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PLANT SCIENCE

GROWTH, DEVELOPMENT, AND UTILIZATION OF CULTIVATED PLANTS

FIFTH EDITION

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Preface

Enter the fascinating and colorful world of plant science through the fifth edition of *Plant Science,* now in color. Discover why we depend on plants and the people who know how to grow them for our survival.

Find out how plants provide sustenance for our bodies and add enjoyment to our lives (food for body and soul). Learn how to grow, maintain, and utilize plants to benefit people and the environment. Whether your interests range from running the family farm to managing a tournament golf course, or directing an international business, rewarding, challenging, and fulfilling careers are open to anyone skilled in plant science.

Human survival absolutely depends on the ability of plants to capture solar energy and convert that energy to a form that can be used as food. The captured energy stored in plant tissues also provides fiber and oil for fuel, clothing, and shelter.

The production of plants that meet our needs for survival is an important application of the knowledge of plant science; however, the essentials for nutrition and shelter can be provided by relatively few plant species. Life would be boring, though, if those few were the only species produced for our needs.

Plants have tremendous economic impact in developed and developing nations. The career opportunities created by the need for people with an understanding of plant growth are unlimited. *Plant Science* is written for anyone with an interest in how plants are grown and utilized for maintaining and adding enjoyment to human life as well as improving and protecting the environment.

The beginning chapters of the text provide the fundamentals of environmental factors, botany, and plant physiology that affect plant growth. The later chapters integrate the aforementioned topics into strategies for producing plants for food, fiber, recreation, and environmental stewardship.

The fifth edition of *Plant Science* has been updated to include the most recent statistics, production methods, and issues concerning the production and utilization of plants. This revision has been reorganized to present the topics in a more logical order and to reflect the changing information needs of those who grow plants for a living.

New information has been added, and out dated information has been deleted. Some information retained from the previous edition has been moved to a different chapter. For example, the climate chapters have been combined into one chapter.

The information on managing soil, water, and nutrients has been combined into one chapter because of the interdependence of these topics. A new chapter in this edition gives an overview of general production and postharvest handling and marketing procedures. It precedes the individual commodity chapters.

BRIEF CONTENTS

*1

History, Trends, Issues, and Challenges in Plant Science

MICHAEL KNEE AND MARGARET MCMAHON

HISTORY

As citizens of the twenty - first century, we tend to pride ourselves on how we have used agriculture to shape the modern world to serve and please us. We have reason to feel that way - our agricultural practices have changed the world. But if we were to use H. G. Wells' time machine to transport us back 150 million years, we would see many plants very similar to those common in our century. We would see some of the same trees that grow in our world, along with other members of the angiosperms, the group of plants to which grasses, flowers, vegetables, fruits, trees, and shrubs belong.

We would also see many plants that no longer exist. Some dinosaurs would be feeding on these plants. As time progresses, the dinosaurs would disap- pear and other animals would appear and evolve, and some would die out.

Plant life would change, some as a result of changes in climate, and become most of the plants we know today. During this time, humans had no influence on changes in life forms that occurred or disappeared.

Humans as a race appeared around 3 million years ago and modern man, Homo sapiens, appeared about 28,000 years ago. For thousands of years, H. sapiens existed without doing much to change how plants grew. As hunters and gatherers, the nomadic tribes followed herds of animals and gathered plant materials along the way. The plants they probably gathered would have been some of the same nuts, grains, and fruits we eat today. Other plants known today would have also provided shelter.

Then something happened around 12,000 to 10,000 years ago (perhaps earlier according to reent archaeological finds) that had a dramatic impact not only on human lifestyle, but the entire global ecosystem.

Humans began the purposeful growing or cultivation of plants to improve the supply of materials obtained from these plants. The science f understanding the cultivation of plants, plant science, was born. Plant cultivation is believed to have started in tropical and subtropical regions in the Middle East and Africa.

By cultivating plants, humans reduced the need to travel to follow the food supply. Those who did the traveling became traders more than gatherers.

TRENDS AND ISSUES AFFECTING PLANT SCIENCE

Background

Traditionally crops are commodities that are exchanged for money in the marketplace. In the case of recreation areas such as golf courses, the use of that field is exchanged for money. According to classical economics, the price of commodities (or user fees) results from the balance between the supply of commodities (recreational areas) and the demand for them. The supply should be influenced by the availability of the resources and raw materials required for production, and the demand should be influenced by the value that consumers perceive in the commodity.

Many people have drawn attention to the mismatch between ecological and money values. If excess fertilizer from a crop pollutes a river, the cost of cleaning up the pollution will not be reflected in the price of the commodity. On the other hand, many people may enjoy seeing an ornamental tree planted by someone else, and it can also help to absorb the carbon dioxide (CO_2) produced by cars, but those benefits seem “free.” Economists call costs and benefits that are not included in the price externalities. Some argue that environmental degradation occurs when no one owns a resource. If land is under common ownership, it will be over-cropped or overgrazed because it is in no one’s interest to conserve the resource. Thus, they refer to the general problem of the tragedy of the commons. According to this view, if everything is privately owned, individuals have an interest in its preservation, those who use resources have to pay the owners, and the value of the resources is reflected in the price of the commodity.

Classical economics assumes that buyers and sellers are fully informed of the value of commodities in the market and make wise decisions that maximize their welfare. However, many people make unwise choices on both sides of the market relationship. In the 1930s, farmers in the American Southwest contributed to soil erosion on their own farms through their crop management practices. The market for tobacco products remains strong after fifty years of health warnings. Individuals may not know all of the consequences of their decisions, and it may take the input from many people to arrive at a full accounting. The tragedy of the commons is not always the case; people are capable of making communal decisions to conserve resources that do not belong to any individual. The soil conservation service was born out of the dust bowl experience. Plant science research and education grew out of a perception of a wider public good to be obtained by applying scientific principles to food production. Now, as you will learn in this book, we need to go beyond production to look at ecological consequences and the consequences for the individuals who consume the produce.

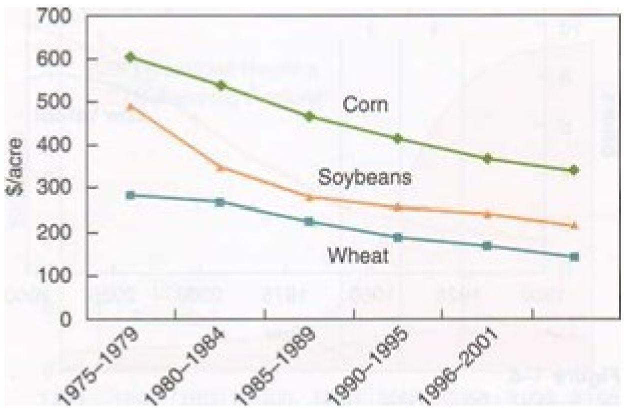


Figure 1-2

Income per acre from selected crops over the past twenty-five years, corrected for inflation by estimating on the basis of 2001 dollar value. Source: Michael Knee.

The payments are supposed to help farms stay in business but end up as one more factor encouraging consolidation in the industry: large farms get more government assistance than small farms do. The number of farms decreased as individual hold-ings got larger in the second half of the century.

Figure 1-3

Number of farms and farm workers during the last century (1910—2000). Source: USDA National Agricultural Statistics Service Information (NASS)

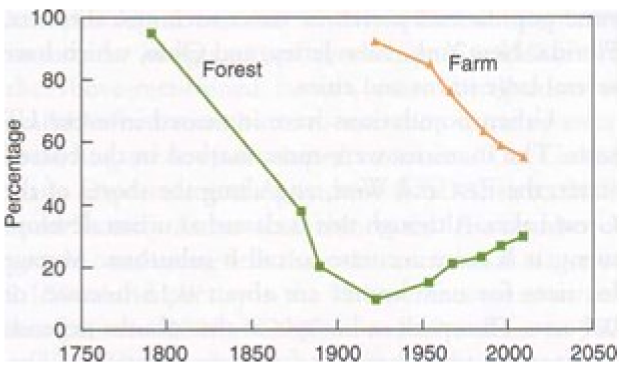


Figure 1-4

Percentage of forested land and farm area in Ohio since European settlement. Source: Michael Knee.

Figure 1-5

Woodland developing on land in Ohio that has not been farmed for 30 years. Source: Margaret McMahon, The Ohio State University.

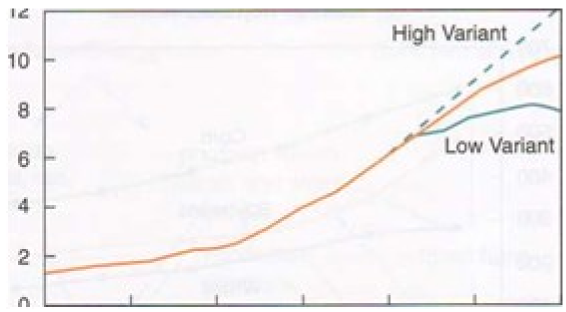
The number of farm workers also continued its long-term decline so that there is now a little more than one full-time worker for each farm. The numbers of farms and farm workers seem to have stabilized toward the end of the century, and these numbers may be minimum sustainable values (Fig. 1-3). Most farms are run as part-time businesses, and about 10 percent of the farms remaining in the United States account for 70 percent of production. The profitability of farming has been helped to some extent by diversifying the uses of staple crops (e.g., ethanol and syrup from corn and tofu

from soybeans) and by adopting alternative crops. The area of farmland has also declined from its high point at the beginning of the twentieth century. In contrast to many other countries, the United States has seen an overall increase in the area of woodland (Fig. 1-4). Some of the increase comes from the conversion and/or reversion of farmland to woodland (Fig. 1-5).

The increase in US population during the last century was mainly in urban areas so that rural population decreased in relative terms from 60 percent in 1900 to 25 percent in 2000. In the upper Midwest, the rural population fell in absolute terms from the middle of the century. This decline was associated with a loss of economic and cultural vitality in rural communities. Such communities were more likely to survive if there were large towns that provided an economic stimulus to the surrounding areas. This may be the reason why rural populations persist in states such as California, Florida, New York, New Jersey, and Ohio, which have several large towns and cities.

Urban populations have increased in every US state. The increases were most marked in the coastal states, the East and West, and along the shores of the Great Lakes. Although this is classed as urban development, it is more accurate to call it suburban. Average lot sizes for new homes are about 0.15 hectare, or 0.4 acre. The spacious lifestyle of the suburbs depends on personal transportation for access to work, shops, and leisure, which accounts for much of our energy demand. Many people have criticized this and other aspects of suburban sprawl, but it leads to new oppor-tunities. The new homes are an expanding market for landscape supplies and services. Surviving farms can market directly to the surrounding population. Families can enjoy a visit to the local farm to buy or pick their own produce. This interaction may help maintain contact and understanding between the mass of the population and the few remaining farmers.

The aesthetic and recreational use of plants is important in urban and suburban areas. The appearance and playability of fields is vitally important to many sports. Golf alone is now equivalent to about two-thirds of major crop sales and involves 12 percent of the US population. The number of golf courses has increased over threefold in the past fifty years.



1900 1925 1950 1975 2000 2025 2050 Year

Figure 1-6

Projections of world population growth. Source: US Global Change Research Program, USGRCP Seminars, http://www.usgcrp.gov/usgcrp/seminars/

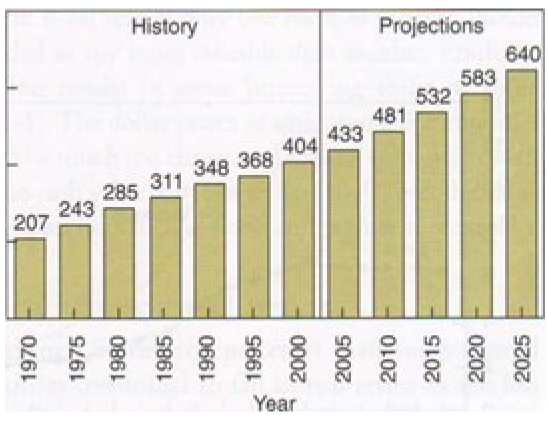


Figure 1-7

History and projection of world energy consumption,

1970—2025. *Sources:* ***History:*** *Energy Information Administration (EIA), International Energy Annual 2001 DOE/EIA-O219 (2001) (Washington, DC: February 2003), www.eia.doe.gov/iea/.* ***Projections:*** *EIA, System for the Analysis of Global Energy Markets (2003).*

MEETING THE CHALLENGES IN PLANT SCIENCE

Many of the changes in the issues of crops and their role in the world have prompted plant scientists to change the focus of their research. For several centuries, plant scientists studied ways to improve crop productivity in a cost-effective way. They studied light, soil, water, and temperature and developed ways of managing or monitoring those factors to influence or predict plant growth. Improved understanding of plant genetics lead to breeders developing plants that would produce more reliably. A scientific approach to pests and their management reduced losses to those factors. Traditional economic analysis was used to see if the new production methods were cost-effective. Great gains were made, but as you have read, increasing evidence showed that some agricultural practices were having negative effects on the environment. Agriculture became the focus of public scrutiny, and a negative public opinion of agriculture developed. This opinion was exacerbated by the fact that most urban dwellers today have very little understanding of their dependence on agriculture. Plant scientists have to find ways to meet our need for food, fuel, and other products and services from plants without negatively affecting the environment. When calculating the cost-effectiveness of a production procedure, costs can no longer include just material and labor costs. The cost to repair any resulting environmental damage must also be factored into cost analysis.

Although it may seem like a relatively simple calculation to factor in environmental costs, it is not. Assessing environmental impact and the cost to repair negative impact can be a challenge. It can be difficult to predict what will happen when a new production practice moves from the lab or experimental field to the real world. For example, genetically engineered plants, sometimes called genetically modified organisms (GMOs), have been created that dramatically reduce the need for pesticides and field tillage. Pesticide runoff and erosion are reduced, which is beneficial for the environment. But there is concern that heritable traits from the GMOs will “escape” and become part of the wild or native plant populations if engineered plants can breed with native plants. The fear is that wild plants with these traits may have serious negative impacts on the ecosystem in which they grow.

Determining the likelihood of a gene escaping requires many long term studies both in the lab and in the field. Organic farming has been proposed as a solution to many problems related to crop production and environmental impact. Organic farming does not allow the use of GMOs and certain types of chemicals for pest control and fertilization. Many organic farms have proved to be successful, thus demonstrating that the process works. However, it is not known if organic farming has the capability to produce the quantities of crop products needed in today's world. Also there is great debate regarding what constitutes organic farming. Some organic farming practices, such as erosion from soil cultivation, may have negative environmental impact.

The public often wants to see plants growing "perfectly"-a very unnatural state for plants. Generally this occurs when plants are used in leisure and recreational settings. Immaculately groomed and weed-free landscapes, flawless floral arrangements, and impeccable golf courses and athletic fields are sources of pride to those who own or use them. Ask any golf course superintendent what his greens committee would say if the fairways and greens had even a few weeds or insect and/or disease problems in them. Who would buy a bouquet if some petals were chewed? Maintaining perfect plants almost certainly has some degree of negative environmental impact.

Plant scientists and growers can find all the current uncertainty and controversy about their fields discouraging and wonder why we should even bother to try to solve seemingly insurmountable problems. We must remember that, although most plants grow very well without human intervention, the cultivated grains and grasses, fruits, vegetables, and ornamentals have become dependent on human intervention to survive. Without cultivation, these plants would likely die out after several generations and be replaced by hardier species such as wild grasses and thistles. But the dependence is mutual-we need these plants to survive and that is why we have to solve the problems.

The estimated 6.5 billion people now living in the world depend on cultivated plants for nourishment and to provide quality to their lives. The global population cannot survive as hunters and gatherers. The need for plant scientists to increase knowledge about crop plants and their place in the ecosystem and the need for professionals who know how to use that knowledge to grow plants in environmentally sound ways will not disappear. In fact, it should increase, perhaps dramatically, if the world population increases as predicted.

Currently, enough food is produced to feed the world's population. However, malnutrition and starvation exist in both developed and undeveloped countries mostly because social and political issues prevent the distribution of food to those who need it. If the social issues cannot be resolved, it will likely become the responsibility of plant scientists and growers to find creative ways to produce food crops locally in starvation-prone areas.

The solution to the loss of small family farms will no longer lie primarily in increasing productivity of traditional crops. New uses for old crops and production strategies for new crops will have to be developed to allow the family farm to remain viable.

Recently, many of the improvements in production were developed not only to reduce labor and increase productivity and profit, but also to allow farmers to be better stewards of the environment. But these improvements come with their own issues. High-oil corn has been bred to yield a product that can be used to replace petrochemicals in some industrial uses but may replace some food crops. No- or low-till farming reduces labor costs and is less detrimental to the soil than traditional cultivation practices are. However, noor low-till farming requires the use of herbicides to control weeds. To make herbicide use more effective and to reduce the

amount of herbicide used, GMOs were developed that are resistant to a very effective herbicide, Roundup®. Weeds are susceptible to the chemical, but Roundup Ready® crops are resistant. As a result, only one or two applications of a single herbicide is required in a season to get the same or better weed control compared to multiple applications of several herbicides in nonresis- tant fields.

A genetically modified corn (Bt®) synthesizes a naturally occurring protein that is lethal to the larva of many species of Lepidoptem, such as corn borer. The production of a natural larval toxin in corn has reduced the need to spray insecticides for control of a very destructive pest. Rice has been genetically modified to produce beta-carotene in the grain (golden rice). Beta- carotene (vitamin A) provides a critical nutritional element that is predicted to save the eyesight of millions of children in areas where vitamin A deficiency causes blindness.

But the public has demonstrated a negative response to each of the aforementioned uses of GMOs. There is fear the Roundup Ready® gene will escape into the native weeds adjacent to the fields where Roundup Ready® crops are being grown, thus creating weeds that are resistant to Roundup® though they would not be resistant to other types of herbicides. The Monarch butterfly (a member of the Lepidoptera species) was at one time thought to be threatened by Bt® corn. Golden rice cannot be grown in many of the areas where vitamin A is needed most because of concern about the beta-carotene gene escaping into the traditional rice crop. Flavr Savr® tomatoes have disappeared from the market because chefs and diners refused to buy or eat them out of fear of what the altered gene would do to human health if consumed. It will be up to those who study and work with crops to determine if there are undue risks with the new plants. However, one approach could work.

Perhaps the best way for plant scientists to meet todays challenges is to include the ecological paradigm of agriculture in all scientific studies. A model for this concept was developed in the College of Food, Agricultural, and Environmental Sciences at The Ohio State University (OSU). As described by the college:

This model is built on four areas of focus: production efficiency, economic viability, environmental compatibility, and social responsibility. A pyramid (Fig. 1-9) has been chosen to provide a visual representation of this model. Each wall of the pyramid represents one of the four dimensions. Four equal walls provide support and strength to each other and emphasize the critical need for balance and integration of the four areas.

FURTHER EXPLORATION

DUM, H. T. 1996. Environmental accounting: Energy and environmental decision making. New York: John Wiley & Sons.

FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS (FAO). 2002. *The state of food and agriculture.* Rome. Available online at http://www.fao.org/ DOCREP/004/y6000e/y6000e00.htm NATIONAL RESEARCH COUNCIL. 2005. *Valuing ecosystem services: Toward better environmental decision-.* Washington, DC: National Academy Press.

*2

Terrestrial Ecosystems and Their Relationship to Cultivating Plants

Almost all terrestrial ecosystems depend on the ability of plants to capture energy from the sun and store it in complex organic molecules. Climate determines the kinds of plants that grow naturally in an area and the rate at which they grow. All of the other organisms in the ecosystem depend on and are influenced by the nature of the vegetation and its productivity. Natural ecosystems are usually more complex than crop ecosystems; they illustrate the gamut of ecological relationships and ecosystem processes and provide a reference point from which we can evaluate crop ecosystems. Generally, the more a crop ecosystem differs from the ecosystem that would occur naturally in an area, the more difficult it is to sustain and the more resource input it requires..

ECOSYSTEM COMPONENTS

An ecosystem consists of a community of organisms in a physical envi-
ronment (Fig. 2-1). The community consists of populations of individual species; different kinds of plants, animals, fungi, bacteria, and so on. A population can be defined as all of the individuals of a species that inhabit a particular environment. The way that we define the environment determines the boundaries of the population. Often we are thinking of a limited area in which the individuals share the available

resources. In an isolated area of woodland, a field, or a greenhouse, the plants may be competing for light, water, or nutrients. However, ecological relationships may extend over larger areas, particularly for animals that can roam from one place to another. Even for plants, pollination may occur between individuals in physically separate environments many miles apart. It is fairly obvious that plants found naturally on differ- ent continents belong to different populations, but if there is any possibility of an cological interaction between individuals of a species, then they can be viewed as belonging to the same population.

We tend to think of ecosystems in terms of the plants and animals that we might see on a visit to a "natural" area in a state park or wilderness location. However, anywhere organisms exist is, in a strict sense, an ecosystem. Many of the most important.

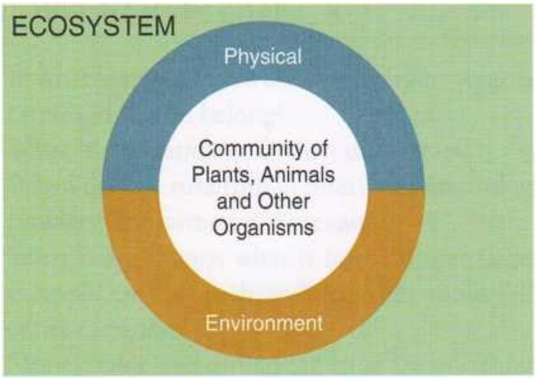


Figure 2-1

An ecosystem consists of a community of organisms in a physical environment (consisting of soil and atmosphere in the case of a terrestrial ecosystem). Source: Michael Knee.

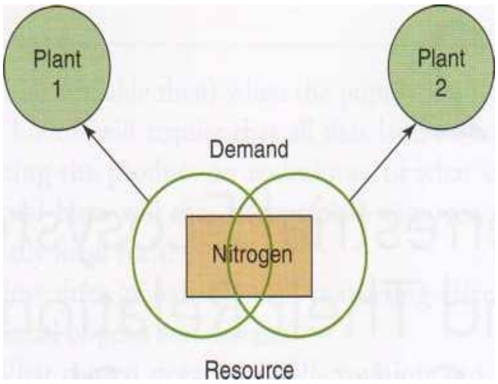


Figure 2-2

Competition occurs when plants of the same or different species attempt to use a resource that is in limited supply. Source: Michael Knee.

organisms and ecological processes in all ecosystems are invisible to us because the organisms are small or because they and the processes occur in the soil. A cornfield or an area of turfgrass may look too simple to qualify as an ecosystem, but a whole community of organisms interacts with the single species of plant, both above and below the ground. Ecology does not disappear when we grow plants in a home or a greenhouse. The physical environment, including the growing medium, may be artificial, but it will be colonized by other organisms, some harmful and some beneficial. Although books and television programs about nature may focus on the animals and birds that enliven natural ecosystems, many of the functions and ecological interactions that sustain the ecosystems are carried out by small invertebrate animals, fungi, and bacteria, and many of these organisms are in the soil. The microflora and -fauna are, relatively speaking, even more important in crop ecosystems, where we generally try to exclude macrofauna (birds and mammals) and noncrop macroflora (in other words, weeds). What distinguishes these "cultivated" ecosystems is that some of the organisms, processes, and interactions that would sustain a natural ecosystem are absent or heavily modified by human intervention. For example, inputs of nutrients are necessary to promote crop growth, or chemicals are needed to suppress disease. We can describe crop production in terms of these inputs and ignore the ecological processes and interactions. However, the goal of sustainable production requires that we minimize the inputs and maximize the contribution of ecosystem processes. By observing the full range of interactions and processes in natural ecosystems, we can learn how to manage crop ecosystems to achieve the goal of sustainability.

The organisms in an ecosystem interact according to the nature of the species and their role in the ecosystem. Each individual organism draws on the resources of the ecosystem to meet its requirements. Plants require light, water, and nutrients for growth and may require pollinators and dispersal agents for reproduction. Competition occurs when more than one organism draws on a resource that is in short supply (Fig. 2—2). The resource might be required for growth or the reproduction of the organism.

In ecosystems with a complete cover of vegetation, the most intense competition among plants is likely to be for light. A plant with a greater leaf area is likely to capture more light, particularly if the leaves are positioned above those of another plant. Trees can capture most of the light and are the dominant vegetation in many parts of the world. However, they have to invest considerable resources in the trunk and branches that support their leaves, which is one factor that limits the size of trees. Vines such as Virginia creeper, English ivy, and poison ivy can compete for light with less structural investment by using the support provided by the trees to grow tall enough to reach sunlight.

Usually a single species cannot utilize all of the resources or the whole of any one resource in the environ-ment. For example, some light does penetrate the canopy in most forests, and herbaceous plants, such as ferns, are adapted to growth in the low-light environment of the forest floor. Many of the trees in temperate forests are deciduous, and for a period in the spring, light is available for herbaceous flowering plants such as bloodroot, Trillium, and Hepatica to grow, flower, and set seed before the trees develop their full canopy. These kinds of plants are called spring ephemerals. The shadeadapted plants and spring ephemerals occupy niches. Niches exist when a resource is partitioned so that different portions of it are accessible to only certain species (Fig. 2-3).

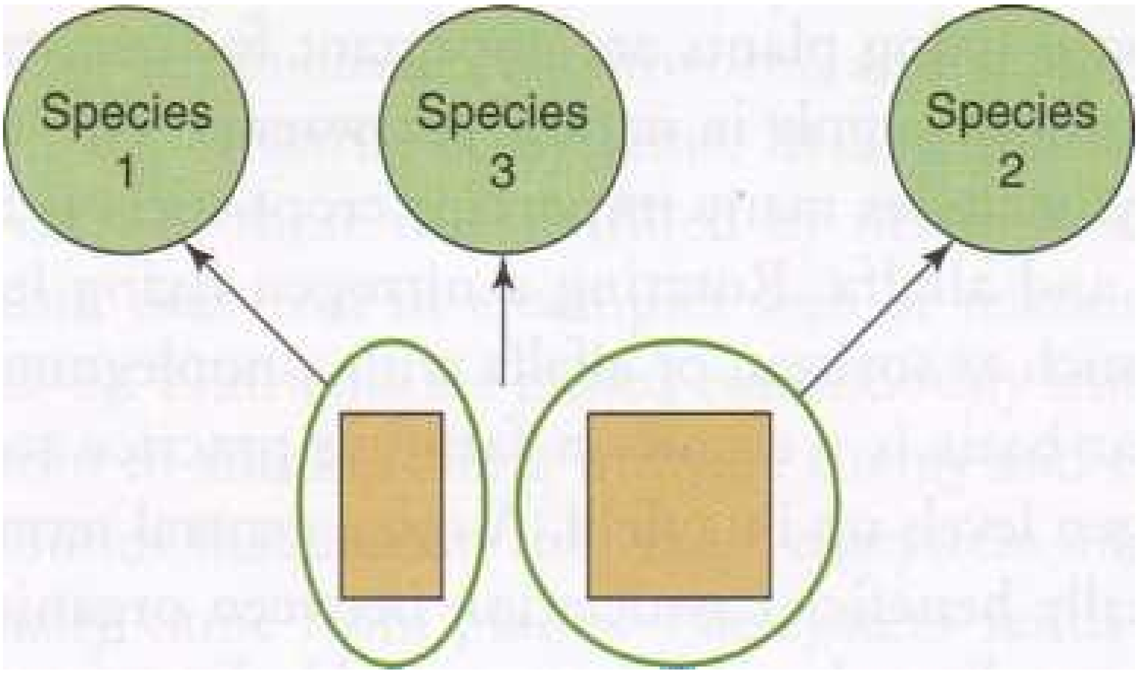


Figure 2-3

Species 1 is able to occupy a niche because species 2 does not use all of the resources. However, species 3 is subject to exclusion because it also needs the resources, but none remain.

Source: Michael Knee.

Although a critical environmental resource may be required for a species to find its niche in an ecosystem, each species has more or less strict requirements for a long list of environmental resources. In the fullest sense, the niche includes everything that is required for an organism to flourish in the environment. For a plant, this list can include light intensity, availability of water, nutrient concentrations, and the presence of the right pollinators. If two plants have identical environmental requirements and they are trying to occupy the same niche, the competition will be more severe than it is for two plants with different requirements. Competition is thus more intense between plants of the same species than it is between plants of different species. For species to coexist in an ecosystem, they must occupy different niches. It can be difficult to see how species requirements differ, for example, when looking at different species of deciduous trees that make up the forest canopy. However, species are separated by their physiological requirements as much as by their more obvious morphological differences.

In healthy, natural ecosystems, every available niche tends to be filled, and consequently resources are fully exploited. It is difficult for new species to colonize the environment because it lacks open niches or unexploited resources, and the result is called exclusion (Fig. 2-3). Thus, annual herbaceous plants cannot colonize mature woodland. If seeds blow in and germinate, the development of the foliage in the canopy during the spring will close off the light before the annual plants can flower and set seed. On the other hand, if some trees come down in a storm, annual plants may be able to colonize the open area or gap until new trees grow and the canopy closes.

Crop ecosystems have one or a few species that do not exploit all of the resources of the environment.

Thus, niches tend to be available for other plants to colonize. We call the other plants weeds, and their presence is a problem to the extent that their resource requirements overlap those of the crop species. One of the strategies in weed control is to plant additional, noncompetitive crop or noncrop plants with the main crop to occupy niches that would otherwise be occupied by weeds.

Resources captured by plants may be lost, however, to predation or parasitism. Plants are consumed by a wide range of animals, which we call herbivores. (We use the term predator for animals that consume other animals). Herbivores include mollusks (slugs and snails), arthropods (insects and mites), mammals, and birds. The diversity and large numbers of herbivores emphasize the importance of plants as a food source in terrestrial ecosystems. Many believe that herbivores do not compete with each other or come close to consuming all of the plant food resources of natural ecosystems because their numbers are kept in check by their own predators. There is a wide range of small predators among the arthropods, and there are many insect- eating birds and mammals. Large predators that feed on birds and mammals are less common because ecosystems cannot support many of them. As the number of herbivores increases, they become easy prey for the predators. Crop ecosystems are usually more vulnerable to herbivory because the number of predators is low or nonexistent. Thus, it may be necessary to use chemicals, introduced predators and parasites (biocontrols), or other means to control slugs, insects, rodents, birds, or deer.

Parasites are organisms that derive their nutrition by living in or on the tissues of another organism, often producing symptoms of disease such as swellings or discolored tissue. Plant parasites include many kinds of viruses, bacteria, and fungi. Some parasites can grow only in the host and are called obligate. Other parasites can grow outside the plant and are called facultative. All viruses are obligate parasites, whereas fungi and bacteria may be obligate parasites or facultative (as when they commonly exist outside the plant in the soil). A few parasitic plants, such as dodders and mistletoes, can infect plants in natural and crop ecosystems. Other classes of plant parasites include nematodes and some insects and mites, particularly those that form galls on leaves and stems.

Parasites differ from herbivores because they cause a disease rather than simply eating their way through the tissue. In a disease, the physiology and often the morphology of the host is altered as its resources are redirected toward the pathogen or disease-causing organism. Parasitism is a long-term relationship between a host and a pathogen, in which the host does not usually die because this would also entail the death of the pathogen. Although the host may not die, it is usually weakened making it vulnerable to attacks by other (secondary) organisms. Parasitoids are animals, often insects, that spend the juvenile phase of their lifecycle in the tissues of another insect. When they emerge as adults, the host is killed. Parasitoids can be helpful in crop ecosystems when they infect herbivorous insects such as caterpillars.

Some associations between organisms are mutually beneficial rather than antagonistic. In natural ecosystems, the roots of most plants are colonized by fungi that draw nutrients from the soil and pass some of them on to the plant. In return, the plant passes sugar and other organic molecules to the fungus. The fungi are known as mycorrhizae and can either live on the surface of the root (ectomycorrhizae) or invade the root tissue (endomycorrhizae) (Fig. 2—4). This relationship is an example of symbiosis, which involves a permanent and close association between two organisms that are known as symbionts.

Mycorrhizae are less common in crop ecosystems, particularly on herbaceous plants, than in the wild. The nutritional requirements of crops are often supplied by fertilizers and fungi are not needed to scavenge for them. However, mycorrhizae are now being supplied to some crops to reduce the need for chemical fertilizers. Lichens that are found on tree trunks, rocks, and the soil surface are formed by the symbiosis of a fungus with an algae species. Another kind of plant symbiosis involves a bacterial symbiont, Rhizobium, that forms the nitrogen-fixing nodules on the roots of many species in the legume family, or Fabaceae and a few other families. Nitrogen-fixing plants are important for maintaining the nitrogen supply in natural ecosystems. The legume family, includes many important crops such as beans, peas, and alfalfa. Rotating a nitrogen-fixing legume crop such as soybean or alfalfa with a nonlegume on a regular basis is a common farming practice to keep nitrogen levels up in a field. A more general term for a mutually beneficial association between organisms is commensalism. In addition to symbiosis, commensal- ism includes looser and less permanent associations such as that between a plant and its pollinating insect.

Although parasitic organisms may be the most conspicuous fungi and bacteria in crop ecosystems, most microorganisms are saprophytes that digest dead plant and animal material at or below the soil surface (Fig. 2-5).

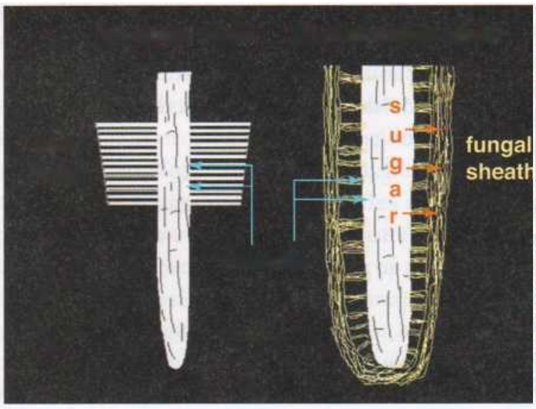


Figure 2-4

Many plant roots form a symbiosis with fungi, a relationship in which the plant supplies sugar to the fungus and the fungus draws mineral nutrients from the soil, which it passes on to the plant. Source: Michael Knee.

Figure 2-5

Recycling is essential for maintaining the supply of nutrients in natural ecosystems, and soil microorganisms are the primary agents in this process. By decomposing the leaf litter and tree trunk in this picture, saprophytes and detritovores are recycling the nutrients in those items. Source: Margaret McMahon, The Ohio State University.

Saprophytes are essential to the survival of the ecosystem because they recycle nutrients that would otherwise be tied up in dead organisms. In natural ecosystems, a few plant species are saprophytic. Saprophytes are aided in their activity by detritovores that break up large pieces of organic matter as they consume it. Earthworms are an important part of this group, which also includes other kinds of worms, many insects, and small mammals. Detritovores and saprophytes may be less important in crop ecosystems than in nature because crops and crop residues are removed and the nutrients are replaced by synthetic fertilizers. They become more important, however, as we try to recycle crop waste and minimize fertilizer inputs to develop more sustainable production systems.

Climate is the main influence on the type of vegetation that develops. The most important climatic variables are temperature, rainfall (or, more correctly, precipitation), and any seasonal variation in both. A key component in the relationship between climate and vegetation is soil. As we will see in Chapter 5, soils are produced from parent material, such as rock, by the interaction of climate and organisms.

Plants are key components of the soil ecosystem and influence all of the other organisms present. Although a world map may show the natural distribution of the different biomes across all of the continents, many of these areas have now been converted to agriculture or urban development. The soils that developed in the biomes differ greatly in their suitability for crop production. In general, the greater the difference between a crop production system and the preexisting biome, the more difficult it is to sustain that system. Sometimes it may even prove to be impossible.

Temperature is primarily influenced by latitude, and within latitudes, it is influenced by the height of the land above sea level. The other factor, moisture availability, is affected by patterns of air circulation around the globe. Air moves in one direction in the winds that we experience at ground level and then rises to the upper atmosphere to flow in the opposite direc-tion, before returning to ground level. This circulation is rather like a donut-shaped mass of air, with the wind moving around it from the hole in the middle to the outside and back. A series of three such systems operates between the equator and each pole (Fig. 2-7).

At the equator, temperatures are high throughout the year. The trade winds from the north and south carry moisture from the oceans and converge in this region. The warm, moisture-laden air rises and cools down so that the moisture condenses as rain. The warmth and readily available water are favorable for plant growth throughout the year, and all kinds of other organisms can benefit from the high productivity of the plants. The tropical rainforests of South America, Africa, India, and southern Asia developed under these conditions and make up the most productive biome, with the greatest range of biological diversity on earth.

The forest is dominated by broad-leaved and evergreen trees whose dense canopy captures most of the light. Rainforest trees include kapok, mahogany, and rosewood. Rainforest soils are shallow, and the tree roots spread outward rather than down. The trees gain stability from their shallow root systems by forming buttress roots. Because of the low-light levels, only a few shade-tolerant plants grow under the canopy; however, the trees provide support to many lianes. Also many herbaceous plants called epiphytes grow on the trunks and branches of the trees. The roots of these epiphytes never reach the soil; they catch their water as it runs down the surface of the tree or from the air itself with specialized aerial roots. Many orchids and bromeliads are rainforest epiphytes.

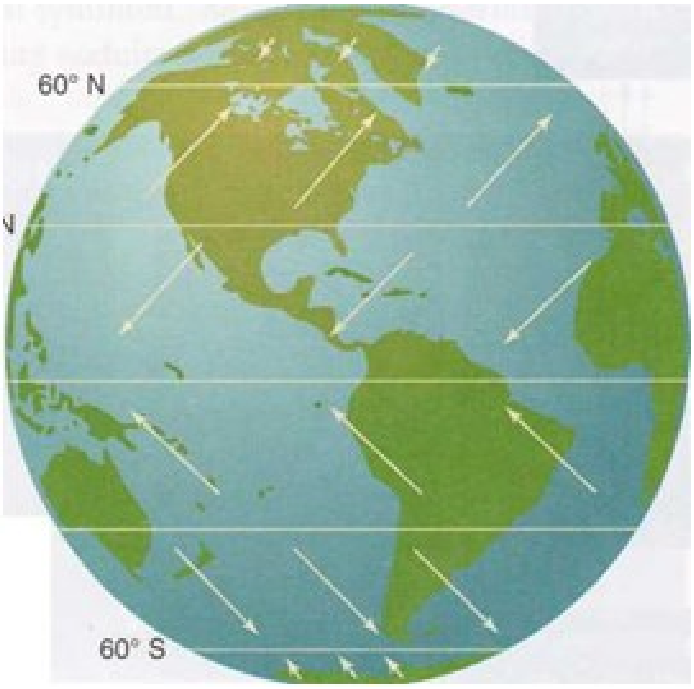


Figure 2-7
Three main belts of surface winds exist in each hemisphere. Each one determines patterns of precipitation and the vegetation that develops. Source: Margaret McMahon, The Ohio State University.

Much of the life of the forest occurs in the canopy, unseen by humans and other groundlings. Most of the nutrients in the ecosystem are also in the canopy and are cycled from one organism to another without passing through the soil. Because of high rates of growth, nutrients are rapidly taken up by plants and rapidly recycled from dead organisms, so rainforest soils contain little in the way of free nutrients. After the forest is cleared, good crops can be raised for a year or two, but the nutrients are soon exhausted. To make matters worse, nutrients are washed out by the rains, and the soils themselves are unstable in the absence of vegetation. So production of annual crops is not easily sustainable in this region.

The plants of this environment are highly specialized and grow slowly or intermittently. They can be slow-growing perennials with succulent stems or leaves that help conserve water. Cacti and yucca are an example of these kinds of plants. They can also be fast-growing annuals such as Ghost Flower (Mohavea confertiflora) or Desert Sunflower (Gerea canescens) that take advantage of occasional rains to complete their life cycles while the moisture is available. Because of slow growth, there is little accumulation of organic matter that can be recycled to build up soil fertility in these ecosystems. Because temperatures can be favorable to plant growth and deserts occupy about two-fifths of the land surface, many people have had the dream of "making the desert bloom." This requires massive amounts of water that can be economically transported or diverted to the desert region. Fertilizers must be used to compensate for the low fertility of the soils. All water sources contain small amounts of salts, even if they are so-called fresh water. The salt level increases when fertilizers are added. When the desert is irrigated, the salts are left behind after the water evaporates from the soil or through plant transpiration. Desert soils are difficult to manage in the long term because the salts tend to accumulate to levels that inhibit the growth of plants.

Moving north or south away from the deserts, the climate becomes moister but temperatures are not con-tinuously favorable for plant growth. In latitudes between 40° and 50° and when there is more than about 75 cm of rainfall, temperate deciduous forest develops (Fig. 2-8).

Ash, oak, maple, hickory, and beech are some of the hardwood species found in temperate forests. These forests develop all of the land masses in the northern hemisphere, but there is little land area in these latitudes in the southern hemisphere so temperate deciduous forest is nearly absent south of the equator. During the summer, the trees in these forests can be almost as productive as those in the tropical rainforests. However, growth nearly ceases in the winter, when most of the trees have lost their leaves. Although lianes, more commonly called vines in this biome, are present in old-growth forests of this type, the canopy is not as favorable a habitat for epiphytes as in the rainforest. However, spring ephemerals which are understory shrubs and herbaceous plants such as trillium (Trillium grandiflorum), dogtooth violet (.Erythronium dens-canis), and bloodroot (Sanguinaria canadensis) can exploit the light that comes through the canopy in the spring before the new leaves are fully formed. (The understory is composed of the plants

that grow under the canopy of other taller plants.) The botanical diversity of the Appalachian forests of North America is a distant second to the rainforest, but it is more readily apparent to a wanderer in the sunlit carpets of spring ephemerals than it is to a ground-based visitor in the comparative (and permanent) gloom of the rainforest.

The annual leaf fall adds a certain amount of nutrients to the litter layer of the temperate deciduous forest. However, the leaves contain only a fraction of the nutrients locked up in the permanent structure of the. tree, and trees manage to withdraw much of the nitrogen and phosphorus from their leaves before they are shed. So forest soils develop slowly and tend to have only a thin organic-rich layer. As with the rainforest soils, fertility can be soon exhausted if not managed properly when crops are grown after the forest is cleared.

The area between the deserts and the forests consist of grasslands and savannas (Fig. 2-9). Tree growth in grassland and savanna is limited to some extent by lack of water, but fire and grazing animals are also important in maintaining these ecosystems. Grassland vegetation survives and may even benefit from a certain level of grazing that woody plants cannot tolerate. Also dead grass is readily ignited by lightning strikes. When fires sweep through grassland, most trees are killed, but grasses and herbaceous perennials, which have their growing points at or below the soil surface, typically survive.

Grasslands and savannas were favored by early people and our first efforts at land management may have been to set fires to provide habitat for animals that we were trying to encourage into or deliberately keep in herds. We still find prairies, meadows, and forest glades attractive but may not fully realize our own role in their ecology. Grassland plants accumulate nutrients in the roots and stems that are renewed from year to year. In temperate climates, the old stems and roots are not fully recycled each year and organic matter builds up over time. This organic matter contains reserves of nutrients and makes up a large part of

Figure 2-8

A clear area under the canopy of a mature temperate forest where other plants cannot grow in the low light. In the spring, however, it is filled with spring ephemerals.

Source: Margaret McMahon, The Ohio State University.

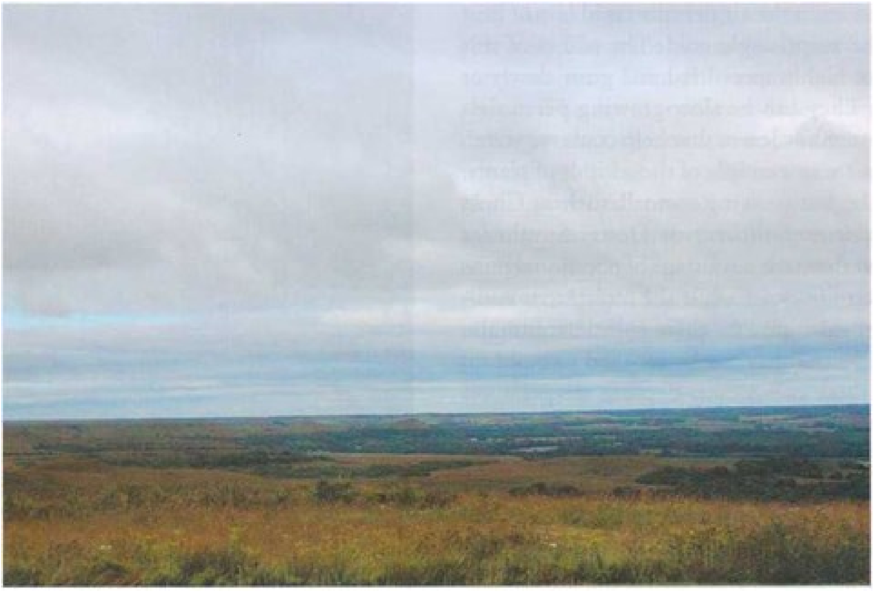


Figure 2-9

The prairie in Kansas is characterized by expanses of grassland interspersed with a few trees and shrubs.

Source: Kimberly Williams, Kansas State University.

the black earths that are characteristic of moist grasslands around the world. The nutrients in such soils can sustain crop production for many years, and the former grasslands of North America, Europe, and Asia have proved to be the world's most productive agricultural land. Agriculture itself originated in such a region, the so-called "fertile crescent" that occupied river valleys from present-day Egypt to Turkey and Iran. Grassland becomes less pro-ductive as it merges with drier regions on its margin. In the United States, for example, the tall grass prairie of the central states gives way to short grass prairie to the west. Attempts to raise productivity with irrigation can meet the same problems of salinization as in the desert. Arid lands can all too easily be turned to desert by over- grazing, and soil erosion can be a devastating consequence of attempted cultivation. The extent to which human beings are responsible for the spread of deserts throughout the world is debatable. Climatic changes, such as unusual and persistent droughts, are certainly involved in the process, but questionable agricultural practices can increase the risk of degradation. This interaction contributed to the US dust bowl of the 1930s, and recovery from it required massive changes in land management. Arid lands are generally sparsely populated, but the quarter billion or so people who live in such areas around the world are among the most vulnerable to climatic change.

At about 60°N, the convergence of arctic winds and the westerlies from lower latitudes creates an upcur- rent leading to precipitation, just as at the equator. Of course, it is much colder at this latitude than at the equator, and the long winter allows for only a short season of plant growth each year. Coniferous trees make up the dominant vegetation in this boreal forest, or taiga, and plant diversity is much lower than in the temperate and tropical forests. Because the conifers are mostly slow-growing evergreens, recycling and the availability of nutrients is lower than in the deciduous forest. Nutrients are also depleted as water drains through soils that are wet for most of the year. This type of vegetation is almost absent from the southern hemisphere because there is little land around 60°C.

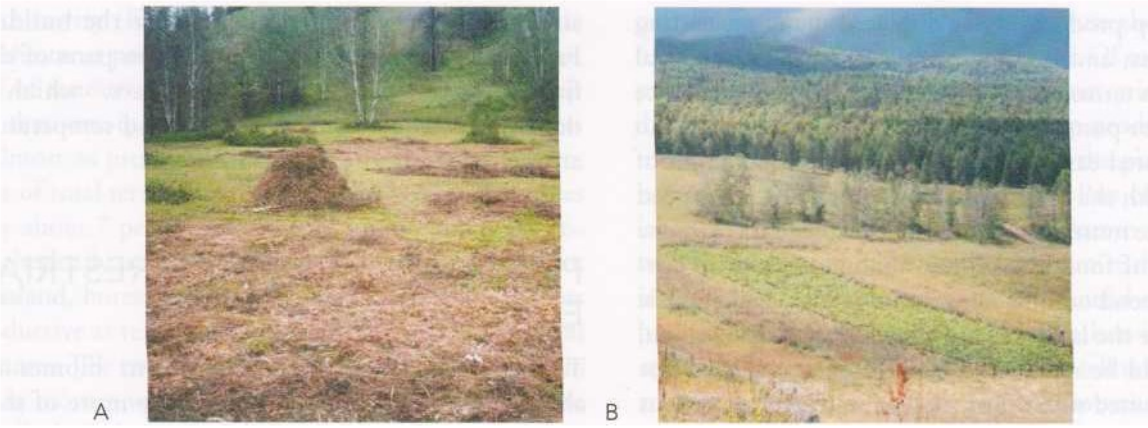


Figure 2-10

In the taiga, farming is done on a very small scale. (A) Hay making in the taiga. (B) A small farm producing fruit and vegetables in the taiga. Source: Margaret McMahon, The Ohio State University.

Figure 2-11

Wetlands provide many important ecological benefits. Source: Margaret McMahon, The Ohio State University.

However, taiga occurs in a band from North America through northern Europe and Asia, making it the second largest biome after the desert. Of course, coniferous trees are a valuable crop for lumber and paper making, but there is little prospect for large-scale production of other kinds of crops in this area (Fig. 2-10).

