

Chapter 18

The Genetics of Viruses and Bacteria

Key Concepts

- 18.1** A virus has a genome but can reproduce only within a host cell
- 18.2** Viruses, viroids, and prions are formidable pathogens in animals and plants
- 18.3** Rapid reproduction, mutation, and genetic recombination contribute to the genetic diversity of bacteria
- 18.4** Individual bacteria respond to environmental change by regulating their gene expression

Framework

A virus is an infectious particle consisting of a genome of single- or double-stranded DNA or RNA enclosed in a protein capsid. Viruses replicate using the metabolic machinery of their bacterial, animal, or plant host. Viral infections may destroy the host cell and cause diseases within the host organism. Viruses may have evolved from plasmids or transposons.

Most bacteria have a circular chromosome and may have additional genes carried on plasmids. In conjunction with the genetic diversity generated by mutation, genetic recombination, and transposable elements, the short generation time of bacteria facilitates their adaptation to changing environments. Individual cells may alter their metabolic response to environmental conditions through feedback inhibition of enzyme activity and the regulation of gene expression.

Chapter Review

The study of viruses and bacteria has provided information about the molecular biology of all organisms and has led to the development of new techniques of manipulating genes that have had an immense impact

on basic research and biotechnology. These microbes are called *model systems* because of their use in studies with broad biological applications.

18.1 A virus has a genome but can reproduce only within a host cell

The Discovery of Viruses: Scientific Inquiry The search for the cause of tobacco mosaic disease led to the discovery of viruses. The infectious agent could not be removed from infected sap by passing it through a filter designed to remove bacteria. Unlike bacteria, the infectious agent could not be cultivated on nutrient media, but it was able to reproduce within plants. In 1935, W. Stanley crystallized the infectious particle, now known as tobacco mosaic virus (TMV). Since that time, many viruses have been seen with the electron microscope.

Structure of Viruses The ability to crystallize viruses indicated that they were not cells. These infectious particles consist of nucleic acid enclosed in a protein coat, sometimes surrounded by a membranous envelope.

Viral genomes may be single- or double-stranded DNA or single- or double-stranded RNA. Viral genes are contained on a single linear or circular nucleic acid molecule.

The **capsid**, or protein shell, is built from a large number of often identical protein subunits (*capsomeres*) and may be rod-shaped (helical), polyhedral, or more complex in shape. **Viral envelopes**, derived from membranes of the host cell but also including viral proteins and glycoproteins, may cloak the capsids of viruses found in animals. Some viruses also contain a few viral enzymes.

Complex capsids are found among **bacteriophages**, or **phages**, the viruses that infect bacteria. Of the seven phages that infect the bacterium *E. coli*, T2, T4, and T6 have similar capsid structures consisting of a polyhedral head and a protein tail piece with tail fibers for attaching to a bacterium.

General Features of Viral Reproductive Cycles Viruses are obligate intracellular parasites that lack metabolic enzymes and other equipment needed to reproduce. Each virus type has a limited **host range** due to proteins

on the outside of the virus that recognize only specific receptor molecules on the host cell surface.

Once the viral genome enters the host cell, the cell's enzymes, nucleotides, amino acids, ribosomes, ATP, and other resources are used to replicate the viral genome and produce capsid proteins. DNA viruses use host DNA polymerases to copy their genome, whereas RNA viruses use virus-encoded polymerases for replicating their RNA genome.

After replication, viral nucleic acid and capsid proteins spontaneously assemble to form new viruses within the host cell, a process called self-assembly. Hundreds or thousands of newly formed virus particles are released, often destroying the host cell in the process.

Reproductive Cycles of Phages A reproductive cycle of a virus that culminates in lysis of the host cell and release of newly produced phages is known as a **lytic cycle**. **Virulent phages** reproduce only by a lytic cycle.

The T4 phage uses its tail fibers to stick to a receptor site on the surface of an *E. coli* cell. The sheath of the tail contracts and thrusts its viral DNA into the cell, leaving the empty capsid behind. The *E. coli* cell begins to transcribe and translate phage genes, one of which codes for an enzyme that chops up host cell DNA. Nucleotides from the degraded bacterial DNA are used to create viral DNA. Capsid proteins are made

and assembled into phage tails, tail fibers, and polyhedral heads. The viral components assemble into 100 to 200 phage particles that are released after an enzyme is manufactured that digests the bacterial cell wall.

Mutations that change their receptor sites and restriction nucleases that chop up viral DNA once it enters the cell help to defend bacteria against viral infection.

