Chapter 38

Angiosperm Reproduction and Biotechnology

Lecture Outline

Overview: Flowers of Deceit

- Male wasps of the species *Campsoscolia ciliata* transfer pollen to the Mediterranean orchid *Ophrys speculum*, although the orchid does not provide energy-rich nectar to the wasp.
  - The shape of the orchid's largest petal and the frill of orange bristles around it vaguely resemble the female wasp.
  - *Ophrys* orchids also emit volatile chemicals with a scent similar to that produced by sexually receptive female wasps.
- This orchid with its wasp pollinator is one example of the many amazing ways in which angiosperms (flowering plants) reproduce sexually.
- Sexual reproduction is not the sole means by which flowering plants reproduce.
- Many species can also reproduce asexually, creating offspring that are genetically identical to them.
- Most angiosperms reward their pollinators with energy-rich pollen or nectar.
  - The symbiotic relationship between plant and pollinator is mutualistic.
- In recent evolutionary times, some species of flowering plants have formed mutualistic relationships with an animal that disperses their seeds, provides them with water and mineral nutrients, and protects them from competitors, pathogens, and predators. In return, the animal gets to eat a fraction of the plants' seeds and fruits.
  - The plant symbionts involved in these mutualistic interactions are crops; the animal symbionts are humans.
- For 10,000 years, plant breeders have altered the traits of a few hundred angiosperm species by artificial selection, transforming them into today's crops.
- With the advent of genetic engineering, the modification of plants has increased dramatically.

Concept 38.1 Flowers, double fertilization, and fruits are unique features of the angiosperm life cycle.

Sporophyte and gametophyte generations alternate in the life cycles of plants.

- The life cycles of angiosperms and other plants are characterized by an alternation of generations, in which haploid (n) and diploid ($2n$) generations take turns producing each other.
  - The diploid plant, the sporophyte, produces haploid spores by meiosis.
  - These spores divide by mitosis to form gametophytes, multicellular male and female haploid plants that produce gametes (eggs and sperm).
  - **Fertilization** results in diploid zygotes, which divide by mitosis to form new sporophytes.

- In angiosperms, the sporophyte is the dominant generation—the large, conspicuous, long-lived plant we see.
- During the evolution of seed plants, the gametophytes became smaller and wholly dependent on the parent sporophyte for nutrients.
- Angiosperm gametophytes are the smallest of all plants, consisting of only a few cells.
- The most important features unique to the angiosperm life cycle are the "three Fs": **f**lowers, double **f**ertilization, and **f**ruits.
- Seed structure and function are also critical to understanding angiosperm life cycles.

Flowers are specialized shoots that bear the reproductive organs of the angiosperm sporophyte.

- Flowers, the reproductive shoots of the angiosperm sporophyte, are typically made up of four whorls of modified leaves called floral organs, which are separated by short internodes.
    - Unlike vegetative shoots, flowers are determinate shoots in that they cease growing once the flower and fruit are formed.
- The four floral organs are the **sepals**, **petals**, **stamens**, and **carpels**.
- Their site of attachment to the stem is the **receptacle**.
- Stamens and carpels are reproductive organs, whereas sepals and petals are sterile.
    - Sepals, which enclose and protect the floral bud before it opens, are usually green and more leaflike in appearance than the other floral organs.
    - In many angiosperms, the petals are brightly colored and advertise the flower to insects and other pollinators.
- Stamens and carpels are the male and female reproductive organs, respectively.
    - A stamen consists of a stalk (the *filament*) and a terminal **anther** containing chambers called microsporangia (pollen sacs) that produce pollen.
    - A carpel has an **ovary** at the base and a slender neck, the **style**.
    - At the top of the style is a sticky structure called the **stigma** that serves as a landing platform for pollen.
    - Within the ovary are one or more **ovules**.
    - Some flowers have a single carpel.
    - In other flowers, several carpels are fused into a single structure, producing an ovary with two or more chambers, each containing one or more ovules.
    - The term **pistil** refers to a single carpel or a group of fused carpels.
- **Complete flowers** have all four basic floral organs; **incomplete flowers** lack sepals, petals, stamens, or carpels.
    - Some incomplete flowers are sterile, lacking functional stamens and carpels; others are *unisexual*, lacking either stamens or carpels.
- Flowers also vary in size, shape, color, odor, organ arrangement, and time of opening.
- Some flowers are borne singly, whereas others are arranged in showy clusters called **inflorescences**.
- Much of floral diversity represents adaptation to specific pollinators.

The male gametophytes of angiosperms are pollen grains.

- Each anther bears four microsporangia, also known as pollen sacs.

- Within the microsporangia are many diploid cells called microsporocytes, also known as microspore mother cells.
- Each microsporocyte forms four haploid **microspores** by meiosis.
- Each microspore then undergoes mitosis to produce an immature male gametophyte consisting of only two cells: the *generative cell* and the *tube cell*.
- Together, these two cells and the spore wall constitute a **pollen grain**.
- The spore wall, produced by the microspore and the anther, has a unique pattern characteristic of the species.
- As the male gametophyte matures, the generative cell passes into the tube cell.
- Then the microsporangium breaks open and releases the pollen.
- A pollen grain may be transferred to a receptive stigmatic surface, where the tube cell produces the **pollen tube**, a long cellular protuberance that delivers sperm to the female gametophyte.
    - As the pollen tube elongates quickly through the style, the generative cell divides to produce two sperm cells, which remain inside the tube cell.
    - The pollen tube grows through the style and into the ovary, where it releases the sperm cells near the female gametophyte.

