5

Plant Physiology

Purpose and Expected Outcomes

The purpose of this chapter is to discuss the primary plant physiological processes and to show how they affect the growth and development of horticultural plants. The discussion includes how an understanding of these processes enables scientists and growers to manipulate them for the higher quality and productivity of plants.

After studying this chapter, the student should be able to

1. Describe the generalized pattern of growth in organisms (sigmoid curve).
2. Describe the generalized phases of plant growth.
3. Discuss vegetative growth and development in plants and how growth patterns are used as a basis for the classification of plants.
4. Describe reproductive growth and development in plants.
5. Describe the role of environmental factors on plant growth and development.
6. Describe specific growth processes—photosynthesis, respiration, transpiration, translocation, and absorption—and their roles in plant growth and development.
7. Discuss specific ways in which growers may manipulate physiological processes for increased plant productivity and quality.

Overview

The genotype of an organism specifies its course of development within a given environment. A tall plant will grow tall, first because it has the *genes* for tallness, and second because it is provided with the appropriate *environment* to support the expression of the tallness trait. In growing to become tall, certain specific physiological activities must occur to provide the materials and energy required to translate genetic information into a physical appearance or phenotype. In other words, it is through physiological processes that genes are expressed.

Physiological processes allow the embryo in a seed to develop into a mature plant. As a plant grows and develops, it does so because of the roles of physiological processes such as *photosynthesis, respiration, transpiration, translocation,* and *absorption.* A variety of external and internal factors affect physiological processes. Light and hormones are notable factors that affect the growth of plants. By understanding how these factors and the processes themselves function, scientists, and eventually growers, are able to manipulate plants to their advantage by altering certain environmental conditions. Some processes may be slowed down and others speeded up. The major physiological processes that affect plant growth and development are discussed in this chapter.

5.1 Growth and Development

Growth and development involve three basic activities:

1. Cellular division
2. Enlargement
3. Differentiation

5.1.1 GROWTH

Growth
A progressive and irreversible increase in size and volume through natural development.

Growth is an irreversible phenomenon that occurs in a living organism, resulting in an increase in its overall size or the size of its parts. Growth is accompanied by energy-dependent metabolic processes. As such, whereas producing a leaf or root is growth, an increase in size due to swelling from water absorption is not.

Cellular Division and Enlargement

Osmosis
The diffusion of water or other solvents through a differentially permeable membrane from a region of higher concentration to a region of lower concentration.

The processes of cell division and enlargement are frequently associated. Cellular enlargement often precedes cellular division, as found in meristematic cells. However, the two processes are regulated independently. Cell enlargement does not induce cell division, and the latter is not always preceded by the former. For cells to enlarge, the rigid cell walls (which are rigid) must first be "loosened." This loosening occurs when certain acids are secreted into the cell walls (cell wall acidification). These acids in turn activate certain pH-dependent enzymes that act on cellulose in the walls. This cell-loosening process is influenced by a plant hormone called *auxin*. In addition to loosening of the cell wall, cellular enlargement requires *positive turgor pressure,* which results as a cell takes in water by **osmosis.** Because enlargement is required for growth and turgor is required for enlargement, the water status of a plant is critical to its growth and development. Cellular enlargement usually occurs in only one direction. Expansion occurs where the cell wall is most elastic. Cell wall elasticity is dependent on the orientation of the cellulose *microfibrils* in the wall. Where longitudinal cellulose microfibrils occur, the cell wall enlarges in a transverse fashion. On the other hand, transverse deposition of microfibrils in the cell walls produces longitudinal expansion. Random cellulose microfibrils produce equal expansion in all directions.

Growth produces an increase in dry matter when the plant is actively *photosynthesizing*. It is influenced by genetic, physiological, and environmental factors. Some plant cultivars are bred to be tall and large bodied, whereas miniature cultivars are bred for other purposes. For example, tomato cultivars used in salads produce small and near bite-size fruits; those used in canning are much larger in size. Plants can be manipulated by the application of chemicals to change their size by either enhancing or inhibiting growth. By changing the environment of the plant (e.g., soil, water, nutrients, temperature, photoperiod, and light intensity), a plant's growth can be enhanced or hindered. These environmental factors of plant growth and development are discussed in Chapter 4.

Growth in an organism follows a certain general pattern described by a *sigmoid curve* (Figure 5–1). The pattern and corresponding developmental stages as they occur in plants are as follows:

1. *Lag growth phase.* The lag phase includes activities in preparation for growth. Dormant cells become active; dry tissue imbibes moisture; cells divide and increase in size; the embryo differentiates.
2. *Logarithmic growth phase.* The logarithmic growth phase is characterized by an increasing growth rate and includes seed germination and vegetative plant growth periods.
3. *Decreasing growth phase.* During the decreasing growth phase, growth slows down. This stage includes flowering, fruiting, and seed filling.
4. *Steady growth phase.* Growth rate either declines or stops during the steady growth phase. This phase is associated with age, or the plant's maturity.

The characteristics of the sigmoid growth pattern vary among species and plant parts. In fruit growth, food materials are translocated from one part of the plant to another. In species such as apple, orange, pear, tomato, and strawberry, fruit growth follows the simple sigmoid growth curve, with variations in characteristics. However, in certain species, including stone fruits, such as plum, peach, and cherry, fruit growth follows a *double sigmoid curve* pattern whereby the single pattern is repeated (Figure 5–2). During the plateau of the first sigmoid curve, the fruit size barely changes; most of the activities involve seed development. In stone fruits, the hardening of the endocarp (pit) occurs during the second phase of fruit development.

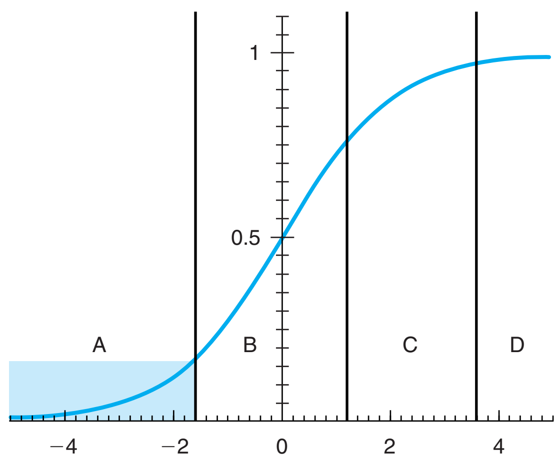


FIGURE 5–1 A typical sigmoid growth curve. (a) lag phase, (b) log phase, (c) decreasing phase, (d) steady phase.

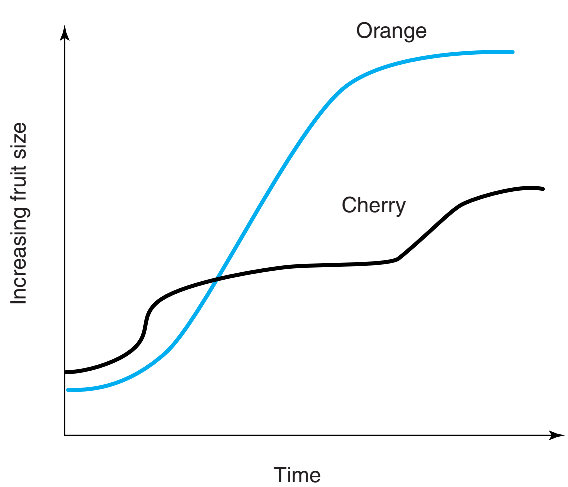


FIGURE 5–2 The sigmoid and double sigmoid growth curves. Stone fruits are characterized by the double sigmoid curve growth pattern. The characteristics of either curve differ from one species to another.

Development

Differentiation
The process of change by which an unspecialized cell becomes specialized.

Cellular Differentiation and Dedifferentiation

Differentiation is the process by which meristematic cells (genetically identical) diverge in development to meet the requirements for a variety of functions. The specialization of cells occurs as a result of differential activation of the cell's genome (total number of genes), resulting in the structure and function of previously genetically identical cells becoming different.

Differentiated cells can revert to meristematic status; when this happens they are said to be *dedifferentiated.* Cells dedifferentiate when the plant structural pattern is disrupted by, for example, wounding. To repair the damage, the cells in the damaged regions first become "deprogrammed" so that they can be reprogrammed to form the appropriate types of cells needed for the repair.

Polarity

Plants and their parts exhibit strong directional differences that are described as polarity. Classic examples of such directional growth and development are the existence of abaxial and adaxial parts of a leaf and the shoot and root ends of a full plant that are very different in structure and function (Figure 5–3). *Polarity* may be influenced by environmental factors such as gravity and light or it may be genetic in origin. In angiosperms, polarity appears to be fixed and difficult to alter. Thus, a stem cutting will always produce roots at the basal end and shoots at the apical end (Figure 5–4). Polar transport of growth hormones (such as auxin) is implicated in this phenomenon.

FIGURE 5–3 Polarity in plants.

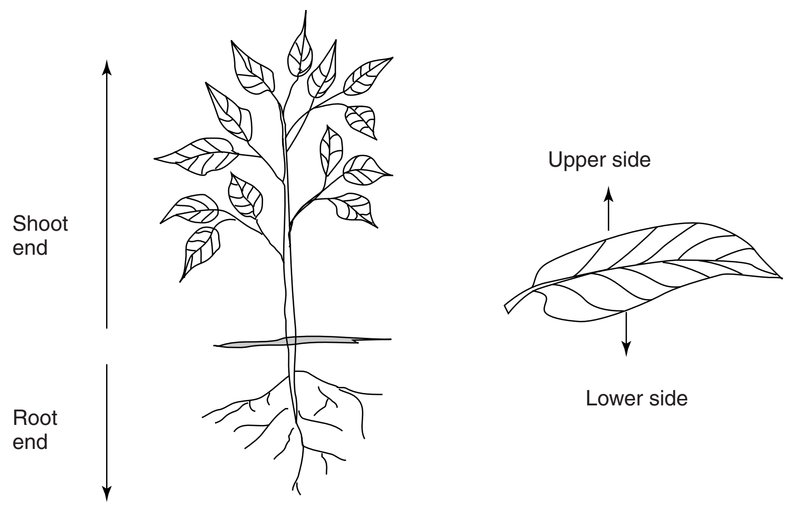
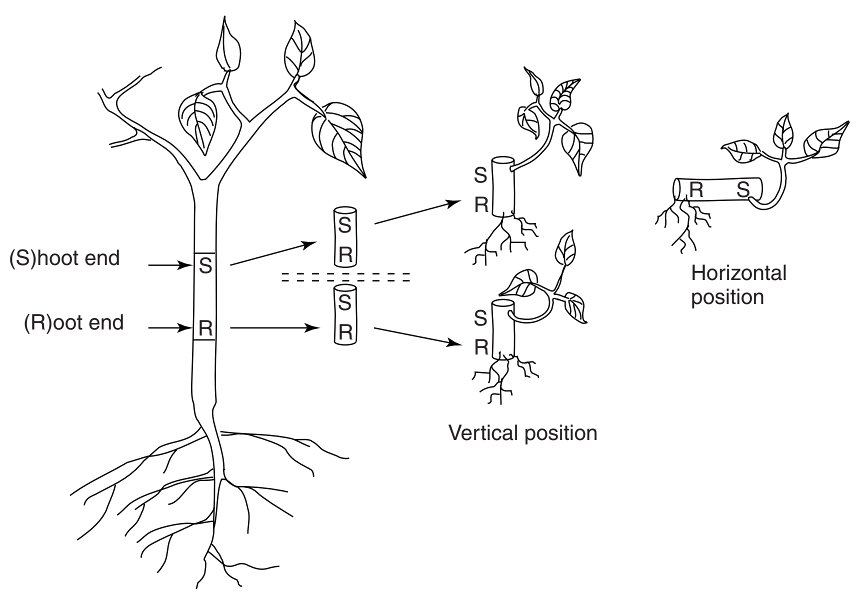


FIGURE 5–4 Polarity in the stem. Auxin transport in the stem is polar. No matter the orientation, rooting will occur only at the root end of the segment of the stem.



5.1.2 THE ROLE OF SIGNALS IN GROWTH AND DEVELOPMENT

Plant growth and development are regulated by complex signals. Plant hormones have been shown to stimulate differentiation of procambium. In tissue culture, the addition of a hormone such as auxin stimulates leaf formation in callus (a mass of undifferentiated tissue). In plants, removing the shoot apex stimulates lateral bud growth. Genetic control similar to that found in animals has been seen in maize studies. Other known control signals are *positional control* (caused by the position of a cell in plant tissue), *biophysical control* (caused by physical pressure generated by growing organs), and *electrical currents* (generated by growing plants).