In the tundra, north of the taiga, the ground is permanently frozen except for a surface layer throughout the year. The short melt period in the summer allows only a low vegetation of dwarf shrubs, sedges, and grasses to develop. Similar vegetation occurs in high mountains. Some of the plants have showy flowers that make the tundra briefly more colorful than the taiga. Alpine plants are attractive for specialist collectors, but there is almost no prospect for crop production in the tundra itself.

PRODUCTIVITY OF TERRESTRIAL ECOSYSTEMS

The relative productivity of different biomes has already been discussed. As we modify more of these areas for human use, it is important to know what effect this modification has on global productivity. The productivity of ecosystems is an indication of how much we can expect to harvest from them without causing loss of species or collapse of the whole ecosystem. Some of the most obvious examples of the failure to consider sustainable harvesting practices are the exploitation of fish stocks and the wood supply in many parts of the world. On a larger scale, productivity is related to the carbon balance of the world. Plant pro-ductivity can be defined in terms of the amount of carbon taken from the atmosphere by photosynthesis. When we change ecosystems for our own use, we may also change the rate at which carbon dioxide is removed from the air, which will have an effect on global climate. We are thinking increasingly in terms of changes that we can implement to maximize atmospheric carbon removal, one way of accomplishing this objective is to maximize plant productivity.

Photosynthesis fixes carbon into organic compounds, but this process is not quite equivalent to plant productivity The plant uses a portion of the organic compounds for its own maintenance. At the end of a growing season, less carbon is retained than was originally fixed. Net primary productivity (NPP) is carbon fixed minus the amount consumed by the plant and returned to the atmosphere through respiration.

It is quite easy to measure the carbon accumulation by a single plant, but it is difficult to measure for complex communities consisting of many species under field conditions. Two-thirds of our planet is covered by water, and it is at least as difficult to estimate the productivity of the oceans as it is for the land. Estimates of productivity have varied greatly over the years, but it is now thought that although terrestrial ecosystems occupy about 30 percent of the surface of the planet, they account for about 55 percent of global photosynthetic productivity. The world's terrestrial ecosystems can be divided into three broad groups of high, intermediate, and low photosynthetic productivity (Fig. 2-12). Tropical forest and savanna are the most productive biomes and account for about half of terrestrial productivity, although they make up less than one-quarter of the land area. Temperate forest is almost as productive but contributes about 10 percent of total terrestrial productivity because it occupies only about 7 percent of the land surface and is photo- synthetically active only part of the year. Temperate grassland, boreal forest, and cropland are about half as productive as temperate and tropical forest and tropical savanna. The contributions to global productivity from these biomes with intermediate productivity tend to match their share of land area (8 percent for temperate grassland, 6 percent for boreal forest, and 10 percent for cropland). One-third of the land surface is occupied by tundra, permanent ice, desert, and semidesert, which contribute about 4 percent of global productivity. Urban areas have about the same productivity as tundra and occupy about 1.5 percent of land surface. In all parts of the world, wetlands tend to be the most photosynthetically productive areas; on average their contribution to productivity is three times their share of land area but because their area is only about 1.8 percent, their total contribution is small. In spite of their natural productivity, we have not yet exploited the inherent productivity of wetlands, with the exception of rice and a few minor crops, probably because it is more difficult to work in flooded fields than on dry land.

In terms of carbon fixation, cropland is usually less productive than the biomes that it replaced. This is particularly true for annual crops because they do not fully occupy the land for most of the year. Of course, crop productivity is not usually the same as net primary productivity of an ecosystem. Usually crop productivity is measured in terms of a specific part of the plant that is harvested, rather than the whole plant. Part of the challenge of production is to maximize this part in relation to total biomass, or in other words to maximize the harvest index. In principle, annual crops are wasteful of primary productivity because most of the fixed carbon is removed at harvest and must be fixed again in the following year to make a new corn or tomato plant. However, perennial crops must allocate part of the fixed carbon to their survival structures and if this is not the part that is harvested, less fixed carbon may be accounted for in the harvest index than from an annual crop. However, some of the most productive crops are perennial plants from which the survival structures are harvested for consumption. Such crops have historically sustained people with limited land and resources, such as the Irish who grew potatoes in the nineteenth century, and the 10 percent of the worlds population that today depends on cassava for its nutrition.

SUCCESSION

Descriptions of biomes can leave the impression that they consist of communities of plants and other organisms that would always be there in the absence of human interference. However, we know that organisms have evolved, landforms have changed, and climate has varied over time. The change in plant communities over time is known as succession. It is often described in terms of the development of vegetation from a blank-slate situation such as a rock surface, a pool of water, or bare soil (Fig. 2-13). These situations may have arisen because of natural causes (an earthquake, volcanic eruption, or the passage of a glacier) or because of human interference.

If there is no soil, succession must begin with soil formation. A rock surface can be colonized by lichens, which trap windblown dust particles and eventually decompose to form a thin layer of soil that can be colonized by mosses. Further soil accumulation allows herbaceous plants to move in. Water might be colonized by floating plants, which decompose and sink to the bottom of a pond that may also be receiving sediment from streams. As the pond becomes shallower, bottom-rooting plants with emergent leaves can colonize, followed by wetland plants. If some kind of soil is already present, fast growing herbaceous plants will exploit the space but will give way to slower-growing plants that can use resources more efficiently. The composition of the ecosystem is always evolving toward the group of organisms that can best exploit the available resources at that time. Succession begins with pioneer species that can survive under special conditions and tend to get displaced as the ecosystem develops. As niches become available in the ecosystem, they are filled by the best available candidates.

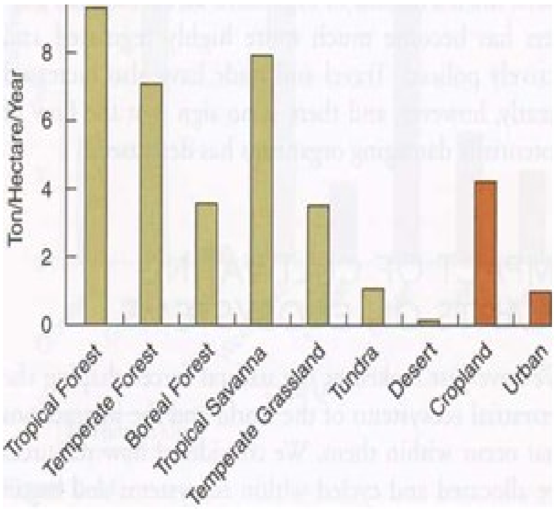


Figure 2-12

The net primary productivity of biomes represents the amount of carbon fixed in photosynthesis for a given area in a year. Source: Michael Knee.

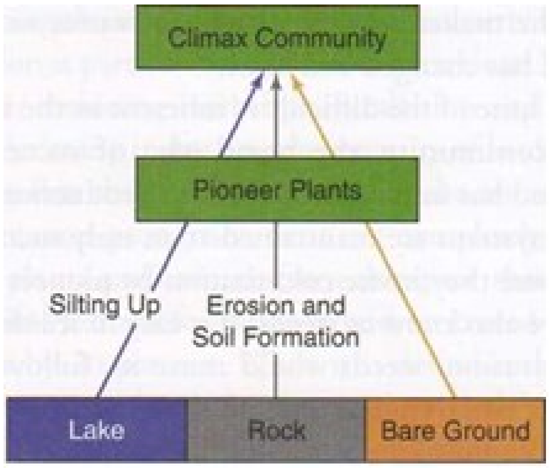


Figure 2-13

All locations in a geographic area tend to develop the same kind of vegetation over time. Source: Michael Knee.

The theoretical end point of succession is known as the climax community. At one time, this point was thought of as a permanent assembly of species that were linked together and would always return after any kind of disturbance. Now it is clear that there is no end point to succession and that species just happen to occur together, not because of necessary associations. The climax community can be seen as a group of species within the broad structure of the biome that is appropriate to the climatic conditions of the area. Over much of the eastern United States, this would be temperate deciduous forest with a mix of forest trees, shrubs, and herbaceous plants. Although we can characterize typical associations such as oak-hickory forest, the makeup of the ecosystem varies with location and has changed over time.

In spite of the difficulties inherent in the idea of a climax community, the broad idea of succession is sound and has implications for crop production. Many crop ecosystems are maintained at an early successional stage where they invite colonization by pioneer species, which we also know as weeds. It is easy to see that without cultivation, weeds would move in, followed by a thicket of woody plants, and the process would culminate in a forest of the longer-lived tree species. The further from the climax community we try to stay, the more work and inputs are required to maintain the ecosystem. The success of the corn belt in part can be explained by the fact that a mix of tallgrass species in the original prairie was replaced by another tallgrass that happens to be physiologically similar. In the temperate zone, we have often been lucky to be able to make drastic changes in the vegetation without suffering excessive losses of soil fertility and structure. In more difficult climates, the consequences have not been so positive, and it can be a good idea to model crop ecosystems on the broad structure of the climax vegetation.

Once a climax community is established, no other species can easily invade because all the niches in the ecosystem are filled and no surplus resources are available to exploit. This outcome is related to the idea of the climax community as a well-defined group of mutually dependent species. However, alien species do invade natural ecosystems, often with quite disastrous consequences, and this outcome is part of the evidence that no unchangeable association exists between the species in a climax community. Long-standing species may be well-adapted to secure the resources that they need from the environment, but they are also vulnerable to pathogens and herbivores, which are equally well-established in the environment. While an alien species may not be able to exploit the resources as efficiently as natives, it may be immune to the diseases and unpalatable to the herbivores. These characteristics would give it a competitive advantage, at least until the pathogens and herbivores catch up with it.

Human beings have a long history of moving plants and other organisms around the world, deliberately or by accident. Many ecosystems have been irreversibly altered by introduced species. In recent years, the movement of organisms across national borders has become much more highly regulated and actively policed. Travel and trade have also increased greatly, however, and there is no sign that the flow of potentially damaging organisms has decreased.

IMPACT OF CULTIVATING PLANTS ON ECOSYSTEMS

We have just looked at the natural forces shaping the terrestrial ecosystems of the world and the interactions that occur within them. We considered how resources are allocated and cycled within ecosystems and began to see how human beings have modified the ecosystems. In many parts of the world, human beings are now the dominant organisms shaping the environ-ment and utilizing its primary productivity. Ten thousand years ago, at the beginning of the agricultural revolution, early farmers could afford to burn vegetation to clear areas for crops without worrying about the ecological consequences (which were largely unknown, of course). At that time, perhaps 5 million people lived on earth. Today, with a global population of more than 6 billion people and rapidly rising, the impact on the environment is impossible to ignore. As we try to fit even more people onto the planet, we need to be more aware of our use of its resources. In this chapter, we will consider most of the ways in which we make use of plants and the ecological impact of that use. In the interest of space rather than scientific reasons, forest crops will not be included, although we will look to forests for the absorption of much of the carbon dioxide that we generate in our lives.

Human impact on natural ecosystems is both physical and biological. Worldwide we now deliberately choose or influence the organisms that inhabit about 35 percent of the land surface of the earth. As we saw in the previous chapter, much of the remaining area is desert or tundra, with low productivity and biological diversity (Fig. 2-14). Thus, we exclude or even deliberately exterminate organisms in many of the most diverse and productive regions of the earth. Some ecologists allege that we have started an era of mass extinction of species like those that have occurred in geological history from meteoric impacts or other physical causes. This proposition is somewhat controversial, and people often argue about the value of preserving

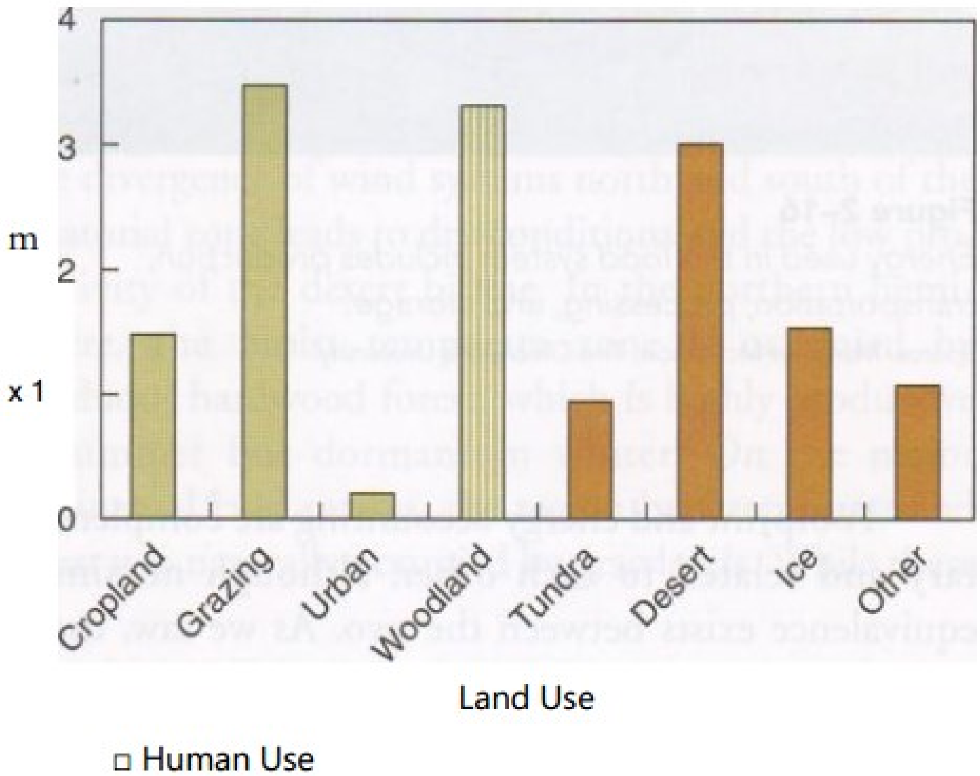


Figure 2-14

Global land use. The shaded columns indicate land used by people. Woodland is striped because it includes areas that are natural and unexploited, natural but managed or harvested, and planted purely for economic use. In a sense, all areas are used for carbon dioxide absorption, if nothing else.

Source: US Global Change Research Program, http://www.globalchange.gov/

individual species or populations of species. However, we cannot escape the fact that we are increasingly presented with the choice about whether to try to preserve plants and animals from extinction or to allow them to disappear. Having admitted the existence of this debate, we will spend the rest of the chapter focusing on the physical cost of providing the crop plants that we utilize or consume. The physical cost comprises the land and energy inputs required in crop production.

Energy requirements and land use are the basis for two ways of evaluating the environmental impact of human activity. Accounting for energy inputs enables us to evaluate the efficiency of technological systems such as crop production, and we can look at energy demand in relation to availability on a national or global level. The land area required for the same activities is a measure of their contribution to the human footprint. The total human footprint is an estimate of the land area required by an individual, a geographic area, a sociopolitical group, or the world population taken as a whole. It accounts for the space required to provide all of the items we use in our lives and to absorb all of the wastes that we generate. Thus, crop production contributes to our footprint not just through the area required to grow crops, but also the areas required to provide inputs of fuel and chemicals, to transport the produce, and to absorb the wastes produced.

A footprint analysis often takes account of the area of land without regard for the intensity of use. Thus, a square meter of land occupied by a home is not differentiated from a square meter of forest that provides lumber or pasture that provides meat or dairy products. But the home uses the area almost entirely for human purposes, whereas the forest or pasture can support many other organisms. A more sophisticated equation is:

Much of our footprint on the planet is related to energy use. Most of our energy consumption is based on fossil fuels, and a footprint is associated with extraction, processing, and distribution of these fuels. However, a far greater footprint arises from the carbon dioxide produced as the fuel is burned to generate energy. This requires 8 hectares of forest for each person in the United States. Cropland makes a smaller contribution to carbon absorption because much of the carbon is returned to the atmosphere as the crop is consumed. The maintenance of forest for carbon fixation is a low-intensity component of our total footprint because we can allow natural ecosystems to perform this function. It is important that the most productive forests in equatorial Asia, Africa, and South America should not be converted to farmland. It has been said that we should probably pay for them to be maintained because we use their services. In fact, in 2008, the World Bank had committed $165 million dollars to offer to tropical countries for “carbon offset credits” for preserving their forests. Carbon credits can be bought by countries that emit large amounts of C02> essentially allowing them to buy a place to sequester the carbon. Other organizations, such as Carbon Conservation and Merrill Lynch, are also involved in "payment for preservation" programs.

Agriculture accounts for only about 2 percent of US energy use, so it can make only a minor contribution to energy conservation. However, because it accounts for less than 1 percent of gross domestic product, it is using above average amounts of energy and has to be regarded as an energy intensive industry (Fig. 2-15). Production of fertilizer accounts for nearly half of agricultural energy use in the United States. If the whole world adopted a similar mechanized and high-input agriculture, it would require about 10 percent of current global energy consumption. Most of the energy used for our food supply is consumed (for transportation, processing, and storage) after produce leaves the farm. It is difficult to account for all of the energy inputs between the farm and the dinner table, but the food sector has been estimated to account for up to 10 percent of total energy consumption. Surprisingly, less than 10 percent of this energy, or 1 percent of total energy consumption, is used in transport. Much of the energy is consumed in food marketing and preparation in the home (Fig. 2—16). If the rest of the world adopted this aspect of our lifestyle, it would use up about half of the worlds energy supply.

SUMMARY AND REVIEW

Plants provide the energy that drives almost all terrestrial ecosystems. An ecosystem consists of populations of dif-ferent species of organisms in a physical environment.

Microclimates exist everywhere and vary from the prevailing climate because of a feature such as body of water, land mass, building, and other features. The environment in a microclimate may be more favorable or less favorable to plant growth than the general climate in the area. Growers can use growing strategies that account for microclimate effects.

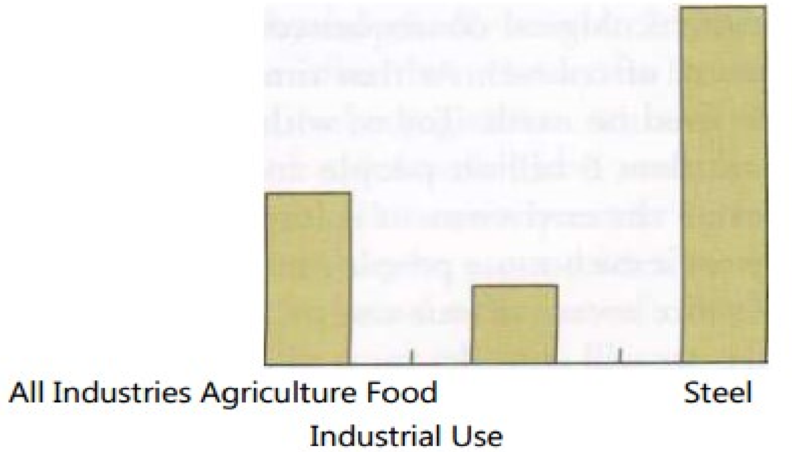


Figure 2-15

Energy use by US industries in 2000, in relation to contribution to gross domestic product. Agriculture appears to be energy intensive partly because profit margins are low. Food manufacture adds value to its raw materials and appears more energy efficient. Source: Earth Observing System Data and Information System, http://esdis.eosdis.nasa.gov/

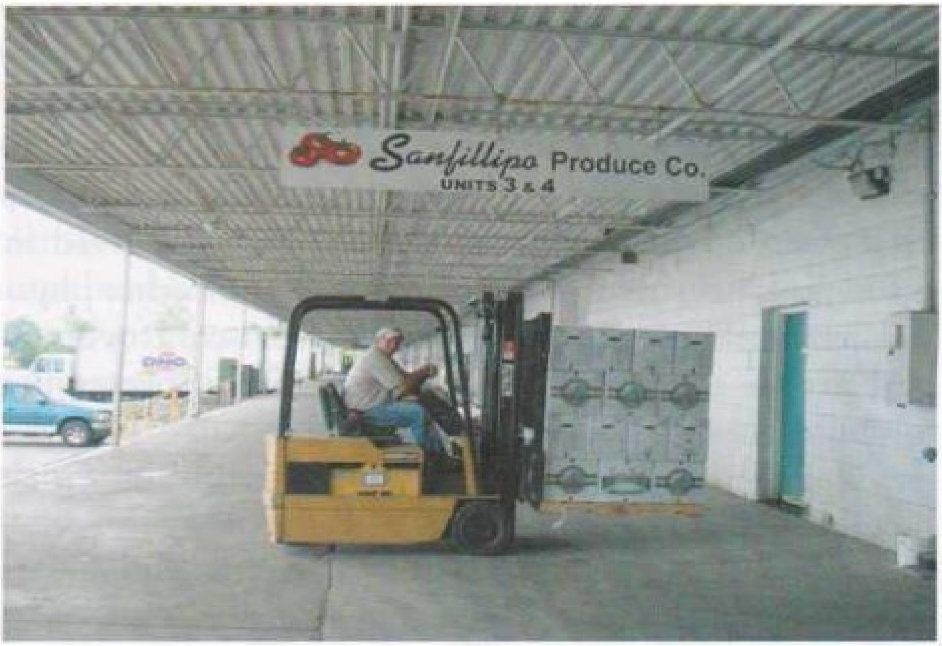


Figure 2-16

Energy used in the food system includes production, transportation, processing, and storage.
Source: Margaret McMahon, The Ohio State University.

Many of the ecoregions that were most suitable for crop production have now been destroyed. The remaining natural areas of the planet are too dry or too cold for agricultural exploitation. Terrestrial ecosystems account for about half of global carbon fixation, but this proportion has been reduced by conversion to agriculture and urban development. Soils and ecosystems develop over time in a process known as succession to a stable climax community. Most crop ecosystems are maintained at an early, unstable successional stage that requires significant energy input to maintain.

Agricultural and other human uses now dominate the ecology of nearly all of the most photosynthetically productive terrestrial areas of the earth. Crop plants and farm animals have replaced the organisms that inhabited these areas, even to the extent that we are causing extinction of other species. We can summarize our impact on global ecology in terms of the land or the energy that is used for human purposes, including crop production. Land/energy use is summarized in the concept of the human footprint. While crop production represents a small fraction of total footprint and energy use, the intensity of land and energy use for crops is higher than many for other industries. The food supply system (processing, transportation, and storage) uses much more energy after it leaves the farm than was used in production.

Areas were not as productive as forests, highly fertile soils developed, and they became some of the world's most productive agricultural areas. To the north of the temperate deciduous forest, coniferous trees predominate in the taiga, or boreal forest; further north still, the subsoil is permanently frozen and trees cannot grow.

The natural ecosystems that occur in different parts of the world can be grouped together in biomes. Each biome is a collection of ecosystems with similar climate, soil type, and vegetation, and these three elements are interrelated. Temperature and precipitation are the main climatic factors. Temperature is determined mainly by latitude and height above sea level. Precipitation patterns are related to the predominant wind patterns that occur in three bands in the northern and southern hemispheres. Temperature and precipitation are consistently high in the equatorial region, leading to continuously high rates of growth and low nutrient availability in the soil for the tropical rainforest. The divergence of wind systems north and south of the equatorial zone leads to dry conditions and the low productivity of the desert biome. In the northern hemisphere, the moist temperate zone is occupied by deciduous hardwood forest, which is highly productive in summer but dormant in winter. On the major continental land masses, the region between forest and desert was naturally occupied by grasslands. While these.

KNOWLEDGE CHECK

1. Briefly describe the parts of an ecosystem.
2. What distinguishes the ecosystem created by cultivating plants from natural ecosystems?
3. What is meant by a niche in ecosystems?
4. Why is it usually easy for weeds to get established among cultivated plants?
5. Although disease parasites often do not directly kill a plant they infect, the plant will often die. Why?
6. What is the beneficial relationship that mycorrhizae have with plants? That Rhizobium has?
7. What role do saprophytes and detritivores have in ecosystems? When do they become most important in plant cultivation systems?
8. What is a biome?
9. How do global wind patterns affect the creation of the major biomes?
10. What types of plants are found in: tropical rainforest, desert, temperate forests, grasslands and savannas, taiga, tundra?
11. What is a microclimate?
12. Describe two ways cultivating plants has impacted biomes.
13. Of the major biomes, which are the most photo- synthetically productive?
14. Are crop systems usually more or less photosyn- thetically productive than the native plants they replaced?
15. What is a harvest index?
16. Describe ecosystem succession. In terms of succession, what is the difficulty with maintaining many of our crops?

17. How does cultivating crops impact our carbon footprint?

18. What is the concept of "carbon credits"?

19. Give two reasons why the United States uses so much energy for its food supply.

FURTHER EXPLORATION __

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2. HUNTER, M., D. LINDENMAYER, and A. CALHOUN. 2007. *Saving the Earth as a career.* Hoboken, NJ: Wiley-Blackwell.

3. NATIONAL RESEARCH COUNCIL. 2005. *Valuing ecosystem services: Toward better environmental decisionmaking.* Washington, DC: National Academy Press.

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*3

Growing Plants for Human Use

MICHAEL KNEE

key learning concepts

After reading this chapter, you should be able to:

- Discuss why plants must be cultivated for human use.
- Describe the many ways plants are needed and used by humans.
- Describe how growing plants impacts our energy use and carbon footprint.

The previous chapter looked at ecosystems and the impact humans have on them. You learned about our energy footprint. Now let's look at why we grow plants and take a closer look at how our need for plants and the way we grow them influences ecosystems, the energy footprint, and society.

PLANTS FOR HUMAN USEO

Nutrition

A healthy diet requires an energy source such as carbohydrate or fat, pro-tein, linoleic acid, and various vitamins, minerals, and water. Apart from the minerals and water, these requirements are complex organic molecules that start with photosynthesis. Plants are essentially the only terrestrial organisms that convert inorganic carbon, oxygen, hydrogen nitrogen, and sulfur to organic forms through photosynthesis. This characteristic is why they are called autotrophs (meaning "self-feeder"), whereas humans and just about everything else that live on land are heterotrophs (or "other feeders") because they feed off autotrophs or other heterotrophs.

When we look at cultivated plants, we see that only a small percentage of all the plant species in existence feed the world's people either directly or indirectly (through animals). These plants are:

1. Cereal crops - wheat, maize (corn), rice, barley, oats, sorghum, rye, and millet. (Over half the world's food supply comes from the photosynthetic activity of these crops.)
2. Roots and tubers - potatoes, sweet potatoes, and cassavas.
3. Oil crops - soybeans, corn, peanuts, palm, coconuts, sunflowers, olive, and safflower.
4. Sugar - sugar cane and sugar beets.
5. Fruit crops - bananas, oranges, apples, pears, and many others.
6. Vegetable crops - tomatoes, lettuce, carrots, mel- ons, asparagus, and so forth.

Fruits and vegetables add to the variety and palatability of our daily meals and supply much-needed vitamins and minerals.

Table 3-1 shows some of the common crops ranked in relation to the calories and proteins produced per unit of land area. Not all of the total production of food materials becomes available for human consumption. Much is lost during harvesting, transportation, and marketing, primarily from attacks by insects, diseases, birds, and rodents. Also, some of the production is saved to be used as seed for future plantings.

Adults need 2000 to 3000 kcal of energy per day, depending on their size and level of activity. This energy can be provided by carbohydrates, which are typically found in plant foods. So twenty-four to thirty-six slices of bread is one way to get our daily energy requirement. Lipids provide energy in more condensed form, and 9 to 14 oz of vegetable oil can provide our energy for the day (Fig. 3-1). Fats are more characteristic of animal foods, but many health problems are associated with consumption of animal fats partly because they tend to be saturated fats, which lack double bonds in their fatty acids. Unlike animals, plants can make polyunsaturated fatty acids (PUFAs) such as linoleic and linolenic acids. Apart from the health benefits of PUFAs, we need linoleic acid to make hormones such as prostaglandin, and plant oils are a more direct source than animal fats. We can also derive energy from protein-rich foods such as meat. Eating only meat for our energy needs is wasteful and probably unhealthy because of the need to excrete the excess nitrogenous material.

Table 3-1

SOME IMPORTANT FOOD CROPS RANKED ACCORDING TO CALORIE AND PROTEIN PRODUCTION PER UNIT OF LAND AREA

Rank	**Calories Produced per Unit Area**	**Protein Produced per Unit Area**
1	Sugar cane	Soybeans
2	Potato	Potato
3	Sugar beets	Corn
4	Corn	Peanuts
5	Rice	Sorghum
6	Sorghum	Peas
7	Sweet potato	Beans
8	Barley	Rice
9	Peanuts	Barley
10	Winter wheat	Winter wheat

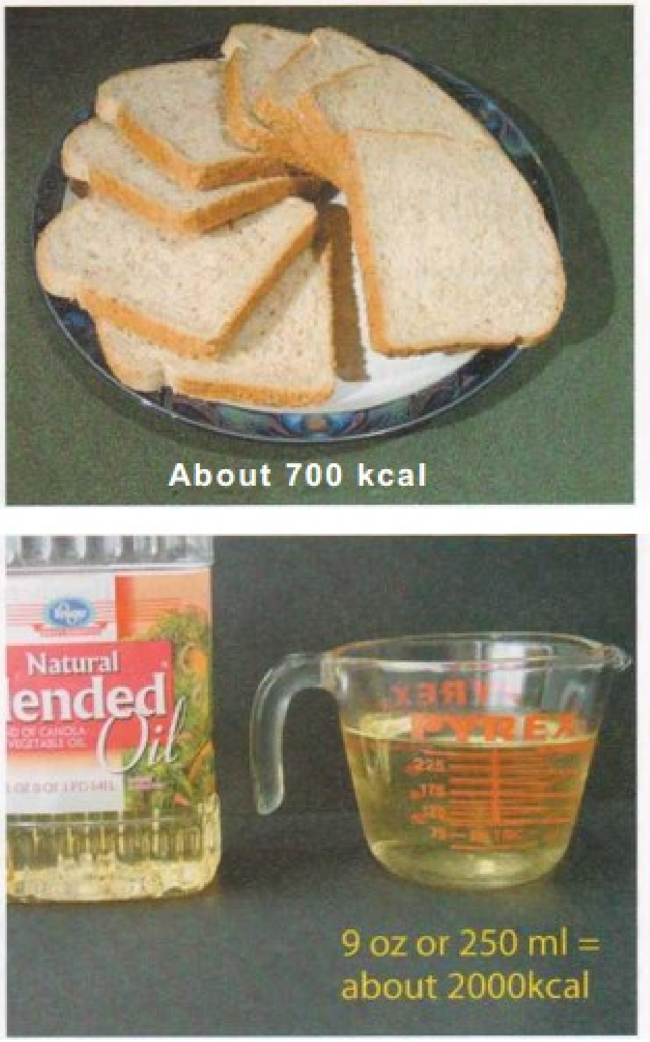


Figure 3-1
Comparative amounts of bread (carbohydrate) and vegetable oil (lipid). Source: Margaret McMahon, The Ohio State University.

Most nutritionists believe that reliance on plant foods as an energy source is healthy because the energy providing carbohydrates is associated with indigestible fiber, which protects us from colon disorders and other so-called diseases of affluence. Of course, these benefits come only with unrefined carbohydrates, such as whole wheat or brown, unpolished rice. Purified carbohydrates such as refined sugar or starch are not as beneficial and carry their own health risks.

An adult needs about 70 grams of protein in a day. Plant foods, especially cereal grains and pulses (peas and beans), often provide enough protein along with the energy that they supply. However a plant diet may not satisfy our protein requirement because it may be deficient in one or more of the amino acids that we require. The essential amino acids are leucine, isoleucine, valine, threonine, methionine, phenylalanine, tryptophan, and lysine; children also require histidine. Plants make these and the rest of the twenty amino acids that make up proteins, but plant proteins often have only a low proportion of some of the essential amino acids, particularly the sulfur-containing acid, methionine, and the basic amino acid, lysine. No common plant food provides the right balance of amino acids, so we would need to overeat to meet our dietary requirements. An exception is the so-called "miracle grain," quinoa (Chenopodium quinoa), which provides enough of the essential amino acids along with its energy content. Animals, being more closely related to us, have a similar amino acid composition and generally provide better-quality protein. Eggs are generally regarded as providing perfect protein and are given a protein score of 100. A balanced diet can be achieved on a plant diet supplemented with a small amount of meat or other animal food. Alternatively, the deficiencies of individual plant foods can be remedied to a large extent by combining them. Grains tend to be low in methionine, whereas pulses (legumes) are low in lysine. A mixture of a grain and a pulse provides a more balanced protein. Many cultures in different parts of the world have based their diet on such mixtures: rice and soybeans in China, wheat and chick peas in the Middle East, corn and beans in South -America (Fig. 3-2).

Carbohydrates, lipids (fats), and proteins are the bulk constituents of our diet. We also need small amounts of other organic molecules, called vitamins. We have some ability to make our own vitamin D, depending on the exposure of our skin to sunlight. All of the other vitamins are plant or microbial products. Most vitamins can be obtained from fruits, vegetables, or grains. Grains and grain flours are a poor source of some vitamins, particularly if they are polished or refined. Vitamin C (ascorbic acid) is found only in fresh fruits and vegetables. Some of the fruits and vegetables that are high in vitamin C are: citrus fruit, pineapples, watermelon, cantaloupe, raspberries, blueberries, cranberries, the cole crops (cabbage, broccoli, etc.), peppers, tomatoes, leafy greens (Fig. 3-3A). Vitamin A is derived from carotene, which is found in green, yellow, orange, or red fruits, vegetables, and grains (Fig. 3-3B). Plant foods do not provide vitamin B12 (cyanocobalamin), which is manufactured by bacteria, especially in the guts of ruminant organisms, so it is available to us in dairy products and meat.

Figure 3-2

Grain and pulse crop combinations such as wheat and peas provide a balance of carbohydrates and protein.

Source: Margaret McMahon, The Ohio State University.

Figure 3-3

(A) Fruits and vegetables rich in vitamin C. (B) Green, yellow, orange, and red fruits, vegetables, and grain provide carotene, which is the precursor to vitamin A. Source: Margaret McMahon, The Ohio State University.

In addition to the organic components, we require six major inorganic nutrients (calcium, phosphorus, magnesium, sodium, potassium, and chloride) and seven micronutrients. All can be obtained from plant foods, although they are often more abundant in animal foods. We can assume most of the time that we are getting enough of the nutrients in the food that we normally eat, but calcium, phosphorus, iron, and iodine are the most likely to be deficient and are called critical nutrients.

If an adult needs 3,000 calories of energy per day and if average US yields can be achieved, it would take about 0.15 hectares of wheat or 0.06 hectares of corn to satisfy this dietary requirement for a year. To improve the protein quality of the diet, beans can be substituted for one-quarter of the grain intake. Again assuming average US yields of soybeans, this diet would take about 0.05 hectares. Yields of soybeans are about the same as those for wheat, so the total area required (0.16 hectares) would not change much on a diet of beans and wheat. However, corn yields are much higher, and a diet of corn and beans would take about 0.09 hectares. This diet would be boring, and it would lack important vitamins (particularly A and C) and minerals. The USDA recommended intakes could be supplied by about 400 grams of fruit and vegetables per day, which would require another 0.02 hectares of land (once more assuming typical US yields). So the wheat-based diet would require a total of 0.16 hectares, and the corn-based diet 0.11 hectares (Fig. 3-4). These figures are optimistic because cereal yields in most countries are lower than in the United States, and soybeans are the highest yielding of the pulse crops. The peas and beans that are mostly consumed by people have much lower yields. It is questionable whether the inputs that are used to attain US yields are physically available or environmentally desirable on a worldwide scale. The United States is exceptionally fortunate in having stable and productive soils and an excess of cropland relative to its population. Worldwide there are about 0.25 hectares (0.6 acres) of cropland for each person. With realistic inputs and yields, this land is about enough to provide everyone with a vegetarian diet.

In addition to the land required to grow crops, we should count the area needed to provide the inputs of energy and chemicals that are used in modern production systems. However, chemical inputs of fertilizer and pesticides can reduce the footprint because they increase the yield from a given area. Area is also required to absorb the wastes generated by food pro-duction. In the past, this factor tended to be ignored,

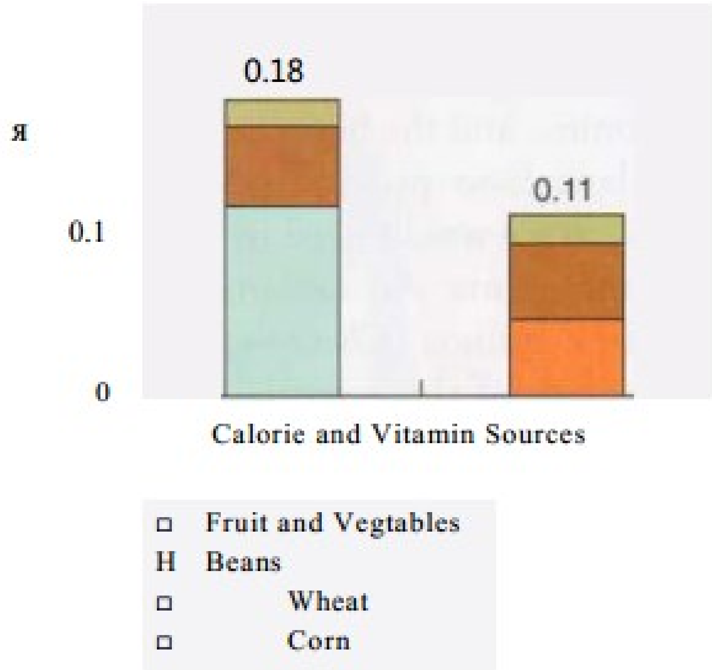


Figure 3-4
Amount of land required to provide an adult with vitamins from 400 g fruits and vegetables, 750 kcal from soybeans, and 2,250 kcal from either wheat or corn. Source: Michael Knee.

with the result that groundwater and surface water became contaminated. Now many crop production facilities large and small use fertilization and pest control practices that minimize chemicals leaching into the groundwater. Many growers provide some kind of buffer vegetation to prevent soil particles and fertilizer from running off from cropland into streams and lakes. Plant waste can often be recycled by composting or incorporation into soil or by feeding it to animals. Animal wastes are often spread on the land. Major problems still occur, however, when wastes cannot be recycled back into the production of crops.

Crop production has become concentrated and specialized in regions and countries around the world. For example, California and

Florida produce more than 60 percent of the fruits and vegetables grown in the United States, which means that crops are often transported thousands of miles between production and consumption points. Although some argue from an ecological perspective that we should consume local produce, the energy costs of transport are much lower than for out-of-season production in a greenhouse (Table 3—2). On the other hand, the nutrient flows arising from food transport do present some problems. The nutrients in the produce are removed from the area where the crop was grown. For example, several coun-tries in Africa and South America produce high-value horticultural crops for export to Europe and North America. These crops tend to have a high potassium content, so an essential plant nutrient is being exported and may not be easy to replace.

The sewerage system transporting human wastes can also be viewed as part of the agricultural footprint. Like animal manure and urine, human waste contains a high level of nutritional elements. Although some municipalities have found ways of composting this waste, it cannot be recycled in food crop production because it is often contaminated with heavy metals and chemicals.

In moist temperate parts of the world, it is easy to forget how much water is needed to produce crops. It can take a ton of water to produce a kilogram of grain, and the water needed to produce our food is at least 500 times our direct intake. In dry areas, a large land surface may be needed to collect water to be used for irrigation to grow crops. The necessity for water in arid locations causes political problems in places such as the American Southwest, the Middle East, and Africa.

Each person in an industrialized country requires about 1 hectare of cropland, which is about 12 percent of their total footprint. While it seems that food consumption is not a major part of the footprint, the area is far greater than it was once thought to be. Furthermore, if everyone lived in an industrial economy, agriculture would occupy all of the world’s land. Because most of the presently unused land is too cold or too dry to support crop production, agricultural use is clearly impossible. The problem arises because people are not eating beans and corn, these crops are being fed to animals, and only 10 percent of the energy that is available in food crops is being recovered in the meat or other animal products. Because of specialization, the crops are often produced on one farm and then fed to animals on another farm that may be hundreds of miles away. The crop grower needs fertilizer to maintain high yields, whereas the stock farm has the problem of disposing of animal wastes, which contain the same nutrients as the fertilizer. Currently, this method is apparently the most profitable way to raise animals, and it is cheaper to buy inorganic fertilizer than to take animal waste back to the cornfields. However, this would most likely change if total energy costs of raising the animals are accounted for..

Forage, Fiber, and Fuel

Ruminant animals can extract energy from plant materials that are indigestible for us, so if they are fed on forage crops or allowed to graze on pasture, the energy recovery can be as high as 50 percent of what we might have obtained from crops grown for human consumption. Although soil problems and climatic limitations make it unlikely that we can increase the area of cropland substantially, much of the land that is unsuitable for crop production can provide grazing for animals. Thus, it should be possible to provide a varied diet for a world population advancing toward 10 billion if we reserve the best land for the production of crops for human consumption and confine animals to grazing on marginal land or limit their consumption to crop wastes. Grazing needs to be managed so that it does not lead to degradation of the soils and vegetation that supports it. On every continent, large land areas have been converted to unproductive scrub or near-desert through overgrazing. The difficulty of managing sustainable grazing is greatest in tropical countries, where the demand for food is often most acute. In principle, pasture can support higher levels of biodiversity than can fields from which crops are harvested. European countries are increasingly seeing the advantage of maintaining countryside that is ecologically diverse and also attractive for visitors.

Historically, farming provided many useful products in addition to food. Most of our clothing and textiles in general were made of plant and animal fibers. Animal skins were used to make most of our footwear and some of our clothing. Agriculture made some contribution to structural materials used for houses and other buildings. Straw was and still is used as a roofing material (thatch) and combined with clay to make bricks. Forestry, however, has been a much more important source of construction materials and fuel. Agriculture provided plant and animal fats that were burned for light but was of minor importance as a source of heat. Forestry and farming compete in providing paper and cardboard; the cheaper products are usually made from wood pulp and the higher grades are made from herbaceous plant fibers such as cotton and hemp. Plants also provided dyes, perfumes, medicines, and other specialized chemical ingredients. Today most of these nonfood materials have been more or less replaced by synthetic materials, often produced from petrochemicals.

Only about 2.5 percent of cropland is devoted to fiber crops, both in the United States and worldwide. Cotton (Gossypium spp.) is the most important and best-known plant fiber crop. Jute (Corchorus spp.) is probably the next most important; it is grown in tropical countries such as Bangladesh and used for coarse string and fabrics such as burlap. Other fiber crops include flax and bamboo, both of which are used for fabrics, and hemp which is used for fabric, rope, and other products (discussed in the following paragraph). The market for natural fibers is stagnant or declining. Although cotton is and is likely to remain a major crop, it is unlikely that production and the area of fiber crops will increase in the near future.

One crop that shows promise of increasing though is hemp (Cannabis sativa), which has growth potential as there is a high demand for its fiber for clothing and other uses. Hemp has a deep root system, which can aid in reconditioning a compacted soil. Unfortunately, hemp grown for fiber is the same species as marijuana. Marijuana plants produce the drug tetrahydro-cannabinol (THC). As a result, the production of hemp for fiber is illegal in many areas of the world. Although closely related, the two types of Cannabis are very different in morphological characteristics. Fiber hemp has the long, unbranched, and sturdy stems required for fiber production. Hemp leaves are relatively small with low THC content. In contrast, the marijuana-type plant is more branched with larger leaves that have high THC levels. Morphological identification of one plant from the other is not difficult.

Because the hemp plant has environmental benefit as a field crop and because the fiber from hemp produces an excellent clothing fabric, many countries, such as Canada, are once again allowing it to be grown, although under strict government control. Currently, hemp production in the United States is illegal but increasing pressure on government agencies is forcing a reevaluation of that policy.

Biofuels result from the processing of plants to produce biodiesel and ethanol for use mainly in internal combustion engines. Oil from soybeans (Glycine max) and other oil crops such as sunflower (Helianthus annus) and canola (Brassica rapa) is extracted and processed to be used as biodiesel fuel. The starches and sugars in corn (Zea mays), sugarcane (Saccharum ojficinarum), and switchgrass (Panicum virgatum) are fermented to produce ethanol. The advantage of these over fossil fuels is that they are renewable and they sequester CO2 during their growing cycle thereby reducing the carbon footprint. Also, the oilseed meal from crops processed for biodiesel and the fermentation residue from ethanol production can be used as animal feed. However, because the crops used are often food crops (e.g., corn, soybeans, sugarcane), using them for fuel negatively affects the food supply for humans and domesticated animals. Even if the crops are not food (e.g., switchgrass), they may occupy land that was formerly used for food crops. Energy is required to produce the fuels so the net gain in fuel energy may be as low as 50 percent.

When the fourth edition of this book was being written in 2003, it was thought that using food crops for fuel would not greatly impact the food supply for many years. However, the use of biofuel sources increased so quickly that by 2007 some food commodities were already being negatively impacted. Corn for human and animal consumption became much more expensive. Also, land that had been used for other crops, such as wheat, was converted to grow crops for biofuels, thus reducing the supply and raising the price of the displaced food crops.

Although corn is one of the most productive ethanol crops, it is not the ideal fuel crop. It requires high-quality land and inputs of fertilizer for efficient production. Furthermore, the gasohol process uses the kernel, the most nutritious part of the plant, which is less than 50 percent of the total dry weight. It would be more advantageous if the fuel crop could be grown on low-quality land and if the fuel could be derived from the whole plant or waste after high-value crops have been harvested. Most of the whole plant or waste is cellulose and no economically viable process converts cellulose to ethanol at present, which is unfortunate because the critical need in the United States and other western countries is for fuel that can be used for transportation.

Nonfuel oil Apart from fiber and biofuel, the major nonfood use of crops is for oil-based industrial products. Tropical oil crops, such as coconut (Cocos nucifera) and oil palm (Elaeis guineensis), are the main

sources of oils used in soaps and detergents. Temperate oil crops, such as canola and soybean (Glycine max), are not suitable for these uses but they are used in the manufacture of lubricants and plastics. Concerns about the future availability of petroleum and the pollution produced by the petrochemical industry have led to suggestions that we should return to using plants as chemical feedstock for detergents, plastics, pharmaceuticals, and other industrial chemicals. Biotechnology could be used to increase the production of existing chemicals or introduce new chemicals into crop plants. For this approach to be economically feasible, the chemical must be sufficiently valuable and the market must be large enough to recover development and production costs.

The current annual value of the US plastics industry, at $110 billion, exceeds that of major agricultural commodities, at $90 to $100 billion. Genetically manipulated canola and soybeans could be used to produce adipic acid, which is used in the manufacture of nylon. For agriculture to capture this $2 billion market, about 5 percent of the total US crop area would be required for canola and 15 percent for soybean. Small molecules like adipic acid must be processed to produce plastic polymers such as nylon. The direct production of plastics in plants is a more attractive possibility. Arabidopsis plants (Fig. 3-5) have been engineered to produce small amounts of polyhydroxybu- tyrate, which suggests that production of plastics in

Figure 3-5

In the future, plants such as Arabidopsis may be genetically engineered to produce chemicals for use in manufacturing, pharmacy, and other industries. Source: Margaret McMahon, The Ohio State University.

plants is feasible. Much development is required, however, and a major commitment of cropland would be necessary to make a significant contribution to the total consumption of plastics. The most rewarding applications of biotechnology may be in the production of high-value therapeutic and diagnostic proteins in plants. These proteins are impossible to produce synthetically and are required only in small quantities. So production of transgenic plants expressing proteins such as vaccines against malaria or rabies could be a profitable small-scale enterprise.

Before the industrial revolution, most of the fuels and raw materials (except for metals) used to manufacture everyday goods were of biological origin. These sources were gradually supplanted by coal and oil, but even in 1930 about 30 percent of raw materials came from plants. At that time, the dominant source was coal, whereas today over 80 percent of chemicals used in industry are petroleum products. Some suggest that this trend will be reversed so that 50 percent of chemical feedstock will be biological by 2050. However, this reversal would require a massive restructuring of the chemical industry and diversion of land from food production.

Medicine

Plants are the source of many drugs and medicines. In fact, until the last century, most medicines were derived directly from plants. From the earliest history of modern humans, the shaman and wise elders of a tribe used herbs to treat diseases and disorders among tribal members. Much of this wealth of plant lore is in danger of being lost as indigenous cultures are absorbed into modem civ-ilizations. Ethanobotany, the study of plant usage by indigenous cultures and the preservation of that knowledge about plants, has become an important branch of plant science.

Today, about 25 percent of pharmaceuticals are based on plant products, and the rest are produced synthetically. One example of a modern-day medicine that can trace its roots to usage by Native Americans is aspirin. Salicylic acid, the pain-relieving component of aspirin, is found in the bark of willow trees (Salix). Native Americans chewed willow bark to relieve pain.