The female gametophyte of an angiosperm is an embryo sac.

- Among angiosperm species, there are more than 15 variations in the development of the female gametophyte, also known as an **embryo sac**.
- The development of the embryo sac occurs within the carpel's ovary, in the tissue within each ovule called the megasporangium.
- Two *integuments* (layers of protective sporophytic tissue that eventually develop into the seed coat) surround each megasporangium except at a gap called the *micropyle*.
- The *megasporocyte* (or megaspore mother cell) in the megasporangium of each ovule enlarges and undergoes meiosis, producing four haploid **megaspores**.
- Only one megaspore survives; the others disintegrate.
- As the surviving megaspore grows, its nucleus divides by mitosis three times without cytokinesis, resulting in one large cell with eight haploid nuclei.
- Membranes then partition this mass into a multicellular female gametophyte—the embryo sac.
    - Three of the cells within the embryo sac are near the micropyle: the egg cell and two cells called synergids.
    - The synergids flank the egg cell and help attract and guide the pollen tube to the embryo sac.
    - At the opposite end of the embryo sac are three antipodal cells of unknown function.
    - The remaining two nuclei, called polar nuclei, are not partitioned into separate cells but instead share the cytoplasm of the large central cell of the embryo sac.
- The ovule, which will eventually become a seed, now consists of the embryo sac and two surrounding integuments.

Pollination is the transfer of pollen from an anther to a stigma.

- Pollination, which brings male and female gametophytes together, is the first step in the chain of events that leads to fertilization.
- Some plants, such as grasses and many trees, release large quantities of pollen on the wind to compensate for the randomness of this dispersal mechanism.
    - At certain times of the year, the air is loaded with pollen, as anyone plagued by pollen allergies can attest.

- Some aquatic plants rely on water to disperse pollen.
- Most angiosperms interact with insects or other animals that transfer pollen directly between flowers.

Double fertilization gives rise to the zygote and endosperm.

- After landing on a receptive stigma, the pollen grain absorbs moisture and germinates, producing a pollen tube that grows between the cells of the style toward the ovary.
- The nucleus of the generative cell divides by mitosis to produce two sperm.
- Directed by a chemical attractant produced by the two synergids, the tip of the pollen tube enters the ovary, probes through the micropyle, and discharges its two sperm near or within the embryo sac.
    - A gradient in GABA, a chemical that functions as a neurotransmitter in animal cells, may be the critical signal for attracting the pollen tube.
- Both sperm fuse with nuclei in the embryo sac.
    - One sperm fertilizes the egg to form the zygote.
    - The other sperm combines with the two polar nuclei to form a triploid ($3n$) nucleus in the central cell of the female gametophyte.
    - This large cell will give rise to the **endosperm**, a food-storing tissue of the seed.
- The union of two sperm cells with different nuclei of the embryo sac is called **double fertilization**.
- Double fertilization ensures that the endosperm will develop only in ovules where the egg has been fertilized.
    - Double fertilization prevents angiosperms from squandering nutrients.
- Normally nonreproductive tissues surrounding the embryo have prevented researchers from observing fertilization in plants, but recently scientists have been able to isolate sperm cells and eggs and observe plant fertilization *in vitro*.
- The first cellular event after gamete fusion is an increase in cytoplasmic Ca^{2+} levels, which also occurs during animal gamete fusion.
- In another similarity to animals, plants establish a block to polyspermy, the fertilization of an egg by more than one sperm cell.
    - In plants, a deposition of cell wall material may mechanically impede sperm.
    - In maize, this barrier is established within 45 seconds after the initial sperm fusion with the egg.

The ovule develops into a seed containing an embryo and a supply of nutrients.

- After double fertilization, the ovule develops into a seed, and the ovary develops into a fruit enclosing the seed(s).
- As the embryo develops, the seed stockpiles proteins, oils, and starch.
    - Initially, these nutrients are stored in the endosperm.
    - Later in seed development in many species, the storage function is taken over by the swelling storage leaves (cotyledons) of the embryo itself.
- Endosperm development usually precedes embryo development.
- After double fertilization, the triploid nucleus of the ovule's central cell divides, forming a multinucleate "supercell" having a milky consistency.
    - The endosperm becomes multicellular when cytokinesis partitions the cytoplasm between nuclei.

- Cell walls form, and the endosperm becomes solid.
- Coconut "milk" is an example of liquid endosperm, and coconut "meat" is an example of solid endosperm. The white fluffy part of popcorn is also solid endosperm.

- In grains and most other monocot species, the endosperm is rich in nutrients, which it provides to the developing embryo.
- In most eudicots, the food reserves of the endosperm are completely exported to the cotyledons before the seed completes its development, and consequently the mature seed lacks endosperm.

The embryo develops within the seed.