5.2 Organic Compounds of Plant Cells

Major and minor inorganic chemicals obtained by plants from the soil are discussed in Chapter 4. These inorganic elements are utilized by the plant to synthesize the organic components of cells. Water is one of the most abundant inorganic compounds in plant cells. Carbon, hydrogen, and oxygen occur in all organic molecules. Sulfur and phosphorus occur in very few organic molecules and, even then, only in small amounts. The major classes of cellular organic constituents are *carbohydrates, lipids, proteins,* and *nucleic acids.* Of these, proteins and nucleic acids are relatively large molecules and hence are called *macromolecules.*

5.2.1 CARBOHYDRATES

Carbohydrates are the most abundant organic molecules in nature. In plants, they are the principal components of cell walls. They are also the primary energy-storage molecules in most organisms. Carbohydrates are made up of three elements—carbon (C), hydrogen (H), and oxygen (O)—usually in the ratio of 1:2:1 of carbon to hydrogen to oxygen. The general molecular formula of carbohydrates is thus $(CH_2O)_n$. The three principal kinds of carbohydrates—*monosaccharides, disaccharides,* and *polysaccharides*—are classified on the basis of the number of sugar molecules they contain.

Monosaccharides

Monosaccharides ("one sugar"), or *simple sugars,* consist of a chain of subunits with the basic structure $(CH_2O)_n$. Simple sugars are thus the building blocks of carbohydrates. Sugar names have the suffix *-ose* and a prefix that indicates the number of carbon atoms each sugar contains. For example, a *pentose sugar* has five carbons, and a *hexose sugar* has six carbons. Hexoses and pentoses are the most important simple sugars in plants. They occur as cell wall constituents and are important in energy aspects of cellular function. Glucose, a hexose, is used in the synthesis of other complex molecules such as starch (see polysaccharides). It is a major product of photosynthesis. The sweet taste of ripened fruits is due in part to the glucose and fructose sugars, as well as hexose sugars. Fructose can be converted to glucose and hence perform the functions of glucose. Ribose sugar is a constituent of deoxyribonucleic acid (DNA) and ribonucleic acid (RNA).

Disaccharides

Disaccharides consist of two monosaccharides joined by the process of *condensation* (removal of a water molecule by an enzyme-catalyzed process). Disaccharides can be broken down into component molecules by **hydrolysis** (addition of a water molecule to each linkage). *Sucrose*, or common table sugar from sugarcane or sugar beet, is a disaccharide consisting of glucose and fructose. Whereas the sugar transported in animal systems is commonly glucose, sucrose is the form in which sugars are most often transported in plants.

Hydrolysis
The breakdown of complex molecules to simpler ones, resulting from the union of water with the compound.

Polysaccharides

A *polymer* is a large molecule consisting of identical or similar molecular subunits called *monomers.* These monomers can polymerize into long chains. When three or more sugar molecules polymerize, the product is a polysaccharide. In most plants, accumulated sugars are stored in seed, leaves, stems, and roots in the form of a polysaccharide called *starch.* Starch is made up of two different polysaccharides—*amylose* and *amylopectin.* Amylose consists of glucose molecules linked in a nonbranching pattern (1,4-linkages), whereas amylopectin consists of molecules linked in a branching pattern (1,6-linkages). The figures in the linkage patterns refer to the position of carbons in the rings involved in the linkage. In certain species, such as temperate grasses, the commonly stored polysaccharides in leaves and stems are polymers of fructose called *fructans.*

Polysaccharides are important structural compounds. The most important in plants is cellulose, a polymer of β-glucose monomers (instead of α-glucose, as in starch) in 1,4-linkages. Cellulose is the most abundant polymer in nature. The molecular arrangement in this compound makes cellulose chains more rigid than starch, even though they consist of the same monomers. Cellulose is resistant to enzymes that readily hydrolyze starch and other polysaccharides. The biological functions of starch and cellulose are thus different. In fact, once incorporated into the cell wall as a constituent, cellulose cannot be utilized as a source of energy by plants. In ruminant animals such as cattle, it takes the action of microbes in the digestive tract to make cellulose an energy source. Other important polysaccharides in plants are *pectin*, a polymer of *galacturonic acid,* a six-carbon sugar containing an acid group, and *hemicellulose* (composed of a complex mixture of sugars).

5.2.2 LIPIDS

Lipids are a group of fats and fatlike substances. They differ in two major ways from carbohydrates. Lipids are not water soluble, unlike most carbohydrates. Also, lipids structurally contain a significantly larger number of C-H bonds and as a result release a significantly larger amount of energy in oxidation than other organic compounds. Lipids can be classified as follows.

Fats and Oils

Fats and *oils* have a similar chemical structure, consisting of three fatty acids linked to a *glycerol*, a three-carbon alcohol molecule. This structural arrangement is the origin of the term *triglyceride.* Fats and oils are storage forms of lipids called *triglycerides.* Whereas fats are solid at room temperature, oils remain liquid. Cells synthesize fats from sugars. Plants, as previously indicated, store excess food as starch. To a limited extent, fat is stored as droplets within the chloroplasts of some species of plants such as citrus.

Triglycerides differ in nature by the length of their fatty acid chains and the number of hydrogen atoms to which their carbons are linked. They are said to be saturated when most carbon atoms are linked to hydrogen atoms, or unsaturated, when some carbon atoms are double-bonded to hydrogen. Triglycerides containing unsaturated fatty acids tend to behave like oils, and are fluid or liquid at room temperature. Unsaturated fatty acids are found in plants such as corn and peanut, both of which are sources of edible oil.

Phospholipids

Phospholipids differ from triglycerides in that only two of the three fatty acids are attached to glycerol, the third one being attached to a phosphate group. The presence of the phosphate at the end of the phospholipid molecule makes this end of the fatty acid molecule water soluble (the other end remains water insoluble). Phospholipids are important cellular membrane constituents.

Cutin, Suberin, and Waxes

Cutin, suberin, and *waxes* make up a group of lipids that are insoluble and create a structural barrier layer in plants. Cutin and suberin form the structural matrix within which waxes are embedded. Waxes consist of fatty acids combined with a long-chain alcohol. The cutin-wax complex forms a water-repellent layer that prevents loss of water from the protected area. The outer walls of epidermal cells have a protective layer called a cuticle that consists of cutin embedded with wax. Suberin occurs in significant amounts in the walls of cork cells in tree bark.

5.2.3 PROTEINS

Proteins are structurally more complex than carbohydrates and lipids. They are composed of building blocks called *amino acids,* which are nitrogen-containing molecules. Amino acids polymerize by linkage of *peptide bonds* (a bond formed between two amino acids) to produce chains called *polypeptides*. The twenty commonly occurring amino acids are used to form all proteins by bonding in a variety of sequences. The basic structure is the same for all amino acids—an *amino group,* a *carboxyl group,* and a *hydrogen atom* bonded to a *central carbon atom.* What distinguishes amino acids is the unique *R group.* The R group may be *polar* or *nonpolar* (according to its tendency to dissolve in a polar solvent such as water), polar groups being more soluble in water than nonpolar ones. An amino acid may have a *net charge* (either positive or negative) or be *neutral* (no net charge). Of the twenty commonly occurring amino acids, fifteen are neutral, three are basic, and two are acidic.

Enzymes

Enzymes are large, complex, globular proteins that act as *catalysts* in biochemical reactions. Catalysts accelerate the rate of chemical reactions by lowering the energy required for activation. That is, reactions can be sped up while occurring at relatively low temperatures. In the process of the reaction, these substances remain unaltered and are hence reusable. An enzyme has an *active site* to which the *substrate* (the substance acted on by the enzyme) attaches to form an enzyme-substrate complex. A substrate might be a compound such as glucose or adenosine triphosphate (ATP). These substances are changed into new products at the end of the reaction.

Enzyme
A complex protein that speeds up a chemical reaction without being used up in the process.

About 2,000 enzymes are known to occur in nature. Each enzyme catalyzes a specific reaction. Sometimes an enzyme-catalyzed reaction requires the presence of a third substance in order to proceed. These additional substances are called *cofactors* and may be organic or inorganic. Inorganic cofactors are also called *activators* and are usually metallic ions required in trace amounts in plant nutrition, such as iron, magnesium, and zinc. Organic cofactors (e.g., nicotinamide adenine dinucleotide [NAD^+] and nicotinamide adenine dinucleotide phosphate [$NADP^+$]) are called *coenzymes.* These substances accept atoms that are removed by the enzyme during the reaction. Enzymes that remove hydrogen atoms from substrates are called *dehydrogenases.*

5.2.4 NUCLEIC ACIDS

Nucleic acids are chemicals involved in hereditary aspects of cellular life. They are polymers of nucleotides that consist of a *phosphate group,* a *five-carbon sugar,* and a *nitrogenous base.* The two major types of nucleic acids are *DNA* and *RNA.*

Deoxyribonucleic acid (DNA) is the genetic material of living organisms. It consists of *nitrogenous bases, sugar,* and *phosphate.* There are four bases: *adenine (A), cytosine (C), guanine (G),* and *thymine (T).* Adenine and guanine are called *purines,* and cytosine and thymine are *pyrimidines.* The letters *A, C, G,* and *T* are the genetic alphabets. The sugar is a *pentos* (five-carbon ring) and is of the *deoxyribose variety.* The sugar and base link up to form a *nucleoside,* which then combines with a phosphate to form a *nucleotide.* Nucleotides link up to produce a chain called a *polynucleotide,* in which the sugar and phosphate form a backbone from which the bases extend. Two polynucleotide chains pair up in an antiparallel (running in opposite sequence) and complementary fashion. That is, *A* always pairs with *T* (by a double hydrogen bond), and *G* always pairs with *C* (by a triple bond). The pair of chains then winds or coils up into a *double helix.*

DNA
Deoxyribonucleic acid (DNA) is the genetic material organisms inherit from their parents.

TABLE 5–1 Selected Examples of C3, C4, and CAM Plants

Common Name	Scientific Name
C_3 Plants	
Kentucky bluegrass	*Poa pratensis*
Creeping bentgrass	*Agrostis tenuis*
Sunflower	*Helianthus annuus*
Scotch pine	*Pinus sylvestris*
Tobacco	*Nicotiana tabacum*
Peanut	*Arachis hypogaea*
Spinach	*Spinacia oleracea*
Soybean	*Glycine max*
Rice	*Oryza sativa*
Wheat	*Triticum aestivum*
Rye	*Secale cereale*
Oats	*Avena sativa*
C_4 Plants	
Crabgrass	*Digitaria sanguinalis*
Corn	*Zea mays*
Bermuda grass	*Cynodon dactylon*
Sugarcane	*Saccharum officinale*
Sorghum	*Sorghum vulgare*
Pigweed	*Amaranthus*
Euphorbia	*Euphorbia* spp.
Millet	*Pennisetum glaucum*
Sedge	*Carex* spp.
CAM Plants	
Wax plant	*Hoya carnosa*
Snake plant	*Sansevieria zeylanica*
Maternity plant	*Kalanchoe diagremontiana*
Pineapple	*Ananas comosus*
Spanish moss	*Tillandsia usneoides*
Jade plant	*Crassula argentea*
Ice plant	*Mesembryanthemum spp.*
Century plant	*Agave americana*
Cacti (many spp.)	

The information in the DNA is decoded by the process of *protein synthesis*. The genetic message occurs in the sequence of nitrogenous bases. The sites of protein synthesis are outside of the nucleus on the ribosomes in the cytoplasm. Copies of the nuclear DNA must first be made and transported to the ribosomes to serve as *templates*. Another nucleic acid, called *ribonucleic acid (RNA),* is responsible for this genetic transport. The RNA differs from DNA in the types of sugar.

5.3 Plant Growth Processes

Plant growth processes provide the raw materials and the energy required for building new tissues and nurturing them to maturity. The major processes are discussed in the following sections.

5.3.1 PHOTOSYNTHESIS

Photosynthesis accounts for more than 90 percent of the dry matter yield of horticultural plants and is the ultimate source of food and fossil fuel. Photosynthesis is the single most important chemical reaction in nature. It impacts the environment significantly through its effects on the oxygen content of the air. This major physiological process is important not only because of its tremendous impact on a variety of functions in nature but also because an understanding of the process enables scientists to maximize its rate for higher crop productivity.

Photosynthesis *The process by which plants convert light to chemical energy.*

Photosynthesis is a reaction occurring in green plants whereby plants utilize water and the energy of sunlight to fix inorganic carbon dioxide in the form of organic compounds, releasing oxygen in the process. In other words, the sun's energy is transformed by plants through photosynthetic processes into chemical energy usable by other living organisms. The importance of this process is more readily apparent when we understand that plants are ultimately the source of all food. Plants may be used *directly* as food (e.g., vegetables, fruits, grains, nuts, and tubers) or may be used by animals and then *indirectly* become available through animal products (e.g., poultry, fish, meat, and dairy products). Lest we limit the importance of plants to food, it should be made clear that plants are also sources of materials for fuel, clothing, and medicines. They are utilized widely in the beautification of the landscape and performance of other functional roles.