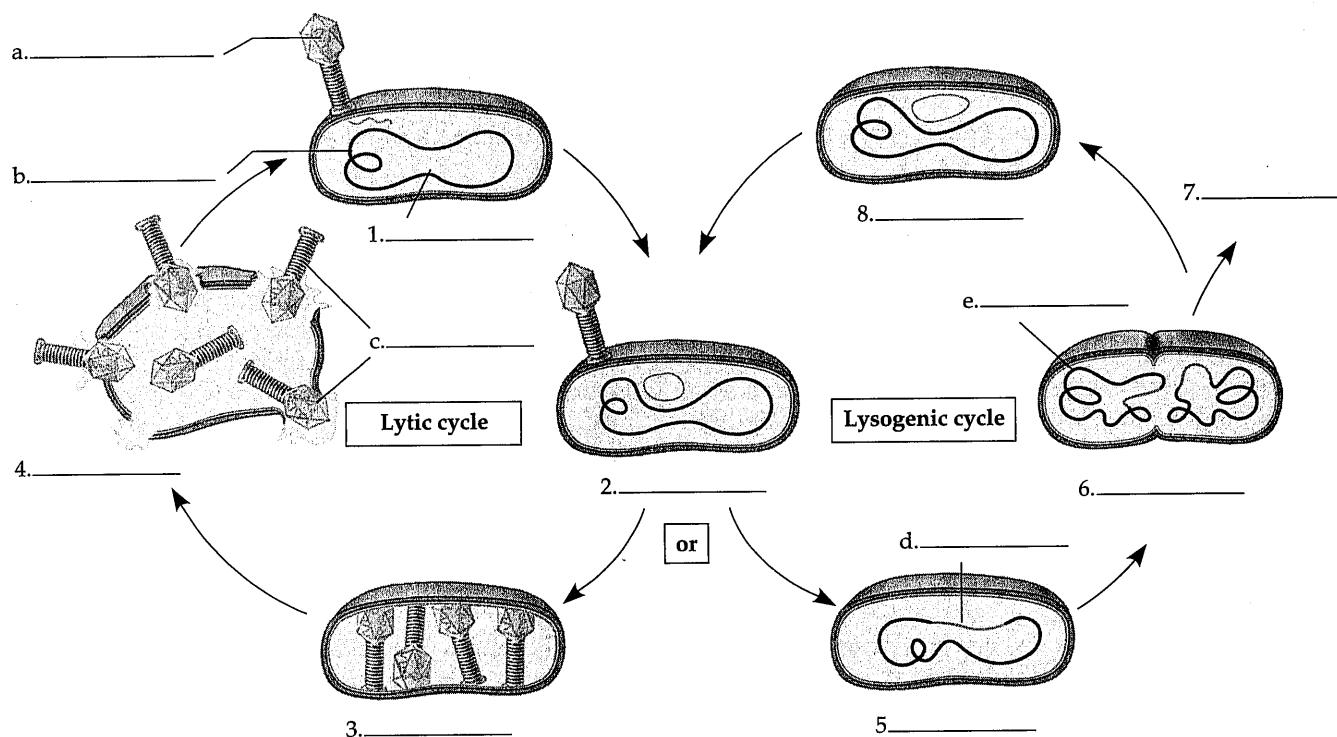
In a **lysogenic cycle**, a virus reproduces its genome without killing its host. **Temperate phages** can reproduce by the lytic and lysogenic cycles.

When the phage lambda (λ) injects its DNA into an *E. coli* cell, it can begin a lytic cycle, or its DNA may be incorporated by genetic recombination into the host cell's chromosome and begin a lysogenic cycle as a **prophage**. Most of the genes of the inserted phage genome are repressed by a protein coded for by a prophage gene. Reproduction of the host cell replicates the phage DNA along with the bacterial DNA. The prophage may exit the bacterial chromosome, usually in response to environmental stimuli, and start the lytic cycle. Complete Interactive Question 18.1 to review the lytic and lysogenic cycles.

Expression of prophage genes may cause a change in the bacterial phenotype. Several disease-causing bacteria would be harmless except for the expression of prophage genes that code for toxins.

■ INTERACTIVE QUESTION 18.1

In this diagram of a lytic and lysogenic cycle, describe steps 1–8 and label structures a–e.



Reproductive Cycles of Animal Viruses Animal viruses are classified based on their type of genome. A viral envelope surrounds the capsid of almost all animal viruses that have RNA genomes. Glycoproteins extending from the viral membrane attach to receptor sites on a host cell plasma membrane, and the two membranes fuse, transporting the capsid into the cell. The viral genome replicates and directs the synthesis of viral proteins. Glycoproteins are produced and embedded in the ER, and then transported to the plasma membrane, where new viruses bud off within an envelope derived from the host's plasma membrane and bearing viral glycoproteins.

