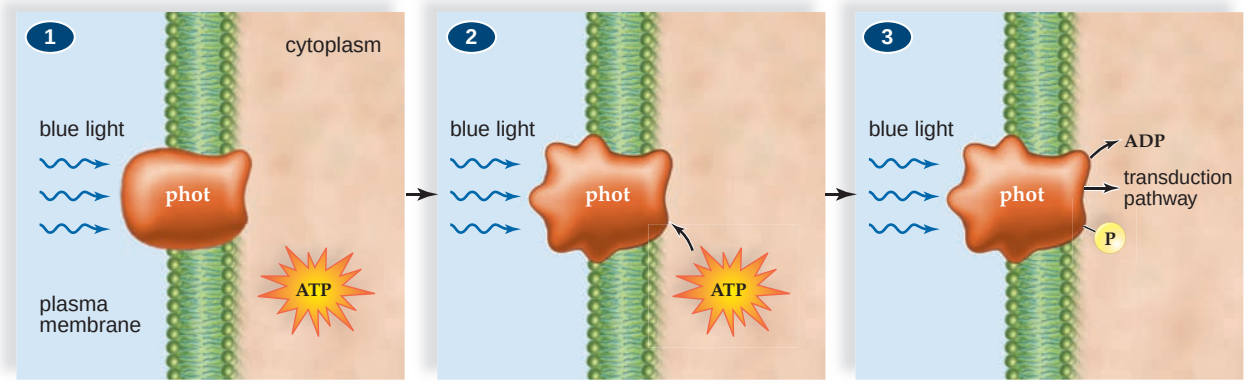
FIGURE 26.12
Phototropin.

In the presence of blue light, a photoreceptor called phototropin (phot) is activated and becomes phosphorylated. A transduction pathway begins.



part of the cell where they come in contact with cytoskeletal elements. The connection between amyloplasts and auxin is uncertain. Perhaps they cause stems and roots to respond differently to auxin: The upper surface of a root elongates so that the root curves downward and the lower surface of a stem elongates, so that the stem curves upwards.

Phototropism

As discussed previously, positive **phototropism** of stems occurs because the cells on the shady side of the stem elongate due to the presence of auxin. Curving away from light is called negative phototropism. Roots, depending on the species examined, are either insensitive to light or exhibit negative phototropism.

Through the study of mutant *Arabidopsis* plants (see page 479), it is now known that phototropism occurs because plants respond to blue light (Fig. 26.12). (1) When blue light is absorbed, the pigment portion of a photoreceptor, called phototropin (phot), undergoes a conformation change. (2) This change results in the transfer of a phosphate group from ATP (adenosine triphosphate) to a protein portion of the photoreceptor. (3) The phosphorylated photoreceptor triggers a transduction pathway that, in some unknown way, leads to the entry of auxin into the cell.

Thigmotropism

Unequal growth due to contact with solid objects is called **thigmotropism** [Gk. *thigma,* touch, and *tropos,* turning]. An example of this response is the coiling of tendrils or the stems of plants, such as the stems of pea and morning glory plants (Fig. 26.13).

A flowering plant grows straight until it touches something. Then the cells in contact with an object, such as a pole, grow less while those on the opposite side elongate. Thigmotropism can be quite rapid; a tendril has been observed to encircle an object within 10 minutes. The response endures; a couple of minutes of touching can bring about a response that lasts for several days. The response can also be delayed; tendrils touched in the dark will respond once they are illuminated. ATP (adenosine triphosphate) rather than light can cause the response; therefore, the need for light may simply be a need for ATP. Also, the hormones auxin and ethylene may be involved since they can induce curvature of tendrils even in the absence of touch.

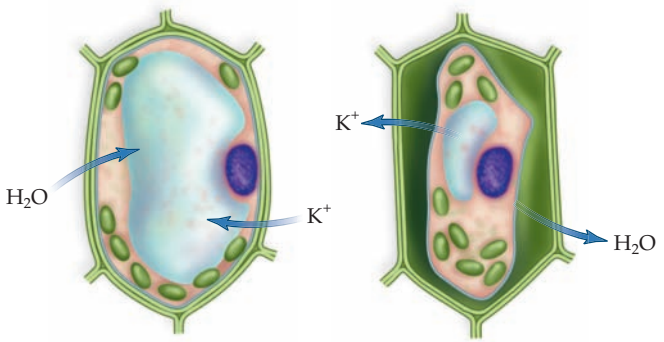
Thigmomorphogenesis is a touch response related to thigmotropism. In the former case, however, the entire plant responds to the presence of environmental stimuli, such as wind or rain. The same type of tree growing in a windy location often has a shorter, thicker trunk than one growing in a more protected location. Even simple mechanical stimulation—rubbing a plant with a stick, for example—can inhibit cellular elongation and produce a sturdier plant with increased amounts of support tissue.

FIGURE 26.13 **Coiling response.**

The stem of a morning glory plant, *Ipomoea,* coiling around a pole illustrates thigmotropism.

Nastic Movements

Recall that a plant cell exhibits turgor when it fills with water:



Cell is turgid Cell is limp

In general, if water exits the many cells of a leaf, the leaf goes limp. Conversely, if water enters a limp leaf, and cells exhibit turgor, the leaf moves as it regains its former position. **Turgor movements** are dependent on turgor pressure changes in plant cells. In contrast to tropisms, turgor movements do not involve growth and are not related to the source of the stimulus.

Turgor movements can result from touch, shaking, or thermal stimulation. The sensitive plant, *Mimosa pudica*, has compound leaves, meaning that each leaf contains many leaflets. Touching one leaflet collapses the whole leaf (Fig. 26.14). *Mimosa* is remarkable because the progressive response to the stimulus takes only a second or two.

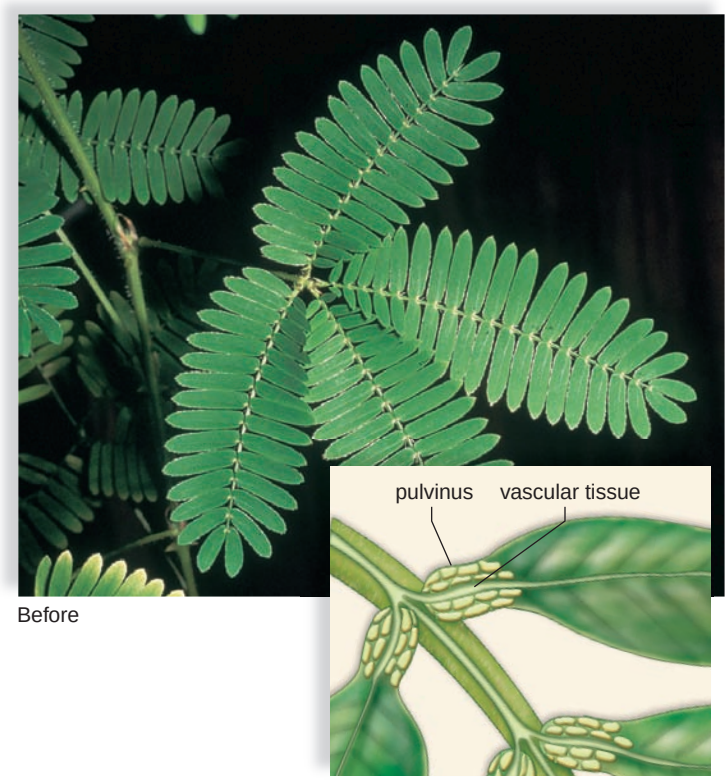
The portion of a flowering plant involved in controlling turgor movement is a thickening called a pulvinus at the base of each leaflet. A leaf folds when the cells in the lower half of the pulvinus, called the motor cells, lose potassium ions (K^+), and then water follows by osmosis. When the pulvinus cells lose turgor, the leaflets of the leaf collapse. An electrical mechanism may cause the response to move from one leaflet to another. The speed of an electrical charge has been measured, and the rate of transmission is about 1 cm/sec.

A Venus flytrap closes its trap in less than 1 second when three hairs at the base of the trap, called the trigger hairs, are touched by an insect. When the trigger hairs are stimulated by the insect, an electrical charge is propagated throughout the lobes of a leaf. Exactly what causes this electrical charge is being studied. Perhaps (1) the cells located near the outer region of the lobes rapidly secrete hydrogen ions into their cell walls, loosening them, and allowing the walls to swell rapidly by osmosis; or (2) perhaps the cells in the inner portion of the lobes and the midrib rapidly lose ions, leading to a loss of water by osmosis and collapse of these cells. In any case, it appears that turgor movements are involved.

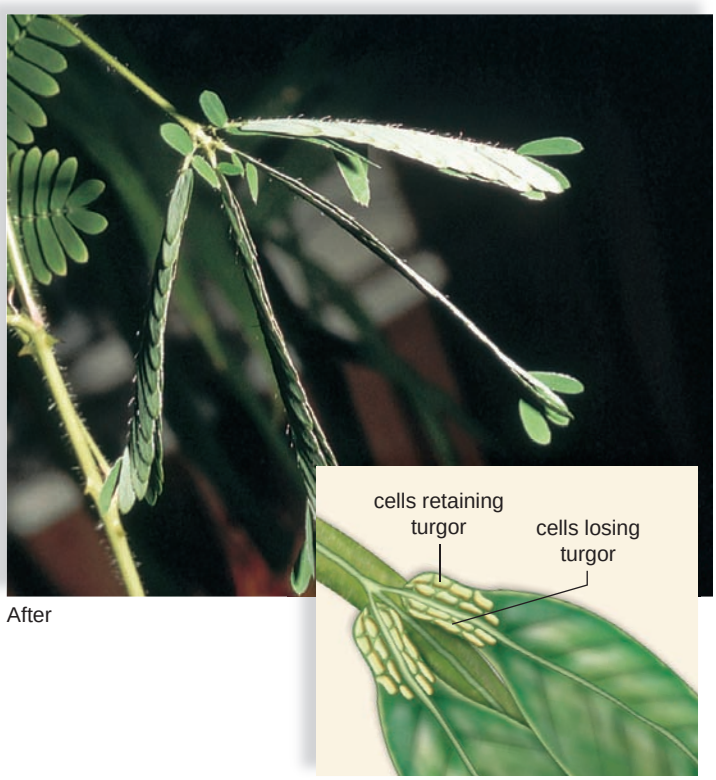
Venus flytrap, *Dionaea*

Sleep Movements and Circadian Rhythms

Leaves that close at night are said to exhibit sleep movements. Activities such as sleep movements that occur regularly in a 24-hour cycle are called **circadian rhythms.** One of the most common examples occurs in a houseplant called the prayer plant (*Maranta leuconeura*) because at night the leaves fold upward



Before



After

FIGURE 26.14 Turgor movement.

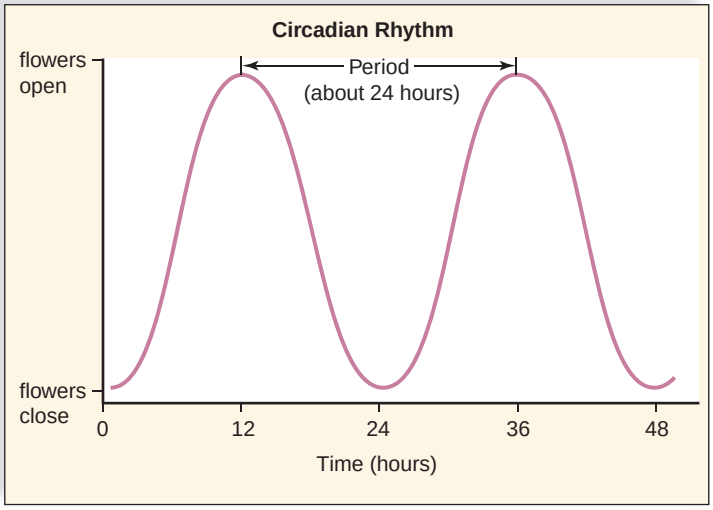
A leaf of the sensitive plant, *Mimosa pudica,* before and after it is touched.

Prayer plant (morning) Prayer plant (night)

a.

Morning glory (morning) Morning glory (night)

b.



c.

FIGURE 26.15 Sleep movements and circadian rhythms.

a. The leaves of a prayer plant, *Maranta leuconeura,* fold every 24 hours at night. **b.** The flowers of the morning glory, *Ipomoea leptophylla,* close at night. **c.** Graph of circadian rhythm exhibited by morning glory plant.

into a shape resembling hands at prayer (Fig. 26.15, *top*). This movement is also due to changes in the turgor pressure of motor cells in a pulvinus located at the base of each leaf.

To take a few other examples, morning glory (*Ipomoea leptophylla*) is a plant that opens its flowers in the early part of the day and closes them at night (Fig. 26.15, *bottom*). In most plants, stomata open in the morning and close at night, and some plants secrete nectar at the same time of the day or night.

To qualify as a circadian rhythm, the activity must (1) occur every 24 hours; (2) take place in the absence of external stimuli, such as in dim light; and (3) be able to be reset if external cues are provided. For example, if you take a transcontinental flight, you will likely suffer jet lag because your body will still be attuned to the day/night pattern of its previous environment. But after several days, you will most likely have adjusted and will be able to go to sleep and wake up according to your new time.

Biological Clock

The internal mechanism by which a circadian rhythm is maintained in the absence of appropriate environmental stimuli is termed a **biological clock.** If organisms are sheltered from environmental stimuli, their biological clock keeps the circadian rhythms going, but the cycle extends. In prayer plants, for example, the sleep cycle changes to 26 hours when the plant is kept in constant dim light, as opposed to 24 hours when in traditional day/night conditions. Therefore, it is suggested that biological clocks are synchronized by external stimuli to 24-hour rhythms. The length of daylight compared to the length of darkness, called the photoperiod, sets the clock. Temperature has little or no effect. This is adaptive because the photoperiod indicates seasonal changes better than temperature changes. Spring and fall, in particular, can have both warm and cold days.

Work with *Arabidopsis* (see Science Focus, pages 478–79) and other organisms suggests that the biological clock involves the transcription of a small number of "clock genes." One model proposes that the information-transfer system from DNA to RNA to enzyme to metabolite, with all its feedback controls, is intrinsically cyclical and could be the basis for biological clocks. In *Arabidopsis,* the biological clock involves about 5% of the genome. These genes control sleep movements, the opening and closing of stomata, the discharge of floral fragrances, and the metabolic activities associated with photosynthesis. The biological clock also influences seasonal cycles that depend on day/night lengths, including the regulation of flowering.

While circadian rhythms are outwardly very similar in all species, the clock genes that have been identified are not the same in all species. It would seem, then, that biological clocks have evolved several times to perform similar tasks.

Check Your Progress 26.2A

1. Roots grow toward water. Explain why this is adaptive.
2. If a plant is in a horizontal position and rotated horizontally, would the stem or the root exhibit gravitropism?
3. Many bat- and moth-pollinated plants open every 24 hours at night and often produce scent during the evening only. Explain why this is adaptive.

Photoperiodism

Many physiological changes in flowering plants are related to a seasonal change in day length. Such changes include seed germination, the breaking of bud dormancy, and the onset of senescence. A physiological response prompted by changes in the length of day or night in a 24-hour daily cycle is called **photoperiodism** [Gk. *photos,* light, and *periodus,* completed course]. In some plants, photoperiodism influences flowering; for example, violets and tulips flower in the spring, and asters and goldenrod flower in the fall. Photoperiodism requires the participation of a biological clock, which can measure time, and it also requires the activity of a plant photoreceptor called phytochrome.

Phytochrome

Phytochrome [Gk. *phyton,* plant, and *chroma,* color] is a blue-green leaf pigment that is present in the cytoplasm of plant cells. A phytochrome molecule is composed of two identical proteins (Fig. 26.16). Each protein has a larger portion where a light-sensitive region is located. The smaller portion is a kinase that can link light absorption with a transduction pathway within the cytoplasm. Phytochrome can be said to act like a light switch because, like a light switch, it can be in the down (inactive) position or in the up (active) position. Red light prevalent in daylight activates phytochrome, and it assumes its active conformation known as P_{fr}. When P_{fr} moves into the nucleus, it interacts with specific proteins, such as a transcription factor. The complex activates certain genes and inactivates others. The active form of phytochrome P_{fr} is so called because it absorbs far-red light. Far-red light is prevalent in the evening and it serves to change P_{fr} to P_r, which is the inactive form of phytochrome.

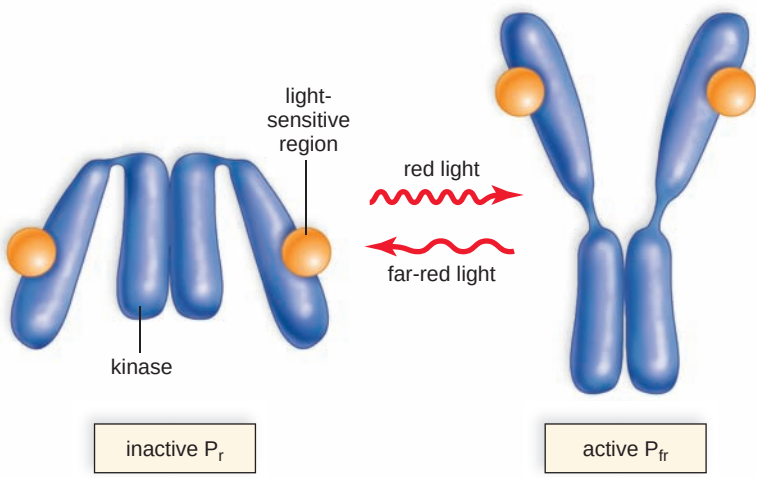


FIGURE 26.16 Phytochrome conversion cycle.