The general chemical reaction of photosynthesis is

$$6CO_2 + 12H_2O \xrightarrow[\text{light energy}]{\text{green plant}} C_6H_{12}O_6 + 6O_2 + 6H_2O$$

This reaction occurs in the chloroplasts, using chlorophyll as an enzyme. Carbon dioxide comes from the air and water from the soil.

Phases of Photosynthesis

Light-Dependent Reactions **LIGHT** The nature of the electromagnetic spectrum is discussed in Chapter 4. Figure 4–4 shows that visible light is only a small portion of the vast electromagnetic spectrum. Only certain wavelengths of light are involved in photosynthesis. These specific wavelengths depend on the *absorption spectrum* (the range of wavelengths of light absorbed) of the various pigments involved in photosynthesis. A pigment may absorb a broad range of wavelengths, but certain ones are more effective than others in performing specific functions. The *action spectrum* of a pigment describes the relative effectiveness of different wavelengths of light for a specific light-dependent process such as flowering or photosynthesis.

Light-Independent Reactions The light-independent reactions stage is also collectively called the *dark reaction* of photosynthesis. At this stage, carbon dioxide is reduced to carbohydrate, a process called **carbon dioxide fixation.** This stage does not depend directly but rather indirectly on light, since the ATP and NADPH required are produced by the light-dependent reactions. Further, the two chemicals do not accumulate in the cell but are used up as fast as they are produced. The fixation of carbon dioxide (CO_2) comes to a halt soon after the light supply is terminated.

Carbon Dioxide Fixation *A cyclical series of reactions in which carbon dioxide is reduced to carbohydrate.*

Carbon dioxide fixation occurs by one of two major pathways, which are distinguished by the first product formed. These are the three-carbon (C_3) pathway and the four-carbon (C_4) pathway.

1. *The Calvin cycle.* Named after its discoverer, the first product of the *Calvin cycle* is a three-carbon compound. Thus this pathway is also called the *C_3 pathway.* Plants that photosynthesize by this pathway are called *C_3 plants.* Carbon dioxide enters the cycle and becomes covalently bonded to a five-carbon sugar with two phosphate groups called *ribulose 1,5-bisphosphate (RuBP)* (Figure 5–5). This process (fixation) is catalyzed by the enzyme *RuBP carboxylase,* also commonly called *rubisco*. Because this enzyme is abundant in chloroplasts, rubisco is said to be the most abundant protein in nature. The overall process can be summarized by the following equation:

$$6CO_2 + 12NADPH + 12H^+ + 18ATP \rightarrow 1\text{ glucose} + 12NADP^+ + 18ADP + 18P_i + 6H_2O$$

The intermediate product is *glyceraldehyde 3-phosphate.*

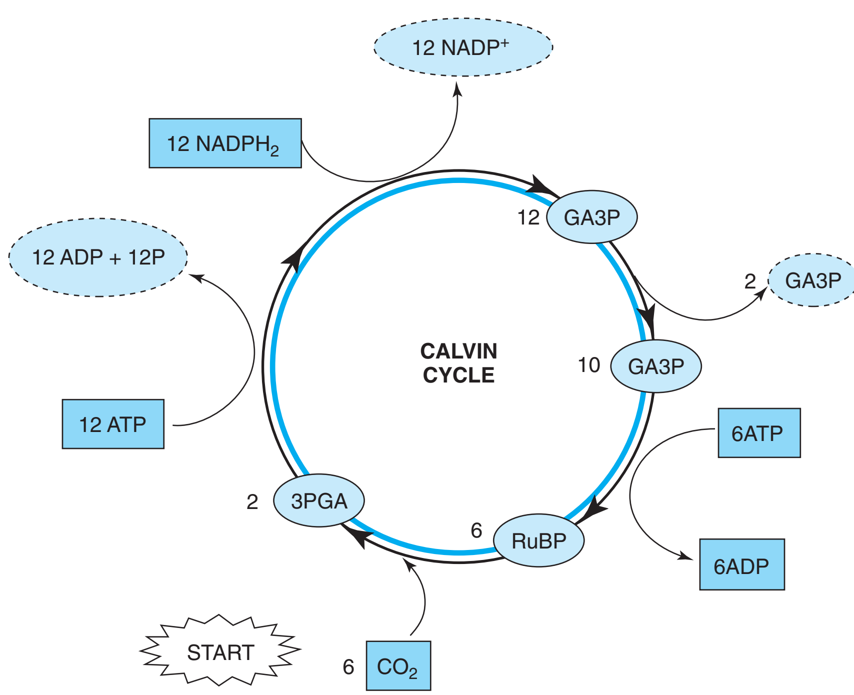
Glucose is indicated in the preceding summary equation, but in practice, photosynthesizing cells generate a minimal amount of this sugar. Most of the fixed carbon dioxide is either converted to sucrose (which is the principal form in which sugar is transported in plants) or stored in the form of starch.

2. *The four-carbon pathway.* Many plants are known to be able to fix carbon dioxide by a pathway whose first product is a four-carbon substance. This pathway is also called the *C_4 pathway,* and plants that photosynthesize by this pathway are called *C_4 plants.* First, a CO_2 molecule is bonded to *phosphoenol pyruvate (PEP),* a three-carbon acceptor compound, resulting in the production of *oxaloacetate.* The reaction is catalyzed by the enzyme *PEP carboxylase* (Figure 5–6).

C_4 plants are less efficient than C_3 plants in terms of the energy requirements in fixing CO_2. To fix one molecule of CO_2, C_4 plants need five ATPs, whereas C_3 plants need only three. However, C_4 plants have higher photosynthetic rates than C_3 plants and also are able to continue photosynthesizing under conditions such as high temperatures and high light intensity when C_3 plants cannot (Figure 5–7). Generally, C_4 plants are adapted to tropical conditions. Select examples of both categories of plants are presented in Table 5–1. Under hot, sunny skies, C_3 plants undergo a process called *photorespiration* (light-dependent production of glycolic acid in chloroplasts and its subsequent oxidation in peroxisomes). C_4 plants use CO_2 more efficiently and hence are able to function at only partially closed stomata, as occurs on hot, sunny days.

C_3 and C_4 plants are different structurally. The bundle sheath cells of C_3 leaves have small chloroplasts. Photosynthesis occurs only in the mesophyll cells. However, the bundle sheath cells of C_4 plants are large and contain large chloroplasts. These chloroplasts exhibit the Calvin cycle, while the mesophyll cells exhibit the C_4 pathway. All plants known to use the C_4 pathway are flowering plants. In

FIGURE 5–5 The Calvin cycle or C_3 pathway of carbon dioxide fixation.



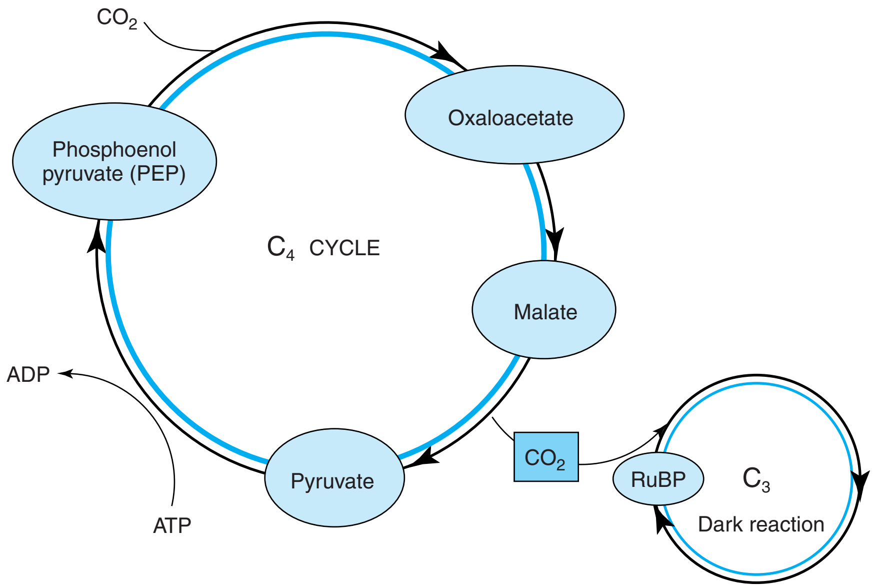


FIGURE 5–6 The C_4 pathway of carbon dioxide fixation.

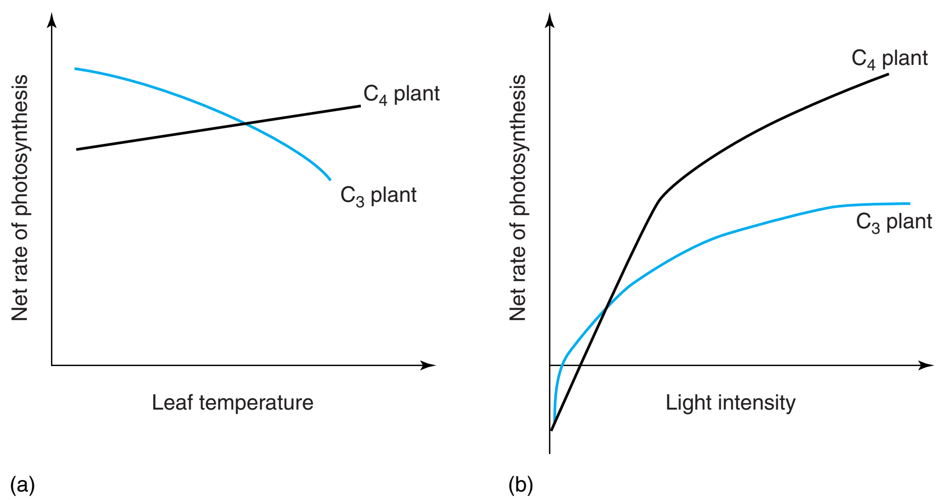


FIGURE 5–7 The relative rates of photosynthesis in C_3 and C_4 plants as influenced by (a) temperature and (b) light intensity.

lawns, where C_4 species such as crabgrass *(Digitaria sanguinalis)* occur among C_3 species such as Kentucky bluegrass *(Poa pratensis),* the crabgrass grows rapidly in summer and tends to suppress the fine-leafed species with its broad leaves.

3. *The Crassulacean acid metabolism.* The Crassulacean acid metabolism (CAM) is a photosynthetic pathway that allows certain plants to fix carbon dioxide in the dark by the activity of PEP carboxylase. Because the stomata of leaves are closed during the hot day, CAM plants depend on CO_2 that accumulates in the leaf during the nighttime. This reaction provides *malic acid,* which accumulates in the vacuoles of cells. During the next light period, the malic acid is decarboxylated. The resulting CO_2 is transferred to the Calvin cycle within the same cell.

Most CAM plants inhabit environments in which moisture stress and intense light prevail. Many are succulents such as members of the cactus (Cactaceae), stone crop (Crassulaceae), and orchid (Orchidaceae) families. Houseplants with CAM include wax plant *(Hoya carnosa)* and snake plant *(Sansevieria zeylanica).*

CAM plants are relatively slower growing than C_3 or C_4 plants under favorable conditions. They grow more slowly because plants, by nature, tend to conserve moisture and in so doing close the stomata most of the day, thus limiting the CO_2 intake needed for fixation.

Environmental Factors Affecting Photosynthesis

The rate of photosynthesis is affected by a number of factors, including light intensity, carbon dioxide concentration, temperature, water availability, photoperiod, and growth and development.

Light Intensity Light is important for the production of ATP and NADPH. Thus, at low light intensities, these products are not produced in adequate amounts. However, when light intensity is extreme, other factors such as CO_2 may be limited, causing the rate of photosynthesis to decline.

Maximum photosynthesis occurs near noon. For most houseplants and trees, such as oak, the photosynthetic rate is not affected by an increase in light intensity. Many houseplants are shade loving, and other plants such as turf grasses, corn, and some fruit trees are sun loving. For example, Bermuda grass (a tropical grass) responds to changes in light intensity. The horticultural practice of pruning trees permits light to penetrate the canopy so that more leaves can receive direct sunlight for increased photosynthesis. Plants grown in high light intensities tend to have broader and thicker leaves than those grown in lower light intensities. The quality of leaf vegetables is thus influenced by light intensity.

Carbon Dioxide Concentration Rapid photosynthesis can deplete cells of carbon dioxide. An increase in carbon dioxide concentration is beneficial to C_3 plants, since they have a high *CO_2 compensation point* (the equilibrium concentration of carbon dioxide at which the amount evolved in respiration is equal to the amount fixed by photosynthesis). C_4 plants have a lower CO_2 compensation point than C_3 plants because the former are more efficient in trapping CO_2. Some commercial growers enrich the greenhouse atmosphere with an artificial source of carbon dioxide (from liquid carbon dioxide or by burning methane or propane) to grow plants such as orchid (*Cattleya* spp.), carnation *(Dianthus caryophyllus),* and rose (*Rosa* spp.). This method of providing supplementary greenhouse carbon dioxide is called *carbon dioxide fertilization*. This practice may be necessary during the winter when carbon dioxide levels in airtight greenhouses may be lowered to a degree where photosynthesis could be limited on sunny days. However, unless the purpose of providing additional carbon dioxide is to increase productivity, the carbon dioxide concentration in winter may be readily restored by frequent ventilation of the facility rather than adopting carbon dioxide fertilization.

