin and flesh of the apple develop from the receptacle and base of the perianth. A ripe apple, although mostly water, contains about 12% sugar, 1% fiber, and negligible amounts of fat and protein. Approximately 50% of the apples harvested are consumed as fresh fruit, with the remainder being processed into applesauce, apple butter, apple cider, apple juice, cider vinegar, dried apples, and canned apples.

Although there are thousands of varieties of apple, only a few can be found in the modern supermarket. In the past, many more varieties were available to consumers; virtually gone from the market are old staples such as Baldwin, Early Harvest, Fall Pippin, and Gravenstein. Today, Red Delicious, Golden Delicious, and Granny Smith are the most common apples seen. The red delicious apple was first discovered in Iowa in the 1870s, but its popularity can be traced to the growth of the large supermarket chains during the 1950s and 1960s. It became the generic “red apple” to the American consumer. Other commercially important red apples include the Rome, Jonathan, and McIntosh. A popular red-gold variety is Jonagold, considered by many experts as the top-ranking apple. It was created from a cross between Golden Delicious and Jonathan apples. The Golden Delicious, the leading yellow apple, arose by chance on a West Virginia farm in 1910. The Granny Smith is a tart green apple that originated in New Zealand. Growers are constantly developing new varieties. One of the newest is Gala, a red and yellow apple also developed in New Zealand. Fuji was created by Japanese breeders who crossed a Red Delicious with the heirloom Ralls Janet. Its sweetness and crispiness have made it a popular variety.

The world’s most extensive collection of apple varieties is maintained in Geneva, New York, at the Agricultural Experiment Station run by Cornell University and the

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**Figure 6.5** The apple blossom is being pollinated by a bee.

**Figure 6.6** In this longitudinal section of the apple fruit, the brown line (exocarp) delineates the true ovary wall from the outer accessory tissue. The endocarp is the brown papery material surrounding each seed or pip.
Plant Genetic Resources Unit of the U.S. Department of Agriculture (USDA). More than 5,000 apple trees are planted on this 50-acre farm; these consist of 2,500 apple varieties, with two trees of each variety. An additional 500 types are stored as seeds at this repository. The apples come from all over the world and include wild apples, modern cultivars, and obsolete cultivars. In an attempt to preserve the genetic diversity of apples, researchers from Geneva have traveled throughout central Asia searching for unique apples. In addition to cultivating these varieties, the Geneva Repository distributes over 3,000 specimens (as seeds or scions) each year to apple researchers throughout the world. This facility can be considered a modern-day Johnny Appleseed.

**Oranges and Grapefruits**

The citrus family (Rutaceae) is the source of many edible fruits; sweet oranges (*Citrus sinensis*), grapefruits (*C. paradisi*), tangerines (*C. reticulata*), lemons (*C. limon*), and limes (*C. aurantifolia*) come to mind most immediately. But there are also pummelos (*C. grandis*), citrons and etrogos (*C. medica*), bergamots (*C. bergamia*), sour oranges (*C. auran- tium*), and kumquats (*Fortunella japonica*). Most of these species are native to southeastern Asia, where they were undoubtedly cultivated by native peoples. Brought by caravan from the East, the citron was the first citrus fruit known to Western civilization; it was widely grown throughout the Mediterranean area during Greek and Roman times, being spread by the Jewish people, for whom it had religious significance. Centuries later, Europeans became acquainted with sour oranges, lemons, and limes when Arabic traders during the Middle Ages introduced them from the East. It was not until the sixteenth century, however, that the sweet orange, the most familiar type today, was brought to Europe by Portuguese traders. It is believed that these first sweet oranges came from India, but later oranges were brought from China, which is believed to be the country of origin, as reflected in its scientific name, *Citrus sinensis*.

Spanish and Portuguese explorers introduced citrus to the New World; by 1565 sour orange trees were growing in Florida. After Florida became a state in 1821, the wild groves of sour oranges became the rootstocks for the sweet orange industry. Florida soon became, and remains, the leading orange-producing state. Valencia oranges are the main variety cultivated in Florida; this is a thin-skinned, seeded orange grown primarily for juice. Citrus was brought to California by the Spanish missionaries in the eighteenth century. Today, we associate the navel orange with California, but these oranges have their origins in Bahia, Brazil. In 1870, an American missionary stationed in Bahia was impressed by the appearance and flavor of a local variety and sent 12 saplings to the USDA in Washington, D.C. The USDA propagated the trees and offered free plants to anyone wishing to grow them. In 1873, a Riverside, California, resident, Mrs. Luther Tibbets, received two trees that were such a success that they were soon widely propagated. In fact, it is believed that all navel oranges today are descendants of Mrs. Tibbets’s trees.

