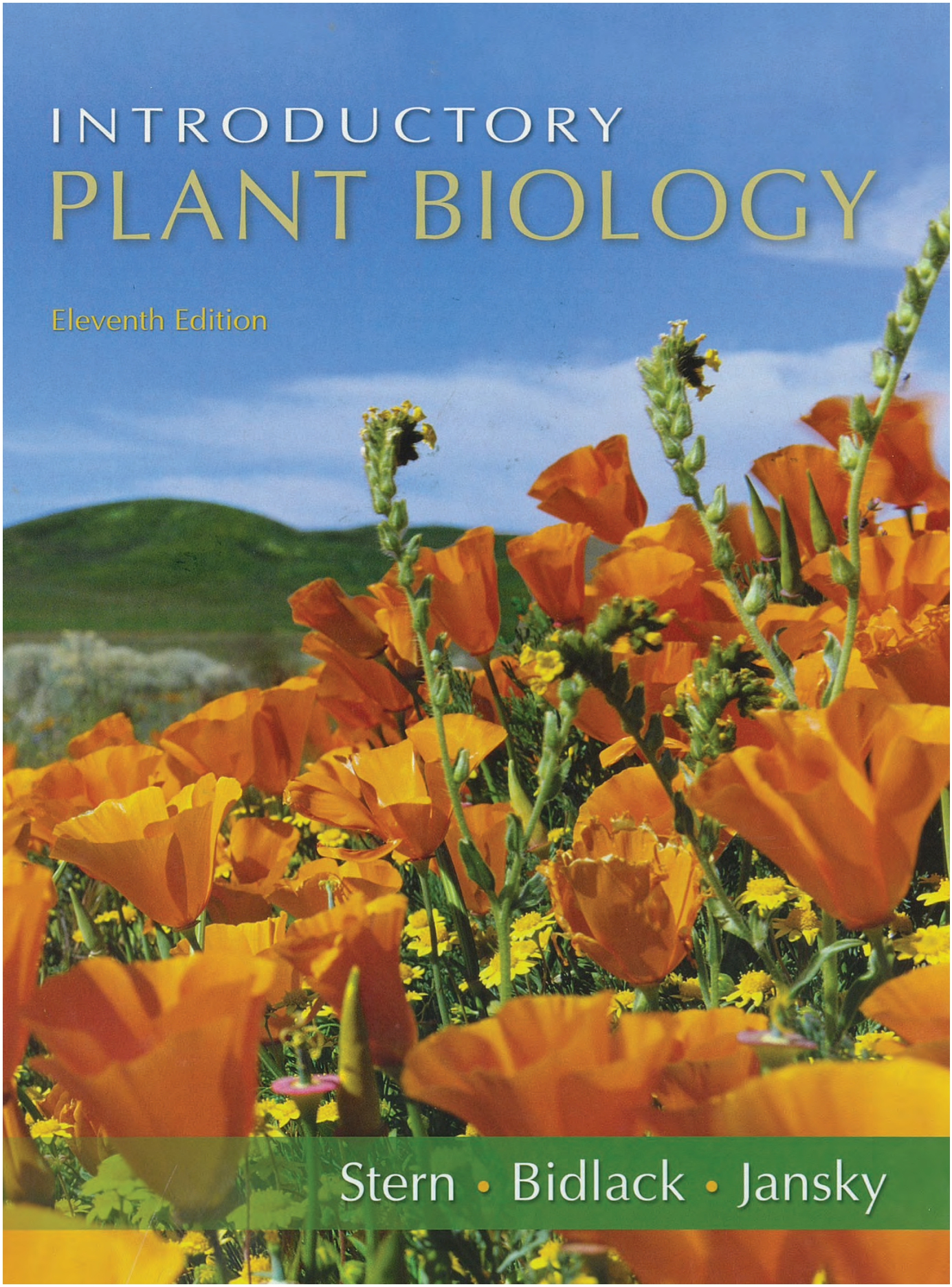


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Edition Eleven

INTRODUCTORY

PLANT BIOLOGY

Kingsley R. Stern
California State University ~ Chico

James E. Bidlack
University of Central Oklahoma

Shelley H. Jansky
University of Wisconsin ~ Madison

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INTRODUCTORY PLANT BIOLOGY, ELEVENTH EDITION

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About the Cover

In 1815, a Russian exploratory group sailed its vessel into San Francisco Bay and dropped anchor. The explorers noted the beauty of the surrounding hills, which were covered with thousands of bright golden to orange flowers. These flowers became known as California poppies (*Eschscholzia californica*). The poppies' generic name honors Johann Friedrich Gustav von Eschscholtz, the ship's surgeon. When the scientific name was published formally, the "t" in Eschscholtz was inadvertently omitted.

California poppies grow in well-drained soils in virtually any area with a Mediterranean climate. They are native plants in locations below 6,000 feet, including Baja, California, other western states, and western Texas. More than 90 subspecies, varieties, and forms of poppy exist in the literature; many varieties are developed horticulturally. The California poppy was formally named California's state flower in 1903. It is illegal to pick California poppies (or any other wildflowers in the state) within 25 feet of a highway or road.

Antelope Valley, in northern Los Angeles County, is the site of a 1,745-acre poppy reserve. The entire area is covered with poppies in bloom in the spring. The cover image was photographed near Lancaster, California.

This book is printed on recycled, acid-free paper containing 10% post consumer waste.

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About the Authors



Jim Bidlack, Kingsley Stern, and Shelley Jansky at Kingsley's office residence in Paradise, California.

In late 1999/early 2000, Kingsley Stern and McGraw-Hill Publishers initiated a search to find outstanding scientists to join the author team for *Introductory Plant Biology*. With nearly three decades of publishing this successful textbook, it was clear to Dr. Stern and the people at McGraw-Hill that new botanists would help to further enrich the content and continue the dedication and hard work needed for future editions. Many professors using the text came to mind but several, in particular, had expressed the desire, knowledge, and enthusiasm to become successful authors. After review of these individuals, Dr. Stern hand-picked two botanists, Dr. Jim Bidlack and Dr. Shelley Jansky, to work with him. Over the years, the team has corresponded directly through personal meetings, dozens of phone calls, and hundreds of e-mails, to improve upon and update content in the book. This eleventh edition reflects their continued teamwork and dedication to the profession of plant biology and related disciplines.

Kingsley R. Stern

Kingsley R. Stern received his undergraduate education at Wheaton College, where he majored in botany. In graduate school, he continued his studies in botany, while minoring in zoology and horticulture. He received his Master's Degree from the University of Michigan at Ann Arbor, and his Ph.D. from the University of Minnesota at Minneapolis. He took additional graduate courses at the University of Illinois in Urbana, and at the Hopkins Marine Station of Stanford University in Pacific Grove, California. While pursuing his studies, Dr. Stern held part-time positions as an instructor in biology at Hamline University and as an instructor in botany at the University of Minnesota, where he received a Conway McMillan Research Fellowship. After accepting a position as Assistant Professor of Botany at California State University in Chico, he was promoted to Associate, and then Full Professor. In 1987, while on leave, he was a Visiting Professor of Botany at the Manoa campus of the University of Hawaii. During his tenure at California State University, Dr. Stern taught eight different courses, several of which he introduced to the curriculum, and was on the committees of over 50 graduate students. To date, an estimated 15,000 students have enrolled in his classes. He has received several grants from the National Science Foundation in support of biosystematic investigations in Fumariaceae (Fumitory Family). These investigations, which included studies at the Swedish National Pollen Laboratory in Stockholm, eventually led to the publication of about 20 research papers in professional journals. Dr. Stern's academic awards include being named Outstanding Professor at California State University in 1993, and receiving the school's Distinguished Service Award in 1999 for establishing and developing the University Herbarium, which grew from 2,000 to more than 74,000 specimens. Dr. Stern was most recently honored

...

at the 100th Meeting of the Botanical Society of America, where he accompanied many world-famous botanists in recognition with the Society's Centennial Award.

Editor's Note: Known as a dedicated botanist and teacher, Kingsley passed away a few days after completing final revisions on the eleventh edition.

James E. Bidlack

Jim Bidlack received a B.S. Degree in Agronomy, with a Soil & Crop Option, from Purdue University in 1984 and continued his education with a Master's Degree in Crop Physiology at the University of Arkansas in 1986. Upon completing a Ph.D. in Plant Physiology at Iowa State University in 1990, Jim joined the teaching faculty at the University of Central Oklahoma (UCO) where he is a Professor of Biology. His first paper was published from undergraduate research at Purdue University on the use of synthetic growth regulators to stimulate seed germination. Subsequent work at Arkansas, Iowa, and Oklahoma focused on soybean physiology, cell wall chemistry, and alternative crops, as well as teaching responsibilities in plant biology. Equipment and student salaries for Jim's research projects have been funded by grants from the National Science Foundation (NSF) and the United States Department of Agriculture (USDA). About a dozen refereed publications, as well as 40 popular articles and abstracts, have resulted from this work. Jim has been active with campus organizations, serving two terms as the local President of the American Association of University Professors (AAUP), and sponsoring Alpha Tau Omega Fraternity, Circle K International Club, and Mortar Board Honor Society. He has been recognized with UCO's Presidential Partner's Excellence in Teaching Award; University Merit Awards in Service, Research, and Teaching; Biology Club Teaching Award; and Pre-Med Teaching Award, as well as AAUP's Distinguished Scholar and Service Awards. Some of Jim's additional responsibilities have included participation on NSF and USDA Review Panels, membership on the National Biology Editorial Board for the Multimedia Educational Resource for Learning and Online Teaching (MERLOT) Project, and Executive Directorship of the Metabolism Foundation. He and his wife, Amy, enjoy hiking and fishing, and spend free time with their daughter, Hanna, at family farms in Oklahoma and Nebraska.

Shelley H. Jansky

Shelley H. Jansky received a Bachelor's Degree in Biology from the University of Wisconsin–Stevens Point in 1982, and M.S. and Ph.D. degrees in Plant Breeding and Plant Genetics from the University of Wisconsin–Madison in 1984 and 1986, respectively. Her graduate work focused on developing methods to incorporate genes from wild relatives of potato into the cultivated potato. Then, she spent four years as an Assistant Professor at North Dakota State University, teaching courses in plant breeding and plant propagation, and performing research in the potato breeding program. She taught courses in botany, genetics, horticulture, and plant genetics at the University of Wisconsin–Stevens Point from 1990 until 2004. In 2004, she moved to Madison, Wisconsin, where she is a Research Geneticist with the U.S. Department of Agriculture and a professor in the Department of Horticulture at the University of Wisconsin–Madison. Her potato research program focuses on utilization of wild potato relatives for improvement of cultivated potato varieties. She received the University of Wisconsin–Stevens Point Excellence in Teaching Award in 1992 and the University Scholar Award in 2000. She lives near Madison, where she enjoys fishing, gardening, sailing, and swimming with her husband, John, and two children, Mark and Kristin.

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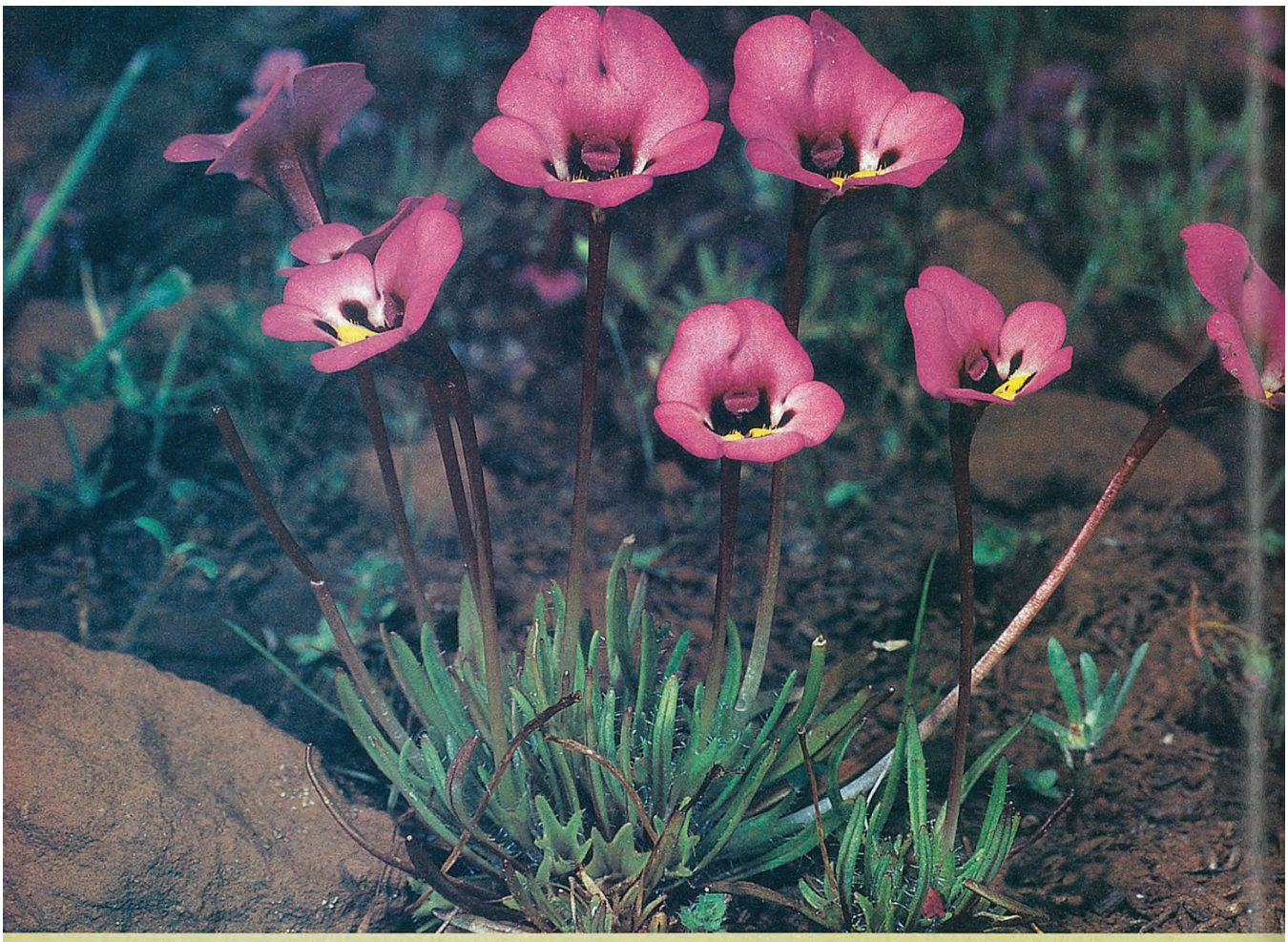
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CHAPTER

13

Genetics

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Quantitative Traits
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Linkage and Mapping
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Summary
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Learning Online

Narrow-tubed monkey flowers (*Mimulus angustatus*), a vernal pool species of northern California. *(Courtesy Robert A. Schlising)*

OVERVIEW

In this chapter, the topic of genetics is introduced with the story of Barbara McClintock's discovery of transposable elements ("jumping genes") in corn. The chapter progresses from genetics at the molecular level to the cellular level (cytogenetics) to the organismal level (Mendelian genetics and related topics) and then finishes with population genetics (the Hardy-Weinberg law).

Some Learning Goals

1. Identify components of a DNA molecule and know how they are arranged in the molecule.
2. Describe the functions of DNA.
3. Describe how a DNA molecule replicates.
4. Know the function of transcription and outline its steps.
5. Know the function of translation and outline its steps.
6. Distinguish between somatic and germ-line mutations.
7. Describe the significance of translocations and inversions.
8. Distinguish between aneuploids and polyploids.
9. Understand the significance of Mendel's experiments with peas.
10. Give the ratios of the offspring in the first two generations from a monohybrid and a dihybrid cross. Describe the genotypes involved.
11. Distinguish between genotype and phenotype; heterozygous and homozygous.
12. Be able to solve simple genetics problems involving dominance and incomplete dominance.
13. Show how genes may interact with each other to influence phenotype.
14. Explain how genotype influences phenotype.
15. Describe features of a quantitative trait.
16. Describe where extranuclear DNA is located and how it differs from nuclear DNA.
17. Explain how linkage can produce ratios that deviate from Mendelian ratios.
18. Describe the Hardy-Weinberg law.

Every so often, someone comes along who is able to push beyond our limits of understanding in science and change the way we view the natural world. Barbara McClintock was one of the most significant scientists in 20th-century biology because she caused a major shift in the way we view gene organization. She was a geneticist who carried out most of her work at the Cold Spring Harbor laboratory in New York in the 1940s and 1950s. While looking at corn seedlings for one of her genetic studies, she noticed that streaks of color often appeared where they did not seem to belong. There were patches of yellow in green leaves or patches of green in white leaves. She also noticed spots of color in corn kernels that should have been colorless, based on her genetic studies (Fig. 13.1). Instead of ignoring these plants as genetic oddities, McClintock undertook years of research to identify the cause of these patterns.

In the early 1950s, McClintock published work introducing the concept of **transposition,** or the movement of a piece of a chromosome to another chromosomal location. A **transposable genetic element** (or *jumping gene* in popular literature) is a gene or a small DNA fragment that can move to a new location on the same chromosome or even to another chromosome. If it moves into an existing gene, then the function of that gene is disrupted. A transposable element can also move out of a gene and restore its original function. So, the patches of yellow in green leaves were regions where transposable elements were inserted into a gene involved in chlorophyll synthesis. Green areas on white leaves resulted



Figure 13.1 Part of an ear of corn showing the effects of transposable elements. The speckles in the center kernel are clusters of cells in which a transposable element has removed itself from a purple pigment gene so purple pigment is produced. Yellow areas in that kernel do not express purple pigment because the transposable element has interrupted that pigment gene.

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when a transposable element moved out of a chlorophyll synthesis gene and allowed it to function again.

McClintock was a highly respected figure in the field of genetics and was able to describe in detail the actions of several transposable elements in corn. Accordingly, even though the concept of movable genes was difficult to fit into the framework of conventional genetics, McClintock's ideas were generally accepted by her peers. Before long, transposable elements were found in other organisms as well.

The discovery of the structure of DNA by James Watson and Francis Crick in 1953 ushered in the new field of **molecular genetics.** At that time, geneticists thought of McClintock's work as a remnant of a previous era and not relevant to modern genetics. However, studies of DNA and gene structure transformed the concept of a gene. Genes were no longer abstract entities but were actual sequences of nucleic acids that could be isolated and characterized. The concept of mutation within a gene became believable. In addition, numerous studies found transposable elements in other organisms.

McClintock's work was formally recognized in 1983 when she was awarded a Nobel Prize. We now know that transposable elements are widespread and have probably been in organisms for a long time. We do not know, however, if they represent genetic parasites causing mutations as they move about an organism's genetic material or if they perform valuable functions. One theory is that they allow nature to tinker with chromosomes much as human genetic engineers do. It may be evolutionarily beneficial to copy, move, and rearrange pieces of chromosomes, creating new and occasionally better combinations of genes within an organism.

MOLECULAR GENETICS

In Chapter 3, we mentioned that chromosomes in the nucleus of each cell carry genetic information that is passed on from one generation to the next. Chromosomes are composed of two types of large molecules—DNA and protein. Until the early 1950s, most scientists believed that proteins carried the genetic information because they thought that the 20 amino acids in proteins could provide more diversity than the four bases in DNA. We now know, of course, that DNA is responsible for carrying genetic information.

Structure of DNA

Chromosomes are composed of chromatin, which is DNA and associated proteins. A DNA molecule is a simple, elegant chain of building blocks called **nucleotides.** Each nucleotide consists of three parts: (1) a nitrogen-containing compound, called a **base;** (2) a 5-carbon sugar, named **deoxyribose;** and (3) a phosphate group. Both the nitrogenous base and the phosphate group are bonded to the sugar (Fig. 13.2). Four types of nucleotides occur in DNA. Each has a unique

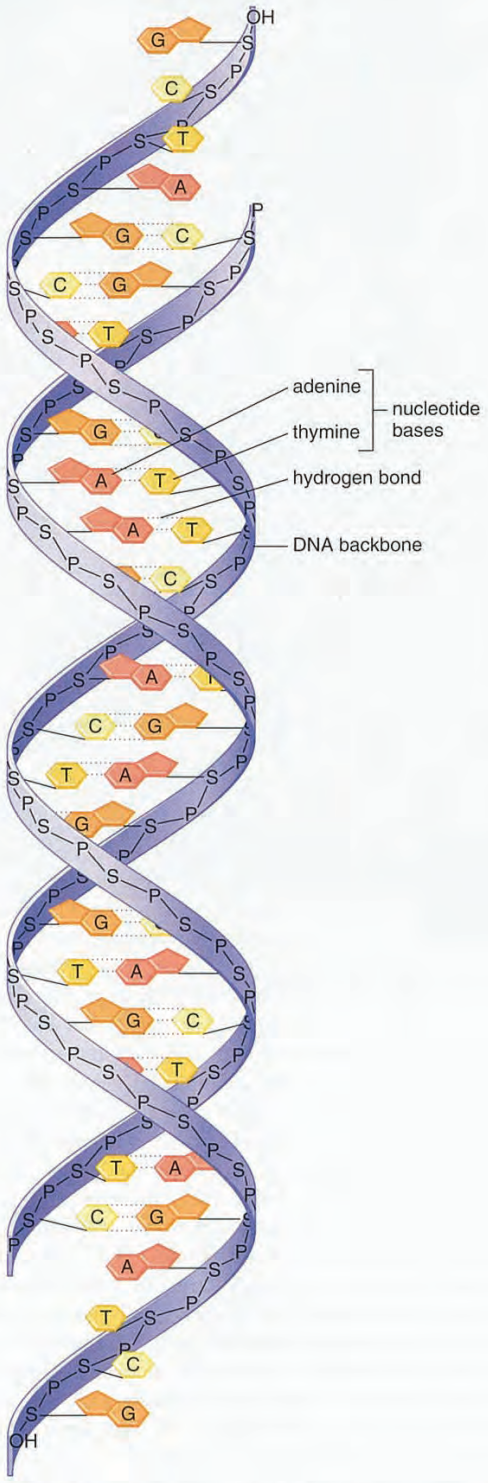


Figure 13.2 Structure of a DNA molecule. In this enlargement of a small portion of a DNA molecule, the rungs of the twisted ladder formed by the two entwined spiraling strands consist of nitrogen-containing bases supported by alternating units of sugar (S) and phosphate (P) molecules. The purines adenine or guanine (A or G) occur opposite the pyrimidines thymine or cytosine (T or C). The purines and pyrimidines opposite each other are held together by hydrogen bonds linking the nitrogenous bases of the paired molecules. The double helix is 2 nanometers wide.

nitrogenous base, but all have the same phosphate group and deoxyribose sugar. Two of the bases—**adenine** (A) and **guanine** (G)—are called **purines.** Each has a molecular structure that resembles two linked rings. The other two bases—**cytosine** (C) and **thymine** (T)—are called **pyrimidines.** They each have a molecular structure consisting of a single ring.