- The first mitotic division of the zygote splits the fertilized egg into a basal cell and a terminal cell, which gives rise to most of the embryo.
- The basal cell continues to divide, producing a thread of cells, the suspensor, that anchors the embryo to its parent.
    - The suspensor functions in the transfer of nutrients to the embryo from the parent and, in some plant species, from the endosperm.
    - As the suspensor elongates, it pushes the embryo deeper into the nutritive and protective tissues.
- The terminal cell divides several times and forms a spherical proembryo attached to the suspensor.
- Cotyledons begin to form as bumps on the proembryo.
    - A eudicot, with its two cotyledons, is heart-shaped at this stage.
    - Only one cotyledon develops in monocots.
- After the cotyledons appear, the embryo elongates.
    - Cradled between the cotyledons is the embryonic shoot apex with the apical meristem of the embryonic shoot.
    - At the opposite end of the embryo axis is the apex of the embryonic root, also with a meristem.
- After the seed germinates, the apical meristems at the tips of the shoot and root sustain primary growth as long as the plant lives.
- During the last stages of maturation, a seed dehydrates until its water content is only about 5–15% of its weight.
- The embryo stops growing and enters **dormancy** until the seed germinates.
    - The embryo and its food supply are enclosed by a protective **seed coat** formed by the integuments of the ovule.
    - Dormancy may be imposed by the presence of an intact seed coat, or the embryo may be dormant.
- In the seed of a common bean (a eudicot), the embryo consists of an elongate structure, the embryonic axis, attached to fleshy cotyledons.
    - Below the point at which the fleshy cotyledons are attached, the embryonic axis is called the **hypocotyl**.
    - The hypocotyl terminates in the **radicle**, or embryonic root.
    - The portion of the embryonic axis above where the cotyledons are attached, and below the first pair of miniature leaves, is the **epicotyl**.
    - The epicotyl, young leaves, and shoot apical meristem are collectively called the *plumule*.
- The cotyledons of the common bean are packed with starch before the seed germinates because they absorbed carbohydrates from the endosperm when the seed was developing.

- However, the seeds of some eudicot species, such as castor beans *(Ricinus communis)*, retain their food supply in the endosperm and have very thin cotyledons.
- The cotyledons absorb nutrients from the endosperm and transfer them to the embryo when the seed germinates.
- The embryo of a monocot has a single cotyledon.
  - Members of the grass family, including maize and wheat, have a specialized cotyledon called a *scutellum*.
  - The scutellum is very thin, with a large surface area pressed against the endosperm, from which the scutellum absorbs nutrients during germination.
- The embryo of a grass seed is enclosed by two sheathes: a **coleorhiza**, which covers the young root, and a **coleoptile**, which covers the young shoot.

Seed dormancy is an adaptation for tough times.

- As a seed matures, it dehydrates and enters a dormancy phase, a condition of extremely low metabolic rate and suspended growth and development.
- The conditions required to break dormancy and resume growth and development vary among species.
  - Some seeds germinate as soon as they are in a suitable environment.
  - Others remain dormant until some specific environmental cue causes them to break dormancy.
- Seed dormancy increases the chances that germination will occur at a time and place most advantageous to the seedling.
  - For example, seeds of many desert plants germinate only after a substantial rainfall, thus ensuring enough water to complete development.
  - Where natural fires are common, many seeds require intense heat to break dormancy, allowing them to take advantage of open space with reduced competition.
  - Where winters are harsh, seeds may require extended exposure to cold to break dormancy.
  - Small seeds such as lettuce require light for germination and break dormancy only if they are buried near the surface.
  - Other seeds require a chemical attack as they pass through an animal's digestive tract before they can germinate.
- The length of time that a dormant seed remains viable and capable of germinating varies from a few days to decades or even longer, depending on the species and on environmental conditions.
  - Most seeds are durable enough to last for a year or two until conditions are favorable for germination.
  - Thus, the soil has a pool of nongerminated seeds that may have accumulated for several years.
  - This is one reason vegetation reappears so rapidly after a fire, drought, flood, or other environmental disruption.
- Germination of seeds depends on **imbibition**, the uptake of water due to the low water potential of the dry seed.
  - Imbibition causes the expanding seed to rupture its seed coat and triggers metabolic changes in the embryo that enable it to resume growth.
- Following hydration, enzymes begin digesting the storage materials of the endosperm or cotyledons, and the nutrients are transferred to the growing regions of the embryo.
- The first organ to emerge from the germinating seed is the radicle, the embryonic root.

- Next, the shoot tip must break through the soil surface.
  - In garden beans and many other eudicots, a hook forms in the hypocotyl, and growth pushes it above ground.
  - Stimulated by light, the hypocotyl straightens, raising the cotyledons and epicotyl.
  - Thus, the delicate shoot tip and bulky cotyledons are pulled upward rather than pushed tip-first through the abrasive soil.
- As it rises into the air, the epicotyl spreads its first foliage leaves (true leaves).
- These foliage leaves expand, become green, and begin making food by photosynthesis.
- After the cotyledons have transferred all their nutrients to the developing plant, they shrivel and fall off the seedling.
- Corn and other grasses, which are monocots, use a different method for breaking ground when they germinate.
  - The coleoptile, the sheath enclosing and protecting the embryonic shoot, pushes upward through the soil and into the air.
  - The shoot tip then grows straight up through the tunnel provided by the tubular coleoptile.

The ovary develops into a fruit adapted for seed dispersal.

- As the seeds are developing from ovules, the ovary of the flower is developing into a **fruit**, which protects the enclosed seeds and aids in their dispersal by wind or animals.
  - Fertilization triggers hormonal changes that cause the ovary to begin its transformation into a fruit.
  - If a flower has not been pollinated, fruit usually does not develop, and the entire flower withers and falls away.
- Fruits are classified into types, depending on their developmental origin.
  - Most fruits are derived from a single carpel or several fused carpels and are called **simple fruits**.
    - Some simple fruits are fleshy, like a peach, whereas others are dry, like a pea pod or nut.
  - An **aggregate fruit** results from a single flower that has more than one carpel, each forming a small fruit. The fruitlets are clustered together on a single receptacle.
    - The strawberry is an aggregate fruit, consisting of an enlarged receptacle embedded with tiny one-seeded fruits.
  - A **multiple fruit** develops from an inflorescence, a group of flowers tightly clustered together. When the walls of the ovaries thicken, they fuse together and form one fruit, as in a pineapple.
  - In some angiosperms, other floral parts as well as the ovaries contribute to the fruit. Such fruits are called **accessory fruits.**
    - In apples, the fleshy part of the simple fruit is derived mainly from the swollen receptacle; only the core of the apple fruit develops from the ovary.
- The fruit usually ripens about the same time its seeds are completing their development.
- For a dry fruit such as a soybean pod, ripening is little more than the aging and drying out of fruit tissues, allowing the fruit to open and release the seeds.
- The ripening of fleshy fruits is more elaborate, with its steps controlled by the complex interactions of hormones.
  - Ripening results in an edible fruit that serves as an enticement to the animals that help spread the seeds.