The inactive form of phytochrome (P_r) is converted to the active form P_{fr} in the presence of red light, which is prevalent in daylight. P_{fr}, the active form of phytochrome, is involved in various plant responses such as seed germination, shoot elongation, and flowering. P_{fr} is converted to P_r whenever light is limited, such as in the shade or during the night.

FIGURE 26.17 Phytochrome control of shoot elongation.

a. If red light is prevalent, as it is in bright sunlight, normal growth occurs. **b.** If far-red light is prevalent, as it is in the shade, etiolation occurs. These effects are due to phytochrome.

Functions of Phytochrome

The $P_r \rightarrow P_{fr}$ conversion cycle is now known to control various growth functions in plants. P_{fr} promotes seed germination and inhibits shoot elongation, for example. The presence of P_{fr} indicates to some seeds that sunlight is present and conditions are favorable for germination. This is why some seeds must be only partly covered with soil when planted. Germination of other seeds, such as those of *Arabidopsis,* is inhibited by light, so they must be planted deeper. Following germination, the presence of P_{fr} indicates that sunlight is available and the seedlings begin to grow normally—the leaves expand and become green and the stem branches. Seedlings that are grown in the dark etiolate—that is, the shoot increases in length, and the leaves remain small (Fig. 26.17). Only when P_r is converted to P_{fr} does the seedling grow normally.

Flowering. Flowering plants can be divided into three groups on the basis of their flowering status:

1. **Short-day plants** flower when the day length is shorter than a *critical length.* (Examples are cocklebur, goldenrod, poinsettia, and chrysanthemum.)
2. **Long-day plants** flower when the day length is longer than a critical length. (Examples are wheat, barley, rose, iris, clover, and spinach.)
3. **Day-neutral plants** are not dependent on day length for flowering. (Examples are tomato and cucumber.)

The criterion for designating plants as short-day or long-day is not an absolute number of hours of light, but a critical number that either must be or cannot be exceeded. Spinach is a long-day plant that has a critical length of 14 hours; ragweed is a short-day plant with the same critical length. Spinach, however, flowers in the summer when the day length increases to 14 hours or more, and ragweed flowers in the fall, when the day length shortens to 14 hours or less. In addition, we now know that some plants require a specific sequence of day lengths in order to flower.

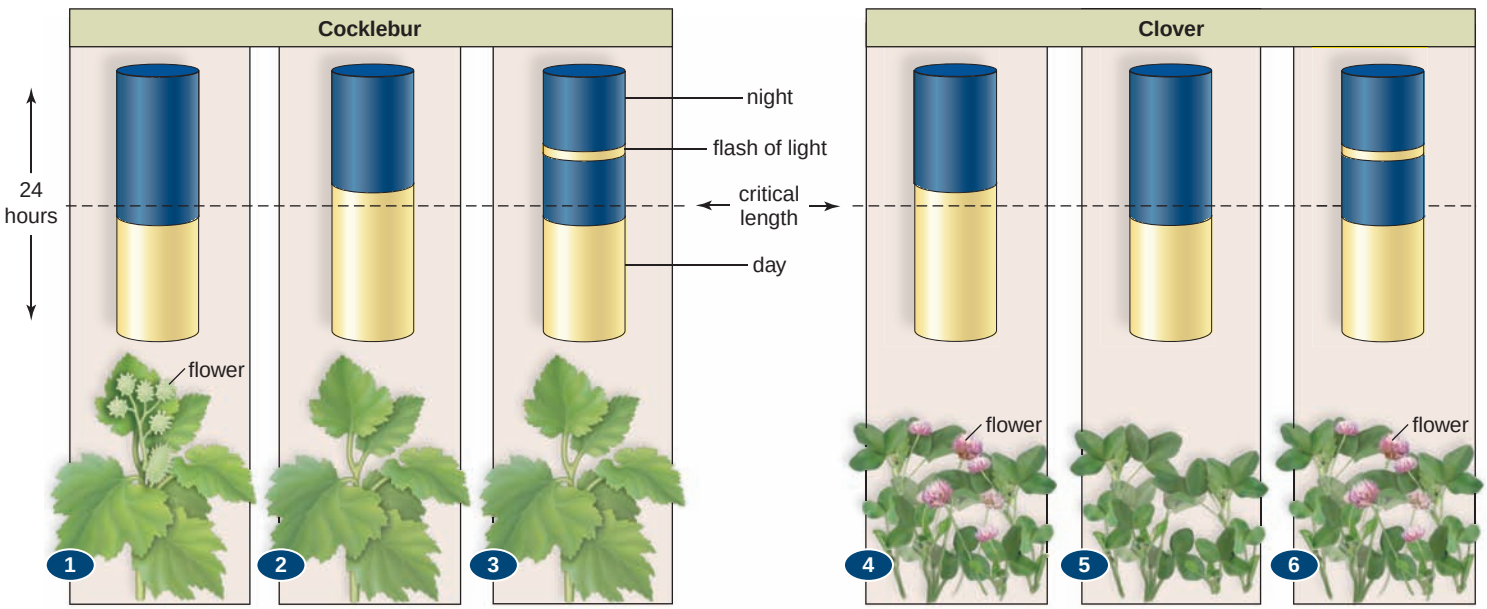
Soon after the three groups of flowering plants were discovered, researchers began to experiment with artificial lengths of light and dark that did not necessarily correspond to a normal 24-hour day. These investigators discovered that the cocklebur, a short-day plant, will not flower if a required long dark period is interrupted by a brief flash of white light. (Interrupting the light period with darkness has no effect.) On the other hand, a long-day plant will flower if an overly long dark period is interrupted by a brief flash of white light. They concluded that the length of the dark period, not the length of the light period, controls flowering. Of course, in nature, short days always go with long nights, and vice versa.

To recap, let's consider Figure 26.18:

- Cocklebur is a short-day plant (Fig. 26.18, *left*). (1) When the night is longer than a critical length, cocklebur flowers. (2) The plant does not flower when the night is shorter than the critical length. (3) Cocklebur also does not flower if the longer-than-critical-length night is interrupted by a flash of light.
- Clover is a long-day plant (Fig. 26.18, *right*). (4) When the night is shorter than a critical length, clover flowers. (5) The plant does not flower when the night is longer than a critical length. (6) Clover does flower when a slightly longer-than-critical-length night is interrupted by a flash of light.

Check Your Progress 26.2B

1. Describe the structure of phytochrome and how it functions in plant cells.
2. A plant is a long-day plant. Explain why the plant will still flower if the long day is interrupted by a period of darkness.



a. Short-day (long-night) plant

b. Long-day (short-night) plant

FIGURE 26.18 Photoperiodism and flowering.

a. Short-day plant. When the day is shorter than a critical length, this type of plant flowers. The plant does not flower when the day is longer than the critical length. It also does not flower if the longer-than-critical-length night is interrupted by a flash of light. **b.** Long-day plant. The plant flowers when the day is longer than a critical length. When the day is shorter than a critical length, this type of plant does not flower. However, it does flower if the slightly longer-than-critical-length night is interrupted by a flash of light.

Flowering Plants Respond to the Biotic Environment

Plants are always under attack by herbivores (animals that eat plants) and parasites. Fortunately, they have an arsenal of defense mechanisms to deal with insects and fungi, for example (Fig. 26.19).

Physical and Chemical Defenses

A plant's cuticle-covered epidermis and bark, if present, do a good job of discouraging attackers. But, unfortunately, herbivores have ways around a plant's first line of defense. A fungus can invade a leaf by way of the stomata and set up shop inside a leaf, where it feeds on nutrients meant for the plant. Underground nematodes have sharp mouthparts to break through the epidermis of a root and establish a parasitic relationship, sometimes by way of a single cell, which enlarges and transfers carbohydrates to the animal. Similarly, the tiny insects called aphids have styletlike mouthparts that allow them to tap into the phloem of a nonwoody stem. These examples illustrate why plants need several other types of defenses not dependent on the outer surface.

The primary metabolites of plants, such as sugars and amino acids, are necessary to the normal workings of a cell, but plants also produce so-called **secondary metabolites** as a defense mechanism. Secondary metabolites were once thought to be waste products, but now we know that they are part of a plant's arsenal to prevent predation. Tannins, present in or on the epidermis of leaves, are defensive compounds that interfere with the outer proteins of bacteria and fungi. They also deter herbivores because of their astringent effect on the mouth and their interference with digestion. Some secondary metabolites, such as bitter nitrogenous substances called **alkaloids** (e.g., morphine, nicotine, and caffeine), are well-known to humans because we use them for our own purposes. The seedlings of coffee plants contain caffeine at a concentration high enough to kill insects and fungi by blocking DNA and RNA synthesis. Other secondary metabolites include the **cyanogenic glycosides** (molecules containing a sugar group) that break down to cyanide and inhibit cellular respiration. Foxglove (*Digitalis purpurea*) produces deadly cardiac and steroid glycosides, which cause nausea, hallucinations, convulsions, and death in animals that ingest them. Taxol, an unsaturated hydrocarbon, from the Pacific yew (*Taxus brevifolia*), is now a well-known cancer-fighting drug.

Foxglove

Even with regard to secondary metabolites, predators can be one step ahead of the plant. Monarch caterpillars are able to feed on milkweed plants, despite the presence of a poisonous glycoside, and they even store the chemical in their body. In this way, the caterpillar and the butterfly become poisonous to their own predators (Fig. 26.19). Birds that become sick after eating a monarch butterfly know to leave them alone thereafter.

Alfalfa plant bug

Fungus infection

Monarch caterpillar and butterfly

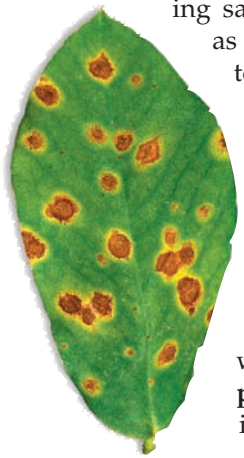
FIGURE 26.19 Plant predators and parasites.

Insects are predators and fungi are parasites of flowering plants.

Wound Responses

Wound responses illustrate that plants can make use of transduction pathways to produce chemical defenses only when they are needed. After a leaf is chewed or injured, a plant produces *proteinase inhibitors*, chemicals that destroy the digestive enzymes of a predator feeding on them. The proteinase inhibitors are produced throughout the plant, not just at the wound site. The defense hormone that brings about this effect is a small peptide called **systemin** (Fig. 26.20). Systemin is produced in the wound area in response to the predator's saliva, but then it travels between cells to reach phloem, which distributes it about the plant. A transduction pathway is activated in cells with systemin receptors, and the cells produce proteinase inhibitors. A chemical called jasmonic acid, and also possibly a chemical called salicylic

acid, are part of this transduction pathway. Salicylic acid (a chemical also found in aspirin) has been known since the 1930s to bring about a phenomenon called systemic acquired resistance (SAR), the production of antiherbivore chemicals by defense genes. Recently, companies have begun marketing salicylic acid and other similar compounds as a way to activate SAR in crops, including tomato, spinach, lettuce, and tobacco.



Hypersensitive response to fungus invasion

Hypersensitive Response

On occasion, plants produce a specific gene product that binds (like a key fits a lock) to a viral, bacterial, or fungal gene product made within the cell. This combination offers a way for the plant to "recognize" a particular pathogen. A transduction pathway now ensues, and the final result is a **hypersensitive response (HR)** that seals off the infected area and will also initiate the wound response just discussed.

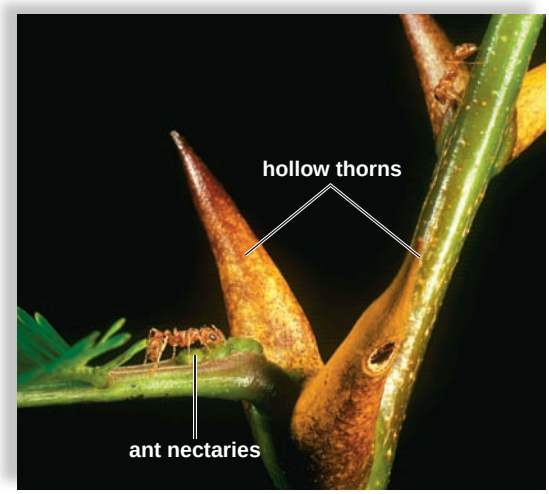
Indirect Defenses

Some defenses do not kill or discourage a herbivore outright. For example, female butterflies are less likely to lay their eggs on plants that already have butterfly eggs. So, because the leaves of some passion flowers display physical structures resembling the yellow eggs of *Heliconius* butterflies, these butterflies do not lay eggs on this plant. Other plants produce hormones that prevent caterpillars from metamorphosing into adults and laying more eggs.

Certain plants attract the natural enemies of caterpillars feeding on them. They produce volatile molecules that diffuse into the air and advertise that food is available for a carnivore (an animal that eats other animals). For example, lima beans produce volatiles that attract carnivore mites only when they are being damaged by a spider mite. Corn and cotton plants release volatiles that attract wasps, which then inject their eggs into caterpillars munching on their leaves. The eggs develop into larvae that eat the caterpillars, not the leaves.

Relationships with Animals

Mutualism is a relationship between two species in which both species benefit. As evidence that a mutualistic relationship can help protect a plant from predators, consider the bullhorn acacia tree, which provides a home for ants of the species *Pseudomyrmex ferruginea.* Unlike other acacias, this species has swollen thorns with a hollow interior where ant larvae can grow and develop.



Mutualism between ants and a plant

In addition to housing the ants, acacias provide them with food. The ants feed from nectaries at the base of leaves and eat fat- and protein-containing nodules called Beltian bodies, which are found at the tips of the leaves. In return, the ants constantly protect the plant by attacking and stinging any would-be herbivores because, unlike other ants, they are active 24 hours a day. Indeed, when the ants on experimental trees were removed, the acacia trees died.

Check Your Progress **26.2C**

1. What are several ways that flowering plants protect themselves from insect predators?

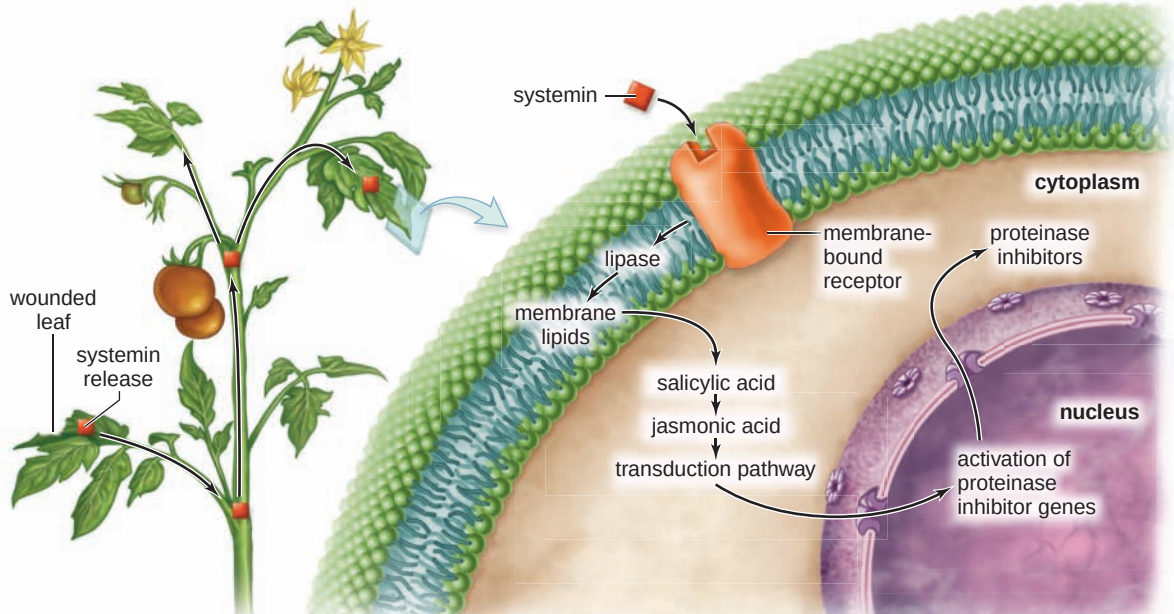


FIGURE 26.20
Wound response in tomato.

After wounded leaves produce systemin, it travels in phloem to all parts of a plant where it binds to cells that have a systemin receptor. These cells then produce jasmonic acid, a molecule that initiates a transduction pathway and, in that way, leads to production of proteinase inhibitors, which limit insect feeding.

