

Chapter 38

Angiosperm Reproduction and Biotechnology

Lecture Outline

Overview

- 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.
- The propagation of flowering plants by sexual and asexual reproduction forms the basis of agriculture.
- 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.

A. Sexual Reproduction

1. *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, giving rise to multicellular male and female haploid plants—the **gametophytes**.
 - The gametophytes produce gametes—sperm and eggs.
 - Fertilization results in diploid zygotes, which divide by mitosis to form new sporophytes.
- In angiosperms, the sporophyte is the dominant generation, the conspicuous plant we see.
 - Over the course of seed plant evolution, gametophytes became reduced in size and dependent on their sporophyte parents.
 - Angiosperm gametophytes are the most reduced of all plants, consisting of only a few cells.
- In angiosperms, the sporophyte produces a unique reproductive structure, the flower.
 - Male and female gametophytes develop within the anthers and ovules, respectively, of a sporophyte flower.
 - Pollination by wind, water, or animals brings a male gametophyte (pollen grain) to a female gametophyte contained in an ovule embedded in the ovary of a flower.
 - Union of gametes (fertilization) takes place within the ovary.
 - Ovules develop into seeds, while the ovary itself develops into the fruit around the seed.

2. *Flowers are specialized shoots bearing the reproductive organs of the angiosperm sporophyte.*

- Flowers, the reproductive shoots of the angiosperm sporophyte, are typically composed of four whorls of highly modified leaves called floral organs, which are separated by very short internodes.
 - Unlike the indeterminate growth of vegetative shoots, flowers are determinate shoots in that they cease growing once the flower and fruit are formed.
- The four kinds of floral organs are the **sepals, petals, stamens, and carpels**.
 - Their site of attachment to the stem is the **receptacle**.
- 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 pollen sacs.
 - The pollen sacs 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 others, several carpels are fused into a single structure, producing an ovary with two or more chambers, each containing one or more ovules.
- The anthers and the ovules bear sporangia, where spores are produced by meiosis and where gametophytes later develop.
 - The male gametophytes are sperm-producing structures called **pollen grains**, which form within the pollen sacs of anthers.
 - The female gametophytes are egg-producing structures called **embryo sacs**, which form within the ovules in ovaries.
- Pollination is the transfer of pollen from an anther to a stigma.
 - It begins the process by which the male and female gametophytes are brought together so their gametes can unite.
 - Pollination occurs when pollen released from anthers is carried by wind, water, or animals to land on a stigma.
 - Each pollen grain produces a pollen tube, which grows down into the ovary via the style and discharges sperm into the embryo sac, fertilizing the egg.
 - The zygote gives rise to an embryo.
 - The ovule develops into a seed, and the entire ovary develops into a fruit containing one or more seeds.
 - Fruits carried by wind, water, or animals disperse seeds away from the source plant where the seed germinates.
- Numerous floral variations have evolved during the 130 million years of angiosperm history.

- Plant biologists distinguish between **complete flowers**, those having all four organs, and **incomplete flowers**, those lacking one or more of the four floral parts.

- A **bisexual flower** is equipped with both stamens and carpels.

- All complete and many incomplete flowers are bisexual.

- A **unisexual flower** is missing either stamens (therefore, a carpellate flower) or carpels (therefore, a staminate flower).

- A **monoecious** plant has staminate and carpellate flowers at separate locations on the same individual plant.

- For example, maize and other corn varieties have ears derived from clusters of carpellate flowers, while the tassels consist of staminate flowers.

- A **dioecious** species has staminate flowers and carpellate flowers on separate plants.

- For example, date palms have carpellate individuals that produce dates and staminate individuals that produce pollen.

- In addition to these differences based on the presence of floral organs, flowers vary in size, shape, and color.

- Much of this diversity represents adaptations of flowers to different animal pollinators.

- The presence of animals in the environment has been a key factor in angiosperm evolution.

3. Male and female gametophytes develop within anthers and ovaries, respectively; pollination brings them together.

- The male gametophyte begins its development within the sporangia (pollen sacs) of the anther.

- Within the sporangia are microsporocytes, each of which will form four haploid **microspores** through meiosis.

- Each microspore can give rise to a haploid male gametophyte.

- A microspore divides once by mitosis and produces a generative cell and a tube cell.

- The generative cell will eventually form sperm.

- During maturation of the male gametophyte, the generative cell passes into the tube cell.

- The tube cell, enclosing the generative cell, produces the pollen tube, which delivers sperm to the egg.

- This is a pollen grain, an immature male gametophyte.