Many other modern medicines are directly derived from plant materials. Examples include quinine, which is used to treat malaria, and the heart medication, digitalis. Morphine, opium, codeine, and heroin are all pain-relieving extracts of the opium poppy (Papaver somniferum). Cocaine, another painkiller, is derived from the coca plant (Erythroxylum coca). However, each of these pain-relieving drugs also has addictiveproperties. Addiction to these chemicals has become a major problem worldwide, as is finding alternative crops for farmers who grow illegal crops.

One of the newest plants to be recognized for its medicinal benefits is a yew (Taxus) that produces taxol, a chemical that shows promise in the treatment of cancer. The taxol-producing species grows wild in the Pacific Northwest and is now being evaluated as a potential crop plant for areas where it would grow well.

Pleasure, Ornamental, and Recreational Uses

After looking at the challenges of obtaining food and industrial resources from plants, it may seem frivolous to consider the ways in which plants give pleasure. However, strong reasons for consuming or using plants in these ways lead to some of the most profitable plant-based industries. In rich countries, food consumption is driven as much by hedonic (pleasure-giving) factors as nutritional require-ments. We consume particular foods because of the sensory stimuli of appearance, texture, taste, and aroma that they provide. Some of the plant products that we consume provide pleasure but no nutritional benefit; they may even be harmful to our health. Tobacco and various forms of alcohol fall in this category, although they also represent some of the most profitable ways of using land. However, because of tobaccos connection to cancer and other health problems, the demand for the crop has dropped. Like opium poppy farmers, tobacco farmers are now looking for alternative crops to grow.

Tropical countries can find it much more profitable to grow coffee or tea for export than to produce staple food crops. The craving for sweets is one of the most pervasive human desires and underlies our demand for sugar. Sugar provides energy but we do not really need it in our diet. Sugarcane in the tropics and sugar beet in temperate countries tend to be more profitable than staple food crops and often supplant the staples. In the United States, the bulk of the market for sweetener has been taken over by corn syrup. About 8 percent of the corn crop is used in this way, which (like ethanol production) helps raise corn prices.

Since neolithic times, human beings have coevolved with agricultural plants and animals. People have shaped plants and animals through selection and breeding, and these organisms have influenced our physiology, psychology, and sociology. As cities developed, people were less intimately involved with plants and animals in their daily lives. It is even possible to forget that bread, meat, or milk were once part of living organisms. However, people retain an affinity for plants and animals: our desire for pets and ornamental plantsmay be an aspect of a deep-seated human tendency that E. O. Wilson has called “biophilia” (Fig. 3-6). One of the most persistent, if minimal, expressions of biophilia is the desire for cut flowers or potted plants in the home or workplace. In cool-temperate areas, these plants are mostly produced in greenhouses. Because of the high market value of floral crops, greenhouse production can be more profitable than vegetables production. However, as we saw with vegetables, it is often cheaper in energy and economic terms to produce cut flowers in warmer countries and then transport them to the United States or Europe. Flowers are generally more perishable than vegetables, however, and it is usually necessary to ship them by air, so the energy advantage may not be so great, especially as fuel costs rise.

Lack of space and limited transportation encouraged intensive development of cities in Europe in the nineteenth century. There was little room for plants where people lived, but even today nearly every home has plants in small gardens, windowboxes, in pots and vases inside the home, and even on rooftops. In the twentieth century, the United States developed a new kind of city with extensive open space between houses and other buildings. While 75 percent of Americans are said to live in urban areas, it is more accurate to say that most of them live in suburbs. Cities and suburbs themselves occupy an area equivalent to about half the area of cropland in the United States. Built-up areas are expanding at a rate equivalent to 0.5 percent of crop area per year. Many argue that this expansion occurs at the expense of agriculture and will cause farm commodity prices to rise by taking land out of production and reducing the supply of agricultural products.

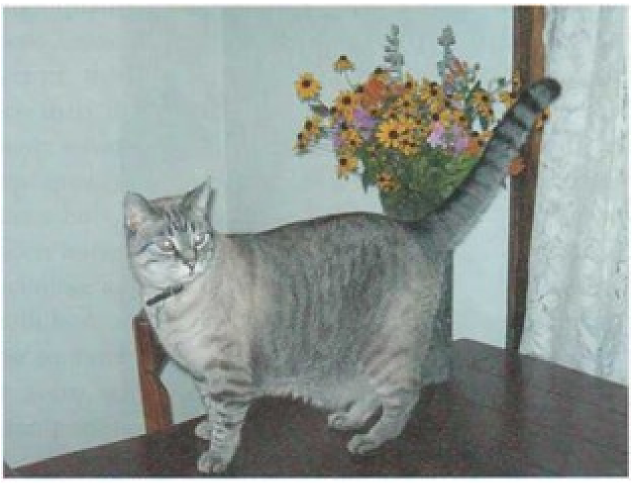


Figure 3-6

Biophilia is the term used to describe our desire for pets and ornamental plants. Source: Margaret McMahon, The Ohio State University.

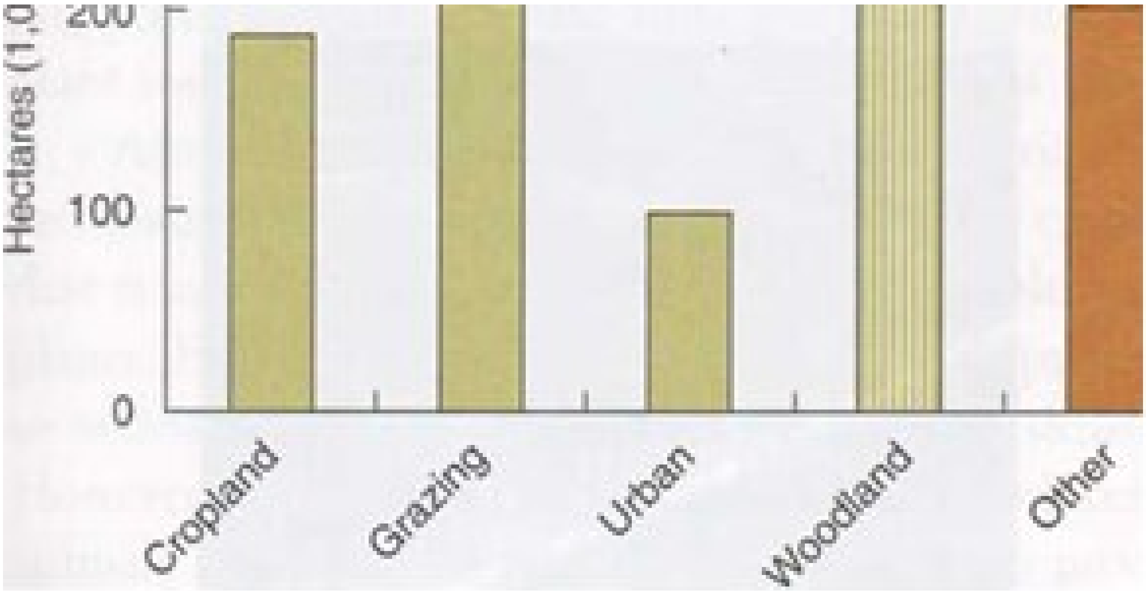


Figure 3-7

Land use in the United States. The areas of human use are shaded. Woodland is highlighted because some of it is unused (compare with Fig 2-14 on page 29). Source: Michael Knee.

Rooftop gardens or green roofs are becoming much more popular in the United States. A new area of the construction and ornamental industries is developing around this, including architectural design, production of suitable plants, installation, and maintenance. Very little land in the urban and suburban biome is used for plants that we need for food or fiber (Fig. 3-8). However, in many cities, small "urban farms" are now being created on plots of land that are not suitable for development. These "farms" provide both food and ornamental plants and plant products to local residents.

There are thousands of ornamental species, most of which are not native to the US. The introduction of so many species occurred because early European settlers struggled not only to grow food, but to make a congenial home out of the North American forest and prairie. Most of the native flora did not seem attractive and was removed. New plants were brought deliberately or by accident to repopulate the land. The trend continues today with most of the new ornamental species being nonnative. As a result, a modern landscape may include plants from different biomes: spruce from the boreal forest, cannas from the tropics, yucca from the desert, and hostas from the temperate forest (Fig. 3-9). A large part of the economic and environmental cost of landscapes results from the attempt to maintain nonnative plants in unfavorable climates. Another downside to this humanmade diversity is that, after introduction to the United States, some ornamental plants have escaped to become agricultural weeds. Others have become invasive and displaced native species. This creates a serious disruption in the ecosystem and negatively affects the lifecycles of species dependent on the native plants.

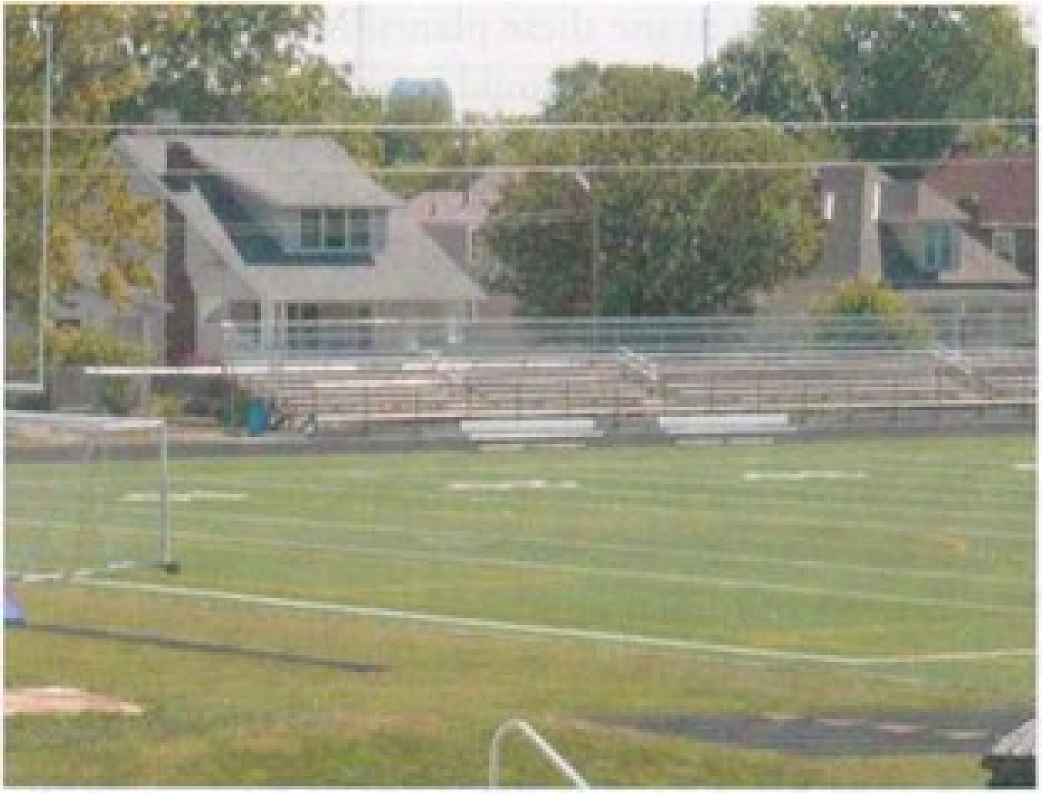


Figure 3-8

The "suburban biome" consists of plants that we look at or utilize for aesthetic appeal, sports, and recreation rather than for food, fiber, or industrial purposes.

Source: Margaret McMahon, The Ohio State University.

Figure 3-9

These plants come from many different biomes and have different environmental requirements which can create challenges to maintaining the plants.

Source: Margaret McMahon, The Ohio State University.

Many people have argued recently that we should use native plants to try to create landscapes with a more distinctively American style and heritage and to avoid the problems that come with nonnative plants. However, strong social and cultural reasons lead most people to continue to plant landscapes using the introduced species.

The scale of urban areas and the cultivated landscapes within them means that agriculture can no longer be regarded as the only significant source of pollution from fertilizers and pesticides. About the same rate of fertilizer application is recommended for turf as for corn or other cereals. Environmental Protection Agency (EPA) data imply that more pesticides, mostly herbicides, are applied to lawns than to agronomic crops. The productivity promoted by these chemical applications is mostly unwanted. Fruits, seeds, and even flowers are regarded as a nuisance when they drop from ornamental plants onto sidewalks. Almost every homeowner is encumbered by a surplus of grass clippings throughout the summer and leaves in the fall. The disposal of this waste has created problems in landfills and other waste collecting facilities. Several municipalities now have mulching/composting facilities and sell the mulch and compost to help pay for the cost of collecting the waste. Many homeowners now collect grass clippings for use as mulch or compost. Some chip their own wood waste for use as mulch.

Nurseries, greenhouses, and sod farms provide the plants for the urban environment (Fig. 3-10). These crops with purely aesthetic value are produced in about 6,800 hectares of greenhouses and 280,000 hectares of open area, which corresponds to about 0.15 percent of the US crop area or about 1 percent of the area used for corn. Yet the combined value of the ornamental crops is about 50 percent of the value of corn. Ornamental crops are much more labor intensive than are other crops, accounting for nearly 20 percent of US agricultural labor costs. But on the other hand, these enterprises provide jobs for many people, from day laborers to corporate executives. Ornamentals may also require more intensive use of fertilizers and pesticides than traditional agriculture. However, many green-houses and nurseries now practice water and fertilizer recycling and use low environmental impact methods of pest control whenever possible.

Figure 3-10

(A) Nurseries, (B) greenhouses, and (C) sod farms provide most of our ornamental and recreational plants. Source: A and в, Margaret McMahon, The Ohio State University; C, Dave Gardner, The Ohio State University.

Although only a few crops provide most of the material for our food and fiber needs, there are an inestimable number of crops grown on a smaller scale for many different reasons. These crops provide variety in our diets, materials for manufacturing, pharmaceuticals, health aids, perfumes, etc. In addition, many different plants are grown for ornamental and recreational use. These relatively small-scale crops can play a very important role in local and regional economies.

SUMMARY AND REVIEW

The human nutritional requirements for carbohydrate, fat, protein, vitamins, and minerals can be met from plant sources, with the important exception of vitamin B12. Assuming average US yields, adequate nutrition can be obtained from the less than 0.25 hectares of cropland that is available for each of the 6 billion people on the planet. Energy and nutrients are lost when crops are fed to animals, and less people can be fed in this situation. However, meat and dairy products can be produced by animals that graze on land unsuitable for crop production. The wastes generated by the food production system and by human and animal consumption of the food are part of the human footprint. Waste management is an important consideration when growing plants.

Historically, farming provided raw materials for the manufacture of textiles, fuels, and various chemicals, including dyes, perfumes, and medicines. Today, many of these materials are produced from synthetic (usually petrochemical) sources. As oil supplies diminish, however, there is renewed interest in plant sources.

In the future, plants may be used to produce not only traditional products for industrial use but new products, especially chemicals, that result from genetically engineering the plants.

The production of sugar, alcohol, and tobacco for enjoyment can be highly profitable, but they are not a necessary part of nutrition and can even be harmful. In the case of tobacco, alternative crops are being developed. Other crops are appreciated for their visual appeal or recreational use. For the urban and suburban population, flowers, turfgrass, shrubs, and trees are an important part of the environment. These crops are at least as demanding as agriculture for energy and chemical inputs and generate significant quantities of waste. Non-native landscape plants can become invasive and displace native biodiversity.

Displacing native diversity can negatively impact the environment. Practices that reduce the ecological impact of ornamental and recreational plants are as important as those practices for food, fiber, and fuel crops.

KNOWLEDGE CHECK

1. What is the advantage of plant fats over animal fats in the human diet?
2. What is the advantage of having a little meat in a human diet?
3. Why do we say that using chemical inputs of fertilizer and pesticides both raises and lowers our energy footprint?
4. What happens to the mineral nutrients (that would normally be recycled back into the soil after a plant dies) when a crop is harvested and shipped to another location? How does that influence the need to add fertilizer for the next crop?
5. What advantage is there to grazing animals on land that is not suitable for other types of crop production?
6. Why is it illegal to grow hemp in the United States and why is there an interest in making it legal?
7. What are the two main types of biofuels and what are some of the plants used for each?
8. Describe two of the issues associated with growing plants for biofuels.
9. What kinds of chemicals are likely to be the most rewarding to produce in genetically engineered plants?
10. What is biophilia and how does it relate to the kinds of plants we grow?
11. Why do we now have to consider urban and suburban landscapes as significant sources of environmental pollution?
12. What are some ways that nurseries and greenhouses are reducing their footprint on the environment?

FOOD FOR THOUGHT

1. Eighty percent of our food energy comes directly or indirectly from six major crops (wheat, corn, rice, sweet potato, white potato, and cassava or manioc). Many people in the world eat little other than one or two of these crops and lack the balanced nutrition that comes with eating a wide variety of fruits, vegetables, and grains. What are some ways you would suggest to get more variety into the diets of those people?

2. If you were asked to give your opinion on the use of biofuels to lower our reliance on petroleum based fuels, what would you say and why would you say it?

3. If you are ever considering plants to landscape the yard where you live, what types of plants would you want to use and why would you want to use those types?

FURTHER EXPLORATION

POWERS, L. E., AND R. MCSORLEY, 2000. *Ecological principles of agriculture.* Albany, NY: Delmar SIMPSON, B. AND M. OGORZALY. 2000. *Economic botany: Plants in our world.* 3rd ed. Columbus, OH: McGraw-Hill THOMPSON, J. W. AND K. SORVIG, 2000. *Sustainable landscape construction.* Washington, DC: Island Press.

UNITED STATES GOVERNMENT. 2006. Energy crops: Corn, oil seeds, wheat, rice, residue. Washington,

DC: Progressive Management. *Note:* This is a two-CD set featuring over 50,000 pages of government documents in PDF form. Its long title is

21st Century Guide to Energy Crops and Biofuels, Agricultural Residue, Corn and Wheat Stover, Rice Straw, Oil Seeds, Switchgrass, Feedstocks, Sugars, Biorefineries, Ethanol, Syngas.

WILSON, E. O. 1996. *Biophilia.* Cambridge, MA: Harvard University Press.

*4

Climate

MICHAEL KNEE AND MARGARET MCMAHON

key learning concepts

After reading this chapter, you should be able to:

- Describe the factors that create climate.
- Explain the interaction between climatic variables and how they vary from location to location.
- Describe how climate factors influence plant growth and determine what plants can grow in an area.
- Discuss what can be done to modify climate factors to improve crop growth.

Climate

Climate is defined as the prevailing weather conditions of an area.

It includes the intensity and duration of solar radiation; the tempera-ture, rainfall, and wind speed and direction that may be expected; and how these characteristics vary according to the season. These character- istics may be summarized as averages or ranges of expected variation to define climate. Because variation or instability in climatic variables is itself an aspect of climate, the summary values may not correspond to the actual weather experienced at a particular time. So weather is defined by the actual values of climatic variables and is not the same as climate.

The climate of an area is determined primarily by the input of solar radiation, which varies with latitude and season. Solar radiation deter-mines or influences all of the other variables that make up climate.

Climate is modified by local features such as altitude, the presence of land or water, and barriers to air circulation. Large-scale features such as continental land masses, mountain ranges, or oceans contribute to macroclimate. Similar but smaller effects can be caused by small-scale features such as buildings, ponds, or depressions in the ground; these fea-tures can contribute to a microclimate.

As we saw in Chapter 2, climate determines the kind of natural vegetation that grows in an area, but vegetation also has a modulating effect on climate, which can occur on a large or a small scale. A large area of forest can make the climate more moist, whereas a small group of trees may act as a windbreak or provide shade. Various human activities also modify climate, often inadver-tently. Areas of human settlement tend to be heat islands, with higher temperatures than the surrounding countryside. Forest clearance tends to lead to drier climates. Dust and other pollutants generatedby human activity reduce light intensity and can increase rainfall.

All plants are characterized by their climatic adaptation. Wild plants evolved to survive and grow optimally in the climatic conditions of their natural habitats. The requirements might apply to a whole species, but there are often ecotypes whose adaptation differs from other members of the same species. For example, one ecotype might have greater tolerance to cold, require a shorter growing season, or require a longer day length for flowering than. The same adaptations occur in cultivated plants, and we can improve a plant's success in an area by exploiting ecotypic variation through the selection of plants adapted to local conditions.

SOLAR RADIATION

The major energy input for the earth comes as electromagnetic radiation from the sun. The sun itself gives off a smooth and continuous spectrum of radiation from shortwave UV light to long-wavelength infrared. Atmospheric components absorb some wavelengths in this range more than others so that the spectrum has peaks and valleys. Much of the solar radiation is in the infrared wavelengths, and only about 40 percent of the energy occurs between 400 and 700 nanometers (nm), the region that supports plant photosynthesis (Fig. 4—1).

The intensity of solar radiation is highest at the equator and decreases at higher and lower latitudes for two reasons, both relating to the angle at which the radiation is received (Fig. 4-2). At the equator, the angle of the sun is always close to 90° relative to the earths surface. The radiation travels the least distance through the atmosphere and reaches the minimum surface area. Moving toward the poles, the angle of approach decreases toward zero so that light travels further through the atmosphere and spreads over a wider surface area. The result is that the intensity at noon at 40°N is about 60 percent of the value at the equator. Clouds absorb a high proportion of incoming radiation and accentuate the difference between latitudes (Fig. 4-3).

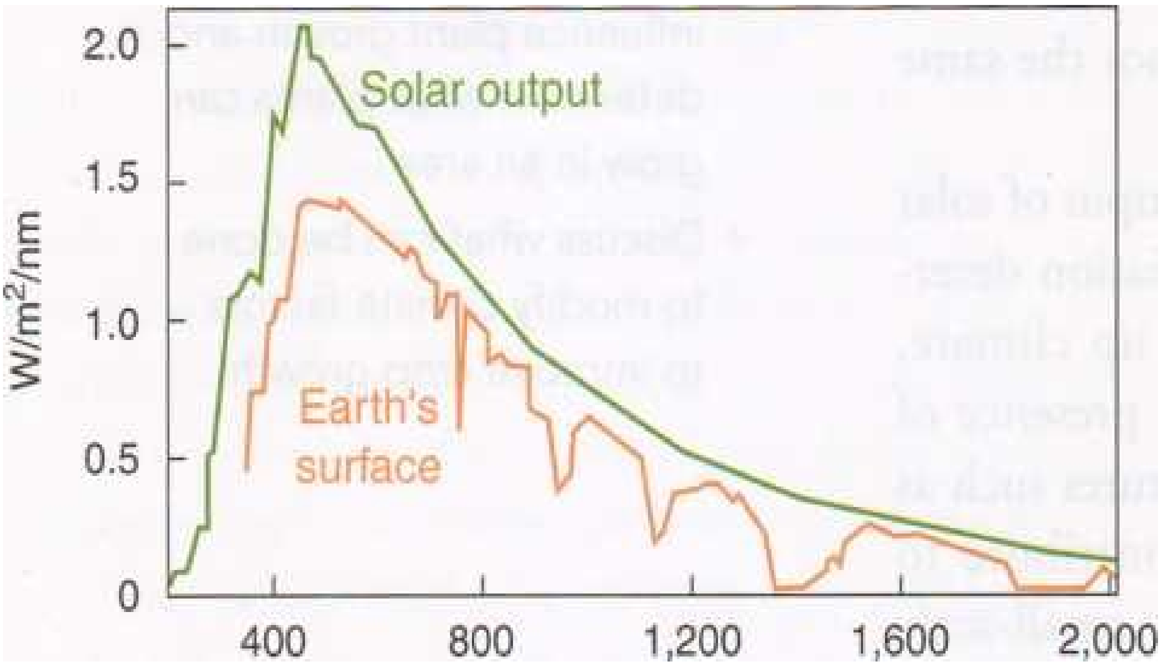


Figure 4-1
Effect of atmosphere on the spectrum of solar radiation.

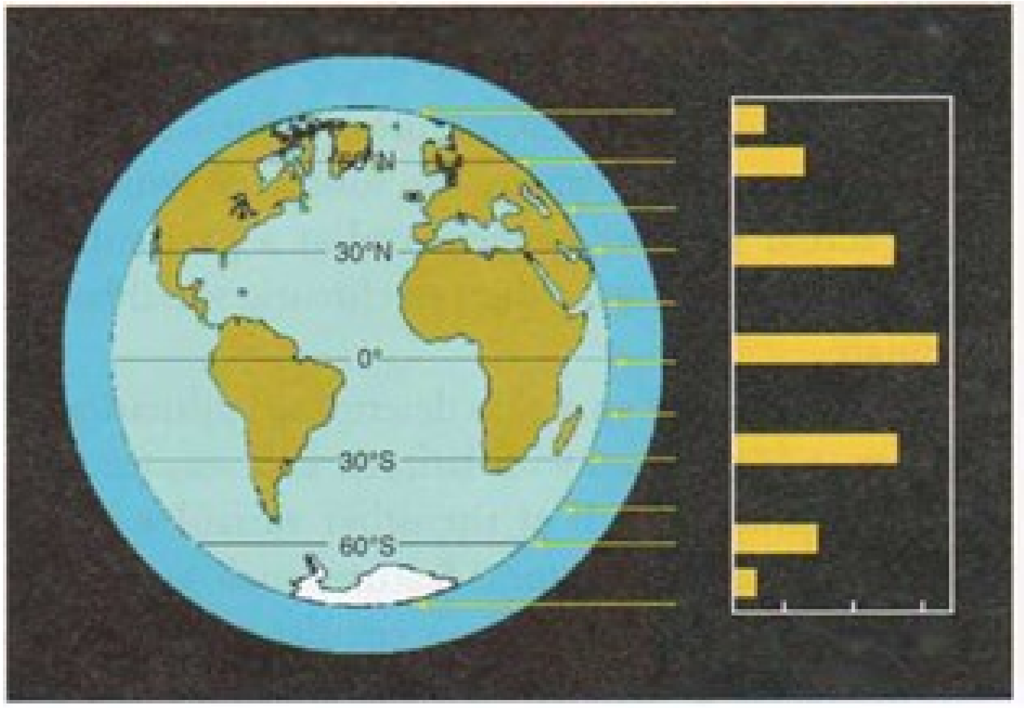


Figure 4-2

Solar energy reaching the earth's surface. Solar radiation passes through more air and is spread over a wider area at higher latitudes. Source: Michael Knee.

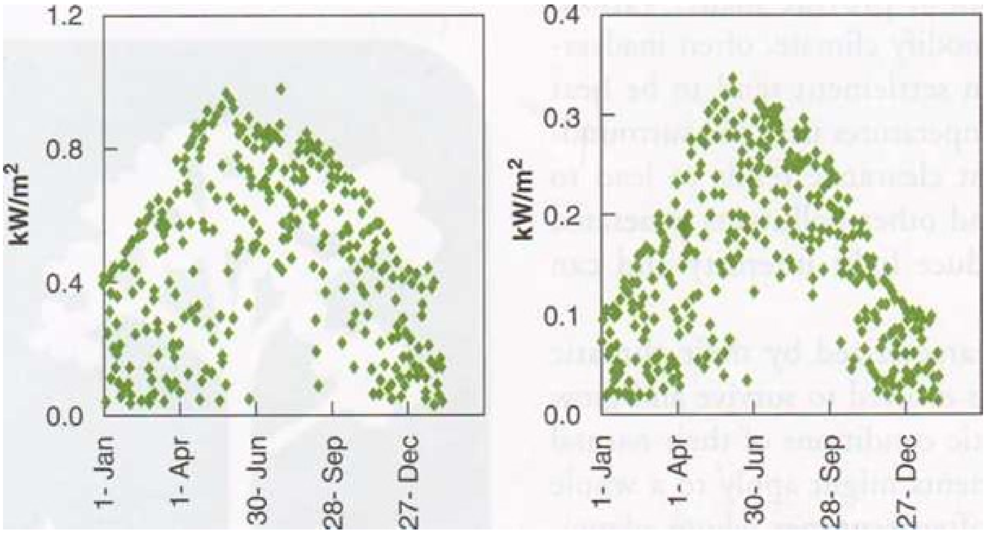


Figure 4-3

Example of variation in solar radiation over a year in Columbus, Ohio (40°N), showing peak radiation at noon and the average for the day. The upper boundary points represent clear skies. Cloudy conditions reduce radiation, particularly in the winter months.

Source: Michael Knee.

Because the earth revolves once in twenty-four t:urs- the average day length throughout the world is twelve hours. However, day length varies through the year recluse of the tilt of 14.5° in the earth's axis (Fig. 4-4). A: the summer solstice, the tilt is toward the sun, and нy _ength varies from twelve hours at the equator to twenty-four hours at the pole. At the winter solstice, : tilt is away from the sun, and day length varies from . it the pole to twelve hours at the equator. At the t tins; and autumn equinox, the axis is not tilted rela- trv; to the sun, and day length is twelve hours every- ~ere on earth. In Hawaii, at 20°N, day length varies titr esn 10.8 and 13.2 hours; in Columbus, Ohio, at -r: n, it varies between 9.2 and 14.8 hours; and in Anchorage, Alaska, at 60°N, it varies between 5.6 and 18.4 hours. Variations in day length add to the effect of variation in light intensity with latitude. In higher latitudes, winter is doubly unfavorable for plant photosynthesis and growth because of short days and low light intensities. On the other hand, cool-season vegetables can grow fast and large during the long cool days of summer in Norway beyond the Arctic Circle. Greenhouses allow for the production year-round of plants, but low light in the winter can make it difficult for the plants to photosynthesize enough to produce quality plants and sufficient yield.

When light intensity is too low for adequate photosynthesis, artificial light can be used. However, even the most efficient artificial light sources convert only a fraction of the electrical energy to photosyntheti- cally active radiation. Thus, it is expensive to achieve light intensities similar to sunlight and almost impossible to do so on a large scale. High intensity discharge

(HID) lights are the only type of artificial light source currently available that can be used in greenhouses to promote growth of high-value crops when natural light intensity or duration is too low. HID's are most effective when used to supplement solar light and not as the sole source of light.

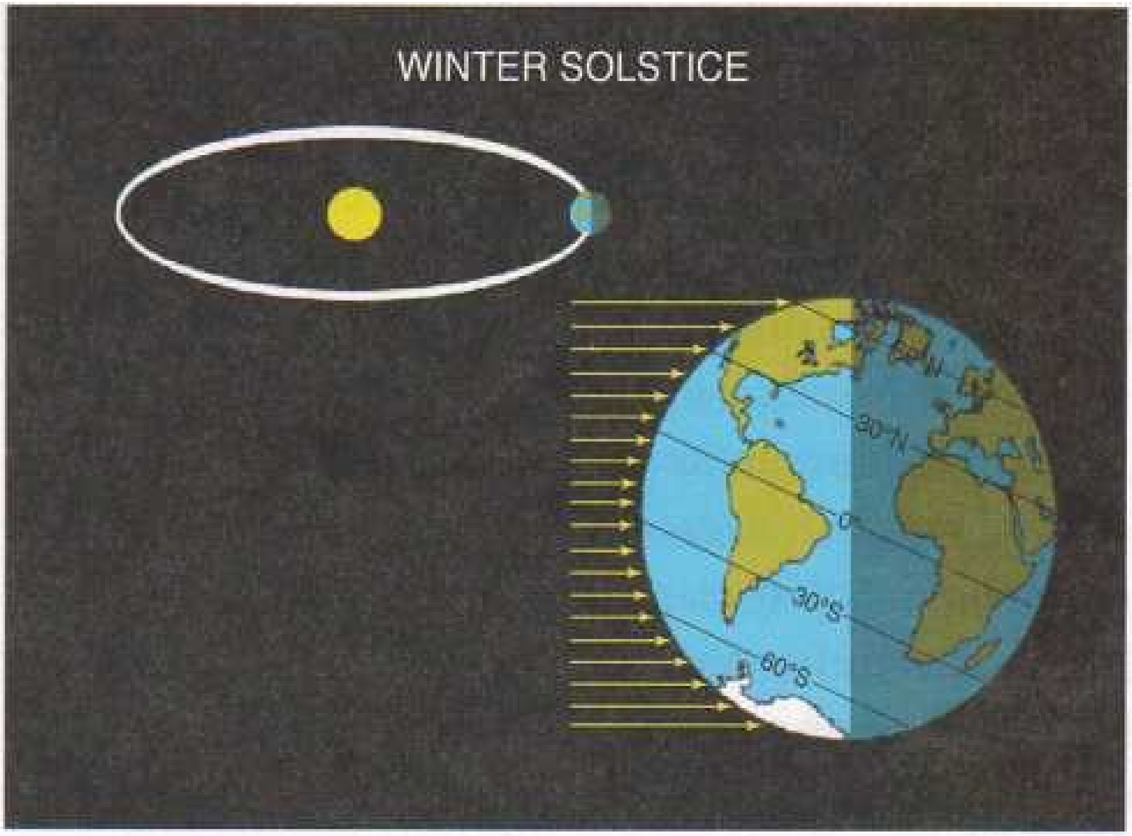


Figure 4-4

The tilt in the earth's axis causes variation in maximum intensity of solar radiation and day length throughout the year.

Source: Michael Knee.

Day length has more subtle effects on plant growth apart from photosynthesis. Like other organisms, plants have a biological clock and can keep track of the duration of light and dark. Some plants flower and bud-break occurs in many trees when days exceed a certain critical length. Conversely, other plants flower and leaf fall occurs in trees when days are shorter than a certain critical length. Plants that flower in response to day length are photoperiodic and the response is called photoperiodism. Plants that flower when the light period exceeds a critical length are called long day plants. Short day plants are those that flower when the light period is less than a critical length. A short day with a night break of a few minutes has been shown to be equivalent to a long day. For this reason, some have argued that short- and long-day plants would be better described respectively as long-night plants and short- night plants. However, because the terms short- and long-day plants still predominate, they will be used in this book.

As with light intensity, plants are often adapted to the conditions of their natural habitat. So ten hours could count as a short day for a tropical plant but a long day for a plant from northern latitudes. That is, when the day is longer than 10 hours, the tropical plant will not flower and when the day length is less than 10 hours, the northern plant will not flower. When a plant species occurs over a wide range of latitudes, local ecotypes are often adapted to the local day length. This feature applies to flowering dogwood (Cornus florida) and many other ornamental trees in North America. If northern ecotypes are taken to the south, bud-break can occur too soon and flowers can be injured by late frosts. Similarly, soybeans are short day plants and varieties have different critical day lengths. A variety developed for Minnesota would be ill-suited for Kentucky.

Plants tend to adapt to the light conditions prevailing in their natural environment. Plants growing in open environments in the tropics grow well at higher light intensities than do those from higher latitudes. Of course, the presence of taller vegetation, particularly trees in forests and jungles, reduces the light intensity reaching lower vegetation. Under a continuous forest canopy, the light intensity may be 1 to 10 percent of that above the canopy. Plants of the forest floor have adapted to

photosynthesize and grow under these conditions and often cannot tolerate direct exposure to the sun. Indoor light levels are similar to those of the forest floor. That is why many indoor plants are understory species, such as ivies and ferns from temperate forests and Spathiphyllum and Epipremnum from tropical forests.

Plants adapted to high light often grow tall and spindly when they are shaded by other plants. This is called the shade avoidance response. Both photoperi- odism and shade avoidance are examples of photomorphogenesis, which means plant shape determined by light quality. Part of the process by which photomorphogenesis occurs involves a light-absorbing protein called phytochrome. This protein responds differently to light in the red (centered at 660 nm) and far-red (centered at 730 nm) regions of the spectrum. The state of the protein and the response of the plant are affected by the relative energy at these wavelengths. There are naturally occurring variations in the amount of red and far-red light reaching the earth's surface and the phytochrome molecule responds to these variations. For example, the end of the day is marked by a decrease in the ratio of red to far-red (R:FR) light. This shift in ratio allows the plant to sense daylength.

The shade avoidance response occurs because leaves absorb more red light than far-red light so that plants growing in the shade of other plants experience a lower R:FR than unshaded conditions. Far-red light promotes stem elongation so the low R:FR accounts for the spindly growth. Although the spindly growth results in a weaker plant, by rapidly growing tall, the plant can become taller than its neighbors and begin to capture more light for photosynthesis and become stronger.

The sensing of light for photoperiodic and other photomorphogenic responses occur at much lower light intensities than are needed by most plants for photosynthesis. So it is quite possible to use lower intensity artificial light to promote flowering in long- day plants or prevent flowering in short-day plants. However, when shade material is used to prevent flowering in long-day plants or to promote it in short-day plants, almost all of the light must be blocked by using opaque material When using shade to control photope-riod, it is particularly important to avoid accidental light exposure during the dark period. The intensity of street lighting in urban areas is enough to cause problems of delayed leaf-fall and premature bud-break in shrubs and trees through similar effects.

When crops are grown in rows oriented north- south, the plants tend to experience more far-red light as the sun moves from east to west than do plants in rows oriented east—west. Soybean plants in north-south rows have been shown to have longer internodes and smaller leaves than soybean plants in east-west rows. Greenhouse crops often grow too tall because they are grown closely together and the shade avoidance response is induced. One way to reduce plant height is to give the plants more space. In addition to the photomorphogenic crowding response, the plants are not exposed to the mechanical stimulation of wind and weather, which inhibits stem elongation in outdoor plants. Photomorphogenic responses may be involved in differences in plant growth observed when crops are grown with different-colored mulches on the soil surface. Current research is investigating the potential of far-red-absorbing filters to control stem elongation in the greenhouse. For a more detailed description of photomorphogenic response and control see Chapters 8 and 24.

MOISTURE AVAILABILITY

Nearly all of the world's water (97.6 percent) is in the oceans and much of the remainder (2.1 percent) is frozen. Groundwater accounts for 0.3 percent of the total, while only 0.01 percent exists as fresh water in lakes and streams. A tiny but important fraction (0.001 percent) is present in the atmosphere. Plants can draw on a fraction of the water in the ground, but much of it is below the depth of root penetration. We can use fresh water to supplement the supply in the soil for the growth of crops, but the available water would soon be exhausted if there were not some way of replacing it. Groundwater and the surface fresh-water supply are replenished through the hydrologic cycle (Fig. 4-5), which is driven by the input of solar energy, both directly as radiant heat that promotes evaporation of water and indirectly through air currents that move water vapor from one area to another. Water vapor then can precipitate as rain or snow bringing fresh water to that area.

Water evaporates from open-water surfaces, the ground, and from plants. Evaporation from plants involves the process of moving water through the plant and evapotranspiration, often just called transpiration. Evapotranspiration cools the plant to keep it from overheating. For most plants, photosynthesis cannot occur without simultaneous transpiration. As water vapor escapes through pores in the leaf surface called stomata, the carbon dioxide needed for photosynthesis enters the leaf through the pores at the same time.

The amount of water vapor that air can absorb depends on air temperature: the cooler the air, the less water it can hold. As moisture-laden air rises or moves to

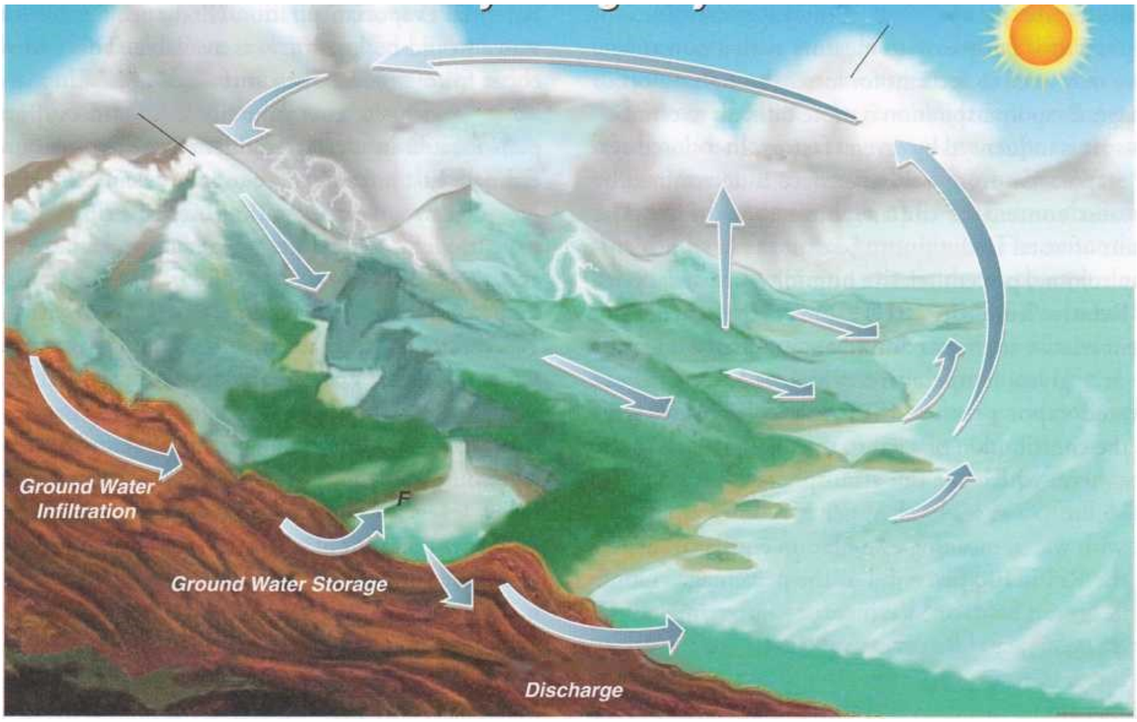


Figure 4-5
The hydrologic cycle. Source: U S Geological Survey,
http://ga.water.usgs.gov/edu/watercycleprint.htmi

cooler regions of the earth, condensation forms fog close to the ground or clouds in the upper atmosphere.

If we want to find out the suitability of an area for crop production or determine the day-to-day waterneeds of crops, we need to know the relationship between the supply of water or precipitation and the demand by the plants in terms of evapotranspiration. Precipitation is fairly easy to measure with a rain gauge, but we may need to account for losses through runoff or drainage. Evapotranspiration is more difficult to estimate because it is influenced by several factors. In a closed system, evaporation from a water surface is determined by the water content of the air above the surface. The amount of water in the air can be expressed as a percentage by volume, percent relative humidity, or partial pressure. Relative humidity (RH) expresses the actual water content relative to the maximum amount that the air can hold at a given temperature, which is known as the saturated vapor pressure (SVP). Partial pressure indicates the contribution of a gas to the total pressure of the atmosphere, which for the atmosphere is around 102 kPa (15 lb/in.2) at sea level. When air comes to equilibrium with water, meaning evaporation equals condensation, the RH is 100 percent, but the percentage volume that the air can hold, or SVP, increases with temperature. It is also possible to identify a temperature for any actual vapor pressure or percentage volume at which RH would be 100 percent; this point is called the dew point. RH tends to be 100 percent when it has just rained or when the temperature drops and the dew point is reached because the partial pressure becomes equal to the SVP. At other times, RH is less than 100 percent and the difference between the actual vapor pressure and the SVP is called the vapor pressure deficit (VPD). Evaporation and plant transpiration are influenced by VPD rather than humidity. Much more water evaporates at 70 percent humidity at 30°C than 70 percent at 10°C because the VPD is much higher at 30°C.

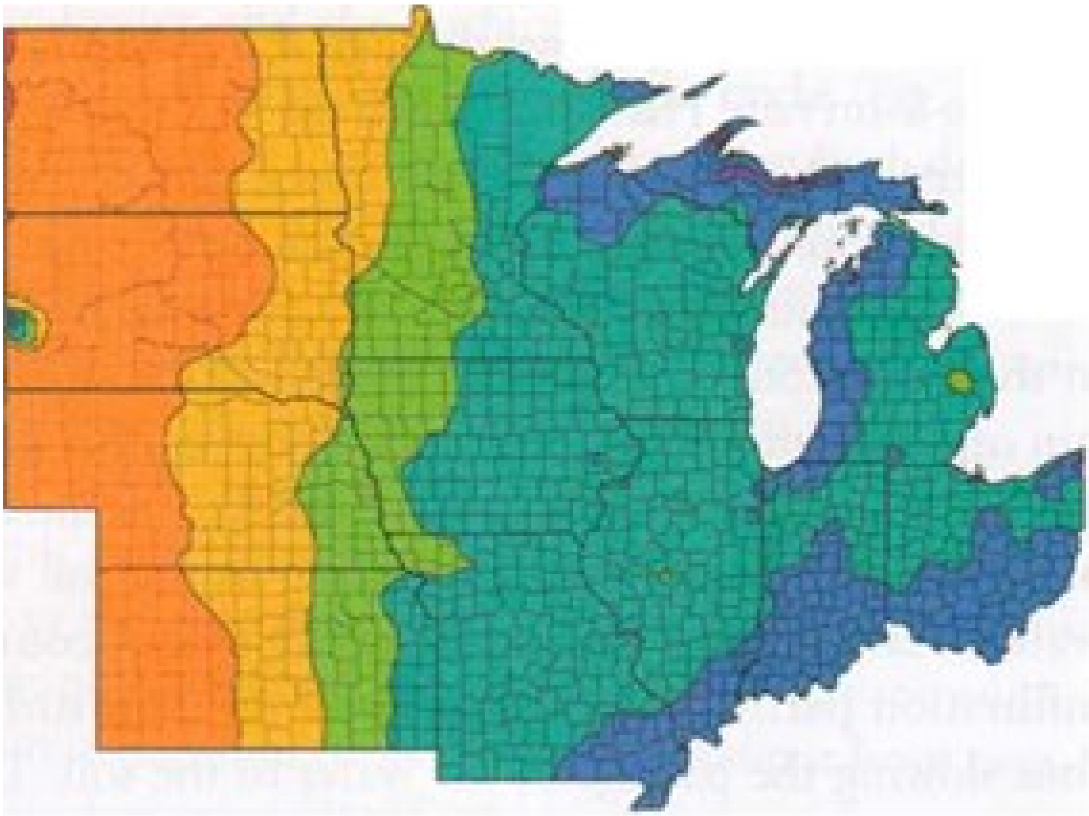


Figure 4-6

The balance between potential evapotranspiration and precipitation in the central United States. East of 95°, precipitation exceeds evapotranspiration. Precipitation is spread nearly uniformly throughout the year. However, high evapotranspiration rates in the summer often exceed precipitation during that season, causing drought conditions at times. Source: USDA.

The balance between evapotranspiration and precipitation defines whether the climate is moist or dry and whether irrigation is likely to be necessary to produce crops. In the United States, east of about 95°W, there is a surplus of precipitation over EtQ, but rainfall is spread throughout the year and Et0 regularly exceeds precipitation in the summer (Figs. 4-6 and 4-7).

Thesituation is more extreme in areas such as the Pacific Northwest, where there is a Mediterranean climate and most of the rain falls in the winter (Fig. 4-8). (A Mediterranean climate is characterized by cool, wet winters and warm, dry summers.) Soil typically holds about 100 cm of water in the plant root zone. After the soil is saturated, the excess water runs off or drains away. It is important for spring planting that the soil should be fully charged with water, but waterlogged conditions are harmful for most crops. In many parts of the United States, it is necessary to install drainage systems to get rid of a seasonal excess of water. Successful water management involves regulating the availability of water to meet evaporative demand. Of course, if water is not present, evaporation does not occur and actual Et is much lower than Et0. For most crops, this

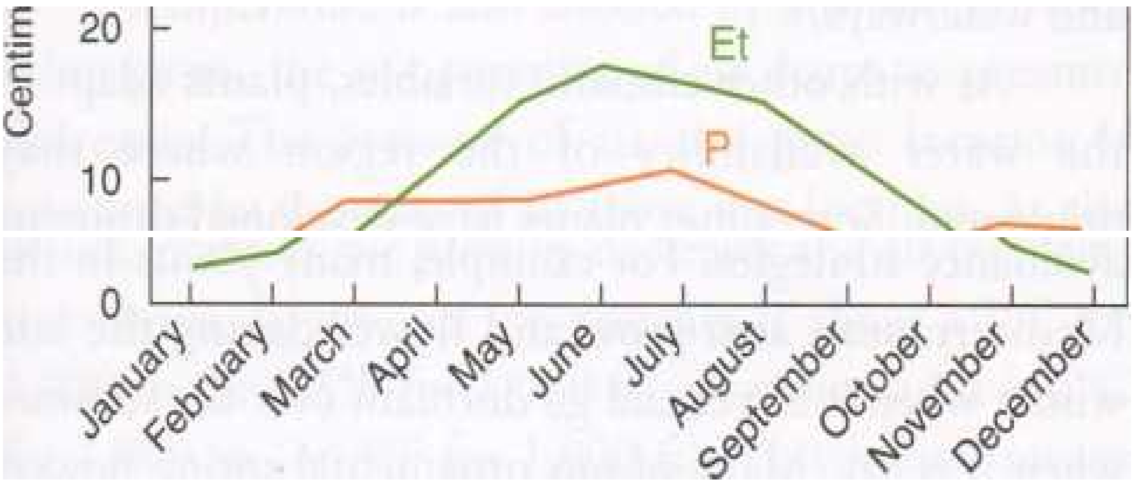


Figure 4-7

Seasonal variation in precipitation and evapotranspiration in Indianapolis, Indiana. Source: US Department of Commerc

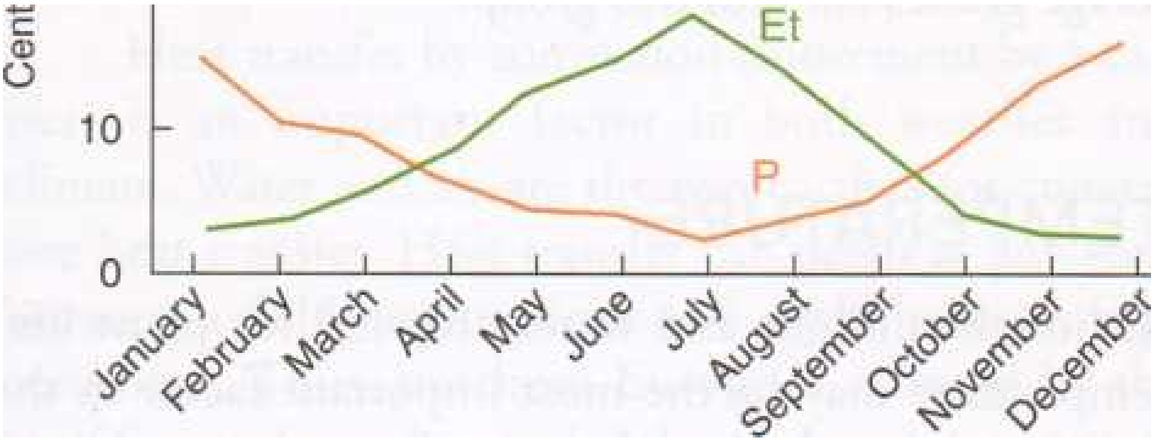


Figure 4-8

Seasonal variation in precipitation and evapotranspiration in Seattle, Washington, which has a Mediterranean climate. situation means that in the short term, they stop growing; if the drought persists, they will die.