Connecting the Concepts

Behavior in plants can be understood in terms of three different levels of organization. On the species level, plant responses that promote survival and reproductive success have evolved through natural selection. At the organismal level, some part or the entire plant responds to a stimulus. And at the cellular level, receptors receive signals, transduction pathways transform them, and genes or metabolic pathways react to them.

We can illustrate these three perspectives by answering the question, why do plants bend toward the light? On the species level, those plants that bend toward the light will be able to produce more organic food and will have more offspring. On the organismal level, elongation of the stem on the shady side causes the stem to bend toward the light. On the cellular level, after auxin is received by a plant cell, cellular activities cause its walls to expand.

The response of both the organism and the cell involve three steps: (1) reception of the stimulus, (2) transduction of the stimulus, and (3) response to the stimulus. Can you designate these steps on the cellular level? A light stimulus causes auxin to enter cells on the shady side, cellular activities is the second step, and stretching of the cell wall is the third step.

If animals were being considered instead of plants, the same type of biological explanations would apply. Plants and animals, and indeed all organisms, share common ancestors, even back to the very first cell(s). Recall that evolution explains both the unity and diversity of living things. Organisms are similar because they share common ancestors; they are different because they are adapted to different ways of life.

summary

26.1 Plant Hormones

Like animals, flowering plants use a reception-transduction-response pathway when they respond to a stimulus. The process involves receptor activation, transduction of the signal by relay proteins, and a cellular response, which can consist of the turning on of a gene or an enzymatic pathway.

Auxin-controlled cell elongation is involved in phototropism and gravitropism. When a plant is exposed to light, auxin moves laterally from the bright to the shady side of a stem.

Gibberellin causes stem elongation between nodes. After this hormone binds to a plasma membrane receptor, a DNA-binding protein activates a gene leading to the production of amylase. Amylase is an enzyme that speeds the breakdown of amylase.

Cytokinins cause cell division, the effects of which are especially obvious when plant tissues are grown in culture. Abscisic acid (ABA) and ethylene are two plant growth inhibitors. ABA is well known for causing stomata to close, and ethylene is known for causing fruits to ripen.

26.2 Plant Responses

When flowering plants respond to stimuli, growth and/or movement occurs. Tropisms are growth responses toward or away from unidirectional stimuli. The positive phototropism of stems results in a bending toward light, and the negative gravitropism of stems results in a bending away from the direction of gravity. Roots that bend toward the direction of gravity show positive gravitropism. Thigmotropism occurs when a plant part makes contact with an object, as when tendrils coil about a pole.

Nastic movements are not directional. Due to turgor pressure changes, some plants respond to touch and some perform sleep movements. Plants exhibit circadian rhythms, which are believed to be controlled by a biological clock. The sleep movements of prayer plants, the closing of stomata, and the daily opening of certain flowers have a 24-hour cycle.

Phytochrome is a pigment that is involved in photoperiodism, the ability of plants to sense the length of the day and night during a 24-hour period. This sense leads to seed germination, shoot elongation, and flowering during favorable times of the year. Daylight causes phytochrome to exist as P_{fr}, but during the night, it is reconverted to P_r by metabolic processes. Phytochrome in the P_{fr} form leads to a biological response such as flowering. Short-day plants flower only when the days are shorter than a critical length, and long-day plants flower only when the days are longer than a critical length. Actually, research has shown that it is the length of darkness that is critical. Interrupting the dark period with a flash of white light prevents flowering in a short-day plant and induces flowering in a long-day plant.

Flowering plants have defenses against predators and parasites. The first line of defense is their outer covering. They also routinely produce secondary metabolites that protect them from herbivores, particularly insects. Wounding causes plants to produce systemin, which travels about the plant and causes cells to produce proteinase inhibitors that destroy an insects digestive enzymes. During a hypersensitive response, an infected area is sealed off. As an indirect response, plants temporarily attract animals that will destroy predators, and going one step further, plants have permanent relationships with animals, such as ants, that will attack predators.

understanding the terms

abscisic acid (ABA) 480
abscission 480
alkaloid 488
apical dominance 475
auxin 475
biological clock 485
cellular response 474
circadian rhythm 484
coleoptile 475
cyanogenic glycoside 488
cytokinin 477
day-neutral plant 487
dormancy 477
ethylene 480
gibberellin 476
gravitropism 482
hormone 474
hypersensitive response (HR) 489
long-day plant 487
photoperiodism 486
phototropism 483
phytochrome 486
receptor 474
secondary metabolite 488
senescence 477
short-day plant 487
statolith 482
systemin 488
thigmotropism 483
transduction pathway 474
tropism 482
turgor movement 484

Match the terms to these definitions:

a. _____ Biological rhythm with a 24-hour cycle.
b. _____ Directional growth of plants in response to the Earth's gravity.
c. _____ Dropping of leaves, fruits, or flowers from a plant.

d. _____ Plant hormone producing increased stem growth between nodes; also involved in flowering and seed germination.

e. _____ Relative lengths of daylight and darkness that affect the physiology and behavior of an organism.

reviewing this chapter

1. Name and describe the three stages of signal transduction in plant cells. 474
2. Why does removing a terminal bud cause a plant to get bushier? 475
3. What experiments led to knowledge that a hormone is involved in phototropism? Explain the mechanism by which auxin brings about elongation of cells. 475–76
4. Gibberellin research supports the hypothesis that plant hormones initiate a reception-transduction-response pathway. Explain. 476–77
5. What is the function of cytokinins? Discuss experimental evidence to suggest that hormones interact when they bring about an effect. 477
6. What are some of the primary effects of abscisic acid and how does it bring about these effects? 480
7. What hormones are involved in abscission? How does ethylene bring about ripening of fruits? 480–81
8. Tropisms are responses to stimuli. Why are stems said to exhibit positive phototropism but negative gravitropism? 482–83
9. What are nastic movements, and how do turgor pressure changes bring about movements of plants? 484–85
10. What is a biological clock, how does it function, and what is its primary usefulness in plants? 485
11. Define photoperiodism, and discuss its relationship to flowering in certain plants. 486–87
12. Describe the structure of phytochrome and its response to red and far-red light. 486
13. What mechanisms allow a plant to defend itself? 488–89

testing yourself

Choose the best answer for each question.

1. During which step of signal transduction is a second messenger released into the cytoplasm?
   a. reception
   b. response
   c. transduction
   d. final step
2. Which of the following plant hormones causes apical dominance?
   a. auxin
   b. gibberellins
   c. cytokinins
   d. abscisic acid
   e. ethylene
3. Internode elongation is stimulated by
   a. abscisic acid.
   b. ethylene.
   c. cytokinin.
   d. gibberellin.
   e. auxin.
4. Which of these is related to gibberellin activity?
   a. initiation of bud dormancy
   b. amylase production
   c. fruit ripening.
   d. Both b and c are correct.
5. _____ always promotes cell division.
   a. Auxin
   b. Phytochrome
   c. Cytokinin
   d. None of these are correct.
6. In the absence of abscisic acid, plants may have difficulty
   a. forming winter buds.
   b. closing the stomata.
   c. Both a and b are correct.
   d. Neither a nor b is correct.
7. Ethylene
   a. is a gas.
   b. causes fruit to ripen.
   c. is produced by the incomplete combustion of fuels such as kerosene.
   d. All of these are correct.
8. Which of the following plant hormones is responsible for a plant losing its leaves?
   a. auxin
   b. gibberellins
   c. cytokinins
   d. abscisic acid
   e. ethylene
9. Which is not a plant hormone?
   a. auxin
   b. cytokinin
   c. gibberellin
   d. All of these are plant hormones.

For questions 10–14, match each statement with a hormone in the key.

KEY:

a. auxin
b. gibberellin
c. cytokinin
d. ethylene
e. abscisic acid

10. One rotten apple can spoil the barrel.
11. Cabbage plants bolt (grow tall).
12. Stomata close when a plant is water-stressed.
13. Stems bend toward the sun.
14. Coconut milk causes plant tissues to undergo cell division.
15. You bought green bananas at the grocery store this morning. However, you want a ripe banana for breakfast tomorrow morning. What could you do to accomplish this?
16. Which of the following statements is correct?
    a. Both stems and roots show positive gravitropism.
    b. Both stems and roots show negative gravitropism.
    c. Only stems show positive gravitropism.
    d. Only roots show positive gravitropism.
17. The sensors in the cells of the root cap are called
    a. mitochondria.
    b. central vacuoles.
    c. statoliths.
    d. chloroplasts.
    e. intermediate filaments.
18. A student places 25 morning glory (see Fig. 26.13) seeds in a large pot and allows the seeds to germinate in total darkness. Which of the following growth or movement activities would the seedlings exhibit?
    a. gravitropism, as the roots grow down and the shoots grow up
    b. phototropism, as the shoots search for light
    c. thigmotropism, as the tendrils coil around other seedlings
    d. Both a and c are correct.
19. Circadian rhythms
    a. require a biological clock.
    b. do not exist in plants.
    c. are involved in the tropisms.
    d. are involved in sleep movements.
    e. Both a and d are correct.

20. Plants that flower in response to long nights are
    a. day-neutral plants.
    b. long-day plants.
    c. short-day plants.
    d. impossible.

21. Short-day plants
    a. are the same as long-day plants.
    b. are apt to flower in the fall.
    c. do not have a critical photoperiod.
    d. will not flower if a short day is interrupted by bright light.
    e. All of these are correct.

22. A plant requiring a dark period of at least 14 hours will
    a. flower if a 14-hour night is interrupted by a flash of light.
    b. not flower if a 14-hour night is interrupted by a flash of light.
    c. not flower if the days are 14 hours long.
    d. not flower if the nights are longer than 14 hours.
    e. Both b and c are correct.

23. Phytochrome plays a role in
    a. flowering.
    b. stem growth.
    c. leaf growth.
    d. All of these are correct.

24. Phytochrome
    a. is a plant pigment.
    b. is present as P_{fr} during the day.
    c. activates DNA-binding proteins.
    d. is a photoreceptor.
    e. All of these are correct.

25. Primary metabolites are needed for _____ while secondary metabolites are produced for _____.
    a. growth, signal transduction
    b. normal cell functioning, defense
    c. defense, growth
    d. signal transduction, normal cell functioning

26. Which of the following is a plant secondary metabolite used by humans to treat disease?
    a. morphine
    b. codeine
    c. quinine
    d. penicillin
    e. All but d are correct.

27. Which of these is mismatched?
    a. cuticle—first line of defense
    b. secondary metabolite—growth response
    c. systemin—wound response
    d. acadia and ants—mutualism

28. Which of these would account for sleep movements in prayer plants?
    a. turgor movements
    b. biological clock
    c. daylight
    d. phytochrome

29. Plants etoliate when they need
    a. fertilizer.
    b. water.
    c. daylight.
    d. phytochrome.

30. Which is part of phytochrome structure?
    a. protein kinase
    b. photoreceptor
    c. P_r and P_{fr}
    d. All of these are correct.

31. Which of these is an indirect defense?
    a. secondary chemical
    b. making a predator think that butterfly eggs are already on the leaves
    c. inviting ants to live on a plant
    d. All of these are correct.

thinking scientifically

1. You hypothesize that abscisic acid (ABA) is responsible for the turgor pressure changes that permit a plant to track the sun (see photograph on page 473). What observations could you make to support your hypothesis?
2. You formulate the hypothesis that the negative gravitropic response of stems is greater than the positive phototropism of stems. How would you test your hypothesis?

bioethical issue

Environmental Activism

The government paid the owner of Pacific Lumber some $500 million so that 3,500 acres of redwood trees along the coast of the Pacific Northwest would be preserved. Activists thought the deal was unfair—they wanted 60,000 acres preserved. Any less and there would not be enough habitat to keep the marbled murrelets, an endangered seabird, from sinking into oblivion. Besides, it would take hundreds of years for the trees to regrow to their original size.

Activists feel betrayed by their own representatives in the government. After all, the owner of Pacific Lumber is a big contributor to the reelection campaigns of elected officials who approved the deal. Under the circumstances, what would you do to save the trees? Some activists climbed the trees and refused to come down even while the trees were being cut. In September of 1998, David Chain, 24, lost his life when a tree fell on him and crushed his skull. What is the proper action for activist groups when they feel their government is letting them down? Should they defy the law, and if so, what is the proper response of government officials?

Biology website

The companion website for *Biology* provides a wealth of information organized and integrated by chapter. You will find practice tests, animations, videos, and much more that will complement your learning and understanding of general biology.

http://www.mhhe.com/maderbiology10

27

Flowering Plants: Reproduction

The flowering plants, or angiosperms, are the most diverse and widespread of all the plants, and their means of sexual reproduction, centered in the flower, is well adapted to life on land. The flower shields the female gametophyte and produces pollen grains that protect a male gametophyte until fertilization takes place. The presence of an ovary allows angiosperms to produce seeds within fruits. Seeds guard the embryo until conditions are favorable for germination.

The evolution of the flower permits pollination not only by wind but also by animals. Flowering plants that rely on animals for pollination have a mutualistic relationship with them. The flower provides nutrients for a pollinator such as a bee, a fly, a beetle, a bird, or even a bat. The animals, in turn, inadvertently carry pollen from one flower to another, allowing pollination to occur. Similarly, animals help flowering plants disperse their fruits and, therefore, seeds. As we learn in this chapter, the diversity of flowering plants can, in part, be attributed to their relationships with a great variety of animals.

Honeybee on landing platform of a yellow aster.

concepts

27.1 Sexual Reproductive Strategies

As in animals, sexual reproduction in plants is advantageous because it can generate variety among the offspring due to the process of meiosis and fertilization. In a changing environment, a new variety may be better adapted for survival and reproduction than either parent.

Life Cycle Overview

When plants reproduce sexually, they alternate between two multicellular stages. As also described on page 412, a diploid stage alternates with a haploid one. (1) In flowering plants, the diploid sporophyte is dominant, and it is the generation that bears flowers (Fig. 27.1) (2) A **flower,** which is the reproductive structure of angiosperms, produces two types of spores by meiosis, microspores and megaspores. (3) A **microspore** [Gk. *mikros,* small, little] undergoes mitosis and becomes a pollen grain, which is either windblown or carried by an animal to the vicinity of the female gametophyte. (4) In the meantime, the **megaspore** [Gk. *megas,* great, large] has undergone mitosis to become the female gametophyte, an embryo sac located within an ovule found within an ovary. (5) At maturity, a pollen grain contains nonflagellated sperm, which travel by way of a pollen tube to the embryo sac. (6) Once a sperm fertilizes an egg, the zygote becomes an embryo, still within an ovule. (7) The ovule develops into a **seed,** which contains the embryo and stored food surrounded by a seed coat. The ovary becomes a fruit, which aids in dispersing the seeds. (8) When a seed germinates, a new sporophyte emerges and through mitosis and growth becomes a mature organism.

Notice that the sexual life cycle of flowering plants is adapted to a land existence. The microscopic female gametophytes develop completely within the sporophyte and are thereby protected from desiccation. Pollen grains (male gametophytes) are not released until they develop a thick wall. No external water is needed to bring about fertilization in flowering plants. Instead, the pollen tube provides passage for a sperm to reach an egg. Following fertilization, the embryo and its stored food are enclosed within a protective seed coat until external conditions are favorable for germination.

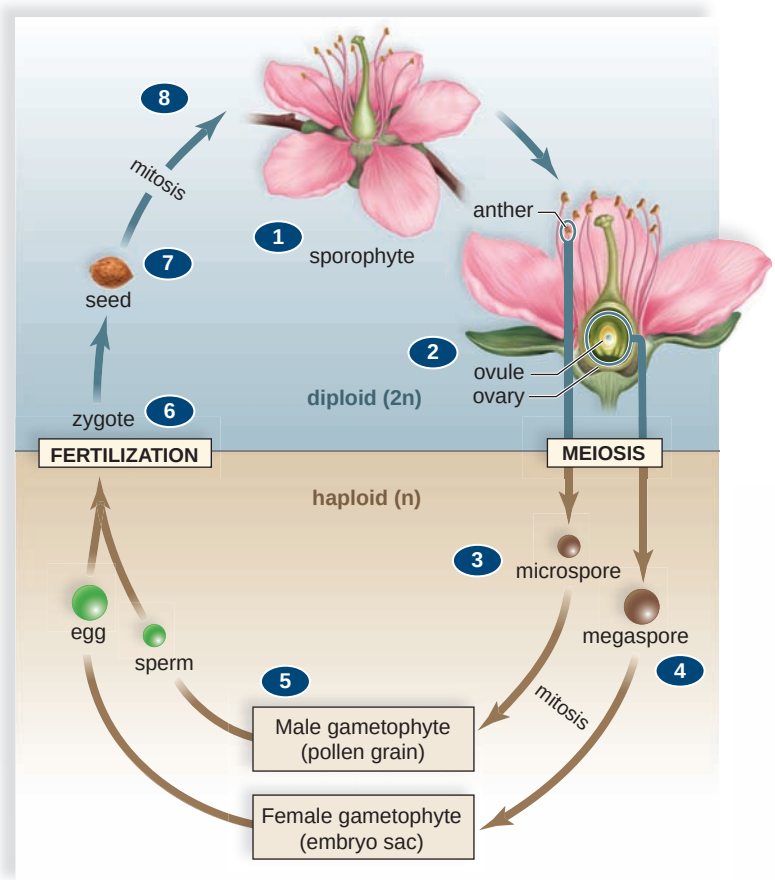


FIGURE 27.1 Sexual reproduction in flowering plants.