- The “pulp” of the fruit becomes softer as a result of enzymes digesting components of the cell walls.
- The color changes from green to red, orange, or yellow.
- The fruit becomes sweeter as organic acids or starch molecules are converted to sugar, which may reach a concentration as high as 20% in a ripe fruit.

~~Concept 38.2 Plant reproduce sexually, asexually, or both.~~

- ~~Many plants clone themselves by **asexual reproduction**, in which offspring are derived from a single parent without genetic recombination.~~
- ~~Asexual reproduction is an extension of the capacity of plants for indeterminate growth.~~
  - ~~Meristematic tissues with dividing undifferentiated cells can sustain or renew growth indefinitely.~~
  - ~~Parenchyma cells throughout the plant can divide and differentiate into various types of specialized cells.~~
- ~~Detached vegetative fragments of some plants can develop into whole offspring.~~
  - ~~In **fragmentation,** a parent plant separates into parts that re-form into whole plants.~~
  - ~~In some species, the root system of a single parent gives rise to many adventitious shoots that become separate root systems, forming a clone.~~
  - ~~A ring of creosote bushes in the Mojave Desert of California is believed to be at least 12,000 years old.~~
- ~~A different method of asexual reproduction, called **apomixis**, is found in dandelions and some other plants.~~
  - ~~These plants produce seeds without their flowers being fertilized.~~
  - ~~A diploid cell in the ovule gives rise to the embryo, and the ovules mature into seeds.~~
  - ~~Dandelion seeds are dispersed by the wind.~~
  - ~~This method of reproduction combines asexual reproduction and seed dispersal.~~
- ~~Introducing apomixis into hybrid crops is a goal of great interest to plant breeders because apomixis would allow hybrid plants to pass on their desirable genomes intact to their offspring.~~

~~Both sexual and asexual reproduction have advantages and disadvantages.~~

- ~~Many plants are capable of both sexual and asexual reproduction, and each offers advantages in certain situations.~~
- ~~An important advantage of asexual reproduction is that there is no need for a pollinator.~~
  - ~~This may be beneficial if plants of the same species are sparsely distributed and unlikely to be visited by the same pollinator.~~
- ~~When reproducing asexually, a plant passes on all of its genes to its offspring. When reproducing sexually, however, it passes on only half of its genes.~~
- ~~If a plant is superbly suited to a stable environment, asexual reproduction has advantages.~~
  - ~~A plant can clone many copies of itself rapidly.~~
  - ~~If the environmental conditions remain stable, the clones will be well suited to the environment.~~
- ~~Generally, the clones produced by asexual reproduction are not as frail as the seedlings produced by sexual reproduction.~~

Formatted: Bullets and Numbering

Formatted: Bullets and Numbering

Formatted: Bullets and Numbering

Formatted: Bullets and Numbering

Formatted: Bullets and Numbering

- ~~The clones are usually mature vegetative fragments of the parent plant, which is why asexual reproduction in plants is also known as **vegetative reproduction**.~~

Formatted: Bullets and Numbering

- ~~Seed germination gives rise to a fragile seedling that is exposed to predators, parasites, wind, and other hazards.~~
- ~~In the wild, only a small fraction of seedlings endure long enough to become parents.~~
- ~~Plants must produce enormous numbers of seeds to compensate for low individual survival rates and to provide ample genetic variation for natural selection to screen.~~
- ~~Flowering and fruiting in sexual reproduction are an expensive method of plant propagation in terms of the resources consumed.~~

- ~~In unstable environments, where evolving pathogens and other variables affect survival and reproductive success, sexual reproduction can be advantageous because it generates variation in offspring.~~
  - ~~In contrast, the genotypic uniformity of asexually produced plants puts them at great risk of local extinction if there is a catastrophic environmental change, such as a new strain of disease.~~

Formatted: Bullets and Numbering

- ~~Seeds produced by sexual reproduction can disperse to new locations and wait for favorable growing conditions.~~
  - ~~Seed dormancy suspends growth until hostile environmental conditions are reversed.~~

Formatted: Bullets and Numbering

- ~~Although the major advantage of sexual reproduction is increasing the genetic diversity of offspring, some flowers, such as garden peas, self-fertilize.~~
  - ~~This process, called "selfing," can be a desirable attribute in some crop plants because it ensures that a seed will develop.~~

Formatted: Bullets and Numbering

~~Plants have various mechanisms that prevent self-fertilization.~~

- ~~The various barriers that prevent self-fertilization contribute to genetic variety by ensuring that sperm and eggs come from different parents.~~
- ~~**Dioecious** plants cannot self-fertilize because different individuals have either staminate (lacking carpels) or carpellate (lacking stamens) flowers.~~
- ~~In plants with bisexual flowers, a variety of mechanisms may prevent self-fertilization.~~
  - ~~For example, in some species, stamens and carpels mature at different times.~~