The envelopes of herpesviruses come from the host nuclear membrane. The herpesvirus' double-stranded DNA can remain latent as a minichromosome in the host cell nucleus until it initiates herpes infections in times of stress.

RNA viruses infect plants, some bacteria, and animals. The single-stranded RNA of animal class IV viruses can serve directly as mRNA. The RNA genome of class V viruses must first be transcribed into a strand of complementary RNA (using a viral enzyme packaged inside the capsid) that then serves as mRNA and a template for making genome RNA.

In the complicated reproductive cycle of **retroviruses** (class VI), the viral RNA genome is transcribed into double-stranded DNA by a viral enzyme, **reverse transcriptase**. This viral DNA is then integrated into a chromosome, where it is transcribed by the host cell into viral RNA, which acts both as new viral genome and as mRNA for viral proteins. **HIV (human immunodeficiency virus)** is a retrovirus that causes **AIDS (acquired immunodeficiency syndrome)**. The integrated viral DNA remains as a **provirus** within the host cell DNA. New viruses, assembled with two copies of the RNA genome and reverse transcriptase within a capsid, bud off covered in host cell plasma membrane studded with viral glycoproteins.

■ INTERACTIVE QUESTION 18.2

Summarize the flow of genetic information during replication of a retrovirus. Indicate the enzymes that catalyze this flow.

Enzymes: _____ → _____ → _____

Evolution of Viruses Viruses contain a genetic program, but it can only be expressed within a host cell.

The genomes of viruses are often more similar to those of their host cells than to the genomes of viruses infecting other hosts. Recent sequencing of viral genomes, however, has found genetic similarities among viruses that otherwise seem distantly related. Viruses may have evolved from fragments of cellular nucleic acids that moved from one cell to another and eventually evolved special packaging. Sources of viral genomes may have been plasmids, self-replicating circles of DNA found in bacteria and yeast, and transposons, segments of DNA that can change locations within a cell's genome.

18.2 Viruses, viroids, and prions are formidable pathogens in animals and plants

Viral Diseases in Animals The symptoms of a viral infection may be caused by toxins produced by infected cells, toxic components of the viruses themselves, cells killed or damaged by the virus, or the body's defense mechanisms fighting the infection.

Vaccines are variants or derivatives of pathogens that induce the immune system to react against the actual disease agent. Vaccinations have greatly reduced the incidence of many viral diseases.

Unlike bacteria, viruses use the host's cellular machinery to replicate, and few drugs have been found to treat or cure viral infections. Some antiviral drugs resemble nucleosides and interfere with viral nucleic acid synthesis.

Emerging Viruses The emergence of "new" viral diseases may be linked to the mutation of an existing virus (as in influenza viruses), the spread from one host species to another (as in hantavirus), or the dissemination of an existing virus to a more widespread population (as in HIV).

Viral Diseases in Plants Most plant viruses are RNA viruses. Plant viral diseases may spread through *vertical transmission* from a parent plant or through *horizontal transmission* from an external source. Plant injuries increase susceptibility to viral infections, and insects can act as carriers of viruses.

Viral particles spread easily through the plasmodesmata, the cytoplasmic connections between plant cells. Reducing the spread of disease and breeding resistant varieties are the best preventions of plant viral infections.

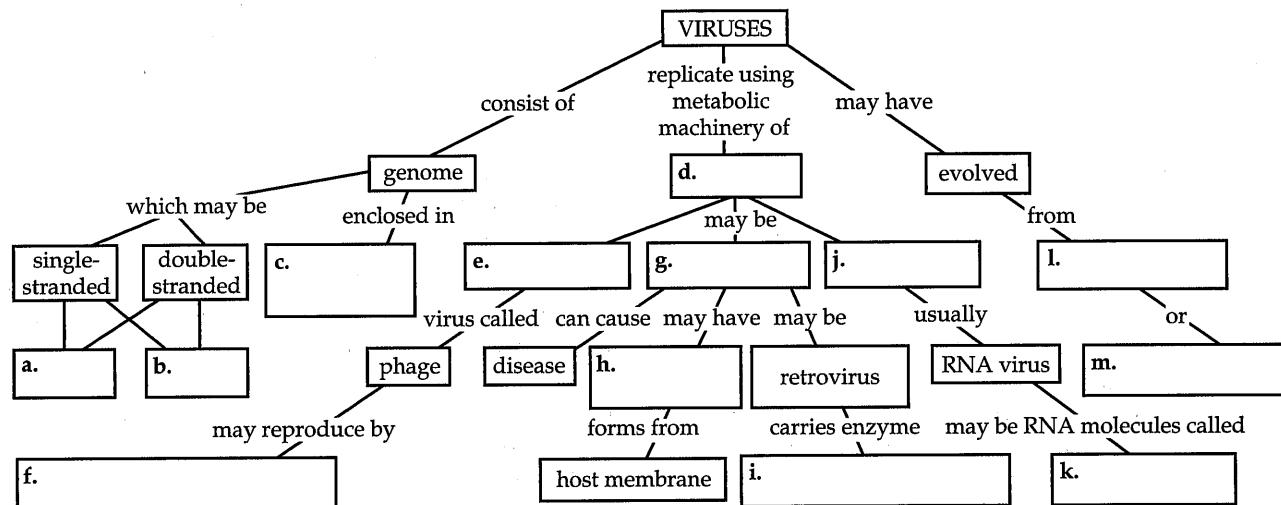
Viroids and Prions: The Simplest Infectious Agents **Viroids** are very small infectious molecules of circular RNA that can disrupt the metabolism of a plant cell and severely stunt plant growth.