Temperature Photosynthetic rate is decreased in cold temperatures because the fixation stage is temperature sensitive. However, under conditions in which light is a limiting factor (low light conditions) the effect of temperature on photosynthesis is minimal. Generally, if light is adequate, the photosynthetic rate is found to approximately double the rate in plants in temperate areas for each 10°C (18°F) rise in temperature. The quality (sugar content) of certain fruits such as cantaloupe is reduced when they are grown under conditions in which the photosynthetic rate is reduced but respiration is high because of high temperatures. C_3 plants grow poorly at high temperatures. For example, lawn grasses that follow the C_3 pathway perform poorly in summer, whereas C_4 plants that are weeds, such as crabgrass, thrive.

Water Availability When plants grow under conditions of moisture stress because of low soil moisture or dry winds that accelerate transpiration, enzymatic activities associated with photosynthesis in the plants slow down. Stomata close under moisture stress, reducing carbon dioxide availability and consequently decreasing the photosynthetic rate.

Photoperiod The duration of day length (photoperiod) affects photosynthesis in a directly proportional way. Generally, plants that are exposed to long periods of light photosynthesize for a longer time and as a result tend to grow faster. In the winter season when sunlight is less direct and of shorter duration, growing plants indoors is more successful if additional lighting at appropriate intensity is provided to extend the period of natural light.

Growth and Development The general plant growth and development needs also influence the rate of photosynthesis. The photosynthetic rate is lower in a young expanding leaf than in a fully expanded one. On the other hand, as plant leaves begin **senescence** (an aging process involving degradation of proteins), the photosynthetic rate in mature leaves declines and eventually ceases in certain species.

Senescence
The breakdown of cell components and membranes that leads to the death of a cell.

Other factors affect the rate of photosynthesis. One such factor is nutrition (deficiency of nitrogen and magnesium, which are both required by chlorophyll, can decrease the rate). Environmental pollutants such as ozone and sulfur damage horticultural plants by causing loss of chlorophyll in leaves and thus reducing the available photosynthetic surface.

5.3.2 RESPIRATION

Respiration may occur in an environment that is oxygen rich or oxygen deficient.

Aerobic Respiration

Aerobic respiration accomplishes the reverse of photosynthesis by using oxygen from the air to metabolize organic molecules into carbon dioxide and water to release stored energy in the form of ATP. In fact, the primary purpose of respiration is this energy-production function. *Polysaccharides* are stored in different forms by different organisms; for example, bananas store it as sucrose, whereas onions store it as fructose. The general reaction that occurs in mitochondria in the cytoplasm is as follows:

$$C_6H_{12}O_6 + 6O_2 \rightarrow 6CO_2 + 6H_2O + \text{energy}$$

Respiration consists of three distinct stages. The first reaction, *glycolysis,* occurs in the cytoplasm, where glucose is broken down into pyruvic acid. In the first part, ATP is converted to ADP; in the second part, ADP is converted to ATP. Pyruvic acid from glycolysis enters the mitochondria to complete the next two phases, which are the *Krebs cycle (tricarboxylic acid cycle* or *citric acid cycle)* and the *electron transport chain* (requires oxygen). This three-phase process is called *aerobic respiration,* since it requires oxygen. When oxygen is limited, another form of respiration, called *anaerobic respiration* (or *fermentation*), occurs, the end product being alcohol.

Glycolysis **Glycolysis** ("sugar splitting") occurs in the cytoplasm of the cell. It involves the breaking down of glucose into pyruvic acid (Figure 5–8). In a series of reactions two, three-carbon sugar phosphates are produced from one, six-carbon glucose molecule. The sugar phosphates are then converted to pyruvic acid (a pyruvate), accompanied by the production of ATP and the reduction of NAD^+ to NADH. The overall equation for glycolysis is as follows:

Glycolysis
The initial phase of all types of respiration in which glucose is converted to pyruvic acid without involving free oxygen.

$$\text{glucose} + 2NAD^+ + 2ADP + 2P_i \rightarrow 2\ \text{pyruvic acid} + 2NADH + 2H^+ + 2ATP + 2H_2O$$

In effect, one glucose molecule is converted into two molecules of pyruvic acid. The formation of ATP by the enzymatic transfer of a phosphate group from a metabolic intermediate to ADP is called *substrate-level phosphorylation.*

Krebs Cycle The Krebs cycle occurs in the mitochondrion, following the entry of pyruvic acid from glycolysis. The series of enzyme-catalyzed reactions involved in this cycle constitute what is called *oxidative decarboxylation* (Figure 5–9). The reactions may be summarized by the following equation:

$$\text{oxaloacetic acid} + \text{acetyl CoA} + ADP + P_i + 3NAD^+ + FAD \rightarrow \text{oxaloacetic acid} + 2CO_2 + CoA + ATP + 3NADH + 3H^+ + FADH_2$$

FIGURE 5–8 A summary of glycolysis.

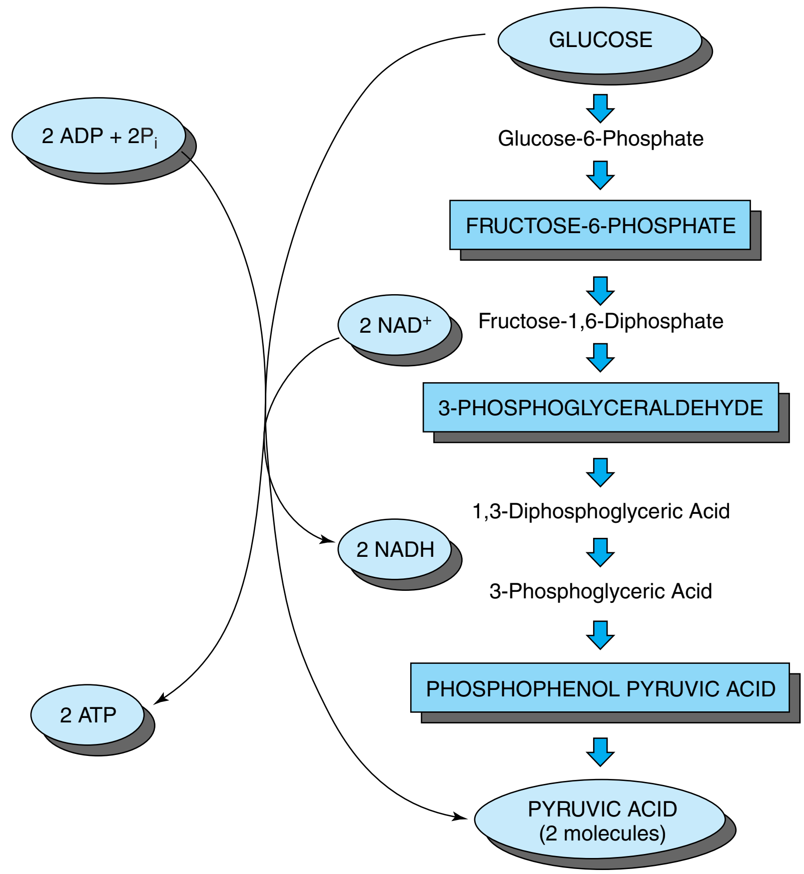


FIGURE 5–9 A summary of the Krebs cycle. The cycle always begins with acetyl CoA, which is its only real substrate.

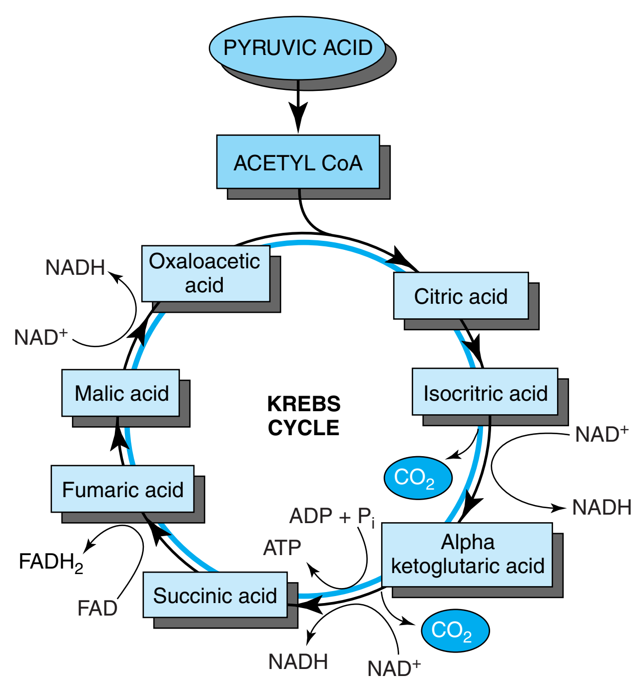


TABLE 5–2 Energy Produced from Aerobic Respiration

Metabolic Reaction	*Coenzyme Type Produced*	*ATP Yield Coenzyme*	*Total*
Glycolysis	(Direct)	2	2
	2 NADH	2	4
Oxydative decarboxylation of pyruvate to acetyl CoA	2 NADH	3	6
Krebs cycle	(From GTP)	2	2
	6 NADH	3	18
	2 $FADH_2$	2	4
Net yield of ATP			36

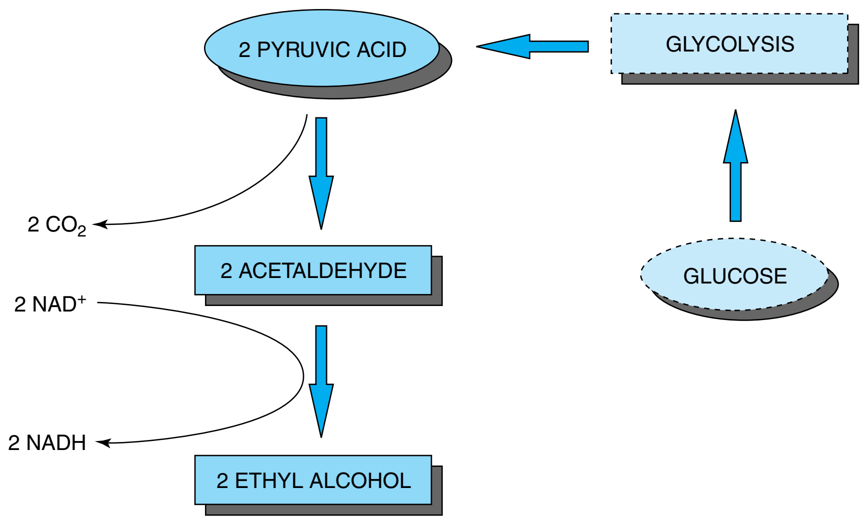


FIGURE 5–10 A summary of the process of fermentation.

Energy Yield in Respiration The energy yield from the respiration of one molecule of glucose is presented in Table 5–2. The net yield of 36 ATPs from aerobic respiration of one molecule of glucose is common to most organisms.

Anaerobic Respiration

Aerobic respiration results in the complete oxidation of pyruvic acid to CO_2 and water. When oxygen is absent, pyruvic acid (or pyruvate) is not the end product of glycolysis. Instead, pyruvate is broken down to *ethyl alcohol* (ethanol) and CO_2 in most plant cells (Figure 5–10). This anaerobic process is called *anaerobic respiration,* or alcoholic fermentation. In some bacteria, the end product is lactic acid, and thus the process is called *lactate* **fermentation.** The anaerobic respiratory pathway is very inefficient. In aerobic respiration, the initial energy of 686 kilocalories (kcal) per mole of glucose yields 263 kcal (39 percent) at the end of the process, which is conserved in 36 ATP molecules. In fermentation, only 2 ATP molecules are produced, representing about 2 percent of the available energy in a molecule of glucose.

Fermentation *The metabolic breakdown of an organic molecule in the absence of oxygen or with low levels of oxygen to produce end products such as ethanol and lactic acid.*

When horticultural plants are grown in mud (air is limited), they are forced to respire anaerobically. Similarly, houseplants die when they are overwatered or grown in containers with poor drainage because they are unable to respire aerobically; instead they resort to anaerobic respiration, which yields very little or no energy at all. Fermentation, however, is a very important process utilized in the alcoholic beverage industry. Wine (from grapes) and apple cider are a few products that depend on anaerobic respiration.