Providing water in order to grow crops where natural precipitation is inadequate during some or all of the growing season is one aspect of climate that can be and is modified on a large scale. Irrigation has a long history and allows us to grow many crops in areas that otherwise would be unsuitable for growing. Water was supplied to crops through open irrigation channels in the Middle East in prehistoric times. The water flowed by gravity to furrows in the fields much as it does in many parts of the world today (Fig. 4—9). Now, large areas are often irrigated with water piped under pressure to some form of overhead irrigation (Fig. 4—10). This method can result in losses because the water may fall outside the crop area and a proportion evaporates before it reaches the root zone. Smaller-scale irrigation of horticultural crops, including ornamentals, often aims to supply the water more directly to the plant roots through trickle-feed pipes or spray emitters close to the soil surface (Fig. 4-11). In a moist climate, water can be held in local ponds or lakes to supply irrigation during periods of water deficit. In a dry climate, irriga-tion may supply the entire water needs of the crop. The water may be drawn from a distant source or from underground aquifers.

Figure 4-9
Irrigation channels in Iraq.
Source: Margaret McMahon, The Ohio State University.

Figure 4-10
Overhead irrigation of field crop. Source: USDA Natural Resource Conservation Service, http://photogallery.nrcs.usda.gov/

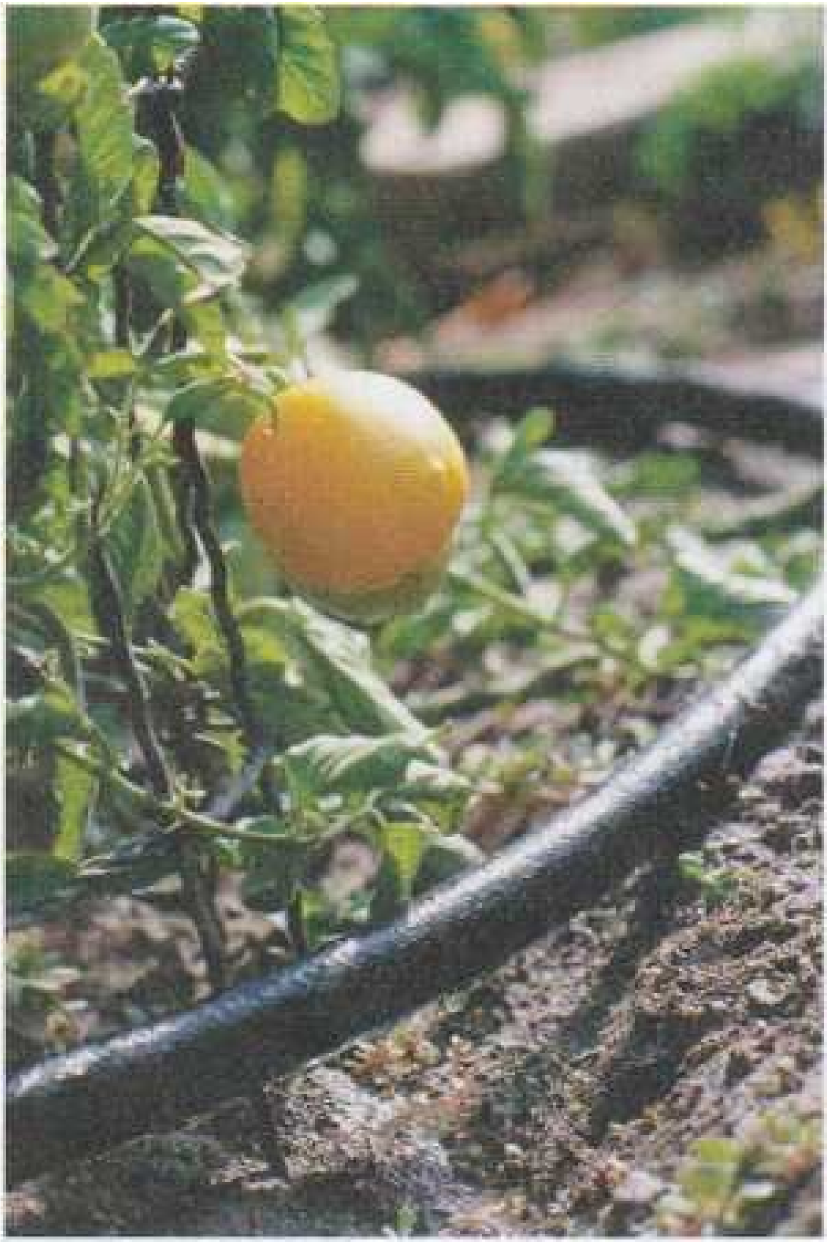


Figure 4-11

Trickle or drip irrigation puts water on the surface of the water near the plants, thereby reducing evaporation compared to overhead irrigation. Source: USDA Natural Resource Conservation Service (NRCS), http://photogallery.nrcs.usda.gov/

TEMPERATURE

Although sunlight and water are vital for plant life, temperature may be the most important factor in the decision about whether a crop can be grown or when to plant a crop in a given location. We generally think of sunshine as providing warmth, but wind and water move huge amounts of thermal energy around the planet.

Gain and loss are equal at about 35° to 40°.

The amount of energy received in " 5 way varies greatly according to geographic position rsLirive to ocean currents and prevailing winds.

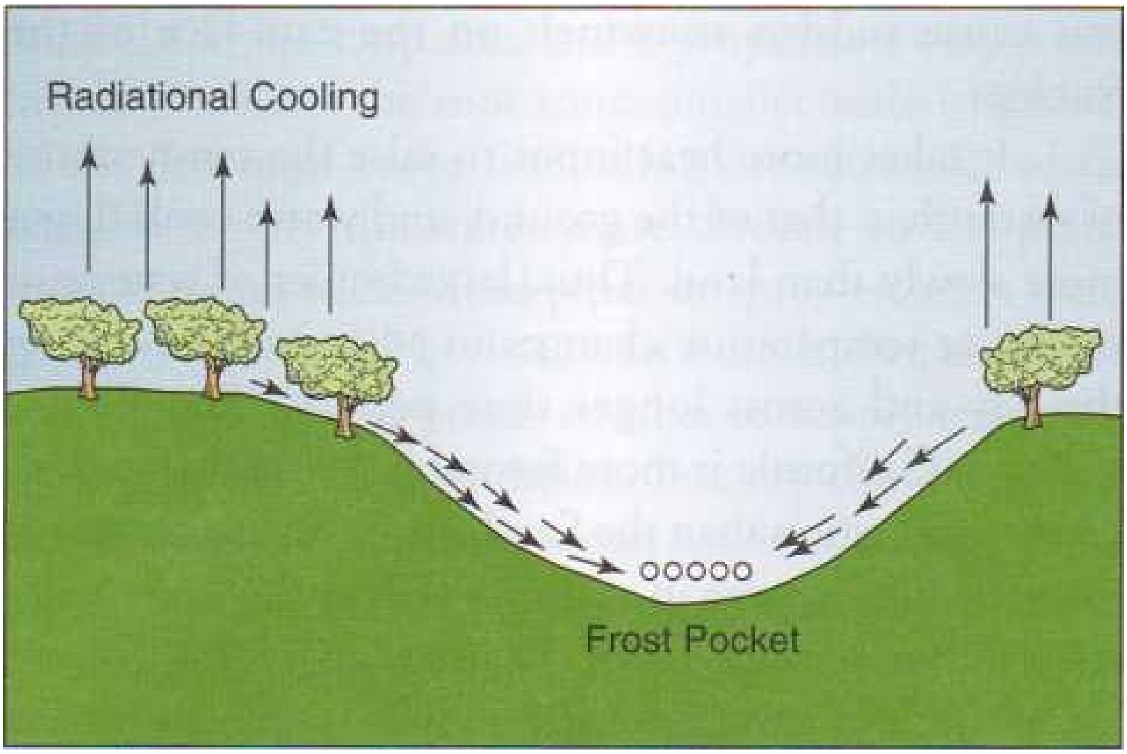


Figure 4-13

On a clear night, heat lost from the ground leads to cooling of the air, which rolls down slopes and leaves warmer air above it. Source: Michael Knee.

The cumulative result of these factors is that cities can be as much as 5°C warmer than the surrounding countryside. A dome of warm air exists over cities, forming the so-called urban heat island or dome. Warm air flows out toward the suburbs, which can be 2° to 3°C warmer than the countryside.

Figure 4-14

It feels hotter in the city than in the country because heat is absorbed and radiated by buildings and paved surfaces rather than being used to drive evapotranspiration.

US plant hardiness zones are defined according to the minimum temperatures that can be expected. Over the years, growers have gathered experience about the minimum temperatures that particular plants can survive. The USDA has created - and recently updated as of 2009a Plant Hardiness Zone Map that shows the minimum temperatures that can occur throughout the country (Fig. 4-15). We can match plants to zones and generally be confident of their survival. However, the plant hardiness zone map shows normal minimum temperatures; occasional extreme temperatures can still result in plant death.

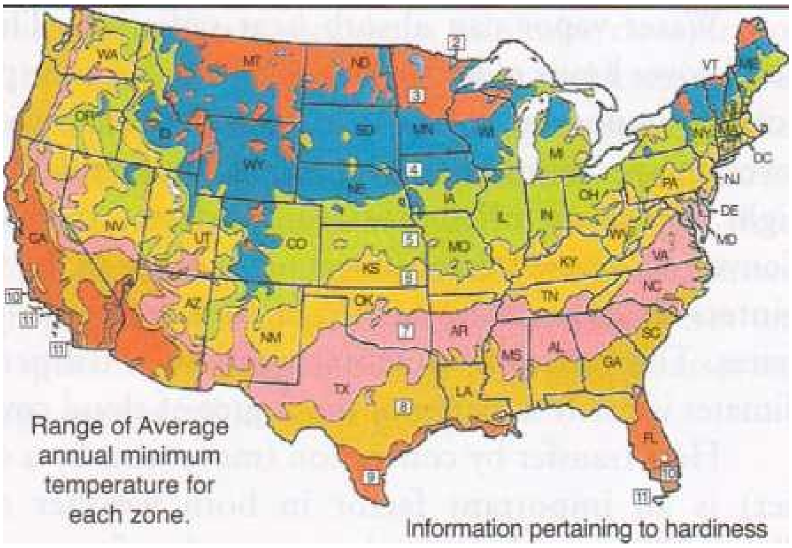


Figure 4-15

USDA plant hardiness zones are defined by usually expected minimum temperatures, not the average winter temperature or the extreme lows recorded. Source: USDA, http://www.usna.usda .gov/Hardzone/ushzmap.htm

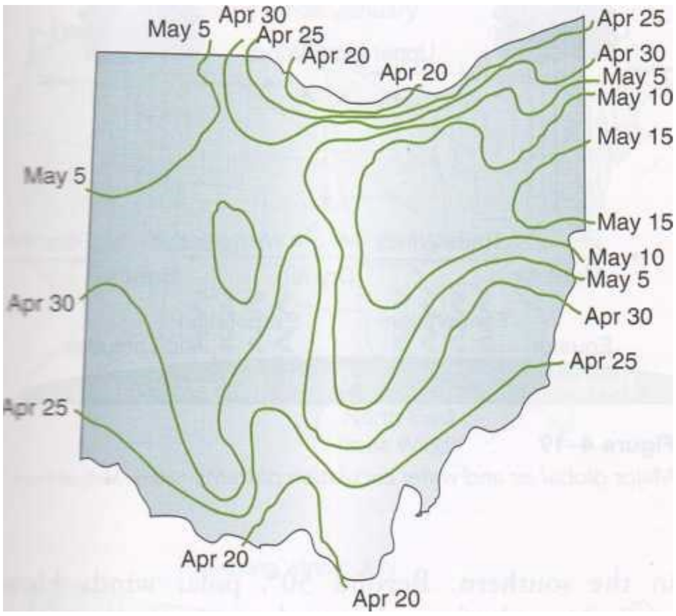


Figure 4-16

Eation in the date when there is a 50 percent chance that ': more frosts will occur in Ohio. Similar data are available for zz^er states at http://www.ncdc.noaa.gov/oa/climate/ rzateclimatologists.html

Springtime temperatures are critical for both annuals and perennials. Many seeds can be planted only arter the danger of frost has passed, and spring-flowering perennials, including many fruit crops, can be injured by late frosts. Maps showing expected dates of last frost can be used to decide when to sow seeds and to select ireas suitable for fruit production (Fig. 4-16). Other maps can show the expected dates of first frost in the i jtumn. For many crops, this point marks the end of the growing season. If a mature crop cannot be harvested by this time, there is little point in growing it Fig. 4—17). A cotton plant grows well in the summer in Ohio, but the growing season is just not long enough to illow mature cotton bolls to be harvested. For most plants in the temperate zone, the minimum is between 0° and 5°C, and the maximum is around 35°C. Many tropical plants are injured below 10°C and show optimal growth around 35°C Fig. 4-18). Spring- and early summer-flowering plants rach as pansies and winter annual weeds may grow well at cool temperatures but die in the summer because of heat.

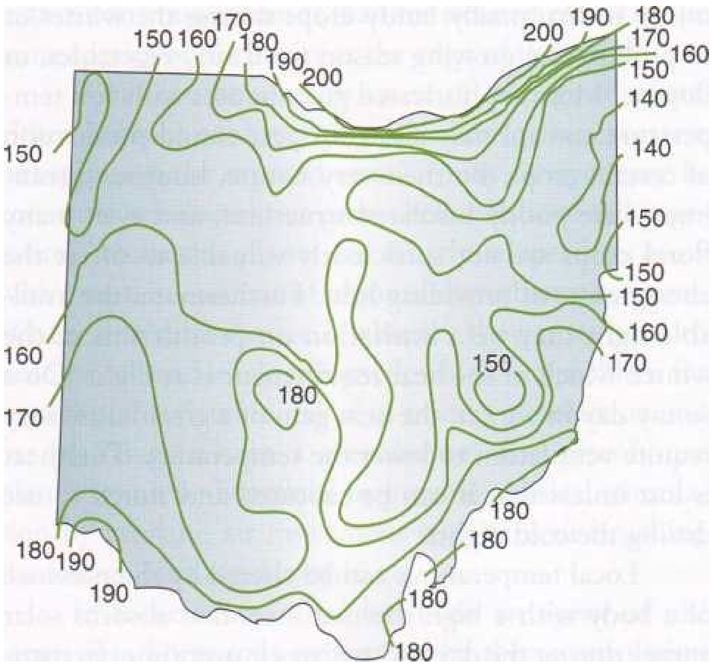
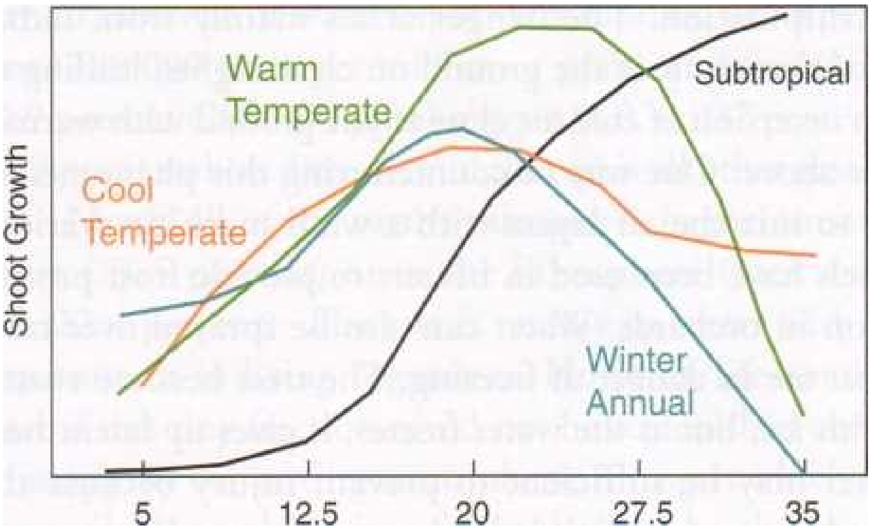


Figure 4-17

Map showing the growing seasons for the state of Ohio. The growing season is defined as the time between the average dates for the last frost in the spring and the first frost in the autumn. Similar data are available for other states at http:// www.ncdc.noaa.gov/oa/climate/stateclimatologists.html



Temperature, °C
Figure 4-18
Growth of different kinds of plants in relation to temperature.

Water can also be sprayed over trees that are in danger of freezing. The trees become coated with ice, but as the water freezes, it gives up latent heat that may be sufficient to prevent injury because the buds freeze at a slightly lower temperature than water.

AIR MOVEMENT AND COMPOSITION

Winds are driven by differences in air pressure resulting from corresponding differences in the input of solar energy. Air movement around the earth is dominated by three belts of wind in both the northern and southern hemispheres. Although the winds move air masses between different latitudes, the rotation of the earth gives them an easterly or westerly shift via the Coriolis effect. The trade winds blow toward the equator from a northeast direction in the upper atmosphere and a southeast direction in the southern. Between about 30° and 50° latitude, winds blow in opposite directions: southwest in the northern hemisphere and northwest

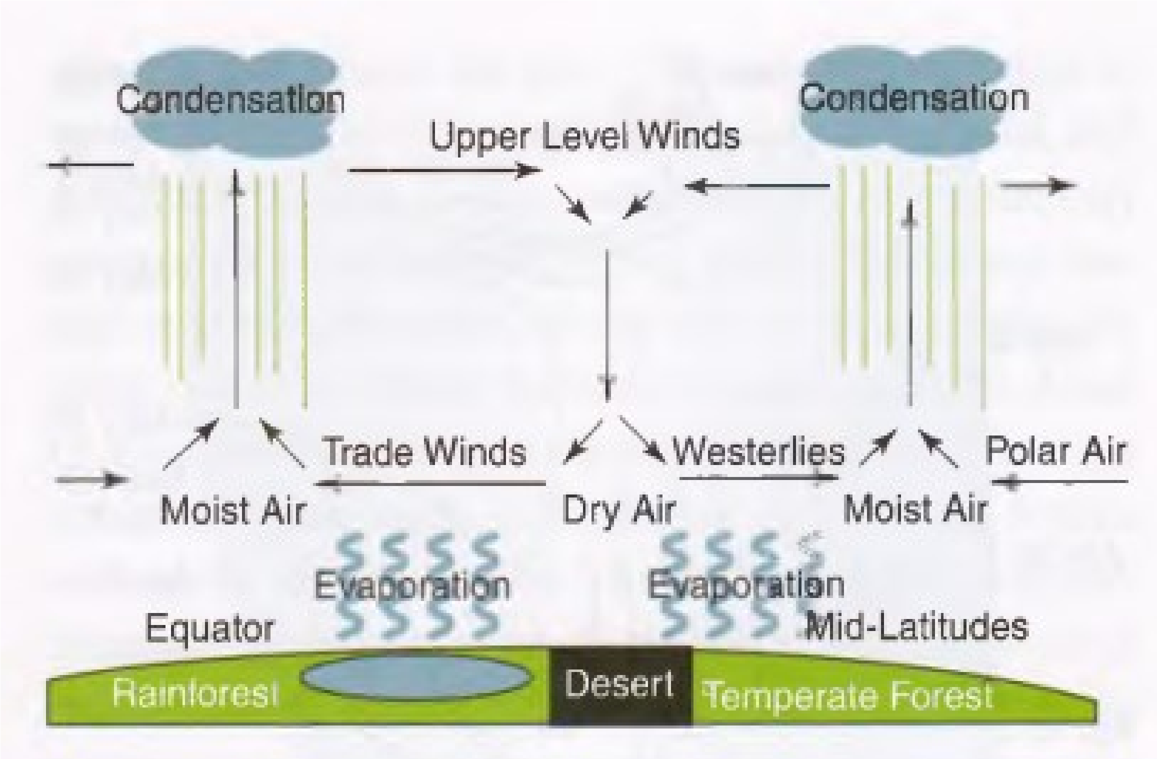


Figure 4-19
Major global air and water circulation patterns. Source: Michael Knee.

in the southern. Beyond 50°, polar winds blow predominantly from the northeast in the northern hemisphere and southeast in the southern. These surface-level winds are accompanied by upper-level winds blowing in the opposite direction. The conver-gence of the trade winds at the equator leads to an updraft of air, from which rain falls as it cools. The divergence of prevailing winds around 30° latitude is associated with a downdraft that carries moisture away and results in low rainfall (Fig. 4-19).

Air circulation tends to be more orderly in the southern hemisphere than in the northern, where large land masses capture the sun's heat and

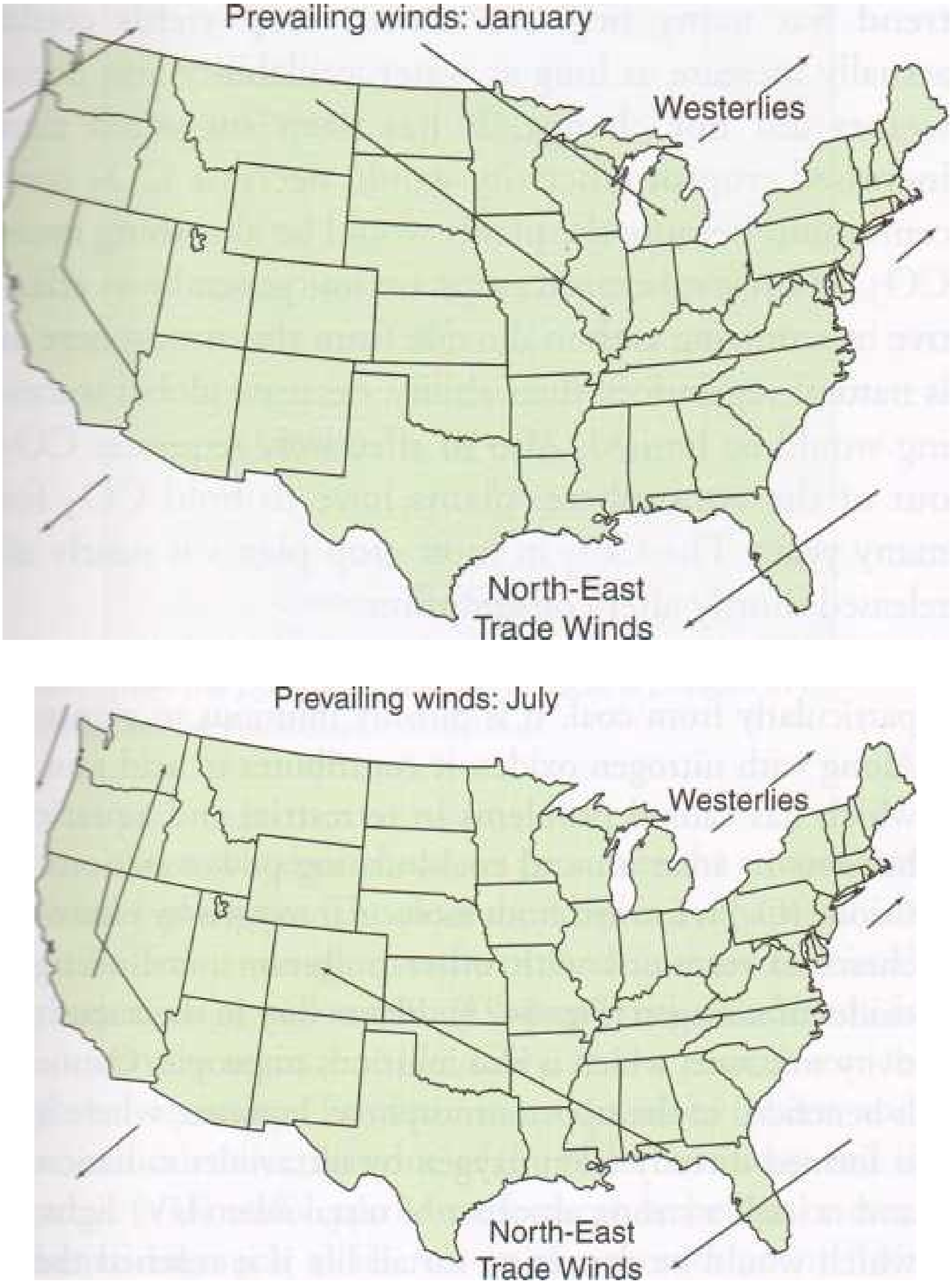


Figure 4-20
Prevailing winds in the United States in summer and winter.

give rise to high pressure areas that break up the circulation patterns. The high pressure areas shift, leading to changes in the weather. In the central United States, summer weather is dominated by southeast winds bringing moistureladen air from the Gulf of Mexico, whereas in the winter, northwest winds bring polar air (Fig. 4-20). Sudden shifts can occur in these patterns, particularly in the spring and autumn, leading to unstable weather. When a cold front meets a mass of warm, moist air, powerful air currents can lead to thunderstorms. When crosswinds blow through the rising clouds, conditions are set for tornado development.

On a more local level, bodies of water affect air circulation because they warm up more slowly than the land does in the daytime and cool more slowly at night. This characteristic leads to an onshore breeze toward the land in the morning and an offshore wind in the evening. In mountainous areas, breezes tend to blow up valleys and hillsides as they warm up during the day, but cool air flows in the opposite direction at night. Buildings tend to slow down air circulation in urban areas; however, depending on the height and distribution of buildings, areas of turbulence or convergence of winds can produce strong gusts. Air movement tends to be slowed down by vegetation. This effect is most noticeable under a continuous canopy of herbaceous or woody vegetation. Air tends to move across the top of the canopy rather than through it (Fig. 4-21).

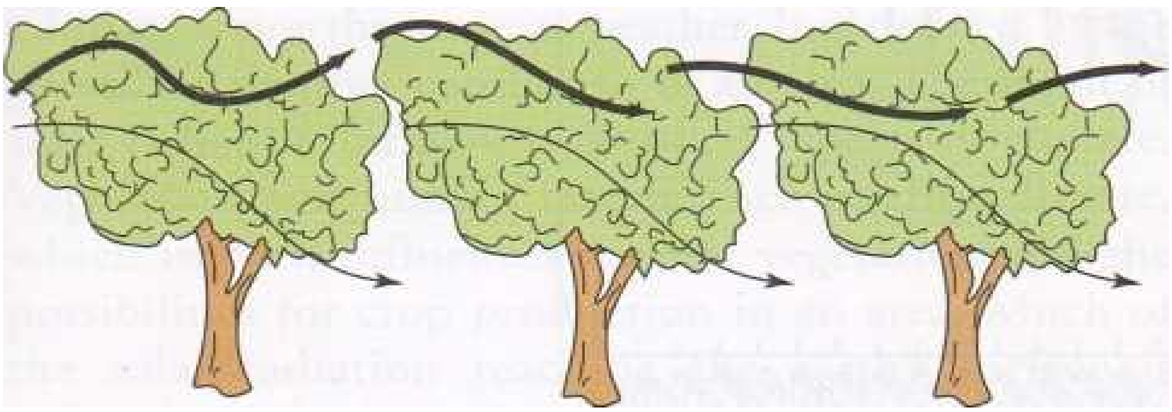


Figure 4-21

Air movement within plant canopies is generally slower than outside the canopies. The thicker the line, the faster the air movement. Source: Michael Knee.

Humidity tends to be higher within the canopy than above it because of limited air exchange. Because transpiration is related to vapor pressure deficit and wind speed, water loss tends to be much lower for plantswithin continuous stands than for isolated plants of the same species or for plants at the edge of the stand.

In some areas, wind has been an agent of soil formation. Loess soils are formed by the accumulation of wind-blown particles. As with water, however, wind is an agent of soil erosion, which is a problem particularly in the drier parts of the western United States and other arid parts of the world.

ATMOSPHERIC COMPOSITION

Dry air (absence of water vapor) is comprised of 78 percent (780,000 parts per million or ppm) nitrogen (N), 20.9 percent (209,000 ppm) oxygen (O), 0.037 percent (370 ppm) carbon dioxide, and the rest is all other gases.

Nearly all of the earth's nitrogen is in the atmosphere (77.5 percent) or in the lithosphere (rock and soil, 22.4 percent). The rest is mainly in water with a tiny amount in living organisms.

In the last century, the same reaction was developed on an industrial scale in the Haber—Bosch process.

This effect is mostly undesirable in natural ecosystems and contributes to eutrophication of bodies of water, the disappearance of

Nitrogen-fixing plant species (which are no longer competitive), and apparently forest decline in the United States and Europe.

Survival is produced by plants and algae during photosynthesis. Land plants account for about 60 percent of global photosynthesis, which keeps the balance between oxygen and carbon dioxide (C02) at about 600 to 1. By competing so effectively for carbon dioxide and keeping it at low levels, plants and algae modify the climate of the earth. As is now well known, carbon dioxide absorbs infrared radiation from the earth so that heat is retained in the atmosphere. This phenomenon is loosely referred to as the greenhouse effect. The level of oxygen in the atmosphere is so high (209,000 parts per million or ppm) that it is not much affected by slight changes in the balance of oxygen and carbon dioxide.

Ozone (O3) is formed from molecular oxygen by photochemical reactions with other pollutants, including oxides of nitrogen (Fig. 4-23). Plants vary in their sensitivity to ozone, which is also injurious to people. Ozone is beneficial in the upper atmosphere, however, where it is formed directly from oxygen by ultraviolet radiation and is itself a strong absorber of ultraviolet (UV) light, which would be damaging for all life if it reached the earth's surface in a large amount. Some UV light though is required for the production of flavonoids, the plant pigments that give plants some of their distinctive colors on leaves and flowers. Ultraviolet light also plays a role in how some insects detect plants.

Monthly Mean Carbon Dioxide

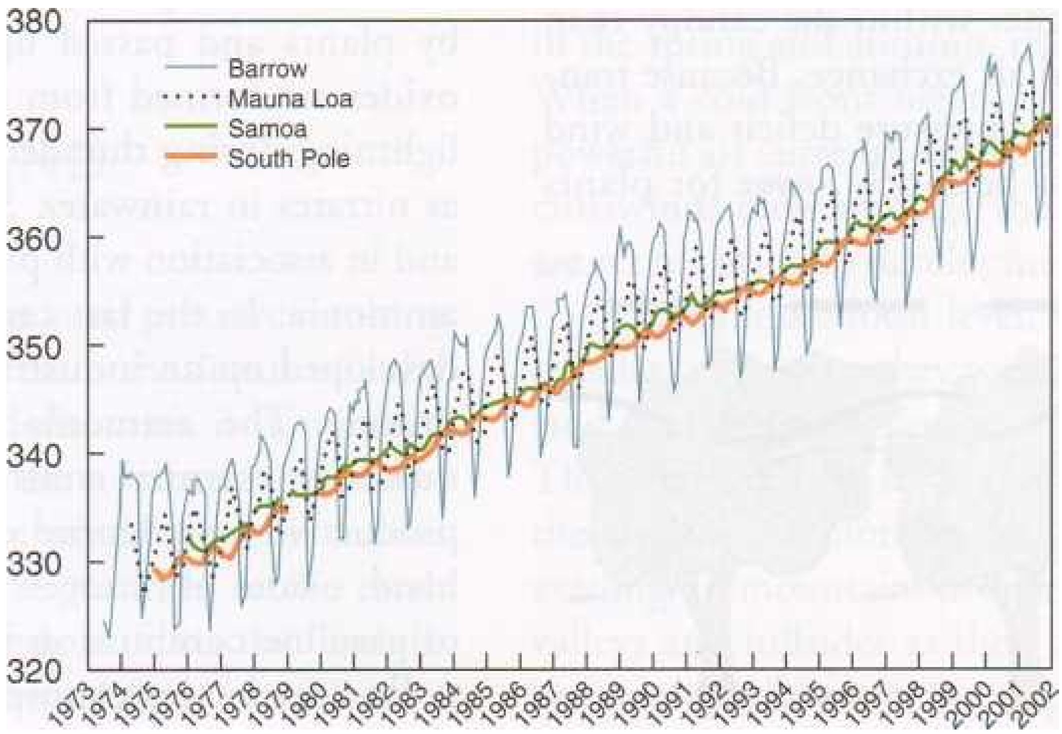
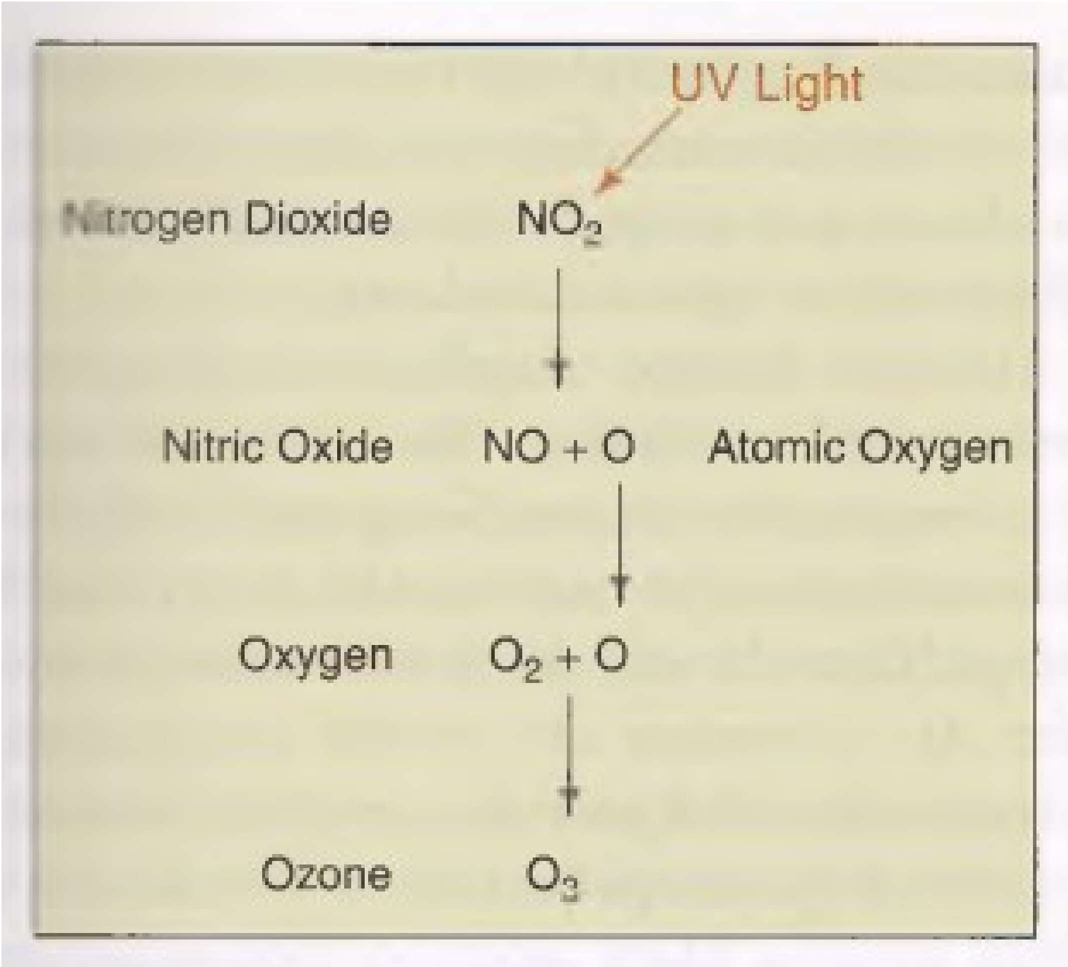


Figure 4-22

Generally, rising carbon dioxide levels show seasonal variation, depending on the photosynthetic activity of vegetation. Data shown here through May 2002. Source:



Fgure 4-23

***The** component of solar radiation promotes ozone forma the pollutant nitrogen dioxide is present in the Z ’ -B" atmosphere. Source: Michael Knee.*

Several hydrocarbons are present in the atmosphere in trace quantities. The most abundant is methane, which irises from sewage treatment and intensive animal production as well as natural sources, such as wetlands. It i5 not very toxic, but like CO2, it is a contributor to global warming.

SUMMARY AND REVIEW

Climate is not the same as weather. It is defined by the prevailing weather conditions of an area. The input of solar radiation influences all other aspects of climate. Vegetation and human interference modify climate, which in turn influences natural vegetation and the possibilities for crop production in an area. Much of the solar radiation reaching the earth's surface is infrared, while about 40 percent is photosynthetically active radiation between 400 and 700 nm. Away from the equator, the intensity of solar radiation decreases and the duration of daylight varies throughout the year.

Cloud cover further decreases light intensity. Plants are adapted to the light conditions of their natural habitat. Day length influences processes such as flowering, leaf-fall, and bud-break. The spectral quality of light reflecting from or passing through foliage changes, which affects the growth of neighboring plants. Although it is uneconomic to supply high-intensity artificial light for photosynthesis on a large scale, supplementary lighting may be used to control development and flowering along with increasing photosynthesis of greenhouse crops.

FURTHER EXPLORATION

CHRISTOPHERSON, R. W. 2008. *Geosystems: An introduction to physical geography*. 7th ed. Upper Saddle River, NJ: Prentice Hall.

HUNTER, M., D. LINDENMAYER, and A. CALHOUN. 2007. *Saving the Earth as a career*. Hoboken, NJ: Wiley-Blackwell.

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*5

DON ECKERT

key learning concepts

After reading this chapter, you should be able to:

- Discuss the concept that soil ecology is a complex system made up of many living and nonliving components.
- Describe the components that make up a soil ecosystem and how they interact.
- Describe the factors that influence soil formation and give soil its physical and chemical characteristics.

People often refer to soil dismissively as dirt and probably regard it as dead stuff. However, it is an important part of the living world; along with climate, it determines the composition and function of the ecosystems that can exist in different areas. Plants live in the soil as much as they live in the air. Some of the oxygen that plants require comes from the soil and enters the roots. Many if not most of the ecological interactions between plants and other organisms occur below ground. Most of the individual organisms in an ecosystem and a large part of the biomass exist in the soil. Over time, the composition and properties of the soil are influenced by soil organisms. As you will learn later in the chapter, soil is the product of the interaction of parent material, climate, topography, and soil organisms over time. This chapter looks at how these factors interact to produce the different kinds of soils found around the world.

DEFINITION OF SOIL

Soils differ around the world, but they are basically composed of weathered rock, air, water, decomposed organic material, and various organisms, all working together in a complex ecosystem capable of supporting the growth of land plants. Not all soils will have all of these components. The type of components and their relative amounts determine what kinds of plants can grow in that soil. Soil is a very complex and dynamic system of many interacting factors and components that affect and are affected by plants. Soil consists of:

1. A solid fraction; that is, rock fragments and minerals.
2. An organic fraction; the decayed and decaying residues of plants, microbes, and soil animals.
3. A liquid fraction, including water and dissolved minerals.
4. A soil atmosphere or soil air.

The voids found between the solids are called **pore spaces.** Pore spaces vary in size and continuity and are an important physical property of soils.

The kind of soil and its ability to support plant growth are influenced by the relative amounts of each of these four components. Typically, a natural soil is approximately half solids and half pore space. The solid phase of the soil might average 40 to 45 percent mineral and 5 to 10 percent organic material by riile the pore space might be filled with.

Igneous rocks (i.e., lava, magma) are formed from :he hardening of various kinds of molten rock material and are composed of minerals such as ~uartz and feldspar.

1 Sedimentary rocks are generally unconsolidated :nd composed of rock fragments that have been transported and deposited by wind, water, or glaciers. Limestone, sandstone, and shale are examples.

Metamorphic rocks form from igneous or sedimentary rocks that have been subjected to sufficiently high pressures and temperatures to change their structure and composition. Slate, gneiss, 5chist, and marble are examples of metamorphic rocks.

FACTORS INVOLVED IN SOIL FORMATION

Soil is derived from rocks, minerals, and decaying organic matter. The two major processes in soil formation are (1) accumulation and (2) transformation of the parent material. Parent material accumulates from the breakdown of rocks by weathering.

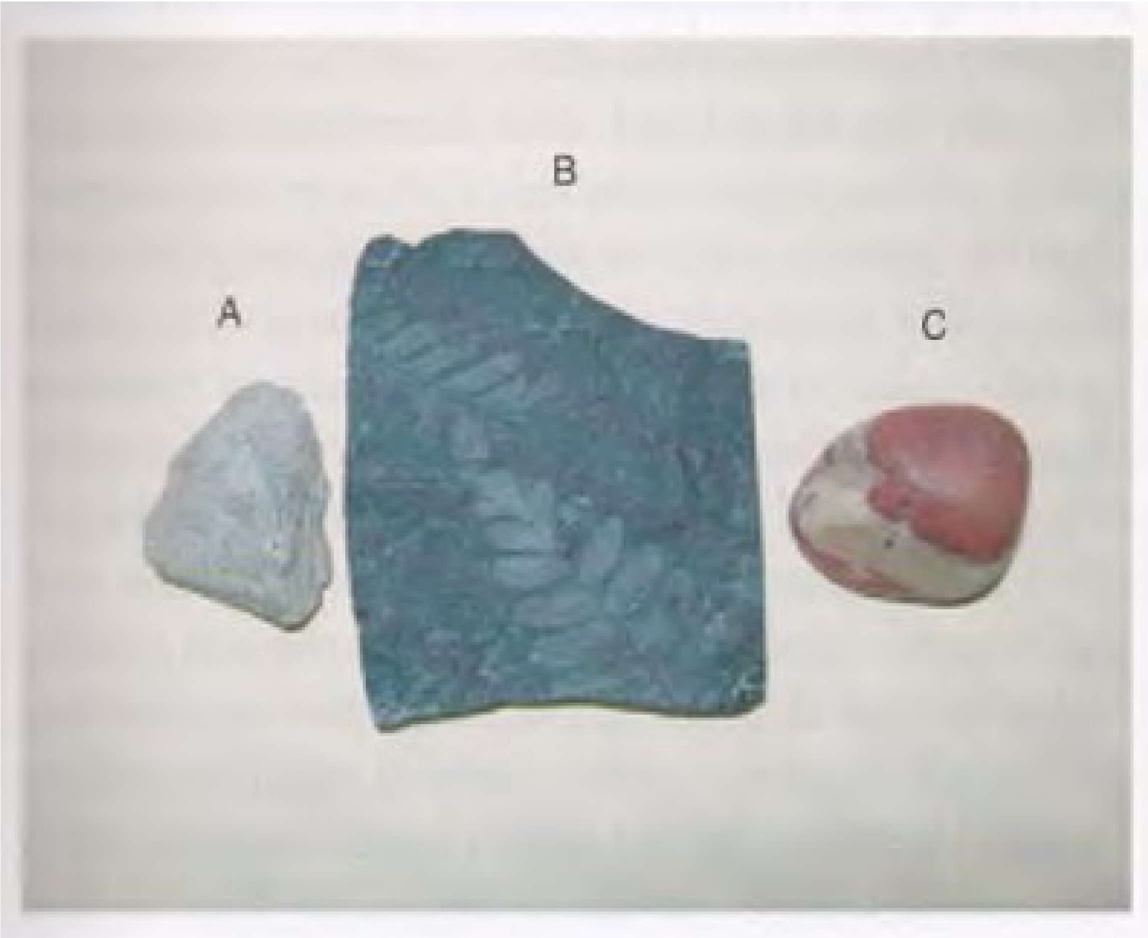

Figure 5-1

Parent rocks from which soil can be formed: (A) igneous, B) sedimentary, and (C) metamorphic.

Source: Margaret McMahon, The Ohio State University

This process must occur before soil can begin to form. The parent material accumulates as an unconsolidated mass that later differentiates into characteristic layers called horizons. A horizon is a distinct layer of soil having physical and/or chemical differences resulting from soil-forming processes as seen in a vertical cross section. Differentiation occurs by mechanical separation and/or transformation of the parent material. As the process continues, the horizons generally become more distinguishable and finally develop into a soil profile. A soil profile is a vertical section of soil extending through all its horizons from the surface to the parent material.

The factors responsible for soil formation are: (1) parent material, (2) climate, (3) biology, (4) topography, and (5) time.

Parent Material

The formation and accumulation of material by chemical and physical weathering of parent rocks is the first step in the development of soil.

Physical Weathering Physical weathering is the physical breakdown of large pieces of rock into smaller and smaller pieces. Changes in temperature greatly affect the rate of physical weathering. Differential rates of contraction and expansion caused by temperature changes bring about cracking and peeling of the outer layers of rocks by a process called exfoliation. A second process occurs due to the presence of different materials within a rock, each with its own characteristic coefficient of expansion. Because of these differences, sudden large temperature changes cause uneven expansion or contraction, cracking the rocks. A third process is the cracking of rocks caused by the expansion of water as it freezes in rock fissures.

The mechanical action of glaciers causes rocks embedded in the ice to scrape against other rocks as the glacier moves. This action grinds the rocks into increasingly smaller rock fragments. This physical process is powerful: it reached a tremendous magnitude during the Ice Ages (Pleistocene epoch). The product of glacial weathering is called glacial till, and it comprises rock particles ranging in size from clay to boulders. This material is deposited beneath, beside, and at the terminus of the melting glacier.

Physical weathering is also caused by moving water, as in stream erosion, sheet erosion, rill erosion, or wave action (Fig. 5-2). The action is similar to that of glaciers. Water from rains and melting snow moves rapidly down streambeds, carrying parent rock frag-ments of varying sizes. As these fragments move along, they are gradually worn down to create smaller and smaller particles, eventually forming parent material. In arid regions, wind acts similarly to water. Coarse sand particles (parent material) are swept along the ground with sandblasting action wearing away other larger parent rocks.

The action of plant roots can sometimes physically break down parent rocks. For example, a tree root growing into a crack in a rock can ultimately fracture the rock. While this example is not considered weathering, it is a physical soil-forming process. In this case, some chemical weathering must occur first to provide nutrients for the plants before they can begin to grow.

Chemical Weathering Chemical weathering entails four distinct processes.

Figure 5-2

Massive gullies formed by severe stream erosion during periods of heavy rainfall. This gully is beyond reclamation by practicable methods. Source: USDA Natural Resources Conservation Service, http://photogallery.nrcs.usda.gov/

Dissolution is the process by which the constituents of parent material dissolve in water or weak, naturally occurring acids and are leached away. Chloride, nitrate, and sulfate salts are generally very soluble in water and can be leached by rainfall alone.

Hydration adds molecular water to another compound to form a hydrated material more vulnerable to pulverization. An example is calcium sulfate (CaSO^ absorbing water to form gypsum (CaS04 • 2 H2O), a hydrated calcium sulfate:

CaS04 + 2 H2O —* CaS04 • 2 H20

Hydrolysis is the reaction between a compound and water to form a more soluble product. In the following hydrolysis reaction, potassium ions (K+) are made more available to plants by the reaction of the slowly soluble feldspar mineral (KAlSigOg) with water (H20) to form soluble potassium hydroxide (KOH):

KAlSi3Og + H20 -> HAlSi3Og + KOH

Oxidation reactions form oxides of parent material by reaction with oxygen. For example, ferrous oxide (FeO) reacts with oxygen (02) to yield ferric oxide (Pe2Oз), a product more oxidized than the reactant:

FeO + 02 —2 Fe203

Climate

The climate affects soil formation. In areas of high rainfall, soils are often highly leached and acidic in reaction. Chemical weathering proceeds at a rapid rate, especially if high rainfall is coupled with high temperature. The fertility level of soils formed under high rainfall is generally low because many of the plant nutrients are leached from the root zone. Many of these soils are red or yellow in color, indicating a relatively high percentage of iron oxide, which remains after other elements have been removed.