The nucleotides in a DNA molecule are bonded to each other in such a way that they form a chain that looks like a ladder twisted into a spiral, or a helix. Each of the two sides of the "ladder" is composed of alternating sugar and phosphate groups (Fig. 13.3). Each sugar is also bound to a base. Hydrogen bonds hold each base on one side of the helix to another base on the other side, making the "rungs" of the ladder. Although the structure of a DNA molecule is very simple—alternating sugar and phosphate groups on the outside and pairs of bases in the middle—it provides all the genetic diversity on the planet. The variation comes in the form of base pairs. A single chromosome contains a DNA molecule that is often hundreds of millions of base pairs in length. The sequence of base pairs on a DNA molecule determines whether, for example, that DNA will direct the synthesis of a chlorophyll molecule or a hemoglobin molecule.

As mentioned earlier, in the early 1950s, James Watson and Francis Crick began to unravel the mystery of DNA structure. Much of their work involved piecing together existing information to develop a model. They knew Linus Pauling had postulated that the structure of DNA might be similar to the structure of protein. Pauling had shown part of the structure of some proteins to be helical and maintained by hydrogen bonds between the amino acids. Watson and Crick also knew from X-ray work by Rosalind Franklin and Maurice Wilkins that DNA molecules are composed of regularly repeating units in a helical arrangement. Finally, studies by Erwin Chargaff indicated that the amount of pyrimidine nucleotides (cytosine + thymine) in DNA equals the amount of purine nucleotides (adenine + guanine). This suggested to Watson and Crick that purines pair with pyrimidines.

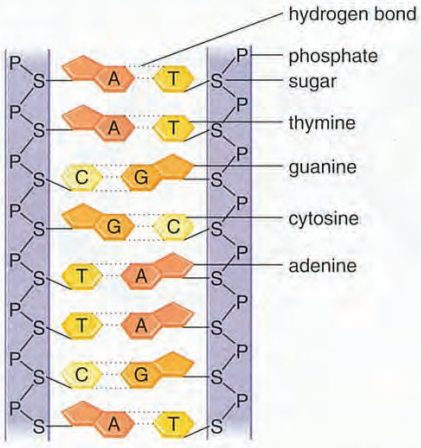


Figure 13.3 The pairing of nucleotides in a tiny portion of a molecule of DNA. The variations in sequences of pairs are virtually unlimited.

When they had put together all the facts, Watson and Crick concluded that a DNA molecule consists of a double helix whose two strands appear to be wrapped around an invisible pole—one strand spiraling in one direction and the other strand spiraling at the same angle in the opposite direction. They also concluded that nucleotides are linked in ladder-like fashion between the two strands. Furthermore, in order for the nucleotides to fit precisely in the DNA molecule, two linked purines or two linked pyrimidines would either be too wide or too narrow. However, a purine and a pyrmidine linked together would fit perfectly. Accordingly, they concluded that the ladder rungs had to consist exclusively of purine-pyrimidine pairs. In order for hydrogen bonds to form correctly between base pairs, guanine must pair with cytosine, and thymine must pair with adenine. Watson and Crick's DNA molecule is now universally accepted as an authentic representation.

DNA Functions

The DNA in a cell must perform four major tasks. It must (1) store genetic information; (2) copy that information for future generations of cells; (3) express that information; and (4) occasionally change its message, or **mutate.**

Storage of Genetic Information

Most DNA in plants resides in the nucleus. The nucleus is a compartment in which proteins that interact with DNA are concentrated. This compartmentalization is important because it creates an environment in which biochemical reactions are optimized by high concentrations of substrates and the enzymes that act on them.

The genetic information in a DNA molecule resides in the sequence of nucleotides along the rungs of the ladder. The sequence GAATCC, for example, codes for a different set of amino acids than CTTAGA. Early scientists were fooled by the simplicity of a DNA molecule and did not believe it could provide information for the survival of all organisms on earth. However, the DNA in a typical plant cell contains millions or billions of base pairs. A barley plant with 5 billion base pairs of DNA in its nucleus could produce $4^{5,000,000,000}$ different DNA sequence combinations! This provides more than enough genetic variability for the plant.

At this point, we need to introduce some important concepts, beginning with that of the gene. We are all familiar with the idea that genes control physical traits, such as eye color in people and height in plants. How do they do that? From a molecular perspective, a **gene** is a segment of DNA (several thousand base pairs long) that directs the synthesis of a protein. That protein is then used by the cell as structural or storage material, or it influences the activities of the cell by acting as an **enzyme.** As you recall from Chapter 2, enzymes are organic catalysts. Any activity in the cell, from photosynthesis to cell-wall construction, absolutely depends

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on enzymes to facilitate chemical reactions. Therefore, all activities of the cell are controlled by enzymes, which require genes for their synthesis. Each kind of organism has many different genes in its **genome,** which is a term for *the sum total of DNA in an organism's chromosomes.* A relatively simple organism such as a bacterium typically has several thousand genes in its genome. On the other hand, more complex eukaryotic organisms usually have between 10,000 and 50,000 genes per genome. The differences between organisms lie in the differences in the composition of their genomes. Organisms that are very dissimilar—for example, bacteria and higher plants—will have many differences in their DNA sequences. The genomes of similar organisms, such as domestic plants and their wild relatives, are very similar, yet different enough to account for dramatic differences in appearance.

Replication (Duplication) of Information

DNA must duplicate itself precisely in order to pass along its information from generation to generation. DNA replication occurs during the S phase of the cell cycle (see Chapter 3). Differences between the DNA of one organism and that of another lie in the sequence of the four possible types of ladder rungs and their total number. If the four nucleotides are synthesized in living cells, then what tells the cell exactly how to put them together to form DNA molecules with proper nucleotide sequences?

Watson and Crick predicted that if the two strands of DNA are "unzipped" by an enzyme breaking the hydrogen bonds between the nucleotides down the middle of the ladder, then each separated chain provides all the information needed to put together a new ladder (Fig. 13.4). In other words, since guanine can pair only with cytosine, and vice versa, a guanine nucleotide synthesized by the cell can lock on, or bond, only to a thymine nucleotide. If the two strands of a DNA molecule "unzip," then individual nucleotide "building blocks" can line up next to each of the single chains in precise sequence and be bonded together to form a new chain; each single chain acts as a mold or template for the creation of a new double-stranded DNA molecule. When replication is complete, two double helices have been created from a single one. Each new DNA molecule consists of one strand from the original molecule and another built using that parental strand as a template. This is called **semiconservative replication.**

Replication is a remarkably rapid and precise process. During DNA replication, nucleotides are added by the enzyme **DNA polymerase** at an amazing rate of approximately 833 per second in prokaryotes and 33 per second in eukaryotes. However, even at this rate, a plant chromosome that is, for example, 200 million base pairs long, would take 70 *days* to replicate. Because a cell must replicate its DNA before it undergoes mitosis, this replication rate is far too slow for normal plant growth. How is this problem resolved for the cells? In two ways: (1) replication proceeds simultaneously in both directions on the chromosome, cutting the replication time in half; and (2) replication begins at several to many points on a chromosome nearly simultaneously.

The nucleus contains enzymes that are capable of "proofreading" during replication. They detect and correct mismatched base pairs, such as guanine paired with adenine or thymine paired with cytosine. Consequently, about only one in every million nucleotides added during replication is incorrectly paired. However, each nucleus of a corn plant contains 4 billion base pairs of DNA. Therefore, about 4,000 mutations (changes in DNA sequence) occur with each cell division.

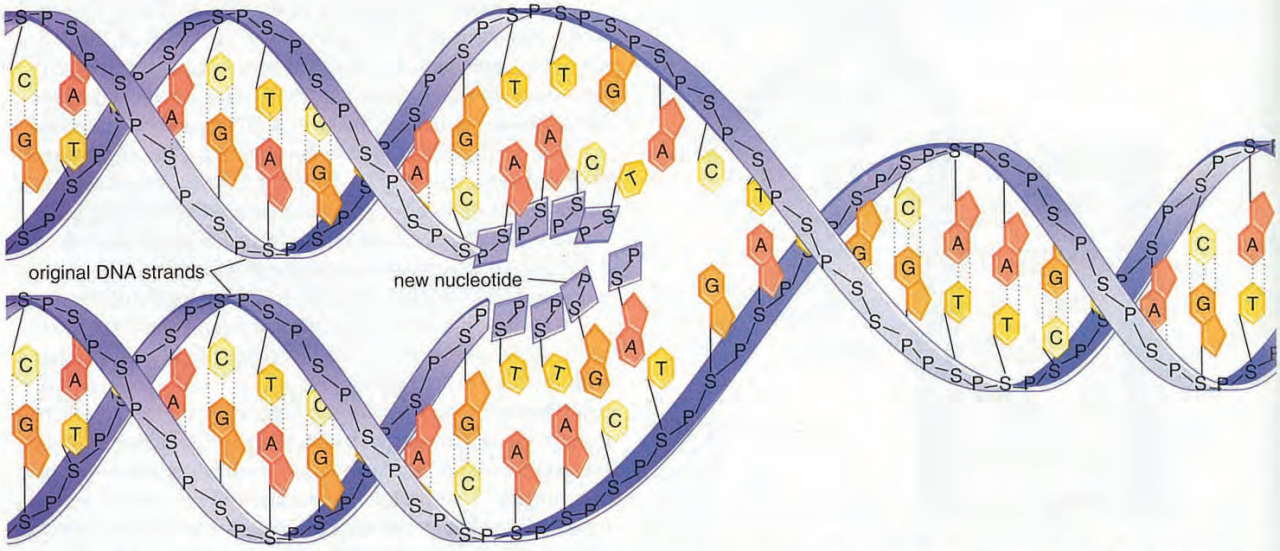


Figure 13.4 Replication (duplication) of DNA. A molecule replicates by "unzipping" along the hydrogen bonds, which link the pairs of nucleotides in the middle, and then each half serves as a template for nucleotides available in the cell. As the new nucleotides fit into the appropriate places and are linked together, a double helix is re-formed for each original half.

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The Polymerase Chain Reaction (PCR)

How many times have you said to yourself, "Why didn't I think of that?" Many scientists must have had that thought when Kary Mullis described the polymerase chain reaction (PCR) in 1984. While Mullis was driving to his cabin in northern California one evening, he was thinking about a method for determining nucleotide sequences in DNA molecules. The technique used DNA replication enzymes to synthesize short strands of DNA in a test tube. After running through several scenarios in his head, he realized that he could create a chain reaction in a test tube. Every reaction would double the amount of DNA synthesized, causing an exponential growth in the number of DNA molecules created. Twenty cycles of DNA replication would create from a single molecule a million identical DNA molecules. For years scientists had worked with replication enzymes in DNA synthesis experiments, but none of them had conceived the power of a chain reaction in a test tube.

The polymerase chain reaction allows scientists to replicate (duplicate) specific DNA sequences in small test tubes. The reaction requires DNA polymerase, nucleotides (actually nucleoside triphosphates, the high-energy precursors to nucleotides), short (approximately 20 nucleotide) single-stranded DNA molecules called *primers,* and DNA from an organism to serve as a template. The reaction follows these steps:

1. The primer is made with the aid of a DNA synthesizer. The primer DNA sequence is critical because it determines what piece of an organism's DNA will be replicated during the PCR reaction.
2. DNA polymerase, nucleotide building blocks, primers, and DNA template are mixed together in a small test tube.
3. The test tube is placed in a *thermal cycler.* This machine is capable of rapidly heating and cooling samples.
4. The tube is heated to approximately 94°C to separate the template DNA into single-stranded molecules. In a living cell, enzymes carry out this process. In an experimental setting, however, heat provides a simple way to make the DNA single-stranded.
5. The tube is then cooled to 35°C to 60°C. This allows the primers to locate and bind to complementary base sequences on the template DNA. Remember that DNA molecules are typically double helices with adenine-thymine pairs and guanine-cytosine pairs.
6. The tube is heated to 72°C, which is the optimal temperature for the DNA polymerase used in PCR reactions. Because the enzyme for PCR is derived from thermophilic (heat-loving) bacteria, it is not destroyed by heating (see Chapter 17). DNA polymerase locates the short, double-stranded regions where primers have bound to template DNA; it then uses nucleotide building blocks to make double-stranded DNA near the primer.
7. Steps 4 through 6 are repeated 20 to 30 times.

After completion of the PCR reaction, millions of copies of a double-stranded DNA molecule are present in the test tube. The real power of the reaction, though, comes from its ability to amplify only the DNA sequence adjacent to the primer binding site. This allows a researcher to make an endless supply of a specific segment of DNA. The illustration (Box Figure 13.1) shows how a target DNA sequence is amplified through cycles of PCR.

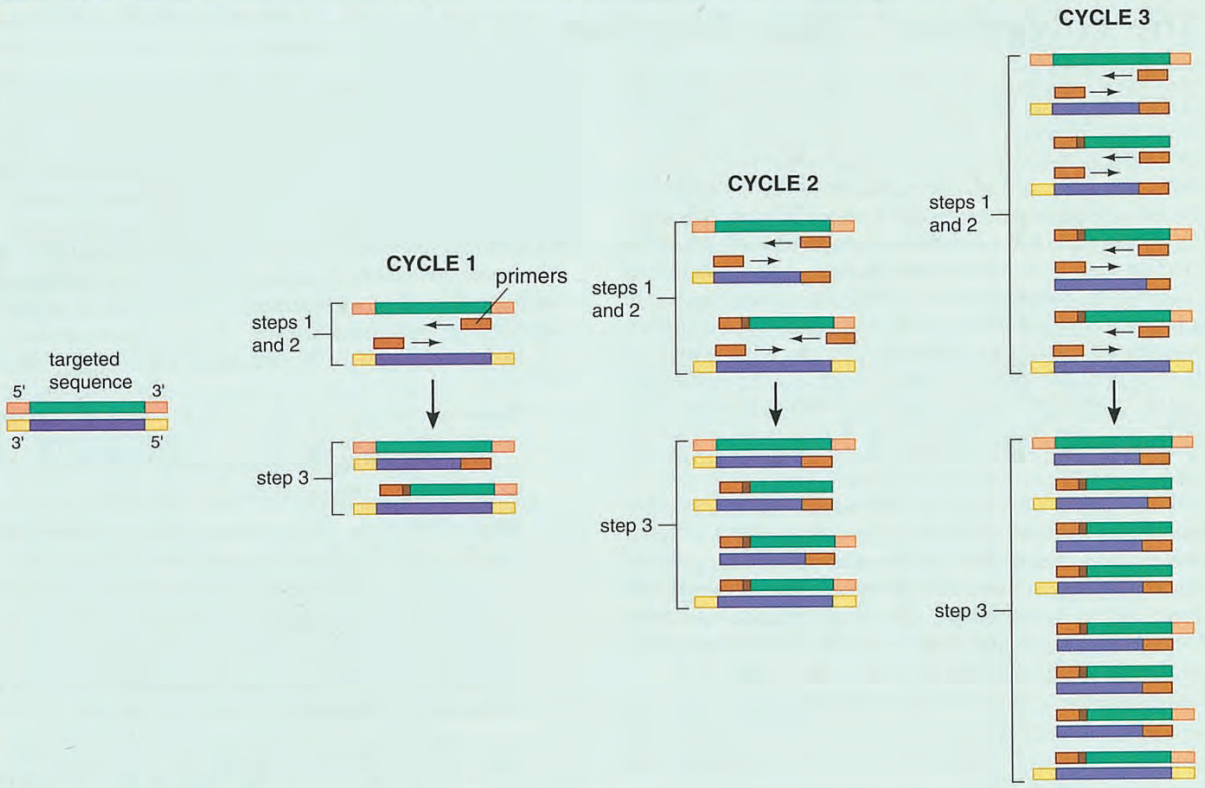
The polymerase chain reaction has become a standard tool in many research laboratories. Countless applications for this technique have been developed and more are on the way. PCR is an important tool because (1) large quantities of DNA can be synthesized from very small samples and (2) only the target DNA sequence is amplified.

How is the PCR reaction used today? Here is a short list of examples:

1. **Forensics.** Samples of hair, blood, and skin contain enough DNA to be amplified by PCR. A comparison of amplified DNA samples from a crime scene with DNA from a suspect can provide compelling evidence.
2. **Disease detection.** Primers have been developed specifically to amplify DNA from pathogens. For example, a person's blood could provide template DNA for the PCR reaction with a primer that binds only to a sequence from the human immunodeficiency virus (HIV). Then, even low levels of DNA produced by the virus would be amplified by PCR. This makes early disease detection possible. PCR is also being used to identify pathogens in plants.
3. **Food safety.** Pathogens in food can be detected quickly and accurately using PCR. Primers specific for pathogenic strains of *Escherichia coli* can detect very low levels of the pathogen in hamburger. Similar tests are available for detection of the organisms that cause *Salmonella* poisoning and botulism, among others.
4. **Fetal testing.** A small sample of fetal tissue can be amplified using primers specific to DNA regions that, in mutant form, cause human diseases. Primers are available to detect sickle cell anemia, phenylketonuria, cystic fibrosis, hemophilia, and Huntington's disease, to name a few. Of course, a moral dilemma is created if the fetus tests positive.
5. **Evolutionary relationships.** DNA from extinct animals can be amplified and compared with the DNA of modern relatives. With the use of PCR, DNA from a 120-million-year-old weevil and from a 250-million-year-old bacterium have already been extracted and amplified.
6. **Conservation efforts.** DNA from tissue samples collected at poaching sites can be amplified and compared to the DNA of pelts from suspected poachers. PCR also allows scientists to determine whether commercial products containing ivory, meat, or feathers were taken from endangered species.
7. **Genetics of dung.** Even DNA from dung can be amplified with PCR! Scientists trying to understand why the giant ground sloth became extinct have located 20,000-year-old dung in caves. PCR amplification of the dung is being used for comparison with modern relatives. In addition, careful choice of primers allows researchers to amplify DNA from the animal's food and its parasites.

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P.S.I. PLANT SCIENCES INQUIRY



Box Figure 13.1 Polymerase chain reaction (PCR) technology.

Only a few examples have been presented here. Application of PCR seems to be limited only by our imagination. We are capable of performing this amazingly simple, yet powerful reaction because we understand the elements responsible for DNA replication. The next time, then, when you are asked to memorize the steps in a biological process, don't grumble about it. Instead, see if you can look at it in a unique way and make your friends wonder, "Why didn't I think of that?"

Expression of Information

Since the nature and structure of DNA is of fundamental importance to its ability to control the form and function of organisms, there appears to be a paradox. If every cell in an organism contains the same genetic information, then why do cells within a plant differ from each other? That is, why is a bark cell so different from a leaf cell?

The answers to these questions stem from the fact that each cell in a multicellular plant contains the same DNA information, but different subsets of this master plan are read in each cell type. For example, a plant has epidermal cells that secrete a protective waxy cuticle, and it also has mesophyll cells that are highly specialized for photosynthesis. The epidermal cells express genes (read DNA sequences) that encode enzymes necessary to build a waxy cuticle. Mesophyll cells, on the other hand, will not express cuticle genes but do express a set of genes that encode enzymes for chlorophyll synthesis. One of the most active areas of biology research today is directed toward understanding how organisms control gene expression.

A cell's environment can influence the set of genes expressed by that cell. Many cellular changes occur as a result of the expression of new sets of genes induced by hormones (see Chapter 11). We know, for example, that an epidermal cell expresses genes for cell elongation if the hormone auxin is present; when mesophyll cells are moved from dark into light, many dramatic changes in gene expression occur as genes for the photosynthetic machinery are turned on.

The expression of genetic information requires two processes. First, the information coded by DNA is *transcribed.* During **transcription,** a copy of the gene message is made using RNA (ribonucleic acid) building blocks. RNA is similar

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to DNA with a few important differences. First, RNA nucleotides contain **ribose** sugars instead of **deoxyribose** sugars. Ribose contains one more oxygen atom than deoxyribose. Second, thymine is replaced by **uracil,** another nitrogenous base. Finally, RNA molecules are typically single-stranded. After transcription has been completed in the nucleus, the RNA is modified and then travels to the cytoplasm, where *translation* occurs. During **translation,** the RNA message provides the information necessary to construct proteins. It might help to remember the following when you are trying to distinguish between transcription and translation. During transcription, a nucleic acid, RNA, is made using another nucleic acid, DNA, as a template. This is analogous to a stenographer transcribing shorthand to longhand. During translation, a protein is made using a nucleic acid (RNA) as a template. This is analogous to a court reporter who transcribes notes based on combinations of letters and words into the text record of the court's proceedings.

Transcription Three different types of RNA are made by transcription. Chromosomes contain genes for the production of *messenger RNA (mRNA), transfer RNA (tRNA),* and *ribosomal RNA (rRNA).* Messenger RNA will be translated to produce proteins, while tRNA and rRNA will be used as part of the machinery for translation.

The mechanism of RNA synthesis is relatively simple. It involves the addition of RNA nucleotides to single-stranded DNA molecules, using complementary base pairing, similar to DNA replication. **RNA polymerase** is responsible for assembling the RNA strand. However, while all regions of the genome are replicated, only a very small portion of the genome is transcribed. In most eukaryotes, less than 10% of the DNA in the genome contains genes. The remainder is **noncoding DNA.** The transcription machinery must therefore search through millions of base pairs to identify small regions that contain genes. How does it do that? We have unraveled some of this mystery, but have much to learn. At the beginning of every gene, a DNA sequence called a **promoter region** acts as a flag to signal the transcription machinery scanning the DNA that a gene is ahead. This causes the transcription enzymes to associate with one strand of the DNA molecule and begin to make a copy of the gene. The complementary DNA strand is not used for transcription. A *terminator* DNA sequence at the end of each gene signals the transcription enzymes to fall off the DNA molecule. At this point, a single-stranded RNA molecule, called a **transcript,** has been made using one strand of a gene as a template. The transcript will undergo several modifications and move to the cytoplasm before translation begins.

As we mentioned before, not every gene is expressed in every cell. In addition to identifying genes, the transcription machinery must determine which genes to transcribe, or express. This is a very complex process and involves interactions among genes and signals from the environment. In addition, cells must control the amount of each type of protein they produce. Until recently, scientists thought that the large amount of nonprotein-coding DNA in the genome represents evolutionary "junk." That is, this DNA is what is left over from failed experimentation by organisms during evolution. On the contrary, it now appears that this nonprotein-coding DNA is fundamental to the control of gene expression. Because nonprotein-coding DNA is not translated, scientists never see protein products. However, RNA transcription products from these sequences appear to carry out an amazing array of activities that control the amount of protein cells produce from conventional "coding" genes.