Formatted: Bullets and Numbering

  - ~~Alternatively, a flower may be arranged in such a way that it is mechanically unlikely that an animal pollinator could transfer pollen from the anthers to the stigma of the same flower.~~
  - ~~The most common anti-selfing mechanism is **self-incompatibility**, the ability of a plant to reject its own pollen and that of closely related individuals.~~
  - ~~If a pollen grain from an anther happens to land on a stigma of a flower on the same plant, a biochemical block prevents the pollen from completing its development and fertilizing an egg.~~
- ~~The self-incompatibility systems in plant are analogous to the immune response of animals.~~
  - ~~Both are based on the ability of organisms to distinguish "self" from "nonself."~~

Formatted: Bullets and Numbering

  - ~~The key difference is that the animal immune system rejects nonself, whereas self-incompatibility in plants is a rejection of self.~~
- ~~Recognition of "self" pollen is based on genes for self-incompatibility, called *S*-genes, with dozens of different alleles in a population.~~
- ~~If a pollen grain has an allele that matches an allele of the stigma on which it lands, the pollen tube fails to grow.~~

- ~~Depending on the species, self-recognition blocks pollen tube growth by one of two molecular mechanisms: gametophytic self-incompatibility or sporophytic self-incompatibility.~~
- ~~In gametophytic self-incompatibility, the *S*-allele in the pollen genome governs the blocking of fertilization.~~
  - ~~For example, an S_1 pollen grain from an S_1S_2 parental sporophyte will fail to fertilize eggs of an S_1S_2 flower but will fertilize an S_2S_3 flower.~~

    Formatted: Bullets and Numbering
  - ~~An S_2 pollen grain will not fertilize either flower.~~
- ~~Self-recognition of this kind involves the enzymatic destruction of RNA within a pollen tube.~~
  - ~~RNA-hydrolyzing enzymes are produced by the style and enter the pollen tube and attack its RNA only if the pollen is of a "self" type.~~

    Formatted: Bullets and Numbering
- ~~In sporophytic self-incompatibility, fertilization is blocked by *S*-allele gene products in tissues of the parental sporophyte that adhere to the pollen wall.~~
  - ~~Neither an S_1 nor S_2 pollen grain from an S_1S_2 parental sporophyte will fertilize eggs of an S_1S_2 flower or a S_2S_3 flower.~~

    Formatted: Bullets and Numbering
  - ~~Sporophytic incompatibility involves a signal transduction pathway in the epidermal cells of the stigma that prevents germination of the pollen grain.~~
- ~~Some crops, such as peas, maize, and tomatoes, routinely self-pollinate without difficulty.~~
- ~~Plant breeders frequently hybridize different varieties of a crop plant to combine the best traits of the varieties and counter the loss of vigor that can result from excessive inbreeding.~~
  - ~~To obtain hybrid seeds, breeders must prevent self-fertilization by laboriously removing anthers from the parent plants that provide the seeds or by developing male sterile plants.~~

    Formatted: Bullets and Numbering
- ~~Eventually, it may be possible to impose self-incompatibility on species that are normally self-compatible.~~
- ~~Basic research on mechanisms of self-incompatibility may therefore lead to agricultural applications.~~

~~Vegetative propagation of plants is common in agriculture.~~

- ~~Various methods have been developed for the asexual propagation of angiosperms.~~
- ~~These methods are based on the ability of plants to form adventitious roots or shoots.~~
- ~~Most houseplants, woody ornamentals, and orchard trees are reproduced asexually from plant fragments called cuttings, which are typically pieces of shoots or stems.~~
- ~~At the cut end, a mass of dividing, undifferentiated cells called a **callus** forms, and then adventitious roots develop from the callus.~~
  - ~~If the shoot fragment includes a node, then adventitious roots form without a callus stage.~~

    Formatted: Bullets and Numbering
- ~~Some plants, including African violets, can be propagated from single leaves.~~
- ~~In other plants, specialized storage stems can be cut into several pieces and develop into clones.~~
  - ~~For example, a piece of a potato including a vegetative bud or "eye" can regenerate a whole plant.~~

    Formatted: Bullets and Numbering
- ~~A twig or bud from one plant can be grafted onto a plant of a closely related species or a different variety of the same species.~~
- ~~Grafting makes it possible to combine the best properties of different species or varieties into a single plant.~~
- ~~The plant that provides the root system is called the **stock**, and the twig grafted onto the stock is the **scion**.~~
  - ~~For example, scions of French vines, which produce superior grapes, are grafted onto roots of American varieties, which are more resistant to certain soil pathogens.~~