Respiration is the source of energy for all life processes. Since it depends on products of photosynthesis (the two processes work in opposite directions), it is critical that a desirable relationship between them be maintained for proper growth and development of plants. If food is broken down faster than it is manufactured, plant growth will be severely hampered. This imbalance may cause the eventual death of certain plants when they are grown in the shade. Whereas light is required for photosynthesis, it is not required for respiration, and hence the latter proceeds even in shade. Fortunately, photosynthesis generally occurs at a higher rate than respiration, such that there are excess photosynthates for growth or production of fruits and seed through storage. It is estimated that a photosynthetic rate of about 8 to 10 times higher than the respiration rate is required for good production of vegetables.

To decrease respiration of carbohydrates, the temperature may be lowered to slow the reaction. However, this action also slows the photosynthetic rate. A warm temperature, moderate intensity of light, and adequate supply of water are desired for maximizing the photosynthetic rate. This condition occurs on warm, bright days with cool night temperatures of about 5°C (9°F) colder than day temperatures. Respiration is reduced during the cool period of the night, while adequate duration and intensity of light exist during the day for photosynthesis.

Respiration does not occur only when plants are growing. Freshly harvested plant produce should be stored appropriately to prevent degradation from respiration. For some plants, such as apple, proper storage may mean the provision of cold storage at about 0°C (32°F); other plants, such as banana and flowers, require less cold storage conditions (about 10°C [50°F]). Anaerobic respiration may be detrimental to most plants, but it may be utilized to reduce respiration rate during storage of certain vegetable crops and fruits.

5.3.3 TRANSPIRATION

Transpiration
The loss of water from plant surfaces by evaporation and diffusion.

The other two major plant growth processes—**transpiration** and translocation—are associated with the movement of water in plants. The movement of water in the soil is discussed in Chapter 4.

Species such as corn *(Zea mays)* lose large amounts of water, whereas others, such as tomato *(Lycopersicon esculentum),* lose only moderate amounts of water during cultivation. Other plants such as cowpea *(Vigna sinensis)* are relatively highly resistant to water loss by transpiration. Transpiration occurs through the stomata, the pores through which the much-needed CO_2 for photosynthesis passes. Transpiration is regulated by closure of the stomata, an event that excludes CO_2 and reduces the rate of photosynthesis. However, respiration produces some CO_2 that can be trapped and used by plants after the stomata have closed.

The stomata open or close according to changes in turgor pressure in the guard cells. Water in most cases is the primary factor that controls stomatal movements. However, other factors in the environment also affect stomatal movements. Generally, an increase in CO_2 concentration in the leaf causes stomatal closure in most species. Some species are more sensitive than others to the effects of CO_2. Similarly, the stomata of most species open in light and close in the dark. An exception to this feature is plants with CAM pathways of photosynthesis. Photosynthesis uses up CO_2 and thus decreases its concentration in the leaf. Evidence suggests that light quality (wavelength) affects stomatal movements. Blue and red light have been shown to stimulate stomatal opening. The effect of temperature on stomatal movements is minimal, except when excessively high temperatures (more than 30°C [86° F]) prevail, as occurs at midday. However, an increase in temperature increases the rate of respiration, which produces CO_2 and thereby increases the CO_2 concentration in the leaf. This increase in CO_2 may be part of the reason stomata close when the temperature increases.

Apart from environmental factors, many plants have been known to accumulate high levels of abscisic acid, a plant hormone. This hormone accumulates in plants under conditions of moisture stress and causes stomata to close.

Transpiration is accelerated by several environmental factors. The rate of transpiration is doubled with a more than 10°C (18°F) rise in temperature. Transpiration is slower in environments of high humidity. Also, air currents may accelerate the transpiration rate by preventing water vapor from accumulating on the leaf surface.

Certain plants are adapted to dry environments. These plants (called *xerophytes*) have special anatomical and physiological modifications that make them able to reduce transpiration losses. These species, which include a large number of succulents, are able to store and retain large amounts of water. Physiologically, the plants photosynthesize by the CAM pathway and close their stomata at night.

5.3.4 HOW WATER MOVES IN PLANTS

Water moves in plants via the conducting elements of the xylem. It moves along a water potential gradient from soil to root, root to stem, stem to leaf, and leaf to air forming a continuum of water movement. The trend is for water to move from the region of highest water potential to the region of lowest water potential, which is how water moves from the soil to the air. Transpiration is implicated in this water movement, because it causes a water gradient to form between the leaves and the soil solution on the root surface. This gradient may also form as a result of the use of water in the leaves. Loss of moisture in the leaves causes water to move out of the xylem and into the mesophyll area, where it is depleted. The loss of water at the top of the xylem vessels causes water to be pulled up. This movement is possible because of the strong cohesive bond among water molecules. The movement of water up the xylem according to this mechanism is explained by the *cohesion-tension theory.* It is the cohesiveness of water molecules that allows water to withstand tension. Water is withheld against gravity by capillarity. The rise is aided by the strong adhesion of water molecules to the walls of the capillary vessel.

Capillary flow is obstructed when air bubbles interrupt the continuity of the water column, called *embolism.* This event is preceded by *cavitation,* the rupture of the water column. Once the tracheary elements have become embolized, they are unable to conduct water. In the cut flower industry, the stems of flowers are cut under water to prevent embolism.

Water enters the plant from the soil via the root hairs, which provide a large surface area for absorption. Once inside the root hairs, water moves through the cortex and into the tracheary elements. There are three possible pathways by which this movement occurs, depending on the differentiation that has occurred in the root (e.g., presence of endodermis, exodermis, or a transcellular pathway suberin). Water may move from cell to cell, passing from vacuole to vacuole. Sometimes water may move via the *apoplastic pathway,* through the cell wall, or the *symplastic pathway,* from protoplast to protoplast through the pores in the plasmodesmata (minute cytoplasmic threads that extend through openings in the cell wall and connect the protoplast of adjacent living cells).

Root pressure plays a role in water movement, especially at night when transpiration occurs to a negligible degree or not at all. Ions build up in the xylem to a high concentration and initiate osmosis, so that water enters the vascular tissue through the neighboring cells. This pressure is called root pressure and is implicated in another event, *guttation,* whereby droplets of water form at the tips of the leaves of certain species (e.g., lady's mantle [*Achemilla vulgaris*]) in the early morning. These drops do not result from condensation of water vapor in the surrounding air but rather are formed as a result of root pressure forcing water out of hydathodes. Root pressure as a water movement mechanism is least significant during the daytime when water moves through plants at peak rates. Further, some plants such as pine (conifers) do not develop root pressure.

Root Pressure
The development of positive hydrostatic pressure in the xylem followed by osmotic uptake of water.

The absorption and movement of water in plants occurs via the xylem vessels. Inorganic nutrients are also transported through these vessels. Solutes are moved against a concentration gradient and require an *active transport* mechanism that is energy dependent and mediated by carrier protein. Some amount of exchange between xylem and phloem fluids occurs such that inorganic salts are transported along with sucrose and some photosynthetic products are transferred to the xylem and recirculated in the transpiration stream.

5.3.5 TRANSLOCATION

Translocation is the long-distance transport of organic solutes through the plant. Photosynthetic products are moved out of the leaves and into the assimilate stream from the *sources* (especially leaves but also storage tissue) to where they are used or stored *(sinks)*. The primary translocation source (leaves) is located above the primary sink (root). However, the movement of organic solutes is not unidirectional or fixed.

During vegetative growth, assimilates are distributed from leaves to growing parts in upward and downward directions. However, when the plant enters the reproductive phase of growth, developing fruits require large amounts of assimilates and hence there is redistribution so that most of the flow from neighboring sources and even from distant ones are redirected to the fruits. Movement in the assimilate stream occurs via the phloem vessels as *sap*, a fluid consisting mainly of sugar and nitrogenous substances (Figure 5–11).

Phloem transport is believed to occur by the mechanism of *pressure flow.* This hypothesis suggests that assimilates are moved from translocation sources to sinks along a gradient of hydrostatic pressure (turgor pressure) of osmotic origin. Sugar is asserted to be transported in the phloem from adjacent cells in the leaf by an energy-dependent active process called *phloem loading.* The effect of this process is a decrease in water potential in the phloem sieve tube, which in turn causes water entering the leaf in the transportation stream to move into the sieve tube under osmotic pressure. The water then acts as a vehicle for the passive transport of the sugars to sinks, where they are unloaded, or removed, for use or storage. The water is recirculated in the transpiration stream because of the increased water potential or the sink resulting from the phloem unloading.

5.4 DEVELOPMENTAL STAGES OF GROWTH

A growing plant seedling goes through a number of developmental changes:

embryonic → juvenile → transitional → maturity → senescence

5.4.1 EMBRYONIC STAGE

The seed consists of an embryo or miniature plant. Until the conditions for germination are right, the embryo remains dormant. *Seed dormancy* is said to occur when a viable seed fails to germinate under favorable environmental conditions. This biological mechanism is especially advantageous when plants are growing in the wild. It ensures that seeds will germinate only when adequate moisture and other necessary environmental

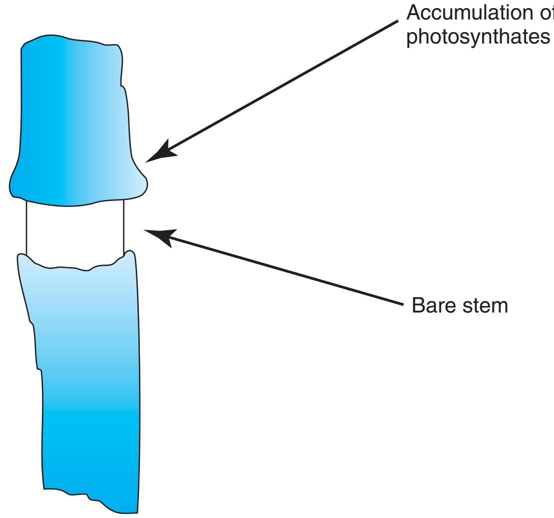


FIGURE 5–11 Accumulation of carbohydrates and sugars above the position of girdling or stem that interrupts the continuity of the phloem.

conditions exist to sustain growth after germination. The condition may be physical (*physical* **dormancy**) or physiological *(physiological dormancy)* in origin. A frequent source of physical dormancy is the presence of an impervious seed coat that does not permit water imbibition for germination. In modern cultivation, such seeds may be mechanically scratched (a process called scarification) to make the seed coat permeable to water. Persistence of seed dormancy may cause undesirable delay in germination, resulting in nonuniform seed germination and consequently an incomplete stand and irregular maturity in the field that leads to unnecessary delays in harvesting. Leguminous species are most plagued by mechanical seed dormancy because of an impervious seed coat.

Dormancy
The failure of seeds, bulbs, buds, or tubers to grow due to internal factors or unfavorable environment.

Dormancy may be caused by physiological causes stemming from chemicals in various parts of the seed or the fruit that inhibit germination. Certain desert species require a good soaking rain in order to leach away a germination inhibitor before seeds will germinate. Consequently, adequate moisture is ensured for the young seedlings to become established and be able to fend for themselves before a dry spell occurs. Seeds seldom germinate while they are in the fruit. However, once excised and washed, the mature seeds promptly germinate. In tomato, the chemical *coumarin* is implicated in this inhibitory condition. Abscisic acid is another chemical known to impose seed dormancy in plants.

In some species, seed maturity lags behind fruit ripening. In the American holly *(Ilex opaca),* an *after-ripening* process is required to bring the embryo in the seed to maturity, without which it will not be able to germinate. Seed dormancy in certain situations can be broken through a cold temperature treatment (*cold* **stratification**). In these species, seeds germinate after a brief storage at temperatures above freezing (e.g., 5°C [41°F]).

Stratification
The practice of exposing imbibed seed usually to cold temperatures for a period of time prior to germination in order to break dormancy.

Buds can also become dormant under certain environmental conditions. *Bud dormancy* is a period of quiescence during which growth is temporarily suspended. Bermuda grass becomes dormant and changes color to a dull brown with the onset of cold temperature. It resumes active growth in spring. Both flower and vegetative buds may experience dormancy. Buds on the same plant have different dormancy characteristics. Just as seed dormancy protects seeds from damage due to adverse weather, woody plants in temperate climates are protected by internally imposed dormancy. Such dormancy ensures that new growth does not occur until the danger of damage from adverse temperatures is minimized. However, the requirements for breaking dormancy vary between the two structures (vegetative and reproductive). In plants such as peach and cherry, the period of cold treatment required to break dormancy is shorter for flower buds than for vegetative buds. If a peach cultivar with a long *low chill requirement* is grown, insufficient chilling can cause some fruiting to occur in the absence of vegetative growth.

5.4.2 JUVENILE STAGE

Juvenility starts after germination and is the stage during which the plant undergoes vegetative growth without any reproductive activities. The period of juvenility is variable among species, being several weeks in some and several years in others. Certain species display telltale characteristics of this stage. For example, in the English ivy *(Hedera helix),* immature (juvenile) plants trail or climb and have three to five deeply lobed palmate alternative leaves. When mature, the plants produce upright shoots with nonlobed ovate opposite leaves. In fruit trees, juvenile branches appear on older ones as vertical shoots (Figure 5–12). These shoots, called *suckers,* or **water sprouts,** may occur at the base of mature tree trunks. Another trait of juvenility is the retention of leaves or juvenile plant parts through the winter, as occurs in oak trees. In *Acacia melnoxylon,* juvenile leaves have compound bipinnate forms, but mature plants have simple leaves.