Prions are protein infectious agents that may be linked to several degenerative brain diseases, such as mad cow disease and Creutzfeldt-Jacob disease in

humans. Prions apparently spread disease by converting normal cellular proteins into the defective form of the prion.

■ INTERACTIVE QUESTION 18.3

Complete the following concept map that summarizes these sections on viruses.



18.3 Rapid reproduction, mutation, and genetic recombination contribute to the genetic diversity of bacteria

The Bacterial Genome and Its Replication The circular bacterial chromosome contains about 100 times more DNA than a typical virus, but only one-thousandth as much DNA as a typical eukaryotic genome. This double-stranded DNA molecule is tightly packed into a region of the cell called the **nucleoid**. Many bacteria also have plasmids, small rings of DNA with a few genes.

Replication of the bacterial chromosome proceeds bidirectionally from a single origin prior to binary fission.

Mutation and Genetic Recombination as Sources of Genetic Variation Most bacteria in a colony are genetically identical to the parent cell. Mutations, although statistically rare, produce a great deal of genetic diversity because bacteria reproduce so rapidly. Considering all 4,300 *E. coli* genes, there may be 9 million mutations per day per human host.

Genetic recombination, the combining of genetic material from two sources, also adds to the genetic diversity of bacterial populations. Evidence that genetic recombination occurs in bacteria is provided by growing two mutant strains of *E. coli*, each of which is un-

able to produce a particular amino acid, together in a liquid medium. When later transferred to minimal media, numerous colonies grow that are now able to synthesize both amino acids.

Mechanisms of Gene Transfer and Genetic Recombination in Bacteria The mechanisms of genetic recombination in bacteria are different from the eukaryotic mechanisms of meiosis and fertilization.

Bacteria can take up segments of naked DNA in a process called **transformation**. The foreign DNA is integrated into the bacterial chromosome by an exchange involving crossing over. Many bacteria have surface proteins specialized for uptake of DNA from closely related species. *E. coli* can be artificially induced to take up foreign DNA, a procedure important to biotechnology.

Phages can transfer genes from one bacterium to another by a process called **transduction**. In *generalized transduction*, a random piece of host DNA is accidentally packaged within a phage capsid and introduced into a new bacterium; in *specialized transduction*, bacterial genes adjacent to a prophage insertion site are excised with the prophage from the bacterial chromosome. By either method, recombination occurs when the newly introduced bacterial genetic material replaces the homologous region of a bacterial chromosome.

■ INTERACTIVE QUESTION 18.4

What type of phage and reproductive cycle would cause specialized transduction?

In **conjugation**, two cells temporarily join by appendages called sex pili and the donor cell transfers DNA to a recipient cell. The ability to form pili and donate DNA usually results from the presence of an **F factor**, a special piece of DNA that is either part of the chromosome or a plasmid.

Plasmids are small, circular, self-replicating DNA molecules. Some plasmids, called **episomes**, can reversibly incorporate into the cell's chromosome. Temperate viruses are also considered to be episomes. Plasmid genes are not required for reproduction and survival under normal conditions, but may confer advantages to bacteria in stressful environments.

Bacterial cells containing the F factor on the **F plasmid** are called **F⁺**. The F plasmid replicates in synchrony with the bacterial chromosome, and **F⁺** cells pass the trait to offspring cells. During conjugation, a single strand of the plasmid DNA is transferred through a mating bridge to the recipient cell. In this *rolling-circle replication*, the single parental strands in both cells replicate, and the recipient cell is now also an **F⁺** cell.