    Formatted: Bullets and Numbering

- ~~The quality of the fruit is not influenced by the genetic makeup of the stock.~~
- ~~In some cases of grafting, however, the stock can alter the characteristics of the shoot system that develops from the scion.~~
  - ~~For example, dwarf fruit trees are made by grafting normal twigs onto dwarf stock varieties that retard the vegetative growth of the shoot system.~~ **Formatted:** Bullets and Numbering
  - ~~Because the seeds are produced by the scion part of the plant, they give rise to plants of the scion species if planted.~~
- ~~Plant biotechnologists have adopted *in vitro* methods to create and clone novel plant varieties.~~
  - ~~Whole plants are cultured from small explants (small tissue pieces) or even single parenchyma cells on an artificial medium containing nutrients and hormones.~~ **Formatted:** Bullets and Numbering
  - ~~The cultured cells divide and form an undifferentiated callus.~~
  - ~~Through manipulations of the hormonal balance, the callus that forms can be induced to develop shoots and roots with fully differentiated cells.~~
  - ~~Once roots and shoots have developed, the test-tube plantlets can be transferred to soil, where they continue their growth.~~ **Formatted:** Bullets and Numbering
  - ~~This test-tube cloning can be used to clone a single plant into thousands of copies by subdividing calluses as they grow.~~ **Formatted:** Bullets and Numbering
  - ~~This technique is used to propagate orchids and to clone pine trees that deposit wood at an unusually fast rate.~~
- ~~Plant tissue culture facilitates genetic engineering of plants.~~
  - ~~Most techniques for introducing foreign genes into plants start with small pieces of plant material or single plant cells.~~ **Formatted:** Bullets and Numbering
  - ~~**Transgenic** plants are genetically modified (GM) plants that have been genetically engineered to express a gene from another species.~~
  - ~~Test-tube culture makes it possible to regenerate a GM plant from a single cell into which foreign DNA has been incorporated.~~
- ~~Another approach combines **protoplast fusion** with tissue culture methods to invent new plant varieties that can be cloned.~~
  - ~~Protoplasts are plant cells that have had their cell walls removed enzymatically by fungal cellulases and pectinases.~~ **Formatted:** Bullets and Numbering
  - ~~It is possible in some cases to fuse two protoplasts from different plant species that would otherwise be incompatible.~~
  - ~~The hybrids can regenerate the cell wall, be cultured, and produce a hybrid plantlet.~~
- ~~This technique has successfully developed a hybrid between a potato and a wild relative called black nightshade.~~
  - ~~The nightshade is resistant to an herbicide that is commonly used to kill weeds.~~ **Formatted:** Bullets and Numbering
  - ~~The hybrids are also resistant, so that a farmer can "weed" a potato field with an herbicide without killing the potato plants.~~

~~Concept 38.3 Humans modify crops by breeding and genetic engineering.~~

~~Humans have created new plant varieties by artificial selection.~~

- ~~Humans have intervened in the reproduction and genetic makeup of plants for thousands of years.~~

- ~~Despite their lack of understanding of the scientific principles of plant breeding, Neolithic (late Stone Age) humans domesticated most crop species over a relatively short period about 10,000 years ago.~~
- ~~Selective breeding by humans has created plants that could not survive or reproduce in the wild.~~
  - ~~For example, maize cannot spread its seeds naturally.~~
  - ~~Humans artificially selected for a larger central axis (the "cob"), permanent attachment of the maize kernels to the cob, and permanent protection by tough, overlapping leaf sheathes (the "husk").~~

Formatted: Bullets and Numbering

- ~~For domesticated crop plants, genetic modifications began long before humans started altering crops by artificial selection.~~
  - ~~For example, the wheat groups that we harvest are the result of natural hybridizations between different species of grasses.~~
  - ~~Such hybridization is common in plants and has long been exploited by breeders to introduce genetic variation for artificial selection and crop improvement.~~

Formatted: Bullets and Numbering

- ~~Plant breeders scrutinize their fields carefully and travel to other countries searching for domesticated varieties or wild relatives with desirable traits.~~
  - ~~The natural rate of mutation is too slow and unreliable to produce all the mutations that breeders would like to study.~~
  - ~~Breeders may hasten mutations by treating large batches of seeds or seedlings with X-rays, radiation, or chemicals.~~

Formatted: Bullets and Numbering

Formatted: Bullets and Numbering

- ~~After finding a desirable trait in a wild species, for example, breeders cross the wild species to a domesticated variety.~~
  - ~~Progeny that inherit the desirable trait from the wild parent may also inherit many undesirable traits, unsuitable for agriculture.~~
  - ~~Progeny continue to be examined for the desired trait, until the progeny with the wild trait resemble the original domesticated parent in their agricultural attributes.~~

Formatted: Bullets and Numbering

- ~~Some breeding methods rely on distant hybridization between two species of the same genus.~~
  - ~~For example, a cross between two species of the genus *Musa* produced the familiar Cavendish banana.~~

Formatted: Bullets and Numbering

- ~~Distant crosses often result in the abortion of the hybrid seed during development because the embryo begins to develop but the endosperm does not.~~
  - ~~Hybrid embryos may be rescued by surgically removing them from the ovule and culturing them *in vitro*.~~

Formatted: Bullets and Numbering

- ~~Less commonly, distant hybridization occurs between members of two different genera.~~
- ~~A cross between wheat *(Triticum aestivum)* and rye *(Secale cereale)* produced a novel grain called triticale, which contains a copy of all the chromosomes from both species.~~
- ~~When triticale was first produced in the 1870s, it was considered merely a botanical oddity.~~
- ~~In the mid-1900s, however, plant breeders realized that triticale could potentially be developed into a crop with the yield and quality of bread wheat and with rye's tolerance of cold stress, moisture stress, and poor acid soils.~~
  - ~~The early triticales were tall, late-maturing plants that tended to fall over, were partially sterile, and were low-yielding.~~
  - ~~Early triticales set shriveled seeds that germinated poorly and were of poor quality for milling and baking.~~

Formatted: Bullets and Numbering

- ~~Through continued artificial selection, these problems were overcome, and triticale is now grown on more than 1 million hectares worldwide.~~
- ~~Triticale is nutritionally superior to rye, and the flour blends better with wheat in the baking of bread.~~