The sporophyte bears flowers. The flower produces microspores within anthers and megaspores within ovules by meiosis. A megaspore becomes a female gametophyte, which produces an egg within an embryo sac, and a microspore becomes a male gametophyte (pollen grain), which produces sperm. Fertilization results in a zygote and sustenance for the embryo. A seed contains an embryo and stored food within a seed coat. After dispersal, a seed becomes a new sporophyte plant.

Flowers

The flower is unique to angiosperms (Fig. 27.2). Aside from producing the spores and protecting the gametophytes, flowers often attract pollinators, which aid in transporting pollen from plant to plant. Flowers also produce the fruits that enclose the seeds. The evolution of the flower was a major factor leading to the success of angiosperms, with over 240,000 species. Flowering is often a response to environmental signals such as the length of the day (see page 486). In many plants, a flower develops when shoot apical meristem that previously formed leaves suddenly stops producing leaves and starts producing a

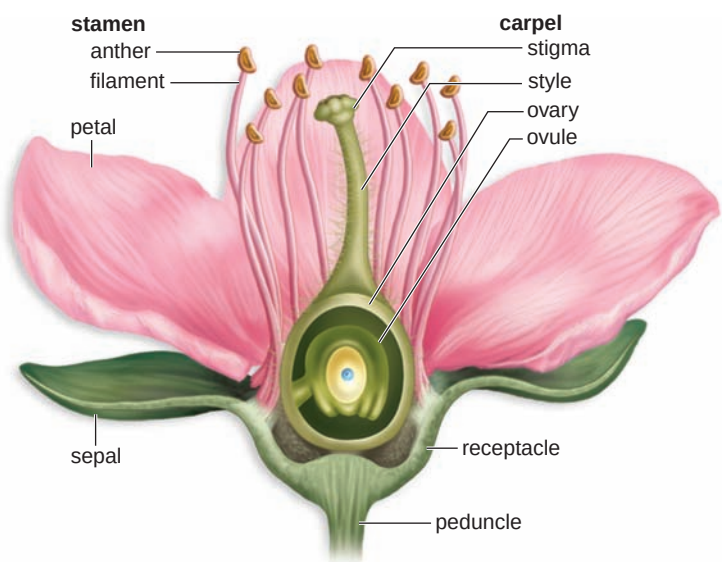


FIGURE 27.2 Anatomy of a flower.

A complete flower has all flower parts: sepals, petals, stamens, and at least one carpel.

flower enclosed within a bud. In other plants, axillary buds develop directly into flowers. In monocots, flower parts occur in threes and multiples of three; in eudicots, flower parts are in fours or fives and multiples of four or five (Fig. 27.3).

Flower Structure

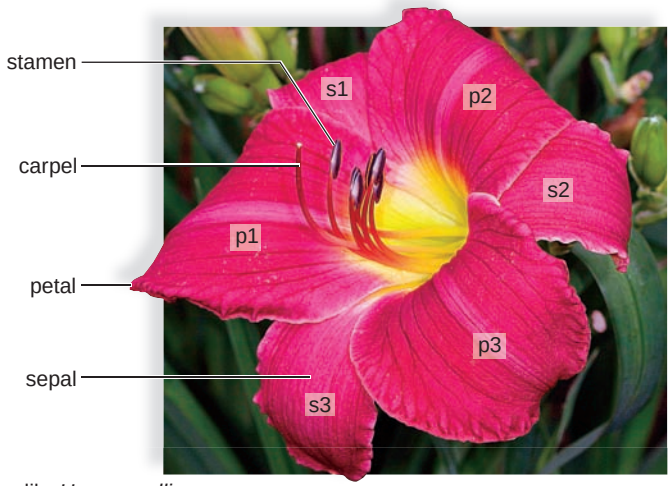
A typical flower has four whorls of modified leaves attached to a receptacle at the end of a flower stalk called a peduncle.

1. The **sepals,** which are the most leaflike of all the flower parts, are usually green, and they protect the bud as the flower develops within. Collectively, the sepals are called the **calyx.**
2. An open flower next has a whorl of **petals,** whose color accounts for the attractiveness of many flowers. The size, the shape, and the color of petals are attractive to a specific pollinator. Wind-pollinated flowers may have no petals at all. Collectively, the petals are called the **corolla.**
3. **Stamens** are the "male" portion of the flower. Each stamen has two parts: the **anther,** a saclike container, and the **filament** [L. *filum,* thread], a slender stalk. Pollen grains develop from the microspores produced in the anther.
4. At the very center of a flower is the **carpel,** a vaselike structure that represents the "female" portion of the flower. A carpel usually has three parts: the **stigma,** an enlarged sticky knob; the **style,** a slender stalk; and the **ovary,** an enlarged base that encloses one or more **ovules** (see Fig. 27.2).

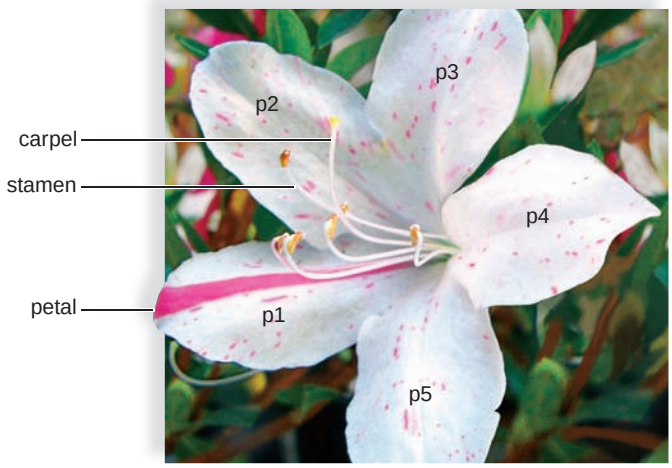
Ovules [L. *ovulum,* little egg] play a significant role in the production of megaspores and, therefore, female gametophytes. A flower can have a single carpel or multiple carpels. Sometimes several carpels are fused into a single structure, in which case the ovary is compound and has several chambers, each of which contains ovules. For example, an orange develops from a compound ovary, and every section of the orange is a chamber.

Variations in Flower Structure

We have space to mention only a few variations in flower structure. Not all flowers have sepals, petals, stamens, or carpels. Those that do are said to be *complete* and those that do not are said to be *incomplete.* Flowers that have both stamens and carpels are called *perfect* (bisexual) flowers; those with only stamens and those that have only carpels are *imperfect* (unisexual) flowers. If staminate flowers and carpellate flowers are on one plant, the plant is *monoecious* [Gk. *monos,* one, and *oikos,* home, house] (Fig. 27.4). Corn is an example of a plant that is monoecious. If staminate and carpellate flowers are on separate plants, the plant is *dioecious.* Holly trees are dioecious, and if red berries are a priority, it is necessary to acquire a plant with staminate flowers and another plant with carpellate flowers.



a. Daylily, *Hemerocallis* sp.



b. Festive azalea, *Rhododendron* sp.

FIGURE 27.3 Monocot versus eudicot flowers.

a. Monocots, such as daylilies, have flower parts usually in threes. In particular, note the three petals and three sepals, both of which are colored in this flower. **b.** Azaleas are eudicots. They have flower parts in fours or fives; note the five petals of this flower. p = petal, s = sepal

a. Staminate flowers

b. Carpellate flowers

FIGURE 27.4 Corn plants are monoecious.

A corn plant has clusters of staminate flowers (**a**) and carpellate flowers (**b**). Staminate flowers produce the pollen that is carried by wind to the carpellate flowers, where ears of corn develop.

Life Cycle in Detail

In all land plants, the sporophyte produces haploid spores by meiosis. The haploid spores grow and develop into haploid gametophytes, which produce gametes by mitotic division. Flowering plants, however, are *heterosporous*—they produce microspores and megaspores. Microspores become mature male gametophytes (sperm-bearing pollen grains), and megaspores become mature female gametophytes (egg-bearing embryo sacs).

Development of Male Gametophyte

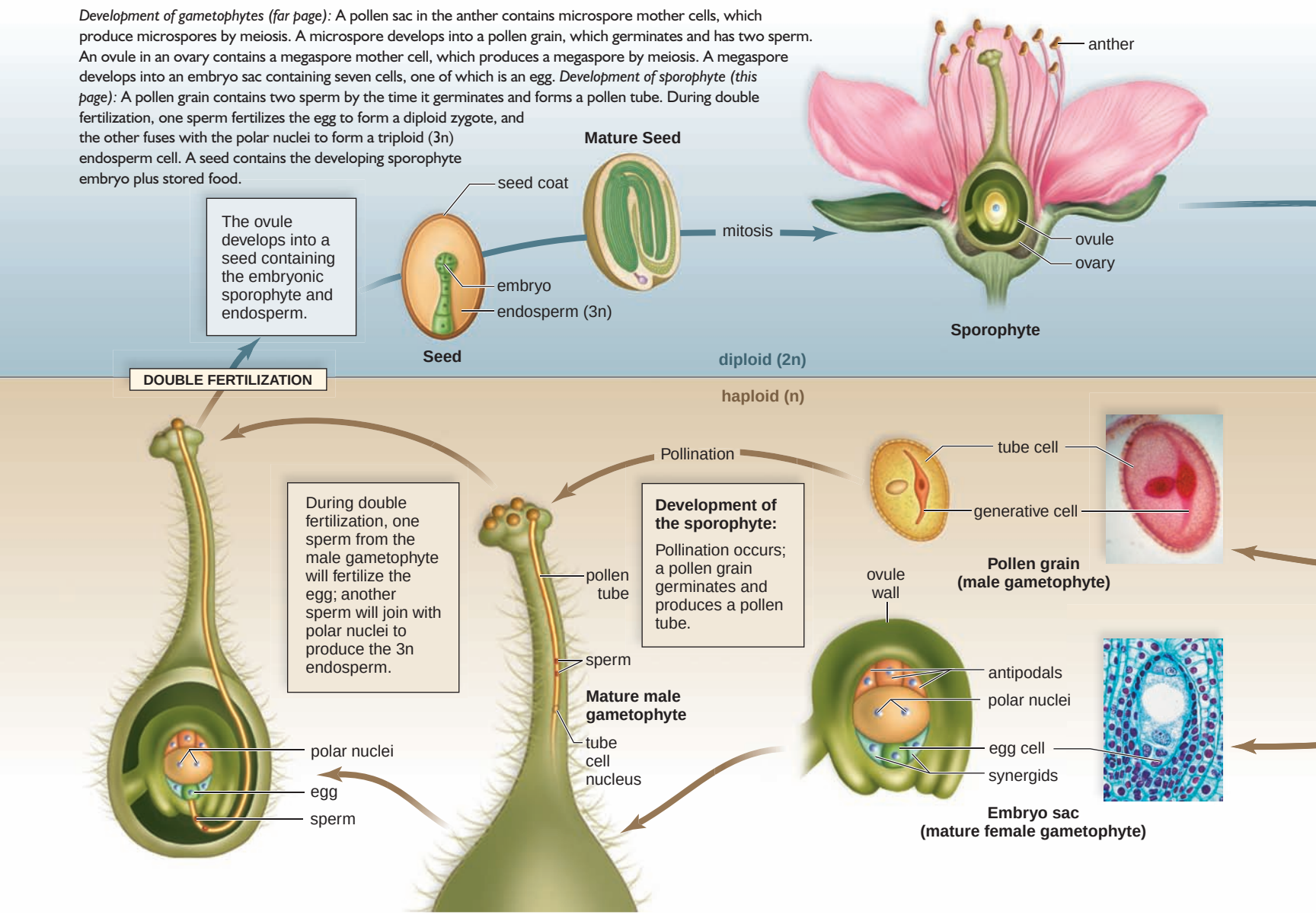
Microspores are produced in the anthers of flowers (Fig. 27.5). An anther has four pollen sacs, each containing many microspore mother cells. A microspore mother cell undergoes meiosis to produce four haploid microspores. In each, the haploid nucleus divides mitotically, followed by unequal cytokinesis, and the result is two cells enclosed by a finely sculptured wall. This structure, called the **pollen grain,** is at first an immature **male gametophyte** that consists of a tube cell and a generative cell. The larger tube cell will eventually produce a *pollen tube.* The smaller generative cell divides mitotically either now or later to produce two sperm. Once these events take place, the pollen grain has become the mature male gametophyte.

Development of Female Gametophyte

The ovary contains one or more ovules. An ovule has a central mass of parenchyma cells almost completely covered by layers of tissue called integuments except where there is an opening, the micropyle. One parenchyma cell enlarges to become a megaspore mother cell, which undergoes meiosis, producing four haploid megaspores (Fig. 27.5). Three of these megaspores are nonfunctional, and one is functional. In a typical pattern, the nucleus of the functional megaspore

FIGURE 27.5 Life cycle of flowering plants.

Development of gametophytes (far page): A pollen sac in the anther contains microspore mother cells, which produce microspores by meiosis. A microspore develops into a pollen grain, which germinates and has two sperm. An ovule in an ovary contains a megaspore mother cell, which produces a megaspore by meiosis. A megaspore develops into an embryo sac containing seven cells, one of which is an egg. *Development of sporophyte (this page):* A pollen grain contains two sperm by the time it germinates and forms a pollen tube. During double fertilization, one sperm fertilizes the egg to form a diploid zygote, and the other fuses with the polar nuclei to form a triploid (3n) endosperm cell. A seed contains the developing sporophyte embryo plus stored food.

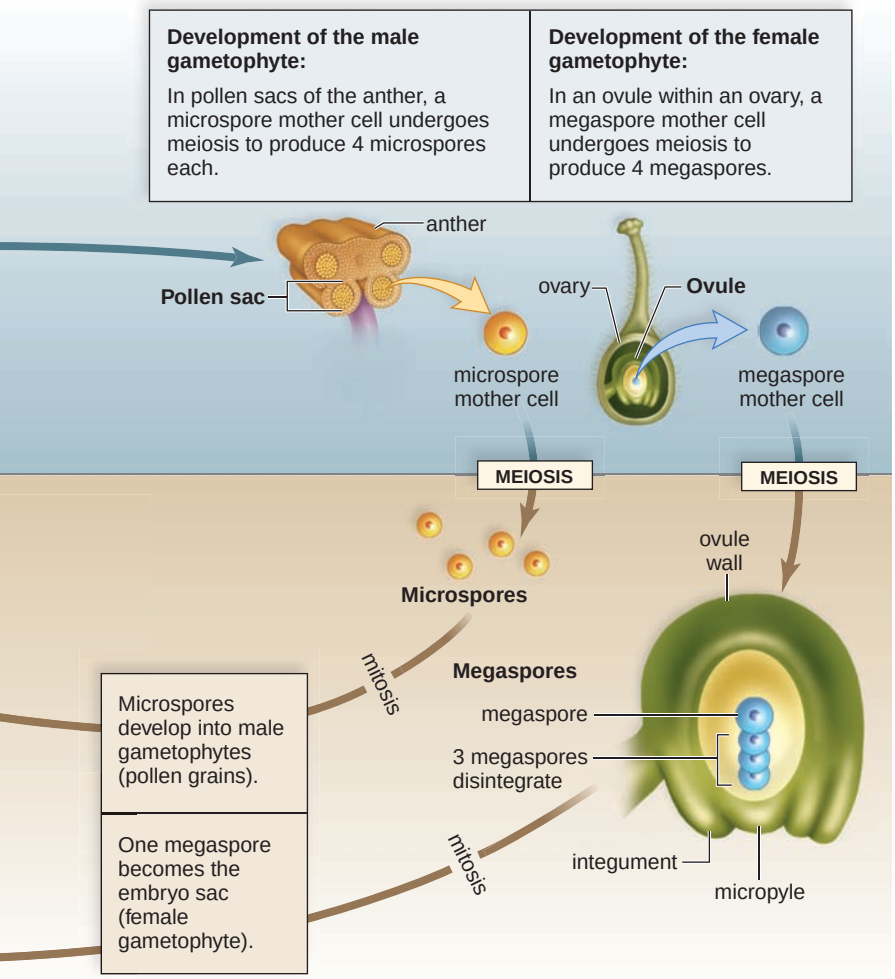


divides mitotically until there are eight nuclei in the **female gametophyte** [Gk. *megas*, great, large]. When cell walls form later, there are seven cells, one of which is binucleate. The female gametophyte, also called the **embryo sac,** consists of these seven cells:

- one egg cell, associated with two synergid cells;
- one central cell, with two polar nuclei;
- three antipodal cells

Development of New Sporophyte

The walls separating the pollen sacs in the anther break down when the pollen grains are ready to be released. **Pollination** is simply the transfer of pollen from an anther to the stigma of a carpel. Self-pollination occurs if the pollen is from the same plant, and cross-pollination occurs if the pollen is from a different plant of the same species.