Cells in which the F factor is inserted into the bacterial chromosome are called **Hfr** cells, for "high frequency of recombination." When these cells undergo conjugation, one parental strand of part of the F factor transfers an attached strand of the bacterial chromosome to the

recipient cell. Movements disrupt the mating, usually resulting in a partial transfer of genes and F factor. Replication in both donor and recipient cells produces double-stranded DNA. Crossovers between the new DNA and the recipient cell's chromosome produce new genetic combinations in this recombinant **F⁻** bacterium.

R plasmids carry genes that code for antibiotic-destroying enzymes. R plasmids also have genes coding for sex pili and are transferred to nonresistant cells during conjugation, creating the medical problem of antibiotic-resistant pathogens.

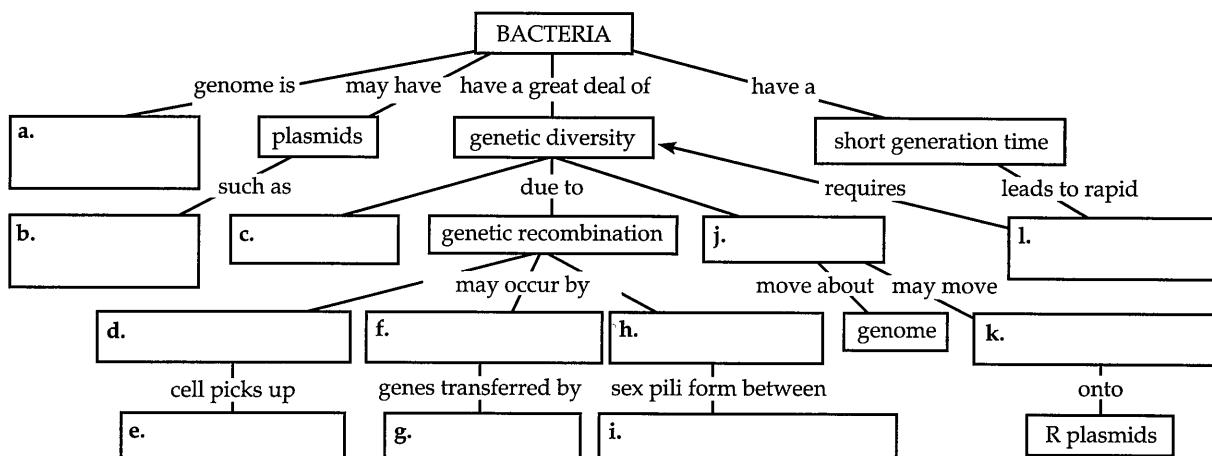
Transposition of Genetic Elements **Transposable genetic elements**, or **transposable elements**, are mobile segments of DNA that may move within a chromosome and to and from plasmids. In "cut-and-paste" transposition, the transposable element simply changes location; in "copy-and-paste" transposition, the transposable element first replicates, thus remaining in its original position and also inserting in a new location. Unlike other forms of genetic recombination where alleles exchange between homologous regions, transposable elements can move genes to totally new areas.

Insertion sequences are the simplest transposable element, consisting of only a transposase gene and inverted repeats, which serve as recognition sites for transposase. Transposase is the enzyme responsible for the cutting and ligating of DNA required for transposition. Insertion sequences cause mutations when they insert within a gene or in regulatory regions.

Transposons contain other genes carried between two insertion sequences or inverted repeats. They may confer selective advantage by moving beneficial genes, such as those for antibiotic resistance, about in the bacterial genome.

■ INTERACTIVE QUESTION 18.5

Complete the following concept map that summarizes the genetic characteristics of bacteria.



18.4 Individual bacteria respond to environmental change by regulating their gene expression

Feedback inhibition, typical of biosynthetic pathways, allows regulation of enzyme activity in response to short-term environmental fluctuations. Regulation of gene transcription controls enzyme production as metabolic needs change. F. Jacob and J. Monod first described the *operon model* for gene regulation in 1961.

Operons: The Basic Concept Genes for the different enzymes of a single metabolic pathway may be grouped together into one transcription unit and served by a single promoter. An **operator** is a segment of DNA within the promoter region or between it and the enzyme-coding genes that controls the access of RNA polymerase to the genes. An **operon** is the DNA segment that includes the clustered genes, the promoter, and the operator.

Operons are normally “on.” A **repressor** is a protein that binds to a specific operator, blocking attachment of RNA polymerase and thus turning the operon “off.” **Regulatory genes** code for repressor proteins. These allosteric proteins, which may assume active or inactive shapes, are usually produced at a slow but continuous rate. The activity of the repressor protein may be determined by the presence or absence of a **corepressor**.