On the other hand, soils developed in arid climates are not highly leached. Calcium and magnesium carbonates tend to accumulate, and chemical weathering proceeds at a much slower rate. Soils formed under arid conditions often contain excessive quantities of salts other than carbonates, and are not productive until the amounts of salts are reduced. Land can be desalinated by flooding with water and leaching the salts downward through the soil profile. Fields treated in this manner must possess excellent subsurface drainage, either natural or improved by human intervention. If heavily The soil is home to a great diversity of organisms ~om all of the five kingdoms: Plantae, Animalia, Fungi, Protista, and Monera. These organisms are involved in all possible types of ecological interaction, md many of them have profound effects on soil chemistry, structure, and function. Many soil organisms have not yet been classified or characterized.

Bacteria are the most abundant soil organisms; some of them are parasites of plants and other soil organisms, but many are involved in decomposition and recycling of nutrients in soil organic matter. Some have the ability to fix atmospheric nitrogen.

Fungi may also be parasites, but most of the fungi in the soil are saprophytes, breaking down soil organic matter. The roots of nearly all plants in the wild are associated with mycorrhiza which are fungi that assist in plant uptake of nutrients and water.

Soil Protista include algae that can carry out photosynthesis at the soil surface and protozoa that are predators of soil bacteria. Soil animals include nematodes, mollusks (slugs and snails), annelids (including earthworms), and arthropods (mites, insects, millipedes, spiders, etc.). These groups can be subdivided into herbivores, microbivores, predators, and detritovores.

The nonliving organic components of the soil are residues of plants and animals. The amount and kind of these organisms are influenced by the climate. For example, the climate of an area determines the quantity of biomass produced on a site, which in turn influences the soil-forming processes.

Vegetation aids soil formation by supplying organic matter in the form of dying and decomposing plants. Grasses decompose into a different kind of organic residue than do trees. Also, the amount of organic matter varies according to the amount and type of vegetation (Fig. 5-3). Peat soils form where reeds, sphagnum moss, and grasses grow and where decomposition of the organic matter is minimized. Soils in arid regions normally contain low amounts of organic matter because of the limited growth of desert grasses, shrubs, and cacti.

The amount of organic matter in soil is influenced by the difference between the rates of accumulation and decomposition of organic material. In cases where decomposition rates are very high, the organic fractionsalted water accumulates in the soil, it can cause the soil to disperse and become waterlogged. Such degradation can render soils useless for future production unless expensive remediation practices are employed.

ECOLOGY

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Figure 5-3

The organic matter produced from the decomposition of forest litter is different from that produced from prairie grasses. In this example, the forest is not so dense that it excludes grasses, and both types of vegetation are present and produce organic matter. Source: USDA Soil Conservation Service.

The amount of organic matter in soil is influenced by the difference between the rates of accumulation and decomposition of organic material. In cases where decomposition rates are very high, the organic fraction accumulates very slowly. Thus, the amount of organic matter remains low. Consider the case where temperatures are high and rainfall or irrigation keeps the soil moist. Under these conditions, the rate of decomposition nearly equals the rate of accumulation, and the organic matter content changes little over time.

Figure 5-4

Prairie grasses such as these in Kansas produce a high level of organic matter in the topsoil.

Source: Kimberly Williams, Kansas State University.

On the other hand, in cool areas or sometimes under anaerobic conditions, decomposition is inhibited and organic matter accumulates. Many factors affect the rates of accumulation or decomposition, all of which play a role in determining the amount of organic matter present in a given soil at a particular time and location.

The type of root system produced by the different plant species also influences soil formation. Dense fibrous root systems of grasses often lead to soils with a deep, organic rich A horizon, such as some of the Mollisols (prairie soils) formed in the central United States (Fig. 5-4) and in some areas of eastern Europe.

Topography

Topography influences drainage and runoff. Steep slopes are subject to erosion because water flows downhill quickly, with little percolating into the soil. Resulting erosion leads to the formation of shallower soils because the soil surface is removed almost as quickly as it is formed. In depressional areas, however, deposition of eroded material leads to formation of deeper soils. Gentle slopes that are heavily covered with vegetation slow the water flow and allow more time for water to percolate into the soil, permitting the development of a well-defined profile. The same is true even of flatter areas. Rapid surface runoff causes more erosion, and if vegetation is removed or absent, deep gullies can be cut into the gently sloping land (Fig. 5—5). Soil on very flat land is more subject to wind erosion than water erosion. The presence or absence of plant material influences wind erosion in the same way as water erosion.

Topography has a marked effect on climate. High altitudes mean lower soil and air temperatures, which influence the amount and type of vegetation. As you learned in the previous chapter, In dry air, the decrease is about 10°C for 1,000 m (or 5.5°F for 1,000 ft); in moist air, it is 6°C for 1,000 m (or 3°F for 1,000 ft). Thus, an increase in elevation changes the kind and type of vegetation. Grasses and deciduous trees grow at lower elevations, with coniferous evergreens at higher

Figure 5-5

Sloping topography accelerates rill erosion, which removes topsoil. Constant removal of topsoil exposes the parent material to weathering and more rapid soil formation. Source: USDA Natural Resources Conservation Services, http://photogallery.nrcs.usda.gov/

***Figure** 5-6*

Figure 5-6. The type of vegetation present can greatly influence the characteristics of the soil at different delations.

Time

As they develop, mature soils differentiate into well-defined profiles consisting of three principal horizons (Fig. 5-7). The surface layer, the A horizon, varies in depth and contains most of the plant roots. This leached zone often lacks some of the important mineral nutrients, but it does contain the largest amount of organic matter.

Hard-to-decompose rocks such as granite require millions of years to form parent material; softer rocks 4 uch as limestone require less time. Interactions between biological and chemical agents reacting with parent material over long periods of time differentiate the soil into horizons. Soils without well-developed horizons are classified as young soils, even though the parent material may have been present for a great many centuries. The organic matter makes the A horizon permeable and dark-colored, and the A horizon is normally the zone of greatest biological activity in the soil profile.

Figure 5-7

A soil profile showing different horizons.Source: USDA Image Gallery, http://www.ars.usda.gov/is/graphics/photos/

Below the A horizon is the B horizon, the zone of accumulation. Plant nutrients, silts, clays, and other materials from the upper layer are leached into and accumulate in this horizon. The color is generally lighter than that of the A horizon, and less organic matter is present (although the roots of deep-rooted plants do reach into the B horizon).

The C horizon consists of unweathered to slightly weathered material from which the A and B horizons are formed. It can also include accumulated calcium carbonates or other salts.

The factors affecting soil formation are obviously interrelated. Parent material affects, along with other factors, the capacity of the soil to support plant life, which in turn influences the kind of vegetation. Topography and temperature also influence vegetative growth. Temperature interacts with organic matter. Topography, temperature, and time influence parent rock conversion into parent material, each interacting to yield different soil formation and soil characteristics. Thus, each factor affects and is affected by all the others. It would be difficult to say that any one is more important than another in soil formation.

PHYSICAL PROPERTIES OF SOIL

Soil Texture

An important physical property of soil is its texture. Soil texture is defined as the percentage of sand, silt, and clay particles in a soil. Soil particles vary in size

from coarse rock fragments (>2 mm) to those so small (<0.002 mm) than an electron microscope is needed to observe them (Table 5-1). To measure soil texture, the soil particles are separated into their respective sizes and the percentage in each size category is calculated. A textural classification is then made with the aid of a soil textural triangle (Fig. 5-8).

Soil texture influences many of the soil's properties related to crop production (Table 5-2). The distribution of different particle sizes determines the ability of soils to hold and transmit water. Soil with a high percentage of sand loses water quickly, retaining little for plant use. Plants growing in these soils will experience water deficits sooner after wetting than those grown in loam or clay soils. Texture also influences soil aeration. In soils largely composed of very fine clay particles, movement of both air and water can be limited.

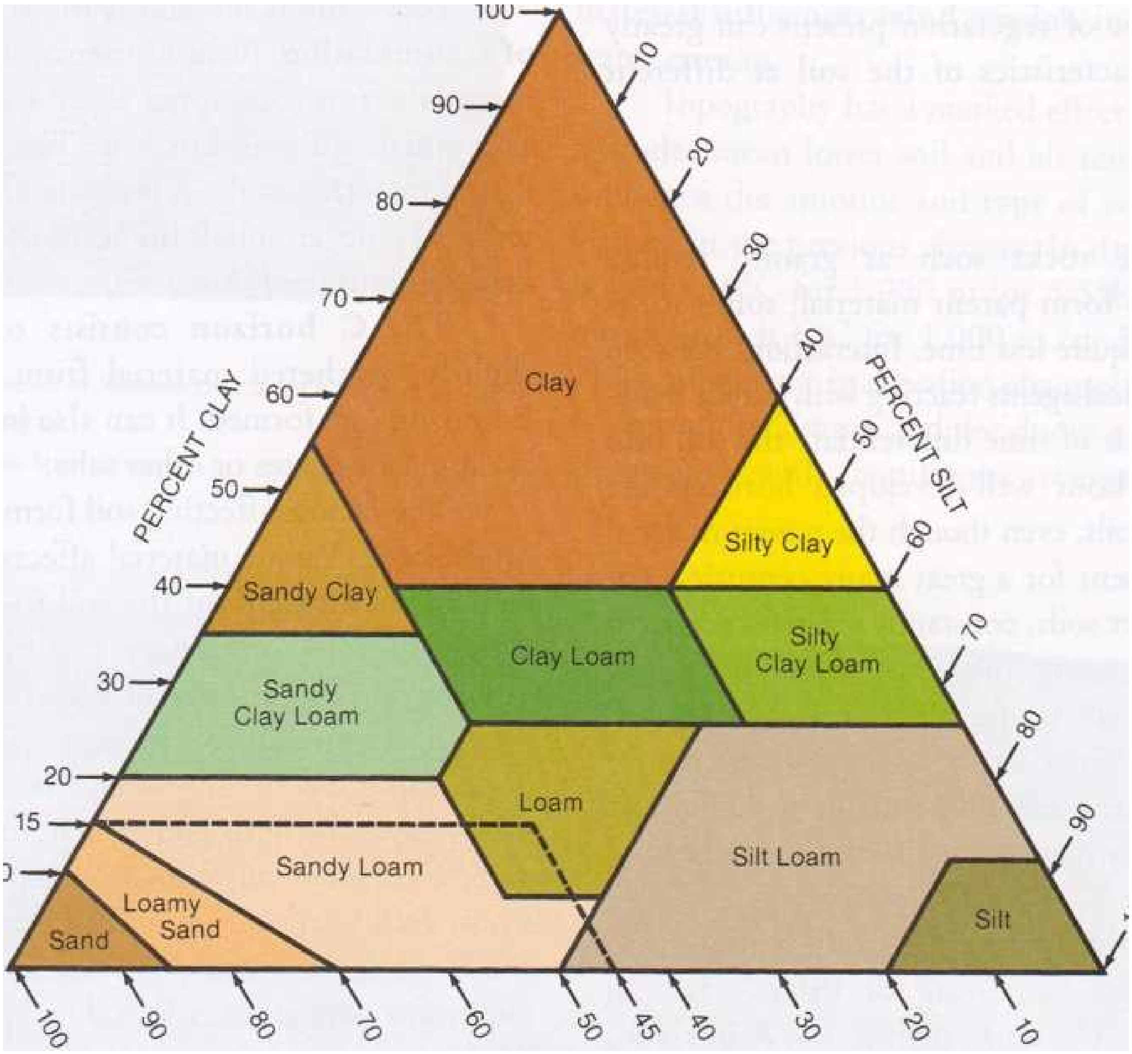


Figure 5-8

A soil textural triangle. To illustrate how the triangle works, assume that a sample of soil has been analyzed and found to contain 45 percent sand, 15 percent clay, and 40 percent silt. On the triangle, locate the 45 percent value on the sand (bottom) axis and draw a line parallel to the lines in the direction indicated by the arrow. Next, locate either the 15 percent value for clay on the clay axis (left side of triangle) or the 40 percent silt on the silt axis (right side of triangle), and draw another parallel line along either of the two axes in the direction indicated by the respective arrows. The two lines intersect in the loam area of the triangle; thus, this soil is classified as a loam. Source: *USDA.*

Plant roots need oxygen for respiration, and soils with low rates of gaseous diffusion restrict respiration and plant growth. Also, many benefl- soil microorganisms require well-aerated soils.

A soil consisting of a mixture of 40 percent sand, -1 percent silt, and 20 percent clay produces a loam > oil that retains sufficient water for good plant growth ind permits its movement without restricting aeration. Due to their excellent water-holding properties, loams are usually excellent soils for crop production.

The ease of tillage (plowing, disking, cultivating) is influenced by soil texture. Sandy or loam soils at the proper moisture content are easier to till than clay soils. Root penetration is sometimes restricted in soils of high clay content. Other factors being equal, most crops grow better in loam soils than in either sandy or clay soils.

Soil Structure

Soil structure is defined as the arrangement of primary soil particles into secondary units, that is, the manner in which individual primary particles clump and hold together. The secondary unit (aggregate) is a clump of soil particles that acts as an individual larger particle with specific characteristics. The kind of soil structure is determined not only by the relative amounts of each primary particle but also by the manner in which these particles are arranged into aggregates. The size and form of aggregation is known as the structure of soil.

Descriptive words are used to classify soil structure, for example, prismatic, subangular blocky, blocky, columnar, platy, and granular. These words describe the shape, character, and appearance of the aggregates (Fig. 5—9). Aggregates may vary from a fraction of a centimeter to several centimeters in diameter and may be held together strongly or weakly.

CHEMICAL PROPERTIES OF SOIL

Effect of Climate

The type of parent material predominately influences the chemical characteristics of young soils. As weathering proceeds, soils tend to show the effects of climate, and the resemblance to parent material lessens or disappears. The chemical properties of the soil are determined largely by the colloid-sized (not visible with an ordinary microscope) aluminosilicate clay minerals.

In the temperate zones, chemical weathering is less intense in arid regions than it is in humid regions. Soluble salts released by weathering are not lost by leaching from soils in arid regions.

In tropical zones, with higher temperature and more rainfall than temperate regions, weathering and leaching are greater. The silicate and aluminosilicate minerals are more weathered, resulting in soils known as Oxisols. These soils contain high concentrations of iron and aluminum oxides, are generally red to reddish brown in color, and are low in fertility and organic matter. Even though large amounts of vegetation are produced, organic matter is low because dead plant matter is rapidly decomposed by high microbial activity.

In the cold humid regions, forest vegetation, mainly conifer trees, combine with climatic factors to produce Spodosol soil groups. The silica content of these soils is high in the surface layer in contrast to the iron and aluminum content in the Oxisols because the parent material of these soils is usually silica sand. These soils are highly leached and inherently low in plant nutrients. Organic compounds produced by decaying conifer needles form acid solutions that dissolve iron and aluminum oxides and basic compounds (calcium and magnesium salts). The ions are leached to

lower depths in the soil profile and redeposited there together with some aluminum and dissolved organic matter to produce a dense layer 60 to 90 cm (2 to 3 ft) below the surface. These soils can be identified by an ashy, bleached white layer immediately above the dense layer. This layer is known as the E horizon, and it forms between the A and B horizons.

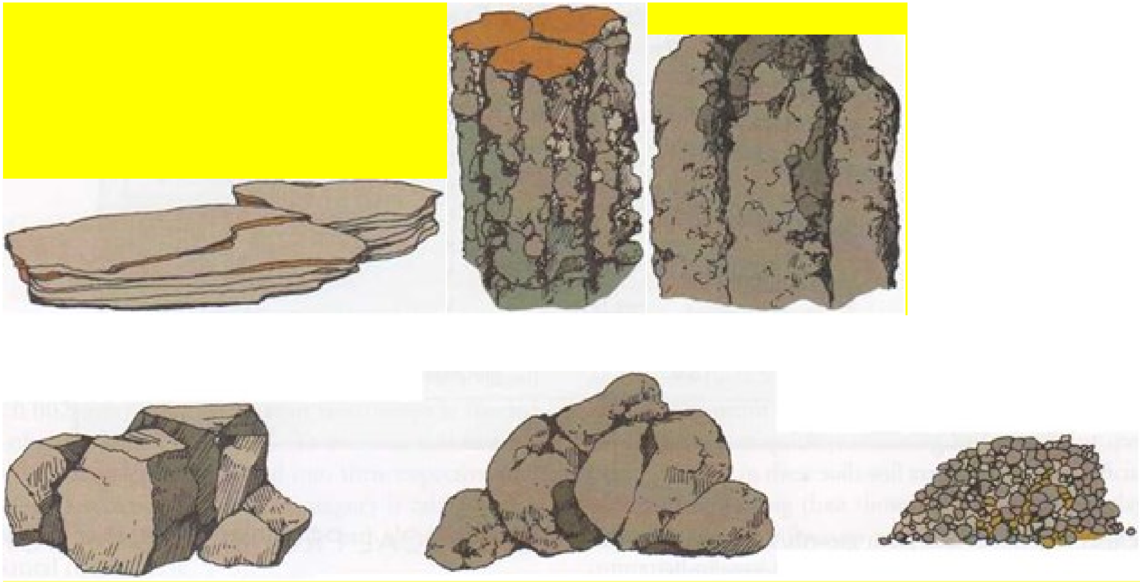


Figure 5-9

Several kinds of soil structure: (A) platy, (B) prismatic, (C) columnar, (D) angular block, (E) subangular blocky, and (F) granular.

lower depths in the soil profile and redeposited there together with some aluminum and dissolved organic matter to produce a dense layer 60 to 90 cm (2 to 3 ft) below the surface. These soils can be identified by an ashy, bleached white layer immediately above the dense layer. This layer is known as the E horizon, and it forms between the A and B horizons.

Soil Acidity and Alkalinity

The acidity or alkalinity of the soil is expressed as its pH. pH is defined as the negative logarithm of H+ activity in the soil solution:

$$pH = -\log [H+]$$

It does not include any H+ adsorbed to the CEC or otherwise not dissolved in solution. pH is not a fixed characteristic of soil and, depending on a number of conditions, varies over time. Values for pH vary considerably among soils ranging from about 4.0 for an acid soil to 10.0 for an alkaline soil (Fig. 5-10).

Most plants do not grow well in highly acid or highly alkaline soils. In general, most plants will grow in the pH range of 5 to 7. However, most of these plants have a narrower range of optimum pH (Table 5—3).

The availability of nutrients to plants is influenced by soil pH. Some nutrients are available in greatest amounts at one pH while others are most available at a different pH (Fig. 5-11). Managing soil pH is an important strategy in fertility management as you will learn in Chapter 14.

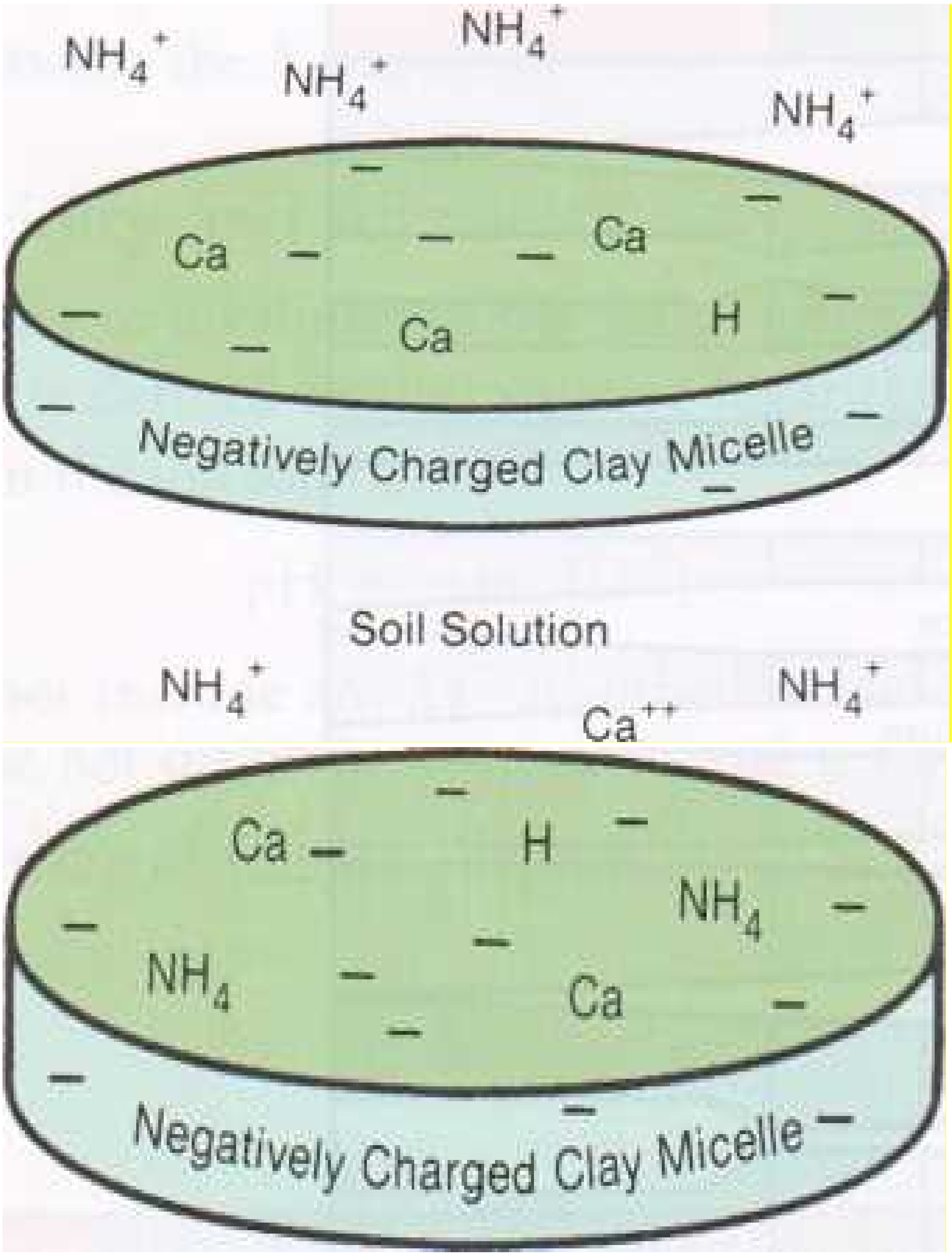
Soils in climates with high rainfall and humidity generally tend to be acid, while those found in arid climates tend to be alkaline. In wet climates, the base elements (sodium, potassium, calcium, and magnesium) are removed from the soil by leaching as well as by the harvested crops that have absorbed them. As the base elements are lost, the exchange sites on the clay colloids become occupied with hydrogen ions, making the soil acid.

Normally, sudden and large changes in soil pH do not occur. Change is generally gradual, especially with fine-textured soils. These and other soils resist such change due to buffering.

Cation Exchange Capacity An important property of clay and of the organic humus fraction of the soil is its ability to attract and hold cations—positively charged ions, some of which are essential plant nutrients (for example: NH4+, Ca+, K4"). Clay colloids carry thousands of negative charges throughout the clay particle and at the broken edges of the clay's layers. Thus, a clay colloid acts as a large, highly negatively charged particle (anion) (Fig. 5-12). A soil's capacity to hold cations is called its cation exchange capacity (CEC). It is called exchange capacity because cations are held very loosely by the colloids, and can be replaced, or "exchanged" with cations in the soil water (often called the soil solution). Ions on the CEC are held tightly enough, however, to prevent their leaching in percolating water. Organic matter has a greater net negativity than clay and has a higher CEC.

calcium (Ca^{++}) > magnesium (Mg^{++}) potassium (K^{+}) > ammonium ($NH4^{+}$) sodium(Na^{+}) > hydrogen(H^{+})

Most plant nutrients are cations and can be held by soil particles. The most notable exception is nitrate ($NO3^{-}$), which is not held and is



Ca clay + 4NH/ ► $(NH_4)_2$ clay + Ca^{++} + $2NH_4^+$

Figure 5-12

Not all cations are attracted to or held by the CEC with equal energy. The strength of attraction for some cations when present in equivalent amounts is:

readily leached out of the root zone. Cation exchange capacity is influenced somewhat by soil acidity: it is greater under alkaline than under acidic conditions. The difference is slight in mineral soils, but it can be substantial in soils containing large quantities of organic matter.

Saline and Sodic Soils

Saline soils contain unusually large quantities of soluble salts. The soluble salts are typically chlorides and sulfates of calcium (Ca"^{4}"), magnesium (Mg^{44-}), and sodium (Na^+), although other soluble cationic salts may contribute as well. Sodic soils differ from saline soils because a large percentage (over 15 percent) of the total cation exchange sites of the soil are occupied specifically by sodium ions (Table 5-4). Displacement of the sodium (Na^+) ion is the main objective in reclamation of a sodic soil. Agriculturally, saline and sodic soils are problem soils that require special handling for successful farming. Excessive amounts of soluble salts are harmful to plants and, when cations are predominantly monovalent (with a single charge), they have adverse effects on soil structure. Soils can be classified on the basis of the kind and amount of salts present, as shown in Table 5-4.

SOIL ORGANISMS

A microscopic examination of a soil sample reveals a wide variety of animal and plant life, some beneficial and essential to human well-being, and some harmful, often causing problems for people, their livestock, or crop plants. The animals include earthworms, gophers, insects, mice, millipedes, mites, moles, nematodes, slugs, snails, sowbugs, and spiders. Plants, plant-like organisms, and microorganisms in the soil include actinomycetes, algae, bacteria, and fungi.

Soil organisms act both chemically and physically on the soil. They digest plant residues and other organic matter enzymatically, and may physically move the residues from one place to another, mixing it with the soil. Earthworms and burrowing animals mix large quantities of material with the soil mass. The kind and amount of soil organisms depend on several factors, including climate, vegetation, soil pH, fertility level, soil temperature, and soil moisture.

The roots of higher plants are a good source of organic matter. Their decomposition by soil organisms produces organic acids and gluelike materials that bind soil particles together to form the aggregates necessary for good soil structure. Following the decomposition of roots, open channels are left in the soil, improving drainage and aeration. Organisms also decompose stems, leaves, and other crop residues.

Certain beneficial fungi called mycorrhiza live in association with plant roots. These fungi help the plants take in water and certain mineral nutrients such as phosphorus. In return, the fungus receives carbohydrates from the plant. Such a relationship between two dissimilar organisms living together for mutual benefit is called **symbiosis.**

Nitrogen fixation, sulfur oxidation, and nitrification are processes carried on by soil bacteria essential to higher plants. Many legumes develop nodules on their roots that contain ***Rhizobium***, a nitrogen-fixing bacteria (Fig. 5—13) that has a symbiotic relationship with the plant. As the legume grows, the bacteria convert unavailable atmospheric nitrogen (N2) into nitrogenous compounds that the legumes use while the plant furnishes energy to the bacteria. When these legumes die and decomposes the nitrogen compounds become a source of nitrogen for succeeding plants.

Elemental sulfur is not immediately available to higher plants; it must first be oxidized to the sulfate form. Autotrophic *Thiobacillus* bacteria bring about this transformation through a complicated series of reactions. Under certain conditions, autotrophic bacteria oxidize iron and manganese to compounds that are less soluble and thus less available to plants. The action of these bacteria helps prevent toxic amounts of iron and manganese from being taken up by the plants.

Not all soil organisms are beneficial. Some of the most injurious plant pests are soil borne. For example, nematodes attack and destroy plants in a wide range of species. Phylloxera, an aphid that attacks grape

Figure 5-13
Nodules of Rhizobium bacteria on a legume (soybean).
Source: Margaret McMahon, The Ohio State University.

roots, devastated large vineyard areas until resistant rootstock cultivars were developed. Pathogenic soil-borne bacteria and fungi are also responsible for significant crop losses.

SOIL ORGANIC MATTER

The soil's organic matter content has a profound effect on its biological, chemical, and physical properties. Through the decomposition (composting) of organic matter, many nutrients become available to crop plants. Organic matter provides food and energy for soil organisms. Most organic matter, except for a small animal fraction, comes from plants. By weight, about 90 percent is made up of carbon, hydrogen, and oxygen. The remainder is usually nitrogen, sulfur, phosphorus, potassium, calcium, and magnesium plus a minute amount of microelements.

The speed of organic matter decomposition varies according to its chemical composition. It is rapid for simple carbohydrates and slow for fats and lignins. Essentially the decomposition reaction is the oxidation of carbon compounds to carbon dioxide, water, and energy:

(CH20)H + 02-» C02 + H20 + energy

Proteins, fats, and other complex compounds decompose in a multitude of reactions to form amino acids, ammonia, nitrates, phosphates, carbon dioxide, and other compounds. After complete decomposition, a complex, amorphous, colloidal substance called humus remains that is resistant to further decomposition. This is the material that helps improve soil structure, imparts the dark color to the soil mineral fraction, and increases the soil's water-holding and cation exchange capabilities. For example, the cation exchange capacity of a mineral soil ranges from about 10 to 50 cmol kg-1, while the capacity of humus ranges from about 100 to 300 cmol kg-1. Being colloidal in size, humus acts similarly to clay colloids in cation exchange reactions, but it is composed chiefly of carbon, hydrogen, and oxygen with small amounts of other elements, while clay colloids largely consist of aluminum, silicon, and oxygen.

Carbon:Nitrogen Ratio

Under natural conditions, there is a close relationship between the amount of carbon and the amount of nitrogen in the soil. This carbon:nitrogen (C:N) ratio is nearly constant at about 12 parts of carbon to one part nitrogen, worldwide. Variations when present seem to correlate with climate, especially temperature and rainfall. For instance, the C:N ratio tends to be smaller (less carbon, more nitrogen) in arid and warmer regions than in humid and cooler regions. For a period of time in an area that has had a high input of organic material with a high C:N, nitrogen is tied up by the organisms that are causing the decomposition (Fig. 5-14).

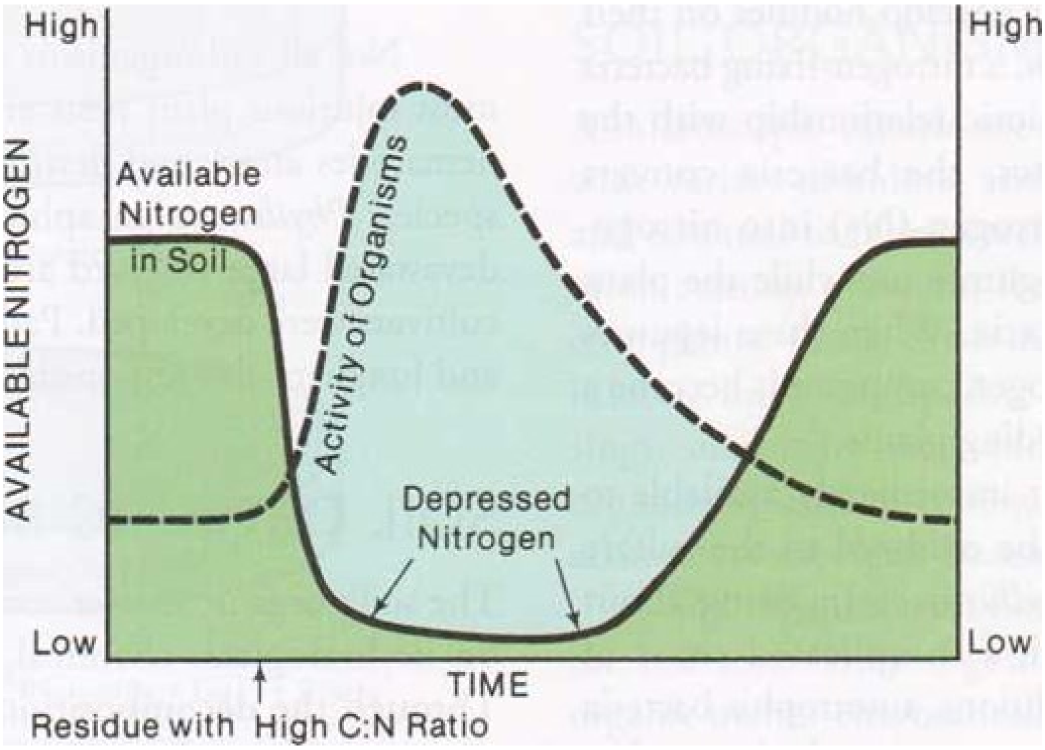


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Figure 5-14
The relationship between the available nitrogen in a soil and the activity of soil microorganisms after a heavy application of organic matter with a high C:N ratio

Eventually, the organic residues decompose to the level where the soil organisms exhaust their supply of food and begin to die. The nitrogen from the decomposing organisms is then returned to the soil and made available to plants again at about the original nitrogen level.

<u>*SUMMARY AND REVIEW*</u>

Soils form a complex ecosystem composed of biological organisms, living and dead; inorganic materials; water; and air. The interaction over time of many factors including parent material, physical and chemical weathering, types of organisms present, the topography of the area, and other climate factors influence the formation and properties of soil.

Physical soil properties include texture (percentage of sand, silt, and clay particles) and structure the arrangement of the primary particles). Soils with good structure have enough pore (air) spaces that are 'arge enough to transmit water and air without restriction and sufficient smaller pores that retain some water against the pull of gravity. Chemical soil properties include cation exchange capacity (CEC), soil acidity and alkalinity, and salinity. Cation exchange capacity is the ability of the soil to exchange cations it already holds with cations in the soil water. This factor is very important in fertility management.

Soil acidity and alkalinity affect the availability of nutritional elements to the plant. Saline soils naturally contain large quantities of soluble salts. These salts may be harmful to plants if they are present in great enough quantities.

Soil organisms play a crucial role in determining soil characteristics. They create pore space by their tunneling activities. They add organic material when they die and decay. They often form beneficial and sometimes even necessary symbiotic relationships with the roots of plants growing in the soil. On the other hand, plant pathogen and herbivore organisms that can infest or feed on roots can also be a part of the soil ecosystem.

Soil degradation occurs when erosion removes the productive A horizon, making it difficult for plants to grow well. It also occurs when the deposition or organic material becomes less than its decomposition resulting in an overall loss of organic material.

KNOWLEDGE CHECK

1. What are the five basic components of soil?
2. How does pore space relate to a productive soil?
3. What is field capacity of a soil?
4. What is parent material?
5. What is a soil horizon? What is a soil profile?
6. What is physical weathering?
7. List the four processes of chemical weathering.
8. Why are soils that are formed in regions of very high rainfall or very low rainfall usually not productive?
9. How do plant roots add to the organic material in the soil?

10. What role do bacteria and fungi play in soil formation?
11. Ҳосилдор тупроққа олам ғоваки қандай алоқаси бор?
12. What are mvcorrizha and how do they help plants?
13. What kind of topography promotes water erosion? Wind erosion?
14. How do plants influence erosion?
15. Even though some deserts have been in existence for thousands of years, why is the soil there considered to be very young?
16. In which soil horizon are the most roots and biological activity found?
17. What is soil texture and what are the components that contribute to a soil's texture?
18. What is soil structure?
19. What are the differences between mollisols, spo- dosols, and oxisols?

FURTHER EXPLORATION

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*6

Plant Growth and Development

JAMES D. METZGER

key learning concepts

After reading this chapter, you should be able to:

- Know the difference between plant growth and plant development and understand ways to measure each.
- Understand the factors that affect plant growth and development and what the effects are.
- Understand how those factors can be manipulated to control plant growth and development.
- Recognize the categories of plant hormones, understand their role in plant growth and development, and how they are used to control plant growth and development.

DEFINITIONS AND MEASUREMENTS

What is plant growth and how is it measured? We generally think of growth as an irreversible increase in volume or dry weight (biomass). The swelling of wood after it becomes wet is not growth because the wood will shrink upon drying. Growth can be measured as increases in fresh or dry weigh, or in volume, length, height, or surface area. As its gross size increases, a plant's form and shape change as directed by genetic factors with influence from the environment. Plant growth is a product of living cells, with all their myriad metabolic processes. A definition of plant growth is as follows: size increase by cell division and enlargement, including synthesis of new cellular material and organization of subcellular organelles. Plant development is its progress through its lifecyle. Figure 6-1 shows the difference between growth and development. Stages of development include seed germination, growth of vegetative organs and tissues, initiation and maturation of reproductive organs and tissues, fertilization, seed development and maturation, and senescence and death. With perennials, some of these are repeated many times during the complete lifestyle. Asexual propagation would substitute cutting rooting or some other initial stage for seed germination.

HOW THE PLANT GROWS

The importance of meristems in the growth of plants must be clearly understood. In dicotyledonous plants, vegetative buds at the shoot tips (apical meristems) and in the axils of leaves contain meristematic (actively dividing) cells that are capable of producing millions of cells along a longitudinal axis. Cell division, together with cell elongation and expansion, causes the shoots to grow. A growing point at a shoot tip, with its meristematic region producing new cells year after year for many hundreds of years, can account for the towering height of the redwood, Douglas fir, and other forest trees. Similar meristematic cells are also located in the root tip, just behind the root cap.

The thickening of the trunks of dicotyledonous trees is due to secondary growth produced by another meristematic region, the vascular cambium. It is a cell aver that lies between the xylem and the phloem and encircles the tree from the roots to almost the top of the snoot. Cells of this vascular cambium also have the capability of dividing, producing both the permanent woody xylem tissues toward the inside that give the tree its girth md mechanical strength and the more fragile transitory phloem cells to the outside. External to the vascular cambium is another meristematic region, the cork cambium, vhich produces the cork in the bark layer.

Figure 6-1

The poinsettia on the right has more growth while the one on ***Tie*** *eft is more developed.*

In mature plants, vegetative apical meristems can become reproductive meristems and produce the floral parts needed for seed production.

Factors Affecting Plant Growth and Development

Genetic and environmental factors interact to determine how a plant grows and develops. Some of the most important ways these factors influence plant growth and development follow.

Genetic Factors One of the marvels of biology is the manner in which the off-spring of plants and animals resemble, yet differ from, their parents. A peach tree, not a cherry tree, grows from a germinated peach seed. In a field planted with wheat seed, wheat plants develop, not oats or barley. The organism developing by cell division and elongation from the fertilized egg—the zygote—in every case is under the genetic control of the genes inherited from the parents at the time of fertilization.

As the plant enlarges from the fertilized egg or zygote to its mature size, many developmental processes take place. Genes direct the synthesis of proteins that can be enzymes, structural proteins such as the mitotic spindles, and special proteins called transcription factors that regulate the activity of structural genes and other regulatory genes. At any given time, some of the organisms genes are transcriptionally active, while others are silent. The control of gene activity depends on the cell type, environmental conditions, or the particular stage of development. As development proceeds, genes are activated and deactivated, depending on signals received in the nucleus. The control of development through selective gene activation and deactivation is mediated mostly (but not entirely) through the action of transcription factors that turn on or turn off genes.

What are the signals that trigger the action of the regulatory genes? Although not clearly understood, biotic signals are believed to include plant hormones, certain inorganic ions, coenzymes, and other metabolites. The classes of hormones that most affect plant growth and development are auxin, gibberellin, cytokinin, and ethylene. A full discussion of the biological function these and other hormones and their uses as chemical plant growth regulators is at the end of this chapter. Environmental factors such as temperature or light can also function as signals during certain developmental stages. Thus, the particular combination of genes directs the form and size that each plant is finally to assume, as altered by environmental influences, either beneficial or deleterious. Many of the measures we use to control plant growth and development ultimately work by activating and deactivating gene transcription.

Environmental Factors You learned about these factors in other chapters of this book, but for a quick refresher and in the context of affects on plant growth and development, we will review them here.

Light The sun is the source of energy for photosynthesis (the production of carbohydrates), but a substantial amount of radiation is lost because of absorption and refraction as it passes through the atmosphere. The atmosphere does not absorb very much of the sun's radi-ation with wavelengths of 400 to 700 nm; this is important because this band of radiation, which is commonly referred to as visible light or photosynthetic active radiation (PAR), is the most important to life on earth. Plants have many mechanisms to most efficiently capture light for photosynthesis. These mechanisms often involve changes in the way the plant grows and develops.

Radiation passing through the earth's atmosphere can be refracted, or scattered, resulting in significant reflection of light back into outer space and thus reducing the amount of light available for photosynthesis. In addition to absorption and scattering, the amount of light reaching the earth's surface depends on the angle of incidence of the sunlight, that is, the angle that a beam of sunlight, makes with the earth's surface. An angle of incidence of 90° has the maximum amount of light striking an area. As the angle of incidence decreases from 90°, a greater proportion of the incident light is reflected, which explains why so much more sunlight is reflected around sunrise and sunset than at midday. An angle of incidence of 90° also spreads the light out over a greater region (Fig. 6-2). The angle of incidence of sunlight has two major effects on crop growth. First, light intensity is directly related to plant photosynthetic rates. As the sun rises the angle of incidence increases, light intensity increases, so does photosynthetic activity until the photosynthetic machinery is saturated. Then photosynthetic activity gradually declines as the day progresses toward sunset.

Not only does the angle of incidence affect the intensity of light, it also affects the amount of light entering the leaf and available for absorption by chlorophyll. Light striking a surface has two possible fates: it may penetrate the surface, where it is either absorbed by or transmitted through the material, or it can be reflected. The proportion of incident light that is either absorbed or transmitted by (or reflected from) a surface varies with the angle of incidence.

Light that is reflected from the surface of a leaf is lost for photosynthesis. Some plants such as soybean can compensate for the reduced light intensity and increased reflection at low solar angles through heliotropic movements, in which leaf angles are adjusted so that the sun's rays are normal, or perpendicular, to the leaf during most of the day. Heliotropic movements are also used to lower the amount of light absorbed by reducing the angle of incidence of sunlight.

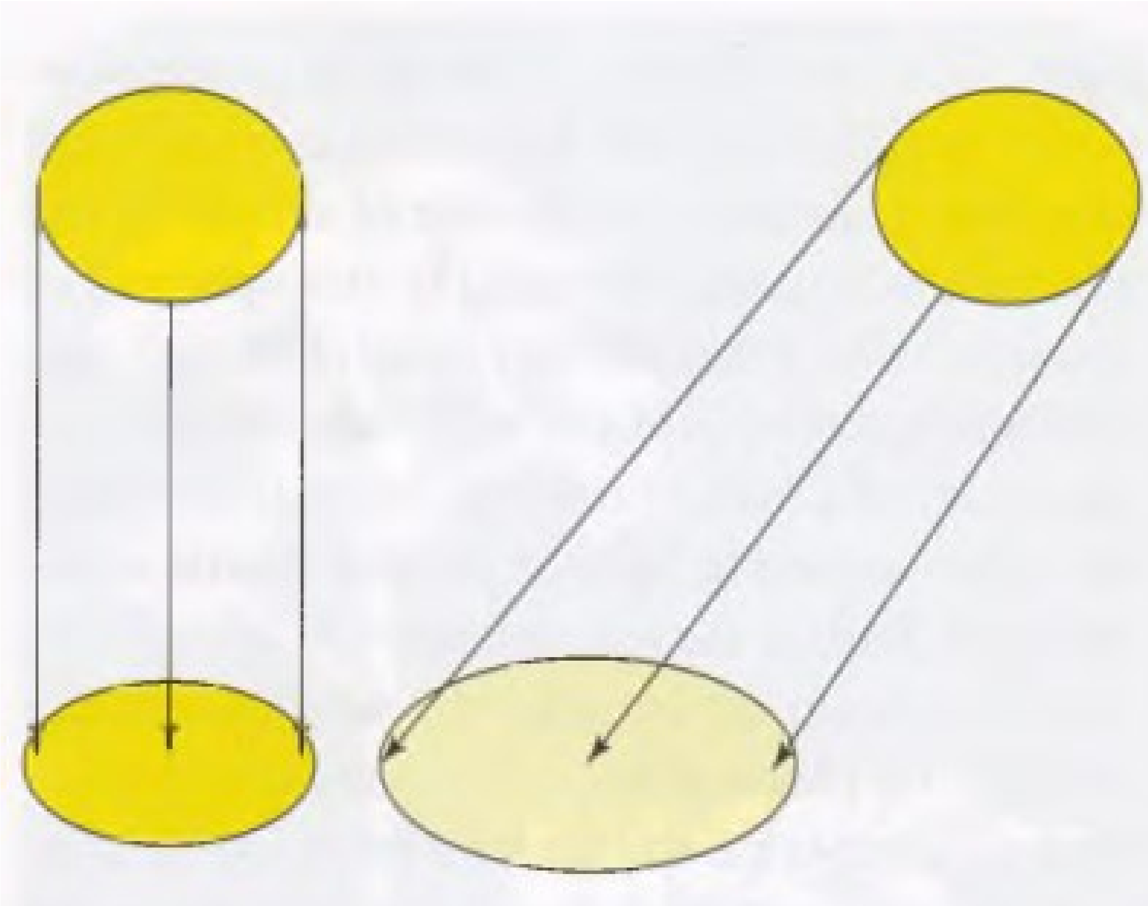

Figure 6-2

The effect of angle of incidence on how much light strikes an area.Source: Margaret McMahon, The Ohio State University.

on the leaf when overheating might occur. Leaves are not the only plant organ that moves in response to solar movement. Perhaps the best known example of heliotropism occurs in Helianthus annus (sunflower) which gets both its scientfic and common name from its ability to keep its flowers facing the sun all day.

Another characteristic of light that is important for plant processes is quality. Light quality does not refer to how beneficial the light is for the plant, but rather to the relative quantity of individual component wavelengths contained in an incident beam of light. Better terms for light quality are spectral composition or spectral distribution, but these have not yet gained widespread acceptance by plant scientists. The band of wavelengths that affect plant processes range from about 380 nm to

800 nm, but individual processes such as photosynthesis have much more narrow requirements for the specific wavelengths that are most effective. For example, blue and red light at 440 and 650 nm, respectively, are much more effective in driving photosynthesis than is green light. Other light-controlled processes have different spectral requirements.

Light also affects plant growth and development through photomorphogenesis. Photomorphogenesis describes several highly integrated processes that are regulated to produce the shape or form of the plant, and they include seed germination in light-sensitive seeds, de-etiolation (the greening of young seedlings when they emerge from the soil), and stem growth in plants competing for light with other plants. A characteristic that distinguishes most photomorphogenic responses from photosynthesis is the relative insensitivity to light intensity. In fact, most photomorphogenic responses are fully induced by light intensities that are below the compensation point for photosynthesis. In addition, photomorphogenic responses typically have more specific requirements for the spectral composition of the incident light than does photosynthesis.

Most photomorphogenic responses are regulated by the phytochrome pigment system. Phytochrome is a pigment that has two interconvertible forms: a red light absorbing form and a far-red light absorbing form. Far-red light is the region of the spectrum with wavelengths between 700 and 800 nm, but the far-red absorbing form of phytochrome absorbs maximally in the region of 720 to 740 nm. As shown in Figure 6-3, a phytochrome molecule in the red absorbing form is converted to the far-red absorbing form following irradiation with red light. Irradiation with far-red light is required for the phytochrome molecule to be converted back to the red absorbing form. As a consequence, the relative amounts of the far-red absorbing form compared to the red absorbing form are proportional to the ratio of red to farred (R:FR) light in the environment. During most of the day, the R:FR ratio is about 1.2:1, so roughly speaking, about two-thirds of the total pool of phytochrome is in the far-red absorbing form. This is important because the far-red absorbing form resulting from

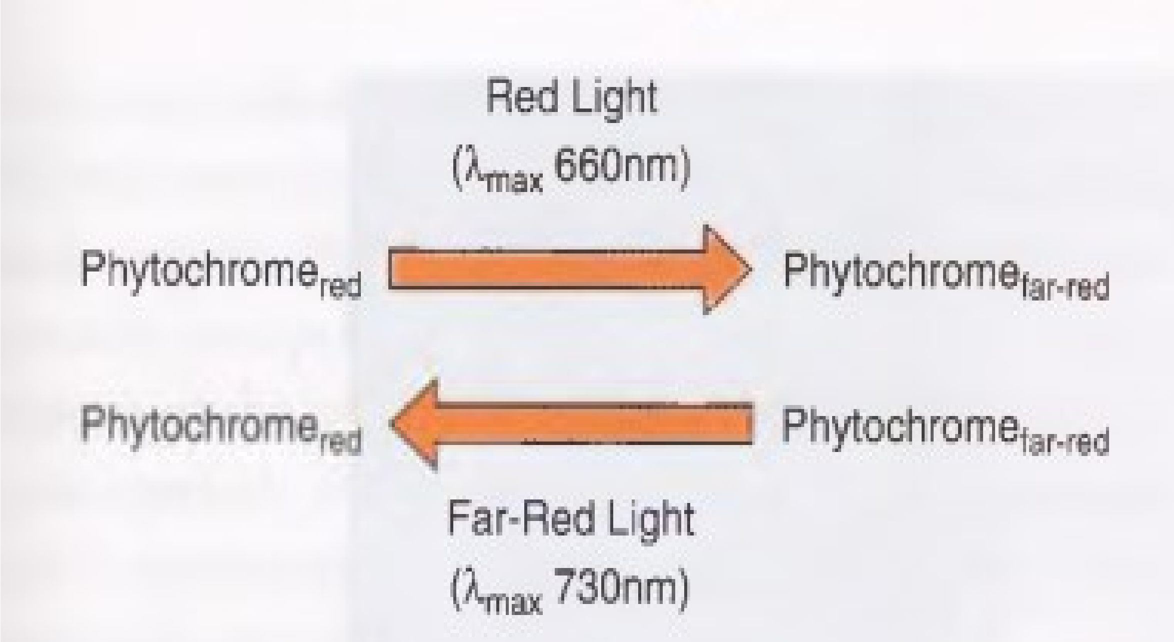

Figure 6-3

How red and far-red light affect phytochrome. Phytochrome$_{rec}$*i can absorb only red light, while phytochromef*$_{gr\cdot rec}$*i can absorb only far-red light. The wavelength of light that is most effectively absorbed by the phytochrome molecule is signified by X-max- Slightly longer and shorter wavelengths are also absorbed, but less effectively.*

irradiation with red light leads to different biological reactions compared to the red- absorbing form. Thus, plants have a highly sensitive system for sensing changes in the light environment by continuously measuring the R:FR ratio. The R:FR ratio declines dramatically as light penetrates through leaf canopies because red light is efficiently absorbed by chlorophyll, while the far-red light is either transmitted or reflected (Fig. 7-4). In some dense canopies, for example in a cornfield, R:FR ratios can be as low as 0.05. The R:FR ratio of light impinging on an individual plant is highly dependent on how close and, of course, how big are the neighboring plants.