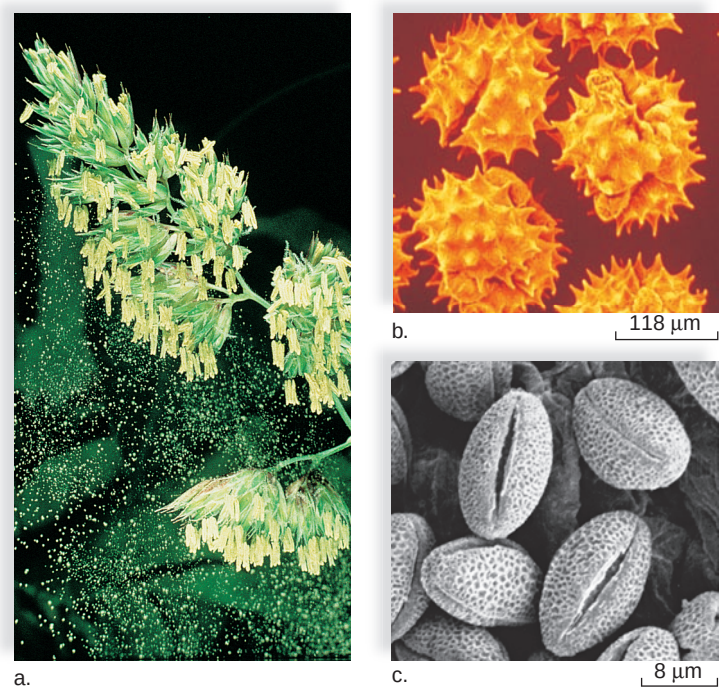


FIGURE 27.6 Pollination.

a. Cocksfoot grass, *Dactylus glomerata,* releasing pollen. **b.** Pollen grains of Canadian goldenrod, *Solidago canadensis.* **c.** Pollen grains of pussy willow, *Salix discolor.* The shape and pattern of pollen grain walls are quite distinctive, and experts can use them to identify the genus, and even sometimes the species, that produced a particular pollen grain. Pollen grains have strong walls resistant to chemical and mechanical damage; therefore, they frequently become fossils.

When a pollen grain lands on the stigma of the same species, it germinates, forming a pollen tube (see Fig. 27.5). The germinated pollen grain, containing a tube cell and two sperm, is the mature male gametophyte. As it grows, the pollen tube passes between the cells of the stigma and the style to reach the micropyle, a pore of the ovule. When the pollen tube reaches the micropyle, **double fertilization** occurs. As expected, one of the sperm unites with the egg, forming a 2n zygote. Unique to angiosperms, however, the other sperm unites with two polar nuclei centrally placed in the embryo sac, forming a 3n endosperm nucleus. This endosperm nucleus eventually develops into the **endosperm** [Gk. *endon,* within, and *sperma,* seed], a nutritive tissue that the developing embryonic sporophyte will use as an energy source. Now the ovule begins to develop into a seed. One important aspect of seed development is formation of the seed coat from the ovule wall. A mature seed contains (1) the embryo, (2) stored food, and (3) the seed coat (see Fig. 27.8).

Cross Pollination

Some species of flowering plants—for example, the grasses and grains—rely on wind pollination (Fig. 27.6), as do the gymnosperms, the other type of seed plant. Much of the plant's energy goes into making pollen to ensure that some pollen grains actually reach a stigma. Even the amount successfully transferred is staggering: A single corn plant may produce from 20 to 50 million grains a season. In corn, the flowers tend to be monoecious, and clusters of tiny male

flowers move in the wind, freely releasing pollen into the air. Most angiosperms rely on animals—be they insects (e.g., bumblebees, flies, butterflies, and moths), birds (e.g., hummingbirds), or mammals (e.g., bats)—to carry out pollination. The use of animal pollinators is unique to flowering plants, and it helps account for why these plants are so successful on land. By the time flowering plants appear in the fossil record some 135 MYA, insects had long been present. For millions of years, then, plants and their animal pollinators have coevolved. **Coevolution** means that as one species changes, the other changes too, so that in the end, the two species are suited to one another. Plants with flowers that attracted a pollinator enjoyed an advantage because, in the end, they produced more seeds. Similarly, pollinators that were able to find and remove food from the flower were more successful. Today, we see that the reproductive parts of the flower are positioned so that the pollinator can't help but pick up pollen from one flower and deliver it to another. On the other hand, the mouthparts of the pollinator are suited to gathering the nectar from these particular plants.

science focus

Plants and Their Pollinators

A plant and its pollinator(s) are adapted to one another. They have a mutualistic relationship in which each benefits—the plant uses its pollinator to ensure that cross-pollination takes place, and the pollinator uses the plant as a source of food. This mutualistic relationship came about through the process of coevolution—that is, the codependency of the plant and the pollinator is the result of suitable changes in the structure and function of each. The evidence for coevolution is observational. For example, floral coloring and odor are suited to the sense perceptions of the pollinator; the mouthparts of the pollinator are suited to the structure of the flower; the type of food provided is suited to the nutritional needs of the pollinator; and the pollinator forages at the time of day that specific flowers are open. The following are examples of such coevolution.

Bee-Pollinated Flowers

There are 20,000 known species of bees that pollinate flowers. The best-known pollinators are the honeybees (Fig. 27A*a*). Bee eyes see a spectrum of light that is different from the spectrum seen by humans. The bees' visible spectrum is shifted so that they do not see red wavelengths but do see ultraviolet wavelengths. Bee-pollinated flowers are usually brightly colored and are predominantly blue or yellow; they are not entirely red. They may also have ultraviolet shadings called nectar guides, which highlight the portion of the flower that contains the reproductive structures. The mouthparts of bees are fused into a long tube that contains a tongue. This tube is an adaptation for sucking up nectar provided by the plant, usually at the base of the flower.

Bee flowers are delicately sweet and fragrant to advertise that nectar is present. The nectar guides often point to a narrow floral tube large enough for the bee's feeding apparatus but too small for other insects to reach the nectar. Bees also collect pollen as food for their larvae. Pollen clings to the hairy body of a bee, and the bees also gather it by means of bristles on their legs. They then store the pollen in pollen baskets on the third pair of legs. Bee-pollinated flowers are sturdy and irregular in shape because they often have a landing platform where the bee can alight. The landing platform requires the bee to brush up against the anther and stigma as it moves toward the floral tube to feed. One type of orchid, *Ophrys*, has evolved a unique adaptation. The flower resembles a female wasp, and when the male of that species attempts to copulate with the flower, the wasp receives pollen.

Moth- and Butterfly-Pollinated Flowers

Contrasting moth- and butterfly-pollinated flowers emphasizes the close adaptation between pollinator and flower. Both moths and butterflies have a long, thin, hollow proboscis, but they differ in other characteristics. Moths usually feed at night and have a well-developed sense of smell. The flowers they visit are visible at night because they are lightly shaded (white, pale yellow, or pink), and they have strong, sweet perfume,

a. b.

FIGURE 27A Pollinators.
a. *A bee-pollinated flower is a color other than red (bees cannot detect this color) and has a landing platform where the reproductive structures of the flower brush up against the bee's body.* ***b.*** *A butterfly-pollinated flower is often a composite, containing many individual flowers. The broad expanse provides room for the butterfly to land, after which it lowers its proboscis into each flower in turn.*

Many examples of the coevolution between plants and their pollinators are given in the Science Focus on these pages. Here, we can note that bee-pollinated flowers are usually yellow, blue, or white because these are the colors bees can see. Bees respond to ultraviolet markings called nectar guides that help them locate nectar. Humans do not use ultraviolet light in order to see, but bees are sensitive to ultraviolet light. A bee has a feeding proboscis of the right length to collect nectar from certain flowers and a pollen basket on its hind legs that allows it to carry pollen back to the hive. Because many fruits and vegetables are dependent on bee pollination, there is much concern today that the number of bees is declining due to disease and the use of pesticides.

Check Your Progress 27.1

1. What specific part of a flower produces male gametophytes? Female gametophytes?
2. Contrast the development and structure of the male gametophyte and the female gametophyte.
3. What are the products of double fertilization in angiosperms?

which helps attract moths. Moths hover when they feed, and their flowers have deep tubes with open margins that allow the hovering moths to reach the nectar with their long proboscis. Butterflies are active in the daytime and have good vision but a weak sense of smell. Their flowers have bright colors—even red because butterflies can see the color red—but the flowers tend to be odorless. Unable to hover, butterflies need a place to land. Flowers that are visited by butterflies often have flat landing platforms (Fig. 27A*b*). Composite flowers (composed of a compact head of numerous individual flowers) are especially favored by butterflies. Each flower has a long, slender floral tube, accessible to the long, thin butterfly proboscis.

Bird- and Bat-Pollinated Flowers

In North America, the most well-known bird pollinators are the hummingbirds. These tiny animals have good eyesight but do not have a well-developed sense of smell. Like moths, they hover when they feed. Typical flowers pollinated by hummingbirds are red, with a slender floral tube and margins that are curved back and out of the way. And although they produce copious amounts of nectar, the flowers have little odor. As a hummingbird feeds on nectar with its long, thin beak, its head comes into contact with the stamens and pistil (Fig. 27B*a*).

Bats are adapted to gathering food in various ways, including feeding on the nectar and pollen of plants. Bats are nocturnal and have an acute sense of smell. Those that are pollinators also have keen vision and a long, extensible, bristly tongue. Typically, bat-pollinated flowers open only at night and are light-colored or white. They have a strong, musty smell similar to the odor that bats produce to attract one another. The flowers are generally large and sturdy and are able to hold up when a bat inserts part of its head to reach the nectar. While the bat is at the flower, its head is dusted with pollen (Fig. 27B*b*).

Coevolution

There are many examples of plant and animal coevolution, but how did this coevolution come about? Some 200 million years ago, when seed plants were just beginning to evolve and insects were not as diverse as they are today, wind alone was used to carry pollen. Wind pollination, however, is a hit-or-miss affair. Perhaps beetles feeding on vegetative leaves were the first insects to carry pollen directly from plant to plant by chance. This use of animal motility to achieve cross-fertilization no doubt resulted in the evolution of flowers, which have features, such as the production of nectar, to attract pollinators. Then, if beetles developed the habit of feeding on flowers, other features, such as the protection of ovules within ovaries, may have evolved.

As cross-fertilization continued, more and more flower variations likely developed, and pollinators became increasingly adapted to specific angiosperm species. Today, there are some 240,000 species of flowering plants and over 900,000 species of insects. This diversity suggests that the success of angiosperms has contributed to the success of insects, and vice versa.

a. b.

FIGURE 27B More pollinators.
a. *Hummingbird-pollinated flowers are curved back, allowing the bird to insert its beak to reach the rich supply of nectar. While doing this, the bird's forehead and other body parts touch the reproductive structures.* **b.** *Bat-pollinated flowers are large, sturdy flowers that can take rough treatment. Here the head of the bat is positioned so that its bristly tongue can lap up nectar.*

27.2 Seed Development

Development of the embryo within the seed is the next event in the life cycle of the angiosperm. Plant growth and development involves cell division, cell elongation, and differentiation of cells into tissues and then organs. Development is a programmed series of stages from a simple to a more complex form. Cellular differentiation, or specialization of structure and function, occurs as development proceeds.

Stages of Eudicot Development

Figure 27.7 shows the stages of development for a eudicot embryo.

Zygote and Proembryo Stages

1 Immediately after double fertilization, we can make out the zygote and the endosperm. The zygote (true green) is small with dense cytoplasm. 2 The zygote divides repeatedly in different planes, forming several cells called a proembryo. Also present is an elongated structure called a suspensor. The suspensor transfers and produces nutrients from the endosperm and these allow the embryo to grow.

Globular Stage

3 During the globular stage, the proembryo is largely a ball of cells. The root-shoot axis of the embryo is already established at this stage because the embryonic cells near the suspensor will become a root, while those at the other end will ultimately become a shoot.

The outermost cells of the plant embryo will become dermal tissue. These cells divide with their cell plate perpendicular to the surface; therefore, they produce a single outer layer of cells. Recall that dermal tissue protects the plant from desiccation and includes the stomata, which open and close to facilitate gas exchange and minimize water loss.

The Heart Stage and Torpedo Stage Embryos

4 The embryo has a heart shape when the **cotyledons,** or seed leaves, appear because of local, rapid cell division. 5 As the embryo continues to enlarge and elongate, it takes on a torpedo shape. Now the root and shoot apical meristems are distinguishable. The shoot apical meristem is responsible for aboveground growth, and the root apical meristem is responsible for underground growth. Ground meristem, which gives rise to the bulk of the embryonic interior, is also now present.

The Mature Embryo

6 In the mature embryo, the epicotyl is the portion between the cotyledon(s) that contributes to shoot development. The plumule is found at the tip of the epicotyl and consists of the shoot tip and a pair of small leaves. The hypocotyl is the portion below the cotyledon(s). It contributes to stem development and terminates in the radicle or embryonic root.

The cotyledons are quite noticeable in a eudicot embryo and may fold over. Procambium is visible at the core of the embryo and is destined to form the future vascular tissue responsible for water and nutrient transport.

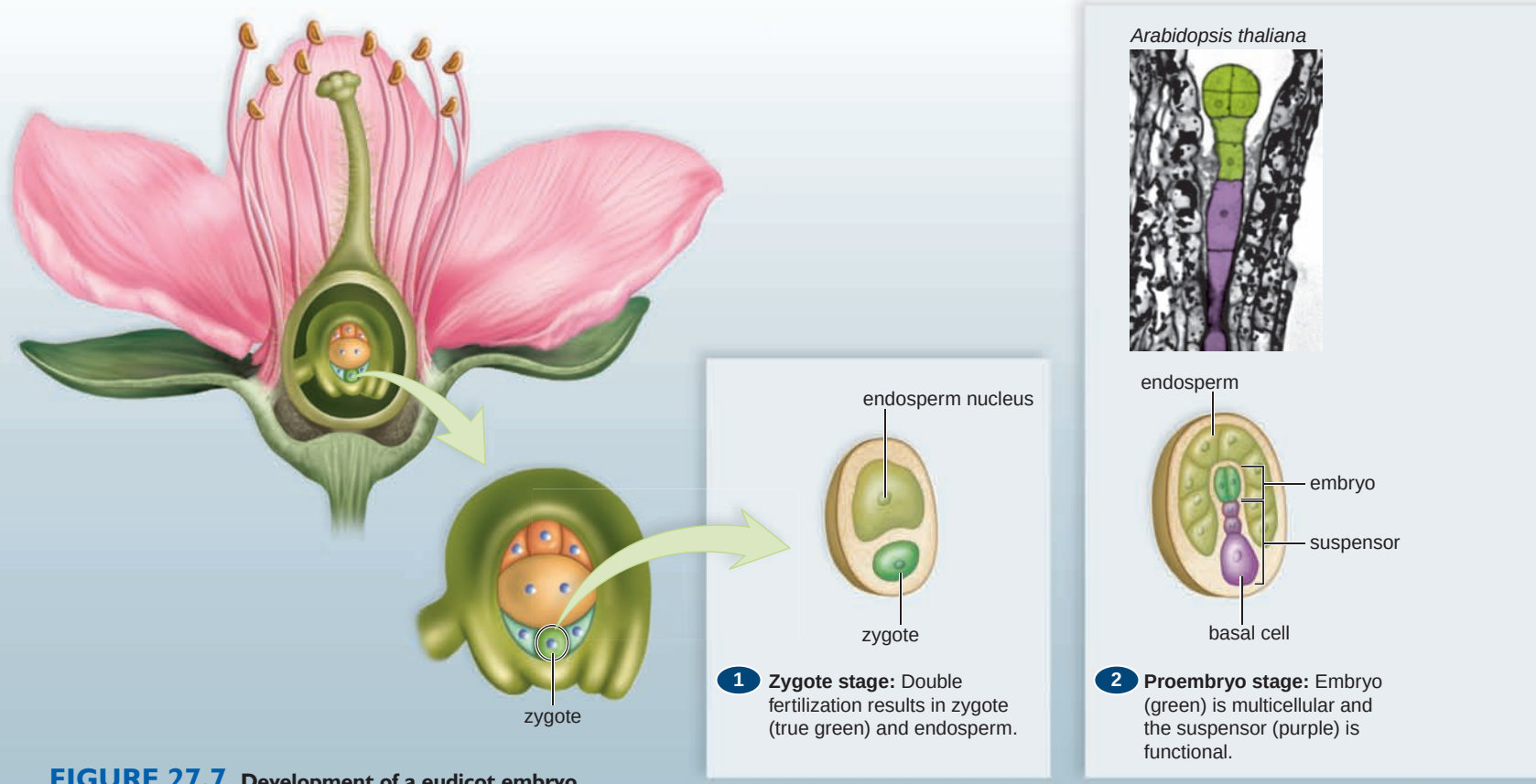


FIGURE 27.7 **Development of a eudicot embryo.**

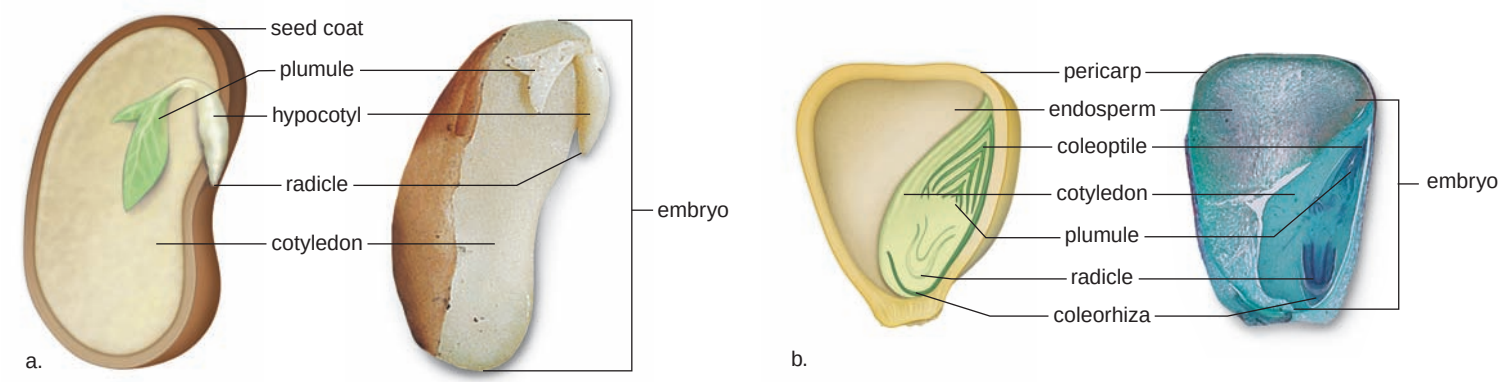


FIGURE 27.8 Monocot versus eudicot.

a. In a bean seed (eudicot), the endosperm has disappeared; the bean embryo's cotyledons take over food storage functions. The hypocotyl becomes the shoot system, which will include the plumule (first leaves). The radicle becomes the root system. **b.** The corn kernel (monocot) has endosperm that is still present at maturity. The coleoptile is a protective sheath for the shoot system; the coleorhiza similarly protects the future root system. The term pericarp is explained in the next section.