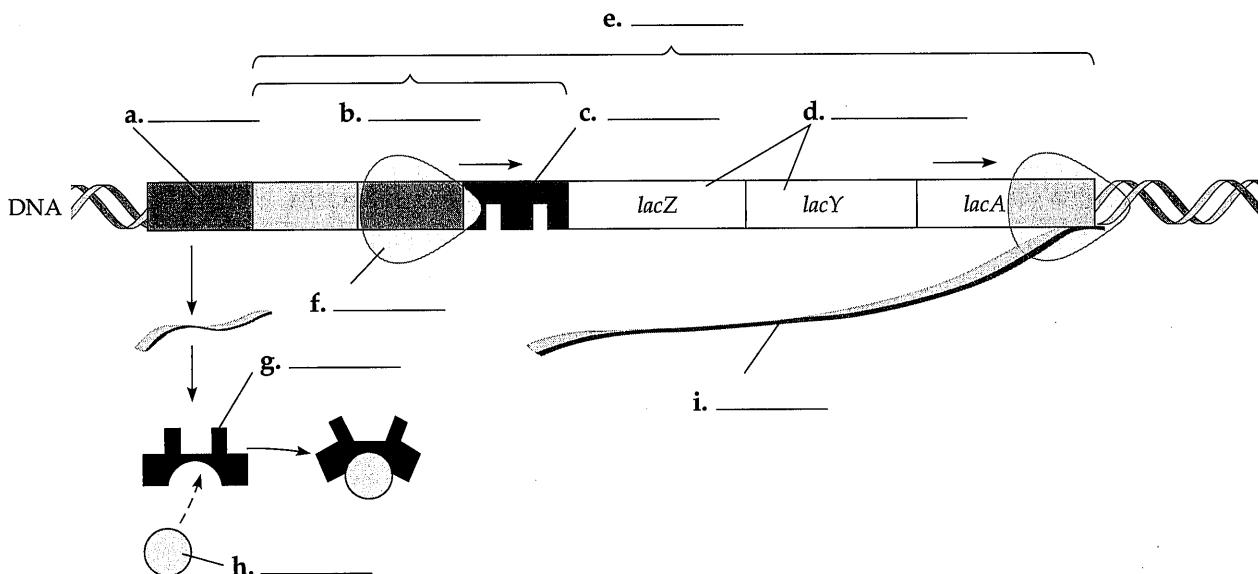
In the *trp* operon, tryptophan is the corepressor that binds to the repressor protein, changing its conformation into its active state, which has a high affinity for the operator and switches off the *trp* operon. Should the tryptophan concentration of the cell fall, repressor proteins are no longer bound with tryptophan and become inactive, the operator is no longer repressed, RNA polymerase attaches to the promoter, and mRNA for the enzymes needed for tryptophan synthesis is produced.

Repressible and Inducible Operons: Two Types of Negative Gene Regulation The transcription of a *repressible operon*, such as the *trp* operon, is inhibited when a specific small molecule binds to a regulatory protein. The transcription of an *inducible operon* is stimulated when a specific small molecule interacts with a regulatory protein.

The *lac* operon, controlling lactose metabolism in *E. coli*, is an inducible operon that contains three genes. The *lac* repressor, coded for by the regulatory gene, *lacI*, is innately active, binding to the *lac* operator and switching off the operon. Allolactose, an isomer of lactose, acts as an **inducer**, a small molecule that binds to and inactivates the repressor protein, so that the operon can be transcribed.

■ INTERACTIVE QUESTION 18.6

In the following diagram of the *lac* operon, an operon for inducible enzymes, identify components a through i.



■ INTERACTIVE QUESTION 18.7

a. Repressible enzymes usually function in _____ pathways. The pathway's product serves as a _____ to activate the repressor and turn off enzyme synthesis and prevent overproduction of the product of the pathway. Genes for repressible enzymes are usually switched _____ and the repressor is synthesized in an _____ form.

b. Inducible enzymes usually function in _____ pathways. Nutrient molecules serve as _____ to stimulate production of the enzymes necessary for their breakdown. Genes for inducible enzymes are usually switched _____ and the repressor is synthesized in an _____ form.

Positive Gene Regulation *E. coli* cells preferentially use glucose as their source of energy and carbon skeletons. Should glucose levels fall, transcription of operons for other catabolic pathways can be increased through the action of the allosteric regulatory protein *catabolite activator protein* (CAP), which is an **activator**. **Cyclic AMP** (cAMP) accumulates in the cell when glucose is scarce and binds with CAP, changing it to its active shape. The active CAP attaches above the promoter region and stimulates transcription by facilitating the binding of RNA polymerase.