Nonprotein-coding genes are also responsible for making some of the machinery needed for translation. Chromosomes contain genes for building tRNA. When transcribed, these genes produce molecules of tRNA approximately 80 nucleotides long. The single-stranded RNA produced by transcription spontaneously forms base pairs in some regions, creating a three-dimensional molecule of a characteristic shape. Transfer RNA will act as the "translator" during translation. One end of the tRNA molecule binds to the mRNA, while the other end carries a specific amino acid. There is at least one form of tRNA for each of the 20 amino acids. Each form of tRNA has a specific *anticodon* loop. The **anticodon** is a sequence of three nucleotides that recognizes a codon on mRNA and base pairs with it. An amino acid binds to the other end of the tRNA with the aid of an enzyme that specifically identifies both a single tRNA strand and its proper amino acid.

Genes for rRNA are also transcribed in the nucleus. This RNA is used to construct **ribosomes,** which act as workbenches during protein synthesis. A ribosome is composed of a large and a small subunit, each containing a specific combination of rRNA molecules and proteins. The rRNA molecules create the three-dimensional structure of a ribosome and help to orient the proteins, most of which appear to assist with the assembly of new proteins during translation. It is believed that mRNA slides between the large and small subunits during translation. All ribosomes in a cell are identical and capable of reading any mRNA.

Translation RNA transcripts that can be decoded into proteins are called *mRNAs.* It seems puzzling that a nucleic acid with only four possible nucleotides (adenine, uracil, cytosine, and guanine) can be used to make a protein polymer that may have 20 different amino acids. One nucleotide is incapable of encoding one amino acid. Even two nucleotides together could be combined in a maximum of only 16 different ways. It turns out that the genetic code is based on trios of nucleotides we earlier referred to as *codons.* Like words and sentences, codons and genes can be read from one direction only, thereby preventing the possibility of expressing the wrong amino acid. There are 64 possible ways to combine nucleotides, taking three at a time. This is more than enough to encode all 20 amino acids. The order of nucleotides on an mRNA molecule (determined by the sequence of nucleotides in a gene during transcription) determines the sequence of amino acids added during translation. For example, the codon AUG (adenine-uracil-guanine) on an mRNA encodes the amino acid methionine, whereas the

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codon AGU on an mRNA encodes the amino acid serine. The genetic code (Fig. 13.5) shows the matching of each three-nucleotide codon with a specific amino acid. With few exceptions, the genetic code is universal. In other words, the same code is used in bacteria, plants, and animals.

As mentioned before, tRNAs act as translators, or decoders, during translation. The anticodon part of the tRNA binds to the mRNA codon by base pairing with it, while the other end of the tRNA molecule has, according to the genetic code, the correct amino acid bound to it. In a sense, then, we can think of tRNAs as the dictionary used to decode an mRNA during translation.

The start of translation is usually signaled by a ribosome in the cytoplasm binding to the mRNA and scanning it for the first AUG codon. This sets the reading frame because each set of three nucleotides is translated in succession after the first AUG. A start tRNA with the amino acid methionine and an anticodon that base-pairs with the AUG on the mRNA joins the mRNA and the ribosome, forming a three-part complex (Fig. 13.6). Another tRNA that base-pairs to the next codon and has its correct amino acid attached inserts in the complex next to the start tRNA. An enzyme in the ribosome then links the two adjacent amino acids together to begin to form a protein. As translation continues, new tRNAs base-pair to each mRNA codon in order, and new amino acid linkages are made. For example, an mRNA with the sequence AUG-AAG-UGU will be translated into a protein with the sequence methionine-lysine-cysteine until a stop codon (UGA, UAA, or UAG) is reached. At that point, a newly made protein is released from the complex.

To summarize, the flow of information in a cell is from the DNA genome in the nucleus, which is transcribed into mRNA, to the cytoplasm, where the mRNA is translated into protein. Because these processes occur in all living organisms, it has come to be known as the *Central Dogma of Molecular Genetics* (Fig. 13.7). Truly, a cell's identity is determined by the genes it expresses, which, in turn, produce the myriad of proteins required for its survival and function.

Mutation

When my six-year-old son recently told a friend that his Mom was a scientist, the boy asked, "Can she make mutants?" While the term *mutation* may conjure up images of *Teenage Mutant Ninja Turtles,* most mutations are not so dramatic. In fact, as mentioned earlier, **mutations,** or changes in DNA sequence, happen every time DNA replicates. In addition to DNA replication errors and other spontaneous types of changes, agents called **mutagens** can alter DNA sequences. Ultraviolet light, ionizing radiation, and certain chemicals act as mutagens. DNA repair enzymes can

Codon	Amino Acid	Codon	Amino Acid	Codon	Amino Acid	Codon	Amino Acid
UUU	phe (phenylalanine)	UCU	ser (serine)	UAU	tyr (tyrosine)	UGU	cys (cysteine)
UUC	phe	UCC	ser	UAC	tyr	UGC	cys
UUA	leu (leucine)	UCA	ser	UAA	STOP	UGA	STOP
UUG	leu	UCG	ser	UAG	STOP	UGG	trp (tryptophan)
CUU	leu	CCU	pro (proline)	CAU	his (histidine)	CGU	arg (arginine)
CUC	leu	CCC	pro	CAC	his	CGC	arg
CUA	leu	CCA	pro	CAA	gln (glutamine)	CGA	arg
CUG	leu	CCG	pro	CAG	gln	CGG	arg
AUU	ile (isoleucine)	ACU	thr (threonine)	AAU	asn (asparagine)	AGU	ser
AUC	ile	ACC	thr	AAC	asn	AGC	ser
AUA	ile	ACA	thr	AAA	lys (lysine)	AGA	arg
AUG	met (methionine) (start)	ACG	thr	AAG	lys	AGG	arg
GUU	val (valine)	GCU	ala (alanine)	GAU	asp (aspartic acid)	GGU	gly (glycine)
GUC	val	GCC	ala	GAC	asp	GGC	gly
GUA	val	GCA	ala	GAA	glu (glutamic acid)	GGA	gly
GUG	val	GCG	ala	GAG	glu	GGG	gly

Figure 13.5 The genetic code. There are 64 different codons, each of which consists of 3 bases and nucleotides, and specifies 1 of the 20 amino acids plus *stop* and *start* information.

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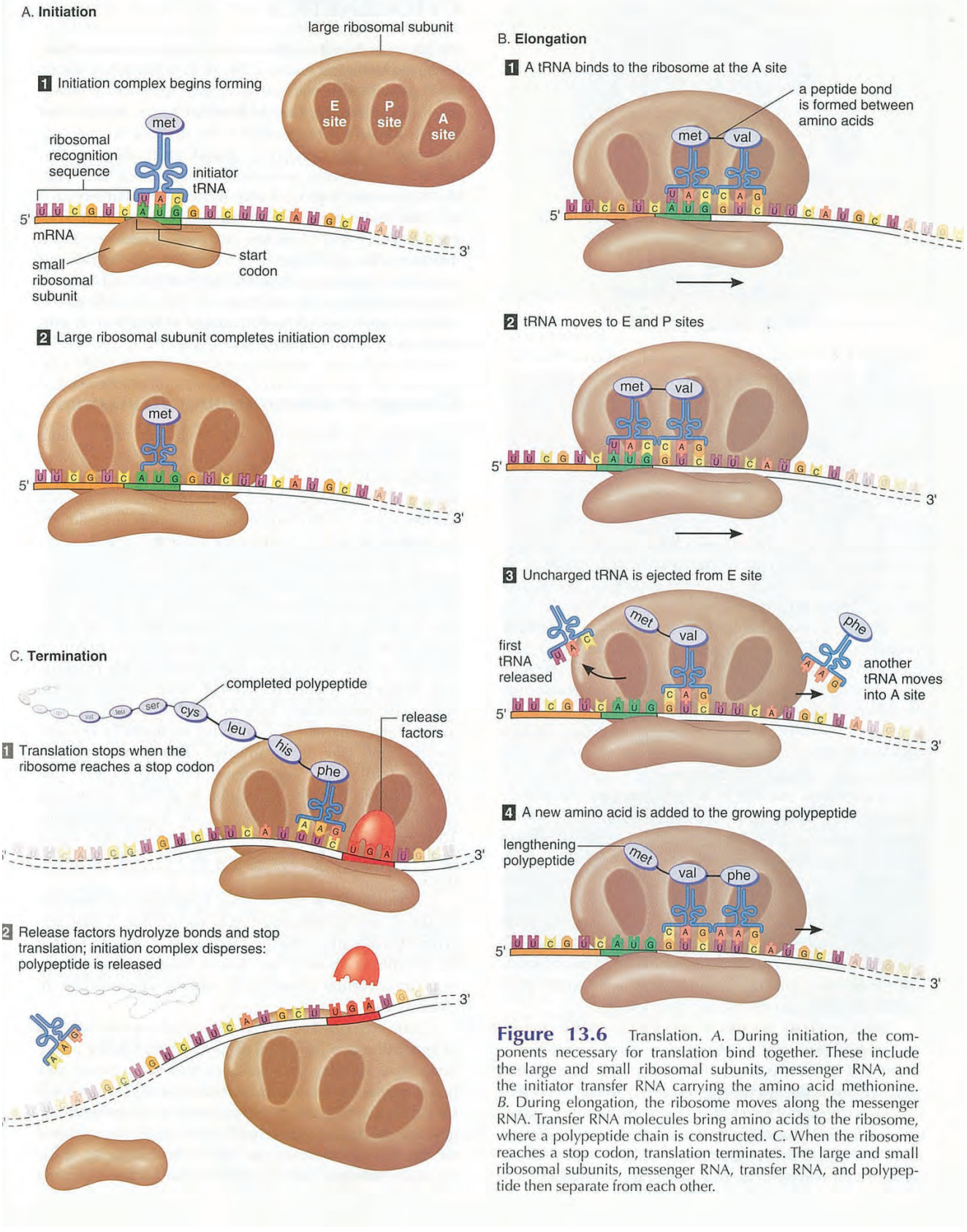


Figure 13.6 Translation. *A.* During initiation, the components necessary for translation bind together. These include the large and small ribosomal subunits, messenger RNA, and the initiator transfer RNA carrying the amino acid methionine. *B.* During elongation, the ribosome moves along the messenger RNA. Transfer RNA molecules bring amino acids to the ribosome, where a polypeptide chain is constructed. *C.* When the ribosome reaches a stop codon, translation terminates. The large and small ribosomal subunits, messenger RNA, transfer RNA, and polypeptide then separate from each other.

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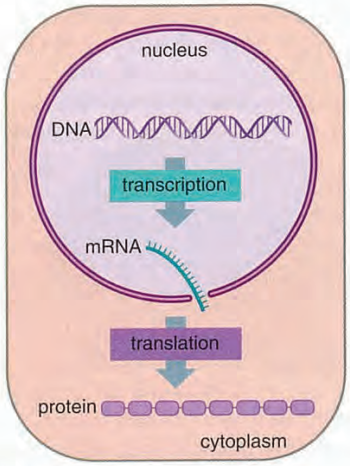


Figure 13.7 The Central Dogma of Molecular Genetics. The flow of information in a cell proceeds from the DNA in the nucleus via mRNA to the cytoplasm, where information from the mRNA is translated into proteins.

often find and correct damaged DNA. If left uncorrected, though, a permanent change in DNA sequence, or mutation, occurs. Most mutations are *silent,* with no visible consequence of the DNA alteration. Remember that most DNA in a cell is noncoding. Even altered coding sequences may produce functional proteins.

Mutations are either *somatic* or *germ-line.* A **somatic mutation** occurs in a body cell and will exist in all cells produced by mitosis of the mutant cell. A somatic mutation may show up as a *sport,* or a branch that looks different from the others on a tree. These types of mutations are sometimes sources of new types of horticultural plants. Navel oranges and Red Delicious apples originated from sports and have been clonally propagated by grafting (see Chapter 14).

A **germ-line** mutation occurs in tissue that will produce gametes, or sex cells. Unlike somatic mutations, germ-line mutations will be passed on to future generations through seeds. A germ-line mutation is generally not apparent until it is passed on to offspring, which will carry the altered DNA in all cells. This mutation has now become a permanent feature of that plant's lineage. Germ-line mutations are important for the genetic improvement of horticultural and agronomic plants. They are responsible for variability in all traits, including flower color and fragrance, fruit taste and texture, grain yield and quality, and disease and stress tolerance.

While we tend to think of mutations as "bad," they are an essential feature of DNA. All the genetic variability in nature has arisen as a result of mutation. The accumulation of mutations is the mechanism that drives evolution of species (see Chapters 15 and 16). That variability was essential for the first plants, which lived in the ocean, to become established on land; it continues to be necessary for plants to survive and compete in an ever-changing environment.

CYTOGENETICS

During the middle of the 20th century, corn cytogenetics dominated the biological sciences, due in large part to the efforts of Barbara McClintock and other corn geneticists, including Roland Emerson, George Beadle, Charles Burnam, and Marcus Rhoades. **Cytogenetics** is the study of chromosome behavior and structure from a genetic point of view. This includes chromosome movement during meiosis and mitosis, chromosome pairing during meiosis, and chromosomal variation due to changes in chromosome structure and number. Chapters 3 and 12 discuss chromosome behavior during mitosis and meiosis, respectively. Therefore, this section will emphasize changes in chromosome structure and number. These changes occur at low frequency, but since their effects are often large, they can have a dramatic influence on the evolutionary success of populations or species.

Changes in Chromosome Structure

Occasionally, a chromosome will break into two or more pieces. Enzymes may repair the damage, leaving the chromosome unaltered. However, sometimes a broken chromosome may become reorganized before the pieces are attached together again. The most significant events from an evolutionary perspective include *inversions* and *translocations*.

An **inversion** results when a piece of a chromosome is broken and reinserted in the opposite orientation. For example, if the chromosome contains genes ABCDE in that order, then an inversion might create a chromosome with the genes in this order: AB**DC**E. The inverted chromosome can pair up with the normal homologous one at meiosis, but crossing-over within the inverted region will create gametes that do not survive because they contain some duplicated chromosomal regions and are missing other segments of chromosomes. Plants carrying an inverted chromosome therefore are less fertile than normal ones. The only gametes that are passed on from one generation to another are those in which crossovers occurred only outside the inverted region. Therefore, allele combinations within an inverted region are not rearranged by meiosis and are inherited together as blocks.

A **translocation** results when a piece of a chromosome breaks off and becomes attached to another one. A plant carrying a translocation, like one carrying an inversion, will not be as fertile as a normal one. This is because some gametes from translocation plants carry unusual combinations of chromosomes.

Translocations and inversions can be important factors in **speciation** (the formation of new species) during evolution. Plants carrying chromosomes from these events may become reproductively isolated from normal plants and will eventually develop into new species. Crosses between the new species and the old one will produce offspring with low fertility and, therefore, a poor reproductive capacity. These types of events have been important in the evolution of many

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plants. For example, cultivated rye (*Secale cereale*) and four wild species (*S. vavilovii, S. africanum, S. montanum, S. silvestre*) each contain 14 chromosomes. However, translocations have resulted in the wild species being reproductively isolated from the cultivated species. Genetic exchange among these species is limited by translocations.

Changes in Chromosome Number

Compared to animals, plants are remarkably tolerant of changes in chromosome number. Mistakes made during the pairing and separation of chromosomes during meiosis can result in gametes carrying extra or missing chromosomes. If one of these gametes is involved in fertilization, then the resulting zygote will be *aneuploid.* An **aneuploid** plant carries an extra one or more chromosomes or, less commonly, is missing one or more chromosomes. For example, the cells in a carrot plant typically contain nine pairs of homologous chromosomes, for a total of 18 chromosomes. An aneuploid carrot plant would have 19 chromosomes if it had an extra copy of one chromosome or 17 chromosomes if it was missing one of a pair. As you would expect, aneuploid plants generally differ in appearance from their normal counterparts due to the effects of extra or missing doses of many genes. Geneticists use aneuploids to determine the chromosomal locations of genes.

Occasionally, meiosis may completely fail to halve the chromosome number, producing gametes with the somatic (body cell) chromosome number. These are called 2*n* gametes. If these gametes are involved in fertilization, then the resulting offspring are *polyploid.* A **polyploid** plant has at least one complete extra set of chromosomes. Using the carrot example, a polyploid carrot could have 27 chromosomes (three sets of nine chromosomes). Polyploid plants are often larger and higher-yielding than their diploid counterparts. For this reason, many of our cultivated plants are polyploid. These include potato, cotton, peanut, wheat, oats, strawberry, and sugar cane (Fig. 13.8). The larger and longer-lasting flowers of polyploids make them attractive as ornamental plants; marigold, snapdragon, lily, and hyacinth are among the numerous examples of ornamental polyploids. In addition, triploid plants (polyploids containing three copies of each chromosome) are sterile and do not produce seeds. Seedless fruits, such as bananas and watermelons, are triploid. In Chapter 15, polyploidy is discussed as an important mechanism for the production of interspecific hybrids in nature.



Figure 13.8 Leaves of potato plants. *Left:* A tetraploid. *Right:* A diploid.



Figure 13.9 Gregor Mendel. Photo ca. 1870s, Brünn, Moravia. *(Courtesy Brooklyn Botanic Gardens, New York. Print at Hunt Institute, Pittsburgh, PA.)*

MENDELIAN GENETICS

Genetics as a science originated about a generation before its significance became appreciated in the scientific community as a whole. An Austrian monk, Gregor Mendel (Fig. 13.9) taught between 1853 and 1868 in what became the Czechoslovakian city of Brno. In the monastery there, he carried out a wide range of studies in physics, mathematics, and natural history. He also became an authority on bees and meteorology and kept notes on experiments involving two dozen different kinds of plants. Today, he is best known for the studies he conducted with peas.

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Mendel published the results of his studies on pea plants in a biological journal in 1866 and sent copies of his paper to leading European and American libraries. He also sent copies to at least two eminent botanists of the time. His work, nevertheless, was completely ignored or overlooked until 1900, when three botanists (Eric von Tschermak of Austria, Carl Correns of Germany, and Hugo de Vries of Holland), working independently in their own countries, reached the same conclusions as Mendel. Each, as a result of library research, came across Mendel's original paper.

Mendel's Studies

Peas, unlike many flowering plants, are *self-fertile.* In other words, a pollen grain of a pea flower can germinate on its own stigma, allowing a sperm cell to fertilize an egg and the ovule to develop into a viable pea seed. Although Mendel did not know about mitosis and meiosis, he had noticed that if a pea plant grew to a certain height, its offspring, if grown under the same conditions, would always reach approximately the same height, generation after generation. He wondered what would happen if he crossed a tall plant with a short one. Would the offspring be intermediate in height?

To make such a cross, Mendel needed to prevent self-pollination. He did so by reaching into a flower of one plant and removing the stamens before the pollen had matured. Then, he took pollen from another plant and applied it by hand to the stigma of the first flower. He also covered the experimental flowers with small bags to prevent insects from bringing pollen from other flowers after the cross had been made.

When Mendel made such crosses, the results were astonishing. All of the offspring were tall. There were no short or intermediate plants. He found, however, that if he allowed the offspring plants to pollinate themselves, they produced offspring in a ratio of approximately three tall plants to one short plant (Fig. 13.10).

Mendel then tried crosses between peas with smooth seeds and those with wrinkled seeds. He also crossed green-seeded plants with yellow-seeded ones and several others with pairs of contrasting characteristics.

Mendel referred to the original plants involved in making the crosses as the **parental generation (P)** and their offspring were the **first filial (F_1)** generation. Filial means "of or relating to a son or daughter." The offspring of F_1 plants were called the **second filial (F_2)** generation.

There are several reasons why Mendel was successful in developing a model for inheritance when countless others before him failed. He performed carefully planned and



Figure 13.10 Two generations of offspring in peas. The F_1 generation is composed of tall plants and was created by crossing a true-breeding tall plant with a true-breeding dwarf (short) plant. The F_2 generation is composed of 75% tall plants and 25% dwarf plants, and was created by intercrossing F_1 plants.

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executed crosses between pure-breeding parents. Each parent was genetically stable for the trait under study—a green-seeded parent produced only green-seeded offspring. Mendel also counted the number of offspring in each cross, something none of his predecessors had done. His use of his math background to apply statistical analyses to his data was unique, allowing him to develop and test inheritance models. Finally, he chose traits under simple genetic control. His predecessors usually studied traits such as weight, which is controlled by many genes and strongly influenced by environment. A summary of some of Mendel's data is shown in Table 13.1.

As Mendel began to collect data in his experiments, he realized that there must be elements in the pea plant responsible for controlling traits such as seed color and stem height. He referred to this unknown agent as a *factor.* He also deduced that each plant must have two such factors for each characteristic, since even though all the offspring of an F_1 generation appeared identical, the F_2 generation revealed some plants with one characteristic and others with the contrasting form.

These discoveries and deductions came to be known as the **law of unit characters.** Stated simply, this law says that *factors, which always occur in pairs, control the inheritance of various characteristics.* Today, we know that the paired factors are **alleles** of genes. Alleles are alternative forms of a gene. For example, the seed color gene has an allele for yellow color and an allele for green color. Genes are always at the same position (**locus**) on homologous chromosomes (see Chapter 12). We also now know that there are typically thousands of genes on every chromosome.

From his data and analyses, Mendel also deduced that one allele may conceal the expression of the other. For example, in the F_1 generation following a cross between green-podded and yellow-podded parents, all the plants had green pods. However, both parents obviously had to contribute something to the cross, since some of the F_2 plants had green pods while others had yellow pods. This deduction led to another principle, known as the **law of dominance.** This principle says that *for any given pair of alleles, one may mask the expression of the other.* The expressed allele is referred to as **dominant,** and the one that is not expressed (masked) is **recessive.** In the green-podded by yellow-podded cross, the green-pod allele is dominant, and the yellow-pod allele is recessive.

Mendel's crosses also made it clear that a plant's having green pods did not indicate whether or not both members of the pair of alleles controlling pod color were present, because the dominant one could mask the expression of the recessive one. To distinguish between the physical appearance of an organism and the genetic information it contains, we use the terms *phenotype* and *genotype.* **Phenotype** refers to the physical appearance of the organism, while **genotype** refers to the genetic information responsible for contributing to that phenotype. We customarily use words to describe phenotypes and letters to designate genotypes.

In Mendel's crosses, for example, seven pairs of phenotypes are shown as parents; these phenotypes include yellow seeds and green seeds, smooth seeds and wrinkled seeds, green pods and yellow pods, and so on. In designating the genotypes of each of these plants, a capital letter is used to indicate the dominant member of a pair of genes; *the same letter* in lowercase is used to indicate the corresponding recessive allele. In the green-podded × yellow-podded pea cross, for example, green is dominant over yellow. If a plant has a green phenotype, then its genotype could be either *GG* or *Gg.* The genotype of yellow-podded plants would always be *gg.* The plant is said to be **homozygous** if both alleles of a pair are identical (e.g., *GG* or *gg*) and **heterozygous** if the pair is composed of contrasting alleles (e.g., *Gg*). Mendel's true-breeding parents were homozygous for the traits he studied.

It is amazing that, nearly 150 years ago, Mendel was able to develop hereditary laws that are widely recognized today. Remember that he did his work before anyone knew about chromosomes, meiosis, or genes.