Botanically, a citrus fruit is a hesperidium. The thick rind is impregnated with oil glands, a characteristic of the family. Fragrant essential oils attract animals for fruit and seed dispersal and are important commercially for perfumes and cosmetics. Within the fruit, the individual carpels are filled with many one-celled juice sacs. Although the carpels are always distinct, their ease of separation varies with the type and variety of fruit. Navel oranges are noted for their seedless condition and for the navel, which is actually a small aborted ovary near the top of the fruit. Although widespread cultivation of navel oranges is a fairly recent phenomenon, Europeans were aware of navel oranges in the seventeenth century. Navel oranges have probably appeared spontaneously many times throughout the history of orange growing.

The color development in oranges is not related to ripening. The orange color associated with the fruit develops only under cool nighttime temperatures; in tropical climates the fruits stay green. In most areas, a deep orange color is needed for successful marketing, and growers use various methods to achieve the desired color. The most widely used method involves exposing the ripened fruit to ethylene, which promotes the loss of chlorophyll, thereby making the orange carotenes visible. As a group, the citrus fruits are high in vitamin C. Those that are orange-colored also provide some beta-carotene (precursor to vitamin A) and calcium.

The largest citrus fruits are pummelos (*Citrus grandis* or *C. maxima*), which can be up to 12 inches (30 cm) in diameter and have a thick yellow rind. There may be up to 14 carpels, with pulp varying from pale yellow to deep red and from slightly sweet to markedly acidic. Although pum- melos are well known throughout Asia, it is only in recent years that they have started appearing in grocery stores in the United States. They are especially popular in cities with a large Chinese population and are a favorite for Chinese New Year festivities.

Pummelos are native to Southeast Asia and have been widely cultivated throughout that area. It is believed that pummelos may be one of the ancestral species in the genus *Citrus*. Arab traders introduced pummelos to Spain in the twelfth century. Pummelo seeds were brought to the Western Hemisphere in the seventeenth century by an English sea captain, James Shaddock, on a return voyage from the East Indies; by 1696 the fruit was being cultivated in Barbados and Jamaica. In many areas, pummelos are also known as shaddocks in tribute to this seventeenth-century sea captain.

Pummelos’ most enduring claim to fame is as one of the ancestors of the grapefruit. It is generally believed that grapefruits arose as a natural hybrid between pummelos and sweet oranges on the island of Barbados during the eighteenth century. The grapefruit was first described in 1750, when it was called a forbidden fruit. The name *grapefruit*, which refers to the fact that fruits develop in grapelike clusters of
three or more, was first used in 1814, and grapefruits were botanically characterized as a separate species and named *Citrus paradisi* in 1837.

The first U.S. grapefruit trees were planted in Florida in the early nineteenth century, and the first commercial groves were established in 1875. By the beginning of the twentieth century, the Florida grapefruit industry was going strong, and today Florida is the world’s leading grapefruit producer. Noteworthy grapefruits are the Texas Ruby Reds, which initially developed as a mutation from a pink-fleshed grapefruit tree in 1929. About half of the U.S. grapefruit crop is processed into juice or fruit sections.

Grapefruit juice made medical headlines after the first report of a grapefruit juice–drug interaction in 1991. Since that time, hundreds of studies have been performed to determine the mode of action and which prescription drugs are affected. Among the prescription drugs that show interaction with grapefruit juice are various types of tranquilizers, antihistamines, calcium channel blockers (used to lower blood pressure and to treat heart disease), cholesterol-lowering drugs, and immunosuppressants. The grapefruit juice effect centers on the enzyme CYP3A in the intestinal wall that normally metabolizes drugs and thereby regulates their uptake. Grapefruit juice inactivates or inhibits the enzyme, causing a greater uptake of the drugs and elevated drug levels in the bloodstream. In some instances, the drug levels have been dangerously high and have resulted in death. A study in 2006 looked at compounds called furanocoumarins, which are plentiful in grapefruit juice but are found in insignificant concentrations or not at all in most other citrus juices, as the responsible culprits. Researchers processed grapefruit juice by removing its furanocoumarins. Subjects were given a blood-pressure lowering medication with either furanocoumarin-free grapefruit juice, normal grapefruit juice, or orange juice. Over a 24-hour period, the medication lingered about twice as long in those who had drunk normal grapefruit juice as in those who had drunk either processed grapefruit juice or orange juice.

Today, many prescription drugs carry warnings to avoid taking with grapefruit juice; however, research is being conducted on ways to use grapefruit juice therapeutically to enhance drug uptake. Some day instructions on a bottle of pills may say “take only with grapefruit juice.”