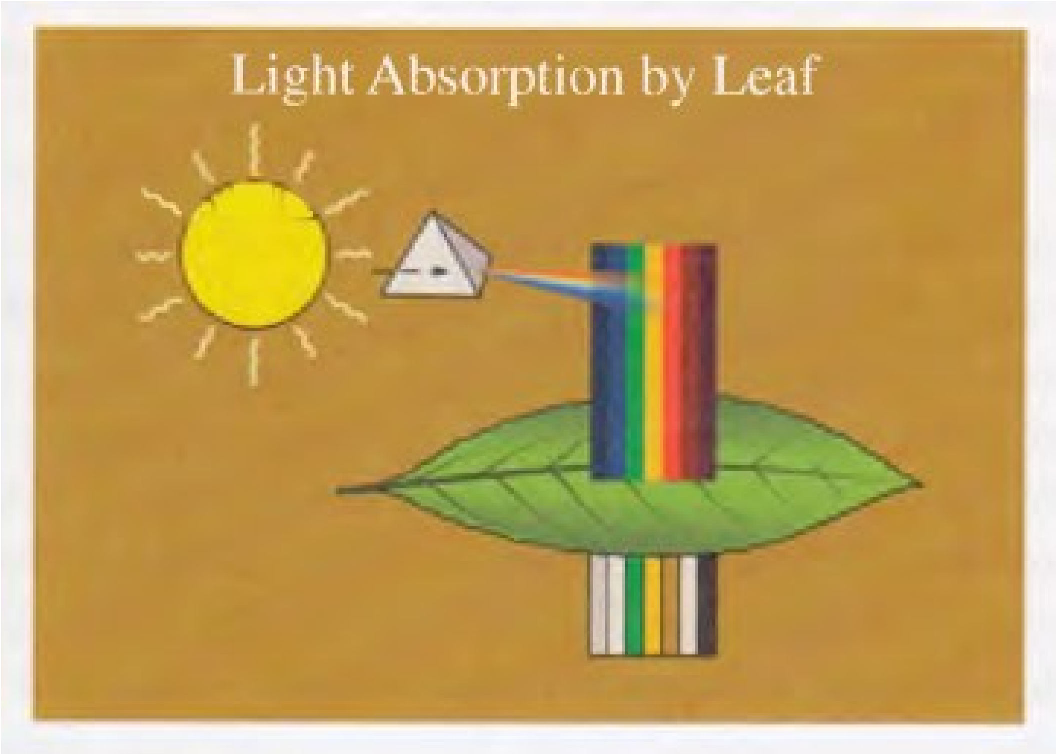

Figure 7-4

Diagram of how a leaf selectively absorbs light for photosynthesis. The dark red line on the far-right represents far-red which is not involved in photosynthesis but has other important effects on plants. Source: Margaret McMahon, The Ohio State University.

The information contained in the R:FR ratio provides an accurate means to sense neighboring plants and to respond so that it can compete for resources, especially light (shade avoidance response).

Plants compete for light by redirecting growth and development so that they produce leaves that are above the leaves of their neighbors. It is no surprise then that plant architecture is highly dependent on the R:FR ratio under which the plant grows. Plants grown in light conditions in which the R:FR ratio is high (for example, open sunny areas) are typically compact, with dark green leaves and more branches and tillers. Plants respond to a decline in the R:FR ratio with increased height, reduced branching, and smaller stem diameters (Fig. 7-5). Chlorophyll synthesis declines when the R:FR ratio is low, so plants appear chlorotic even though soil fertility is adequate. These changes in plant architecture result in tall, spindly plants that are more prone to lodge (fall over) under typical field conditions and are more easily damaged during shipment. Such plants are also more susceptible to disease and environmental stress. Reduced branching and tillering under low R:FR ratios also results in lower yields. The practical implication of the neighbor detection system is that a maximum number of plants can be grown in an area; any number above the maximum means that yield or quality is adversely affected.

Another pigment system mediating photomorphogenic responses is the cryptochrome system. In contrast to phytochrome, this pigment is a blue light photoreceptor. Cryptochromes are a family of molecules that are involved in photomorphogenic responses as well as circadian (daily) rhythms. A blue light receptor, different than cryptochrome, called phototropin, is responsible for phototropism (movement in response to light) (heliotropism is a type of phototropism) and it may be involved with stomate opening. For the most part, above-ground organs such as stems, leaves, and flowers bend toward a unidirectional beam of light and are said to exhibit a positive phototropic response. The bending in positive phototropic responses is due to increased cell growth on the side away from the light source. It is believed that the plant hormone auxin accumulates on the shaded side, promoting cell expansion. In some species, the roots exhibit a negative phototropic response; that is, they grow away from the light source. Cryptochrome and phototropin complement the functions of phytochrome in providing the plant with more complete information about the light environment in which it is growing.

Another characteristic of light that is important to plant growth and development is duration. Photoperiodism is the photomorphogenic response to variations in daylength. Numerous aspects of plant growth and development are controlled by photope-riod including flowering (which will be discussed in more detail later in this chapter); induction of bud dormancy in woody species; and the formation of vegetative propagules such as bulbs, tubers, corms, and runners (stolons).

Figure 6-5

Right: plant was grown under a filter that blocked far-red but not red light (high R:FR). Center: plant was grown under normal sun light. Left: plant was grown under a filter that blocked red but not far-red (low R:FR). The intensity of photosynthetically active light was the same for all three plants. Source: Margaret McMahon, The Ohio State University.

All photoperiodically controlled processes can be categorized into three basic response types: long-day plants (LDPs); short-day plants (SDPs); and day- neutral plants (DNPs); which are photoperiodically insensitive (there are actually more response types, but the three described here represent the vast majority of species). The designation as a long- or short-day plant is not based on the absolute length of the day, but rather if the photoperiodically controlled process is induced only at daylengths longer or shorter than specific daylength, called the critical daylength (CDL). A plant with photoperiodically controlled process that is induced only when the days are longer than the critical daylength is considered an LDP for that process, while an SDP represents the inverse situation: the process is induced only when the daylength is shorter than the CDL. It is important to understand that no direct relationship exists between the response type and the absolute length of the CDL. For example, consider the flowering response of a typical LDP and an SDP. Red clover is an LDP with a CDL of twelve hours, meaning that it will not flower unless the daylength is longer than twelve hours. In contrast, the CDL for the hardy chrysanthemum, which is an SDP, is fifteen hours, considerably longer than red clover, a so-called longday plant. In general, whether or not a plant is an SDP or LDP determines when the process is induced relative to the summer solstice. In other words, long-day responses are initiated prior to the longest day of the year, while short-day responses are initiated when the days begin to shorten, so that the shorter the CDL, the later in the summer or early fall the process is induced.

Next to flowering, the collection of integrated processes known as the autumn syndrome observed in many woody plants is the most visible photoperiodic process. The autumn syndrome describes a series of processes that occur in plants in temperate climates at the end of the summer in preparation for winter; these processes include acquisition of freeze tolerance; dormancy of buds; and, in deciduous trees, leaf fall. Dormancy is a temporary cessation of growth and is often accompanied by the formation of bud scales, modified leaves that protect the delicate shoot tips from desiccation during winter.

Dormancy is induced by short days in several familiar trees and shrubs, including red maple (Acerrum), redbud (Cercis canadensis), American elm_ .mus americana), eastern hemlock (Tsuga canadensis), i__d weigela {Weigela florida). However, there are some ':rable exceptions in which dormancy and other erects of the autumn syndrome are not controlled by rxDtoperiod. Some examples include ash (Fraxinus гг. . mountain ash (Sorbus spp.), and common fruit rrees such as apple (Malus) and pear (Pyrus).

The critical daylength for dormancy induction zisi vary by several hours among members of a species, especially when individuals from different latitudes are ;: mpared. This variation maximizes the number of reographical areas a species can colonize. Table 7-1 provides a comparison of the approximate critical ex .'lengths for the induction of bud dormancy in vari- : woody plants at three different latitudes. Typically, the higher the latitude, the longer the CDL for the mduction of bud dormancy (and other short-day responses as well). The longer CDL at higher latitudes results in increasingly earlier dates at which buds begin to go dormant, and this process is directly related to earlier onset of winter.

In addition to flowering and bud dormancy, other irvelopmental processes are controlled by photoperiod.

• lany of these processes are related to strategies for sur- val in unfavorable environmental conditions such as me cold temperatures of winter or the hot, dry condi- rions of summer. Many herbaceous perennials survive sinter with the formation of tubers that are protected ry being buried underground; some examples of plants in which tuber formation is a photoperiodically controlled process are potatoes, dahlias, yams, Jerusalem inichokes, and tuberous begonias. In all these cases, raber formation is a short-day process that is initiated at me end of the summer. The formation of vegetative rosettes at the base of certain herbaceous perennials and adventitious crown or root buds are often short-day induced processes that are specially adapted to survive winter.

In contrast, processes relating to vegetative reproduction are often induced in late spring and early summer by long days to take full advantage of the growing season. Examples include runner formation and growth in the strawberry plant and bulb formation in onion, garlic, and related species. (Note that bulb and corm formation in spring blooming ornamental species like tulip, hyacinth, and crocus are not under photoperiodic control.) In commercial onion production, it is important to match the critical daylength of a cultivar with the latitude in which it will be grown. Table 6-2 provides a comparison of the critical daylength for bulb formation in different onion cultivars. It is obvious that some of these cultivars (e.g., Yellow Zittau) would exhibit poor bulb formation if grown, say, in Orlando, Florida (28°N), in which the longest day of the year is about fourteen hours.

Temperature The seasonal variation of light intensity is responsible for the temperature changes from summer to winter in the various temperature zones. To make sure that the crops they grow have enough time to grow and develop, farmers depend on climatic records in their areas to predict the last day of frost in the spring and the number of available growing days before the first killing frost in the fall. The greater the distance from the equator, the fewer the number of available growing days to mature crops. It is possible to grow temperature-sensitive tomatoes in Alaska or northern Europe, but precautions must be taken to protect the seedlings from frost in early spring. Once summer arrives in these northern latitudes, the days are so long and the temperatures are warm enough that plants grow, flower, and set fruit rapidly. The growing season may be short, but plants develop quickly.

All plants have optimal temperatures for maximum vegetative growth and flowering, as noted for plants discussed as crops in subsequent chapters. Most temperate-region plants grow between temperatures of 4°C (39°F) and 50°c (122°F), but these are generally the limits of plant growth. The high temperatures destroy the protoplasm of most cells; however, some spores and seeds can withstand the temperature of boiling water for short periods. At the low temperatures, most plants just fail to grow because of a lack of cell activity. However, there are some arctic or mountain plants that function near freezing, but these are rare exceptions.

Plant parts are injured by very high temperatures, even if the exposure is short. Leaves may be solarized or sunburned when exposed to high light intensities. In the leaf, light energy converts to heat, which destroys the cells. Young trees in orchards are prone to sunscald, which kills the cambium layer just under the thin bark of the trunk and limbs. Injury can be prevented by whitewashing the bark to reflect the heat. Occasionally, plants suffer heat damage when the relative humidity drops suddenly because of hot, desiccating winds. Heat damage in intensively managed systems such as nurseries, golf course and athletic fields, and in greenhouses can be prevented if the relative humidity is increased by misting in the immediate vicinity of the plant.

The most common low-temperature injury is evident after the night of the first killing frost in the fall. Plant surfaces may be coated with frost depending on the dew point temperature, but soon after the sun shines on the leaves, the damage is evident in blackened leaves. The contents of the cells are damaged by the formation of ice crystals that rupture the cell membranes and walls, allowing water to flow out of the protoplasm and desiccating the cells. Frost damage to plants due to heat loss at night by radiation can be avoided to some extent by placing a covering between the plant and the clear sky on a calm night. This covering prevents radiant heat transfer from the leaves to the cold sky. Citrus and grape growers sometimes use smudge pots burning oil to create heat that radiates to the trees. In locations where there are temperature inversions above the plants (slightly warmer temperatures in a layer some distance above the soil than at ground level), wind machines may be useful. The power-driven propellers mix the warm air above with the cool air below, thus preventing low-temperature injury.

Many woody perennials grown in locations with severe winters enter into a rest period—brought on by shortening days in fall—and become resistant to low winter temperatures. A covering of snow or leaf litter or mulch helps the plants withstand the winter because it acts as a good insulator at extremely low temperatures.

Some plants of tropical origin may be injured at temperatures well above the freezing point—for some plants 13°C (55°F) is low enough to cause injury. This is referred to as a chilling injury. The leaves may wilt and never recover and developing fruits may not mature; some examples are avocado, banana, mango, okra, and tomato. Unripe tomatoes, which show pink color, are injured and do not finish the ripening process if refrigerated at 4°C (39°F) or less. Many ornamental foliage plants are susceptible to chilling injury. These plants need protection when being shipped during the winter from warm production areas such as Florida to colder areas. They should also be kept away from cold areas in homes and office buildings.

While we usually think of low temperatures as being injurious or as negatively affecting plant processes, low, nonfreezing temperatures are sometimes used by plants as cues to coordinate growth and development with the changing seasons. Temperatures for these cold-induced processes are usually in the range of 0°C (32°F) to 10°C (50°F). Examples of cold-induced processes include:

0. Seed germination. Some seeds require a period of time (usually several weeks) during which the seeds are imbibed at low temperatures (stratification) before germination is possible. The seeds must be kept moist because dry seeds cannot sense the cold temperatures.

1. Flowering. The cold induction of flowering is called vernalization and will be discussed in more detail later in this chapter.

2. Dormancy breakage. As spring approaches, bud dormancy and other processes (such as freeze tolerance induced in the fall in many woody plants) are gradually lost, while the ability to resume growth is

regained. The environmental cue initiating these changes is often cold temperature. The duration required for complete loss of dormancy is called the chilling requirement. The length of the chilling requirement varies among species and even among cultivars of species.

3. Acquisition of cold and freeze tolerance. For many herbaceous perennials, the low, nonfreezing temperatures (0°C to 10°C) that frequently occur during autumn nights induce the physiological

processes responsible for the ability to survive the freezing temperatures of winter. The freeze tolerance acquired in the autumn is quickly lost when temperature rises the following spring. Unlike the first three cold-induced processes above which require several weeks of cold, the duration of the cold period required to induce maximum freeze tolerance is relatively short—about one to two weeks.

Water Water is very important in the growth and development of plants. As you have or will learn in this book, water is required for: biological processes, as a part of the plant structure, nutrient and metabolite transport, as well as temperature control in the plant. When water is limiting, the above can be affected which impacts how the plant can grow and develop. Water also directly influences how plants grow. When water is plentiful, plants grow more succulently than when water is limited. Much of this difference in growth is due to how the cells that are enlarging are affected. When water is plentiful, the cells are turgid ' filled with water). The plasmalemma presses against the developing cell wall. Under these conditions the wall elongates longitudinally and it is it not as thick as when the plasmalemma is not pressing on it. When water is limiting, the cell can undergo plasmolysis because it is not fully turgid. In plasmolysis the plasmalemma pulls away from the cell wall. Under those conditions as long as plasmolysis is not so severe that the cell desiccates and dies, the developing wall becomes thicker and does not elongate as much. These cells usually are shorter and stronger than cells that developed under turgid conditions, resulting in shorter, stronger stems. A strategy for keeping plants short is to carefully withhold water during cell elongation in the stems. This is called drying down. It should be noted that a grower must pay very close attention when using this practice, as it is often a very short time between drying down and drying up (desiccation), which is not good for plant quality.

Gases The two gases most important to the growth of green plants are carbon dioxide (CO_2) and oxygen (O_2). Carbon dioxide is the third most abundant gas in the atmosphere, behind nitrogen (N_2) and O_2. Although used in great quantities for phototsynthesis, in relative amounts in the atmosphere, CO_2 is very small. Nitrogen is approximately 78 percent (~ 780,000 ppm),

O_2 is approximately 21 percent (~ 210,000 ppm), and CO_2 is approximately 0.035 percent (~ 350 ppm). Stomatal opening and closing is regulated in part by the CO_2 level in the leaf, which is influenced strongly by photosynthesis. When the CO_2 concentration in the leaf cells behind the stomata is lower than that found in the atmosphere, stomata open. The absorption of CO_2 for photosynthesis keeps the concentration lower than atmospheric concentration and the stomata remain open if other conditions (especially water availability) are favorable. When sufficient water is not available to support the plant, the stomates close, thus blocking the entry of CO_2 and dramatically reducing the rate of photosynthesis, which can have a negative impact on growth.

Oxygen is important in the respiration of all plant parts. Respiration is the release of energy captured and stored in the carbohydrates (sugars) synthesized during photosynthesis. The released energy is used to drive the complex biochemical reactions needed for the growth and development of not only plants but also all living organisms. While a low concentration of O_2 is rarely a problem for the aerial portion of the plant, roots can experience low O_2 when the soil is flooded or compacted. As a result overall plant growth is negatively affected.

STAGES OF GROWTH AND DEVELOPMENT

Germination and Early Seedling Growth In general, seed germination occurs in three stages: (1) imbibition (water uptake); (2) increase in biological activity; and (3) radicle (root) and shoot emergence (Fig. 6-6). There are many factors that control the start of germination including water availability, appropriate temperatures, presence or absence of light, as well as others. The specific factors needed vary tremendously among species and even varieties and cultivars within species. However, once a plant's requirements are met, then germination can begin. Germination starts with the seed imibing water. This causes cells to swell and the seed increases in size. Respiration and other biological activity, such as enzyme activity and synthesis, increase, thus decreasing the energy reserves of carbohydrates and lipids. Cells elongate and begin to divide and differentiate. The embryonic root (radicle) and shoot (plumule) emerge. The radicle quickly becomes a functioning root. Leaves emerging from the shoot start to photo- synthesize and the new plant becomes independent of the energy reserves in the seed. Many of the techniques used in growing plants are designed to promote seed germination and seedling development.

Figure 7-6

The seed on the left has not begun to germinate, the center seed has imbibed water, the seed on the right has the radicle and plumule emerging.

Source: Margaret McMahon, The Ohio State University.

Vegetative Growth and Development

Shoot and Root Systems In living plants, we see primarily the shoot system, in all its diverse patterns— from the mosses to the magnificent towering redwoods.

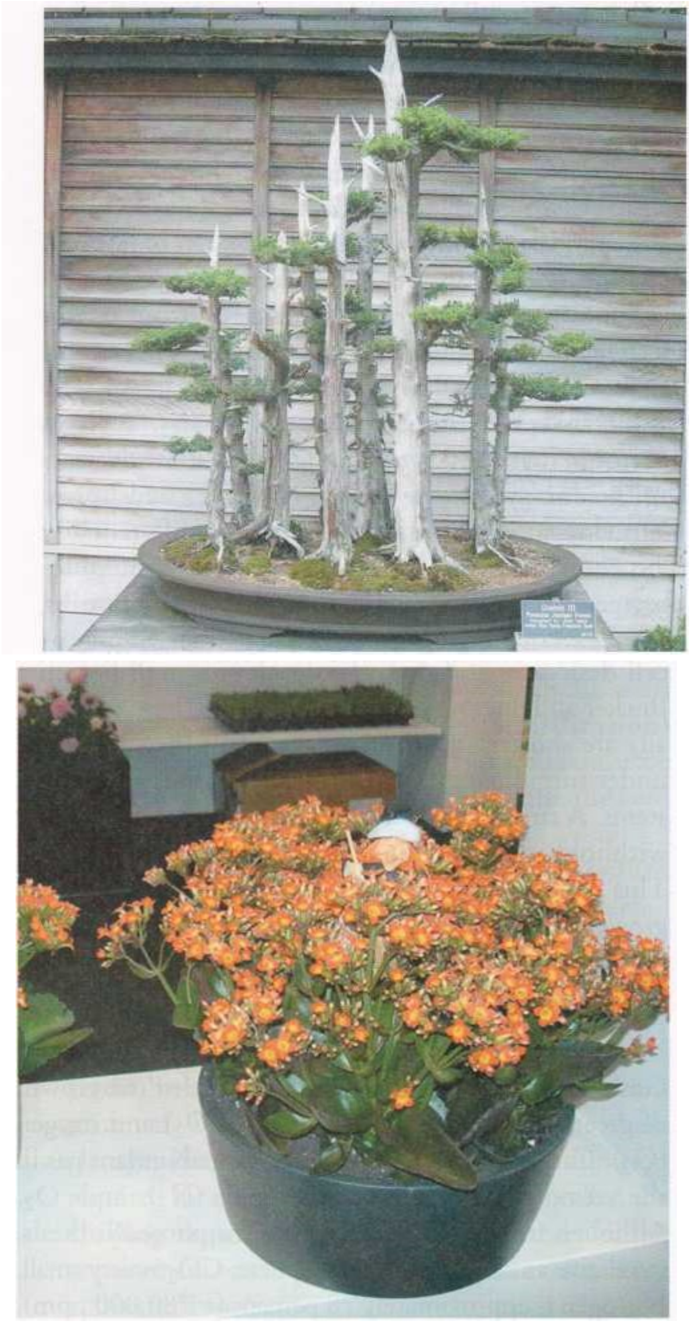

Figure 6-7

Growers of bonsai (left) and potted flowering plants (right) usually want to inhibit vegetative growth to create an effect or enhance aesthetic appeal. Whereas, growers of other crops generally prefer at least initial vegetative growth to be vigorous.

Soil Acidity and Alkalinity

The acidity or alkalinity of the soil is expressed as its pH. pH is defined as the negative logarithm of H+ activity in the soil solution:

$$pH = -\log [H+]$$

It does not include any H+ adsorbed to the CEC or otherwise not dissolved in solution. pH is not a fixed characteristic of soil and, depending on a number of conditions, varies over time. Values for pH vary considerably among soils ranging from about 4.0 for an acid soil to 10.0 for an alkaline soil (Fig. 6-10).

Most plants do not grow well in highly acid or highly alkaline soils. In general, most plants will grow in the pH range of 5 to 7. However, most of these plants have a narrower range of optimum pH (Table 5-3).

The availability of nutrients to plants is influenced by soil pH. Some nutrients are available in greatest amounts at one pH while others are most available at a different pH (Fig. 5-11). Managing soil pH is an important strategy in fertility management as you will learn in Chapter.

Soils in climates with high rainfall and humidity generally tend to be acid, while those found in arid climates tend to be alkaline. In wet climates, the base elements (sodium, potassium, calcium, and

magnesium) are removed from the soil by leaching as well as by the harvested crops that have absorbed them. As the base elements are lost, the exchange sites on the clay colloids become occupied with hydrogen ions, making the soil acid.

Normally, sudden and large changes in soil pH do not occur. Change is generally gradual, especially with fine-textured soils. These and other soils resist such change due to buffering.

Cation Exchange Capacity An important property of clay and of the organic humus fraction of the soil is its ability to attract and hold cations—positively charged ions, some of which are essential plant nutrients (for example: NH4+, Ca+, K4"). Clay colloids carry thousands of negative charges throughout the clay particle and at the broken edges of the clay's layers. Thus, a clay colloid acts as a large, highly negatively charged particle (anion) (Fig. 5-12). A soil's capacity to hold cations is called its cation exchange capacity (CEC). It is called exchange capacity because cations are held very loosely by the colloids, and can be replaced, or "exchanged" with cations in the soil water (often called the soil solution). Ions on the CEC are held tightly enough, however, to prevent their leaching in percolating water. Organic matter has a greater net negativity than clay and has a higher CEC.

pattern, the poinsettias on the right have a determinate pattern.

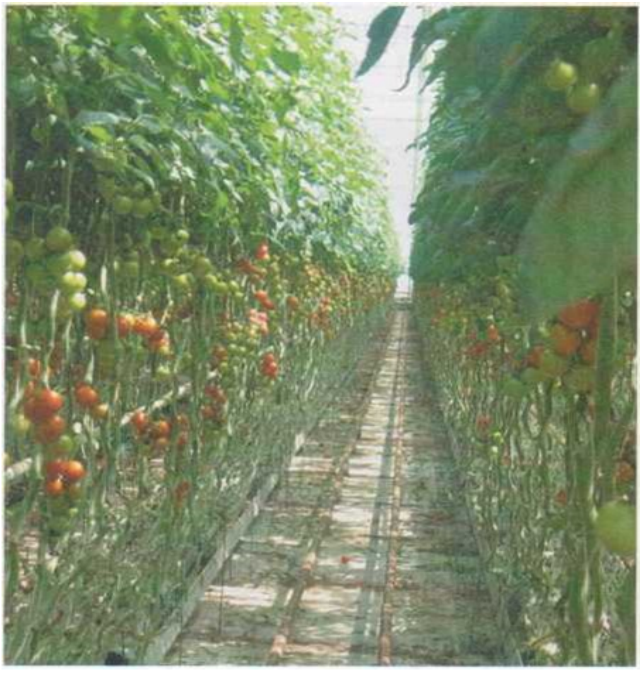

Figure 6-8

The tomatoes shown on the left have an indeterminate growth

Source: Margaret McMahon, The Ohio State University.

Shoot Growth Patterns: Annuals, Biennials, and Perennials Annuals, which are herbaceous (non- woody) plants, complete their life cycle (seed to seed) in one growing season. Shoot growth commences after seed germination and continues in a fairly uniform pattern—provided no environmental influences are limiting—until growth is stopped by frost or some senescence-inducing factor. Flowering, followed by fruit and seed production, occurs at intervals through the growing season. General growth curves for the annuals are shown in Figure 6-9, a detailed growth curve for barley, an herbaceous annual, is shown in Figure 6-10.

Figure 6-11 shows various events in the life cycle of a typical angiosperm annual plant. All these events occur during a single summer growing season.

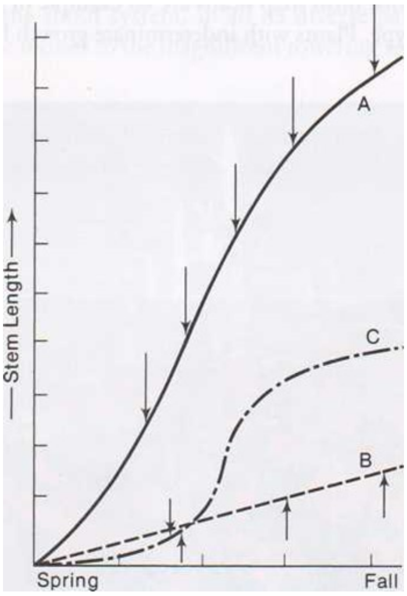

Figure 6-9

Vegetative growth patterns of annual plants.

(A) Indeterminate vine-type plants. (B) Determinate, bush- type plants. (C) Terminal-flowering plants, such as cereals and grasses. Arrows indicate times of flower initiation.

Source: Adaptec! from L. Rappaport and R. M. Sachs, Physiology of Cultivated Plants (Davis, CA: University of California-Davis, 1976).

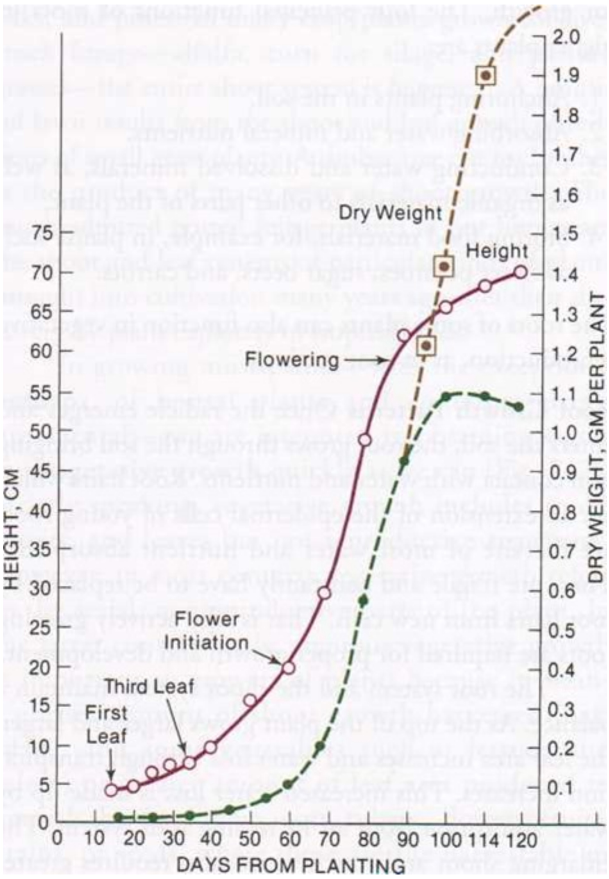

Figure 6-10

Growth curve of a field-grown barley plant from leaf emergence to grain maturity, o = plant height. • = dry weight of plant minus grain we/ght[*]= dry weight of plant plus grain weight.Source: Adapted from G. R. Noggle and G. J. Fritz, Introductory Plant Physiology (Englewood Cliffs, NJ: Prentice Hall, 1976).

The biennials, which are herbaceous plants, require two growing seasons (not necessarily two years) to complete their life cycle (seed to seed). As shown in Figures 6-12 and 6-13, stem growth is limited during the first growing season. The plants remain alive but dormant through the winter. Exposure to chilling temperatures triggers hormonal changes leading to stem elongation, flowering, fruit formation, and seed set during the second growing season. Senescence and death of the plant follows shortly thereafter. Examples of herbaceous biennials are celery, Swiss chard, beets, and cole crops such as cabbage and Brussels sprouts.

Most annual and biennial plants flower and fruit only once before dying. The production of the flowers and fruits or, perhaps, just the flowering stimulus itself apparently causes the plants to senesce and die. In such plants, continued removal of flowers and fruits often delays senescence.

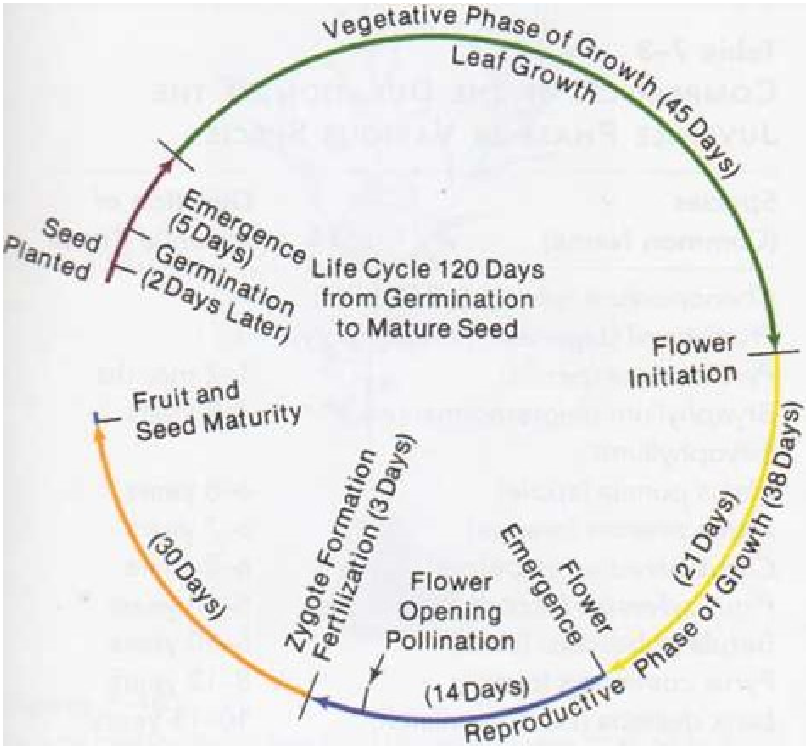

Figure 6-11

Events in the life cycle of a typical annual plant—from seed planting to seed maturity—accomplished in four months.

Source: Adapted from G. R. Noggle and G. J. Fritz, Introductory Plant Physiology (Englewood Cliffs, NJ: Prentice Hall, 1976).

Perennials are either herbaceous or woody. In herbaceous perennials, the roots and shoots can remain alive indefinitely but the shoot system may be killed by frosts in cold-winter regions or by senescence inducing factors. Shoot growth resumes each spring from latent or adventitious buds at the crown of the plant. Figure 6-14 shows typical growth patterns for two types of herbaceous perennials. Many tropical, subtropical and warm-temperate herbaceous perennial ornamental plants (e.g., pelargoniums) are grown as annuals in areas with severe winters, such as the Midwest region of the United States.

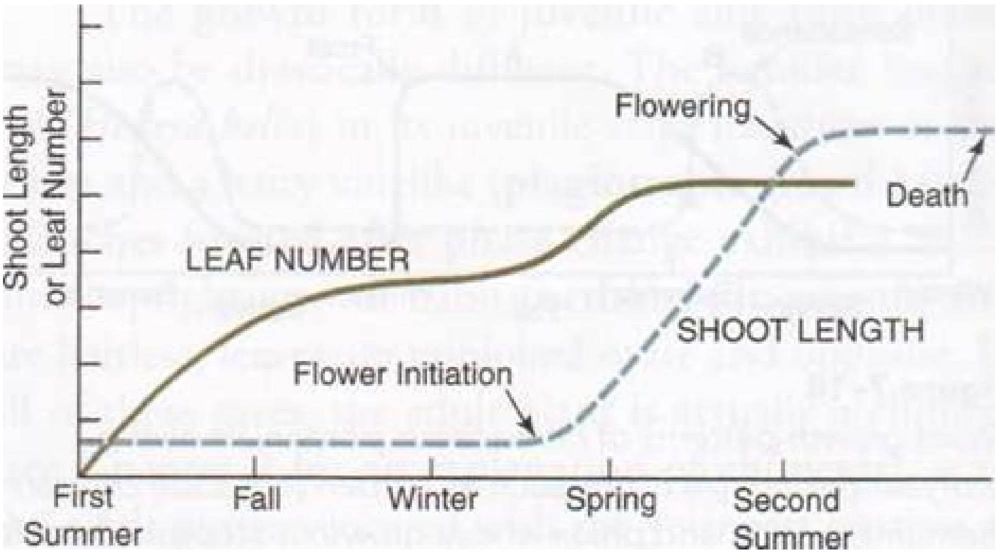

Figure 6-12

Growth curves of biennial plants during the first growing season (vegetative growth only), a required winter chilling- period, and a second growing season (flowering, fruiting, and seed production).Source: Adapted from L. Rappaport and R. M. Sachs, Physiology of Cultivated Plants (Davis, CA: University of California-Davis, 1976).

Hollyhocks are a biennial plant. The plant on the right is two years old and flowering. The one on the left is in its first growing season and will remain vegetative.Source: Margaret McMahon, The Ohio State University.

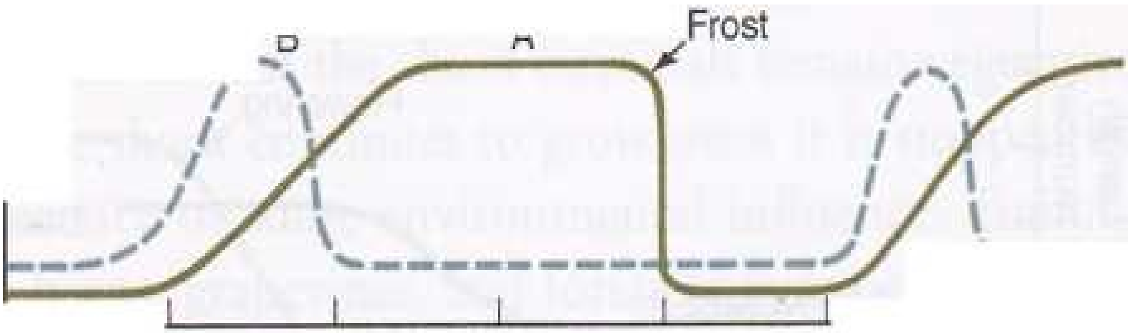

Figure 6-14

Shoot growth patterns of herbaceous perennials over a two-year period. (A) Plants such as garden (outdoor) chrysanthemums, peony, and phlox whose growth is stopped by cold weather in the fall. (B) Bulbous plants such as tulips, narcissus, and hyacinths, whose growth is terminated after spring flowering.Source: Adapted from Rappaport, L., and R. M. Sachs, 1976. Physiology of Cultivated Plants. Davis, CA: UCD Bookstore.

Phase Change: Juvenility, Maturation, Senescence

A newly emerged seedling undergoes a phasic development throughout its life that is essentially the same as in animals. It will pass through embryonic growth; juvenility; a transition stage, which in plants is called phase change; maturity or adult phase; senescence; and death. The juvenile phase is characterized by the inability to reproduce sexually; in angiosperms, plants at this stage cannot flower, even though conditions are permissive. Flowering occurs only in plants that have reached the adult phase following phase change. Adult plants that have not flowered because the conditions are not proper are said to be ripe to flower. The duration of the juvenile phase varies from a week or two up to thirty or forty years in some tree species. It should be noted, however, that plants do not measure time in terms of calendar days, but rather with some factor related to an increase in plant size, probably number of nodes (leaves) produced.

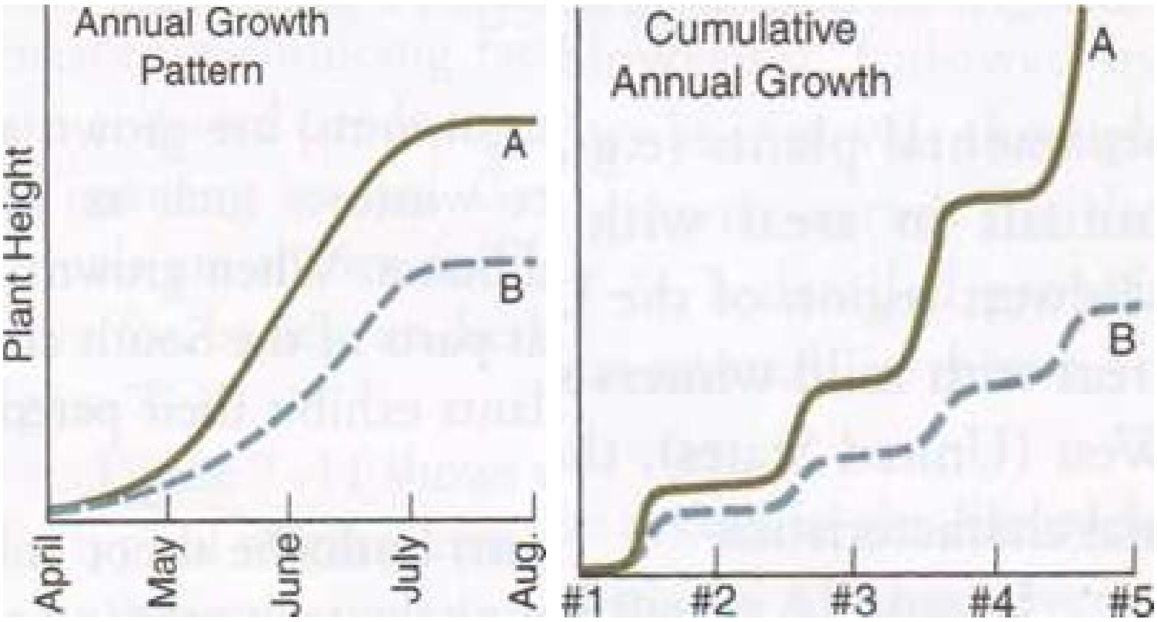

Figure 6-15

(Left) Growth patterns for temperate zone woody perennials in the northern hemisphere during one growing season, and (Right) over a period of several years. (A) Curve for a rapid- growing species such as poplar. (B) Curve for a slow-growing species such as oak.Source: Adapted from L. Rappaport and R. M. Sachs, Physiology of Cultivated Plants (Davis, CA: University of California-Davis, 1976).

The morphology of juvenile and adult plants is often quite different. For example, juvenile acacia leaves are bipinnately compound, while the adult form appears linear (Fig. 6-16). Juvenile eucalyptus trees have opposite leaves that are broad and lack a petiole. Adult eucalyptus leaves assume a different appearance: they become alternate, are narrower, and have a distinct petiole. Juvenile citrus seedlings are thorny, but thorns are not produced after the plant undergoes phase change.

Figure 6-16

Acacia melanoxylon seedling showing phase change from juvenile to mature form. Lower, juvenile leaves have compound bipinnate structure. Upper, mature leaves are actually expanded petioles (phyllodia). Transition stages are evident in between.

Source: D. E. Kester and H. T. Hudson, Plant Propagation: Principles & Practices, 4th ed. © 1983. Adapted by permission of Pearson Education, Inc., Upper Saddle River, NJ.

The growth form of juvenile and adult plants may also be drastically different. The familiar English ivy (Hedera helix) in its juvenile stage has three or five leaves and a hairy vinelike (plagiotropic growth) stem. Branches formed after phase change exhibit a much more upright growth habit (orthotropic growth) and are hairless; leaves are nonlobed ovate and opposite. In all of these cases, the adult plant is actually a chimera (see Chapter 9 for an explanation of chimeras), with the adult portion located with the youngest portion of the plant, while the juvenile portion is found at the base and oldest part of the plant. A summary comparing morphological features of juvenile and adult plants in various species can be found in Table 7—4. Rooting ability of cuttings is one of these features that is of significant economic importance. Plant propagators would like to maintain the juvenile stage in stock plants as long as possible so that cuttings taken from them will root properly and in high percentages.

Table 6-4

COMPARISON OF MORPHOLOGICAL CHARACTERISTICS ASSOCIATED WITH THE JUVENILE AND ADULT STATES OF VARIOUS SPECIES

Characteristic	Species	Juvenile Form	Adult Form
Growth habit	*Hedera helix*	Plagiotropi	Orthotropic
	Ficus pun u la	Plagiotropi	Orthotropic
	Euonymus	Plagiotropi	Orthotropic
Leaf shape	*Cupressus* spp.	Acicular	Scalelike
	Acacia spp.	Pinnate	Phyllodes
	Eucalyptus spp.	Oval,	Lanceolate
	Pinus spp.	Flat,	Scale- and
	Hedera helix	Palmate	Ovate,
Phyllotaxis	*Eucalyptus* spp.	Opposite	Alternate
	Hedera helix	Alternate	Spiral
Anthocyanin in leaves	*Malus pumila*	Present	Absent
	Carya	Present	Absent
	Acer rubrum	Present	Absent
	Hedera helix	Present	Absent
Thorniness	*Robinia*	Thorns	No thorns
	Citrus spp.	Thorns	No thorns
Autumn leaf	*Fagus sylvatica*	Keep	
Abscission in	*Quercus* spp.	Keep	Abscise
	Robinia	Keep	Abscise
	Carpinus spp.	Keep	Abscise
Rooting ability of	*Hedera helix*	Will root	Will not

Quercus spp.	Will root	Will not
Fagus sylvatica	Will root	Will not
Pinus spp.	Will root	Will not
Pyrus malus	Will root	Will not

Source: J. D. Metzger, "Hormones in reproductive development." In P. J. Davies (ed.), *Plant hormones,* 2nd ed. (Berlin: Springer-Verlag, 1995). Used with kind permission of Springer Science and Business Media.

REPRODUCTIVE GROWTH AND DEVELOPMENT

Fruit and seed production involves several phases:

1. Flower induction and initiation
2. Flower differentiation and development
3 Pollination
4. Fertilization
5. Fruit set and seed formation
6. Growth and maturation of fruit and seed
7. Fruit senescence Гул.

Flower Induction and Initiation When a plant is mature, a change can occur in an apical meristem that switches it from being vegetative (producing shoots and leaves) to reproductive (producing flowers) (Fig. 6-17). Some annuals mature and can flower in only a few days or weeks after the seeds sprout; some forest and fruit trees require years before flowering. Once mature, the plant can be induced to flower by becoming sensitive to the conditions of its environment. What brings about the formation of flowers? The majority of agricultural plants are self-inductive for flowering; that is, they initiate or form flowers when they reach a certain morphological maturity that is often determined by how much heat the plant has received (accumulated heat). Most fruit trees, shrubs, woody plants, garden perennials, and vegetable crops (beans, peas, tomatoes, peppers, cucumbers) have self-induced flowering. Growing degree days (GDD) are a way to measure heat accumulation.

For many plants the GDDs needed for flowering or seed maturation is known and can be used to predict or control the time of flowering or harvest. Easter lilies and sweet corn

are two crops where GDDs are important for timing and harvest, respectively. Phenology is the study of lifecycle responses to annual and seasonal variations in temperature and other climate factors. In other plants, flowering is controlled by is daylength (photoperiodic effect) and/or low temperatures (vernalization).

Figure 6-17

Transition of an apical meristem of chrysanthemum from (A) vegetative (note the smooth, rounded surface of the meristem); to (B) floral structures beginning to develop; to (C) fully developed flower bud. Chrysanthemums are in the Asteraceae family, so there are multiple flowers on the flower head or capitulum.Source: Margaret McMahon, The Ohio State University.

Photoperiodism (Daylength) Earlier in this chapter, we discussed the general features exhibited by photoperiodically controlled processes. In this section, we will consider in more detail the photoperiodic control of flowering. The influence of the photoperiod on the flowering of several plant species was first studied in detail by the USDA at Beltsville, Maryland, and the results were published by W. W. Garner and H. A. Allard in 1920. They grew plants in containers that could be wheeled into dark sheds at the end of the workday and returned to the sunlight in the morning. They found that Maryland Mammoth tobacco and certain cultivars of soybeans and cosmos required short days for flower induction. A set number of successive short days was required to complete differentiation (change from vegetative to reproductive growing points or shoot terminals). These plants, such as strawberry, poinsettia, and soybean, were called short-day plants.

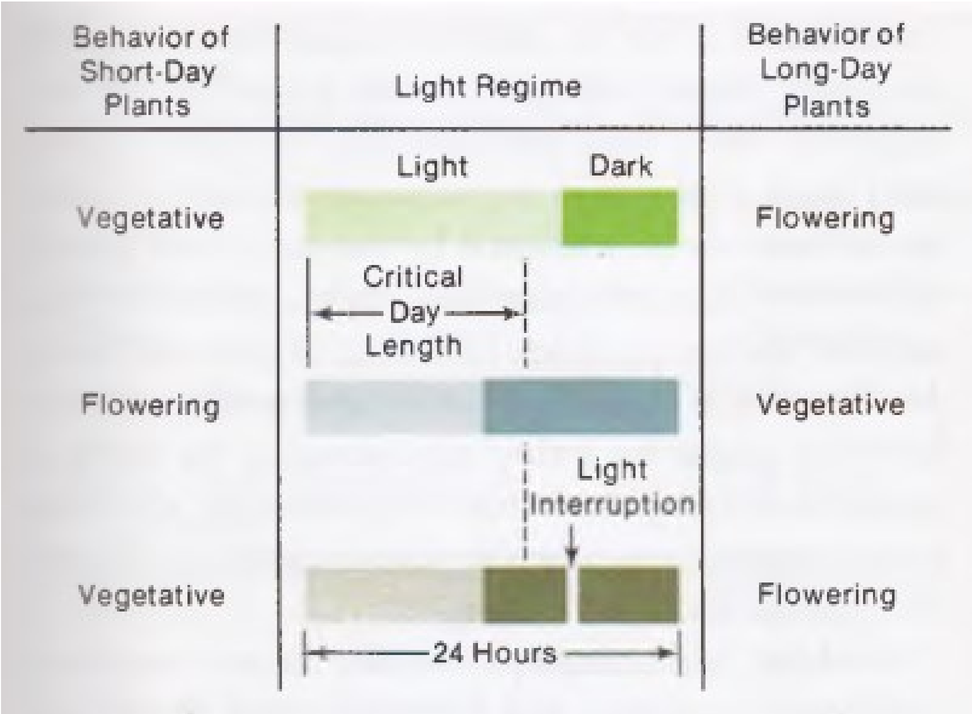

Figure 6-18
Effect of light interruption of the dark period on flowering
- *snort-day and long-day plants.Source: A. W. Galston and P. J.*

This phenomenon whereby daylength controls certain plant processes, as noted above, was termed photoperiodism. Other workers in later experiments

Round this phenomenon to be more complicated and tnat many plants did not fit nicely into these three categories because of interactions of daylength with temperatures.