TABLE 13.1

Summary of Mendel's Data

PARENTS	F_1	F_2
Yellow × green seeds	All yellow	6,022 yellow: 2,001 green
Smooth × wrinkled seeds	All smooth	5,474 smooth: 1,850 wrinkled
Green pod × yellow pod	All green	428 green: 152 yellow
Long stem × short stem	All long	787 long: 277 short
Axial flowers × terminal flowers	All axial	651 axial: 207 terminal
Inflated pods × constricted pods	All inflated	882 inflated: 299 constricted
Purple flowers × white flowers	All purple	705 purple: 224 white

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The Monohybrid Cross

Mendel was successful largely because he carried out well-planned crosses with true-breeding parents. Geneticists today perform similar experiments when trying to understand the genetic basis of uncharacterized traits. A common strategy is to generate a **monohybrid cross.** In this scenario, a single trait is studied. A cross is made between two true-breeding parents differing for that trait, producing an F_1 generation. Then, these F_1 plants are intercrossed to produce an F_2 generation. As an example, we will examine a cross between a homozygous green-podded pea plant and a homozygous yellow-podded one (Fig. 13.11). The genotype of the homozygous dominant parent (green-podded) is *GG*; the genotype of the homozygous recessive parent (yellow-podded) is *gg*. You will recall from Chapter 12 that gametes have only one member of each pair of homologous chromosomes. The gametes of the green-podded parent (*GG*), therefore, will be *G*; the gametes of the yellow-podded parent (*gg*) will be *g*. No matter which egg unites with which sperm of the other parent, all the zygotes of this cross will be heterozygous, with the genotype *Gg*. This means that all individuals in the F_1 generation will have the green-podded phenotype, and all will be heterozygous.

The next step is the actual monohybrid cross. Members of the F_1 generation are crossed with each other (or self-pollinated) to produce an F_2 generation. All of the F_1 plants have the same phenotype (green-podded) and genotype (*Gg*). Each F_1 plant produces two kinds of gametes (*G* and *g*) in roughly equal numbers. When the gametes are produced, half will be *G*, and half will be *g*. A *G* egg may unite with a *G* sperm, producing a *GG* zygote. Alternatively, purely at random, the *G* egg may unite with a *g* sperm producing a *Gg* zygote. The same type of random combinations occur with *g* eggs so that either *Gg* or *gg* zygotes are produced. When all the offspring of a large number of such crosses are counted, a genotypic ratio of 1 *GG*: 2 *Gg*: 1 *gg* is produced. The phenotypic ratio will be approximately three green-podded plants (*GG* and *Gg*) to one yellow-podded plant (*gg*). These four equally possible F_2 offspring are shown at the bottom of Figure 13.11.

The Dihybrid Cross

So far, our examples have involved single genes. However, it is often desirable to study a pair of genes using a **dihybrid cross.** This is especially valuable in gene mapping studies. That topic is discussed later in this chapter. The **law of independent assortment** states that *the factors (genes) controlling two or more traits segregate independently of each other.* This is one law that, while true for many traits, often breaks down.

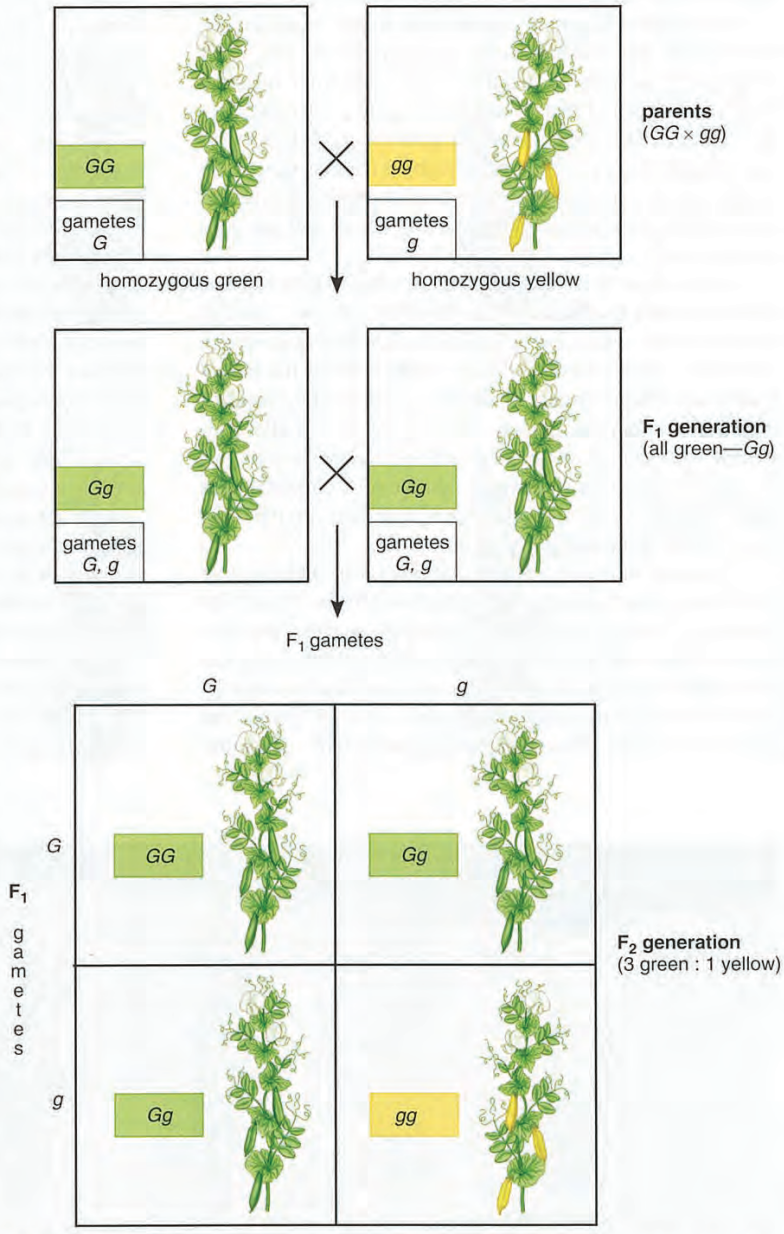


Figure 13.11 A monohybrid cross between a green-podded pea plant and a yellow-podded pea plant. Green (*G*) is dominant; yellow (*g*) is recessive.

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That is because the two genes under study may be physically close to each other on a chromosome. If this is the case, then the genes are basically attached together and will follow each other through meiosis. They do not segregate independently. In this situation, the genes are said to be **linked.** In the dihybrid example that follows, however, we will assume that the pair of genes is **unlinked.** That is, they are on different chromosomes or are far apart on a single chromosome.

Let's consider the genes for plant height and pod color. Recall that tallness in peas is dominant and dwarfness is recessive, while green pod is dominant over yellow pod. The homozygous dominant (*GGTT*) parent will have a green-podded, tall phenotype, while the recessive parent (*ggtt*) will be yellow-podded and dwarf. All the gametes from the dominant parent will be *GT,* and those of the recessive parent will be *gt.* The F_1 generation will be composed of dihybrid (*GgTt*) plants that are green-podded and tall (Fig. 13.12).

When intercrossed to produce the F_2 generation, these dihybrid members of the F_1 generation will produce four types of gametes in equal proportions. The gamete genotypes are *GT, Gt, gT,* and *gt.* Remember that each gamete will carry only one allele of each gene. Since any one of the four kinds of gametes can unite randomly with any of the four kinds of gametes of the other parent, 16 combinations are possible.

In order to avoid confusion when trying to make all possible combinations of gametes, a diagram called a **Punnett square** is used to determine the genotypes of the zygotes. The Punnett square diagram looks somewhat like a checkerboard, with the gametes of one parent across the top and the gametes of the other parent on the left side. To fill in each square on the checkerboard, look at the gamete designation above the square and to the side of it. Multiply the gamete proportions (e.g. 1/4 × 1/4) and add together the gamete letters (e.g., *GT* + *GT*). In Figure 13.11, the first square would therefore be 1/16 *GGTT.*

Nine different zygote genotypes are possible in the 16-box Punnett square. They are produced in a ratio of 1 *GGTT*: 2 *GGTt*: 1 *GGtt*: 2 *GgTT*: 4 *GgTt*: 2 *Ggtt*: 1 *ggTT*: 2 *ggTt*:1 *ggtt.* Four phenotypes are possible in a ratio of 9 green-podded, tall: 3 green-podded, dwarf: 3 yellow-podded, tall: 1 yellow-podded, dwarf. A geneticist observing a 9:3:3:1 ratio from a dihybrid cross can deduce that the genes controlling the two traits are unlinked and are exhibiting dominance. Genetic ratios such as the ones previously outlined are expected when large numbers of individuals are studied. Note in Mendel's data (Table 13.1) that he looked at over 8,000 F_2 offspring following a monohybrid cross involving seed color. With small numbers, chance alone may not produce the expected ratios. Human populations, for example, are divided relatively equally into males and females (a genetically controlled trait), but in smaller groups, such as families, the general population ratio of one male to one female may not be evident.

The Backcross

If a scientific theory is valid, then one should be able to test it experimentally. Mendel himself tested his predictions by means of backcrosses. A **backcross** is a cross between a hybrid and one of its parents. Mendel had found in pea flowers that red color is dominant and that white is recessive. Therefore, all F_1 offspring of a cross between a homozygous red-flowered parent (*RR*) and a homozygous white-flowered parent (*rr*) would be red (*Rr*). The gametes of these F_1 plants would be either *R* or *r,* with each type being produced in equal numbers. If the F_1 hybrid (*Rr*) is crossed to a homozygous recessive plant (*rr*), then half of the offspring would be *Rr.* These plants received the dominant allele from the heterozygous parent and a recessive allele from the homozygous parent. The remaining offspring from the backcross received a recessive allele from the heterozygous parent, so they would be *rr.* Following backcrosses of F_1 hybrids to recessive parents, Mendel observed the expected ratio of 1 red-flowered plant (*Rr*) to 1 white-flowered plant (*rr*). This provided further confirmation for his inheritance theory.

The Testcross

In the F_2 generation of a monohybrid cross, there are two genetically different types of plants that look identical. Homozygous dominant plants look just like heterozygotes. Suppose you are interested in determining which plants are homozygous dominant for the tall allele. How would you identify them? One of the easiest ways is to cross the tall plants with short plants. A cross between a plant with the dominant phenotype and a homozygous recessive plant is called a **testcross.** This cross will determine whether the plant with the dominant phenotype is homozygous or heterozygous. The short plants are homozygous recessive, so you know their genotype. If all the offspring from a cross between a tall plant and a short plant are tall, then the tall plant must be homozygous dominant. If some (approximately 50%) of the offspring are short, then the tall plant must be heterozygous.

Incomplete Dominance

Although the principle of dominance was amply demonstrated by Mendel's crosses, we know now that in many other instances, neither member of a pair of genes completely dominates the other. In other words, some genes exhibit **incomplete dominance** (or absence of dominance), in which a heterozygote is intermediate in phenotype to the two homozygotes. In snapdragons, for example, the F_1 plants of a cross between a red-flowered parent and a white-flowered parent are all pink-flowered. When an F_2 generation is produced from such a cross, the flowers of the offspring appear in a ratio of 1 red: 2 pink: 1 white (Fig. 13.13).

Interactions Among Genes

So far, our discussion of inheritance has focused on single genes or pairs of genes acting independently of each other. This type of autonomous behavior, however, is the exception rather than the rule. Genes are generally responsible for the production of proteins that are components of complex

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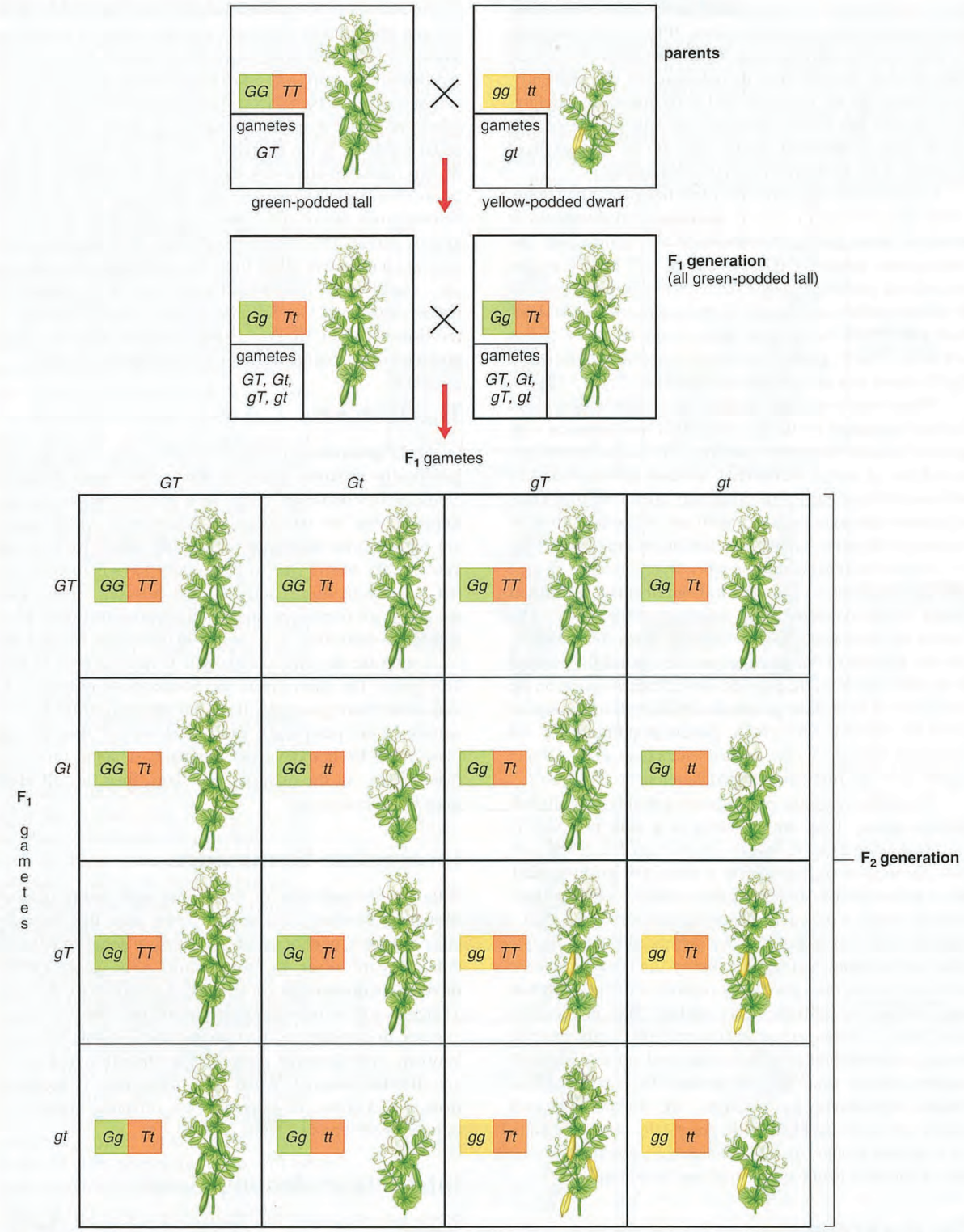


Figure 13.12 A dihybrid cross between a green-podded, tall pea plant and a yellow-podded, dwarf pea plant. Green (*G*) and tall (*T*) are dominant; yellow (*g*) and dwarf (*t*) are recessive.

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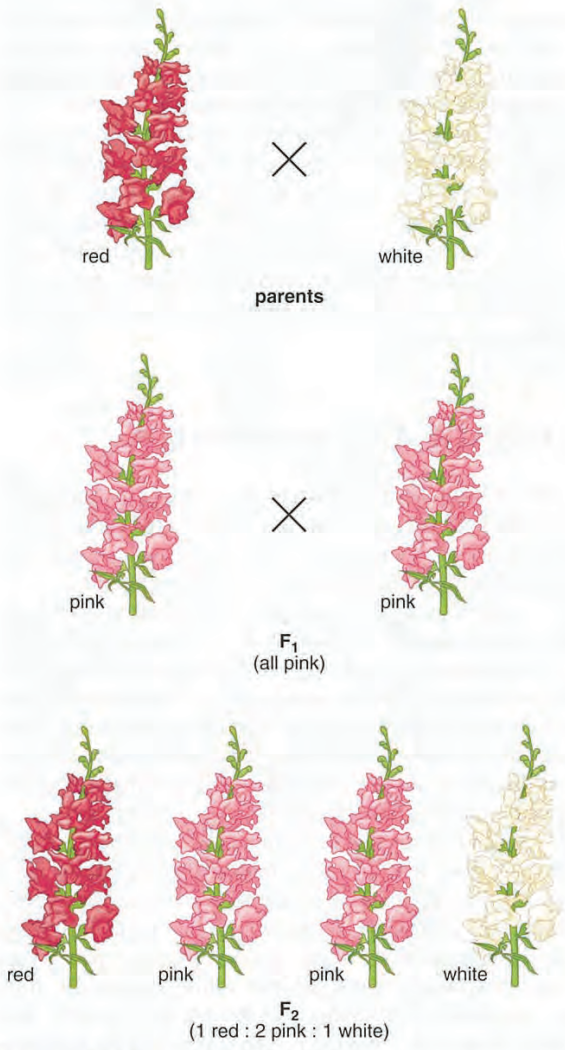


Figure 13.13 Incomplete dominance. A cross between a red-flowered and a white-flowered variety of snapdragons produces F_1 offspring with an intermediate phenotype.

biochemical pathways. It is often necessary to consider the genotype of an individual at more than one locus before a prediction of phenotype can be made. For example, in a plant called blue-eyed Mary (*Collinsia parviflora*), two genes control flower color in a biochemical pathway as follows:

$$\text{colorless} \xrightarrow{\text{gene } W} \text{magenta} \xrightarrow{\text{gene } M} \text{blue}$$

If a plant contains at least one dominant *W* allele, then it can proceed through the first step of the pathway and produce either magenta or blue flowers. The flowers will be magenta if the plant is homozygous recessive for the *M* gene (*mm*) or blue if it has at least one copy of the dominant *M* allele (*MM* or *Mm*), allowing it to complete the second step in the pathway. The enzyme produced by the dominant *W* allele catalyzes a pathway that synthesizes a compound used by the gene *M* enzyme. Therefore, a homozygous recessive (*ww*) plant cannot produce colored flowers even if it contains a dominant *M* allele. Of course, a plant that is homozygous recessive for both genes (*wwmm*) will also produce colorless (white) flowers.

How Genotype Controls Phenotype

Mendel had no way of knowing how his factors (genes) could produce plants that varied in phenotype. However, as our understanding of the molecular basis of genetics increases, so does our ability to explain Mendelian inheritance patterns.

Mendel discovered that the allele for smooth seeds is dominant over the wrinkled seed allele. How does one allele mask the expression of another? Often, the dominant allele codes for a protein that can effectively catalyze a reaction in a cell and produce a phenotype we recognize. The recessive allele, on the other hand, represents a mutant form that has an altered DNA sequence. The protein product that results from transcription and translation of that recessive (mutant) allele is defective. It cannot catalyze the reaction, and, therefore, does not produce a functional product. One copy of the normal allele is usually enough to allow the cell to produce ample quantities of normal protein. Therefore, a heterozygous plant looks normal. A homozygous recessive plant, on the other hand, cannot make any normal protein from its two mutant alleles.

What is the difference between the smooth seed allele and the wrinkled seed one? The smooth pea phenotype (*RR* or *Rr*) produces an enzyme allowing the seeds to accumulate high levels of starch. Seeds with the *rr* genotype do not produce a functional form of that enzyme and so have high levels of sucrose rather than starch. The sucrose in the *rr* seeds causes them to absorb water during development. When they dry, they lose that water and shrivel. The *RR* and *Rr* seeds have lower levels of sucrose and do not absorb as much water during development; consequently, they do not shrivel when they dry. Recent molecular genetic studies have revealed that the *r* allele produces a defective enzyme because it has had an 800-nucleotide piece of DNA inserted into the gene. As you might expect, compared with the normal allele, transcription and translation of the allele carrying this insert produce a much different (and, in this case, nonfunctional) protein. How did the insert get there? The best guess is that a transposable element inserted into the pea chromosome at this location some time during the pea plant's evolutionary history.

Molecular genetics can also explain how other Mendelian traits are expressed. For example, as you recall, flower color in snapdragons is inherited as an incompletely dominant trait. In this case, one copy of the functional allele produces some red pigment, but two copies produce noticeably more pigment. Red-flowered plants therefore have two copies of an allele that is critical in the red pigment synthesis pathway and are *RR*. Pink-flowered plants have one copy of

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that allele, producing light red (pink) pigmentation, and are *RR′*. (We use superscripts instead of upper- and lower-case letters here because we are not looking at complete dominance.) Finally, white plants have two copies of the defective allele (*R′R′*) and cannot make the enzyme necessary for red pigment production.

QUANTITATIVE TRAITS

While simply inherited traits such as snapdragon flower color effectively demonstrate Mendel's principles, many traits are under much more complex genetic control. **Quantitative traits,** such as yield and days to flowering, exhibit a range of phenotypes, rather than the discrete phenotypes studied by Mendel. Typically, they are dramatically influenced by environment. Consider tomato fruit yield as an example of a quantitative trait. Under identical environments, some tomato plants produce more fruit than others due to genetic differences. However, genetically identical plants will also produce different amounts of fruit when grown under different environments. They will produce large yields under optimal growing conditions and lower yields under stressed conditions. Therefore, phenotype (yield in this example) is determined by both genotype and environment. This is the "nature versus nurture" concept. Because quantitative traits are strongly influenced by environment and are generally controlled by many genes, they do not produce typical Mendelian ratios. Instead, statistical tools such as distributions, means, and variances are used to study quantitative traits. Molecular geneticists are able to identify chromosomal fragments, called **quantitative trait loci,** or QTLs, associated with quantitative traits. Presumably, these fragments contain genes that influence the trait and behave like Mendelian genes. Using this approach, quantitative geneticists are beginning to understand the nature of complex traits such as growth rate, fruit quality, and flowering time.

EXTRANUCLEAR DNA

You may recall a statement earlier in this chapter indicating that *most* DNA in plants resides in the nucleus. Where is the remaining DNA found? In plants, **extranuclear DNA** is found in both mitochondria and chloroplasts. According to the **endosymbiont hypothesis,** mitochondria and chloroplasts were free-living bacteria at some time in their evolutionary history. They became incorporated into cells of organisms that evolved into plants and established a symbiotic association. As you might expect, then, the DNA in mitochondria and chloroplasts is similar to bacterial DNA.