As the embryo develops, the integuments of the ovule become the seed coat. The seed coat encloses and protects the embryo and its food supply.

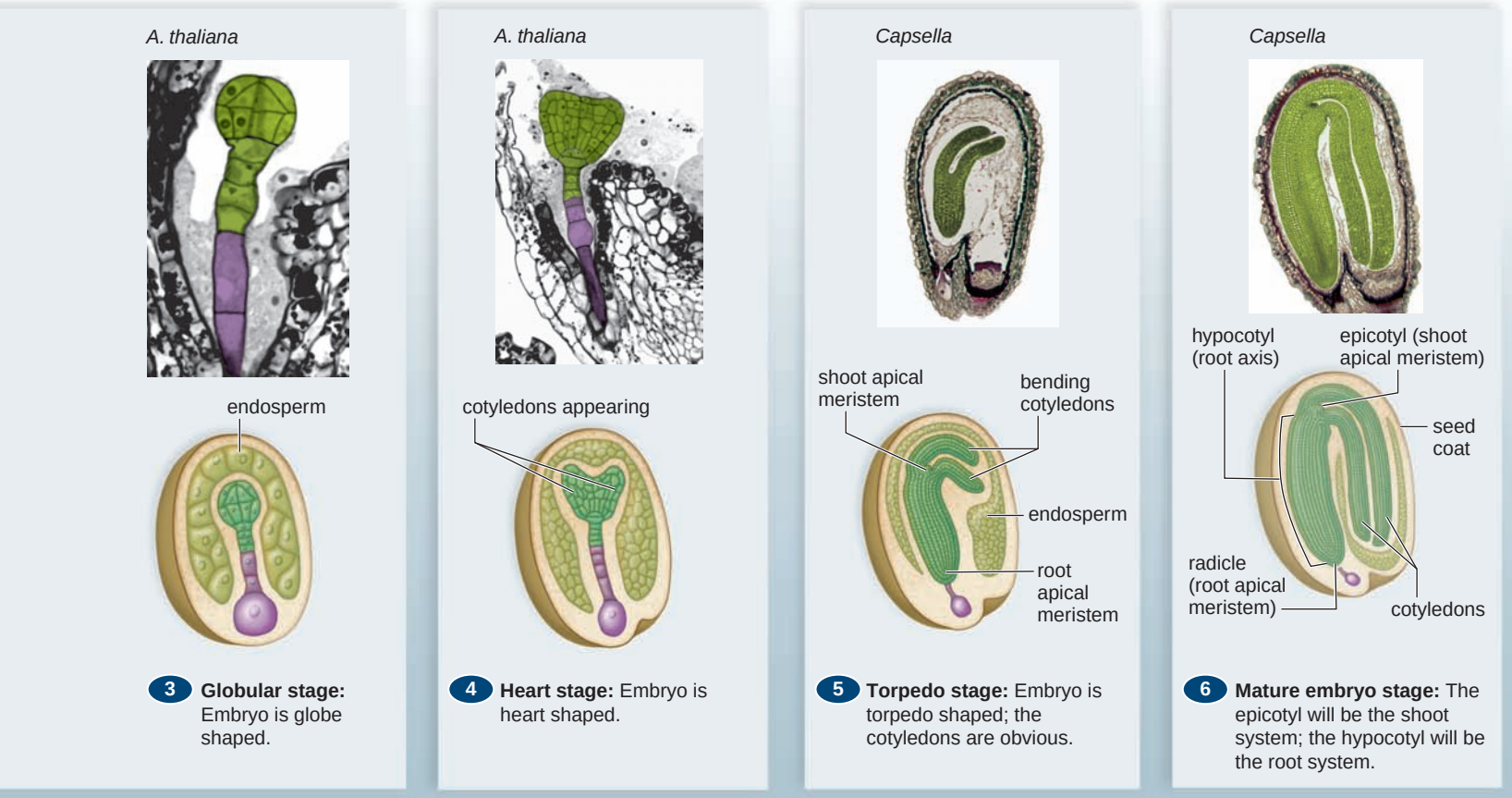
Monocots Versus Eudicot Seeds

Monocots, unlike eudicots, have only one cotyledon. Another important difference between monocots and eudicots is the manner in which nutrient molecules are stored in the seed. In monocots, the cotyledon, in addition to storing certain nutrients, absorbs other nutrient molecules from the endosperm and passes them to the embryo. In eudicots, the cotyledons usually store all the nutrient molecules that the embryo uses. Therefore, in Figure 27.7 we can see that the endosperm seemingly disappears. Actually, it has been taken up by the two cotyledons.

Figure 27.8 contrasts the structure of a bean seed (eudicot) and a corn kernel (monocot). The size of seeds may vary from the dust-sized seeds of orchids to the 27-kg seed of the double coconut.

Check Your Progress 27.2

1. Identify the origin of each of the three parts of a seed.
2. Why are both the seed coat and the embryo 2n?
3. What are cotyledons and what role do they play?

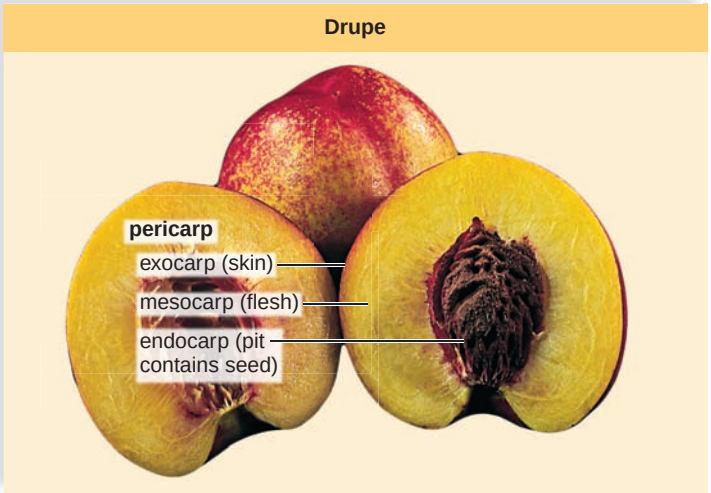


3 Globular stage: Embryo is globe shaped.

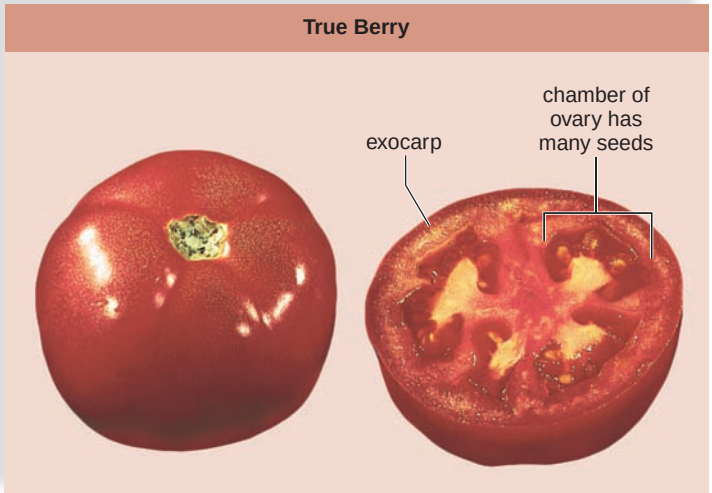
4 Heart stage: Embryo is heart shaped.

5 Torpedo stage: Embryo is torpedo shaped; the cotyledons are obvious.

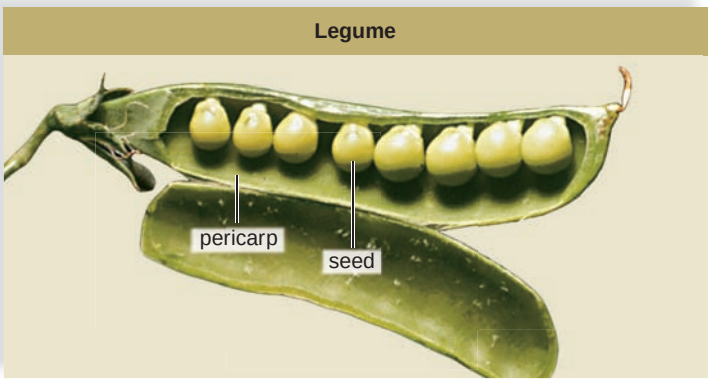
6 Mature embryo stage: The epicotyl will be the shoot system; the hypocotyl will be the root system.



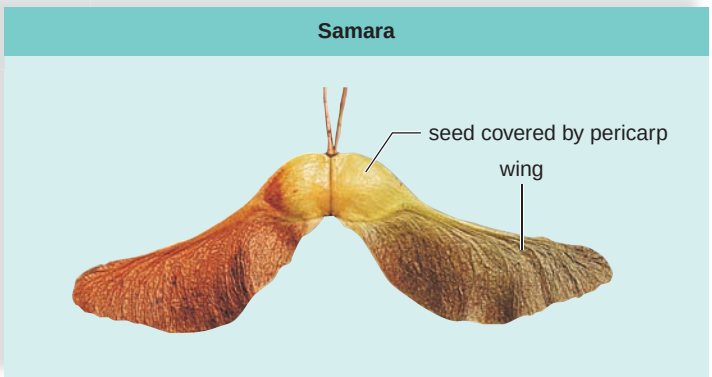
a. A drupe is a fleshy fruit with a pit containing a single seed produced from a simple ovary.



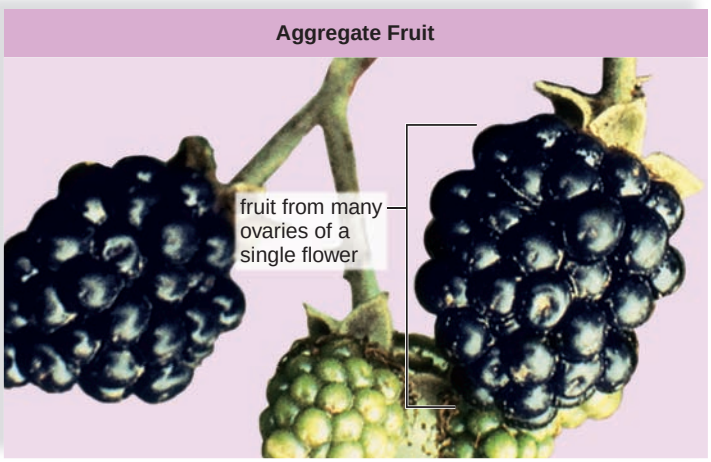
b. A berry is a fleshy fruit having seeds and pulp produced from a compound ovary.



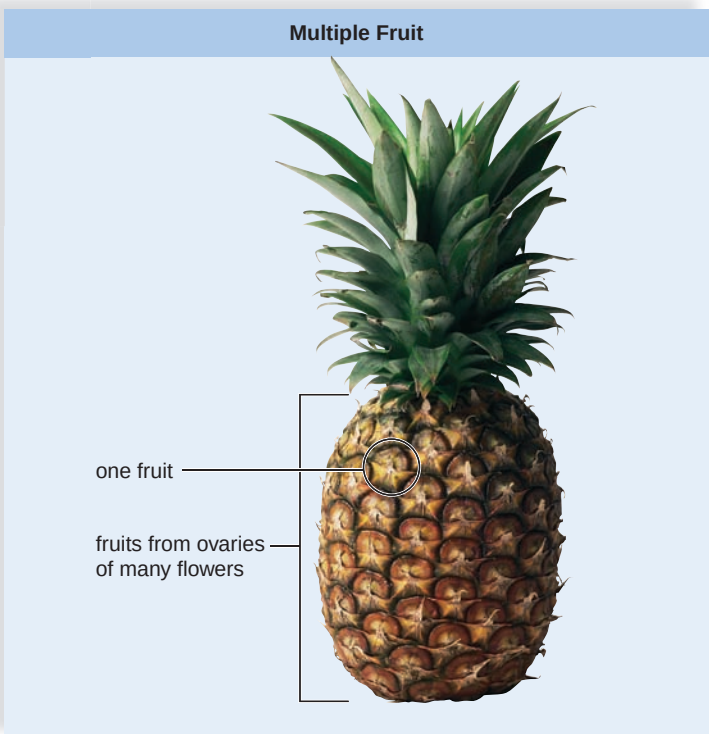
c. A legume is a dry dehiscent fruit produced from a simple ovary.



d. A samara is a dry indehiscent fruit produced from a simple ovary.



e. An aggregate fruit contains many fleshy fruits produced from simple ovaries of the same flower.



f. A multiple fruit contains many fused fruits produced from simple ovaries of individual flowers.

FIGURE 27.9 Fruits.

a. A peach is a drupe. **b.** A tomato is a true berry. **c.** A pea is a legume. **d.** The fruit of a maple tree is a samara. **e.** A blackberry is an aggregate fruit. **f.** A pineapple is a multiple fruit.

27.3 Fruit Types and Seed Dispersal

Most of us have to become accustomed to the botanical definition of a fruit (Table 27.1). A **fruit** is a mature ovary and sometimes, in addition, other flower parts, such as the receptacle. This means that pea pods, tomatoes, and what is usually called winged maple seeds are actually fruits (Fig. 27.9). Fruits protect and help disperse seeds. Some fruits are better at one of these functions than the other. The fruit of a peach protects the seed well, but the pit may make it difficult for germination to occur. Peas easily escape from pea pods, but once they are free, they are protected only by the seed coat.

Kinds of Fruits

Fruits can be simple or compound (Fig. 27.9). A *simple fruit* is derived from a single ovary that can have one or several chambers (Fig. 27.9*a–d*). A *compound fruit* is derived from several groups of ovaries (Fig. 27.9*e–f*). If a single flower had many ovaries, as in a blackberry, then the fruit is an *aggregate* one (Fig. 27.9*e*). In contrast, a pineapple comes from many individual ovaries. Because the flowers had only one receptacle, the ovaries fused to form a large, *multiple fruit* (Fig. 27.9*f*).

As a fruit develops, the ovary wall thickens to become the pericarp, which can have as many as three layers: exocarp, mesocarp, and endocarp.

- The exocarp forms the outermost skin of a fruit.
- The mesocarp is often the fleshy tissue between the exocarp and endocarp of the fruit.
- The endocarp serves as the boundary around the seed(s). The endocarp may be hard, as in peach pits, or papery, as in apples.

Some fruits such as legumes and cereal grains of wheat, rice, and corn are *dry fruits.* The fruits of grains can be mistaken for seeds because a dry pericarp adheres to the seed within. Legumes such as the pea pod (Fig. 27.9*c*) are dehiscent because they split open when ripe. Grains are indehiscent—they don't split open. Humans gather grains before they are released from the plant and then process them to acquire their nutrients. You might be more familiar with fleshy fruits, such as the peach and tomato. In these fruits, the mesocarp is well developed.

