Chapter 38

Angiosperm Reproduction and Biotechnology

Key Concepts

38.1 **Pollination enables gametes to come together within a flower**

38.2 **After fertilization, ovules develop into seeds and ovaries into fruits**

38.3 **Many flowering plants clone themselves by asexual reproduction**

38.4 **Plant biotechnology is transforming agriculture**

Framework

This chapter describes the sexual and asexual reproduction of flowering plants. The flower produces spores that grow into the haploid gametophyte stages of the life cycle: Microspores in the anther develop into pollen grains, and a megaspore in the ovule produces an embryo sac. Pollination and the double fertilization of egg and polar nuclei are followed by the development of a seed with a quiescent embryo and endosperm, protected in a seed coat and housed within a fruit. Seed dormancy is broken following proper environmental cues and the imbibition of water.

Vegetative propagation allows successful plants to clone themselves. Agriculture makes extensive use of this type of plant reproduction by using cuttings, grafts, and test-tube cloning.

Plant biotechnologists are creating genetically modified (GM or transgenic) plants that have such traits as insect and disease resistance, herbicide tolerance, and improved nutritional value. Opposition to the development of GM organisms focuses on human health concerns and the unknown dangers of introducing transgenic plants into the environment.

Chapter Review

38.1 Pollination enables gametes to come together within a flower

Plants exhibit an alternation of generations between haploid (n) and diploid ($2n$) generations. The diploid plant, the sporophyte, produces haploid spores by meiosis. Spores develop into multicellular haploid male and female gametophytes, which produce gametes by mitosis. Pollination brings pollen to the stigma of a flower, and pollen germination brings sperm to the female gametophyte. Fertilization yields diploid zygotes that grow into new sporophyte plants. In angiosperms, the male and female gametophytes have become reduced to only a few cells that develop within the anthers and ovules of the flower.

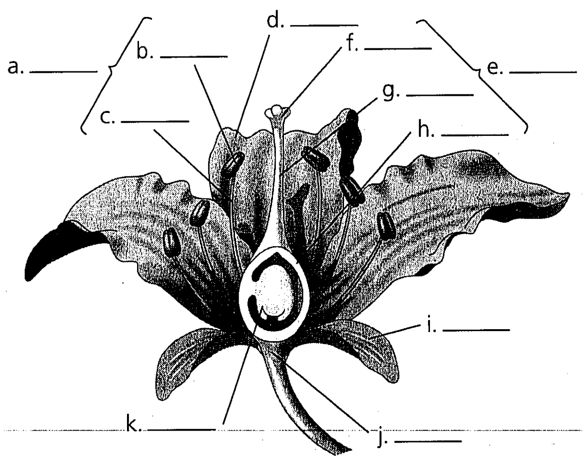
Flower Structure Flowers are determinant, reproductive shoots that usually contain four whorls of modified leaves called floral organs: **sepals, petals, stamens,** and **carpels,** which attach to the stem at the **receptacle.** Sepals enclose and protect the unopened floral bud. Petals are generally more brightly colored and may attract pollinators. Stamens consist of a filament and an **anther,** which contains pollen sacs. A carpel consists of a sticky **stigma** at the top of a slender **style,** which leads to an **ovary.** The ovary encloses one or more **ovules.** A flower may have a single carpel or multiple or fused carpels, which may be referred to as a **pistil.**

A **complete flower** has sepals, petals, stamens, and carpels. **Incomplete flowers** lack one or more of these floral organs. Floral variations include fused or separated floral organs; bilateral or radial symmetry; an ovary that is superior, semi-inferior, or inferior; individual flowers or clusters of flowers called **inflorescences;** as well as diverse shapes, colors, and odors adapted to attract different pollinators.

All complete flowers and some incomplete flowers have both stamens and carpels. Most incomplete flowers are either staminate or carpellate. In **monoecious** plant species, both staminate and carpellate flowers are on the same plant; in **dioecious** species, these flowers are on separate plants.