Some genes involved in photosynthesis and respiration are located in the chloroplast and mitochondrial genomes, respectively. Because many copies of each organelle exist in a plant cell and multiple copies of each gene may be found in each organelle, extranuclear genes do not exhibit Mendelian segregation ratios. In addition, sperm cells rarely carry mitochondria and chloroplasts, so that extranuclear genes are typically passed on to the next generation by only the female parent. This is called **maternal inheritance.**

Leaf variegation in plants such as four-o'clocks exhibits maternal inheritance because it results from mutations in chloroplast synthesis genes. Some herbicides are effective because they inhibit enzymes encoded by chloroplast genes. Genetic engineers are currently trying to manipulate chloroplast genomes to create herbicide-resistant crop plants. See Chapter 14 for a more detailed discussion of genetically engineered plants.

LINKAGE AND MAPPING

There are typically thousands of genes on each chromosome, and the closer the genes are to one another on a chromosome, the more likely they are to be inherited together. Genes that are together on a chromosome are said to be **linked.**

In 1906, just a few years after the basic details of meiosis became known, W. Bateson, R. C. Punnett (after whom the Punnett square is named), and E. B. Saunders became the first to report on linkage in sweet peas. They knew from earlier work with sweet peas that purple flower color was dominant and red was recessive. They also knew that pollen grains with an oblong shape ("long pollen") were dominant and that spherical pollen grains ("round pollen") were recessive.

When Bateson and Punnett crossed a homozygous purple long plant (*PPLL*) with a homozygous red round plant (*ppll*), all the F_1 offspring were purple and long as expected. When they crossed the F_1 plants with one another to obtain an F_2 generation, however, the F_2 offspring phenotypes were produced in numbers that differed markedly from the expected 9:3:3:1 ratio. Puzzled by these results, they tried a backcross, crossing F_1 plants (*PpLl*) with the recessive parent (*ppll*). Again, the expected 1:1:1:1 ratio was not produced. Instead, they obtained a ratio of 7 purple long: 1 purple round: 1 red long: 7 red round. They could not adequately explain what they had observed. In 1910, however, T. H. Morgan, who had observed similarly puzzling ratios in his experiments with fruit flies, correctly theorized that linkage and crossing-over were responsible.

If the genes for purple and red and those for long and round were on separate pairs of chromosomes, then the genotypes of the F_1 would be all *PpLl,* and the homozygous recessive would be *ppll.* A backcross to the F_1 (*PpLl* × *ppll*) should have produced 1 *PpLl*: 1 *Ppll*: 1 *ppLl*: 1 *ppll* instead of the 7:1:1:7 ratio actually obtained. Apparently, the F_1 parent produced many more *PL* and *pl* gametes than *Pl* and *pL* gametes. If we assume the genes are linked, then we can use a slash (/) to separate the alleles on one chromosome from those on the homologous chromosome. The parents were *PL/PL* and *pl/pl.* The first parent would produce gametes containing the *PL* chromosome and the other would produce *pl* gametes. The F_1 plant, then, would be *PL/pl* because it received a *PL*

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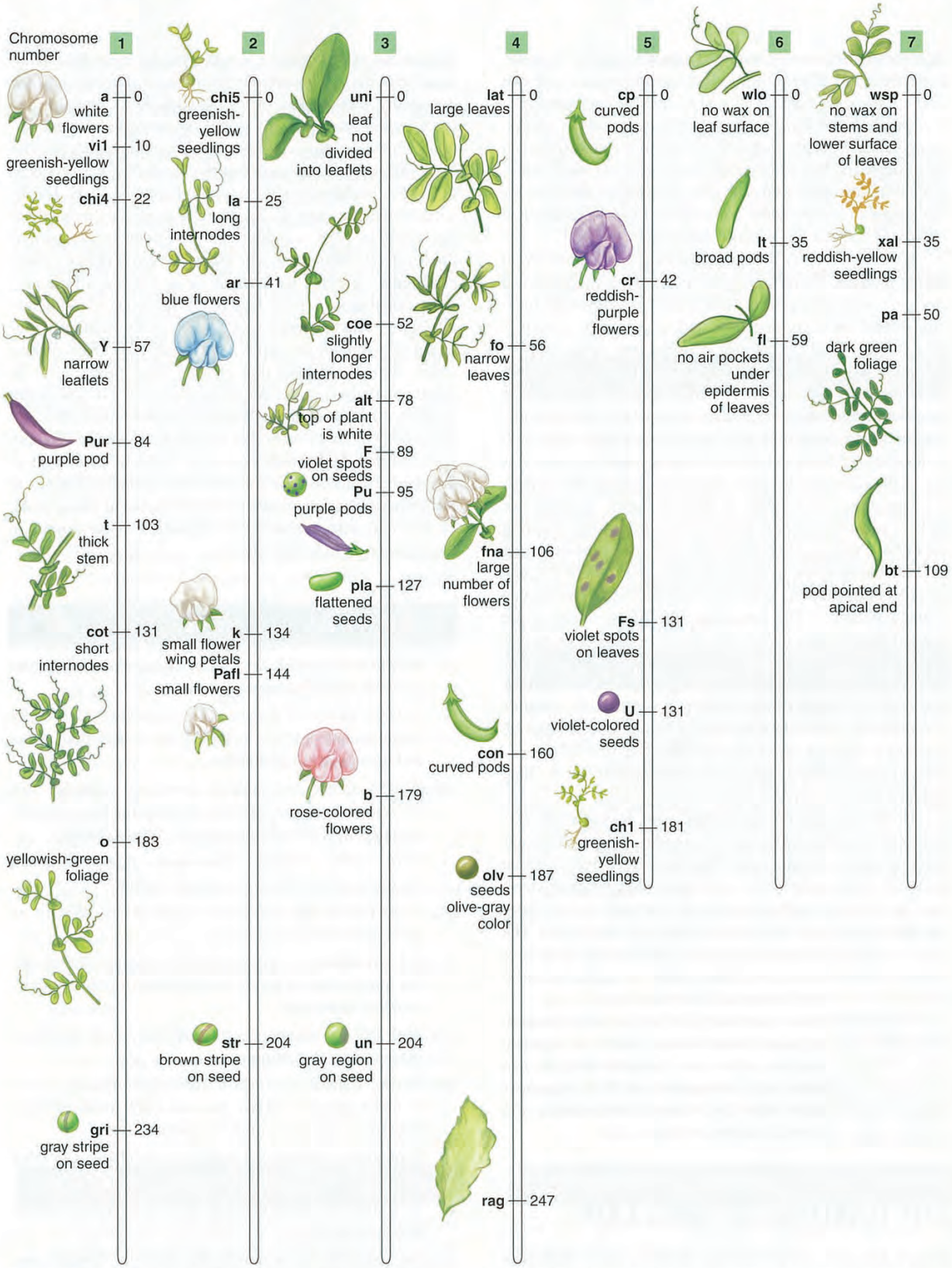


Figure 13.14 A partial genetic map of the pea. Chromosomes 1 through 7 are listed from left to right. Numbers along the right side of each chromosome are map distances. Letters along the left side are gene abbreviations. Drawings illustrate mutant phenotypes.

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chromosome from one parent and a homologous *pl* chromosome from the other. The F_1 plant would produce just two kinds of gametes, namely *PL* and *pl,* and the backcross (*PL/pl* × *pl/pl*) would have produced only two kinds of phenotypes, namely purple long (*PL/pl*) and red round (*pl/pl*) in equal numbers. But some purple round and red long phenotypes were also produced. The only plausible explanation for this seems to be that some crossing-over (see prophase I of meiosis in Chapter 12) occurs between genes *P* and *L.*

Crossing-over is a regular, seemingly random event during meiosis. Therefore, it may occur by chance between any pair of linked genes. Each gene has a specific location (**locus**) on a chromosome and, presumably, crossing-over is more likely to happen between two genes that are far apart on a chromosome than between two genes that are close together. We can use the frequency of crossing-over between genes to create a genetic map of each chromosome. A genetic map is similar to a map of a straight road, with genes corresponding to cities and map distances corresponding to the distances between the cities. A **map unit** equals 1% crossing-over between a pair of genes. Suppose we make a backcross (*PL/pl* × *pl/pl*), and 90% of the offspring are either *PL/pl* or *pl/pl.* These are **parental type** offspring because the gametes from the heterozygous parent (*PL* and *pl*) do not carry chromosomes for which a crossover between *P* and *L* occurred. The remaining 10% of the offspring are **recombinant types** (*Pl/pl* and *pL/pl*) because a crossover occurred between genes *P* and *L* to produce *Pl* and *pL* gametes. Remember that the heterozygous parent contains *P* and *L* on one chromosome and *p* and *l* on the homologous chromosome. The only way, then, it can produce *Pl* and *pL* gametes is through crossing-over. Because 10% of the offspring (and, therefore, gametes) were recombinant, the map distance between genes *P* and *L* is 10 map units.

In Bateson and Punnett's backcross, two of every sixteen (12.5%) of the offspring were produced through recombination due to crossing-over. We can deduce from this that the genes controlling flower color and pollen shape in sweet peas are 12.5 map units apart on a chromosome. It is interesting that Mendel did not observe linkage in his studies. The traits he analyzed happened to be on different chromosomes in peas. Imagine the difficulty he would have encountered if he had chosen to work on genes that were linked.

Linkage maps are essential tools for geneticists because they give us a physical framework in which to organize genes. Massive mapping efforts are currently underway in all major crop plants, with new genes and DNA sequences being added to maps every day. A simplified example of a genetic map of the pea is shown in Figure 13.14.

THE HARDY-WEINBERG LAW

Before Mendel's work became known, most biologists studied quantitative traits and believed that inherited characteristics resulted from a blending of those furnished by the parents. It was difficult to understand why unusual characteristics did not eventually become so diluted that they essentially disappeared. After Mendel, R. C. Punnett and other biologists asked why dominant genes did not eventually completely eliminate recessive ones in breeding populations. After all, a cross between two heterozygotes produces only 25% homozygous recessive individuals. G. H. Hardy, a mathematician, and W. Weinberg, a physician, pointed out the reason in 1908, and their observation became known as the Hardy-Weinberg law. The **Hardy-Weinberg law,** which essentially specifies the criteria for genetic equilibrium in large populations, states that the proportions of dominant alleles to recessive ones in a large, random mating population will remain the same from generation to generation unless there are forces that change those proportions. In small populations, for example, random losses of alleles can occur if, by chance, the individuals carrying those alleles do not mate as often as other individuals. In populations of any size, selection is the most significant cause of exceptions to the Hardy-Weinberg law and can cause dramatic changes in the proportions of dominant to recessive alleles. Discussions of artificial selection and natural selection are found in Chapters 14 and 15, respectively.

Summary

1. McClintock's work with corn changed beliefs about genes and chromosomes.
2. A DNA molecule consists of nucleotides. A typically single-stranded RNA molecule has a different sugar, and uracil instead of thymine.
3. Watson, Crick, and Wilkins developed a model of a DNA molecule, now considered authentic. It is a double-stranded helix resembling a spirally twisted ladder.
4. DNA stores genetic information, replicates itself, expresses its information, and can mutate.
5. A genome is the sum total of the information in an organism's DNA.
6. A DNA molecule replicates by "unzipping"; the resulting single strands serve as templates for two double-stranded molecules.
7. With DNA as a template, mRNA, tRNA, and rRNA are made during transcription.
8. During translation mRNA from transcription is used to make proteins; tRNA decodes mRNA information. Ribosomes are made of rRNA and proteins.
9. Spontaneous or induced mutations are changes in DNA sequence.
10. Inversions and translocations may be important speciation mechanisms.
11. An aneuploid has a normal chromosome number plus or minus one to several chromosomes. A polyploid has extra complete sets of chromosomes.

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12. Gregor Mendel originated the science of genetics while experimenting with peas. The pea varieties he crossed had pairs of contrasting characteristics on homologous chromosomes. Parent plant offspring were called the F_1 generation; the F_2 generation resulted from F_1 plant crosses. F_1 plants, called hybrids, all resembled their parents. F_2 offspring were produced in a 3:1 ratio of plants resembling one or the other parent.
13. The agents controlling the plants' characteristics were called "factors"; Mendel deduced that each plant had two factors (later known as alleles) for each characteristic. His law of unit characters states that "factors, which always occur in pairs, control the inheritance of various characteristics." The suppressing factor was called dominant and its counterpart recessive.
14. Phenotypes (described with words) denote appearance; genotypes (shown with letters) designate genetic makeup. Capital letters designate dominant alleles; lower case letters designate recessive alleles.
15. Paired homozygous plant alleles are identical. Paired heterozygous plant alleles are contrasting.
16. Monohybrid cross offspring are produced in a ratio of 3 dominant phenotypes to 1 recessive phenotype. Dihybrid crosses produce a 9:3:3:1 phenotypic ratio. A backcross between an F_1 hybrid and its recessive parent produces a phenotypic ratio of 1:1 (monohybrid) or 1:1:1:1 (dihybrid). A testcross is used to determine if a plant with the dominant phenotype is homozygous or heterozygous.
17. Compared with homozygotes the heterozygotes are intermediate when dominance is incomplete.
18. Enzymes control biochemical reactions. Genotypes control phenotypes.
19. Quantitative trait genotypes are strongly influenced by environment.
20. Linked genes are inherited together. Bateson, Punnett, and Saunders observed a 7:1:1:7 ratio in a dihybrid cross, and postulated it resulted from linkage and crossing-over.
21. Chromosomal mapping requires calculating crossover percentages to determine the positions of genes on chromosomes.
22. The Hardy-Weinberg law explains why recessives in a population do not disappear. Selection is the most significant cause for seven exceptions to the Hardy-Weinberg law.

Review Questions

1. Using S, P, and B as abbreviations for sugar, phosphate, and base, respectively, draw a DNA double helix in the arrangement you would see if you untwisted the helix so you were looking at a ladder structure.
2. If a DNA molecule had a string of cytosine-thymine base pairs, how would it differ in width from a normal molecule?
3. Explain how DNA replicates.
4. Using the genetic code, determine the amino acid sequence produced by the following gene (DNA) sequence. Remember that during transcription, RNA forms complementary base pairs with DNA. For example, if the DNA sequence is TAG, then transcription would produce an RNA fragment with the sequence AUC. TACACAGCAACT

Discussion Questions

1. Why do you suppose gene expression requires an intermediate RNA molecule? That is, why does the translation machinery read mRNA instead of the gene itself?
2. If proofreading enzymes became more accurate and efficient, then what do you suppose would happen to the speed at which organisms evolve?
3. Mendel's peas were self-pollinating. Describe advantages and disadvantages of self-pollination.

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CHAPTER

14

Plant Breeding and Propagation

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A flower of butterfly pea (*Clitoria ternata*), a tropical vine whose flower construction ensures that both the anthers and pistil touch the backs of visiting insects. The seeds are believed to be toxic to livestock.

OVERVIEW

In this chapter, the processes that have produced and propagated domesticated plants are discussed. Proposed origins of our agricultural societies are presented along with the phenotypic changes that occurred during crop domestication. Plant breeding methods using conventional and nonconventional strategies are outlined. Then, propagation methods using seeds and asexual propagules are discussed.

Some Learning Goals

1. Provide explanations for the shift from hunter-gatherer societies to agricultural ones.
2. Describe phenotypic changes that occurred in plant populations as a result of human selection.
3. Describe breeding methods used for self-pollinating crops.
4. Describe breeding methods used for cross-pollinating crops.
5. Explain the significance of germplasm banks to crop improvement programs.
6. Describe the method used to produce protoplast fusion hybrids.
7. Outline the major steps involved in creating a transgenic plant.
8. Outline the steps involved in growing a crop from seed.
9. Describe how cutting propagation methods produce genetically identical plants.
10. Explain the benefits of grafting and outline the steps involved in making a graft.
11. Provide examples of specialized roots and stems used for asexual propagation.
12. Explain the benefits of micropropagation and outline the steps involved in micropropagation.

CROP PLANT EVOLUTION

"It is clear that the human species is currently an eater of grass seeds. We have become 'canaries.' It is also clear that the world's food supply depends on 12 or 15 plant species. It probably was not always so, although wheat, barley, rice, and maize have been the foundations of our high civilizations. The current trend is for the major crops to become even more major and for the lesser ones to dwindle."[1]

In fact, although there are approximately 250,000 species of flowering plants, only six species—wheat, rice, corn, potato, sweet potato, and cassava—provide 80% of the calories consumed by humans worldwide (Fig. 14.1). An additional eight plants—sugar cane, sugar beet, bean, soybean, barley, sorghum, coconut, and banana—complete the list of major crops grown for human consumption.

In the 2 million years that we have inhabited this earth, we have cultivated plants for only the most recent 10,000 years, or less than 1% of our history. However, in that time, we have dramatically changed the plant landscape and our own lives. Hunter-gatherer societies have given way to agricultural societies and the development of cities and civilizations. Such concentrations of people are vulnerable to catastrophes such as drought and famine. Domesticated plants depend on us for their survival, but we have also become dependent on them for our survival.

1. J. P. Harlan. 1992. *Crops and Man*, 2d ed. Madison, WI: Amer. Soc. Agron.



Figure 14.1 These six foods—corn, rice, wheat, potato, sweet potato, and cassava—meet most of the caloric needs of people worldwide.

We **domesticate** plants by altering them genetically to meet our needs. Strictly speaking, a domesticated plant is one whose reproductive success depends on human intervention. This is an ongoing evolutionary process, and plants are found in a continuum from purely wild to fully domesticated. Our current crop plants continue to evolve as a result of our breeding efforts. It is amazing that, although humans have eaten thousands of types of plants in the past, we currently rely on only a handful to supply almost all of our nutritional needs.

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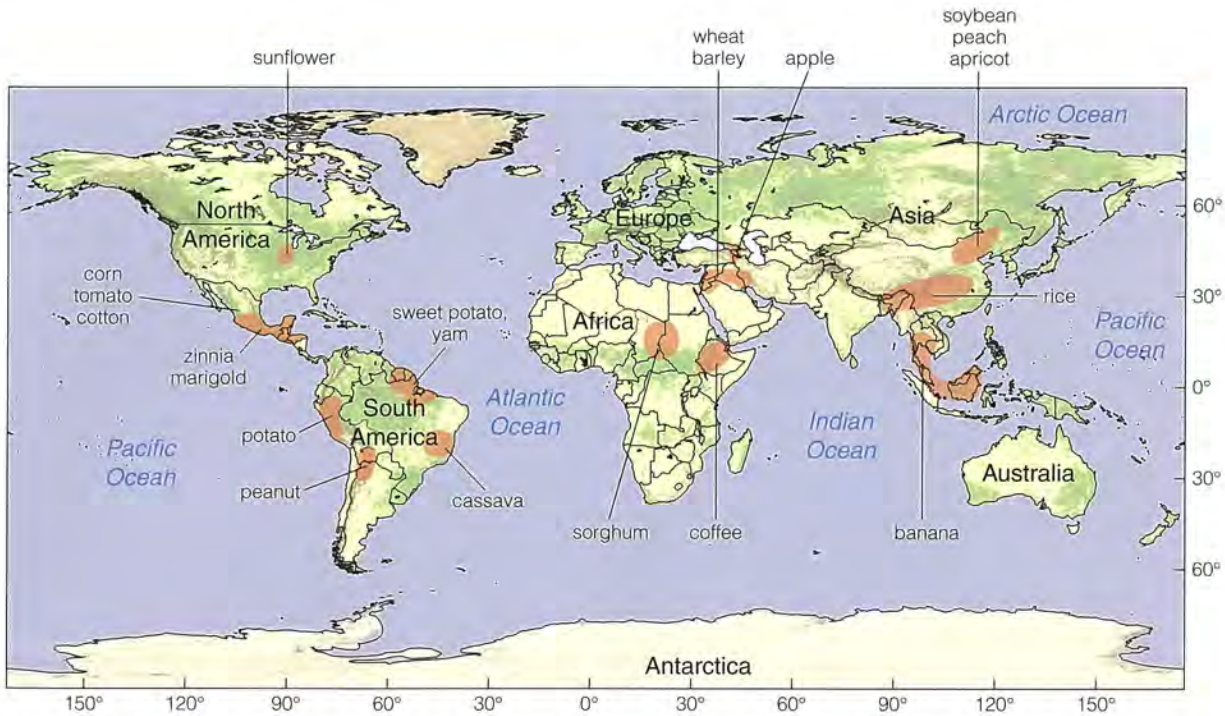


Figure 14.2 Regions of domestication of some crop plants. *(Data from Jack R. Harlan.* Crops and Management, *2nd edition. Am. Soc. Agronomy.)*

Origins of Agriculture

Domestication of crop plants, and the development of industrial societies that followed, is a recent event in our history. Of the 80 billion humans that have lived on this earth, 90% were hunter-gatherers, 6% were farmers, and only 4% were industrialized.[2]

We do not know why most humans shifted from a hunter-gatherer lifestyle to an agricultural one. Several hypotheses exist, but they are purely speculative. Hunter-gatherers may have had better lives than cultivators did. Their diet and health were better, their starvation rate was lower, and they worked far fewer hours. Their work week was only about 20 hours long! Because they had abundant free time, hunter-gatherers may have simply begun to grow plants in gardens as a hobby. They may have begun to cultivate a few plants to supplement lean times in the gathering schedule. Or, they may have had spiritual reasons for growing plants in a protected environment. Because agricultural practices arose independently in many parts of the world over thousands of years, each of these scenarios probably explains why humans began to domesticate plants.

People began to domesticate plants in the Near East around 10,000 years ago. Many agricultural sites from this time period have been located on the western edge of what is now Iran. Domesticated plants were developed in Asia and the New World 1,000 to 3,000 years later. Farming probably began in Africa and the New World about 4,000 years ago.

The first crops domesticated were cereal grains. Root crops and legumes, such as peas and beans, were domesticated 1,000 to 2,000 years later. These were followed by vegetables, and then oil, fiber, and fruit crops. Finally, plants used for forage, decoration, and drugs were first domesticated only about 2,000 years ago. Few crops have been brought into domestication in recent centuries. Plant breeders currently devote much more energy to improving existing crops than developing new ones. The map in Figure 14.2 shows where some of our major crops were domesticated. Sunflower is the only major crop that was domesticated in the present-day United States (Fig. 14.3). For further discussion on the origin of cultivated plants, see Chapter 24.

Evolution Under Domestication

"It is as if man had been appointed managing director of the biggest business of all, the business of evolution . . . whether he is conscious of what he is doing or not, he is in point of fact determining the future direction of evolution on this earth. That is his inescapable destiny, and the sooner he realizes it and starts believing in it, the better for all concerned."[3]

2. See note 1.

3. J. S. Huxley. 1957. *New Bottles for New Wine.* New York: Harper and Sons.

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Figure 14.3 The sunflower is the only major crop that was domesticated in the United States. *(© Stephen P. Lynch)*

As soon as people began sowing seeds of selected plants, instead of simply harvesting wild plants, dramatic genetic changes occurred in those populations in response to selection pressure. The seed dispersal mechanism was probably the first trait altered during domestication. The seeds of wild plants are typically carried away by wind, water, or animals. This minimizes the competition for light and nutrients that results from overcrowding. People most likely gathered seeds from plants that retained them instead of dispersing them. Early domesticators would have focused also on plants with high seed numbers and large seed size (Fig. 14.4). Competition in crowded cultivated plots would favor high seedling vigor and fast germination rate. In addition, while seed dormancy mechanisms are important in wild plants, plants that survived in cultivated gardens were those that germinated immediately upon planting. These changes accumulated over many generations and created the cultivated plants we know today. Many of these plants have been so dramatically altered from their wild forms that they cannot survive without the aid of humans. For example, if a cornfield is abandoned, it will cease to produce any corn plants within just a year or two.