- This two-celled structure is encased in a thick, ornate, distinctive, and resistant wall.

- A pollen grain becomes a mature gametophyte when the generative cell divides by mitosis to form two sperm cells.

- In most species, this occurs after the pollen grain lands on the stigma of the carpel and the pollen tube begins to form.

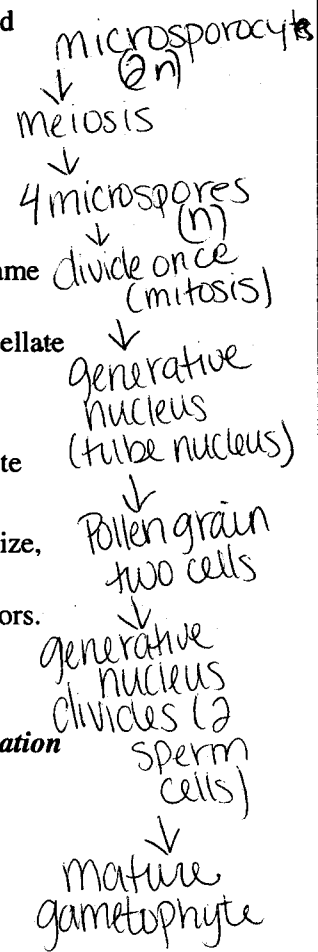
- The pollen tube grows through the long style of the carpel and into the ovary, where it releases the sperm cells in the vicinity of the embryo sac.

- Ovules, each containing a single sporangium, form within the chambers of the ovary.

- One cell in the sporangium of each ovule, the megasporocyte, grows and then goes through meiosis, producing four haploid **megaspores**.

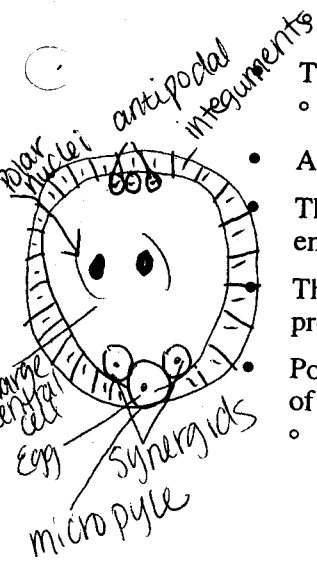
- In many angiosperms, only one megaspore survives.

- This megaspore divides by mitosis three times without cytokinesis, forming in one cell with eight haploid nuclei.



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Membranes partition this mass into a multicellular female gametophyte—the embryo sac.

Three cells sit at one end of the embryo sac: two synergid cells flanking the egg cell.

- The synergids function in the attraction and guidance of the pollen tube.

- At the other end of the egg sac are three antipodal cells of unknown function.

The other two nuclei, the polar nuclei, share the cytoplasm of the large central cell of the embryo sac.

The ovule now consists of the embryo sac and the surrounding integuments, layers of protective tissue from the sporophyte that will eventually develop into the seed coat.

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.

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

- Some flowers self-fertilize or “self,” but most angiosperms have mechanisms that make this difficult or impossible.

- 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 they are unisexual.

- 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.

- Alternatively, they 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.”

- The key difference is that the animal immune system rejects nonself, but 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 and the carpel’s stigma have matching alleles at the *S*-locus, then the pollen grain fails to initiate or complete the formation of a pollen tube.

- Because the pollen grain is haploid, it will be recognized as “self” if its one *S*-allele matches either of the two *S*-alleles of the diploid stigma.

- Although self-incompatibility genes are all referred to as *S*-loci, such genes have evolved independently in various plant families.

Self pollination
Cross pollination

- As a consequence, self-recognition blocks pollen tube growth by different molecular mechanisms.
- In some cases, the block occurs in the pollen grain itself, called gametophytic self-incompatibility.
 - In some species, self-recognition leads to enzymatic destruction of RNA within the rudimentary pollen tube.
 - RNases are present in the style of the carpel, and they can enter the pollen tube and attack its RNA only if the pollen is of a "self" type.
- In other cases, the block is a response by the cells of the carpel's stigma, called sporophytic self-incompatibility.
 - In some species, self-recognition activates a signal transduction pathway in epidermal cells that prevents germination of the pollen grain.
 - Germination may be prevented when cells of the stigma take up additional water, preventing the stigma from hydrating the relatively dry pollen.
- Basic research on self-incompatibility may lead to agricultural applications.
 - Many agricultural plants are self-compatible.
 - Plant breeders sometimes 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 maximize hybrid seed production, breeders currently prevent self-fertilization by laboriously removing anthers from the parent plants that provide the seeds or by developing male sterile plants.
 - Eventually, it may be possible to impose self-incompatibility on species that are normally self-compatible.