■ INTERACTIVE QUESTION 38.1

Identify the flower parts in the following diagram.



Gametophyte Development and Pollination Anthers and ovules contain the sporangia in which spores and gametophytes develop. A pollen grain is the sperm-producing male gametophyte surrounded by a spore wall, and embryo sacs are the egg-producing female gametophytes.

Pollination is the transfer of pollen from an anther to a stigma. The pollen grain grows a tube down the style, releasing its sperm within the embryo sac.

Following fertilization, the zygote develops into an embryo as the ovule containing the embryo develops into a seed. The entire ovary forms a fruit, which aids in seed dispersal.

Within the microsporangium (pollen sac) diploid cells called microsporocytes undergo meiosis to form four haploid **microspores.** A microspore divides once by mitosis to produce a generative cell and a tube cell. The wall surrounding the two cells thickens into the sculptured coat of the pollen grain. A pollen grain develops into a mature male gametophyte when the generative cell, which has moved into the tube cell, divides to form two sperm cells, usually after the tube cell begins to form the pollen tube. After growing through the style, the pollen tube releases the sperm cells near an embryo sac.

The megasporocyte in the single megasporangium of each ovule undergoes meiosis to form four haploid **megaspores,** only one of which usually survives. This megaspore grows and divides by mitosis three times, forming the female gametophyte, called the embryo sac, which typically consists of eight nuclei contained in seven cells. At one end of the embryo sac, an egg cell is lodged between two cells called synergids; three antipodal cells are at the other end; and two nuclei, called polar nuclei, are in a large central cell. The ovule consists of the embryo sac and its surrounding protective sporophyte layers called integuments.

Pollination is accomplished by wind, water, or animals. In Interactive Question 38.1, indicate where pollen is produced and where pollination and fertilization occur.

■ INTERACTIVE QUESTION 38.2

a. Describe the male gametophyte.

b. Describe the female gametophyte.

Mechanisms That Prevent Self-Fertilization Some flowers self-fertilize; this "selfing" ensures that a seed will develop within the fruit but does not increase the genetic diversity of offspring. Self-fertilization may be prevented by temporal or structural mechanisms. In flowers that are **self-incompatible,** a biochemical block prevents the development of pollen that does land on a stigma of the same plant.

The ability of flowers to reject their own pollen, or that of closely related individuals, depends on genes for self-incompatibility called S-genes. A plant population may have dozens of alleles of the S-gene, and if the pollen's allele matches an allele of the stigma, a pollen tube does not develop. In gametophytic self-incompatibility, a matching allele in the developing pollen tube allows RNAases from the carpel to enter and hydrolyze the pollen's RNA. In sporophytic self-incompatibility, self-recognition activates a signal-transduction pathway in stigma cells that blocks pollen germination.

Further research on the molecular basis of self-incompatibility may allow plant breeders to manipulate crop species to assure hybridization.

38.2 After fertilization, ovules develop into seeds and ovaries into fruits

Double Fertilization A pollen grain that lands on a receptive stigma absorbs moisture and germinates. The pollen tube grows through the style, and the generative cell divides to form two sperm. The pollen tube probes through the micropyle, an opening through the integuments of the ovule, and releases its two sperm within the embryo sac. By **double fertilization,** one sperm fertilizes the egg to form the zygote, and the other combines with the polar nuclei to form a triploid nucleus, which will develop into a food-storing tissue called the **endosperm.** Gamete fusion is immediately followed by an increase in cytoplasmic Ca^{2+} levels in the egg and the establishment of a block to polyspermy.

■ INTERACTIVE QUESTION 38.3

What function does double fertilization serve?

From Ovule to Seed The triploid nucleus divides to form the endosperm, a multicellular mass rich in nutrients (proteins, oils, and starch) that are provided to the developing embryo and may be stored for later use by the seedling. In many eudicots, the food reserves of the endosperm are transferred to the cotyledons before the seed matures.