Water Sprouts
A vigorous and vertical-growing shoot produced on the trunk or branches of a tree.

5.4.3 TRANSITIONAL STAGE

The stage of transition occurs between juvenility and maturity. Plants at this stage may display characteristic features of both stages simultaneously. In the transitional stage, mature plants may revert to juvenility with changes in the environment.

FIGURE 5–12 Water sprouts emerging from the side of an established tree. *(Source: Peter Anderson © Dorling Kindersley)*

5.4.4 MATURITY OR REPRODUCTIVE STAGE

The stage of maturity is characterized by reproductive activities (flowering and fruiting). As mentioned previously, plants such as English ivy have a specific adult (or mature) leaf form that is different from the juvenile form. It should be mentioned that the attainment of maturity does not mean activities (such as flowering) occur automatically. The appropriate conditions for flowering and fruiting must prevail for such activities to take place. Though the plant in this phase is relatively stable, the application of growth regulators can induce juvenility in mature tissue. Other activities in mature plants are aging and senescence.

Physiological Maturity
The stage of development at which a plant or, in grain crops, the seed reaches maximum dry weight.

Physiological maturity is the stage at which the plant has attained maximum dry weight. At this stage, it will not benefit from additional growth inputs. To realize the potential yield of a crop that has been well cultivated, it should be harvested at the right time, using the appropriate methods, and then stored under optimal conditions. Since some horticultural crop products are highly perishable (such as fresh fruits, vegetables, and cut flowers), if they are to be harvested for sale at a distant location from the farm, temporary storage is a critical consideration. If crops are not harvested at the right time, their quality may not be acceptable to consumers. A fresh produce may be too fibrous or not succulent enough or it may taste bitter if not harvested at the proper time. In some crops, such as green beans, consumers prefer a tender product and hence growers harvest beans before they are fully mature.

5.5 Phases in the Plant Life Cycle

The pattern of growth takes a flowering plant through two distinct phases in its life cycle: (1) *vegetative growth* and (2) *reproductive growth.* Plants do not grow continuously but have periods in which they are dormant or in a resting phase.

5.5.1 VEGETATIVE PLANT GROWTH AND DEVELOPMENT

The vegetative phase of growth is characterized by an increase in the number and size of leaves, branches, and other characteristics of the shoot. Shoot growth follows certain patterns that may be used as a basis for classifying plants.

Shoot Elongation

In certain plants, most shoot elongation ceases after a period of time, and the terminal part is capped by a flower bud or a cluster of flower buds. Plants with this habit of growth are said to be **determinate.** These plants are also described as bush types and are usually able to stand erect in cultivation. They flower and set seed within a limited period. The pods mature and can all be harvested at the same time. In other plant types, shoot elongation continues indefinitely, such that flower buds arise laterally on the stem and continue to do so for as long as the shoot elongates. Plants with this growth habit are said to be *indeterminate.* Mature pods and flowers occur simultaneously on such plants. Trees behave in this way, as do vines. Some indeterminate vegetables require support (staking) in cultivation. Certain species have growth habits between these two extremes. Breeders sometimes breed for bush or erect plant types in certain crops to adapt them for mechanized culture.

Determinate
The concept of restricted potential whereby a plant or organ has a genetically limited size and cannot grow indefinitely.

Duration of Plant Life

A complete life cycle in flowering plants is the period it takes from seed to seed (i.e., germination to seed maturity). On the basis of life cycle, there are four classes of flowering plants. These classes are discussed in detail in Chapter 2.

1. *Annuals.* Annual plants complete their life cycles in one growing season. They are herbaceous and have no dormancy during the growing season (the dormant stage being the seed). Garden crops are mostly annuals, and so are many bedding plants (e.g., lettuce and petunia). Climatic factors may cause species such as impatiens and tomato to behave like annuals, although they are not true annuals.
2. *Biennials.* Biennial is a less common plant growth pattern found in plants such as evening primrose (*Primula* spp.), sugar beet, carrot, cabbage, and celery *(Apium graveolens).* These herbaceous plants complete their life cycles in two growing seasons. They grow vegetatively in the first season, remain dormant through the winter months, resume active vegetative and reproductive activities in the second season, and finally die. Plants such as carrot and sugar beet are grown for their roots (the storage organs), which are harvested at the end of the first growing season. These plants are often grown as annuals.
3. *Perennials.* Perennial plants live for more than two seasons and may be herbaceous or woody. In climatic zones where frost occurs, herbaceous perennials may lose their vegetative shoots, leaving only the underground structures to go through the winter. Woody perennials, on the other hand, maintain both above- and belowground parts indefinitely. In flowering perennials, the flowering cycles are repeated over and over, year after year. Examples include rhubarb, asparagus, bulbs, tomato, eggplant, fruit trees, and ornamental trees and shrubs. As indicated previously, tomato and eggplant are frequently cultivated as annuals in temperate zones.
4. *Monocarp.* Monocarpic plants are a kind of perennial in the sense that they live for many years. However, they flower only once in a lifetime, after which they die. An example is the century plant.

5.5.2 REPRODUCTIVE GROWTH AND DEVELOPMENT

Reproductive activities occur in phases.

Flower Induction

Most agricultural plants are self-inductive for flowering. However, some need a cold temperature treatment to overcome the resting period, or dormancy. The chemical reaction of flower induction is the first indication that the plant has attained maturity. In certain species, the process is known to be dependent on environmental factors, the most common being temperature and light.

Vernalization
A cold temperature treatment required by certain species in order to induce flowering.

Vernalization **Vernalization** is the cold temperature induction of flowering required in a wide variety of plants. The necessary degree of coldness and duration of exposure to induce flowering vary from species to species, but the required temperature is usually between 0 and 10°C (32 and 50°F). Although some plants such as sugar beet and kohlrabi can be cold sensitized as seed, most plants respond to the cold treatment after attaining a certain amount of vegetative growth. Some plants that need it are not treated because they are cultivated not for flower or seed but for other parts such as roots (in carrot and sugar beet), buds (brussels sprout), stems (celery), and leaves (cabbage). Apple, cherry, and pear *(Pyrus communis)* require vernalization, as do winter annuals such as wheat, barley, oat, and rye. Flowers such as foxglove (*Digitalis* spp.), tulip, crocus (*Crocus* spp.), narcissus (*Narcissus* spp.), and hyacinth (*Hyacinthus* spp.) need cold treatment, which may be administered to the bulbs, making them flower in warmer climates (at least for that growing season). However, they must be vernalized again to flower in subsequent years. In some of these bulbs, the cold treatment is needed to promote flower development after induction but not for induction itself. Sometimes vernalization helps plants such as pea and spinach to flower early, but it is not a requirement for flowering.

In onion, the bulbs are the commercial products harvested. Cold storage (near freezing) is used to preserve onion sets during the winter. This condition vernalizes the sets, which will flower and produce seed if planted in the spring. To obtain bulbs (no flowering), the sets should not be vernalized. Fortunately for growers, a phenomenon of *devernalization* occurs, in which exposure to warm temperatures above 27°C (80°F) for two to three weeks before planting will reverse the effect of vernalization. Onion producers are therefore able to store their sets and devernalize them for bulb production during the planting season.

Flowering in certain species is affected by a phenomenon called *thermal periodicity,* in which the degree of flowering is affected by alternating warm and cool temperatures during production. For example, tomato plants in the greenhouse can be manipulated for higher productivity by providing a certain cycle of temperature. Plants are exposed to a warm temperature of 27°C (80°F) during the day and cooler night temperatures of about 17 to 20°C (63 to 68°F). This treatment causes increased fruit production over and above what occurs at either temperature alone.

Photoperiodism The effect of *photoperiodism* is discussed in detail in Chapter 4. As explained there, photoperiod is a phenomenon whereby day length controls certain plant processes. Further, it is actually the length of darkness, rather than light, that controls flowering, making the terminology a misnomer. Plants such as *Xanthium* require only one long-night (short-day) treatment to induce flowering, whereas others such as poinsettia *(Euphorbia pulcherrima),* chrysanthemum (*Chrysanthemum* spp.), and kalanchoe (*Kalanchoe* spp.) require several days (three to four). Although photoperiodism and vernalization both influence flowering, they seem to do so by different mechanisms and are not interchangeable. That is, a plant that needs both treatments will not flower if only one is provided.

Other Factors Apart from duration of light, its intensity also affects flowering. Under the controlled environment of a greenhouse, light is provided in adequate amounts regarding intensity and duration. When potted flowering plants are purchased for the home, flowering may be poor or lacking because of the low light intensity in most homes. Flowering has been known to be stimulated under conditions of stress from drought or crowding. On the other hand, excessive moisture during the period of flower initiation in philodendrons causes a disproportionate number of seeds to be vegetative. Generally, woody plants tend to flower more copiously in spring if the preceding summer and fall were dry than if these seasons were wet.

Flower Initiation and Development

After being appropriately induced to flower, flowers are initiated from vegetative meristems that change into flowering meristems. This change is an irreversible process. The meristems differentiate into the flower parts. Proper temperature conditions are required for success, since high temperatures can cause flower abortion. The duration of the developmental process varies from one species to another. Time of flower initiation is important in horticulture. Flower primordia are laid down for a few to many months before flowering in many perennial species. For example, in the crocus, flowers in spring are produced from buds initiated in the previous summer. Flower primordia are initiated under a short photoperiod of August to September in plants such as June-bearing cultivars of strawberry.

Flowers can be chemically induced by externally applying certain growth regulators such as auxins. Commercial production of certain crops such as pineapple is aided by artificial flower induction. Other growth regulators are used to control the number of flowers set on a plant.

Pollination

Pollination is the transfer of pollen grains (male gametes) from the anther to the stigma of the flower. If the pollen deposited is from the anther of the recipient flower, or from another flower on the same plant, the pollination process is called *self-pollination*. Nut trees are mostly self-pollinated. Sometimes pollen from different sources is transferred to a flower, as is the case in most fruit trees. This type of pollination mechanism is called *cross-pollination*. Some species may be self-pollinated but have a fair capacity for outcrossing. When different cultivars are planted close together, there is a good chance for outcrossing. Wind and insects are agents of cross-pollination. Wind is particularly important for pollinating plants with tiny flowers such as grasses. Many fruit crops and vegetables are pollinated by insects that are attracted to the bright colors and nectaries of the flowers. In commercial production, growers of certain crops (such as orchard crops and strawberry) deliberately introduce hives of domestically raised bees to aid pollination for a good harvest. Without pollination, flowers will drop off, thus reducing crop yield.

Flowers that are specifically adapted to pollination by bees, wasps, and flies have showy and brightly colored petals. These flowers are usually blue or yellow in color. The nectary is located at the base of the corolla tube and has special structures that provide for convenient landing by bees. Bee flowers include rosemary (*Rosemary officinalis*), larkspur, lupines, cactus (*Echinocereus*), foxglove (*Digitalis purpurea*), California poppy (*Eschscholzia californica*), and orchids of the genus *Ophys.*

Flowers specifically adapted to pollination by moths and butterflies are typically white or pale in color so that they are visible to nocturnal moths. These flowers also have strong fragrance and a sweet, penetrating odor that is emitted after sunset. The nectary of such flowers is located at the base of a long and slender corolla tube. Such nectaries can be reached only by the long sucking mouth parts found in moths and butterflies. Examples of flowers associated with moths and butterflies include the yellow-flowered species of evening primrose (*Oenothera*), pink-flowered *Amarylis belladonna,* and tobacco (*Nicotiana* spp.).

Birds are associated with flowers that produce copious, thick nectar and have very colorful petals (especially red and yellow). These flowers are generally odorless. Examples are bird-of-paradise (*Strelitzia reginae*), columbine (*Aquilegia canadensis*), poinsettia (*Euphorbia pulcherima*), banana, fuchsia, passion flower, eucalyptus, and hibiscus.

Bats pollinate certain flowering species. Similar to "bird flowers," "bat flowers" are generally large and strong, with dull colors. Most of these flowers open at night, when nocturnal bats operate. Some flowers hang down on long stalks below the foliage of the plant. Bat flowers have strong fruitlike or musty scents. Examples are banana, mango, and organ-pipe cactus (*Stenocereus thurberi*).