- ~~Triticale grows well on *marginal land*, agriculturally inferior land that usually has a poor yield.~~
- ~~If we are to feed the burgeoning world population in the 21st century, such marginal lands will have to become more productive.~~
- ~~The term *plant biotechnology* has two meanings.~~
  - ~~In the general sense, it refers to innovations in the use of plants (or substances obtained from plants) to make products of use to humans—an endeavor that began in prehistory.~~
  - ~~In a more specific sense, it refers to the use of GM organisms in agriculture and industry.~~
- ~~The terms *genetic engineering* and *biotechnology* have become synonymous in the media.~~
- ~~Unlike traditional plant breeders, modern plant biotechnologists are not limited to transferring genes between closely related species or varieties of the same species.~~

~~Genetic engineering of crop plants may help to reduce world hunger.~~

- ~~Eight hundred million people on Earth suffer from nutritional deficiencies.~~
- ~~Forty thousand people die each day of malnutrition, half of them children.~~
- ~~There is much disagreement about the causes of such hunger.~~
  - ~~Some argue that food shortages arise from inequities in distribution and that the dire poor simply cannot afford food.~~
  - ~~Others regard food shortages as evidence that the world is overpopulated—that the human species has exceeded the carrying capacity of the planet.~~
- ~~Whatever the social and demographic causes of malnutrition, increasing food production is a humane objective.~~
- ~~Because land and water are the most limiting resources, the best option is to increase yields on the available land.~~
  - ~~There is little "extra" land that can be cultivated if the few remaining pockets of wilderness are to be preserved.~~
- ~~Based on conservative estimates of population growth, farmers will have to produce 40% more grain per hectare to feed the human population in 2020.~~
- ~~Plant biotechnology can help make these crop yields possible.~~
- ~~The commercial use of transgenic crops has been one of the most dramatic examples of rapid technology adoption in the history of agriculture.~~
- ~~Transgenic crops include varieties and hybrids of cotton, maize, and potatoes that contain genes from the bacterium *Bacillus thuringiensis*.~~
  - ~~These "transgenes" encode for a protein (*Bt* toxin) that is toxic to insect pests, thus greatly reducing the need for chemical insecticides.~~
  - ~~The *Bt* toxin used in crops is produced in the plant as a harmless protoxin that becomes toxic only if activated by alkaline conditions within insect guts.~~
  - ~~In the highly acidic stomachs of vertebrates, the protoxin is destroyed without becoming active.~~
- ~~Considerable progress also has been made in developing transgenic plants of cotton, maize, soybeans, sugar beets, and wheat that tolerate certain herbicides.~~

Formatted: Bullets and Numbering

Formatted: Bullets and Numbering

Formatted: Bullets and Numbering

Formatted: Bullets and Numbering

- ~~The cultivation of these plants may reduce production costs and enable farmers to "weed" crops with herbicides that do not damage the transgenic crop plants instead of by heavy tillage, which can cause soil erosion.~~

- ~~Researchers are also engineering plants with enhanced resistance to disease.~~
  - ~~A transgenic papaya resistant to a ring spot virus was introduced into Hawaii and helped to save its papaya industry.~~
- ~~The nutritional quality of plants is also being improved.~~
  - ~~"Golden rice," a transgenic variety of rice with daffodil genes that increase the quantities of vitamin A, has been developed to prevent the blindness that occurs in many of the world's poor whose diet is chronically deficient in vitamin A.~~
  - ~~Recently, a new variety has been produced with even more vitamin A than the original golden rice.~~

~~Biofuels offer the opportunity of reducing fossil fuel dependency.~~

- ~~Global sources of inexpensive fossil fuels, particularly oil, are rapidly being depleted.~~
- ~~The burning of fossil fuels, such as coal and oil, and the resulting release of greenhouse gases increase global warming.~~
- ~~Scientists are searching for economical and nonpolluting technologies that will allow the world to meet its energy demands.~~
- ~~The biomass from extremely fast-growing plants, such as switchgrass *(Panicum virgatum)* and poplar *(Populus trichocarpa)*, may produce a sizable fraction of the world's energy needs in the not-too-distant future.~~
  - ~~Under optimal conditions, poplars can grow 3 to 4 m each year, whereas switchgrass grows well under a wide variety of marginal conditions.~~
- ~~Biopolymers in these plants' cell walls, such as cellulose and hemicellulose, will be broken down into sugars by enzymatic reactions.~~
- ~~These sugars will be fermented into alcohol and distilled to yield **biofuels**.~~
- ~~Compared with gasoline, biofuels from plant biomass would reduce emissions of the greenhouse gas~~ ~~CO_2~~.
  - ~~Biofuel crops reabsorb by photosynthesis the~~ ~~CO_2~~ ~~emitted when biofuels are consumed, creating a cycle that is carbon neutral.~~
- ~~Currently biofuel technology is a controversial topic.~~
  - ~~Critics David Pimentel and Tad Patzek of Cornell University have published estimates that more energy may actually be required to produce biofuels than is produced from the combustion of these products.~~
  - ~~Biofuel advocates, in turn, have questioned the accuracy and currency of the data underlying these estimates.~~

~~The debate over plant biotechnology continues.~~

- ~~Some biologists, particularly ecologists, are concerned about the unknown risks associated with the release of genetically modified organisms (GMOs) into the environment.~~
  - ~~These scientists fear that GMOs could harm human health or the environment.~~
  - ~~Those who want to proceed more slowly with agricultural biotechnology (or end it) are concerned about the unstoppable nature of the "experiment."~~

Formatted: Bullets and Numbering

Formatted: Bullets and Numbering

Formatted: Bullets and Numbering

Formatted: Bullets and Numbering

Formatted: Bullets and Numbering

Formatted: Bullets and Numbering

Formatted: Bullets and Numbering

Formatted: Bullets and Numbering

- ~~Laboratory and field studies continue to examine the possible consequences of using GM crops, including the effects on the health of humans and nontarget organisms and the potential for transgene escape.~~