The regulation of the *lac* operon includes negative control by the repressor protein that is inactivated by the presence of lactose, and positive control by CAP when complexed with cAMP.

Word Roots

capsa- = a box (*capsid*: the protein shell that encloses the viral genome)

conjug- = together (*conjugation*: in bacteria, the transfer of DNA between two cells that are temporarily joined)

lyto- = loosen (*lytic cycle*: a type of viral replication cycle resulting in the release of new phages by death or lysis of the host cell)

-oid = like, form (*nucleoid*: a dense region of DNA in a prokaryotic cell)

-phage = to eat (*bacteriophages*: viruses that infect bacteria)

pro- = before (*provirus*: viral DNA that inserts into a host genome)

retro- = backward (*retrovirus*: an RNA virus that reproduces by transcribing its RNA into DNA and then inserting the DNA into a cellular chromosome)

trans- = across (*transformation*: a phenomenon in which external DNA is assimilated by a cell)

virul- = poisonous (*virulent virus*: a virus that reproduces only by a lytic cycle)

Structure Your Knowledge

1. Create a concept map that describes the lytic and lysogenic cycles of a phage.
2. Create a concept map to develop your understanding of the mechanisms by which bacteria regulate their gene expression in response to varying metabolic needs. Distinguish repressible and inducible operons, which are both examples of negative control, and catabolite activator protein (CAP), which illustrates positive control of gene expression.

Test Your Knowledge

MULTIPLE CHOICE: Choose the one best answer.

1. The study of the genetics of viruses and bacteria has done all of the following *except*
 - a. provide information on the molecular biology of all organisms.
 - b. illuminate the sexual reproductive cycles of viruses.
 - c. develop new techniques for manipulating genes.
 - d. develop an understanding of the causes of diseases.
 - e. show that genetic recombination occurs even in asexual bacteria.
2. Beijerinck concluded that the cause of tobacco mosaic disease was not a filterable toxin because
 - a. the infectious agent could not be cultivated on nutrient media.
 - b. a plant sprayed with filtered sap would develop the disease.
 - c. the infectious agent could be crystallized.
 - d. the infectious agent reproduced and could be passed on from a plant infected with filtered sap.
 - e. the filtered sap was infectious even though microbes could not be found in it.

3. Viral genomes may be any of the following except
 - a. single-stranded DNA.
 - b. double-stranded RNA.
 - c. misfolded infectious proteins.
 - d. a linear single-stranded RNA molecule.
 - e. a circular double-stranded DNA molecule.
4. Retroviruses have a gene for reverse transcriptase that
 - a. uses viral RNA as a template for making complementary RNA strands.
 - b. protects viral DNA from degradation by restriction enzymes.
 - c. destroys the host cell DNA.
 - d. translates RNA into proteins.
 - e. uses viral RNA as a template for DNA synthesis.
5. Virus particles are formed from capsid proteins and nucleic acid molecules
 - a. by spontaneous self-assembly.
 - b. at the direction of viral enzymes.
 - c. by using host cell enzymes.
 - d. using energy from ATP stored in the tail piece.
 - e. by both b and d.
6. A virus has a base ratio of $(A + G)/(U + C) = 1$. What type of virus is this?
 - a. a single-stranded DNA virus
 - b. a single-stranded RNA virus
 - c. a double-stranded DNA virus
 - d. a double-stranded RNA virus
 - e. a retrovirus
7. Vertical transmission of a plant viral disease may involve
 - a. the movement of viral particles through the plasmodesmata.
 - b. the inheritance of an infection from a parent plant.
 - c. a bacteriophage transmitting viral particles.
 - d. insects carrying viral particles between plants.
 - e. the transfer of filtered sap.
8. Bacteria defend against viral infection through the action of
 - a. antibiotics that they produce.
 - b. restriction nucleases that chop up foreign DNA.
 - c. their R plasmids.
 - d. reverse transcriptase.
 - e. episomes that incorporate viral DNA into the bacterial chromosome.
9. Drugs that are effective in treating viral infections
 - a. induce the body to produce antibodies.
 - b. inhibit the action of viral ribosomes.
 - c. interfere with the synthesis of viral nucleic acid.
 - d. change the cell-recognition sites on the host cell.
 - e. produce vaccines that stimulate the immune system.
10. Which of the following is true of prions?
 - a. They are emerging viruses.
 - b. They may spread through vertical or horizontal transmission.
 - c. They probably evolved from transposons.
 - d. They are infectious proteins that may convert brain proteins into misfolded forms.
 - e. They may be transferred between animals by sexual contact.
11. The herpesvirus
 - a. acts as a provirus when its DNA becomes incorporated into the host cell's genome.
 - b. is a retrovirus that uses restriction enzymes to transcribe DNA from its RNA genome.
 - c. has an envelope derived from the host cell's plasma membrane.
 - d. is the retrovirus that has been linked to HIV, the virus that causes AIDS.
 - e. can be used to vaccinate against hepatitis B.
12. The replication of the genome of an RNA virus uses
 - a. DNA polymerase from the host.
 - b. RNA replicating enzymes coded for by viral genes.
 - c. reverse transcriptase to synthesize RNA.
 - d. RNA polymerase from the host.
 - e. restriction nucleases from the host.
13. The replication of the genome of a DNA virus uses
 - a. DNA polymerase from the host.
 - b. RNA replicating enzymes coded for by viral genes.
 - c. reverse transcriptase to make an RNA copy from the DNA.
 - d. RNA polymerase from the host.
 - e. restriction nucleases from the host.
14. Which of the following would never be an episome?
 - a. an F plasmid
 - b. a prophage
 - c. a provirus
 - d. a retrovirus
 - e. All of the above can be episomes.