The first serious attempts to understand the geographic origins of domesticated plants were made by the Russian geneticist Nikolai Ivanovich Vavilov in the 1930s. Based on extensive collecting expeditions carried out worldwide, Vavilov proposed that each crop plant was first domesticated in the region of the world where its genetic diversity is greatest. Tragically, Vavilov's career and life were cut short when he was imprisoned by the Stalin government in 1940 on charges of espionage and, ironically, efforts to harm agriculture. He died in prison 3 years later. Although more recent studies indicate that patterns of crop domestication cannot be adequately explained by Vavilov's *Centers of Origin,* he can be credited with initiating studies that have led to our understanding of the relationships between cultivated plants and their wild relatives. As we will see later, wild relatives of crop plants are valuable sources of genes for modern crop improvement.

PLANT BREEDING

The systematic breeding of crop plants has been carried out only in the past 200 years. Until then, crop improvement was based on simply selecting and planting seeds from desirable plants. This method was moderately effective because plant populations were genetically diverse and could be improved gradually across generations (Fig. 14.5). However, it took an understanding of genetics and plant reproduction, and the training of scientists in these fields, to develop the sophisticated crop-breeding methods we know today.

Plant breeding is accelerated evolution guided by humans rather than nature. Breeders replace natural selection with human selection in order to modify plants genetically to meet our needs. Remember from Chapter 13 that, according to the Hardy-Weinberg law, a population of plants will remain in genetic equilibrium unless an outside force changes its genetic makeup. Plant breeders act as that outside force, molding plant populations to contain higher proportions of alleles that are desirable to humans. Typically, the primary goal of plant-breeding programs is improved yield, with disease resistance, pest resistance, and stress tolerance contributing to yield. With new sources of agricultural land dwindling and the human population continuing to grow, efforts must concentrate on improving the amount of food harvested per acre and developing crops that can grow on low-quality land (Fig. 14.5).



Figure 14.4 Modern corn (*left*) was probably domesticated from teosinte (*right*). *(Teosinte photo courtesy John Doebley)*

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Figure 14.5 Potato tuber diversity. Genetic variation provides the foundation for efforts to improve plants through breeding.

Breeding Methods Using Sexually Compatible Germplasm

Strategies

A plant breeder tends to divide crop plant species into two groups: **self-pollinating** and **cross-pollinating.** A self-pollinating plant is capable of fertilizing itself, while a cross-pollinating one cannot. Breeding methods for self-pollinating plants are radically different from those for cross-pollinating ones. A self-pollinating plant tends to be highly **homozygous** because all of its genes came from the same parent. The plant's mother was also its father! As you might expect, these plants have undergone a significant amount of **inbreeding.** As the species has evolved, it has adapted to and thrives on inbreeding. On the other hand, a cross-pollinating plant is likely to be highly **heterozygous,** because its mother and father were different plants. Cross-pollinating species tend to require a high level of heterozygosity in order to be productive.

Self-pollinated crop plants include wheat, rice, oats, barley, peas, beans, tomatoes, and peppers. Some fruit trees, such as apricots, nectarines, peaches, and citrus fruits are also primarily self-pollinated. The most primitive form of breeding in this group of plants is called **pure-line selection.** This method simply involves collecting seed from each of several plants, growing all the seed from each plant in a row, and selecting the most desirable row. All the plants in a row will be related to each other, since they came from the same plant. The seeds from the best row can then be propagated as a new "pure-line" variety.

A breeder with an understanding of reproductive biology can make crosses between self-pollinating plants. In fact, today, most plant breeders create hybrid populations by crossing desirable parents. Then, as the hybrid plants self-pollinate, highly diverse groups of offspring will be created. These offspring of the self-pollinated hybrids provide the basis for selecting pure-line varieties. Crosses between normal wheat varieties and dwarf plants have been created to develop dwarf varieties. More of the energy in these plants is directed toward producing seeds rather than stalks, resulting in higher yields.

Norman Borlaug, who is known as the "Father of the Green Revolution," was awarded the Nobel Prize in 1970 for developing new strains of wheat in Mexico. The new high-yielding strains, which were produced from crosses with a dwarf variety from Japan, were widely planted. Before the project began in 1944, Mexico had imported wheat for many years, but the new varieties were so successful that, within 20 years, Mexico had quadrupled its wheat production and had enough to export to other countries. India and Pakistan experienced similar gains. It has been argued that, by increasing grain yields in developing countries, Borlaug has saved more lives than anyone in history (Fig. 14.6).

Although the Green Revolution has been a dramatic success, gains have not been unqualified. Irrigation and inorganic fertilizer are needed to support the rapid growth of these plants. Because many inorganic fertilizers are produced from



Figure 14.6 Norman Borlaug, the father of the Green Revolution. *(© Bill Meeks/AP Wide World Photos)*

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fossil fuels, the cost of farming increases with fuel prices. On the other hand, the high-input system of agriculture has allowed food production to increase without a corresponding increase in the amount of land used for farming. This means that in areas where population growth is strong, high-yield farming prevents deforestation of wild areas.

Cross-pollinated species include corn, rye, alfalfa, and clover, as well as most fruits, nuts, and vegetables. The simplest form of selection in cross-pollinated crops is **mass selection.** With this method, many plants from a population are selected, and seeds from these plants are then used to create the next generation. Again, the seeds from the best plants are chosen and propagated, and so on, for many generations. This slowly molds the genetic makeup of the population to fit the breeder's preferences. For example, suppose variations in seed size are due to genetic differences and the breeder always collects from plants with the largest seeds. After several generations of selection, the breeder has genetically altered the population so that a larger proportion of plants carry the genes for large seed size.

Outcrossing (crossing between genetically different plants) in cross-pollinated crops often results in hybrid vigor, or **heterosis.** These plants are large, vigorous, fertile, and high yielding. Conversely, self-pollination of cross-pollinated plants will result in **inbreeding depression** in the form of small size, poor vigor, low reproductive capacity, and a high proportion of abnormal plants, due to the expression of deleterious recessive alleles. Breeders, however, do not avoid inbreeding of cross-pollinated species. In fact, a common breeding method involves forced self-pollination for several generations to create inbred lines in which deleterious alleles have been eliminated. Then, selected inbred lines are crossed to produce **hybrid seed.** Using this method, the most dramatic success story to date involves corn (maize), in which crosses between unrelated inbred lines often produce hybrids that dramatically outyield their parents. In 1908, in one of the earliest hybrid corn studies, plant breeder G. H. Shull crossed two inbred lines of corn, each of which produced 20 bushels per acre. The hybrid offspring yielded 80 bushels per acre, a quadruple increase in yield. Most of the corn in the United States is grown from hybrid seed (Fig. 14.7).

Some early American and European varieties, called **heirloom varieties,** are grown as open-pollinated populations of plants. Each variety is a mixture of genotypes, and all plants are allowed to pollinate each other, or open-pollinate, during seed production. These varieties are not as uniform as modern varieties, but their genetic variability allows them to produce a crop under many different environments. For example, a dry year and an insect pest might severely compromise all the plants in a hybrid variety if the variety is not genetically capable of surviving these conditions. An open-pollinated variety is likely to have some plants that are adapted to drought and others that can resist insect damage. The Seed Savers Exchange in Decorah, Iowa, has been created to preserve and distribute heirloom varieties. Heirloom varieties are important for farm market producers and growers of organic crops. They also contribute genetic diversity to breeding programs.

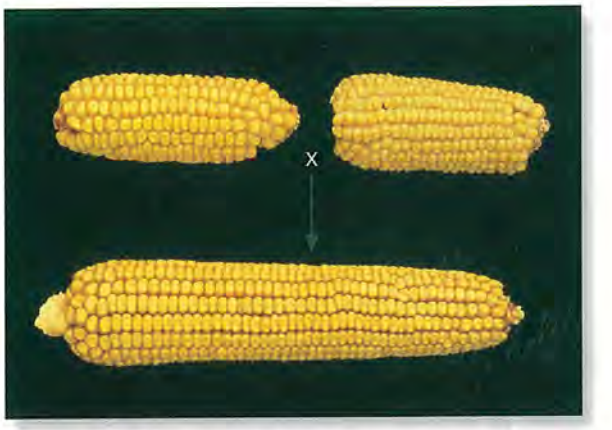


Figure 14.7A Crosses between inbred lines (*top*) often produce high-yielding hybrids (*bottom*). Such hybrid vigor is called *heterosis.*



Figure 14.7B Hybrid corn plants.

Germplasm Collection and Gene Banks

Progress in plant breeding is absolutely dependent on genetic variability. It is impossible to improve a population if there is no genetic variability for the trait of interest. For example, a breeder who needs to develop rust fungus-resistant wheat

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must begin with a population containing at least one plant with some degree of resistance. Plant breeders are, therefore, concerned with the *germplasm* resources of crop plants. A crop plant's **germplasm** is the sum total of its genes. A breeder must have access to crop plant germplasm containing genes for traits that are important for current breeding efforts and in the future, new traits may become important. For example, in a decade or two, we may need to develop plants with resistance to a new pathogen.

The plant varieties used in agriculture today have resulted from centuries of selection for specific traits. They are often genetically uniform and, therefore, may not be good sources of new genetic variability for further advances in breeding. In addition, their homogeneity makes them vulnerable to outbreaks of pests. The Irish potato famine in the mid-1800s occurred because people in that region relied on a few varieties of potatoes for most of their food supply. When a pathogen spread through the fields, all the plants succumbed, and the people lost their entire potato crop. As recently as 1970, 15% of the United States corn crop was wiped out by a fungal pathogen. Genetic uniformity in the corn varieties grown at that time resulted in this significant loss.

In order to meet current and future needs for plant genetic diversity, **gene banks** have been established worldwide. The International Plant Genetic Resources Institute is responsible for coordinating international efforts to collect and conserve crop plant germplasm. The Institute also assists regional and national gene banks. The collaborative efforts of state and federal government agencies, along with private industries, comprise the National Plant Germplasm System in the United States. Scientists regularly conduct collecting expeditions in regions where wild relatives of crop plants are found (Fig. 14.8A). In a similar fashion, botany students often learn how to identify and collect plant specimens for herbariums and museums worldwide (Fig. 14.8B). These skills help professional botanists to bring plant samples back to gene banks, where they are catalogued, propagated, and screened for desirable traits. Some seeds or other **propagules** are put into long-term storage for future needs, while others are given to plant breeders for immediate use.



Figure 14.8A Botanists on a plant-collecting expedition in Peru. *(Courtesy David Spooner)*



Figure 14.8B Botany students learning how to collect and identify plant specimens in the field.

Breeding Methods Using Sexually Incompatible Germplasm

In recent years, powerful new tools have been added to the toolboxes of plant breeders. Most breeding progress today is made using crosses among crop plants and their relatives, as described in the previous section, "Breeding Methods Using Sexually Compatible Germplasm." However, in many breeding programs, species boundaries no longer exist. Through techniques such as *protoplast fusion* and *gene splicing* (discussed in sections that follow), genes from virtually any living organism can be incorporated into crop plants. Everything, therefore, from an antifreeze gene in North Atlantic fish to a pesticide gene in bacteria, is now accessible to breeding programs.

Protoplast Fusion

There are times when a breeder would like to tap into the genetic diversity of a plant species that is distantly related to a crop plant. However, it is impossible to make a cross between the two species and obtain viable seeds. An alternative strategy involves **protoplast fusion.** With this method, cells of each species are grown in a liquid nutrient solution. Then, their cell walls are chemically stripped off to produce protoplasts. The protoplasts of the two species are mixed together and stimulated, with the aid of an electric current or chemical solution, to fuse with each other. When screening the fusion products, a scientist must distinguish between *autofusions,* where two protoplasts of the same species have

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fused together, and *hybrid fusions,* in which the protoplast of one species has fused with that of the other species. One way of doing this involves dyeing the protoplasts of each species with a different color before the fusion event. Then, the scientist can examine the fusions with a microscope and identify protoplasts that show both colors. The selected protoplasts are then carried through a series of *tissue culture* events (see "Micropropagation" on page 261) that cause them to grow into whole plants. These new plants carry genes from two distantly related species. They are called **somatic hybrids** because they resulted from combining (hybridizing) *somatic,* or body, cells from two different plants. In contrast, plants usually reproduce when gamete cells (eggs and sperm) are combined, producing sexual hybrids.

Although protoplast fusion appears to have value for the incorporation of new genes into crop plants, few success stories are currently available. Somatic hybrids have been created between potato cultivars and nontuber-bearing wild relatives. Some are highly resistant to a number of bacterial and fungal diseases, but varieties have not yet been created from the hybrids or their offspring. Tobacco is probably the best example of a commercially successful somatic hybrid. A common variety produced in Canada is the result of a fusion between cultivated tobacco and a wild relative containing a novel form of disease resistance.

Gene Splicing and Transgenic Plants

Genes from virtually any organism, from viruses to humans, can now be inserted into plants, creating **transgenic plants.** The technologies that have been developed to support this work arose from basic research to understand DNA structure and function. **Recombinant DNA** technology is based on the knowledge that DNA behaves the same no matter what organism carries it. Because the DNA code is nearly universal, a plant cell can read a DNA sequence from almost any other organism and produce a foreign gene product.

The serendipitous discovery of **restriction enzymes** paved the way for molecular genetic engineering. These enzymes act as molecular scissors, chopping up DNA into pieces small enough for genetic analysis. In nature, bacteria produce restriction enzymes, protecting themselves from viral pathogens by destroying pieces of foreign DNA. A key feature of these enzymes is their ability to cut DNA at specific sites and create DNA fragments with "sticky" ends. When DNA is cut by certain restriction enzymes, one strand is slightly longer than the other. Each fragment then is a double-stranded DNA molecule with a single-stranded tail at each end. This tail is called a sticky end because it will base-pair with the tail of any other fragment cut with the same enzyme (Fig. 14.9).

How are transgenic plants made? As an example, let's say we would like to insert a bacterial insect resistance gene into a corn plant. First, we need to find the insect resistance gene in the bacterium. This is actually a very difficult task and beyond the scope of this book. As you might expect, finding a specific gene in the enormous genome of eukaryotes is even more difficult and is like looking for a needle in a haystack. Sometimes, if a protein gene product is known, then a machine called a **protein sequencer** can be used to determine the sequence of amino acids in the protein. Then, using information from the genetic code (see Chapter 13), a **DNA synthesizer** produces an artificial gene. An alternative approach is to find the gene in an organism's genome and then use a restriction enzyme to cut the bacterial chromosome on both sides of the gene, but not within the DNA sequence of the gene. After that, the bacterial DNA and a *cloning vector* are cut with the same restriction enzyme. A *cloning vector* is a piece of DNA that can copy itself in a living cell. A common example of a cloning vector is a **plasmid,** a small, circular piece of DNA naturally found in bacteria and capable of replicating independently of the bacterial chromosome. Dozens of custom-made plasmids containing restriction enzyme cutting sites have been created by genetic engineers. If the cut bacterial DNA is mixed with cut plasmids, then their sticky ends will join together and create recombinant DNA. In this case, the recombinant DNA is a plasmid with an insect resistance gene attached to it. *Escherichia coli,* the bacterial workhorse of molecular genetics, can be stimulated to take up the plasmid via a process called **transformation.** When the *E. coli* cells multiply in a flask of nutrient medium, they will replicate their recombinant plasmids. At this point, *E. coli* is cloning our insect resistance gene for us. A culture of the bacterium will contain millions of copies of the gene (Fig. 14.10).

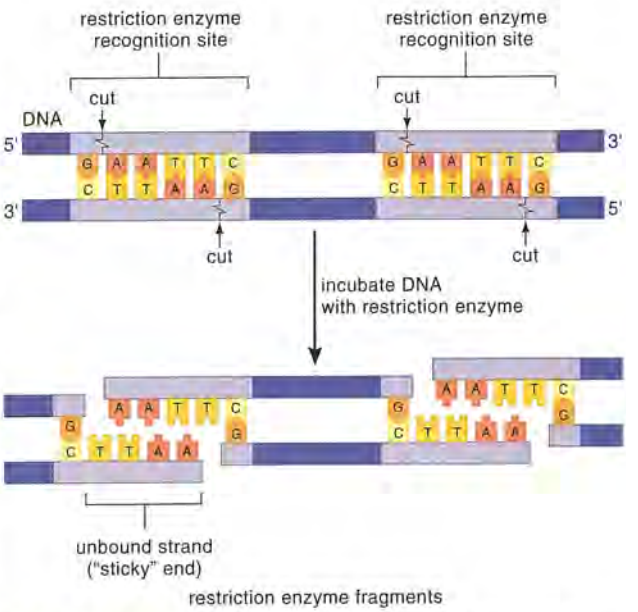


Figure 14.9 Cutting of DNA by a restriction enzyme. Some restriction enzymes are capable of cutting DNA molecules into two strands. One strand, which is slightly longer than the other, has a *sticky end* that can pair with the sticky end of another similarly cut DNA strand. *(From Moore, Clark, and Vodopich, Botany, 2nd edition. ©1998 The McGraw-Hill Companies. All rights reserved.)*

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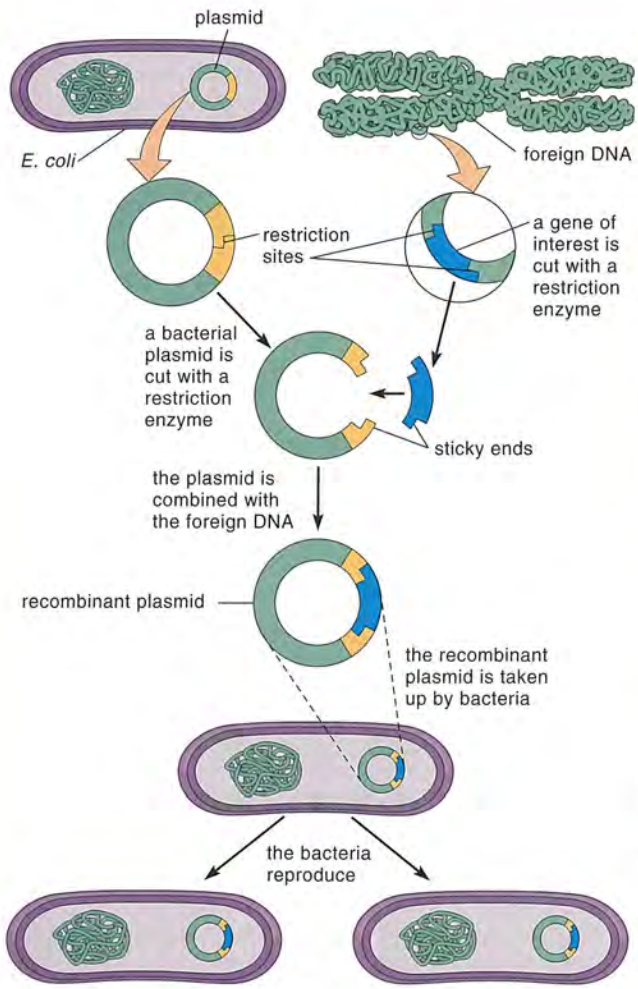


Figure 14.10 Gene cloning by bacteria. A plasmid from a bacterium and a gene of interest from foreign DNA are cut by restriction enzymes. The gene becomes inserted into the plasmid, which is taken up by bacteria. The bacteria multiply. *(From Moore, Clark, and Vodopich,* Botany, *2nd edition. © 1998 The McGraw-Hill Companies. All rights reserved.)*

After our insect resistance gene has been cloned, we have enough copies of it to manipulate and try to insert it into plant cells, again through transformation. We can remove the plasmids from a culture of *E. coli,* use the same restriction enzyme to cut out the resistance gene, and then purify it. Plant cells will not take up foreign DNA as readily as bacterial cells. Nevertheless, a number of techniques to transform plants with foreign DNA have been developed. We will focus on the two major ones.

The most common transformation technique relies on a natural genetic engineer, *Agrobacterium tumefaciens.* This bacterium infects plant cells and then inserts DNA (called **T-DNA,** or transfer DNA) from its plasmids into the plant's chromosomes. This causes the plant to produce cancer-

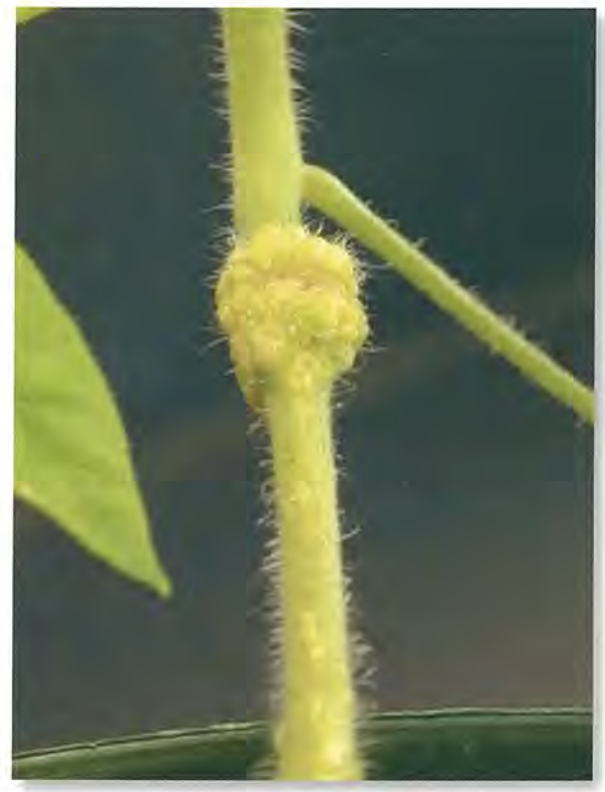


Figure 14.11 A crown gall, caused by the bacterium *Agrobacterium tumefaciens,* on a tomato plant. *(Courtesy Terese Barta)*

like tumors that harbor and feed the bacterium (Fig. 14.11) Human genetic engineers, however, have removed the virulence (disease-causing) genes from the T-DNA region and replaced them with genes of human interest. In our example, we could insert the insect resistance gene into the T-DNA region of the *Agrobacterium* plasmid (Fig. 14.12). Then, we would allow the bacterium to infect corn cells and insert its T-DNA into the chromosomes of those cells. Transformed cells can be cultured to produce whole plants carrying and expressing the insect resistance gene. The gene has now been stably incorporated into a plant chromosome and will be passed on to subsequent generations (Fig. 14.13).