~~Opponents of GMO raise concerns about human health.~~

- ~~Many with the anti-GMO viewpoint suggest that genetic engineering may inadvertently transfer allergens from the gene source to a plant used for food.~~
- ~~To prevent this from happening, biotechnologists are removing genes that encode allergenic proteins from soybeans and other crops.~~
- ~~So far, there is no evidence that GM plants specifically designed for human consumption have adverse effects on human health.~~
- ~~In fact, some GM foods are potentially a healthier alternative to non-GM foods.~~
  - ~~For example, *Bt* maize contains 90% less of a cancer- and birth defect–causing mycotoxin called fumonisin, which is highly resistant to degradation and has been found in high concentrations in some batches of processed maize products.~~

Formatted: Bullets and Numbering

  - ~~Fumonisin is produced by a fungus (*Fusarium*) that infects insect-damaged maize.~~
  - ~~Because *Bt* maize generally suffers less insect damage than non-GM maize, it contains less fumonisin.~~
- ~~GMO opponents lobby for the clear labeling of all foods containing products of GMOs and argue for strict regulations against mixing GM foods with non-GM foods during transport, storage, and processing.~~
  - ~~Similar demands were not raised when "transgenic" crops produced by traditional plant-breeding techniques were put on the market.~~

Formatted: Bullets and Numbering

~~Some commercially grown varieties of wheat derived by traditional plant breeding techniques contain entire chromosomes (and thousands of genes) from rye.~~

~~Ecologists are concerned about possible effects of GM crops on nontarget organisms.~~

- ~~Many ecologists are concerned that the growing of GM crops might have unforeseen effects on nontarget organisms.~~
- ~~One study indicated that the larvae (caterpillars) of monarch butterflies died following laboratory consumption of milkweed leaves heavily dusted with pollen from transgenic *Bt* maize.~~
- ~~This study has since been discredited and affords a good example of the self-correcting nature of science.~~
- ~~When the original researchers shook the male maize inflorescences onto the milkweed leaves in the laboratory, they also rained staminal filaments, opened microsporangia, and other floral parts onto the leaves.~~
  - ~~It was these other floral parts, *not* the pollen, that contained high concentrations of *Bt* toxin.~~

Formatted: Bullets and Numbering

  - ~~Unlike pollen, these floral parts would not be carried by the wind to neighboring milkweed plants when shed under natural field conditions.~~
- ~~In considering the negative effects of *Bt* pollen on monarch butterflies, one must also weigh the effects of an alternative to the cultivation of *Bt* maize—the spraying of non-*Bt* maize with chemical pesticides.~~
  - ~~Such spraying is much more harmful to nearby monarch butterfly populations than *Bt* maize production.~~

Formatted: Bullets and Numbering

- ~~This controversy shows the need for accurate field-testing of all GM crops, and the importance of targeting gene expression to specific tissues.~~

~~Critics fear that introduced genes may escape from transgenic crops into related weeds.~~

- ~~Some scientists raise the possibility that introduced genes may escape from a transgenic crop into related weeds through crop-to-weed hybridization.~~
- ~~In this scenario, spontaneous hybridization between a crop engineered for herbicide resistance and a wild relative, for example, might give rise to a "superweed" that would have a selective advantage over other weeds in the wild and would be difficult to control in the field.~~
- ~~Some crops *do* hybridize with weedy relatives, and crop-to-weed transgene escape is a possibility.~~
- ~~Its likelihood depends on the ability of the crop and weed to hybridize and on how the transgenes affect the overall fitness of the hybrids.~~
  - ~~For example, a desirable crop trait, such as a dwarf phenotype, might be disadvantageous to a weed growing in the wild.~~

Formatted: Bullets and Numbering

- ~~In some cases, there are no weedy relatives nearby with which to hybridize.~~
  - ~~Soybean, for example, has no wild relatives in the United States.~~

Formatted: Bullets and Numbering

- ~~However, canola, sorghum, and many other crops do hybridize readily with weeds.~~
- ~~Many different strategies are being pursued to prevent transgene escape.~~
- ~~One approach is to engineer male sterility into plants.~~
  - ~~Then the plants would still produce seeds and fruit if pollinated by nearby nontransgenic plants, but they would produce no viable pollen.~~

Formatted: Bullets and Numbering

- ~~A second approach involves the genetic engineering of apomixis into transgenic crops.~~
  - ~~When a seed is produced by apomixis, the embryo and endosperm develop without fertilization.~~
  - ~~The transfer of this trait to transgenic crops would minimize the possibility of transgene escape via pollen because plants could be male sterile without compromising seed or fruit production.~~

Formatted: Bullets and Numbering

- ~~A third approach is to engineer the transgene into the chloroplast DNA of the crop.~~
  - ~~Chloroplast DNA in many plant species is inherited strictly from the maternal plant, so transgenes in the chloroplast cannot be transferred by pollen.~~

Formatted: Bullets and Numbering

- ~~A fourth approach is to genetically engineer flowers that develop normally but fail to open.~~
  - ~~Self-pollination would occur, but the pollen would not escape from the flower.~~

Formatted: Bullets and Numbering

- ~~The continuing debate about GMOs in agriculture is a good illustration of the relationship of science and technology to society.~~
- ~~Scientists and the public must assess the possible benefits of transgenic products versus the risks society is willing to take on a case-by-case basis, making decisions based on sound scientific information and testing rather than on reflexive fear or blind optimism.~~