In the zygote, the transverse first mitotic division creates a basal cell and a terminal cell. The basal cell divides to produce a thread of cells, called the suspensor, that anchors the embryo and transfers nutrients to it. The terminal cell divides to form a spherical proembryo, on which the cotyledons (two in eudicots, one in monocots) begin to form as bumps. The embryo elongates and apical meristems develop at the apexes of the embryonic shoot and root.

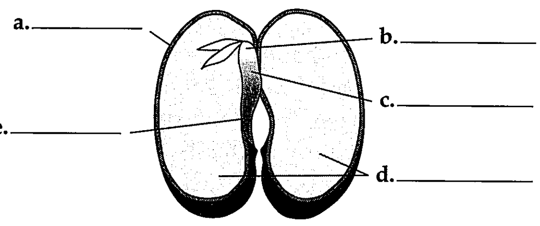
As it matures, the seed dehydrates and the embryo becomes dormant. The embryo and its food supply, the endosperm and/or enlarged cotyledons, are enclosed in a **seed coat** formed from the ovule integuments.

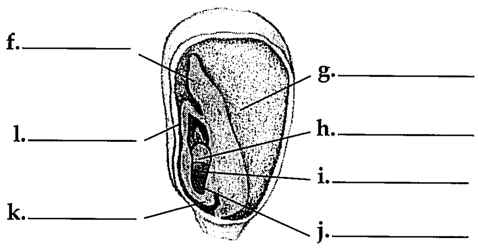
In a eudicot seed, such as a bean, the embryo is an elongated embryonic axis attached to fleshy cotyledons. (Some eudicots have thin cotyledons.) The axis below the cotyledonary attachment is called the **hypocotyl;** it terminates in the **radicle,** or embryonic root. The upper axis is the **epicotyl;** it terminates as a shoot tip with a pair of leaves.

The monocot seed found in members of the grass family has a single thin cotyledon, called a **scutellum,** which absorbs nutrients from the endosperm during germination. A sheath called a **coleorhiza** covers the root, and a **coleoptile** encloses the young shoot.

■ INTERACTIVE QUESTION 38.4

Label the parts in these diagrams of a bean and a corn seed.





From Ovary to Fruit The ovary of the flower develops into a **fruit,** which both protects and helps to disperse the seeds. Hormonal changes following fertilization cause the ovary to enlarge, its wall becoming the pericarp, or thickened wall of the fruit. Fruit usually does not set if a flower has not been pollinated.

A **simple fruit** is derived from a single carpel or several fused carpels; an **aggregate fruit** results from a flower with more than one seperate carpel; a **multiple fruit** develops from an inflorescence, whose many ovaries fuse together to become one fruit. Other floral parts (such as the receptacle) may contribute to what we commonly call a fruit. Such fruits, such as apples, are called accessory fruits.

Fruits usually ripen as the seeds are completing their development.

■ INTERACTIVE QUESTION 38.5

What changes usually occur when a fleshy fruit ripens?

Seed Germination Growth and development are suspended when a seed matures and enters **dormancy.**

Dormancy increases the chances that the seed will germinate when and where the seedling has a good chance of surviving. The specific cues for breaking dormancy vary with the environment and may include heavy rain, intense heat from fires, cold, light, or chemical breakdown of the seed coat. The viability of a dormant seed may vary from a few days to decades or longer.

Imbibition, the absorption of water by the dry seed, causes the seed to expand, rupture its coat, and begin a series of metabolic changes. Enzymes digest stored compounds, and nutrients are sent to growing regions.

The radicle emerges from the seed first, followed by the shoot tip. In many eudicots, a hook that forms in the hypocotyl is pushed up through the ground, pulling the delicate shoot and cotyledons behind it. Light stimulates the straightening of the hook, and the first foliage leaves begin photosynthesis.

■ INTERACTIVE QUESTION 38.6

How does the shoot tip break through the soil in maize and other grasses?