When the *Agrobacterium* transformation technique was first developed, it was not effective in monocots. As a result, an alternative strategy using a **particle gun** was developed especially for use with monocots. This technique actually first used a tiny modified shotgun, with DNA attached to the shot. Today's particle guns are much more refined (and expensive!) than that first prototype, but still rely on shooting DNA into plant tissue. With this technique, very small tungsten or gold pellets are coated with the cloned insect resistance gene. Then the DNA is shot into corn cells and, if enough plant cells are bombarded, some of them will have the gene incorporated into their chromosomes. Precisely how this process works is still a mystery, but through the

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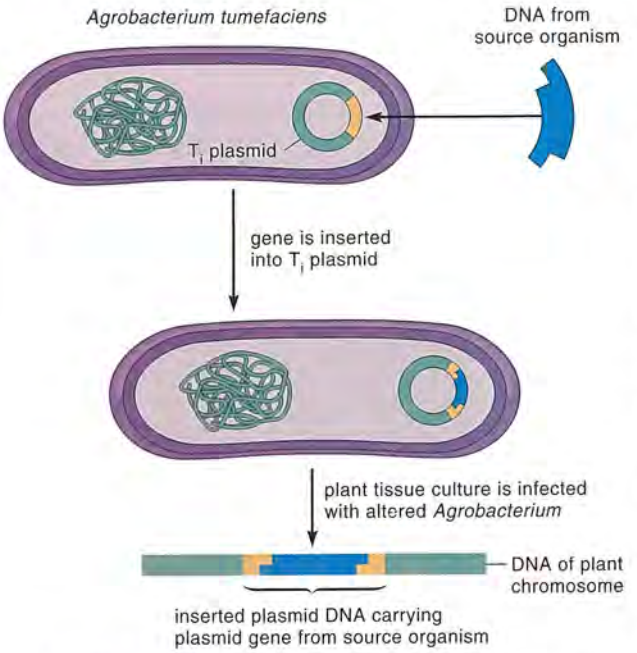


Figure 14.12 Inserting foreign genes into a plant using an *Agrobacterium* T$_i$ plasmid. *(From Moore, Clark, and Vodopich,* Botany, *2nd edition. © 1998 The McGraw-Hill Companies. All rights reserved.)*

use of this technique, foreign genes have been permanently inserted into crop plants. In fact, transgenic corn containing a bacterial insect resistance gene is now widely grown in the United States.

It is difficult to control the number of gene copies inserted during transformation. In addition, genes are inserted at random locations in plant chromosomes during this step. Sometimes, the foreign genes may be inserted in areas of the genome that are not expressed by the plant, or they may insert into a critical portion of a plant gene. In addition, considerable effort is often needed to get the foreign gene expressed at suitable levels in appropriate tissues. Transformation and gene expression, therefore, are the most challenging aspects of transgenic plant production.

Transgenic corn, soybean, cotton, potato, and canola varieties containing herbicide and insect resistance are grown extensively in North America (Fig. 14.14). Traits such as disease, insect, and herbicide resistance are important for the producers of those crops, but you would not notice them as a consumer. The new generation of transgenic crops focuses on traits that will be more obvious. Transgenic plants can act as *bioreactors* to create pharmaceuticals. These plants would provide inexpensive access to vaccines and other medicines,

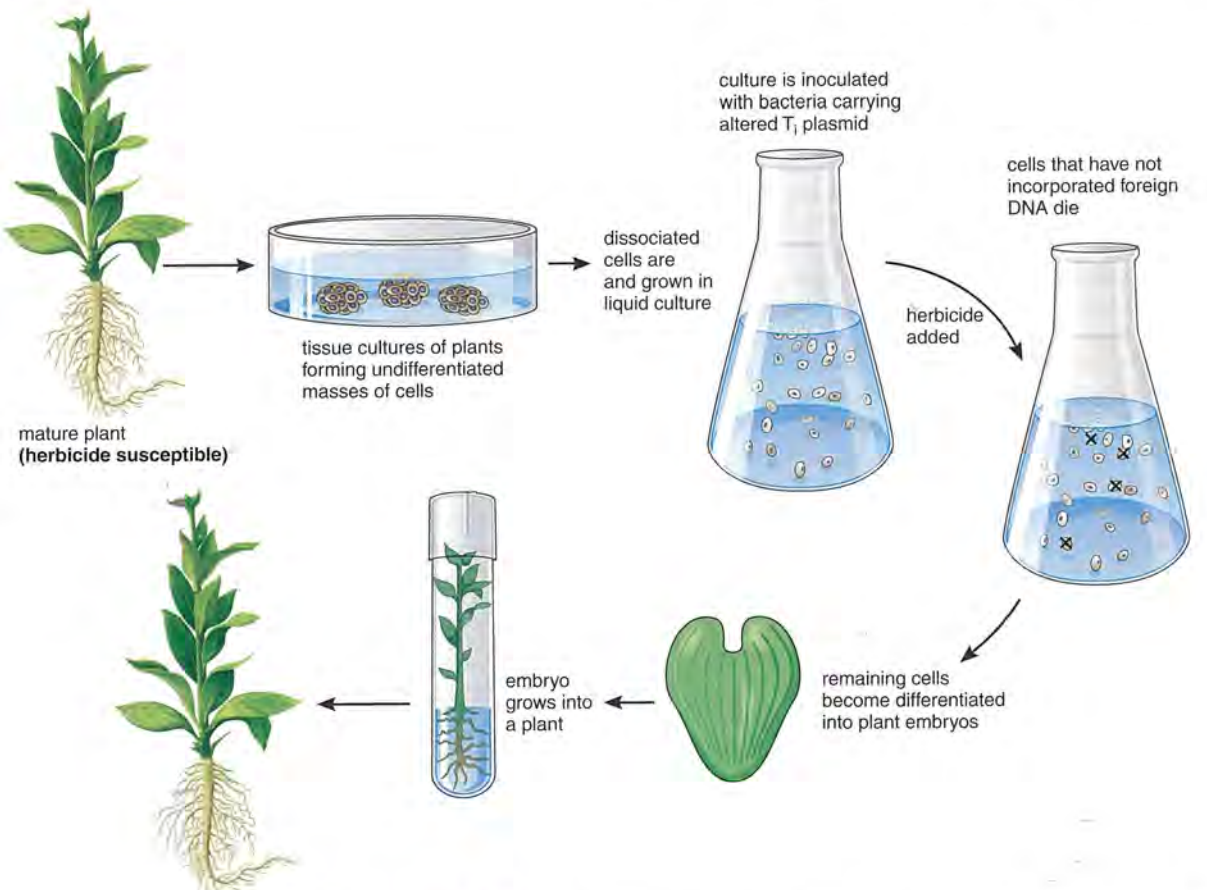


Figure 14.13 Steps in making a transgenic plant. *(From Moore, Clark, and Vodopich,* Botany, *2nd edition. © 1998 The McGraw-Hill Companies. All rights reserved.)*

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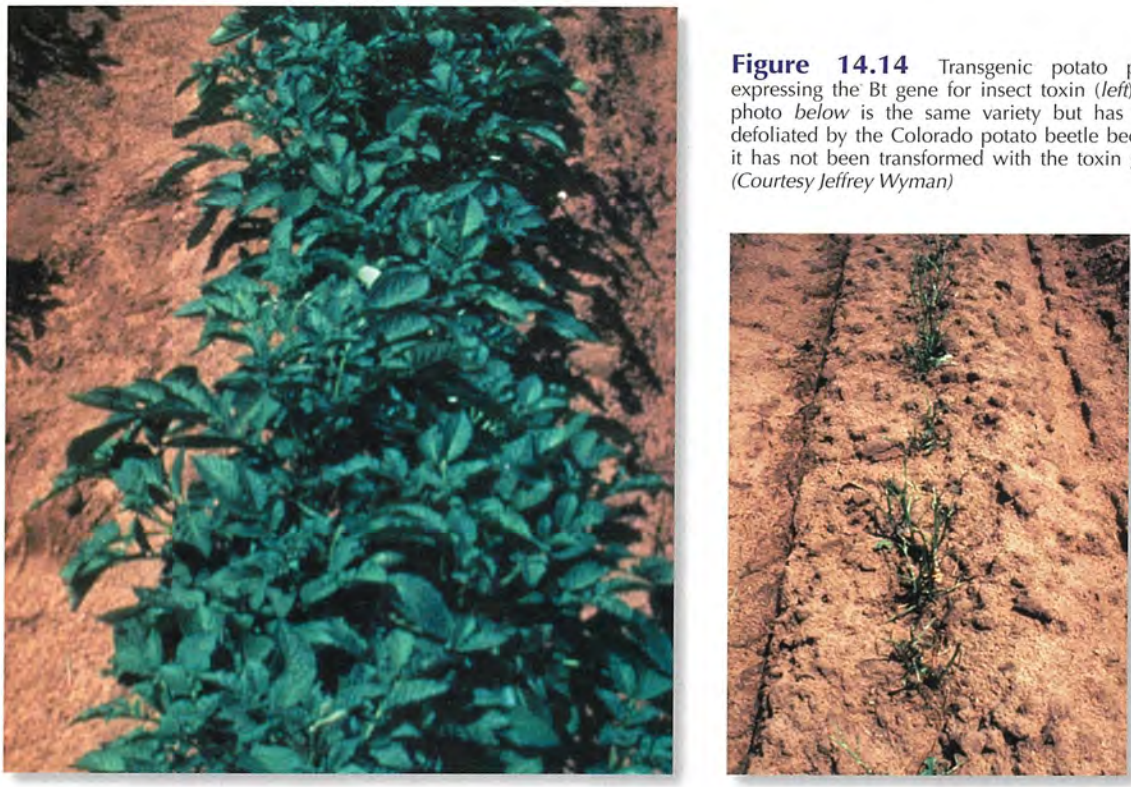


Figure 14.14 Transgenic potato plants expressing the Bt gene for insect toxin (*left*). The photo *below* is the same variety but has been defoliated by the Colorado potato beetle because it has not been transformed with the toxin gene. *(Courtesy Jeffrey Wyman)*

especially in parts of the world where medical facilities are not readily available. People would simply take their medicine by eating potatoes or carrots. For example, transgenic plants are being tested for the production of vaccines against hepatitis B, rabies, cholera, tuberculosis, malaria, acute diarrhea, and even dental cavities. Transgenic plants have also been made to produce a protein that can prevent or delay the onset of insulin-dependent *diabetes mellitus*. At one time, all of our drugs were derived from plants, but we have learned to synthesize many of them in laboratories. Now, we are completing the circle by letting the plants once again create our drugs.

Nonedible transgenic plants are also showing potential in some novel ways. Plants are being created to produce biodegradable polymers in order to reduce our dependence on plastics made from nonrenewable resources. Plants are also being engineered to sequester heavy metals. These transgenics could be grown in contaminated soils where they will pick up wastes such as copper or mercury. Then, they could be harvested and disposed of properly.

Finally, transgenic technology is providing us with ornamental plants never before seen in nature. Most popular cut flowers do not produce blue hues, and efforts are presently being directed toward the development of blue carnations, chrysanthemums, and roses. For example, a violet carnation named Moonshadow contains a petunia gene for blue color (Fig. 14.15). Genetic engineers are also trying to extend the shelf life of cut flowers, mainly by blocking genes for ethylene synthesis. In addition, "flowering-time" genes are being used to develop plants that flower under day-length conditions that would normally prevent flowering; plant architecture



Figure 14.15 The Moonshadow variety of carnation contains a petunia gene for blue color.

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genes are being used to produce either compact or vine-type plants; and fragrance genes have been identified in an effort to restore fragrance quality to roses and carnations.

Pros and Cons of Transgenic Plants

In October 2000, activists called the Green Streets destroyed a test plot of genetically engineered corn at a University of California test facility. In January 2001, a group called the Nighttime Gardeners destroyed a greenhouse containing genetically engineered wheat in Albany, California. And, in February 2001, a group called the Earth Liberation Front burned a research cotton gin in Visalia, California, to protest the development of genetically engineered cotton. In less than 2 years, over 40 antigenetic engineering acts of vandalism have occurred in North America. Why are people so concerned about transgenic crops?

There are approximately 109 million acres of transgenic crops grown worldwide, 68% of which are in the United States. The most common transgenic crops are soybean, corn, cotton, and canola. Most often, these plants contain a gene making them resistant to the herbicide glyphosate, commercially sold as Roundup or an insect resistance gene that produces a protein called Bt toxin (because it is derived from the bacterium *Bacillus thuringiensis*).

On the positive side, proponents of transgenic crops argue that transgenic crops are environmentally friendly because they allow farmers to use fewer and less noxious chemicals for crop production. For example, a 21% reduction in the use of insecticide has been reported on Bt cotton. In addition, when glyphosate is used to control weeds, then other, more-persistent herbicides do not need to be applied.

On the negative side, opponents of transgenic crops suggest that there are many questions that need to be answered before transgenic crops are grown on a large scale. One question deals with the effects that Bt plants have on "nontarget" organisms such as beneficial insects, worms, birds, and even humans who consume the genetically engineered crop. Monarch caterpillars feeding on milkweed plants near Bt cornfields will eat some corn pollen that has fallen on the milkweed leaves. Laboratory studies indicate that the caterpillars can die from eating Bt pollen. However, field tests indicate that Bt corn is not likely to harm monarchs. Remember, too, that application of pesticides (the alternative to growing Bt plants) has been demonstrated to cause widespread harm to nontarget organisms.

Another unanswered question is whether herbicide-resistance genes will move into populations of weeds. Crop plants are sometimes grown in areas where weedy relatives also live. This is especially true outside of the United States. (Remember that most of our crop plants did not originate in the United States, and they do not have wild relatives here.) If the crop plants hybridize with weedy relatives, then this herbicide-resistance gene will be perpetuated in the offspring. In this way, the resistance gene can make its way into the weed population. If this happens, a farmer can no longer use glyphosate, for example, to kill those weeds. This scenario is not likely to occur in many instances because there are no weedy relatives growing near the crop plant. However, in some cases, it may become a serious problem. For example, canola readily hybridizes with mustard weed species and could transfer its herbicide-resistance genes to those weeds. In addition, Canadian farmers have reported that herbicide-resistant canola has invaded wheat fields like a weed and, of course, cannot be killed with a major herbicide.

We know that evolution will occur when transgenic plants are grown on a large scale over a period of time. Of special concern is the development of insect populations resistant to the Bt toxin. This pesticide has been applied to plants for decades without the development of insect-resistant populations. However, transgenic Bt plants express the toxin in all tissues throughout the growing season. Therefore, all insects carrying genes that make them susceptible to the toxin will die. That leaves only the genetically resistant insects to perpetuate the population. When these resistant insects mate, they will produce offspring capable of surviving in the presence of the Bt toxin. Farmers are attempting to slow the development of insect resistance in Bt crops by, for example, planting non-transgenic border rows to act as a refuge for susceptible insects. These insects may allow Bt susceptibility to remain in the population.

Perhaps the most serious concern about the transgenic crop plants currently in use is that they encourage farmers to head farther away from sustainable agricultural farming practices. Transgenics, at least superficially, simplify farming by reducing the choices made by the manager. The planting of a glyphosate-resistant crop encourages a farmer to use that herbicide for the season, probably to the exclusion of all other herbicides and other weed-control practices. In the long run, though, it may be in the best interest of the farmer and the land to use more integrated, sustainable weed-control approaches. Farmers who use Bt transgenics may not feel they need to follow through with integrated pest-management practices that use beneficial insects and timely application of pesticides to control insect pests. In fact, a farmer must decide whether to plant Bt corn even before he knows whether the European corn borer will be a problem during the growing season. In contrast, a more sustainable approach would be to plant non-transgenic corn, monitor the fields throughout the growing season, and then apply a pesticide only if and when it is needed.

The jury is still out on the long-term effects of transgenic plants on our agricultural and natural environments. The "Catch 22" is that we will not know whether transgenic crops cause serious negative consequences until we grow them on a large scale. However, if we do grow them on a large scale and find that the concerns are valid, then we cannot reverse what has been done. Transgenic pollen has been released, and populations of everything from weeds to corn borers have been altered.

In addition to questions regarding environmental safety, human health issues must be addressed. The major concern over the consumption of foods derived from transgenic crops is the potential for the transgene protein product to cause an

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allergic reaction. For example, a Brazil nut gene was added to soybean to increase its methionine content. Methionine is an amino acid commonly added to animal feed. However, this gene produced a protein that caused an allergic reaction in some people. Although the transgenic soybean was being developed as an animal feed, there was concern that it might find its way into the human food chain, and consequently, it was dropped from production. How likely is it that a crop designed for animal feed will end up in human food products? Recently, Starlink corn was found in taco shells, tortilla chips, and corn dogs. Starlink is a variety of transgenic corn containing a gene for Bt toxin and was developed as an animal feed. It has not been approved for human consumption because of concerns that it might cause an allergic reaction. So far, no antibodies to the Starlink protein have been found in people who have experienced a potential allergic reaction after eating these products. The Starlink incident is just the tip of an iceberg faced by the food industry as it tries to keep track of transgenic products.

PLANT PROPAGATION

After we create genetically superior clones or populations of plants through breeding efforts, we must have a method to perpetuate, or propagate, these plants. Plant propagation techniques allow us to grow thousands of acres of a superior corn variety or to have the same day lily variety growing in thousands of yards. Some plants are most easily propagated through sexual reproduction via seed propagation. With other plants, asexual reproduction methods are used more extensively.

Seed Propagation

Hybrid varieties are often grown from the seed produced by crosses between two inbred parents. A common summer job for teenagers in corn-belt regions is detassling corn (removing male flowers). Rows of one inbred parent are planted next to rows of a second inbred parent (Fig. 14.16). Then, the tassels of the first parent are removed to prevent self-pollination. Pollen from the second parent is carried by the wind to the female flowers (the ears) of the first parent and carry out fertilization. The mature ears of the detasseled parent are then collected, and the kernels are harvested as hybrid seed. That seed will be sold to farmers for planting their hybrid cornfields during the next growing season.

Inbred line varieties are typically grown from seed. It is especially easy to generate seed from these varieties. They are simply grown in a field and allowed to self-pollinate. Seeds collected from these plants will grow into a uniform population similar to the plants from which the seeds were collected. For example, if you collect seeds from an inbred green bean variety, you could grow plants that are nearly identical to that variety in appearance and fruit quality. In contrast, seeds collected from a hybrid plant will produce a highly variable population of plants.



Figure 14.16 A field planted for hybrid corn seed production. Rows that have been detassled are adjacent to rows with tassels. Pollen from the tassels will land on ears of detassled plants. Hybrid corn will be harvested from detassled plants.

Commercial seeds usually come from fields planted solely for seed production. The fields are isolated from other fields of the same crop in order to prevent contamination by foreign pollen and mixing of seeds by harvest equipment. Seed quality depends on the health of the plants that produce it. Growing conditions, consequently, are meticulously monitored. Often, the plants are grown in arid regions where irrigation can be controlled and seeds can dry out before harvest. Most grass and forage seed production is concentrated in the Pacific Northwest, while vegetable and flower seeds are generated in the coastal valleys of California. There is also a growing international seed production industry.

When seeds are mature, they are harvested and stored in a controlled environment. The **viability** of most seeds is best maintained in cool, dry storage conditions. Samples are periodically removed from a seed lot and tested for vigor and viability. You may sometimes see the results of these tests on packages of seeds you purchase for your garden. You will also see a date stamped on the seed package. Seeds of some species of plants retain their viability in storage much longer than others. Seeds of green beans, lettuce, onions, and peppers lose their viability after a year or two in storage, while those of beet and tomato may be stored for 5 years or more.

Before planting seeds, steps may be taken to ensure the growth of a vigorous stand of seedlings. In preparation for planting, seeds may be dusted with a **protectant,** such as a fungicide. The red coating on seed corn is such a fungicide. Sometimes, seeds are dusted with beneficial bacteria before planting. Legumes such as peas and beans establish mutualistic associations with bacteria that *fix* nitrogen (convert nitrogen from the air into forms the plants can use). Dusting seeds with these bacteria will encourage that relationship to develop.

It is important to plant seeds in a suitable bed. The soil should be moist enough to allow the seeds to imbibe water, which is essential to begin germination. However, if the soil is soggy, the new roots will not have enough oxygen to keep up with the respiration needed for active growth. Seeds of different species are adapted for growth at different soil

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temperatures. Celery, lettuce, and onion seeds will not germinate in hot summer soil, while tomato, bean, cucumber, and sweet-corn seeds germinate poorly in cool spring soils. Initially, seeds rely on stored food for growth. Fertilizer cannot be utilized until a root system has been established.

In their early stages of growth, seedlings are easily shaded and stunted by weed growth, so weed control is important until the plants can shade the spaces between rows. Seedlings may also compete with each other for light, water, and nutrients, making thinning necessary for production of a good crop.

Asexual Plant Propagation

In recent years, we have heard amazing stories about scientists who have cloned animals such as sheep and cows. Botanists are far ahead in that arena. They have been cloning plants for centuries! Many plants are easy to **propagate** asexually, using vegetative parts rather than seeds. For example, **crown division** is a simple technique in which a plant is separated into several pieces, each of which contains a portion of the crown and root system (Fig. 14.17). This is commonly used for many ornamental perennial plants. A breeder who has identified a superior plant of an asexually propagated species can perpetuate that genotype indefinitely. This avoids the genetic variability and consequent unpredictability that results from seed propagation.

Cuttings

We know that nothing lives forever. Or do we? If you are particularly fond of your grandmother's African violet plant, you can use a leaf to propagate a new plant. As that plant begins to age, you can propagate a new one again from a leaf and eventually pass the plant on to your grandchildren. This plant could be propagated indefinitely and would essentially live forever.



Figure 14.17 Asexual reproduction of a daylily by crown division.



Figure 14.18 Asexual reproduction by cuttings. *Left:* Stem cuttings of an ornamental fig (*Ficus*). *Right:* Leaf cuttings of *Sansevieria*. Note the adventitious roots developing from both types of cuttings.

Propagation of plants from parts such as leaves is called propagation by **cuttings.** If a stem is used as a cutting, it needs to be coaxed into producing **adventitious** roots (roots produced on internodes or other parts of plant organs). Buds on the stem will grow into the shoot system. Leaf and root cuttings, though, must develop both adventitious roots and shoots (Fig. 14.18). The formation of adventitious structures requires plant cells near the wound to **dedifferentiate** (become less specialized) and create a new **meristematic** region.

After a cutting is made, it must be kept in an environment that will allow wound healing and development of new organs. The most critical step is prevention of water loss. Because a stem or leaf cutting has lost its root system, its tissues must be kept moist until roots can once again supply water. This is easily done by keeping the cuttings in an enclosed container to maintain high humidity and to reduce **transpiration.** In commercial production systems, frequent misting or constant fog is used to keep cuttings from drying out. Sometimes, rooting is stimulated by application of a rooting powder containing a growth regulator such as **auxin.** Rooting powders also often contain fungicides to prevent pathogens from entering wounds. The cuttings must be kept in a potting mix such as perlite or vermiculite, which holds water but also drains well. This is preferable to rooting cuttings in water, because oxygen levels in water are low and are quickly depleted as young cells in developing roots undergo respiration. Temperature is also a factor in successfully generating cuttings. Ideally, young roots should be warm enough to enhance growth, while the above-ground parts should be cool enough to minimize growth and transpiration. For this reason, cuttings are often grown on heating pads or in heated beds (Fig. 14.19). Once roots are established, fertilizer helps to stimulate growth.