Figure 6-18 demonstrates how a flash of light (or right break) of sufficient intensity or duration inhibits lowering of a short-day plant (long-night plant) but may induce flowering of a long-day plant (LDP). This information has been useful to commercial chrysanthemum growers who grow these short-day plants on a ear-round schedule. When they want the young plants zo reach a size adequate for flowering, the growers use incandescent or fluorescent lamps over the chrysanthemum plants in the middle of the night, each night for эпе to four hours, depending on time of year and lati- rude. This night break inhibits flowering until the plants reach the desired height. Conversely, when the r.atural daylight of summer is too long for chrysanthemum plants to flower, they cover the plants of proper ;:ze with black cloth or plastic each evening about 6 P.M. ind remove it in the morning at about 8 A.M. This shortens the plant's day (lengthens the night) enough to induce and fully develop the flowers. These manipulations enable growers to have chrysanthemums uni- rormly in flower for every day of the year (Fig. 6-19). Poinsettias flower the same way and could be produced vear-round. However, because of the association with Christmas, the public will purchase poinsettias only for Christmas.

These chrysanthemums were grown during the summer and forced into flowering uniformly by drawing blackout doth over

Further studies have shown that there is a daily rluctuation in the sensitivity to light such that, depending on the time of day, light either inhibits or promotes flowering. This cycle of sensitivity to light is one of

many circadian rhythms exhibited by plants and animals alike. Circadian rhythms are biological rhythms that complete one cycle in approximately 24 hours; they are typically initiated, or entrained, by transitions between darkness and light, as occurs at dawn. (Some circadian rhythms are entrained by the changes in temperature that occur between day and night.) The circadian rhythms of light sensitivity in SDPs and LDPs are qualitatively identical, but they differ in time of day when the promotive and inhibitory stages are maximally expressed

Flowering Signal - As is the case for other photoperiodically regulated processes, the pigment system responsible for sensing light is phytochrome. The phytochrome system is located in the leaf, yet it is the apical meristem that must go through a transition to produce floral organs instead of leaves. Thus, both positive and negative signals are transported via the phloem from the exposed leaves to the apical meristem, the timing of which is determined by the response type and the amount of time that has elapsed after the start of the day. Most of the attention has been focused on the positive signal, which promotes photoperiodic flowering. This signal is sometimes called florigen, or the floral stimulus. The existence of the floral stimulus was discovered by partial leaf removal when plants were placed under the inductive photoperiod for flower formation, then failed to flower. The SDP Xanthium (cocklebur) exposed to

vernalization is not an absolute requirement; they will eventually flower without it. Some species can be vernalized as seeds (beet and kohlrabi), but most plants must reach a minimum size or produce a certain number of leaves to be sensitized by the cold. Bulb plants, such as the hyacinth, narcissus, tulip, and some lilies required low temperatures to induce or promote flower development in the bulb. Growers who produce these as flowering plants for spring sales vernalize the bulbs in coolers then bring them into the greenhouse where the warm temperatures cause the plants to grow and flower. This process is called “forcing.”

Many herbaceous perennials, as well as plants with corms or tubers, and many flowering shrubs and fruit trees require low temperatures to overcome the rest period, but few require low temperatures for flower induction.

Flower Development

Once flowering is induced for whatever reason, there is a change in the apical meristem from vegetative (producing shoots and leaves) to reproductive (producing floral parts). Once the apex has changed to a flower pri- mordium, the process is not reversible. The floral apex may abort, however, if the subsequent environmental conditions are not favorable for full flower development. For example, short day plants are returned to long day conditions. In such a case, the axillary buds below the aborted floral apex usually grow vegetatively (bypass growth) (Fig. 6-20) until daylength or temperature conditions once again are favorable for flower induction.

long noninductive days initiated flowers if light was blocked from a single leaf. Some experiments in which flowering plants (donor) were grafted to nonflowering plants (receptor) caused the latter group to flower. These and other experiments gave rise to the theory that a flowering hormone (named florigen), which might be similar in all plants, was responsible for flower induction. For around seventy years, researchers looked for florigen with no success. Then, in 2001, researchers discovered a gene called CONSTANS that produces a transcription factor protein that acts as the signal for flowering by turning on the FT (flowering locus T) gene that starts the conversion of apical buds to flower buds. The activity of CONSTANS appears to be mediated by phytochrome and chryptochrome. Current research is investigating more thoroughly how this protein works to influence flowering.

There has been considerable documentation to categorize plants as short-day, long-day, or day-neutral. Although not complete, one such list appears in Table

5. The critical daylength of many of the species shown in the table may be changed by a slight shift in temperature above or below the optimum for that species.

Understanding photoperiodic response allows crop producers to select species and cultivars that flower and seed at the right time for their geographic location or market window.

Figure 6-20

These poinsettias are exhibiting the start of bypass growth that resulted from being placed back in long day conditions after flower induction under short days. The flowers have aborted. Source: Margaret McMahon, The Ohio State University.

Low Temperature Induction Some plants, including many of the biennials, require low temperature for flower induction. The term for this is vernalization, which means "making ready for spring." It was first observed in winter wheat over a century ago. Vernalization is any cold temperature treatment that induces or promotes flowering. The temperatures required to vernalize a given plant and the length of the vernalization period vary among species and may even differ among cultivars of the same species. Broadly speaking, however, vernalization temperatures range between 0° and 10°C (32° and 50°F). An example is the olive tree (Olea europaea), which needs chilling temperatures for induction of flower parts. In the kiwifruit (Actinidia deliciosd), there is no evidence of reproductive structures in the bud until after exposure to chilling temperatures. Some of the biennials that require vernalization are beets, Brussels sprouts, carrots, celery, and some garden flowers such as Canterbury bells and foxglove. Winter annuals—such as the cereal crops, barley, oats, rye, and wheat-—also respond to cold by flowering. Some plants, such as lettuce, peas, and spinach, can be induced to flower earlier with vernalization.

The number of days from flower initiation to anthesis (time of flower opening) depends on the species and the cultivar. Generally the time is increased if temperatures are low and decreased with warm temperatures (low and warm being relevant to the temperature requirements of the plant). Extreme changes in temperature however can cause the flowers to abort or be deformed.

Pollination

In the production of most floral crops and flowering shrubs—for example, carnations, petunias, chrysanthemums, roses, and camellias—the flower itself is the desired product. There is little interest in any resulting fruits and seed, except in the case of the plant breeder working with such species. In fact, flower growers often use techniques to prevent pollination in order to slow flower senescence. But in the food crops—the cereals, fruits, and many vegetable species—the postflowering structures are the desired products. It is the fruits, grains, and seeds that are harvested.

Fruit, grain, and seed formation starts with pollination, which is the transfer of pollen from an anther to a stigma in angiosperms. The anther and stigma may be in the same flower (self-pollination), in different flowers on the same plant (self-pollination), in different flowers on different plants of the same clone (self-pollination), or in different flowers on plants of different cultivars (cross-pollination).

Pollen grains come in many sizes and shapes and, while essential for sexual plant reproduction, can be devastating to many people as allergy producers. See Figure 6-21.

Figure 6-22 shows the various parts of a simple flower dependent upon pollination for fruit set.

If a plant is self-fertile, it produces fruit and seed with its own pollen, without the transfer of pollen from another plant. If it is self-sterile, it cannot set fruit and seed with its own pollen, but instead requires pollen from another plant, usually of a different clone. Often this is due to incompatibility, where a plants own pollen will not grow through the style into its embryo sac (Figs. 7-22 and 7—23). Sometimes, too, cross-pollination between two particular cultivars is ineffective because of incom-patibility, which is believed to be due to factors that inhibit pollen tube germination or elongation.

Pollen transfer from the anthers to the stigmas is principally by:

1. Insects (see Fig. 6-24). Insect pollination is common among cultivars with white or brightly colored flower parts and attractive nectar. Most fruit crops, many vegetables, and legume forage crops are pollinated by insects.

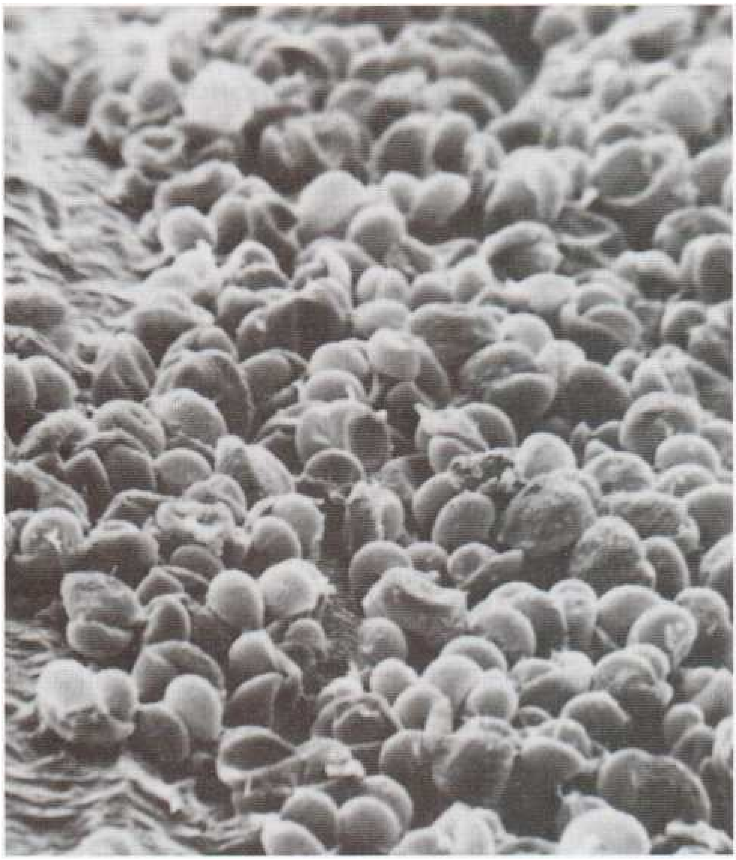

Figure 6-21

Scanning electron micrograph of pollen grains produced in a male cone of red pine (Pinus resinosa). Source: USDA.

Adequate pollination is so important in many crops that considerable efforts are made to aid the bees in their pollen distribution.

Hives are placed in or near the fields needing pollination. Also pollen inserts are placed at the entrances of hives to coat bees with pollen as they enter and exit.

2. Wind. This is the main pollinating agent for plants with inconspicuous flowers—the grasses, cereal grain crops, and forest tree species, as well as some fruit and nut crops such as the olive, walnut, pistachio, and pecan.

Other pollinating agents are water, snails, slugs, birds, and bats.

Figure 6-23 shows a longitudinal section through the pistil of a flower following pollination. Note the elongated pollen tube. A pollen grain that germinated the sticky surface of the stigma has grown down through the style carrying the male gametes to the embryo sac in the ovary.

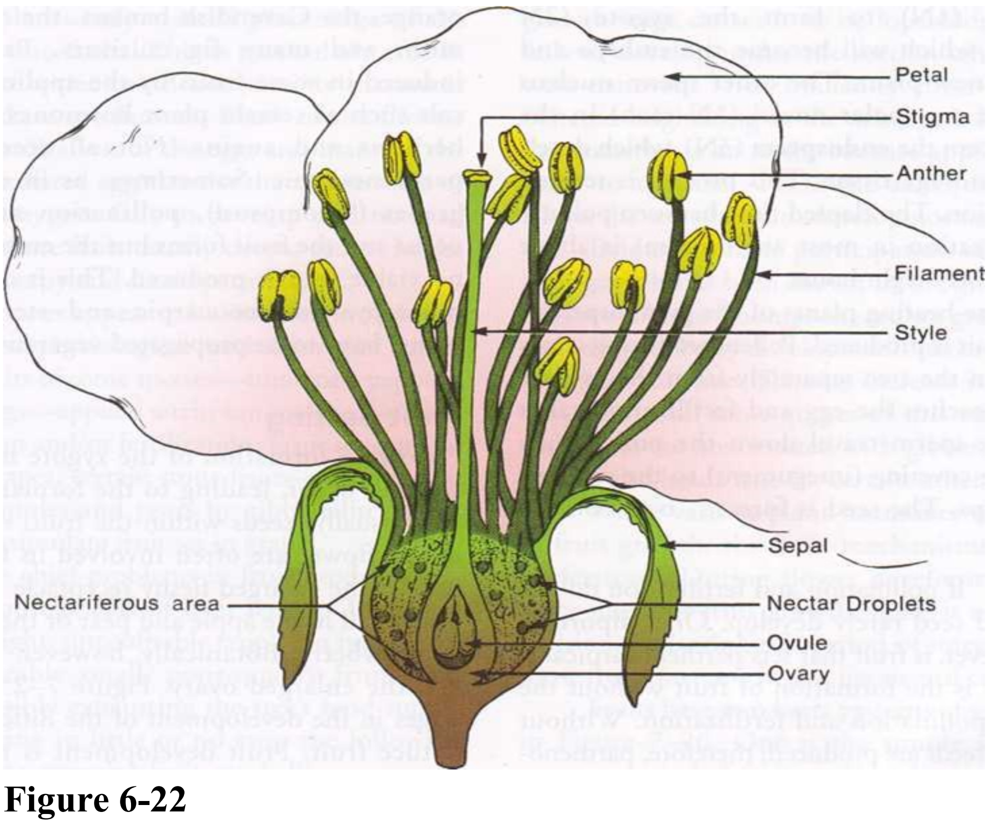

Figure 6-22

Longitudinal section of a cherry flower showing the structures involved in the transfer of pollen from anthers to stigma (pollination). Source: USDA.

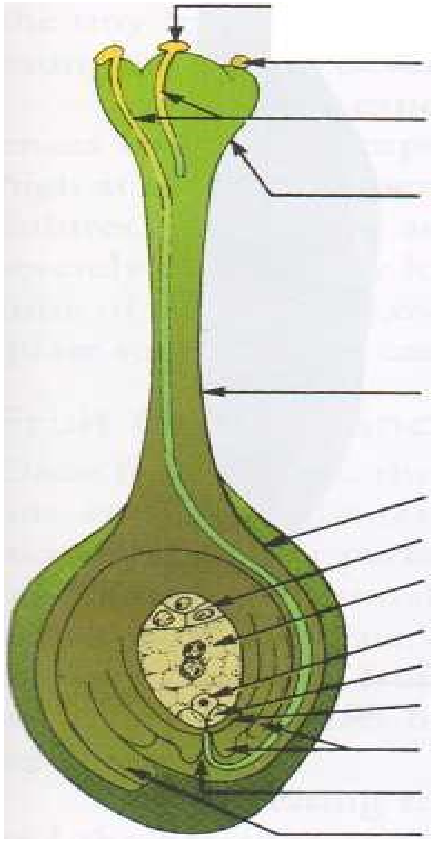

Figure 6-23

A longitudinal section through the carpel of a flower following pollination and just before fertilization

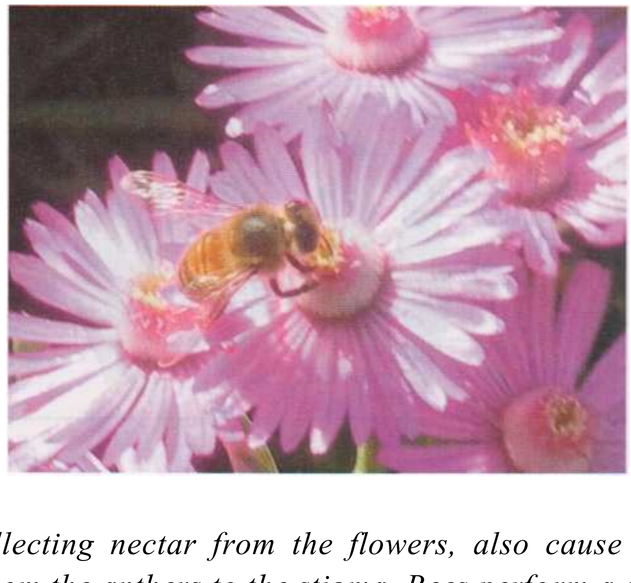

Figure 6-24

Honeybees, collecting nectar from the flowers, also cause pollination by distributing pollen from the anthers to the stigma. Bees perform a great service in the culture of many crops by their pollination activities.

Source: Margaret McMahon, The Ohio State University.

Fertilization

In the angiosperms the pollen tube grows through the micropyle opening in the ovule into the embryo sac and discharges two sperm nuclei (IN each). One unites

fruit crops, many vegetables, and legume forage crops are pollinated by insects.

Adequate pollination is so important in many crops that considerable efforts are made to aid the bees in their pollen distribution. Hives are placed in or near the fields needing pollination. Also pollen inserts are placed at the entrances of hives to coat bees with pollen as they enter and exit.

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Figure 6-23 shows a longitudinal section through the pistil of a flower following pollination. Note the elongated pollen tube. A pollen grain that germinated the sticky surface of the stigma has grown down through the style carrying the male gametes to the embryo sac in the ovary.

In many plants only a small percentage of the flowers develop into fruits. This is particularly true in fruit crops where a tree could not possibly mature as many fruits as there are flowers. Many of the flowers drop without fertilization of the egg, and many of the flowers with a fertilized egg abort at the zygote stage or later. When the zygote fails to develop and no seed forms, the immature fruit usually drops, except in the case of parthenocarpy and stenospermocarpy.

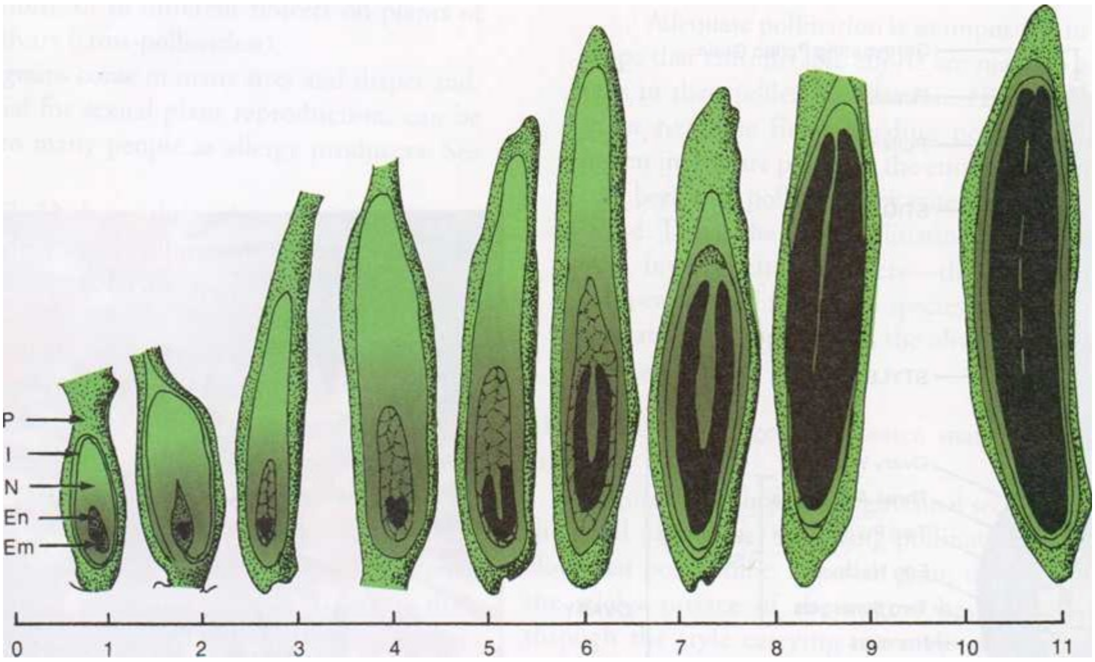

Figure 6-26

Developmental pattern of the tissues in a lettuce fruit, from the fertilized egg to the mature fruit. The ovary wall (the pericarp) is firmly attached to the seed coat (integument), so the structure is correctly considered a fruit and not a seed. P = pericarp;

I = integument; N = nucellus; En = endosperm; Em = embryo.Source: Adapted by H. T.Hartmann and D. E. Kester, Plant Propagation, 4th ed. (Englewood Cliffs, NJ: Prentice Hall, 1983. From H. A. Jones, "Pollination and Life History Studies of the Lettuce (Latuca sativa)," Hilgardia 2 (1927): 425-479.

One of the chief problems in fruit production is obtaining the optimal level of fruit setting. Too low a fruit set gives a light, unprofitable crop. Too heavy a set leads to undesirable small, poor-quality fruits that mature late, possibly exhausting the tree's food supply and often resulting in little or no crop the following year. To overcome excessive fruit set, half—or more— of the fruits are removed at a very early stage, either by hand thinning, machine shaking, or chemical sprays. Interestingly, fruits of some species (the Washington Navel orange, for example) are self-thinning. Most of the tiny fruits originally forming drop, leaving an optimum number to develop to maturity.

As might be expected, temperature strongly influences fruit set. Temperatures that are too low or too high at this critical period are often responsible for crop failures. Peaches are an example of a crop that is often severely damaged by low temperatures that occur at the time of flowering. Low light intensity and lack of adequate soil moisture can also adversely affect fruit set.

Fruit Growth and Development

Once fruit has set, the true fruit and, sometimes, various associated tissues begin to grow. Food materials move from other parts of the plant into these developing tissues. Hormonal substances, such as the auxins, gibberellins, ethylene, and cytokinins, may be involved in some phases of fruit growth just as they are in fruit set. These materials originate in both the developing seeds and fruit.

An interesting relationship between fruit growth and the presence of auxin has been observed in strawberry fruits. Removing some of the achenes (the fruits usually mistaken for seeds) from the surface of the strawberry (botanically the receptacle) at an early growth stage causes it to be lopsided; the strawberry fails to develop under the section where the achenes were removed. The stimulatory effect of some mobile material originating in the achenes is lost. Presumably this material is an auxin because application of auxin paste to the area where the achenes were removed allows the strawberry to develop normally.

Evidence of the participation of gibberellins in fruit growth has been shown in the grape. Application of gibberellin to Thompson seedless grape clusters at an early stage of berry development markedly increases the ultimate fruit size. The size increase is so pronounced that almost all table grapes of this cultivar grown in California are now treated with gibberellin. This effect on size also holds true for certain other grape cultivars.

While various plant hormones may be involved in fruit growth, the basic mechanisms are still barely understood. During flower development and in the early stages of fruit growth, there is considerable cell division. Following this period of intense cell division, most fruits increase in size because of cell enlargement.

Fruits have two basic patterns of growth, as shown in Figure 7-26. One is the simple sigmoid growth curve— typical of fruits such as the orange, apple, pear,

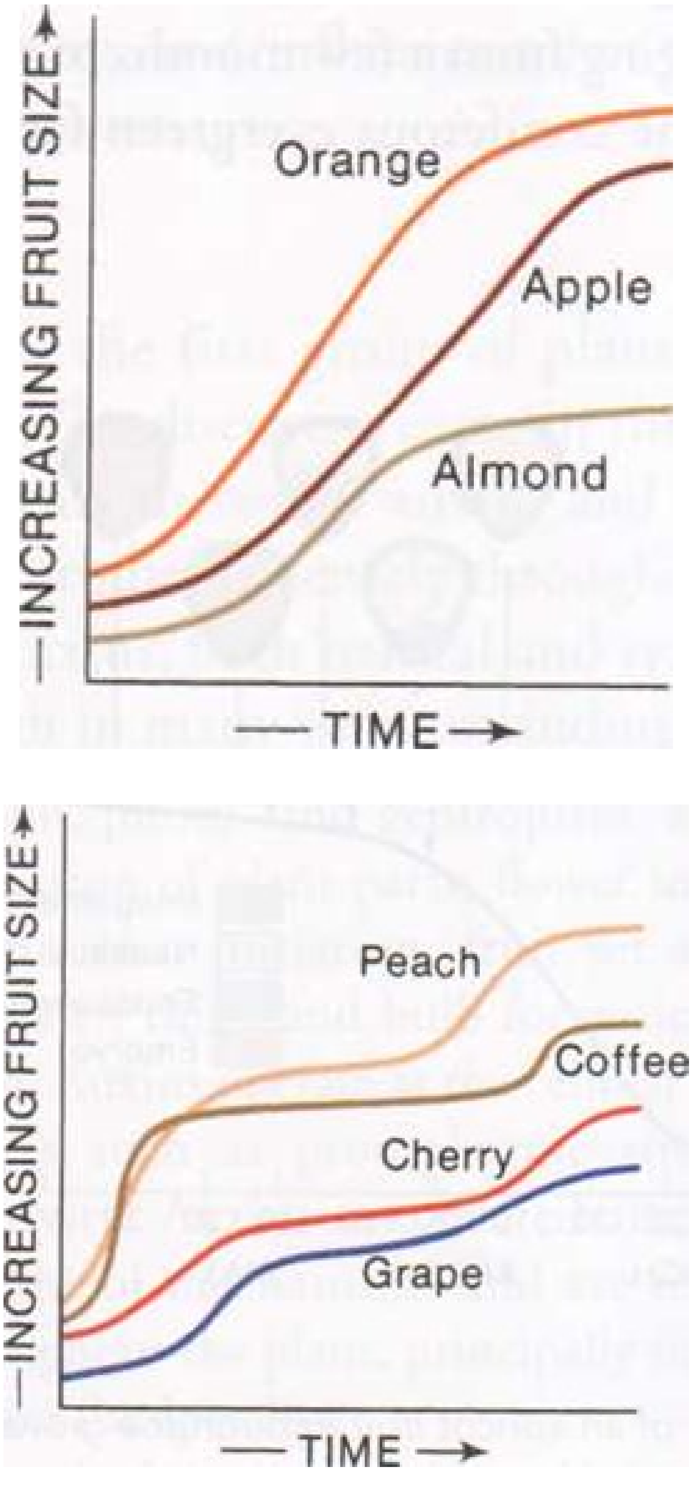

Figure 6-26

Growth curves of representative kinds of fruits showing the two characteristic types. Top: The sigmoid growth curve. Bottom: The double sigmoid growth Curve.Source: D. E. Kester and H. T. Hudson, Plant Propagation: Principles & Practices, 4th ed. © 1983. Adapted by permission of Pearson Education, Inc., Upper Saddle River, NJ.

pineapple, olive, almond, tomato, and strawberry—in which there is a slow start followed by a period of rapid size increase, then a decrease in growth rate near fruit maturity. The second pattern is a double sigmoid growth curve, in which the single sigmoid growth curve is repeated. Near the center of the growth period, the growth curve is flat; the fruit increases little, if at all, in size. The stone fruits—peach, apricot, plum, and cherry—as well as the grape and fig show a double sigmoid growth pattern. In the stone fruits (peach, nectarine, plum), which have a hard endocarp or pit, the pit hardens during the second phase of fruit development. In addition, some important changes take place in seed development within the pit, as illustrated in Figure 7-27.

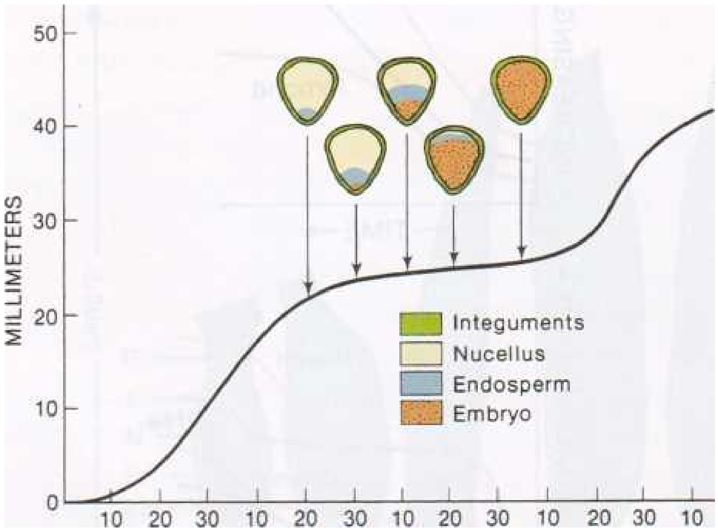

Figure 6-27

Growth curve of an apricot fruit through the growing season. During the second growth period the pit (endocarp) hardens and the seed within the pit develops mostly from nutritive tissue (nucellus and endosperm) to finally consist entirely of the

embryo. Source: Adapted from J. C. Crane and P. Punsri, "Comparative Growth of the Endosperm and the Embryo in Unsprayed and 2,4,5-trichlorophenoxyacetic Acid Sprayed Royal and Tilton Apricots," *Proceedings of the American Society of Horticultural Scientists* 68 (1956): 96-104.

Some fruits as they ripen experience a burst of respiration and a release of high levels of ethylene. These are called climacteric fruits. Apples, apricots, bananas, and tomatoes are example of climacteric fruits. The ripening of many of these fruit can be hastened by treating them with ethylene before or after they are harvested. If these fruit are stored with ethylene sensitive fruit or plants, the ethylene they generate can harm the sensitive plants nearby.

Aging and Senescence

The life spans of the different kinds of flowering plants differ greatly, ranging from a few months to thousands of years. Some of the coniferous evergreen forest trees are the earth's oldest living organisms. Some of the California coast redwoods (Sequoia sempervirens) are known to be over 3,000 years old. Olive trees with huge trunks found in the eastern Mediterranean area are believed to be over 2,000 thousand years old (Fig. 6-28).

Senescence is considered to be a terminal, irreversible deteriorative change in living organisms, leading to cellular and tissue breakdown and death. It is a conspicuous period of physical decline, particularly evident toward the end of the life cycle of annual plants (population senescence) and of individual plants (whole plant senescence), but it can also occur in leaves, seeds, flowers, or fruits (organ senescence). Plants exhibit senescence in different ways. In annuals, the entire plant dies at the end of one growing season, after and probably because of fruit and seed production. In herbaceous perennials, the tops of the plants die at the end of the growing season, perhaps killed by frost, but the shoot grows again in the spring and the roots can live for many years. In deciduous woody perennials, the leaves senesce, die, and fall off each year, but the shoot and root systems remain alive, often for a great many years. Vegetatively propagated clones can extend the "life" of a plant for what theoretically could be indefinitely. For example the Winter Pearmain apple that is cultivated in England, was grown there as early as 1200 CE The Black Corinth grape is a clone that has been grown in Greece for thousands of years. The modern plants of both of these clones are in reality branches from their original plant.

Senescence is usually considered to be due to inherent physiological changes in the plant, but it can also be caused by pathogenic attack or environmental

Figure 6-28

Ancient olive tree fOlea europaeaj growing on the Mount of Olives in Jerusalem. Trees of this species are known to live for several thousand years. Every year to produce olives it has to go through a chilling period in the winter.

ess. As individual trees age, for example, they aremore vulnerable to lethal attacks by fungi, ricteria, and viruses. The long-lived trees mentioned ibcve characteristically have very durable heartwood, :retaining high levels of resins and phenolic com- : : .mds that resist decay.

Considerable study has been given to senescence in plants, particularly in regard to leaves and their it scission. During leaf senescence, DNA, RNA, protons, chlorophyll, photosynthesis, starch, auxins, and cirberellins decrease, sometimes drastically. Senescence 15 not entirely degradation, however; particular mRNAs 2nd proteins are synthesized only in senescing tissues.

A decline in photosynthetic activity of many determinate annuals such as wheat plants following r-owering; the decline in photosynthesis, of course, soon leads to senescence and death. Plant senescence is fastened, too, by the transfer of stored nutrients to the reproductive parts—the flowers, fruits, and seeds—as fie}' develop and mature, at the expense of the root and snoot systems. As a result, senescence can be postponed in many plants by picking off the flowers before seeds start to form. Pollination and fertilization can cause senescency of some flowers and the cessation of further dowering. Removing sweet peas flowers as soon as they start to wither and before seeds form prolongs the dooming period. Just as plant hormones are involved in many plant functions, they are also involved in ienescence. For example, ethylene plays a major role in rruit ripening and deterioration as well as other senescence processes.

PLANT GROWTH REGULATORS

As you have read in the previous sections, plant hormones were mentioned several times as being factors or signals involved in plant growth and development. Because of their importance in plant growth and development, the following section describes both natural =nd synthetic plant hormones as well some chemical plant growth regulators that act on the hormones.

In plants, as in animals, many growth and behavioral patterns and biological functions are controlled by hormones. Hormones are produced in extremely small imounts at one site in the plant and translocated to other sites where they can alter growth and development in that area. Hormones are essentially chemical messengers, influencing the many aspects of plant development.

A distinction must be made between the terms riant hormone and plant growth regulator. A plant hormone is a natural substance (produced by the plant

itself) that acts to control plant activities. Plant hormones that are chemically synthesized can initiate reactions in the plant similar to those caused by the natural hormones. Plant growth regulators, on the other hand, include plant hormones—natural and synthetic—as well as other chemicals not found naturally in plants but that, when applied to plants, influence their growth and development.

There are five traditionally recognized groups of natural plant hormones: auxins, gibberellins, cytokinins, ethylene, and abscisic acid (Fig. 6-29). Recently additional hormones or hormone classes, including the Brassinolides, salicylic acid, and jas- monates, have been identified. The discovery and subsequent study of plant hormones is one of the most exciting and fascinating chapters in the history of plant physiology, partly because their discovery lead to the creation of many new methods of regulating plant growth and development. Despite considerable study of hormones, however, the mechanism of their actions in the plant is still not completely understood.

In addition to natural hormones, synthetic growth regulators have been developed to allow growers to manipulate plant growth and development. Synthetic growth regulators are used to promote rooting, reduce stem elongation, encourage branching, regulate flowering, and influence other aspects of growth and development.

Auxins

Auxins were the first group of plant hormones to be discovered. The discovery came in the mid-1950s, and for many years thereafter auxins and their activities in plants were studied intensely throughout the world.

The auxins, both natural and synthetic, influence plant growth in many ways, including cell enlargement or elongation, photo- and geotropism, apical dominance, abscission of plant parts, flower initiation and development, root initiation, fruit set and growth, cambial activity, tuber and bulb formation, and seed germination. Auxins operate at the cellular level, affecting activities such as protoplasmic streaming and enzyme activity. Auxins are related to many other chemical control mechanisms and are readily transported throughout the plant, principally in an apex-to- base direction (basipetally).

The natural auxins originate in meristems and enlarging tissues, such as actively growing terminal and lateral buds, lengthening internodes, and developing embryos in the seed. Auxins are produced in relatively high amounts in the shoot tip or terminal growing point of the plant and move down the plant through ascular tissues, causing the phenomenon known as ap :cal dominance (blockage of the growth of lateral i-di by the presence of terminal buds). High levels of ; rrin in the stem just above the lateral buds block their —: v.-h. If the shoot tip supplying this auxin is broken : cut off, the auxin level behind the lateral buds is reduced and the lateral buds begin to grow. This is part : rhe reason why, when a shoot tip is removed, many tv shoots arise from buds down along the stem.

One of the most widespread auxins that occurs nat- -ri_y in plants is indoleacetic acid (IAA) (Fig. 6-29).

:eral other natural auxins have also been identified, and -_~.ere are others whose chemical structure is yet unknown.

_ :anv synthetic auxins induce the same effects as natural i xsin. Some of these are indolebutyric acid (IBA), naph- rnaleneacetic acid (NAA), and 2,4-dichlorophenoxyacetic add (2,4-D). (See Fig. 6-29.)

Some important commercial uses of these syn- thetic auxins are:

Adventitious root initiation. One of the first responses attributed to auxins was the stimulation of root formation in stem cuttings. Two synthetic auxins, indolebutyric acid and naphthaleneacetic acid, are now widely used commercially in treating the bases of stem cutting to stimulate the initiation of adventitious roots.

2. Weed control. The synthetic auxin, 2,4-D, is in widespread commercial use as a selective weedkiller that eliminates broad-leaved weeds in grass or cereal fields.

3. Inhibition of stem sprouting. Many kinds of woody ornamental trees produce masses of vigorous sprouts from the base of the trunk that, if not removed, would transform the tree into a bush. Continual removal of these sprouts by hand is costly and time consuming. It has been found that treatment of the tree trunks with the auxin naphthaleneacetic acid at about 10,000 ppm (1.0 percent) strongly inhibits the development of such sprouts.

4. Tissue culture. The initiation of roots and shoots on small pieces of plant tissue cultured under aseptic conditions has become a standard method of micropropagation of some plant species. Often an auxin, such as IAA or 2,4-D, has to be included in the culture medium for roots to initiate.

Gibberellins (GAs)

The gibberellins are a group of natural plant hormones with many powerful regulatory functions. The most obvious is the stimulation of stem growth dramatically,

far more than auxins can. Gibberellins may stimulate cell division, cell elongation, or both, and they can control enzyme secretion.

In some plants, GA is involved in flower initiation and sex expression (male or female flower parts). Fruit set as well as fruit growth, maturation, and ripening seem to be controlled by gibberellin in some species. Senescence of plant parts, particularly leaves, is also affected by GA. Certain dwarf cultivars of peas and corn, if treated with GA, grow to a normal height, indicating that the dwarfed plants lack a normal level of gibberellin (Fig. 6-30).

Gibberellins are also involved in overcoming dormancy in seeds and in buds. Their role in the germination of barley seed has received much study (Fig. 6-31). After the seed has been moistened and placed at room temperature, a natural gibberellin produced in the embryo translocates to the aleurone layer surrounding the endosperm. Triggered by the GA, cells in the aleurone layer synthesize enzymes such as amylases, proteases, and lipases. These enzymes then diffuse throughout the endosperm, hydrolyzing starches and proteins into sugars and amino acids that then become available to the embryo for its growth and development.

The molecular structure of the gibberellins is well known; a typical one is shown in Figure 6-29. By 2000, more than 100 different gibberellins had been discovered in tissues of various plants. Some common ones are GAj, GA3 (gibberellic acid), GA4, and GA7.

studying a disease of rice plants caused by the fungus Gibberella fujikuroi. Plants infected with the fungus grew excessively and abnormally. Extracts from this fungus applied to noninfected plants stimulated the same abnormal growth. By 1939, the active ingredient was extracted from the fungus, crystallized, and named gibberellin. This early work with gibberellin in Japan went unnoticed in the Western world until the early 1950s when a great surge of gibberellin research began, particularly in the United States and England. This research led to the isolation of many different forms of gibberellin extracted from the Gibberella fungus and from higher plants.

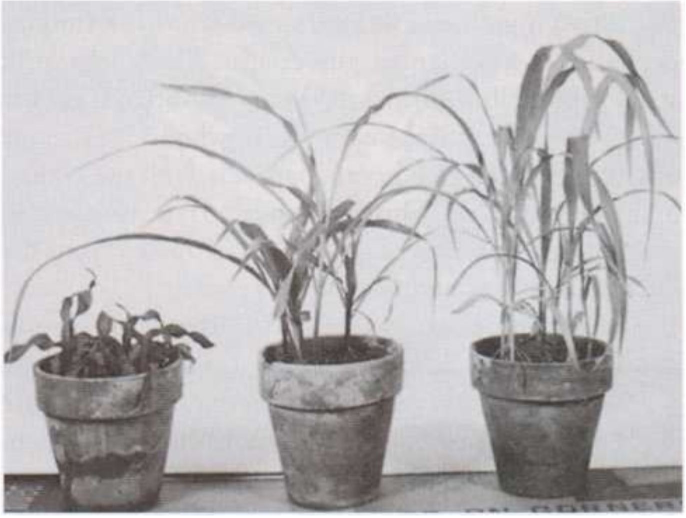

Figure 6-30

Overcoming dwarfness in corn by spraying with gibberellin. Left: Untreated, genetically dwarf corn plants. Center: Nondwarf corn sprayed with gibberellin. Right: Genetic dwarf corn sprayed with gibberellin. Photographs taken six weeks after spraying.Source: From Plant Growth Substances in Agriculture by Robert J. Weaver. W. H. Freeman and Company. Copyright © 1972.

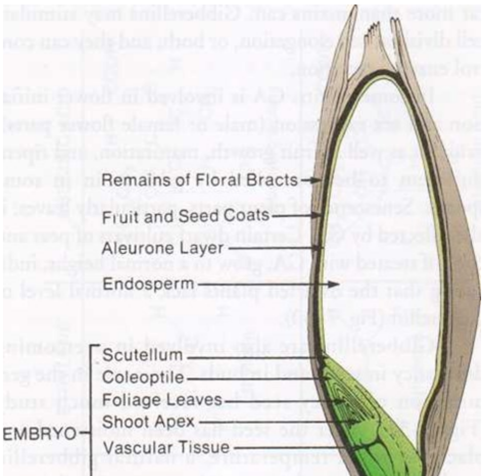

Figure 6-31

Longitudinal section of a barley seed.Source: From a drawing by Peter J. Davies. In A. W. Galston, P. J. Davies, and R. L. Satter, The Life of the Green Plant, 3rd ed. (Edgewood Cliffs, NJ: Prentice Hall, (1980).

Gibberellins were first discovered in 1926 by Japanese researchers Gibberellins are synthesized in the shoot apex of the plant, particularly in new leaf primordial. They are also found in embryos and cotyledons of immature seeds and in fruit tissue. In addition, the root system synthesizes large quantities of gibberellin, which moves upward throughout the plant. GA translocates easily in the plant in both directions, unlike auxin, which moves largely in an apex-to-base direction.

Pharmaceutical companies produce crystalline GA3 as the acid or the potassium salt for research studies and certain commercial applications. These preparations are all obtained from growth of the Gibberella fungus in a process similar to that used to produce antibiotics.

Even though it has been demonstrated that gibberellins occur naturally in many of the higher plants, little is known of the physiological mechanisms of gibberellin action or transport.

Although gibberellins are a powerful and important group of plant hormones involved in many of the plant functions, only a few agricultural uses have been found for them. Some are:

1. Increasing fruit size of seedless grapes. This is the principal commercial application of gibberellin. Practically all vines of the Thompson Seedless grape grown for table use in California are sprayed each year. Berry size of other grape cultivars, such as Black Corinth, is also increased by gibberellin sprays, as shown in Figure 6-32.

2. Stimulating seed germination and seedling growth. Several cases have been reported where soaking seeds in solutions of gibberellic acid before germination greatly stimulates seedling emergence and growth. Such responses have been obtained with barley, rice, peas, beans, avocado, orange, grape, camellia, apple, peach, and cherry. Figure 6-33 shows the stimulation obtained with grape seedlings by gibberellin treatment.

3. Promoting male flowers in cucumbers. When pollen is wanted for hybrid seed production, a single application of GA3 to the leaves stimulates maleness of a cucumber. This has proved an important discovery for hybridizers.

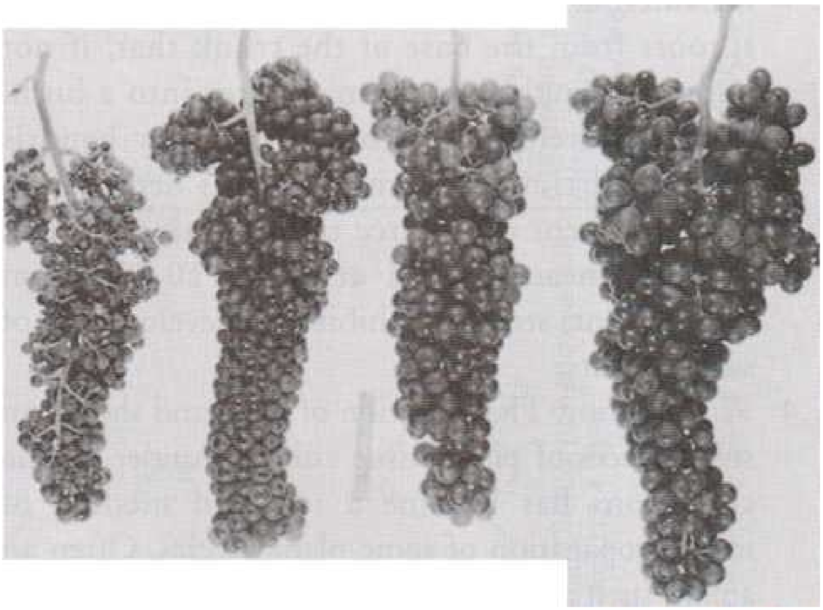

Figure 6-32

Effect of gibberellin sprays on growth of Black Corinth grapes. (A) Untreated control. (B) Stem girdling control.

(C) Plants sprayed at an early growth stage with gibberellin at 5 ppm. (D) At 20 ppm. Photos taken 59 days after spraying.

Source: From Plant Growth Substances in Agriculture by Robert J. Weaver.
W.H. Freeman and Company. Copyright © 1972.

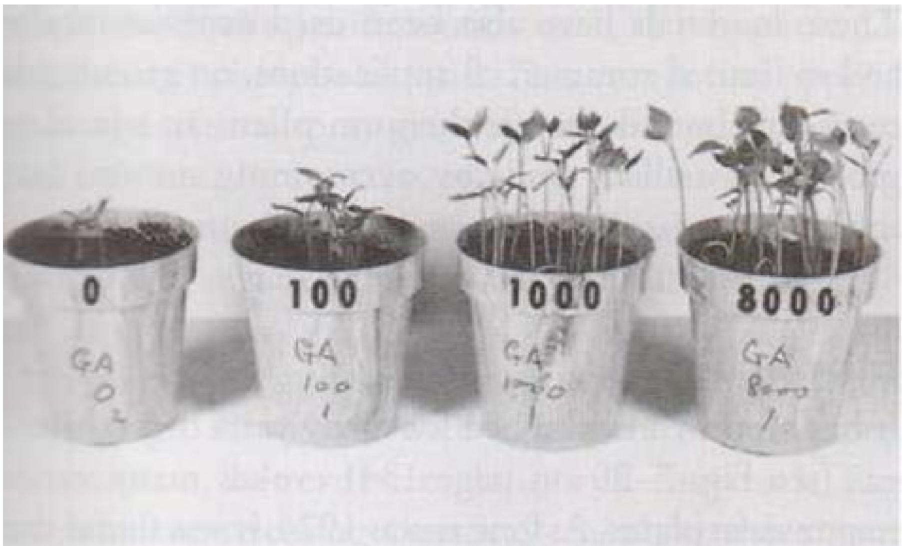

***Figure* 6-33**

Effect of gibberellin on germination and growth of Tokay г'ззе *seeds. Seeds soaked (before planting) at 0, 100, 1,000,*

1. Overcoming the cold requirement for some plants. Azalea plants require six weeks of cool temperatures (8°C or 46°F) to develop flower

buds. Several leaf applications of 1,000 ppm gibberellin completely or partially replace this cold requirement for flower bud development. It has been shown experimentally that gibberellins applied to biennial plants that require a cold period before they flower causes early flowering. Most of these treatments, however, have limited commercial value.

2. Promoting stem elongation. Some ornamental plants such as poinsettias and geraniums can be grown into a tree form (Fig. 6-34) by applying gibberellins to cause stem elongation. As the stem is growing, side branches are removed for a period of time. Then the stem is allowed to grow until several internodes develop. The apical meristem is pinched to stop apical dominance and allow the lateral branches to form. The plant is allowed to grow and produce flowers. In the case of poinset- tia, the plant must be grown in a flower-inducing photoperiod.

Cytokinins

This group of plant hormones primarily promotes cell division but they also participate in a great many aspects of plant growth and development, such as cell enlargement, tissue differentiation, dormancy, different phases of flowering and fruiting, and in retardation of leaf senescence.

Cytokinins interact with auxins to influence differentiation of tissues. As shown in Figure 6-35, externally applied cytokinin alone stimulates bud formation in tobacco stem segments; auxin applied alone causes roots to develop, but when cytokinin plus auxin are applied together, there is a canceling effect—only masses of undifferentiated callus form.

There are both natural cytokinins, such as zeatin, and synthetic forms, such as kinetin and benzylade nine (BA) (see Fig. 6-29 on page 134). There are over 100 known natural and synthetic cytokinins. Cytokinins occur in many plant tissues as both the free hormonal material and as a component of transfer RNA.

Figure 6-34

Left: before the start of short days and flowering. Right: after flowering is complete. 2'zberellins were used to elongate the stems. Lateral branches were also removed from the lower portion of the stem.