38.3 Many flowering plants clone themselves by asexual reproduction

Many plant species produce genetically identical copies of themselves through **asexual reproduction.** Advantages of asexual or **vegetative reproduction** include the production of clones of plants that are well suited to a certain environment and of progeny that are usually not as frail as seedlings. Sexual reproduction generates variation in a population, an advantage when the environment changes. Seeds, which are almost always produced sexually, provide a means of dispersal to new locations and dormancy during harsh conditions.

Mechanisms of Asexual Reproduction Asexual reproduction is an extension of the indeterminate growth of plants in which meristematic tissues can grow indefinitely and parenchyma cells can divide and differentiate into specialized cells. A common type of vegetative reproduction is **fragmentation,** the formation of whole plants from parts of a parent plant. In some species, the root system gives rise to many adventitious shoots that develop into a clone with separate shoot systems. Some plants, such as dandelions, can produce seeds asexually, a process called **apomixis.**

■ INTERACTIVE QUESTION 38.7

What is an advantage of apomixis?

Vegetative Propagation and Agriculture New plants may develop from stem cuttings when a **callus,** or mass of dividing cells, forms at the cut end of the shoot and adventitious roots develop from the callus. Adventitious roots can also form from a node in the shoot fragment.

Twigs or buds of one plant can be grafted onto a plant of a different variety or closely related species. The plant that provides the root system is called the **stock,** and the twig is called the **scion.** Grafting can combine the best qualities of different plants.

In test-tube cloning, whole plants can develop from pieces of tissue, called explants, or even from single parenchyma cells. A single plant can be cloned into thousands of plants by subdividing the undifferentiated calluses as they grow in tissue culture. Stimulated by proper hormone balances, calluses sprout shoots and roots and develop into plantlets, which can be transferred to soil to develop.

Foreign DNA may be inserted into individual plant cells, which then grow into **transgenic** or genetically modified (GM) plants by test-tube culture.

A technique called **protoplast fusion** is being coupled with tissue culture to create new plant varieties. Protoplasts are cells whose cell walls have been enzymatically removed. Protoplasts from different species can be fused and cultured to form hybrid plantlets.

38.4 Plant biotechnology is transforming agriculture

Plant biotechnology refers both to the age-old use of plants to make products for human use and to the use of GM organisms in agriculture.

Artificial Selection Almost all our crop species were first domesticated by Neolithic (late Stone Age) humans about 10,000 years ago. Natural hybridization between different species of plants is common, and humans have exploited such genetic variations using selective breeding and artificial selection to develop and improve crops.

Reducing World Hunger and Malnutrition The serious malnutrition of millions of people may be due to inequities in distribution of food resources or may signal that the world is already overpopulated.

The planting of transgenic crops has increased dramatically over the past several years. Cotton, maize, and potatoes have been engineered to contain genes from *Bacillus thuringiensis* that code for *Bt* toxin, reducing the need for spraying chemical insecticides. Other transgenic crops have been developed that are resistant to a number of herbicides, allowing farmers to "weed" crops without heavy tillage. Some transgenic plants are more resistant to disease or have improved nutritional quality.

The Debate over Plant Biotechnology GM organisms (GMOs) may present an unknown risk to human health or the environment. One concern is the transfer of allergens to a food source. Some GM crops may be safer; *Bt* maize contains less of a cancer-causing mycotoxin.

Many ecologists are concerned about the effect of GM crops on nontarget organisms. All GM crops need to be field tested for nontarget effects.

A serious concern is the escape of herbicide- or disease-resistance genes through crop-to-weed hybridization that may create "superweeds." Various techniques are being developed to help reduce the ability of transgenic crops to hybridize, such as developing male sterility so that transgenic pollen is not produced; introducing genes into chloroplast DNA, which is not present in pollen; and developing "terminator technology" through which seeds are rendered inviable when they mature.