TABLE 27.1

Fruit Classification Based on Composition and Texture

Composition (based on type and arrangement of ovaries and flowers)
Simple: develops from a simple ovary or compound ovary
Compound: develops from a group of ovaries
Aggregate: ovaries are from a single flower on one receptacle
Multiple: ovaries are from separate flowers on a common receptacle
Texture (based on mature pericarp)
Fleshy: the entire pericarp or portions of it are soft and fleshy at maturity
Dry: the pericarp is papery, leathery, or woody when the fruit is mature
Dehiscent: the fruit splits open when ripe
Indehiscent: the fruit does not split open when ripe

Dispersal of Fruits

Many dry fruits are dispersed by wind. Woolly hairs, plumes, and wings are all adaptations for this type of dispersal. The somewhat heavier dandelion fruit uses a tiny "parachute" for dispersal. Milkweed pods split open to release seeds that float away on puffy white threads. The winged fruit of a maple tree has been known to travel up to 10 km from its parent. Other fruits depend on animals for dispersal.

Dispersal by Animals

When ripe, *fleshy colorful fruits,* such as peaches and cherries, often attract animals and provide them with food (Fig. 27.10*a*). Their hard endocarp protects the seed so it can pass through the digestive system of an animal and remain unharmed. As the flesh of a tomato is eaten, the small size of the seeds and the slippery seed coat means that tomato seeds rarely get crushed by the teeth of animals. The seeds swallowed by birds and mammals are defecated (passed out of the digestive tract with the feces) some distance from the parent plant. Squirrels and other animals that gather seeds and fruits bury them some distance away and may even forget where they have been stored. The hooks and spines of clover, bur, and cocklebur attach a dry fruit to the fur of animals and the clothing of humans (Fig. 27.10*b*).

a.

b.

FIGURE 27.10

Fruit dispersal by animals.

a. When birds eat fleshy fruits, seeds pass through their digestive system. **b.** Burdock, a dry fruit, clings to the fur of animals.

Seed Germination

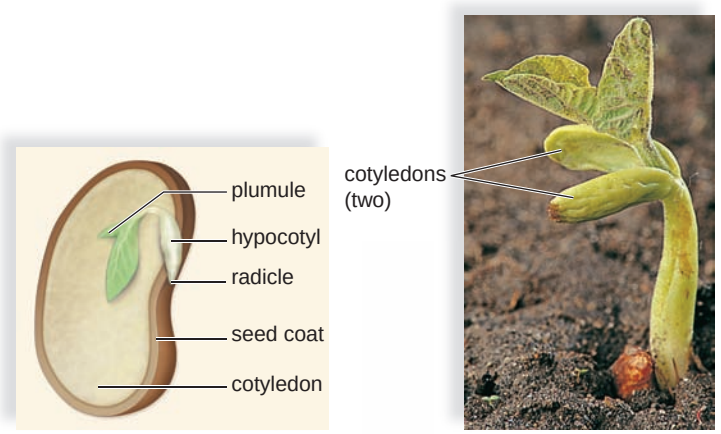
Following dispersal, if conditions are right, seeds may **germinate** to form a seedling. Germination doesn't usually take place until there is sufficient water, warmth, and oxygen to sustain growth. These requirements help ensure that seeds do not germinate until the most favorable growing season has arrived. Some seeds do not germinate until they have been dormant for a period of time. For seeds, *dormancy* is the time during which no growth occurs, even though conditions may be favorable for growth. In the temperate zone, seeds often have to be exposed to a period of cold weather before dormancy is broken. Fleshy fruits (e.g., apples, pears, oranges, and tomatoes) contain inhibitors so that germination does not occur while the fruit is still on the plant. For seeds to take up water, bacterial action and even fire may be needed. Once water enters, the seed coat bursts and the seed germinates.

If the two cotyledons of a bean seed are parted, the rudimentary plant with immature leaves is exposed (Fig. 27.11*a*). As the eudicot seedling starts to form, the root emerges first. The shoot is hook-shaped to protect the immature leaves as they emerge from the soil. The cotyledons provide the new seedlings with enough energy for the stem to straighten and the leaves to grow. As the mature leaves of the plant begin photosynthesizing, the cotyledons shrivel up.

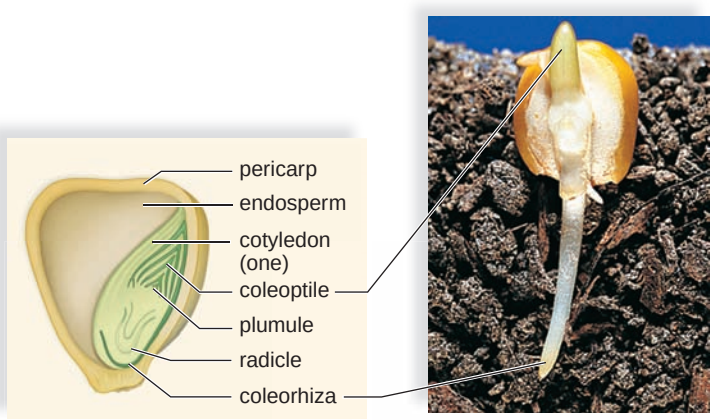
A corn kernel is actually a fruit, and therefore its outer covering is the pericarp and seed coat combined (Fig. 27.11*b*). Inside is the single cotyledon. Also, the immature leaves and the radicle are covered, respectively, by a coleoptile and a coleorhiza. These sheaths are discarded as the root grows directly downward into the soil and the shoot of the seedling begins to grow directly upward. This completes our discussion of sexual reproduction in flowering plants.

Check Your Progress 27.3

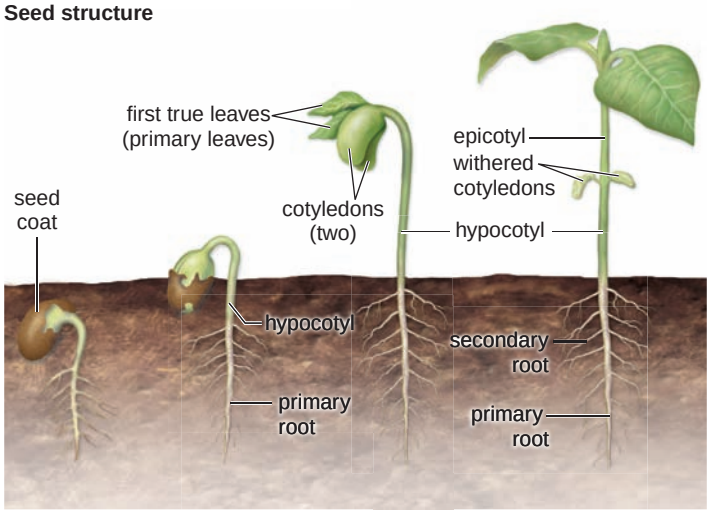
1. How does a dry fruit differ in structure and dispersal from a fleshy fruit?
2. Contrast how a eudicot seedling and a monocot seedling protect the first true leaves.



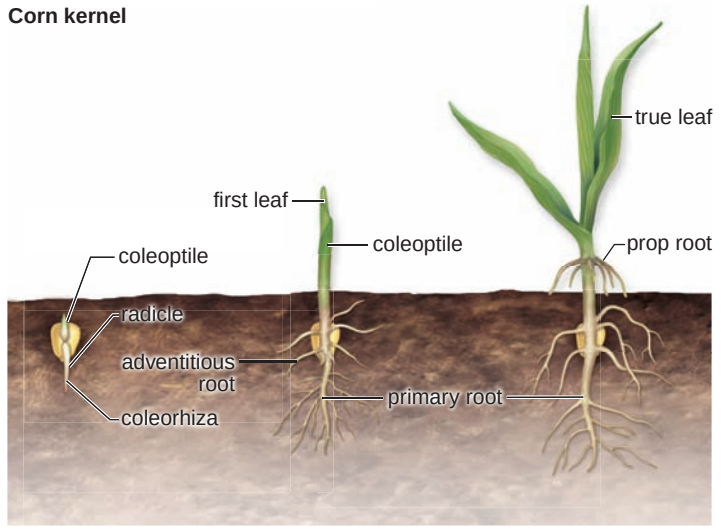
Seed structure



Corn kernel



Bean germination and growth
a.



Corn germination and growth
b.

FIGURE 27.11 Eudicot and monocot seed structure and germination.

a. Bean (eudicot) seed structure and germination. **b.** Corn (monocot) kernel structure and germination.

27.4 Asexual Reproductive Strategies

Asexual reproduction is the production of an offspring identical to a single parent. Asexual reproduction is less complicated in plants because pollination and seed production is not required. Therefore, it can be advantageous when the parent is already well adapted to a particular environment and the production of genetic variations is not an apparent necessity.

Figure 27.12 features a strawberry plant that has produced a stolon. **Stolons** are horizontal stems that can be seen because they run aboveground. As you know, the nodes of stems are regions where new growth can occur. In the case of stolons, a new shoot system appears above the node, and a new root system appears below the node. The larger plant on the left is the parent plant, and the smaller plant on the right is the asexual offspring that has arisen at a node. The characteristics of new offspring produced by stolons are identical to those of the parent plant.

Rhizomes are underground stems that produce new plants asexually. Irises are examples of plants that have no aboveground stem because their main stem is a rhizome that grows horizontally underground. As with stolons, new plants arise at the nodes of a rhizome. White potatoes are expanded portions of a rhizome branch, and each eye is a bud that will produce a new potato plant if it is planted with a portion of the swollen tuber. Sweet potatoes are modified roots; they can be propagated by planting sections of the root.

You may have noticed that the roots of some fruit trees, such as cherry and apple trees, produce "suckers," small plants that can be used to grow new trees. In addition, pineapple, sugarcane, azalea, gardenia, and many other food and ornamental plants have been propagated from stem cuttings. In these plants, a cut stem will automatically produce roots. The discovery that the plant hormone auxin can cause roots to develop has expanded the list of plants that can be propagated from stem cuttings.

Tissue Culture of Plants

Tissue culture is the growth of a tissue in an artificial liquid or solid culture medium. Somatic embryogenesis, meristem tissue culture, and anther tissue culture are three methods of cloning plants due to the ability of plants to grow from single cells. Many plant cells are **totipotent,** which means that each one has the genetic capability of becoming an entire plant.

During *somatic embryogenesis,* hormones are added to the medium and they cause leaf or other tissue cells to generate small masses of cells, which can be genetically engineered before being allowed to become many new identical plants.

FIGURE 27.12

Asexual reproduction in plants.

Meristem tissues at nodes can generate new plants, as when the stolons of strawberry plants, *Fragaria*, give rise to new plants.

Thousands of little "plantlets" can be produced by using this method of plant tissue culture (Fig. 27.13). Many important crop plants, such as tomato, rice, celery, and asparagus, as well as ornamental plants such as lilies, begonias, and African violets, have been produced using somatic embryogenesis. Plants generated from somatic embryos are not always genetically identical clones. They can vary because of mutations that arise spontaneously during the production process. These mutations, called *somaclonal variations*, are another way to produce new plants with desirable traits. Somatic embryos can be encapsulated in hydrated gel, creating artificial "seeds" that can be shipped anywhere.

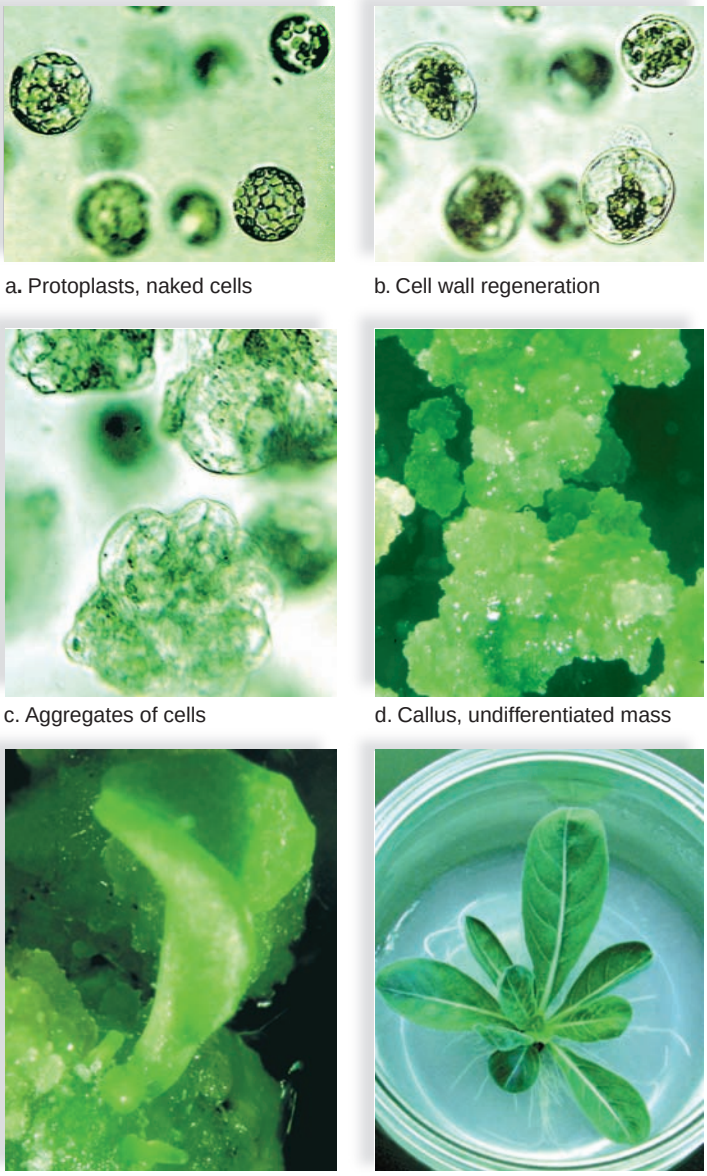


FIGURE 27.13 Asexual reproduction through tissue culture.

a. When plant cell walls are removed by digestive enzyme action, the result is naked cells, or protoplasts. **b.** Regeneration of cell walls and the beginning of cell division. **c.** Cell division produces aggregates of cells. **d.** An undifferentiated mass, called a callus. **e.** Somatic cell embryos such as this one appear. **f.** The embryos develop into plantlets that can be transferred to soil for growth into adult plants.

FIGURE 27.14 Producing whole plants from meristem tissue.

Meristem tissue can also be used as a source of plant cells. In this case, the resulting products are clonal plants that always have the same traits. In Figure 27.14, culture flasks containing meristematic orchid tissue are rotated under lights. If the correct proportions of hormones are added to the liquid medium, many new shoots develop from a single shoot tip. When these are removed, more shoots form. Another advantage to producing identical plants from meristem tissue is that the plants are virus-free. (The presence of plant viruses weakens plants and makes them less productive.)

Anther tissue culture is a technique in which the haploid cells within pollen grains are cultured in order to produce haploid plantlets. Conversely, a diploid (2n) plantlet can be produced if chemical agents, to encourage chromosomal doubling, are added to the anther culture. Anther tissue culture is a direct way to produce plants that are certain to have the same characteristics.

Cell Suspension Culture

A technique called **cell suspension culture** allows scientists to extract chemicals (i.e., secondary metabolites) from plant cells, which may have been genetically modified (see page 255), in high concentration and without having to overcollect wild-type plants growing in their natural environments. These cells produce the same chemicals the entire plant produces. For example, cell suspension cultures of *Cinchona ledgeriana* produce quinine, which is used to treat leg cramping, a major symptom of malaria. And those of several *Digitalis* species produce digitalis, digitoxin, and digoxin, which are useful in the treatment of heart disease.

Check Your Progress 27.4

1. What are the possible benefits of asexual reproduction?
2. How are new plants produced asexually in the wild?
3. How are new plants produced asexually in the laboratory?

Connecting the Concepts

Life as we know it would not be possible without vascular plants, and specifically flowering plants, which now dominate the biosphere. *Homo sapiens* evolved in a world dominated by flowering plants and therefore does not know a world without them. The earliest humans were mostly herbivores; they relied on foods they could gather for survival—fruits, nuts, seeds, tubers, roots, and so forth. Plants also provided protection from the environment, offering shelter from heavy rains and noonday sun. Later on, human civilizations could not have begun without the development of agriculture. The majority of the world's population still relies primarily on three flowering plants—corn, wheat, and rice—for the majority of its sustenance. Sugar, coffee, spices of all kinds, cotton, rubber, and tea are plants that have even promoted wars because of their importance to a country's economy. Although we now live in an industrialized society, we are still dependent on plants and have put them to even more uses. To take a couple of examples, plants produce substances needed to lubricate the engines of supersonic jets and to make cellulose acetate for films. We grow them not only for the products they produce, but also for their simple beauty. For millions of urban dwellers, plants are their major contact with the natural world.