5. 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 extends down the style toward the ovary.
 - The nucleus of the generative cell divides by mitosis to produce two sperm, the male gametes.
 - The germinated pollen grain contains the mature male gametophyte.
 - Directed by a chemical attractant, possibly calcium, the tip of the pollen tube enters the ovary, probes through the micropyle (a gap in the integuments of the ovule), and discharges two sperm within the embryo sac.
- 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 nucleus in the central cell.
 - 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 termed **double fertilization**.
 - Double fertilization ensures that the endosperm will develop only in ovules where the egg has been fertilized.
 - This prevents angiosperms from squandering nutrients.

- Normally nonreproductive tissues surrounding the embryo have prevented researchers from visualizing fertilization in plants, but recently, scientists have been able to isolate sperm cells and eggs and observe 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, this may be through deposition of cell wall material that mechanically impedes sperm.
 - In maize, this barrier is established within 45 seconds after the initial sperm fusion with the egg.

6. 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.
 - It 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 endosperm is rich in nutrients, which it provides to the developing embryo.
 - In most monocots and some dicots, the endosperm also stores nutrients that can be used by the seedling after germination.
 - In many dicots, 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 first mitotic division of the zygote is transverse, splitting the fertilized egg into a basal cell and a terminal cell.
 - The terminal cell gives rise to most of the embryo.
 - The basal cell continues to divide transversely, producing a thread of cells, the suspensor, which anchors the embryo to its parent.
 - The suspensor functions in the transfer of nutrients to the embryo from the parent.
- 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 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 becomes dormant until the seed germinates.
 - The embryo and its food supply are enclosed by a protective **seed coat** formed by the integuments of the ovule.
- In the seed of a common bean, 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**; above it is the **epicotyl**.
 - At the tip of the epicotyl is the plumule, consisting of the shoot tip with a pair of miniature leaves.
 - The hypocotyl terminates in the **radicle**, or embryonic root.
- While the cotyledons of the common bean supply food to the developing embryo, the seeds of some dicots, such as castor beans, retain their food supply in the endosperm and have cotyledons that are very thin.
 - The cotyledons will 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.

7. 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.
- The wall of the ovary becomes the **pericarp**, the thickened wall of the fruit, while other parts of the flower wither and are shed.
 - In some angiosperms, other floral parts contribute to the fruit.
 - In apples, the fleshy part of the fruit is derived mainly from the swollen receptacle, while the core of the apple fruit develops from the ovary.
- Fruits are classified into several types, depending on their developmental origin.
 - A typical fruit is derived from a single carpel or several fused carpels and is called a **simple fruit**.
 - Some simpler fruits are fleshy, like a peach, while others are dry, like a pea pod.

Fig 35.8
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Fig 35.9

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- 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, like a raspberry.
 - 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.
 - The fruit usually ripens about the same time as its seeds are completing their development.
 - For a dry fruit such as a soybean pod, ripening is a little more than senescence of the fruit tissues, which allows the fruit to open and release the seeds.
 - The ripening of fleshy fruits is more elaborate, 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.
 - Color changes from green to red, orange, or yellow.
 - The fruit becomes sweeter as organic acids or starch molecules are converted to sugar.

8. *Evolutionary adaptations of seed germination contribute to seedling survival.*

- As a seed matures, it dehydrates and enters a **dormancy** phase, a condition of extremely low metabolic rate and a suspension of growth and development.
- Conditions required to break dormancy and resume growth and development vary between 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, 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 new opportunities and open space.
 - Where winters are harsh, seeds may require extended exposure to cold.
 - 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 or physical abrasion 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 longer.
 - It depends 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 some other environmental disruption.
- Germination of seeds depends on imbibition, the uptake of water due to the low water potential of the dry seed.
 - This causes the expanding seed to rupture its seed coat and triggers metabolic changes in the embryo that enable it to resume growth.
 - Enzymes begin digesting the storage materials of 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 dicots, a hook forms in the hypocotyl, and growth pushes it aboveground.
 - Stimulated by light, the hypocotyl straightens, raising the cotyledons and epicotyl.
- 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 tough seed gives rise to a fragile seedling that will be exposed to predators, parasites, wind, and other hazards.
 - Because 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.
 - This provides ample genetic variation for natural selection to screen.
 - However, flowering and fruiting in sexual reproduction is an expensive way of plant propagation in terms of the resources consumed.