Fertilization

Fertilization is the union of a sperm from the pollen with the egg of the ovary to form a *zygote.* For this union to occur, the pollen must grow rapidly down the style to unite with the egg in the ovary. In some plants, pollen from a flower is unable to fertilize the eggs

Fertilization
The union of two gametes to form a zygote.

of the same flower, a condition called *self-incompatibility.* These plants, of necessity, must then be cross-pollinated. Most fruit trees are self-incompatible (and thus self-sterile), which may be due to the inability of pollen to germinate on the stigma or unsynchronized maturity of male and female parts of the flower such that the pollen is shed after the stigma has ceased to be receptive or before it becomes receptive (*protandry* and *protogyny,* respectively). Some incompatibility mechanisms are genetic in origin. Plants such as date palms and willows are compelled to cross-pollinate because of a condition called *dioecy,* in which plants are either male or female. This condition arises because staminate and carpellate flowers occur on different plants. In monoecious plants such as corn and oak, both staminate and carpellate flowers are found on the same plant. The stigma should be mature and ready physically and chemically in terms of the presence of fluids in the right concentration and nutrient content, especially certain trace elements such as calcium and cobalt, to stimulate pollen germination.

Fruit Formation and Development

Parthenocarpy
The development of fruit in the absence of fertilization.

Fertilization normally precedes fruit formation. However, under certain conditions, the unfertilized egg develops into a fruit, the result being a seedless fruit. This event is called **parthenocarpy**. Since seedlessness is desired in certain fruits, horticulturalists sometimes deliberately apply certain growth regulators to plants to induce parthenocarpic fruits. In tomato, high temperatures have been known to induce seedlessness. Seeds appear to play a significant role in the growth and development of certain fruits. As such, if the embryo dies or pollination is not complete, some eggs will not be fertilized. Fruits formed as a result of this event are malformed, as is observed in cucumber and apple. In the case of stone fruits (e.g., cherry, peach, and apricot), the death of an embryo results in fruit drop. Each plant has an optimal number of fruits it can support in relation to vegetative matter (leaves). In commercial production, growers of orchard crops undertake what is called *fruit thinning,* whereby the number of fruits set is reduced artificially. Fruit set is adversely affected by improper temperature (high or low), low light intensity, and inadequate moisture and nutrition. As fruits develop, they enlarge and become filled with soluble solids.

Fruit Ripening

There are two basic patterns of fruit ripening—*nonclimacteric* and *climacteric.* Nonclimateric fruit ripening patterns occur in species in which fruits ripen only when they are attached to the parent plant (i.e., vine-ripen only). In these plants, (e.g., cherry, grape, cucumber) it is imperative that fruits are harvested only vine- or tree-ripened for the highest taste and flavor. The process of maturation and ripening is a gradual process that tapers off. Respiration rate in fruits occurs at a gradual rate. On the other hand, climateric fruit ripening is characterized by a rapid rise in respiration rate at the onset of ripening (called respiratory climacteric), followed by a gradual rate as ripening progresses. The fruits of such species (e.g., apple, banana, tomato) can be harvested prematurely and forced to ripen in the warehouse or allowed to vine- or tree-ripen.

Fruit ripening starts after enlargement ceases. The results of ripening are usually a change in color from the breakdown of chlorophyll to reveal other pigments, softening of the fruits (caused by breakdown of pectic substances that strengthen cell walls), and change in flavor (sour to sweet) (Figure 5–13). Ripening is a physiological event that signifies the end of fruit maturation and the onset of senescence. This event is associated with a sudden and marked increase in the rate of respiration of a fruit and the concomitant evolution of carbon dioxide. Levels of enzymes such as hydrolases, synthetases, and oxidases increase. Color change of the fruit exocarp is one event that is visible to the grower in many crops. The color change depends on the crop and cultivar. In banana, raw (unripe) fruit is green and while ripening goes through shades of color changes to yellow. The green chlorophyll is broken down to reveal the hitherto masked yellow color of carotenoids. The acceptable degree of ripening depends on the crop, the consumer (or use), and the marketing system. As ripening progresses, fruits become more

FIGURE 5–13 Ripening of plantain shows a gradual change in color from green to yellow. *(Source: George Acquaah)*

susceptible to fungal attack and rot due to the activities of enzymes. Fruits become softer. Ethylene is associated with ripening; it initiates and also accelerates the process.

Ethylene gas can be biosynthesized in the plant from methionine, an amino acid, with the aid of indoleacetic acid (IAA). In fact, high amounts of endogenous IAA can trigger the production of ethylene in large quantities. Wounding of a plant can stimulate the production of ethylene. Ethylene gas is used in the banana production industry to hasten ripening. Bananas are harvested and shipped green from production centers and are induced to ripen at their destination.

By volume, the CO_2 content of the atmosphere is only about 0.035 percent. To reduce the rate of fruit ripening, the carbon dioxide content of the storage room atmosphere is increased to about 2 to 5 percent, and the oxygen percentage is reduced from 20 percent to between 5 and 10 percent. This environment results in a reduced rate of respiration. Respiration rate can also be slowed by reducing the storage room temperature to about 5°C (41°F). Ripening fruits respire at a higher rate.

Senescence

Senescence precedes death, the final stage in the life cycle of a plant. This phase may occur naturally or be accelerated by environmental conditions including pathogenic attack. During senescence, cells and tissues deteriorate. The effect of senescence is physically visible. In this state of decline, yield progressively decreases and the plant becomes weak. The whole plant eventually dies, as in annuals; however, in deciduous perennials, the leaves drop in the fall season and the rest of the plant remains alive.

Senescence is a complex process that is not clearly understood. It occurs in patterns that appear to be associated with the life cycle of plants (annual, biennial, and perennial). In terms of the ultimate end of living organisms, plants may experience *partial senescence* (in which certain plant organs age and eventually die) or *complete senescence* (in which the whole plant ages and eventually dies). In annual plants, death occurs swiftly and suddenly, and senescence is complete. It occurs after maturity in fruits; dramatically, a whole field of annuals can deteriorate and die in concert in a short period. In biennials, the top portions of the plants wither after the first season and the bottom part remains dormant in the winter. Deciduous perennial plants shed their leaves in fall and resume active growth with a new flush of leaves in spring. Whereas senescence in animals is terminal, growers can employ the horticultural method of pruning (Chapter 19) and nutritional supplementation to revitalize an aged plant.

5.6 Plant Hormones

Plant *hormones* are organic molecules produced in small amounts in one (or several) parts of the plant and then transported to other parts called *target sites,* where they regulate plant growth and development (Figure 5–14). Because of this physiological role, plant hormones are also called *plant* **growth regulators,** a broad term that includes and is often associated with synthetic chemicals that have effects similar to hormones. Plant hormones are classified on the basis of their origin, *natural* or *synthetic.* Unlike animal hormones, which have specificity in site of production and target site, plant hormones tend to be more general with respect to both source and target. There are five basic groups of natural plant hormones: auxins, gibberellins, cytokinins, ethylene, and abscisic acid.

Growth Regulator
A natural or synthetic compound that in low concentrations controls growth responses in plants.

5.6.1 AUXINS

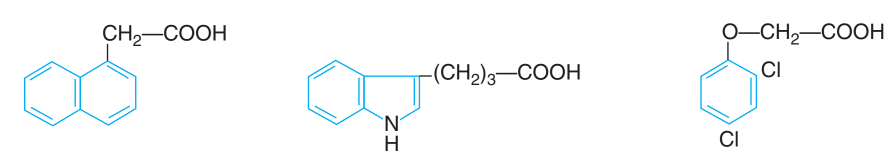
Auxins are produced in meristematic tissue such as root tips, shoot tips, apical buds, young leaves, and flowers. Their major functions include regulation of cell division and expansion, stem elongation, leaf expansion and abscission, fruit development, and branching of the stem. Auxins move very slowly and in a polar (unidirectional) fashion in plants. In shoots, the polarity is *basipetal* (toward the base of the stem and leaves), whereas it is *acropetal* (toward the tip) in roots. Auxin movement is not through defined channels such as sieve tubes (phloem) and vessels (xylem) but through phloem parenchyma cells and those bordering vascular tissues. This hormone is believed to move by an energy-dependent diffusion mechanism. The only known naturally occurring auxin is indole-3-acetic acid (IAA). Synthetic hormones that are auxins include 2,4-dichlorophenoxyacetic acid (2,4-D), which is actually an herbicide for controlling broadleaf weeds such as dandelion in lawns, α-naphthaleneacetic acid (NAA), and indole-3-butyric acid (IBA). Other uses of auxins in horticulture are as follows:

1. As rooting hormones to induce rooting (adventitious) in cuttings, especially when propagating woody plants.
2. To prevent fruit drop (control of abscission) in fruits trees (e.g., citrus) shortly before harvest.
3. To increase blossom and fruit set in tomato.
4. For fruit thinning to reduce excessive fruiting and thus produce larger fruits.
5. For defoliation before harvesting.
6. To prevent sprouting of stored produce, for example, in potato; when applied to certain tree trunks, basal sprouts are suppressed.

The concentration of auxin can be manipulated in horticultural plants in cultivation. Auxins are produced in relatively higher concentrations in the terminal buds than in other parts. This localized high concentration suppresses the growth of lateral buds located below the terminal bud. When terminal buds are removed (e.g., by a horticultural operation such as pruning or pinching), lateral buds are induced to grow because of the abolition of **apical dominance.** This technique makes a plant fuller in shape and more attractive (Figure 5–15). *Phototropism,* the bending of the growing point of a plant toward light, is attributed to the effect of auxins. Light causes auxin to be redistributed from the lit area to the dark side, where it causes cell elongation, leading to curvature (Figure 5–16).

Apical Dominance
The regulatory control of the terminal bud of a shoot in suppressing the development of lateral buds below it.

FIGURE 5–14 Selected synthetic hormones.



α-Naphthaleneacetic acid (NAA)   Indole-3-butyric acid (IBA)   2,4-Dichlorophenoxyacetic acid (2,4-D)

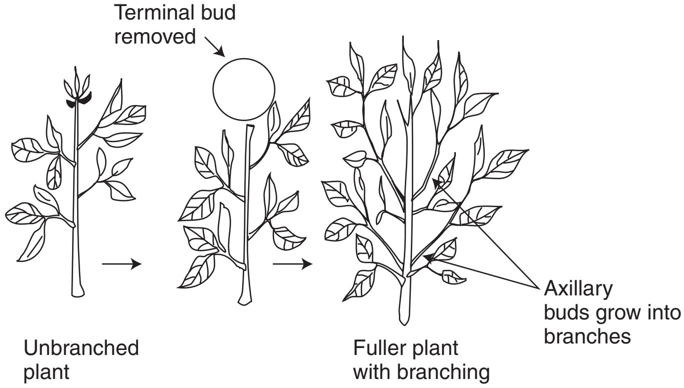


FIGURE 5–15 The effect of abolishing apical dominance in plants.

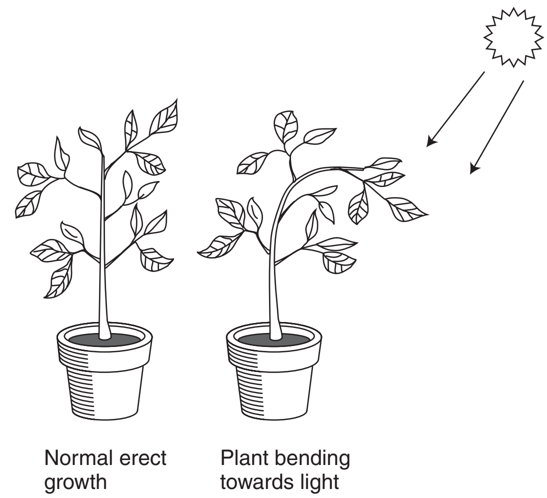


FIGURE 5–16 Phototropism displayed by a plant located near a window.

5.6.2 GIBBERELLINS

Gibberellins are produced in the shoot apex and occur also in embryos and cotyledons of immature seeds and roots. They occur in seed, flowers, germinating seed, and developing flowers. The highest concentration occurs in immature seeds. This class of hormones promotes cell division, stem elongation, seed germination (by breaking dormancy), flowering, and fruit development. In carrot (*Daucus carota*) and cabbage (*Brassica oleracea* var. *Capitata*), among others, exposure to long days or cold is required to induce flowering (*bolting*). Application of gibberellic acid eliminates the need for these environmental treatments. Gibberellins are noted for their ability to overcome dwarfism in plants, allowing compact plants to develop to normal heights. Gibberellic acid is used to induce seedlessness in grapes; the size of seedless grapes is also increased through the application of this hormone. An example is gibberellic acid (GA_1), one of the numerous (more than seventy) closely related terpenoid compounds that occur naturally.