Word Roots

a- = without; **-pomo** = fruit (*apomixis:* the asexual production of seeds)

anth- = a flower (*anther:* the terminal pollen sac of a stamen, inside which pollen grains with male gametes form in the flower of an angiosperm)

bi- = two (*bisexual flower:* a flower equipped with both stamens and carpels)

carp- = a fruit (*carpel:* The female reproductive organ of a flower, consisting of the stigma, style, and ovary)

coleo- = a sheath; **-rhiza** = a root (*coleorhiza:* the covering of the young root of the embryo of a grass seed)

di- = two (*dioecious:* referring to a plant species that has staminate and carpellate flowers on separate plants)

dorm- = sleep (*dormancy:* a condition typified by extremely low metabolic rate and a suspension of growth and development)

endo- = within (*endosperm:* a nutrient-rich tissue formed by the union of a sperm cell with two polar nuclei during double fertilization, which provides nourishment to the developing embryo in angiosperm seeds)

epi- = on, over (*epicotyl:* the embryonic axis above the point at which the cotyledons are attached)

gamet- = a wife or husband (*gametophyte:* the multicellular haploid form in organisms undergoing alternation of generations, which mitotically produces haploid gametes that unite and grow into the sporophyte generation)

hypo- = under (*hypocotyl:* the embryonic axis below the point at which the cotyledons are attached)

mega- = large (*megaspore:* a large, haploid spore that can continue to grow to eventually produce a female gametophyte)

micro- = small (*microspore:* a small, haploid spore that can give rise to a haploid male gametophyte)

mono- = one; **-ecious** = house (*monoecious:* referring to a plant species that has both staminate and carpellate flowers on the same individual)

peri- = around; **-carp** = a fruit (*pericarp:* the thickened wall of fruit)

proto- = first; **-plast** = formed, molded (*protoplast:* the contents of a plant cell exclusive of the cell wall)

scutell- = a little shield (*scutellum:* a specialized type of cotyledon found in the grass family)

sporo- = a seed; **-phyto** = a plant (*sporophyte:* the multicellular diploid form in organisms undergoing alternation of generations that results from a union of gametes and that meiotically produces haploid spores that grow into the gametophyte generation)

stam- = standing upright (*stamen:* the pollen-producing male reproductive organ of a flower, consisting of an anther and filament)

uni- = one (*unisexual flower:* a flower missing either stamens or carpels)

Structure Your Knowledge

1. Draw yourself a diagram of the major events in the life cycle of an angiosperm.
2. List the advantages and disadvantages of sexual and asexual reproduction in plants.
3. List some of the potential benefits and dangers of plant biotechnology.

Test Your Knowledge

FILL IN THE BLANKS

_______ 1. structure from which fruit typically develops

_______ 2. generation that produces spores by meiosis

_______ 3. species with staminate and carpellate flowers on the same plant

_______ 4. female gametophyte of angiosperms

_______ 5. embryonic root

_______ 6. embryonic axis above attachment of cotyledon

_______ 7. protects grass shoot as it breaks through the soil

_______ 8. twig or stem portion of a graft

_______ 9. plant cell from which cell wall is removed

_______ 10. mass of dividing cells at cut end of a shoot

MULTIPLE CHOICE: *Choose the one best answer.*

1. A flower on a dioecious plant would be
   - **a.** complete.
   - **b.** biennial.
   - **c.** incomplete.
   - **d.** staminate or carpellate.
   - **e.** both c and d.

2. Which of the following structures is haploid?
   - **a.** embryo sac
   - **b.** anther
   - **c.** endosperm
   - **d.** microsporocyte
   - **e.** both a and b

3. The terminal cell of an early plant embryo
   - **a.** develops into the shoot apex of the embryo.
   - **b.** forms the suspensor that anchors the embryo and transfers nutrients.
   - **c.** develops into the endosperm when fertilized by a sperm nucleus.
   - **d.** divides to form the proembryo.
   - **e.** develops into the cotyledons.

4. In angiosperms, sperm are formed by
   - **a.** meiosis in the anther.
   - **b.** meiosis in the pollen grain.
   - **c.** mitosis in the anther.
   - **d.** mitosis in the pollen tube.
   - **e.** double fertilization in the embryo sac.