**Chestnuts**

The images of the winter holidays are often filled with the aroma of “chestnuts roasting on an open fire.” These flavorful nuts are products of *Castanea* spp., a genus native to temperate regions of eastern North America, southern Europe, northern Africa, and Asia. In North America, *Castanea dentata*, the American chestnut tree, was one of the most useful trees to the native peoples and settlers. The trees, once some of the most abundant in the Eastern forests, were towering specimens, often reaching heights of 36 meters (120 feet) and diameters of 2 meters (7 feet). The wood was highly prized for furniture, fence posts, telegraph poles, shingles, ship masts, and railroad ties. The high tannin content of the wood made the lumber resistant to decay and was a source of tannins for the tanning of leather.

The nuts have long been consumed by both humans and animals; they can be eaten raw but are more commonly boiled or roasted. The chestnuts can also be made into a rich confectionery paste known as *creme de marrons* (chestnut spread) used in French desserts. Nutritionally, chestnuts are high in starch (approximately 78%) and unusually low in fat (4% to 5%) for a nut.

Usually, three nuts (one-seeded fruits with a stony pericarp) are borne in a spiny bur or husk that splits open at maturity (fig. 6.7a). Each nut is produced by a single female flower, which is borne in a cluster of three; the cluster is subtended by an involucre, a collection of bracts that develop into the spiny bur as the fruits mature. The trees are monococious, with the staminate flowers borne in long slender catkins on the same individual.

The reign of the chestnut trees in American forests began to decline early in the twentieth century because of chestnut blight, a disease caused by the fungus *Cryphonectria parasitica* (formerly known as *Endothia parasitica*). The fungus is believed to have been introduced in 1890 from some Asian chestnut trees brought to New York. The first reported case of the disease was in 1904 at the Bronx Zoological Park. Cankers, localized areas of dead tissue, were noted on several of the trees in the park (fig. 6.7b). Although attempts were made to stop the disease by pruning away diseased branches, the fungus soon spread to all the chestnut trees in the park. By 1950, chestnut blight had spread throughout the natural range of *Castanea dentata* from Maine to Alabama and west to the Mississippi River. Although the trunk of an infected tree dies, the roots are usually not infected. The chestnut’s ability to resprout from the roots has saved the species from extinction. These young saplings can reach heights of 4–6 meters (12–20 feet) before they succumb to the blight. Today, intense research efforts are focusing on various techniques to restore the American chestnut to its former glory. Researchers are field testing a blight-resistant variety of American chestnut. Asian chestnut trees show resistance to the blight fungus, and breeding programs in Connecticut have developed hybrids between the Asian and American species that are also resistant. The hybrids are backcrossed to the American chestnut for several generations with the aim that the only foreign genes remaining in the hybrids are those that confer blight resistance. Biological control, another line of ongoing research, uses a virus that infects *Cryphonectria parasitica*. Strains of the fungus with the virus are hypovirulent (less potent) and do not destroy the chestnut trees. Inoculating infected trees has resulted in disease remission. It is hoped that the combination of resistant trees and biological control may one day restore the American chestnut tree.

In May 2006, a stand of mature chestnut trees that had somehow escaped the blight were found in the Appalachian range in Georgia. The oldest of the half-dozen trees is about
Many of the dessert and snack fruits that we commonly enjoy are not native to North America but had their origins in exotic lands and faraway places. Consider these familiar fruits and their origins: apples (central Asia), oranges (southeastern Asia), peaches (China), bananas (southeastern Asia), watermelons (Africa), and pineapples (Latin America). Today this trend is accelerating, and every year new fruits are introduced to the North American public. The kiwifruit is a good example of a fruit that, within a short time, made the jump from exotic to familiar.

Around 1980 the kiwifruit, *Actinidia chinensis*, began appearing in supermarkets throughout the United States, and soon after many people were enjoying this fuzzy brown egg-shaped fruit. The distinctive flavor of its emerald green flesh is reminiscent of a strawberry-banana-pineapple combination. Its current popularity is the result of successful marketing that began in New Zealand. Originally native to China, the plants were introduced into New Zealand in 1904, where kiwifruit was known as the Chinese gooseberry and often was grown as an ornamental vine. Commercial farming began in the 1930s, and the first exports were delivered to England in 1952. Around this time, marketing strategists renamed the Chinese gooseberry; the new name, kiwifruit, fit because its fuzzy rind resembles New Zealand’s flightless bird, the kiwi. The name change paid off. Sales and exports increased steadily, and by the late 1980s it was an American produce staple. In the United States, cultivation of this berry is found mainly in northern California, with a large percentage of the crop exported to Europe, Japan, and Canada.

One exotic fruit that may be seen more frequently in the near future is the cherimoya, *Annona cherimola*. This tree fruit, native to the uplands of Peru and Ecuador, was first cultivated by the ancient Incas. In appearance, the aggregate fruit looks like a leathery green pinecone. Its custardlike flesh can be scooped out and is delicious with cream or orange juice. Today, cherimoya, described by some as the aristocrat of fruits, is widely grown in Chile, Spain, and Israel and is making inroads in North America through California growers. Atemoya, a new hybrid resulting from a cross between the cherimoya and the closely related sugar apple (*Annona squamosa*), has the advantage of being more tolerant of environmental conditions than either parent and can, therefore, be grown in a wide variety of climates. The sweet taste of atemoya makes this a superb fruit for fresh consumption as well as for frozen desserts.