15. Tiny molecules of naked RNA that may act as infectious agents are

- retroviruses.
- transposons.
- viroids.
- reoviruses.
- prions.

Choose from the following types of genetic variation in bacteria to answer questions 16–20.

- conjugation
- mutation
- transduction
- transformation
- transposon

16. When harmless *Streptococcus pneumoniae* are mixed with heat-killed, broken-open cells of pathogenic bacteria, live pneumonia-causing bacteria are found in the culture.

17. Transfer of genes by viruses is called _____.

18. Transfer of antibiotic-resistant genes to R plasmids may occur this way.

19. The source of most of the genetic variation found in bacterial populations is _____.

20. Two mutant *E. coli* strains, which cannot grow on minimal media, are grown together in complete media (all amino acids supplied). Samples are later transferred to minimal media and numerous colonies are able to grow.

21. Which of the following is *not* descriptive of conjugation between an Hfr and F[−] bacterium?

- The Hfr cell has an F plasmid integrated into its chromosome.
- The Hfr cell forms sex pili and transfers one strand of its chromosome into an F[−] cell.
- Random movements often break the conjugation bridge before the entire single strand of its chromosome and F episome is transferred.
- Hfr conjugation always transfers antibiotic resistance genes between bacteria.
- Crossing over between homologous genes creates a recombinant F[−] cell.

22. A regulatory gene

- has its own promoter.
- is transcribed continuously.
- is not contained in the operon it controls.

- codes for repressor proteins.
- is or does all of the above.

23. Inducible enzymes

- are usually involved in anabolic pathways.
- are produced when a small molecule inactivates the repressor protein.
- are produced when an activator molecule enhances the attachment of RNA polymerase with the operator.
- are regulated by inherently inactive repressor molecules.
- are regulated almost entirely by feedback inhibition.

24. In *E. coli*, tryptophan switches off the *trp* operon by

- inactivating the repressor protein.
- inactivating the gene for the first enzyme in the pathway by feedback inhibition.
- binding to the repressor and increasing the latter's affinity for the operator.
- binding to the operator.
- binding to the promoter.

25. A mutation that renders nonfunctional the product of a regulatory gene for an inducible operon would result in

- continuous transcription of the genes of the operon.
- complete blocking of the attachment of RNA polymerase to the promoter.
- irreversible binding of the repressor to the operator.
- no difference in transcription rate when an activator protein was present.
- negative control of transcription.

26. An insertion sequence

- carries a gene only for transposase between two inverted repeats.
- may transpose genes for antibiotic resistance to R plasmids.
- involves the exchange of homologous regions of DNA.
- is necessary for the F plasmid to incorporate into the bacterial chromosome to form an Hfr cell.
- consists of an inverted repeat sandwiched between two direct repeats.

MATCHING: Match these components of the *lac* operon with their functions:

_____ 1. β -galactosidase	A. is inactivated when attached to allolactose
_____ 2. active CAP	B. codes for repressor protein
_____ 3. allolactose	C. hydrolyzes lactose
_____ 4. operator	D. stimulates gene expression
_____ 5. promoter	E. repressor attaches here
_____ 6. regulator gene	F. RNA polymerase attaches here
_____ 7. repressor	G. acts as inducer that inactivates repressor
_____ 8. gene in operon	H. usually codes for an enzyme