5. The endosperm
   - **a.** may have its nutrients absorbed by the cotyledons in the seeds of eudicots.
   - **b.** is usually a triploid tissue.
   - **c.** is digested by enzymes in monocot seeds following hydration.
   - **d.** develops in concert with the embryo as a result of double fertilization.
   - **e.** is or does all of the above.

6. A seed consists of
   - **a.** an embryo, a seed coat, and a nutrient supply.
   - **b.** an embryo sac.
   - **c.** a gametophyte and a nutrient supply.
   - **d.** an enlarged ovary.
   - **e.** an immature ovule.

7. Which structure protects a bean shoot as it breaks through the soil?
   - **a.** hypocotyl hook
   - **b.** radicle
   - **c.** coleoptile
   - **d.** coleorhiza
   - **e.** seed coat

8. Which of the following is a form of asexual or vegetative reproduction?
   - **a.** apomixis
   - **b.** grafting
   - **c.** test-tube cloning
   - **d.** fragmentation
   - **e.** all of the above

9. Protoplast fusion
   - **a.** is used to study the fertilization of plant egg and sperm.
   - **b.** is the method used to produce test-tube plantlets.
   - **c.** can be used to form new plant species.
   - **d.** occurs within a callus.
   - **e.** is done with a gene gun.

10. In the plant embryo, the suspensor
- **a.** is produced by vertical mitotic divisions within the proembryo.
- **b.** connects the early root and shoot apexes.
- **c.** develops into the endosperm.
- **d.** is analogous to the umbilical cord in mammals.
- **e.** is the point of attachment of the cotyledons.

11. Flower organs have evolved from modified
- **a.** leaves.
- **b.** buds.
- **c.** sporangia.
- **d.** sporophytes.
- **e.** apical meristems.

12. What does self-incompatibility provide for a plant?
- **a.** means of transferring pollen to another plant
- **b.** a means of coordinating the fertilization of an egg with the development of stored nutrients
- **c.** a means of destroying foreign pollen before it fertilizes the egg cell
- **d.** a biochemical block to self-fertilization so that cross-fertilization is assured
- **e.** a means of producing seeds without the need for fertilization

13. Into what does a microspore develop in an angiosperm?
- **a.** the male gametophyte
- **b.** a pollen grain
- **c.** the male sporophyte
- **d.** the embryo sac
- **e.** Both a and b are correct.

14. Many plants form clones that develop after shoots emerge from the same root system. What is an advantage of forming such clones?
- **a.** provide a strong start for new plants
- **b.** disperse offspring to new habitats
- **c.** provide a period of dormancy until specific environmental cues signal regrowth
- **d.** provide a strong root system for a genetically altered shoot system
- **e.** allow for the production of seeds without fertilization

15. Why did it take nearly 20 years for plant breeders to convert the *opaque-2* mutant maize (with higher levels of two essential amino acids) into a variety that had a more durable endosperm?
- **a.** Such genetic recombination between species was restricted by government regulations.
- **b.** Its development was delayed because of concern that the new variety, intended for swine feed, would get mixed with maize intended for human consumption.
- **c.** Traditional plant breeding using hybridization and artificial selection is a time-intensive process.
- **d.** Plant breeders were trying to combine two varieties that were not closely enough related.
- **e.** Few people saw the benefit of improving the protein content of maize, and funding was severely lacking for such research.

16. Which of the following is a technique being developed to reduce the threat of introduced genes for herbicide or insect resistance escaping to closely related weed species?
- **a.** planting a nontransgenic plant border around crop fields to reduce crop-to-weed gene transfer
- **b.** breeding male sterility into transgenic plants so that they have no pollen to be transferred to nearby weeds
- **c.** engineering the gene of interest into chloroplast DNA, which is inherited from the maternal plant and is not transferred by pollen
- **d.** engineering crops, such as soybeans, that have no weedy relatives nearby, or introducing genes for beneficial crop traits that would actually reduce the fitness of hybrid weeds
- **e.** All of the above would reduce the risk of crop-to-weed transgene escape.