*Carambola, Averrhoa carambola*, is another ancient fruit that has recently been introduced to North American markets. Native to Malaysia, the carambola is also known as star fruit because a series of five-pointed yellow stars results from slicing the elongate fluted fruit. This tart fruit adds an appealing shape that brightens up seafoods, salads, desserts, and fruit punches. The fruit can also be squeezed to make a refreshing juice or can be picked green, cooked, and eaten as a vegetable. Presently, star fruits are grown throughout the tropics, with the U.S. cultivation centered in Florida.
While cherimoyas are the aristocrats of fruit in South America, durians, *Durio zibethinus*, are considered the king of fruit throughout much of Southeast Asia (fig. 6.8). The best durians are said to have originated in Malaysia, although Thailand and South Vietnam are the leading producers. Durian trees produce melon-sized fruits that have a thick green rind and are covered with stout spines. Inside the fruit, there are usually five compartments, with smooth, creamy white pulp surrounding the seeds. This pulp, which is typically eaten fresh, is usually described as having a heavenly flavor. By contrast, the most notorious feature of durian fruits is their incredibly foul smell, which has been described as similar to the smell of rotten eggs. The odor is due to the presence of sulfur compounds; in fact, there are 43 sulfur compounds in durians. Some of these are similar to the compounds in onions and garlic; others are similar to the compounds produced by skunks. The odor is so strong that in Singapore, fresh durians are banned in buses, subways, taxis, and airlines. Despite the odor, during the harvest season, thousands of tourists from Japan and other Asian countries come to durian festivals and tours in Malaysia. Durian trees require tropical conditions and abundant rainfall; seedlings introduced to Florida survived only a short time. The trees have been introduced successfully to Hawaii, some Caribbean Islands, and Honduras although so far the plantings are not extensive. Fresh durians have a short shelf life and are seldom shipped out of Asia. However, the United States is the largest importer of frozen durians, which can be found in Asian groceries in major U.S. cities. The world’s smelliest fruit may soon be arriving at your neighborhood market.

After 20 years of research, a scientist at Thailand’s Horticultural Research Institute has created an odorless variety of durian. Without the offensive smell, Chantaburi No. 1 is predicted to become a major export crop for Thailand when commercial production begins in a few years. In the meantime, research is progressing on a durian variety that is both odorless and thornless.

**CHAPTER SUMMARY**

1. Fruits are unique to the sexual reproduction of angiosperms. They protect the enclosed seeds and aid in seed dissemination. Botanically, a fruit is a ripened ovary although in the United States, the legal definition of a fruit is something that tastes sweet and is eaten as dessert.

2. Fruits can be classified according to the characteristics of the fruit wall or pericarp. In fleshy fruits, the pericarp is soft and juicy; berry, hesperidium, pepo, drupe, and pome are all examples of fleshy fruits. In dry fruits, the pericarp is often tough or papery. Dry fruits can also be dehiscent, splitting open along one or more seams to release their seeds. Follicles, legumes, and capsules are examples of dehiscent fruits. Dry fruits that do not split open are indehiscent; examples of this fruit type are achenes, samaras, grains, and nuts. Simple fruits are derived from a single ovary. Aggregate fruits develop from the separate ovaries within a single flower; multiple fruits result from the fusion of ovaries from separate flowers in an inflorescence.

3. Seeds are the end products of sexual reproduction in flowering plants. Each seed contains an embryonic plant, nutrient tissue to nourish the embryo, and a tough outer seed coat. Differences exist between monocot and dicot seeds. Monocotyledonous seeds have a single thin cotyledon whereas dicotyledonous seeds typically have two large cotyledons.

4. Edible fruits have played an important role not only as a significant contribution to the human diet but also in scientific studies and folklore. Once-exotic fruits are becoming commonplace as they are incorporated into the world’s marketplace.

**REVIEW QUESTIONS**

1. What is the function of the fruit in the life cycle of an angiosperm?

2. Give the botanical meaning of the following: berry, nut, legume, grain.

3. What is a seed? What is a fruit?

4. Compare and contrast monocot and dicot seeds in structure and germination.

5. How did the tomato, an Aztec fruit, become the staple of Italian cookery?

6. What factors contributed to the successful introduction of the kiwifruit into North American markets?

7. Although “chestnuts roasting on an open fire” is an American image, most chestnuts eaten in the United States are from Italy. Why?

8. Research the history, uses, and folklore of the following fruits: pineapple, mango, papaya.

**FURTHER READING**


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