Most people fail to appreciate the importance of plants, but plants may be even more critical to our lives today than they were to our early ancestors on the African plains. Currently, half of all pharmaceutical drugs have their origin in plants. The world's major drug companies are engaged in a frantic rush to collect and test plants from the rain forests for their drug-producing potential. Why the rush? Because the rain forests may be gone before all the possible cures for cancer, AIDS, and other killers have been found. Wild plants cannot only help cure human ills, but they can also serve as a source of genes for improving the quality of the plants that support our way of life.

summary

27.1 Sexual Reproductive Strategies

Flowering plants exhibit an alternation of generations life cycle. Flowers borne by the sporophyte produce microspores and megaspores by meiosis. Microspores develop into a male gametophyte, and megaspores develop into the female gametophyte. The gametophytes produce gametes by mitotic cell division. Following fertilization, the sporophyte is enclosed within a seed covered by fruit.

The flowering plant life cycle is adapted to a land existence. The microscopic gametophytes are protected from desiccation by the sporophyte; the pollen grain has a protective wall and fertilization does not require external water. The seed has a protective seed coat, and seed germination does not occur until conditions are favorable.

A typical flower has several parts: Sepals, which are usually green in color, form an outer whorl; petals, often colored, are the next whorl; and stamens, each having a filament and anther, form a whorl around the base of at least one carpel. The carpel, in the center of a flower, consists of a stigma, style, and ovary. The ovary contains ovules.

Each ovule contains a megaspore mother cell, which divides meiotically to produce four haploid megaspores, only one of which survives. This megaspore divides mitotically to produce the female gametophyte (embryo sac), which usually has seven cells. One is an egg cell and another is a central cell with two polar nuclei.

The anthers contain microspore mother cells, each of which divides meiotically to produce four haploid microspores. Each of these divides mitotically to produce a two-celled pollen grain. One cell is the tube cell, and the other is the generative cell. The generative cell later divides mitotically to produce two sperm cells. The pollen grain is the male gametophyte. After pollination, the pollen grain germinates, and as the pollen tube grows, the sperm cells travel to the embryo sac. Pollination is simply the transfer of pollen from anther to stigma.

Flowering plants experience double fertilization. One sperm nucleus unites with the egg nucleus, forming a 2n zygote, and the other unites with the polar nuclei of the central cell, forming a 3n endosperm cell.

After fertilization, the endosperm cell divides to form multicellular endosperm. The zygote becomes the sporophyte embryo. The ovule matures into the seed (its integuments become the seed coat). The ovary becomes the fruit.

27.2 Seed Development

As the ovule is becoming a seed, the zygote is becoming an embryo. After the first several divisions, it is possible to discern the embryo and the suspensor. The suspensor attaches the embryo to the ovule and supplies it with nutrients. The eudicot embryo becomes first heart-shaped and then torpedo-shaped. Once you can see the two cotyledons, it is possible to distinguish the shoot tip and the root tip, which contain the apical meristems. In eudicot seeds, the cotyledons frequently take up the endosperm.

27.3 Fruit Types and Seed Dispersal

The seeds of flowering plants are enclosed by fruits. There are different types of fruits. Simple fruits are derived from a single ovary (which can be simple or compound). Some simple fruits are fleshy, such as a peach or an apple. Others are dry, such as peas, nuts, and grains. Compound fruits consist of aggregate fruits, which develop from a number of ovaries of a single flower, and multiple fruits develop from a number of ovaries of separate flowers.

Flowering plants have several ways to disperse seeds. Seeds may be blown by the wind, attached to animals that carry them away, eaten by animals that defecate them some distance away, or adapted to water transport.

Prior to germination, you can distinguish a bean (eudicot) seed's two cotyledons and plumule, which is the shoot that bears leaves. Also present are the epicotyl, the hypocotyl, and the radicle. In a corn kernel (monocot), the endosperm, the cotyledon, the plumule, and the radicle are visible.

27.4 Asexual Reproductive Strategies

Many flowering plants reproduce asexually, as when the nodes of stems (either aboveground or underground) give rise to entire plants, or when roots produce new shoots.

Somatic embryogenesis is the development of adult plants from protoplasts in tissue culture. Micropropagation, the production of clonal plants as a result of meristem culture in particular, is now a commercial venture. Flower meristem culture results in somatic embryos that can be packaged in gel

for worldwide distribution. Anther culture results in homozygous plants that express recessive genes. Leaf, stem, and root culture can result in cell suspensions that allow plant chemicals to be produced in large tanks.

understanding the terms

anther 495
calyx 495
carpel 495
cell suspension culture 506
coevolution 498
corolla 495
cotyledon 500
double fertilization 497
embryo sac 497
endosperm 497
female gametophyte 497
filament 495
flower 494
fruit 503
germinate 504
male gametophyte 496
megaspore 494
microspore 494
ovary 495
ovule 495
petal 495
pollen grain 496
pollination 497
rhizome 505
seed 494
sepal 495
stamen 495
stigma 495
stolon 505
style 495
tissue culture 505
totipotent 505

Match the terms to these definitions:

a. _____ Flower structure consisting of an ovary, a style, and a stigma.
b. _____ Flowering plant structure consisting of one or more ripened ovaries that usually contain seeds.
c. _____ The gametophyte that produces an egg; an embryo sac in flowering plants.
d. _____ Mature ovule that contains an embryo, with stored food enclosed in a protective coat.
e. _____ Mature male gametophyte in seed plants.

reviewing this chapter

1. Draw a diagram of alternation of generations in flowering plants, and indicate which structures are protected by the sporophyte. Explain. 494
2. Draw a diagram of a flower, and name the parts. 494–95
3. Describe the development of a male gametophyte, from the microsporocyte to the production of sperm. 496
4. Describe the development of a female gametophyte, from the megasporocyte to the production of an egg. 496–97
5. What is the difference between pollination and fertilization? Why doesn't fertilization require any external water? What is double fertilization? 497–99
6. Describe methods of cross-pollination, including the use of animal pollinators. 498–99
7. Describe the sequence of events as a eudicot zygote becomes an embryo enclosed within a seed. 500–501
8. Distinguish between simple dry fruits and simple fleshy fruits. Give an example of each type. What is an aggregate fruit? A multiple fruit? 502–3
9. Name several mechanisms of seed and/or fruit dispersal. 503
10. What are the requirements for seed germination? Contrast the germination of a bean seed with that of a corn kernel. 504
11. In what ways do plants ordinarily reproduce asexually? What is the importance of totipotency with regard to tissue culture? 505–6

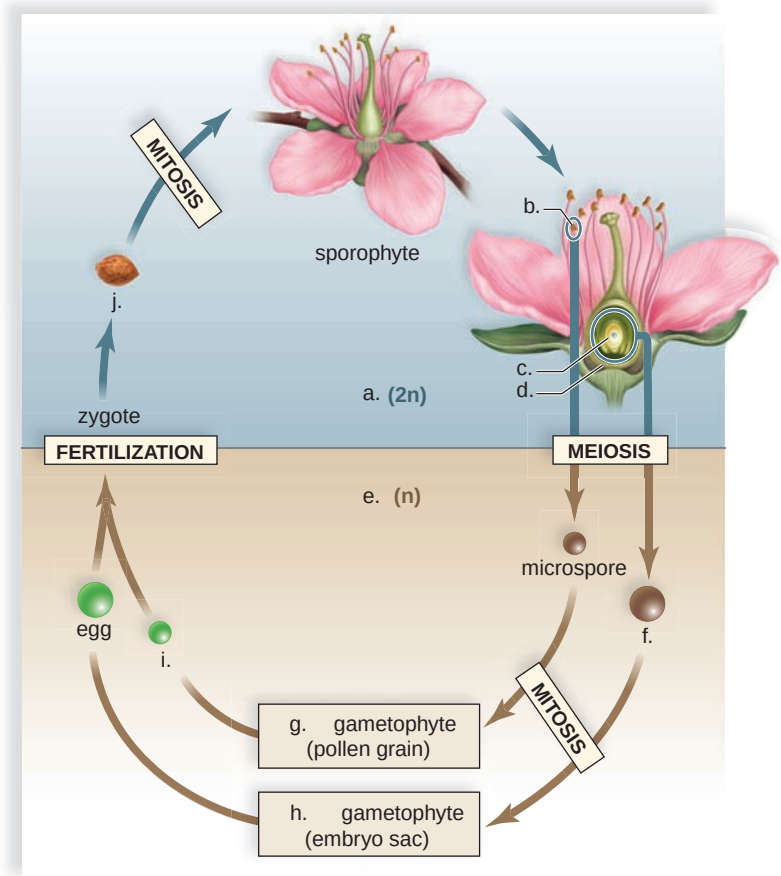
testing yourself

Choose the best answer for each question.

1. In plants,
   a. a gamete becomes a gametophyte.
   b. a spore becomes a sporophyte.
   c. both sporophyte and gametophyte produce spores.
   d. only a sporophyte produces spores.
   e. Both a and b are correct.
2. The flower part that contains ovules is the
   a. carpel.
   b. stamen.
   c. sepal.
   d. petal.
   e. seed.
3. The megaspore and the microspore mother cells
   a. both produce pollen grains.
   b. both divide meiotically.
   c. both divide mitotically.
   d. produce pollen grains and embryo sacs, respectively.
   e. All of these are correct.
4. A pollen grain is
   a. a haploid structure.
   b. a diploid structure.
   c. first a diploid and then a haploid structure.
   d. first a haploid and then a diploid structure.
   e. the mature gametophyte.
5. Which of these pairs is incorrectly matched?
   a. polar nuclei—plumule
   b. egg and sperm—zygote
   c. ovule—seed
   d. ovary—fruit
   e. stigma—carpel
6. Which of these is not a fruit?
   a. walnut
   b. pea
   c. green bean
   d. peach
   e. All of these are fruits.
7. Animals assist with
   a. pollination and seed dispersal.
   b. control of plant growth and response.
   c. translocation of organic nutrients.
   d. asexual propagation of plants.
   e. germination of seeds.
8. A seed contains
   a. a seed coat.
   b. an embryo.
   c. stored food.
   d. cotyledon(s).
   e. All of these are correct.
9. Which of these is mismatched?
   a. plumule—leaves
   b. cotyledon—seed leaf
   c. epicotyl—root
   d. pericarp—corn kernel
   e. carpel—ovule
10. Which of these is not a common procedure in the tissue culture of plants?
    a. shoot tip culture for the purpose of micropropagation
    b. meristem culture for the purpose of somatic embryos
    c. leaf, stem, and root culture for the purpose of cell suspension cultures
    d. culture of hybridized mature plant cells

11. In the life cycle of flowering plants, a microspore develops into
    a. a megaspore.
    b. a male gametophyte.
    c. a female gametophyte.
    d. an ovule.
    e. an embryo.
12. Carpels
    a. are the female part of a flower.
    b. contain ovules.
    c. are the innermost part of a flower.
    d. may be absent in a flower.
    e. All of these are correct.
13. Which of these is part of a male gametophyte?
    a. synergid cells
    b. the central cell
    c. polar nuclei
    d. a tube nucleus
    e. antipodal cells
14. Bat-pollinated flowers
    a. are colorful.
    b. are open throughout the day.
    c. are strongly scented.
    d. have little scent.
    e. Both b and c are correct.
15. Heart, torpedo, and globular refer to
    a. embryo development.
    b. sperm development.
    c. female gametophyte development.
    d. seed development.
    e. Both b and d are correct.
16. Fruits
    a. nourish embryo development.
    b. help with seed dispersal.
    c. signal gametophyte maturity.
    d. attract pollinators.
    e. signal when they are ripe.
17. Asexual reproduction in flowering plants
    a. is unknown.
    b. is a rare event.
    c. is common.
    d. occurs in all plants.
    e. is no fun.
18. Plant tissue culture takes advantage of
    a. a difference in flower structure.
    b. sexual reproduction.
    c. gravitropism.
    d. phototropism.
    e. totipotency.
19. In plants, meiosis directly produces
    a. new xylem.
    b. phloem.
    c. spores.
    d. egg.
    e. sperm.

20. Label this diagram of alternation of generations in flowering plants.



thinking scientifically

1. You notice that a type of wasp has been visiting a flower type in your garden. What web/library research would allow you to hypothesize that this wasp is a pollinator for this flower type?
2. The pollinator for a very rare plant has become extinct. **a.** What laboratory technique would you use to prevent the plant from also becoming extinct? **b.** How might you improve the hardiness of the plant?

Biology website

The companion website for *Biology* provides a wealth of information organized and integrated by chapter. You will find practice tests, animations, videos, and much more that will complement your learning and understanding of general biology.

http://www.mhhe.com/maderbiology10

part VI

Animal Evolution and Diversity

In his book On the Origin of Species, *Charles Darwin says that, while the planet Earth cycles year after year around the sun, "endless forms most beautiful and most wonderful" have appeared and will keep on appearing. This phraseology can certainly be applied to the evolution of animals, whose variety seems without bounds. The fossil record even reveals a myriad of animals that are extinct today, as are the dinosaurs. The search for food, shelter, and mates under a variety of environmental conditions can explain why the diversity of animals is so great.*

Despite their diversity, evolution from a common ancestor has provided animal life with an unbroken thread of unity. At the biosphere level, animals are heterotrophic consumers that require a constant supply of food by way of autotrophs. At the organismal level, their eukaryotic cells usually form tissues and organs with specialized functions. At the molecular level, animals share a common chemistry, including a genetic code that we now know reveals how the many groups of animals are related. This part concentrates on the characteristics of animals, their origin, and evolution as revealed by molecular genetics.

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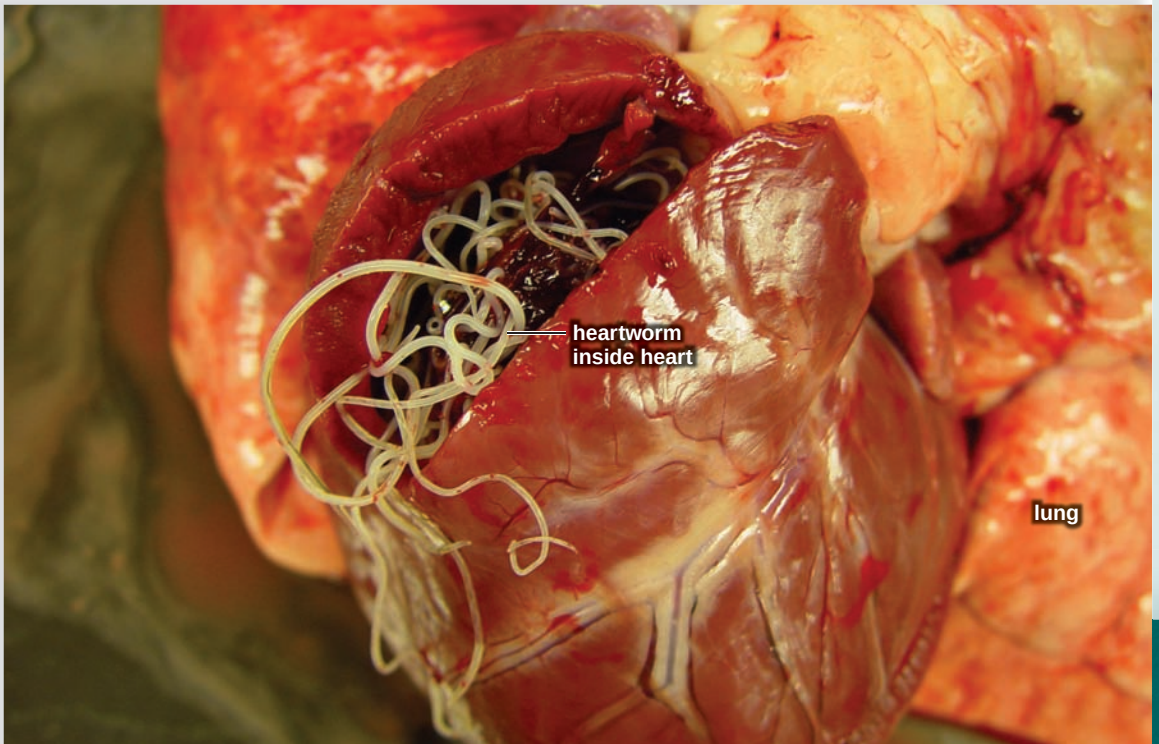
Invertebrate Evolution

When we think of animals, we tend to imagine birds, dogs, fishes, squirrels, and other vertebrates. However, the animals that lack a backbone—invertebrates—are far more diverse and numerous than the vertebrates. They range in size from tiny gnats to the giant and colorful squid; some are as familiar as a housefly—while others, say, the comb jellies—may be unknown to you. Many invertebrates enhance the quality of our lives. For example, coral reefs, built by stony corals, act as storm barriers for the shoreline and provide safe harbors for ships. Bees are insects that pollinate fruit trees—otherwise, they would not be able produce their delectable products.

Still, other invertebrates are harmful to us. Insects called pests feed on and damage crops, making them less valuable or unusable. Working in pairs, certain invertebrates bring about human diseases. For example, mosquitoes serve as vectors for roundworms, whose presence accounts for elephantiasis in humans and heartworm in dogs. Parasites, as well as free-living invertebrates, are adapted to live as they do. In this chapter, you will read about the major groups of invertebrates and the evolutionary ties that bind them together, while allowing them to adapt to particular habitats.

Dirofilaria immitis *is an invertebrate that causes heartworm in dogs.*



concepts