B. Asexual Reproduction

1. Many plants clone themselves by asexual reproduction.

- Many plants clone themselves by **asexual reproduction**.
- Many plants are capable of both sexual and asexual reproduction, and each offers advantages in certain situations.
 - When reproducing asexually, a plant passes on all of its genes to its offspring.
 - When reproducing sexually, 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.
 - The offspring are not as frail as the seedlings produced by sexual reproduction in seed plants.

- They are usually mature vegetative fragments of the parent plant.
- 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.
 - Seeds produced by sexual reproduction can disperse to new locations and wait for favorable growing conditions.
 - Seed dormancy allows growth to be suspended until hostile environmental conditions are reversed.
- 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 fragments of some plants can develop into whole offspring.
- In **fragmentation**, a parent plant separates into parts that re-form into whole plants.
- A variation of this occurs in some dicots, in which 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 produce seed without their flowers being fertilized.
 - A diploid cell in the ovule gives rise to the embryo, and the ovules mature into seeds.
 - These seeds are dispersed by the wind.
 - This combines asexual reproduction and seed dispersal.

2. *Vegetative propagation of plants is common in agriculture.*

- Various methods have been developed for the asexual propagation of crop plants, orchards, and ornamental plants.
 - These can be reproduced asexually from plant fragments called cuttings.
 - These are typically pieces of shoots or stems.
- At the cut end, a mass of dividing, undifferentiated cells called the **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.
 - Some plants, including African violets, can be propagated from single leaves.
- In others, 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.
- 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.
 - This 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.
 - 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 characteristic 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.
 - 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.
 - 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.
 - This test-tube cloning can be used to clone a single plant into thousands of copies by subdividing calluses as they grow.
 - 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 the introduction of foreign genes into plants start with small pieces of plant material or single plant cells.
 - **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 cellulases and pectinases.
 - 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.
- One success of this technique has been the development of 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.
 - The hybrids are also resistant, enabling a farmer to “weed” a potato field with an herbicide without killing the potato plants.

C. Plant Biotechnology

- Plant biotechnology has two meanings.

- One is innovation in the use of plants, or of substances obtained from plants, to make products of use to humans.
 - This began in prehistory.
- In a more specific sense, biotechnology refers to the use of genetically modified (GM) organisms in agriculture and industry.
- Over the past two decades, the terms *genetic engineering* and *biotechnology* have become synonymous in the media.

1. Neolithic humans created new plant varieties by artificial selection.

- Humans have intervened in the reproduction and genetic makeup of plants for thousands of years.
 - Neolithic (late Stone Age) humans domesticated virtually all of our crop species over a relatively short period about 10,000 years ago.
 - Even for these 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.
- 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 selected for a larger central axis (“the cob”), permanent attachment of the maize kernels to the cob, and a permanent protection by tough, overlapping leaf sheathes (“the husk”).
- Maize is a staple in many developing countries.
 - However, because most varieties are a relatively poor source of protein, a diet of maize must be supplemented with other protein sources such as beans.
 - Forty years ago, a mutant maize known as *opaque-2* was discovered with increased levels of tryptophan and lysine, two essential amino acids.
 - This maize is more nutritious, and swine fed with *opaque-2* maize gain weight three times faster than those fed with normal maize.
 - However, the beneficial trait was closely associated with several undesirable ones.
 - It took nearly 20 years for plant breeders, using conventional breeding methods of hybridization and artificial selection, to create maize varieties that had higher nutritional value without the undesirable traits.
 - If modern methods of genetic engineering had been available, the desirable varieties could have been developed in only a few years.
- Unlike traditional plant breeders, modern plant biotechnologists, using the techniques of genetic engineering, are not limited to transferring genes between closely related species or varieties of the same species.
 - Genes can be transferred between distantly related plant species to create transgenic plants.

2. Biotechnology is transforming agriculture.

- Whatever the social and demographic causes of human starvation around the world, increasing food production seems like a humane objective.
 - Because land and water are the most limiting resources for food production, the best option is to increase yields on available land.