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Figure 14.19 Cuttings are often grown on a heated bed to stimulate root development.

Many house plants are easily propagated by cuttings. These include African violet (*Saintpaulia*), snake plant (*Sansevieria*), *Begonia, Coleus,* and *Kalanchoë.* Outdoor plants propagated by cuttings include *Forsythia, Geranium,* rose (*Rosa*), *Spiraea,* raspberry (*Rubus*), and juniper (*Juniperus*). The main advantage of propagation by cuttings is that identical copies of a valuable plant can be made. A major disadvantage is that diseases carried by the mother plant, including those caused by viruses, fungi, and bacteria, are also propagated.

Layering

Layering is a modified form of cutting propagation and works well for some plants that are not easy to propagate by cuttings. This procedure allows the adventitious root system to develop before the new plant part is severed from the parent plant.

Tip layering is used with blackberries, boysenberries, and other plants with flexible stems. The canes are bent over until the tips touch the ground; the tips are then covered with a small mound of soil. Roots form on the portion of buried stem, and eventually, shoots will also appear (Fig. 14.20). These new plants can then be separated from the parent stems. Variations of tip layering include forcing a stem to lie horizontally and covering it with small mounds of soil at intervals, or heaping soil around the base of a plant so that the individual stems produce roots there. Once roots have been established, the individual plantlets or pieces of stem can be cut off from the original parent and grown independently.

Air layering is sometimes used to propagate tropical trees and shrubs. It is useful for producing a few large plants from a single plant with a rigid stem. A branch or main stem

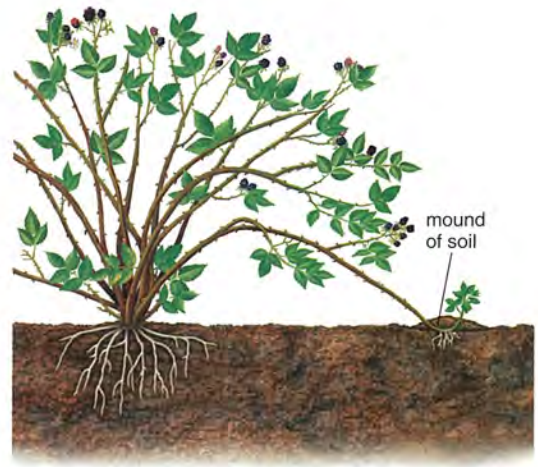


Figure 14.20 Tip layering. The tips of canes are bent to the ground and covered with a small mound of soil. When a new plant has developed at the tip, it can be cut from the parent plant and grown independently.

is wounded with a sterile knife and then may be dusted with a rooting powder. The wound is produced by gashing the stem or, alternatively, by *girdling.* **Girdling** is the removal of a ring of bark around the stem. Damp sphagnum moss is wrapped around the wound, and the area is covered with clear plastic film to retain moisture. Then, aluminum foil is placed over the plastic film to reflect sunlight and prevent overheating (Fig. 14.21). When roots are observed in the moss through the plastic film, the layer is removed from the parent plant and transplanted.



Figure 14.21 Steps in air layering. *A.* Cuts are made at an angle to the axis of a stem of a rooted plant. *B.* Damp sphagnum moss is wrapped around the cut area. *C.* Polyethylene film is wrapped around the moss, and the ends of the film are taped shut. *D.* Aluminum foil is wrapped around the film-covered moss. Adventitious roots develop and protrude through the moss. Then the rooted portion can be cut off and planted.

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Figure 14.22 A brightly colored cactus stem has been grafted on to a green cactus plant.

Grafting

Imagine walking out into your yard in the morning and picking a fresh grapefruit for your breakfast. Then, you go to the same tree at lunchtime and harvest an orange. Later in the day, you pick a lemon off the same tree to squeeze on your fish dinner. Sound impossible? It is not, if you are growing a tree that was created by grafting.

Grafting is a process by which segments of different plants are connected and induced to grow together as one plant. It has been performed as a horticultural art for thousands of years, dating back to around 1560 B.C. Historically, grafting has been performed mainly to clone plants that are difficult to propagate as cuttings. Today, many fruit and nut trees are grafted. Trees are bred for high-quality fruits or nuts. Then, they are grafted onto root systems selected for traits such as winter hardiness, dwarfing, and disease resistance. The top part of the graft is called the **scion.** The bottom portion, that forms the root system, is the **rootstock.** To take grafting a step farther, though, it is possible to graft several different but related plants onto the same rootstock. You could, for example, have grapefruit, orange, and lemon grafted onto the same *Citrus* rootstock. Almond, plum, and apricot can be grafted onto a peach rootstock. Many nurseries sell grafted apple trees containing two or more varieties. Brightly colored novelty cactus plants, which are not capable of photosynthesis, survive because they are grafted onto normal plants (Fig. 14.22).

To describe how grafting is performed, assume we have bred a new extra-juicy variety of apple and would like to graft it onto a young native tree with a hardy root system. In late spring, we would collect some young branches from the tree with the juicy apples (the scions) and keep them in a cooler to inhibit the buds from growing. Then, later in the spring when the rootstock begins to grow, we would bring the scion branches out of the cooler. Using sterilized instruments, we would cut the top of the rootstock diagonally several inches above the soil line. At the same time we would make a diagonal cut in a scion branch that is similar in diameter to that of the rootstock. Successful grafting depends on good contact between the **vascular cambium** of the scion and that of the rootstock. Therefore, we align the scion and rootstock so their cambia are in contact and hold them together with tape or string (Fig. 14.23). The graft union is often also sealed with wax to prevent the wounded tissues from drying out. If the graft is successful, several weeks later, the vascular cambia of the scion and rootstock will have grown together. The tree now consists of a single plant with one variety of rootstock below and a different fruiting variety above. An expanded and illustrated discussion of grafting is given in Appendix 4.

Propagation of Specialized Stems and Roots

If you would like to create a bed of tulips in your garden, you would not plant seeds or rooted cuttings. Instead, you would rely on **bulbs,** which are natural propagules produced by tulip plants. Herbaceous perennials produce shoots that die during the winter, but in the spring, they regrow from underground storage structures. The underground structures that survive over winter may be *bulbs, corms, tuberous roots,* or *rhizomes* (discussed in Chapter 6) (Fig. 14.24). These structures are typically fleshy, with abundant food-storage tissue, and contain buds that will sprout in the spring.



Figure 14.23 A simple graft. The root portion (*stock*) and portion to be grafted onto the stock (*scion*) are cut so that the two parts will fit together with the cambium of both portions in close contact.

Micropropagation

One of the major disadvantages of most asexual propagation techniques is that they also propagate pathogens. Once a plant is diseased, there is no immune system to activate or antibiotic we can administer as a cure. The best way to

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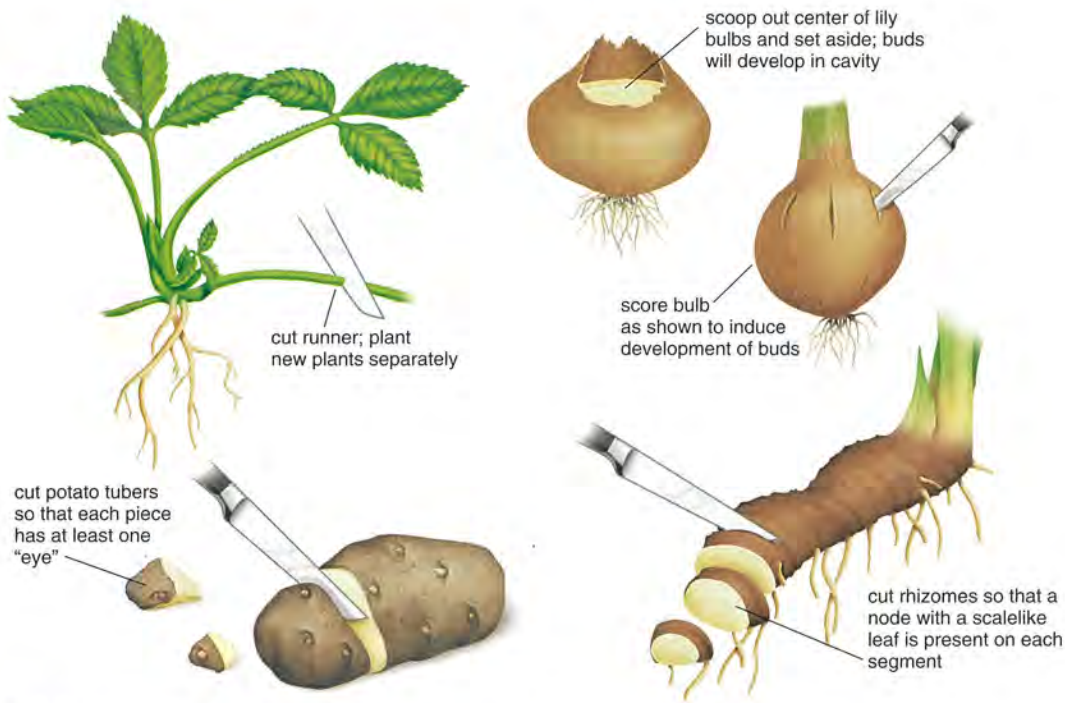


Figure 14.24A Propagation of specialized stems.



Figure 14.24B Some specific examples of specialized stems that are easily propagated asexually. *Left:* A tulip bulb. *Center: Crocus* corms. *Right:* A ginger rhizome.

eliminate the effects of plant disease is to prevent exposure to pathogens. This is nearly impossible in greenhouse and field environments. However, it is possible to maintain plants in a disease-free status if we grow them in sterile test tubes through **micropropagation.** Other advantages of micropropagation include the capacity to grow large numbers of plants in a small area, minimal maintenance required for established plants (they do not need to be watered), and rapid multiplication.

Propagating plants through micropropagation is similar to growing them as cuttings. The major difference is that the plants are grown ***in vitro*** in a sterile **medium** and maintained in special controlled environment rooms. The medium includes a support matrix composed of agar, a gelatinous material extracted from red algae. Inorganic salts are added to the medium to provide macro- and micronutrients, such as nitrogen, phosphorous, calcium, and iron. Sucrose is added to supplement the sugars produced by the plant. In addition, vitamins such as thiamine, nicotinic acid, and inositol are generally included in the growth medium. Commonly, growth regulators are also added. After the ingredients are combined and pH is adjusted, the mixture is poured into *test tubes.* The tubes are then capped and put in an **autoclave** (a large form of pressure cooker) to sterilize them (Fig. 14. 25). When the medium cools, it solidifies like Jell-O™. This acts as the "soil" in the micropropagation system, providing plants with support, nutrients, and water.

Micropropagation, like other forms of asexual propagation, relies on the property of **totipotency** (capacity of a cell to give rise to any structure of a mature organism) of plant cells. Each living cell has the genetic information and, therefore, the capacity to develop into any cell type. Micropropagation usually begins with an excised piece of leaf or stem tissue, or **explant,** and carries it through three steps.

The first step is establishment of explants in **tissue culture.** Micropropagation requires sterile plant material as well as growth media. Plant parts must be **disinfested** to remove surface contaminants without killing the plant tissue. Common disinfestants include bleach and ethanol. This procedure does not remove internal contaminants, including pathogens, so it is important to begin with disease-free plants. After plant parts are disinfested, they are inserted into the

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Figure 14.25 An autoclave, in which pressurized steam is used to sterilize media, glassware, and instruments.



Figure 14.26 A laminar flow hood. A sterile work area is created by blowing sterile air from the back of the hood to the opening in front.

growth medium in test tubes under sterile conditions. Often, a special reach-in chamber, called a **laminar flow hood,** is used for this step (Fig. 14.26). Filtered air is blown across the work surface in the chamber to prevent the introduction

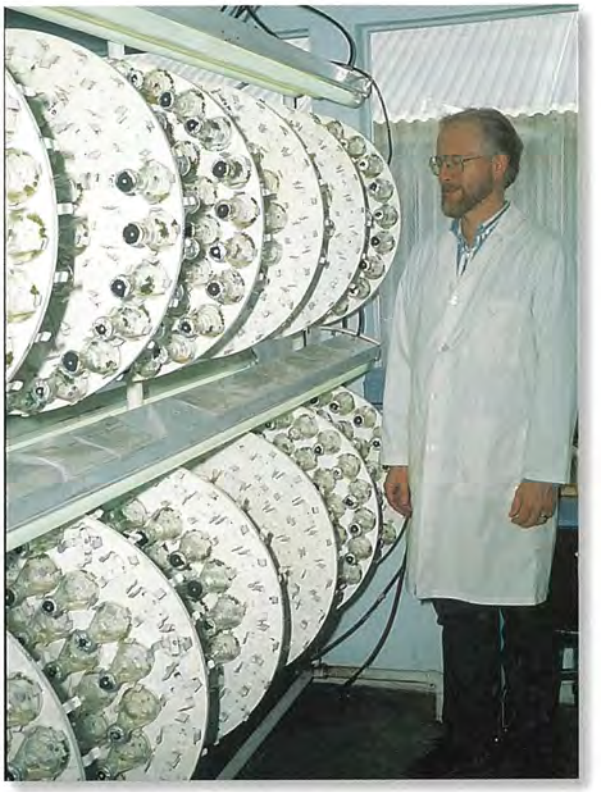


Figure 14.27 Flasks of sterile growing medium to which meristematic tissue has been added. The flasks are slowly rotated under lights. Roots and shoots appear within a few weeks.

of contaminants. Test tubes containing sterile plants are then placed in a clean room with artificial lighting and temperature control. The goal of this first step is to obtain sterile, viable plant tissue cultures (Fig. 14.27).

After cultures are established, they typically will be induced to develop multiple shoots in a multiplication medium. These **microshoots** can be separated and placed in a new medium by a process called **subculturing** (Fig. 14.28). This step is similar to propagation by cuttings, except it is carried out under sterile conditions. It is not unusual to subculture plants every four weeks, making approximately four new plants from every one in a test tube. At this rate, it is theoretically possible to produce a million plants from one plant in just 10 months. Although these multiplication rates are not realized in commercial systems, many tissue culture laboratories have the capacity to produce millions of plants per year.

The third step in micropropagation is root formation. Some explants, such as those from African violets, will spontaneously produce roots in multiplication medium. In other cases, plants are induced to form roots *in vitro* by transferring them to a rooting medium. Compared to the multiplication medium, the rooting medium usually contains reduced levels of cytokinins and increased auxin levels. When possible, the most economical approach is an ***ex vitro*** one, in which microshoots are rooted in potting mix and treated as cuttings.

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Figure 14.28 Plantlets that have developed from cultured meristematic tissue are separated and further cultured to maturity.

The last step in micropropagation is the transfer of plants back to an outdoor environment. This is often the most difficult step. Because the humidity is high in test tubes, plants grown *in vitro* do not produce as much wax on their cuticles as do those grown outdoors. In addition, their stomata do not close as readily in response to water stress. Therefore, tissue culture plantlets must be acclimatized to an outdoor environment. First, the humidity in the growth chamber is reduced for a few weeks before the plants are brought out of their test tubes. Then, when they are transferred to soil in pots, they are maintained in a high-humidity environment for several weeks.

Commercial micropropagation has become a successful venture with a number of plants. Some plants that propagate slowly by other asexual means may be rapidly increased with micropropagation. These include orchids, Boston fern, African violet, and *Hosta.* In some cases, with the use of tissue culture techniques, as many plants can be produced in a month as would be produced in a year with other techniques. New cultivars can also be rapidly multiplied to meet high market demand. For example, new apple rootstocks are often propagated *in vitro* because conventional asexual reproduction methods cannot adequately supply market needs. Tissue culture protocols, using various combinations of nutrients and growth regulators, have been developed for a number of woody plants that are otherwise difficult to root.

Tissue culture is now being used to propagate endangered plant species. Small pieces of just a few plants can be used to establish tissue cultures. Then, nearly unlimited numbers of plantlets can be produced and returned to their natural habitat.

Summary

1. Most of our food is derived from just a handful of plant species.
2. We domesticate plants by genetically altering them to meet our needs.
3. The impetus for the shift from hunter-gatherer to agricultural societies is not clear. Current hypotheses are speculative.
4. Plant domestication began in the Near East approximately 10,000 years ago and spread to Asia, Africa, and the New World.
5. During domestication, plants were selected for nonshattering seeds, high yield, seedling vigor, and absence of seed dormancy.
6. Two methods for improvement of self-pollinated crops are pure-line selection and selection within self-pollinated offspring of hybrid plants.
7. Two methods for improvement of cross-pollinated crops include mass selection and creation of hybrids from inbred lines.
8. Germplasm banks are critical repositories of genetic diversity essential for plant-breeding progress.
9. Protoplast fusion combines entire genomes of related plant species that cannot mate with each other.
10. Transgenic plants contain DNA from foreign organisms. To make a transgenic plant, a gene is spliced out of the donor and inserted into a vector. The vector is inserted into a host, such as a bacterium, which clones the foreign donor DNA. The next steps, transformation of the plant with the cloned foreign gene and expression of that gene, are the most difficult ones to perform.
11. Seed propagation requires production of high-quality seed, an adequate seed storage environment, and appropriate conditions for seedling growth.
12. Cuttings provide a method of asexual propagation for many plant species.
13. Grafting unites pieces of two different, but related, plants and can be used for cloning.
14. Another form of asexual reproduction utilizes natural propagules, such as bulbs, corms, and tubers.
15. Micropropagation is an asexual propagation technique carried out under sterile conditions.

Review Questions

1. Describe the traits that early humans selected during domestication of plants.
2 Explain why knowledge of a plant's reproductive system is important when choosing a breeding strategy.

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3. Outline the steps you would use to create a petunia plant carrying a corn gene for red flower color.
4. Differentiate between a rootstock and a scion.
5. Explain how you would create an apple tree that produces both Granny Smith and Red Delicious apples.
6. Describe the four steps that are usually carried out in micropropagation.

Discussion Questions

1. Suppose you grow a hybrid tomato plant and save some of its seeds to plant in your garden next year. Would those seeds grow into plants that look like the hybrid plant from which you collected them? What if you collected seeds from an inbred line of tomato and planted them?
2. Describe advantages and disadvantages of micropropagation compared with making cuttings in a greenhouse.
3. What might be some advantages of having several varieties of apple or plum on the same tree?
4. Describe advantages and disadvantages of producing a crop of potato plants using asexual (tuber) rather than sexual (true seed) propagation.
5. Many people are opposed to the production of transgenic crop plants. Do you feel that position is justified?

Additional Reading

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CHAPTER

23

Seed Plants: Angiosperms

Overview
Some Learning Goals
Phylum Magnoliophyta—The Flowering Plants
- Development of Gametophytes
- Pollination
- Fertilization and Development of the Seed
- Apomixis and Parthenocarpy
- Trends of Specialization and Classification in Flowering Plants

Pollination Ecology
Herbaria and Plant Preservation
- Methods
- A Word of Caution to Collectors

Summary
Review Questions
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Flowers of the butterfly weed (*Asclepias curassavica*), a native of the tropics from Florida to South America. Parts of the plant are used medicinally in tropical areas. In Mexico, for example, root extracts have been used in the treatment of cancers of the intestinal tract, kidneys, and uterus.

OVERVIEW

This chapter begins with a probe of the differences between angiosperms and gymnosperms and then discusses the origin of flowering plants. The exceptional diversity of the flowering plants is reviewed next, and the chapter continues with a description of the parallel development of the gametophytes in the anthers and ovules. This leads up to pollination, followed by some details of fertilization and the development of a seed. A discussion of trends of specialization and classification in flowering plants is followed by a section on pollination ecology. Plant preservation, including simple herbarium techniques and practice, is next. The chapter closes with a brief survey on the uses of herbaria and a word of caution to plant collectors concerning unnecessary depletion of native floras.

Some Learning Goals

1. Understand the basic differences between angiosperms and gymnosperms.
2. Contrast two principal schools of thought concerning the origin of the flowering plants and the nature of the first flowers.
3. Diagram the life cycle of a flowering plant, indicating shifts from haploid to diploid cells, and vice versa.
4. Compare two types of female gametophyte development and learn how a male gametophyte develops.
5. Know the characteristics of flowers associated with specific types of pollinators.
6. Know major trends of specialization in the flowering plants.
7. Know the functions of a herbarium and the techniques of preparing herbarium specimens.

A flowering plant once saved my life in an unconventional way. While in Washington's Olympic National Park, I was conducting field research on a group of relatively small herbaceous plants known as *bleeding hearts* (Fig. 23.1). At one point, I found myself on a slope of loose shale above a steep cliff. Suddenly, the shale started to move, and before I could do anything about it, I was rapidly sliding on my back, feet first, directly toward the edge of the cliff. There were no bushes, trees, or anything stable I could cling to or grab that would at least slow my journey to doom in an avalanche of shale. Just a few feet before I was to hurtle over the cliff, however, I cannoned into a large clump of bleeding hearts that somehow had rooted securely enough beneath the shale surface to stop my speedy plunge. Obviously, I lived to tell the tale, and it won't surprise you to know that ever since the experience, I have had a special place in my garden for bleeding hearts!

The Pacific bleeding hearts that saved my life are only one of more than 250,000 known species of flowering plants that comprise, by far, the largest and most diverse of the phyla of the Plant Kingdom. These flowering plants are called **angiosperms.**

The term *angiosperm* is derived from two Greek words: *angeion,* meaning "vessel," and *sperma,* meaning "seed." The "vessel" is the **carpel,** which is like an inrolled leaf with seeds along its margins. A green pea pod, for example, is a carpel that resembles a leaf that has folded over and fused at the margins, enclosing the attached seeds. Many flowers have *pistils* (see Chapter 8) composed of either a single carpel or two more united carpels. A seed develops from an *ovule* within a carpel and is part of an *ovary* that becomes a *fruit.* Although the angiosperms generally have organs and tissues similar to those of the gymnosperms, the enclosed ovules and seeds of the angiosperms distinguish them from gymnosperms, which have exposed ovules and seeds.



Figure 23.1 Pacific bleeding hearts (*Dicentra formosa*).

All angiosperms are presently considered to be in the Phylum Magnoliophyta (previously known as the Anthophyta). Other classifications of flowering plants are discussed in Chapter 16. Phylum Magnoliophyta has been divided into two large classes: the Magnoliopsida (dicots) and the Liliopsida (monocots). As indicated in Chapter 16, DNA and cladistic evidence now suggests that two groups of dicots should be recognized. Table 8.1 on page 130 lists the distinguishing features of members of the two classes.

Since Darwin's *Origin of Species* appeared in 1859, there have been two major theories concerning the origin

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