5.6.3 CYTOKININS

Cytokinins are hormones that stimulate cell division and lateral bud development. They have been isolated mainly from actively dividing tissue. Cytokinins occur in embryonic or meristematic organs. Examples of natural cytokinins are isopentenyl adenine (IPA) and zeatin (Z). Zeatin, isolated from the kernels of corn, is the most active naturally occurring cytokinin. Kinetin was first isolated from yeast. Benzyl adenine (BA) is also a commonly used cytokinin. Cytokinins interact with auxins to affect various plant functions. A high cytokinin-auxin ratio (i.e., low amounts of auxin, especially IAA) promotes lateral bud development because of reduced apical dominance. Relatively high amounts of auxin induce root formation in callus. The principal role of cytokinins in plant physiology is the promotion of cell division. They are important in tissue culture work and are more effective when IAA is also added. The effect of cytokinins when used this way is to cause cells to remain meristematic (undifferentiated) in culture, producing large amounts of callus tissue.

5.6.4 ETHYLENE

Ethylene is a gas found in the tissues of ripening fruits and stem nodes. It promotes fruit ripening and leaf abscission. In the horticultural industry, ethylene is used to aid in uniform ripening of apple, pineapple, and banana, and in changing the rind color of fruits (as in orange and grapefruit from green to yellow and tomato from green to uniform red).

On the other hand, ripening apples produce this gas in large quantities, which tends to shorten the storage life of fruits. Storage life can be prolonged by removing the gas with activated charcoal, for example. Ethaphon is used commercially to induce ripening. Ethylene in the growing environment may cause accelerated senescence of flowers and leaf abscission. Commercially, ethylene is used to promote fruit loosening in grape, blueberry, and blackberry to facilitate mechanical harvesting. Carnations close and rosebuds open prematurely in the presence of ethylene. In cucumber and pumpkin, ethaphon spray can increase female flowers (disproportionately) and thereby increase fruit set. Ethylene is also implicated in the regulation of sex expression and promotion of femaleness in cucurbits (cucumber and squash). Male flowers are associated with high gibberellic acid levels but can be changed to females by the application of ethylene.

5.6.5 ABSCISIC ACID

Abscisic acid (ABA) is a natural hormone that acts as an inhibitor of growth, promotes fruit and leaf abscision, counteracts the breaking of dormancy, and causes the stomata of leaves to close under moisture stress. It has an antagonistic relationship with gibberellins and other growth-stimulating hormones; for example, ABA-induced seed dormancy may be reversed by applying gibberellins. Commercial application of ABA is limited partly by its high cost and unavailability.

Plant hormones may also be classified based on their effect on plant growth as *stimulants* or *retardants.* Cytokinins and gibberellins have a stimulating effect on growth and development, whereas ABA inhibits growth. Alfalfa is known to produce the alcohol *triacontanol,* which stimulates growth. Naturally occurring inhibitors include benzoic acid, coumarin, and cinnamic acid. A number of synthetic growth retardants are used in producing certain horticultural plants. Their effect is mainly a slowing down of cell division and elongation. As such, instead of a plant growing tall, with long internodes, it becomes short (dwarf), compact, fuller, and aesthetically more pleasing. Examples of these commercial growth retardants include the following:

1. Daminozide (marketed under trade names such as Alar and B-nine): plants that respond to it include poinsettia, azalea, petunia, and chrysanthemum.
2. Chlormequat (CCC, cycocel): retards plant height in poinsettia, azalea, and geraniums.
3. Ancymidol (A-Rest): effective in reducing height in bulbs, such as Easter lily and tulip, as well as chrysanthemum and poinsettia.
4. Paclobutrazol (Bonzi): used to reduce plant height in bedding plants including impatiens, pansy, petunia, and snapdragon.
5. Maleic hydrazide: used to prevent sprouting of onions and potatoes.

5.7 NONPATHOGENIC (PHYSIOLOGICAL) PLANT DISORDERS

Horticultural plants are plagued by numerous diseases and pests, some of which can completely kill the affected plants. Generally, if a grower observes certain precautions and adopts sound cultural practices, the chance of experiencing a disease problem in plants is reduced drastically. Some diseases are endemic in certain areas. As such, plants that are susceptible to such diseases should not be grown there. If they must be grown in such areas, resistant cultivars should be used; otherwise, disease control measures such as spraying with pesticides will be required for successful production. Other cultural observances such as using high-quality, clean seeds; weed control; right timing of planting; phytosanitation; and preplanting seed treatment will minimize the occurrence of diseases in a production enterprise.

However, many other disorders are *nonpathogenic* (not caused by pathogens) in origin. They are caused by improper or inadequate plant growth environmental conditions—pertaining to light, moisture, temperature, nutrients, and air—as well as improper cultural operation, involving compaction of soil and pesticide application, for example. Since these disorders are nonpathogenic, their effect is localized and usually within complete control of the grower. Further, since plant production under uncontrolled environmental conditions is subject to the uncertainties of the weather, certain disorders are unpredictable and sometimes difficult to prevent.

This section is devoted to nonpathogenic disorders, many of which are weather related. Chapter 4 contains related information. Plants are not affected equally by adverse weather conditions. An important caution to observe when inspecting plants for disorders is not to hastily attribute every disorder to parasitic or pathogenic causes and exercise caution before initiating pest-control measures.

5.7.1 WEATHER-RELATED PLANT DISORDERS

The following are different categories of weather factors and how they inflict damage on horticultural plants when they prevail in adverse levels. It should be emphasized that these factors often interact or interplay in producing an effect. The role of these factors in plant growth has been discussed previously.

Temperature

Extreme Cold Plants in temperate zones may suffer one of two kinds of injury from extremely cold temperatures. Similar to frostbite in humans, plants may suffer from *frost damage* when temperatures suddenly drop below seasonable levels. Affected plants may show signs of wilting overnight. When this cold strikes during the blooming period, the plant may lose most or all of its flowers. Frost damage occurs more frequently in younger tissues, and herbaceous species are more susceptible than woody ones.

A much more severe cold damage called *winter kill* occurs when plants are subjected to prolonged periods of freezing temperatures. Under such conditions, branches may die back (tips wilt); when roots are severely impaired, however, the plant may die. In evergreens, such as pine, extreme cold may cause the foliage to "burn" (turn brown).

Extreme Heat Microclimates, both natural and human-made, occur in the landscape in places such as underneath trees and the eaves of homes. Brick structures absorb heat during the day and radiate it at night. This property is advantageous during the cold months, because radiated heat protects plants in the vicinity from frost. However, in hot months, these same walls, especially those that face south, can create extremely hot microclimates, thereby injuring plants within their spheres of influence. Similarly, the hot asphalt of parking lots, concrete, and some pavements can radiate intense heat that damages plants. Heat-sensitive plants may show marginal scorching of leaves.

Moisture

Excess Moisture Excess moisture overwhelms the pore spaces in the soil leading to waterlogged conditions. Poorly drained soils create anaerobic conditions that lead to root death (root rot), if they persist for an extended period. Plants vary in their response to poor drainage. Root rot eventually results in plant death through stages, starting with stunted growth and yellowing and wilting. Excess moisture received after a period of drought might cause tubers and roots of root crops, as well as the walls of fruits such as tomato, to crack.

Excess Dryness (Drought) Lack of moisture usually is expressed as wilting of plant leaves.

Low Humidity The tips and margins of leaves of tropical plants brown (tip burn) under conditions of low humidity. This browning is caused by rapid transpiration, which overwhelms the rate at which water is moved through the leaf to the ends. As a result, water fails to reach the edges of the leaf, leading to drying and browning.

Light

Intense Light Strong and direct sunlight may scorch certain plants. Potted plants placed in south-facing windows receive direct sunlight unless the presence of a tree in the direction of the sun's rays filters the light. Intense light also causes the foliage of certain plants to bleach and look pale and sickly.

Low Light Inadequate sunlight induces etiolated growth (spindly) and yellowing of leaves. Plant vigor is reduced, and leaves drop prematurely.

Nutrients

Nutrient Deficiency Generally, an inadequate supply of any of the major plant nutrients, especially nitrogen, causes plants to be stunted in growth and leaves to yellow (chlorosis). Deciduous plant leaves may prematurely senesce and defoliate. In addition to yellowing, lack of potassium shows up later as marginal leaf burns of leaves; young and expanding leaves show purple discoloration when phosphorus is lacking in the soil. Calcium deficiency in tomato shows up as *blossom end rot.*

Nutrient Excess Excess acidic soils may cause excess availability of trace elements (e.g., iron and aluminum), which can lead to toxicity in certain plants.

5.7.2 HUMAN-RELATED ACTIVITIES

Industrial Production

Industrialized and heavily populated areas often experience excessive amounts of chemical pollutants in the air. These toxic gases damage horticultural plants. Acute amounts of sulfur dioxide cause chlorosis and browning of leaves and sometimes necrosis (cell destruction and death). Fluoride injury has been recorded in sensitive plants such as ponderosa pine as reddish-brown bands that appear between necrotic and green tissue. Ozone is a major pollutant that is produced primarily from the photochemical action of sunlight on automobile emission. It can cause chlorosis and necrosis in a wide variety of plants.

Pesticide Application

Improper application of pesticides may cause collateral damage to cultivated plants. Applying sprays on a windy day may cause the chemicals to drift onto desirable plants, resulting in deformed leaves, discoloration, and in some cases death of tissue and possibly the entire plant. Herbicide damage appears suddenly and may last through the cropping season. Often, the symptom is bleaching; in severe cases, it may be followed by leaf drop. Unlike the effect of herbicides, collateral damage from insecticides shows up as browning of the foliage.

Fertilizer Application

Chemical fertilizers are frequently applied to houseplants or outdoor plants in production. Eagerness for good yield may lead some growers to overfertilize their plants, resulting in a buildup of excessive fertilizer in the soil. High amounts of salts create *sodic* soil conditions. A higher salt-soil concentration than root fluids can cause dehydration of roots. Instead of the roots absorbing soil moisture, they become depleted of moisture. Plant growth is inhibited under such conditions, and plants wilt (as they would under drought conditions) and eventually die.

SUMMARY

The variety of activities that have been described to occur at various phases in plant growth and development are the results of certain growth processes. These processes provide the raw materials and the energy required for building new tissues and nurturing them to maturity. The major processes include photosynthesis, respiration, transpiration, and translocation. Photosynthesis is the process by which green plants manufacture food from water and nutrients absorbed from the soil and light energy. Photosynthates are translocated to other parts of the plant where, through the process of respiration, the energy locked up in the food is released for use by the plants. Gaseous exchange between the plant and its environment occurs through pores in the leaves called stomata. Plants lose moisture by the process of transpiration. Plant development and growth occur in phases described by a sigmoid curve—a rapid logarithmic growth phase, followed by a decreasing growth phase, and then a steady growth phase. Plants have two general phases in their life cycles—a vegetative phase and a reproductive phase. Based on the duration of the life cycle, plants can be categorized into annuals, biennials, perennials, and monocarps. In flowering plants, a reproductive phase follows a vegetative phase. Flowers are produced and eventually become pollinated and fertilized to produce seed and fruit. When plants are subject to adverse conditions in the environment, they develop a variety of physiological disorders such as wilting, drying, cracking, and abnormal growth.

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Photosynthesis
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Practical Experience

1. *Translocation.* Obtain a young tree (about a year old) and girdle the midsection by carefully removing the bark and making sure to scrape away the phloem layer completely. Maintain the plant under proper growth conditions in which it will be able to photosynthesize adequately. After some time, the upper edge of the girdle should begin to swell from accumulation of photosynthates being translocated down to other parts of the plant from the leaf.
2. *Growth regulators.* Cytokinins and gibberellins stimulate plant growth, and abscisic acid is an inhibitor. Commercial growth regulators are available. Plant geraniums in pots and divide the pots into two groups, each containing plants of equal size. To one set apply a growth regulator (e.g., Cycocel) and leave the other as a control. You may also apply various concentrations of the hormone. Observe the changes in growth after a period by comparing hormone-treated plants with controls.

3. *Apical dominance (pinching).* Obtain young poinsettia plants. Pinch off the apical buds in some plants and leave others unpinched. After a period, observe the changes in the plants' branching.
4. *Fruit ripening.* Obtain two bunches of green bananas. Place one bunch in the open air in the laboratory and tie up another bunch in an airtight plastic bag. The latter will trap the ethylene gas in the bag and accelerate ripening.

OUTCOMES ASSESSMENT

1. Discuss how a horticulturalist may apply the sigmoid growth curve in managing crop production.
2. What crop production management practices may be adopted to optimize photosynthesis?
3. Distinguish between, giving examples plants that use the C_3 and C_4 carbon dioxide fixation in food manufacture.
4. Discuss the roles and importance of aerobic respiration and anaerobic respiration in plant growth and development.
5. Define the following terms, giving their importance in horticultural industry:
   - **a.** Physiological dormancy
   - **b.** Physiological maturity
   - **c.** Vernalization
   - **d.** Transpiration
6. Discuss the occurrence of physiological plant disorders in crop production and their economic importance.
7. Discuss the physiological role of ethylene in plant growth and development, and its application in the horticultural industry.
8. Describe the characteristic features of the embryonic stage of plant development, pointing out how they impact management of plant production.