- Based on conservative estimates of population growth, the world's farmers will have to produce 40% more grain per hectare to feed the human population in 2020.
- Plant biotechnology can help make these plant yields possible.
- The commercial adoption by farmers of transgenic crops has been one of the most rapid cases of technology transfer in the history of agriculture.
 - These crops include cotton, maize, and potatoes that contain genes from a bacterium *Bacillus thuringiensis*.
 - These "transgenes" encode for a protein (*Bt* toxin) that effectively controls several insect pests.
 - This has reduced the need for application of chemical insecticides.
 - *Bt* toxin is produced in the plant as a harmless protoxin that becomes toxic when activated by alkaline conditions in the guts of insects.
 - In the acid guts of vertebrates, the protoxin is destroyed without becoming active.
- Considerable progress has been made in the development of transgenic plants of cotton, maize, soybeans, sugar beat, and wheat that are tolerant of a number of herbicides.
- Researchers have also engineered transgenic plants with enhanced resistance to disease.
 - Transgenic papaya resistant to ringspot virus was introduced to Hawaii, thereby saving the papaya industry.
- "Golden rice," a transgenic variety with a few daffodil genes that increase quantities of vitamin A, is under development.
 - It is hoped that this rice will prevent blindness in those whose diet is chronically deficient in vitamin A.

3. *Plant biotechnology has incited much public debate.*

- Many people, including some scientists, are concerned about the unknown risks associated with the release of GM organisms into the environment.
 - Much of the animosity regarding GM organisms is political, economic, or ethical in nature, but there are also biological concerns about GM crops.
 - The most fundamental debate centers on the extent to which GM organisms are an unknown risk that could potentially cause harm to human health or to the environment.
- One specific concern is that genetic engineering could potentially transfer allergens, molecules to which some humans are allergic, from a gene source to a plant used for food.
 - Biotechnologists are engaged in removing genes that code allergenic proteins from soybeans and other crops.
 - So far there is no credible evidence that any GM plants specifically designed for human consumption have had any adverse effect on human health.
 - Some GM foods are potentially healthier than non-GM foods.
 - *Bt* maize contains 90% less of a carcinogen produced by a fungus that infects insect-damaged maize.
 - Since *Bt* maize suffers less insect damage, it contains less of the fungal carcinogen.
 - GM-organism opponents lobby for clear labeling of all foods made wholly or in part from products of GM organisms and for strict regulations against mixing GM foods with non-GM foods at any stage of food preparation.
 - Biotechnology advocates argue that similar demands were not raised when "transgenic" crops were produced by traditional plant-breeding techniques.

- There are concerns that growing GM crops might have unforeseen effects on nontarget organisms.
 - One study suggested that the caterpillars of monarch butterflies responded adversely and even died after consuming milkweed leaves heavily dusted with pollen from transgenic maize that produced *Bt* toxin.
 - *Bt* toxin is normally toxic to pests closely related to monarch butterflies.
 - This study has since been discredited.
 - When the original researchers shook the male maize inflorescences onto the milkweed leaves in the laboratory, other floral parts rained onto the leaves.
 - It was those floral parts, not the pollen, that contained *Bt* toxin in high concentrations.
 - These floral parts would not be blown by wind to neighboring milkweed plants under normal field conditions.
 - The alternative to transgenic maize, spraying chemical insecticides, is more harmful to monarch populations.
- Probably the most serious concern that some scientists raise is the possibility that introduced genes may escape from a transgenic crop into related weeds through crop-to-weed hybridization.
 - This spontaneous hybridization may lead to a “superweed,” which may have a selective advantage and be difficult to control.
 - 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.
 - Strategies to minimize risk include planting a border of unrelated plants with which the transgenic plants could not hybridize.
 - Another possibility is breeding male sterility in transgenic plants.
 - Alternatively, the transgenes can be engineered into chloroplasts, which are inherited maternally only.
- “Terminator technology” may offer another approach to the problem of transgene escape.
 - Plants that are genetically modified to undergo the terminator process grow normally until the last stages of seed maturation.
 - At this point, a gene expressing a “terminator” protein toxic to plants but harmless to animals is activated in the new seeds.
 - The seeds are inviable.
 - Terminator proteins are only produced if the original seeds are pretreated with a specific chemical.
- There is the potential for seed companies to control supplies of viable seeds.
 - Seeds sold to farmers would be pretreated with the chemical that activates the terminator process.
 - Some argue that poor farmers in developing countries will not be able to produce their own seed, because the plants they grow would produce inviable seeds.
- The continuing debate about GM organisms in agriculture exemplifies the relationship of science and technology to society.
 - Technological advances almost always involve some risk that unintended outcomes could occur.
 - In the case of plant biotechnology, zero risk is unrealistic and probably unattainable.

- Scientists and the public need to assess the possible benefits of transgenic products versus the risks society is willing to take on a case-by-case basis.
- These discussions and decisions should be based on sound scientific information and testing rather than on reflexive fear or blind optimism.