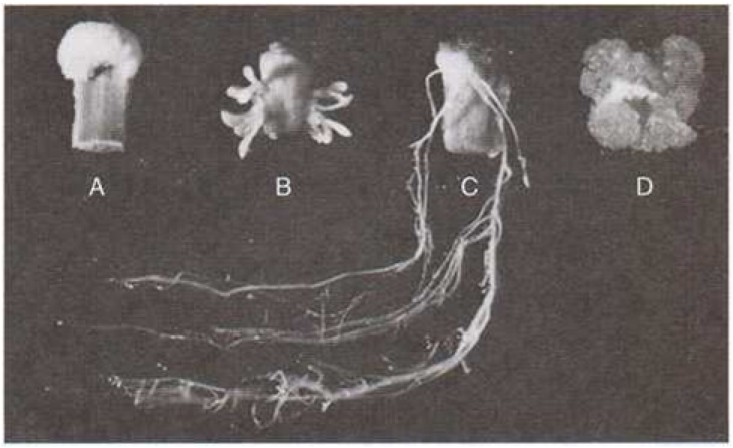

Figure 6-35
Effects o f a cytokinin and an auxin on growth and organ for-
mation in tobacco stem segments. (A) Control, no treatment.
(B) Cytokinin—bu d formation b u t no root formation.
(C) Auxin— root formation with prevention o f bud development.
(D) Cytokinin plus auxin—stimulation o f callus growth b u t no
organ formation. Source: D. E. Kester and H. T. Hudson, Plant Propagation: Principles & Practices,4th ed. © 1983. Adapted by permission of Pearson Education, Inc., Upper Saddle River, NJ

They are found in abundance in embryos and germinating seeds and in young developing fruits—all tissues with considerable cell division. Roots supply cytokinins upward to the shoots.

The mechanism of cytokinin action in the plant is not clear. Cytokinins indirectly increase enzyme activity and increase the DNA produced in some tissues. Their regulatory effects seem to result from interactions with other hormones in the plant.

Cytokinins were discovered when scientists at the University of Wisconsin in 1955 used a synthetic material kinetin, later named a cytokininto cause cell division of tobacco stem pith. After many interesting physiological activities of kinetin became apparent, plants were examined for possible natural similar materials. In 1964 such a material was isolated from young corn seeds by researchers in New Zealand and was named zeatin. An active promoter of cell division known to exist in coconut milk was finally determined to be a zeatin-riboside.

Even though cytokinins are strongly involved in plant growth regulation, no important agricultural uses have been developed for them. In media for tissue culture, however, cytokinin usually must be added to induce shoot development. Applications of cytokinins to green tissue have been shown to delay senescence.

These materials have also been used experimentally, and in limited commercial applications, on greenhouse roses and potted chrysanthemum plants to stimulate growth of axillary buds by overcoming natural bud inhibitors.

Ethylene

It has been well established for many years that ethylene gas (see Fig. 6-29 on page 134) evokes many varied responses in plants. As long ago as 1924, it was found that ethylene could induce fruit ripening; in 1925, it was determined that ethylene could overcome bud dormancy in potato tubers; in 1931, that it could induce leaf abscission; in 1932, that it could induce flowering in pineapple plants; in 1933, that it could cause roots to form on stem cuttings. By the mid-1930s, it was determined that ethylene was itself a plant product, and arguments arose among plant scientists about whether ethylene, a gas, should be considered a plant hormone.

Little further attention was paid to possible roles of ethylene as a natural growth regulator until the development in the 1960s of gas chromatographic techniques that permit the detection of ethylene in concentrations as low as one part per billion. Vast amounts of research of ethylene physiology in the 1960s and 1970s established ethylene as a plant hormone.

Ethylene itself is a tiny molecule (CFI2 = CH2), compared with the other plant hormones. The pathway for ethylene biosynthesis in plants has been fairly well elucidated. Ethylene, as a gas, diffuses readily throughout the plant, moving much like carbon dioxide, and it can exert its influence in minute quantities. Its solubility in water also enhances its movement through the plant. The cuticular coatings on external cell surfaces tend to prevent losses from the plant. Ethylene is apparently produced in actively growing meristems of the plant, in ripening and senescing fruits, in senescing flowers, in germinating seeds, and in certain plant tissues as a response to bending, wounding, or bruising. Synthetic ethylene, from ethephon, applied to plant tissues can cause a great burst of natural ethylene production—an autocatalytic effect.

Just how ethylene exerts its regulatory effects is no better known than the basic mechanisms involved in the action of the other plant hormones. One theory is that ethylene regulates some aspect of DNA transcription or RNA translation, thus changing RNA-directed protein synthesis and, consequently, enzyme patterns. But many other mechanisms are also likely to be in operation.

The possible commercial uses of ethylene were greatly increased with the development in the 1960s of ethylene-releasing compounds such as ethephon (2- chloroethyl) phosphonic acid. This compound applied as an agricultural spray gradually releases ethylene into plant tissues. In contrast to some of the other plant hormones, ethylene and ethylene-releasing chemicals have several valuable commercial applications:

1. Fruit ripening. Ethylene gas, injected into airtight storage rooms, is used commercially to ripen bananas, honeydew melons, and tomatoes. The ethylene-releasing chemical ethephon also ripens tomatoes that are

green but horticulturally mature. To harvest canning tomatoes by machine harvesting equipment, where the entire crop is picked at one time, it is important that most of the fruits be ripe and fully colored at the time of harvest. Spraying the field with an ethylene-releasing material before harvest promotes uniform red color development of the green fruits. Ethephon is used as a preharvest spray to promote uniform ripening of apples, cherries, figs, blueberries, coffee, and pineapple.

2. Flower initiation. Ethylene gas released from ethephon has initiated flowers in several ornamental bromeliad species, including Ananas spp., Aechmea fasciata, Neoregelia spp., Billbergia spp., and Vriesia splendens. Ethephon has been widely used to promote uniform flowering in the cultivated banana.

3. Changing sex expression. Ethylene application to certain plants, such as cucumbers and pumpkins, can dramatically increase the production of female flowers. Some cucumber cultivars produce both female and nonfruiting male flowers on the same plant. Spraying the vines with ethephon causes all flowers to be female, which develop into fruits and thus increase yields. This practice gives results similar to previous studies where auxins were used.

4. Degreening oranges, lemons, and grapefruit. Sometimes the rind of maturing oranges and grapefruits remains green owing to high chlorophyll levels, even though the eating quality, juice content, and ratios of soluble solids to acid are high enough to meet grade standards for harvest. Citrus packers can treat such fruits with ethylene at about 20 ppm for twelve to seventy-two hours. This breaks down the chlorophyll and allows the orange and yellow carotenoid pigments to show.

3 Harvest aids. Certain fruit and nut crops, such as sour cherries and walnuts, are harvested by mechanical tree shakers that shake the trees until the crop falls into catching frames or onto the ground to be picked up later. Often this practice is not completely successful because the fruits or nuts

are so tightly attached that the tree shakers do not remove them. However, by spraying the trees about a week before harvest with an ethylene-releasing compound—ethephon, for example—the abscission-inducing effects of the ethylene result in a much higher percentage of crops removed. Mature cotton plants are sprayed with ethephon to cause the leaves to senesce and abscise, making mechanical harvesting much easier.

1. Growth regulation. One of the physiological effects of ethylene application to plants is a reduction in the growth of stems and leaves. The greenhouse industry recently made use of this fact in controlling excessive growth in floriculture crops. Florel® is a special formulation of ethephon registered for this purpose. Great care must be exercised when using ethylene as a growth regulator because high concentrations of this hormone can cause leaf abscission and other deleterious effects.

Ethylene can also harm plants. It can cause unwanted leaf abscission and can hasten senescence of most flowers. Some fruits give off ethylene as they ripen. The ethylene can harm any ethylene-sensitive produce, including flowers, stored in the same area. The introduction of a few parts per billion of ethylene into the surrounding air causes carnation flowers to close, rose buds to expand prematurely, and orchid flower petals and sepals to develop a water-soaked appearance. The pollination of an orchid flower can generate sufficient ethylene to cause injury to the other parts of the flower. Ethylene can cause flower bud abortion of bulbs during shipment. A few diseased tulip bulbs give off enough ethylene in a packing crate to stop further development of the flower buds within the bulbs. Gas- or oil-fired heaters situated directly in greenhouses can generate toxic levels of ethylene if the units do not burn properly (incomplete combustion) and are not vented adequately. Incomplete combustion generates other unwanted gases such as carbon monox-ide, too. For some commercial flowers such as carnations and geraniums, the deleterious action of ethylene may be blocked with the application of methylcyclo- propene (MCP). MCP has also been shown to be effective at slowing the ripening of climacteric fruit.

Abscisic Acid (ABA)

ABA was originally identified as a component of a complex of inhibitory substances associated with the dormant buds of ash trees and with substances that accumulated in abscising leaves. In fact, the original names for ABA were dormin and abscisin II because researchers believed there was a primary function for ABA in these two processes.

Later, when the chemical structure (see Fig. 7-29 on page 134) was elucidated, dormin and abscisin II were shown to be identical compounds, and the name abscisic acid was adopted. Further research showed, however, that ABA appears to have less influence on dormancy and abscission than the other hormones. Today, ABA is recognized to have two major roles in the life of a plant. First is the regulation of processes in seed development, including the accumulation of seed proteins and the prevention of precocious seed germination, that is, germination while on the mother plant. The second role is one of a mobile stress hormone in which ABA action initiates plants' responses to cold and water stress. One of the most important stress responses mediated by ABA is the closure of stomates when the loss of water from the plant reaches a critical value. Once this critical value is reached, plant cells begin to synthesize large amounts of ABA, which is then transported to the guard cells signaling them to reduce the stomatal aperture, thus minimizing further water loss by transpiration.

ABA is synthesized in both leaves and roots. This characteristic provides the plant with a mechanism to adjust the amount of water loss through transpiration in response to the water status of not only the leaves but also the roots and surrounding soil. For example, during a hot, sunny day, leaves may begin to wilt despite adequate moisture in the soil because more water is lost than can be replaced via the xylem transport system. The reduced leaf water content results in the production of ABA by the mesophyll cells, which signals the guard cells to close the stomates until leaf turgor is restored. On the other hand, as soil moisture reserves are gradually depleted through direct evaporation to the atmosphere and transpiration, the water content of the roots declines commensurately. When a threshold level of water loss is reached, root cells produce ABA, which is transported to the leaves via the xylem, closing the stomates. Thus, plants have a very elegant system for adjusting stomatal apertures to match soil moisture content.

At present, no commercial uses of ABA exist in crop production, although considerable effort was made to see if it could be used as an antitranspirant to minimize transplant shock. The biggest obstacle for such use, besides cost, is the fact that the plant rapidly deactivates ABA, so any effect on depressing transpiration is transient.

Additional Hormones or Hormone Classes

In recent years, four additional hormones or hormone classes have been discovered, indicating that other likely plant hormones are waiting to be discovered. Brassinolides are steroids, closely related in structure to animal steroid hormones such as estrogen and testosterone. In plants, brassinolides appear to function in the regulation of cell division and elongation. Plants lacking brassinolides are dwarf and exhibit weak growth.

A second new hormone is salicylic acid, which coincidentally is the biologically active component of aspirin. This hormone is an important component of plants' response to pathogen attack; it serves as a signal to activate genes involved in pathogen defense. Through a relatively minor chemical modification, plants use a derivative of salicylic acid as a form of interplant communication in an early warning system that a nearby plant is under attack by a pathogen. This modified version is the methyl ester of salicylic acid, which is wintergreen oil. Methyl salicylate is much more volatile than salicylic acid and readily evaporates from the leaves. The vaporized molecules diffuse through the atmosphere and can be absorbed by the leaves of neighboring plants. Once inside living cells, methyl salicylate is easily hydrolyzed to re-form salicylic acid, which can then induce plant defense systems without the plant actually being infected.

While salicylic acid has a major role in pathogen defense, the jasmonates represent a group of compounds involved in systems that defend plants against herbivores. Jasmonates are derived from fatty acids and are similar in structure to the class of animal hormones known as prostaglandins. Jasmonates are also volatile and are the major component of the fragrance associated with jasmine tea and gardenia flowers. The volatile nature of jasmonates provides a mechanism similar to that of methyl salicylate for interplant signaling of attacks by herbivores such as insects.

The last hormone is also involved in herbivore defense. Systemin is unique among plant hormones because it is the only one known to be a peptide (there are several animal peptide hormones—insulin is a well-known example) composed of eighteen amino acids. It is produced in tissue wounded by herbivores and is transported to remote tissues and organs, where it induces defense genes.

Synthetic Growth Retardants

A rather diverse group of growth retardants developed since about 1950 has several important commercial uses regarding ornamental plants, principally in obtaining compact, dwarf-type plants. These materials generally act by slowing, but not stopping, cell division and elongation in subapical meristems, usually without causing stem or leaf malformations. The primary effect of these materials is the opposite of gibberellin, often converting a tall-growing plant into a rosette. Most act by blocking gibberellin synthesis. Plants treated with these growth retardants have a compact, scaled-down appearance, which is often more attractive than larger, untreated plants with a loose, open growth. The treated plants also often have darker, more attractive foliage and more flowers than untreated plants (Fig. 6-36). These chemicals only block gibberellin synthesis, they do not stop its activity or the plant's sensitivity to it. Applying gibberellin to growth regulator treated plants will at least partially overcome the effects of the growth regulator.

Some of the better known synthetic growth retardants are described below:

Daminozide (succinic acid-2, 2-dimenthyl hydrazide; Alar, B-Nine). Tests have shown that daminozide effectively retards growth and stimulates flowering of several kinds of herbaceous and woody ornamental plants and enhances the size and color of various fruit species. Those plants that respond well include chrysanthemums (see Fig. 6-36), various bedding plants (2,500 to 5,000 ppm), and azaleas (2,500 ppm). Sometimes two applications two or three weeks apart are required to maintain the desired dwarf form.

Chlormequat [(2-chloroethyl) trimethylammonium chloride; Cycocel, CCC]. Chlormequat is effective in retarding the height of some ornamental plants.

Figure 6-36
Growth retardation in chrysanthemum plants when treated with a growth retardant, Chrysanthemum x morifolium. "Circus" plants sprayed with daminozide (B-Nine) to retard shoot growth; left: control, no daminozide; center: 2,500 ppm; right: 2,500 ppm sprayed Aug. 14 and again on Aug. 21.

The height of poinsettias may be controlled if chlormequat is applied as a drench to the soil or as a spray to the stems and foliage.

Ancymidol (<x-cyclopropyl(P-methoxyphenyl)-5- pyrimidine-methanol, A-rest®). This growth retardant is very effective for reducing the height of some bulbous and other potted ornamental crops.

Paclobutrazol [2RS, 3RS]-l-[4-chlorophenyl] 4-4- dimethyl-2—1, 4-triazol-yl-pentan-3-ol; Bonzi® P. and its close chemical relative uniconazole (Sumagic®) are very potent growth-retarding chemicals that effectively control the height of many herbaceous and woody ornamentals. The rates used for these chemicals are much lower than for other growth retardants.

Trinexapac-ethyl [4-(cyclopropyl-<X-hydroxy-methylene)- 3,5-dioxocycloheanecarboxylic acid ethyl ester Primo®]. Trinexapac-ethyl is a relatively new growth retardant registered for use in turfgrass. It is relatively specific for monocots.

CHEMICAL REGISTRATION AND USE FOR PLANTS

In the United States, the application of chemicals to plants for commercial use is strictly controlled by Environmental Protection Agency (EPA) regulations. Before the chemicals can be used legally, an EPA registration must be obtained for each crop, stating the dosage allowable and the time of year that application is permissible. Application for registration is usually made by the chemical company manufacturing the material after a patent has been obtained. Regulations for obtaining a registration for use of chemicals

to be applied to food crop plants are much stricter than are those for ornamentals. Most chemical plant growth regulators are forbidden by law to be used on any plants that are grown for human consumption. Chemical use on plants must be in accordance with the law. Before using any chemical, check the label to be certain that the crop you are treating, the rate you are using, and the intended use, along with any other considerations, are in agreement with the label.

SUMMARY AND REVIEW

Growth is the increase in size of a plant by cell division and enlargement. Plant development is progress through the stages of its lifecyle. Growth in plants results from cell division in the meristems and subsequent cell elongation and expansion. Shoot growth can be determinate (shoot elongation ceases with the formation of reproductive structures) and indeterminate (bearing clusters of fruits and flowers along the stem).

Genetic and environmental factors interact to determine plant growth and development. Genetic factors include the overall genetic (DNA) composition of the plant and the active or inactive state of genes at any particular time.

Environmental factors include light, heat, water, and atmospheric gases. Sun light provides the energy for photosynthesis and the accumulation of carbohydrates needed for growth. Changes in light quality or duration direct the shape of the growing plant (photomorphogenesis), including the flowering of photoperiodic plants. Photoperiodic plants flower in response to changes in daylength. Many photogenic responses are mediated by the phytochrome system which senses changes in the amount of red and far-red light striking the plant.

Heat determines how fast most plants grow and develop. Most plants have an optimum growing temperature. Temperatures much below or above the optimum slow growth rate and may be detrimental or even lethal. However, low temperatures can serve as cues for the plant to coordinate growth with the changing seasons. Low temperatures are involved in seed stratification, vernalization, dormancy breaking, development of cold and freeze tolerance.

Water can indirectly influence plant growth because of the role it has in so many plant processes. The presence or absence of water-induced pressure of the plasmalemma on the walls of expanding cells determines the shape and strength of the cell wall and consequently the size and shape of the plant.

The most important atmospheric gases for plants are CO2 (needed for photosynthesis) and O2 (needed for respiration). CO2 concentrations in the leaf influence stomate opening; when internal CO2 is low, the stomates are open. The need for a plant to conserve water (stomates close) and the need to bring in CO2 for photosyntheis (stomates open) can be in conflict. Roots can "drown" in flooded soil because water displaces the O2 needed for root respiration.

Growth starts with germination (seed imbibition followed by radicle and plumule emergence) and early seedling growth. Development of the root and shoot systems follow. Plant growth patterns include annual (complete life cyle including death in one growing season), biennial (life cycle covers two growing seasons), and perennial (life cycle extends for many years). Plants go through juvenile and adult phases. During the juvenile phase, the plant cannot become reproductive even if condtions are right for the development of reproductive organs. At maturity reproductive growth begins as long as environmental factors are appropriate. When a plant becomes reproductive, some or all stem meristems start producing floral parts. For determinate plants, leaf and shoot production stops when the switch is made.

Once the flower matures (it is producing pollen, ovum, or both), pollination and fertilization occurs. Plants can be self-pollinated or cross-pollinated, depending on whether they are self-fertile or self-infertile.

Parthenocarpy is the development of fruit without pollinization and fertilization. Stone fruits and some others such as grape and fig have a double sigmoid pattern where there are periods of rapid growth.

Aging and senescence are the final stages of the life cycle of all plants. Senescence is the terminal and irreversible deterioration in plants leading to death. It is usually caused by natural processes in the plant such as transfer of metabolites from leaves to developing flowers and fruit but can also be caused by pathogen attack or environmental stress. Removing flowers and immature fruit can delay senescence of leaves in some plants and extend the flowering period of others. For temperate biennials and perennials senescence occurs for some but not all tissues and organs at the end of each growing season.

There are five traditionally recognized classes of plant hormones: auxins, gibberellins (GAs), cytokinins, ethylene, and abscisic acid (ABA). Auxins influence cell enlargement, photo- and geotropism, apical dominance, and other growth traits. Gibberellins can promote flower initiation and stem elongation, and can overcome dormancy in seeds and buds. Cytokinins promote cell division and slow leaf senescence and influence other physiological processes. Ethylene promotes senescence and fruit ripening in many species. Unwanted exposure to ethylene can cause severe damage to plants. Abscisic acid (ABA) is involved in seed development and the closing of stomates when plants stressed by low water availability. In some plants, ABA also promotes leaf abscission and/or dormancy. In recent years, four more classes of hormones have been discovered and more are likely to be discovered.

Chemical growth regulators generally promote or inhibit the influence of hormones. Most of them act by blocking the synthesis of gibberellins.

FURTHER EXPLORATION

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CULTIVATED PLANTS: NAMING, CLASSIFYING, ORIGIN, IMPROVEMENT, AND GERMPLASM DIVERSITY AND PRESERVATION

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key learning concepts

- After reading this chapter, you should be able to:
- and classified.
- Use the nomenclature and system of taxonomic classification to identify plants and their relationship to each other.
- Explain how several crops originated and where they were domesticated.
- Discuss the importance of saving germplasm from extinction and the global system created to preserve germplasm.

There are over 500,000 different kinds of plants, and for humans to be able to communicate about them, some method of classifying and naming them had to be developed. The process of developing plant names started over 4,000 years ago, but the first recorded names were attributed to Theophrastus (370-285 BCE). Naming plants, no doubt, began with simple names that referred to the plant's use, growing habit, or other visible attribute. One example is the milk weed—so named because its sap (latex) is milky in appearance. One difficulty with such names is that often they are only used locally. People in one place know the plant by one name, while elsewhere the same plant is known by a different name.

The weed Tribulus terrestris is known as the puncture vine in some areas because the seeds have sharp spines that puncture tires or bare feet; another common name for the same plant in other areas is goat-head because the shape of the seed resembles a goat's head. As plant knowledge expanded and the exchange of this knowledge became desirable, it was obvious that a uniform and internationally acceptable system was needed to name and classify plants.

There are many ways to classify plants, and any system depends on how the classification is to be used. Some classifi cations relate directly to specific environmental requirements of the plant for satisfactory growth. For example, such a classification could categorize plants according to their climatic requirements.

CLIMATIC AND RELATED CLASSIFICATIONS

Farmers and others who grow plants commercially have to be able to identify and name crops. But this alone is not enough. They also have to distinguish which of many crops and plants suit their climate.

Most commercial growers in the United States are working in the temperate zone. For example, some fruit and nut crops grown in the temperate zone are almond, apple, apricot, cherry, peach, pear, pecan, and plum. Fruit growers in a tropical region would have an entirely different choice of crops, such as cacao, cashew and macadamia nuts, banana, mango, papaya, and pineapple. The fruits of the subtropical region, between the temperate zone and the tropics, cannot withstand the severe winters of the temperate zone but may need some winter chilling. Some of these subtropical plants are citrus, date, fig, olive, and pomegranate. Thus, by using climate as a criterion, plants can be classified into distinct groups. The USDA has divided the United States into several different cold hardiness zones, and many plants are classified by their ability to grow in the different zones.

Agronomic crops like grains, forage, fiber, and oil crops and the vegetable and ornamental plants can also be classified by their temperature requirements. For example, some annuals have specific climatic requirements for growth and flowering and are distinguished as winter or summer annuals. Winter annuals are planted in the fall and bloom early the following spring. Summer annuals are planted in the spring and bloom through the summer and fall.

Some crops grow best in certain seasons and are thus classified. For example, warm-season plants such as corn, beans, tomatoes, peppers, watermelons, petunias, marigolds, zinnias, and Bermuda grass grow best where monthly temperatures average 18°C to 27°C (65°F to 80°F), while broccoli, cabbage, lettuce, peas, flowering bulbous plants, snapdragons, cyclamen, and bluegrass are cool-season crops growing best at average monthly temperatures of 15°C to 18°C (60°F to 65°F). Plants can be classified by the seasons in which they are most likely to flower and fruit or when the quality of the product can be expected to be at its maximum. Numerous flower and vegetable cultivars can be classified as early, midseason, or late maturing.

Vegetables are classified into groups according to their edible parts. Some are grown for fruits and seeds, such as the tomato, bell pepper, string bean, pea, and corn. Many are grown for their shoots or leafy parts, such as asparagus, celery, spinach, lettuce, and cabbage. Others are grown for their underground parts (either roots or tubers), such as the carrot, beet, turnip, and potato.

Ornamentals are sometimes classified by use— that is, as houseplants, greenhouse plants, cut flowers, garden plants, street trees, and various classes of landscape plants. Houseplants, which have become very popular, are often classified according to their foliage, flowers, or growth habits. Common foliage plants, which stay green all year, are the philodendrons, dief- fenbachias, and ferns, to name a few. Blooming of some flowering plants may be only seasonal, as in the Easter lily and poinsettia, but the African violet and chrysanthemum are available in flower year-round. Plants outside the home are typically classified by use, for example, bedding plants such as petunias, marigolds, and zinnias, and landscape plants like trees and shrubs.

The forester classifies trees into two broad groups: the hardwoods and softwoods. Some hardwood types are oaks (Quercus), maples (Acer), birch (Betula), and beech (Fagus). Some softwood trees are pines (Pinus) (Fig. 7-1), firs (Abies), redwood (Sequoia) (Fig. 7-2), cedars (Cedrus), and spruce (Piced). Trees are also classified according

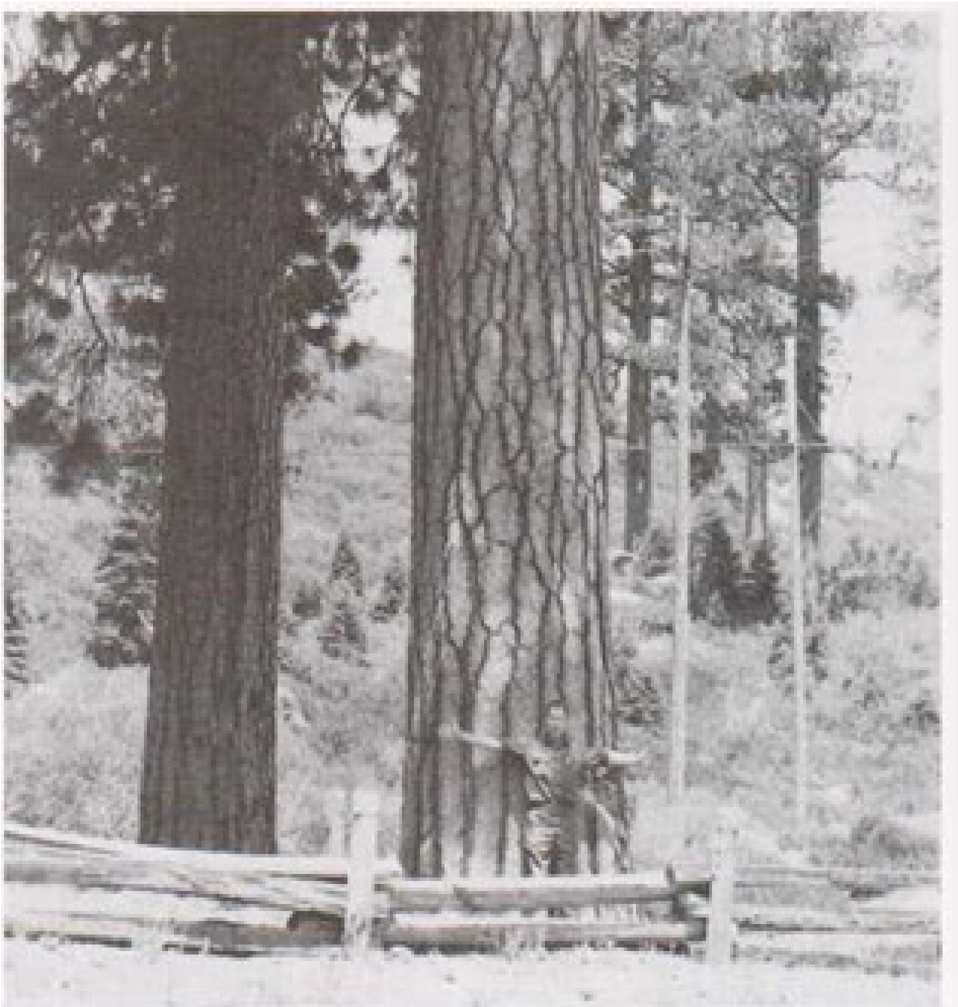

Figure 7-1

Jeffrey pine (Pinus jeffreyi Grev. and Balf.) tree growing in the Sierra Nevada mountains of northern California near Lake Tahoe. This tree is about 2 m (6.5 ft) in diameter at breast height (DBH), the point where lumber trees are measured.

Source: Robert A. H. Legro.

to the hardiness zones in which they can survive. Some can withstand very low temperatures during the winter, whereas others are subject to frost damage and therefore must be grown in a subtropical climate.

COMMON AND BOTANICAL NAMES

Most plants are generally known by their common names because common names are often easier to remember, pronounce, and use. Maple or elm trees

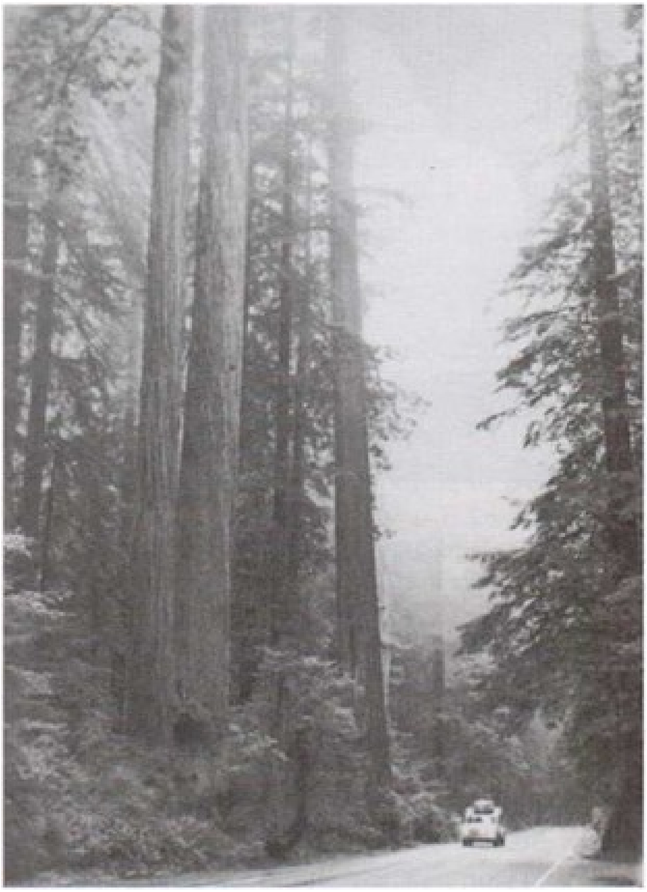

Figure 7-2

A grove of coast redwoods (Sequoia sempervirens D. Don, Endl.) along Highway 101 on "The Avenue of the Giants" in northern California. The camper truck is dwarfed by these majestic trees.

growing along the streets are referred to by common names in everyday conversation. Common names often evolve because of certain plant characteristics.

A common name has value in conversation only if both persons know exactly what plant is being discussed. This is most likely when persons are from the same community and the common name of the plant cannot be mistaken for another. But take the case of the jasmine, a plant known all over the world and prized for its fragrance, flavoring (tea), and landscaping. Many common plant names contain the word jasmine, but such plants do not resemble one another and may not even be closely related botanically. Some of the so-called jasmines are listed below, with the botanical (italicized) name following the common name:

Star jasmine (Jasminum gracillimum)
Star j asmine (Trachelospermum jasminoides)
Blue jasmine (Clematis crispa)
Cape jasmine (Gardenia jasminoides)
Crape jasmine (Tabernaemontana divaricata)
Night jasmine (Cestrum nocturnum)
Night jasmine (Nyctanthes arbor-tristis)

It is obvious from these examples that common names have their limitations for universal written or verbal communication. There are too many and they are too variable to serve most scientific purposes.

DEVELOPMENT OF BOTANICAL CLASSIFICATIONS

Theophrastus (370-285 BCE), a student of Aristotle, classified plants by their texture or form. He also classified many as herbs, shrubs, and trees. He noted the annual, biennial, and perennial growth habits of certain plants, and described differences in flower parts that enabled him to group plants for purposes of discussion. He is known as the father of botany for these signifi-cant contributions.

Carl von Linne (1707-1778), better known as Carolus Linnaeus, devised a system of categorizing plants that led to the modern taxonomy or nomenclature of plants.

Scientific Classification

The scientific system of classification has all living things divided into groups called taxa (sing, taxon) based on physical characteristics. The first taxon, called Domain, divides all living things into two Domains: Prokaryotes (cells having no separate subcel- lular units) and Eukaryotes (cells having subcellular units). The Eukaryote Domain is divided into the four Kingdoms of Fungi, Protista, Plantae, and Animalia. The Plantae Kingdom is divided into two groups: bryophytes (includes mosses and liverworts) and vascular plants. The vascular plants are divided into two subgroups: seedless and seeded. Seedless and seeded plants are further classified by Phyla. Seedless phyla include the Pterophyta (ferns). Seeded phyla include Cycadophyta (cycads), Ginkgophyta (ginkgo), Coniferophyta (conifers), and Anthophyta (angiosperms, which are subdivided into monocotyledon and dicotyledon). Almost all commercially important crop plants are in the seeded group. After phylum, plants are classified in descending rank by class, order, family, genus, and species. Each descending rank more closely defines the physical characteristics common to members of that rank.

PLANT IDENTIFICATION AND NOMENCLATURE

The family is usually the highest taxon commonly included in plant identification or study. Students of plant science are usually required to learn the family, genus, and species of some plants as well as their common names.

Since the early Christian era, naturalists wrote their books in Latin, which was the language of all educated people in Europe. Thus, Linnaeus used names of Latin form. Most of the names he gave, which describe morphological characteristics of the plants, came from Latin words, although some were derived from Greek and Arabic.

The names are usually phonetic and often give a clue to the plant's characteristics, its native habitat, or for whom it is named. Such derivatives are numerous. Names that refer to leaves include folius, phyllon, or phylla, usually as suffixes. The names can also have prefixes, such as macro or micro. Thus, words are created, such as macrophylla (large leaf), microfolius or microphylla (small leaf), illicifolius (holly leaf), and salicifolius (willow leaf). The Latin for flower is flora; add the prefix grand and it becomes grandiflora (large flower), as in Magnolia grandiflora L., the southern magnolia (Fig. 7-3). Shapes or growing habits of plants can be described with altus or alta (tall), arboreus (treelike), comp actus (dense), nanus or pumilus (dwarf), repens or reptans (creeping), and scandens (climbing). Names based on flower or foliage color include albus or leuco (white), argentus (silver), aureus or chryso (gold), rubra, rubens, or coccineus (red), and croceus, flavus, or luteus (yellow). Species names sometimes reflect the plant's place of origin. Examples are australis (southern), borealis (northern), canadensis (from Canada), chinensis or sinensis (from China), chilensis or chileonsis (from Chilt), japonica, nipponica, or nipponicus (from Japan), campestris (field), insularis (island), and montanus (mountain). Sometimes Linnaeus took names, like Narcissus, from classical mythology, or devised names to honor other scientists, like Rudbeckia, honoring Linnaeus' botany professor, Rudbeck.

Each plant has a two-word, or binomial, name1 given in Latin. The first name refers to the plant's genus, the second to its species. The Latin binomial name is international and understood universally.

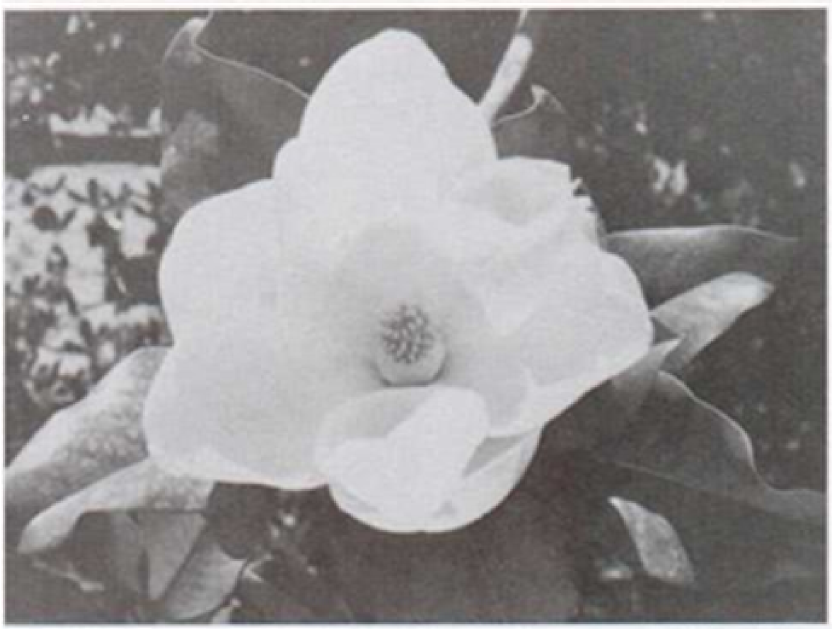

Figure 7-3

The southern magnolia (Magnolia grandiflora L.). The name grandiflora is more than justified; the flower measures 15 cm (6 in.) across.

Complete Linnaean names have a third element— the authority, or the abbreviated name of the scientist who named the species. Consider the name for the common white (Irish) potato, Solanum tuberosum L. The "L." means Linnaeus, and his initial appears commonly, because Linnaeus named so many species. Books and journals often omit the authority for brevity and simplicity, but it is important in determining which taxon is being referred to in situations where different botanists have used different binomials for the same plant. In such cases, the botanical or scientific name that was published first takes precedence.

Wild or naturally occurring plants are named under the rules of the International Code of Botanical Nomenclature. Cultivated plants are named according to the same principles but are covered by the International Code ofNomenclature for Cultivated Plants. Some of the basic rules of nomenclature follow.

The generic name always begins with a capital letter; it is underlined when written by hand or typewriter and italicized in print. Thus, the genus name for potato is Solanum. The specific epithet tuberosum is likewise underlined or italicized. The specific epithet usually begins with a lowercase letter, but it may be capitalized if it is a person's name; it is always correct if written entirely in lowercase. Many of the original species names are frequently capitalized (e.g., Pinus feffreyi Grev. and Balf. or Pinus Jeffrey i Grev. and Balf.).

To complete the binomial name, the authority for describing and naming the plant is given after the genus and species; thus, Solanum tuberosum L. In this text, unless otherwise specified, both the binomials and the authorships agree with those given in Hortus Third, which is a widely recognized compilation of the cultivated plants for the United States and Canada. These authority names are often abbreviated. Each taxonomy book has a list of the full names of these authorities.

When several plants in the same genus are listed, the genus name is given in full for the first plant, then shortened to the first initial (which is always capitalized) for the other plants in the list. As an example, the apricot, the European plum, and the peach are all members of the genus Prunus. Listed as scientific binomials, they would be Prunus armeniaca, P. domestica, and P. persica, respectively. This procedure should not be used if there is any chance of confusion with another genus with the same first initial.

The singular and plural spelling of species is the same. Occasionally the plant genus is known but the exact species is not known because it is difficult or impossible to identify. In such a case, the genus name is given and followed by the lowercase letters "sp." for species (singular) and "spp." for species (plural). An example is Prunus spp. The "spp." usually refers to all of the many species in the genus. However, the "sp." refers to a definite plant whose specific epithet is not known. The "sp." or "spp." is never underlined or italicized.

Subspecific Categories

Sometimes a botanical binomial is not sufficient to identify a species-wild or cultivated. Botanists and horticulturists may form subspecific categories, such as botanical variety, cultivar, and group.

Botanical Variety

A plant group can be so different in the wild from the general species described originally that it warrants a botanical variety classification below that of species. An example of this is Buxus microphylla Sieb. and Zucc. var.japonica Rehd. and Wils., which is native to Japan. The "var." stands for varietas, Latin for "variety." Another botanical variety originated in Korea; it is Buxus microphylla var. koreana Nakai. These botanical varieties are sufficiently different to warrant unique names and authorities to distinguish them from one another. In this case, the name of the variety japonica or koreana is underlined or italicized. When a varietas epithet is formed from a surname, it may or may not be capitalized depending on the personal preference of the author. However, the trend is to not capitalize them, as recommended by the International Codes.

Cultivar

Many kinds of plants that are valuable in agriculture must be propagated with little or no genetic change in the offspring. In agronomy and horticulture, there are cultivated varieties that remain genetically true. These cultivated varieties may be different from botanical varieties and are called cultivars, a contraction of culmated variety. There are two main categories of cultivars—the clones and the lines. If propagated by vegetative methods, they are called clones-, if by seeds (under certain specified conditions), they are called lines. The word cultivar is abbreviated "cv." and the plural is "cvs." A cultivar is often a distinct variant selected by someone who believed it was uniquely different from any plant already in cultivation. The flower color may have changed from red to white because of a mutation, as in some carnations. Perhaps a plant has fewer spines or thorns than does the ordinary species; an example is a Chinese holly (Ilex cor- nuta Lindl. and Paxt.) found to have few or no spines. It was named Ilex cornuta cv. Burfordii. The cultivar name is always capitalized but never underlined or italicized. The term “cv.” after cornuta may be dropped in favor of single quotes around the cultivar name. Either way of expressing the cultivar name is acceptable. Either single quotes or the term “cv.” is used, but never both. Tables or lists usually use “cultivar” or “cv.” in the heading to avoid single quotes around each cultivar name.

Many annual flowers, vegetables, grains, and forage crops are cultivars that are propagated by seed from open pollination. Others are F j hybrids. An example is Petunia X hybrida Hort. Vilm.-Andr.—the hybrid garden petunia. A breeder may develop a new strain that is believed to warrant a cultivar name such as ‘Fire Chief’ or ‘Pink Cascade.’ The parent plants can be maintained and crossed to produce the same Fj hybrid cultivar year after year. Many vegetables and flowering annuals are maintained as cultivars in this manner, with the parents maintained to produce new crops of seed each year for planting. Cultivars of fruit trees, grapes, and woody ornamentals are usually maintained as true-to-type clones by vegetative propagation methods.

Group

The group category is used for some vegetables and some ornamentals such as lilies, orchids, roses, and tulips. It is a category below the species and not used as frequently as the cultivar category. A group includes more than one cultivar of a particular kind of plant. For example, when there are evident differences among plants of the same species, they can be further categorized by a group name. When a species has many cultivars, cultivars that are similar are categorized into groups. For example, cultivars of Brassica oleraceae can be grouped into the Acephala Group (kale and collards), the Alboglabra Group (Chinese broccoli), the Botrytis Group (cauliflower), the Italica Group (broccoli), the Capitata Group (cabbage), and other groups depending on their morphological characteristics. These groups have the same botanical name—Brassica oleracea. The name of the group is written within parentheses between the species name and the cultivar name, as Brassica oler- aceae (Capitata) 'King Cole,' and the group name is always capitalized but not enclosed in single quotes.

Family

The family is a group of closely related genera. The relationship can be based on certain plant structures or on chemical characteristics, such as the presence of latex in the milk weed family ASCLEPIADACEAE, but flower structure is the usual basis for association. The nightshade family SOLANACEAE contains not only Solanum (potato) but also

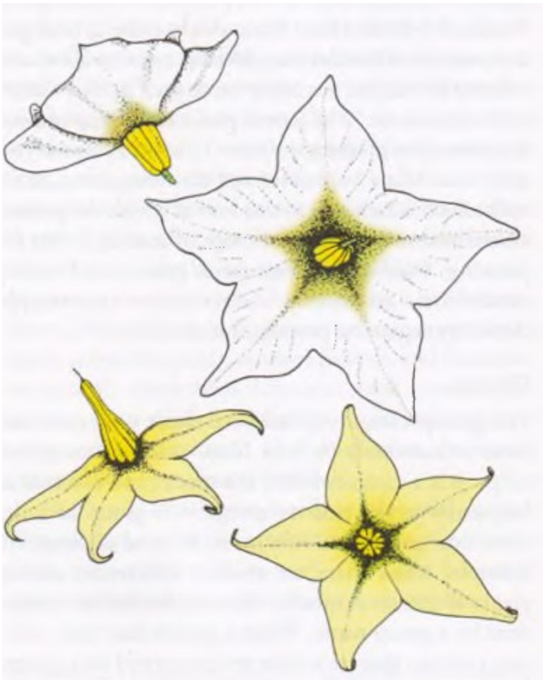

Figure 7-4

Side and front views of potato (upper) and tomato (lower) flowers. These views show the similarities of the flowers of plants in the same family, solanaceae. Source: Moira Tanaka.

Lycopersicon (tomato), Capsicum (pepper), Nicotiana (tobacco), Datura (deadly nightshade), Petunia, and many others. This is a large family (about ninety genera and more than 2,000 species), most of which are native to the tropics. All species in this family have similar flower structures; the similarities between a tobacco, a tomato, and a potato flower, for instance (Fig. 7-4), are readily seen.

The first letter of family names is always capitalized and the names are sometimes underlined or italicized.

The family names may be written entirely in capital (uppercase) letters. Most families' names end with -aceae (pronounced ace-ay-ee) attached to a genus name; for example, SOLANACEAE, ROSACEAE, AMARYLLIDACEAE, LILACEAE, and MAGNOLIACEAE. Eight families, however, did not follow this standard rule. For the sake of uniformity, new names have been adopted for these families. The old names appear in parentheses following the new names:

Asteraceae (compositae)
Brassicaceae (cruciferae)
Poaceae (graminae)
Clusiaceae (guttifereae)
Lamiaciace (labiate)
Fabaceae (leguminosae)
Arecaceae (palmae)
Apiaceae (umbelliferae)

Plant classifications can be studied in detail in various plant biology or taxonomy books and references.

PLANT IDENTIFICATION KEY

See Table 10-1 for a simplified dichotomous key used to identify some commonly known seed-bearing plants (Spermatophyta). To use a key you need to know the vocabulary of plant structure. Examine the plant in question to decide if its characteristics fit in one category or the other offered by the key. Keying plants is a process of elimination by making yes or no decisions to characteristics offered in the key—rejecting those that do not apply (dichotomy).

To use a simplified key (Table 7-1), eliminate the alternative that does not pertain to the plant in question, and then proceed to the next pair of numbers (choices) directly under the proper choice. As an example, the first choice in this key is to determine whether the seeds of the plant being identified are borne naked, as in the cone-bearing plants of the gym- nosperms (Fig. 7-5), or enclosed in an ovary, as in the angiosperms. Once this yes or no decision has been made, the next step is to compare the next pair of descriptions directly under the previously chosen char-acteristic. If the seeds are enclosed within an ovary, the plant in question is an angiosperm and the next pair of numbers to compare is 8. Note that the two 8s are separated by several pairs of subsidiary descriptions. A choice between the two 8s must be made before proceeding further. If the plant in question has parallel- veined leaves and the seeds have one cotyledon, the plant belongs to the

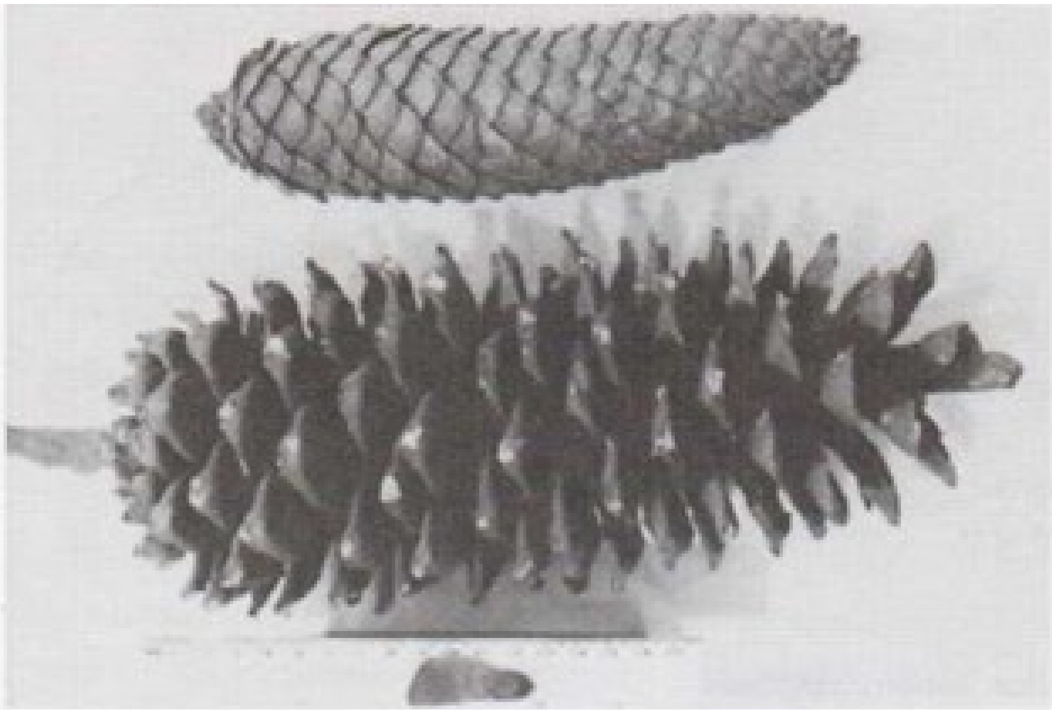

Figure 7-5

Cones of the sugar pine (Pinus lambertiana Dougl.) in closed and open conditions. When the cones dry; the winged seeds, shown on the 17.8-cm (7-in.) ruler, are released and can be disseminated by the wind.

monocotyledon subclass. This procedure is followed until the plant to be identified “fits” a given set of plant characteristics.

A slight variation of a dichotomous key appears in Chapter 25 for the identification of turfgrasses; the number at the end of the phrase in that case indicates the next number to pursue.

Figure 7-6

An inflorescence of the pear (Pyrus communis L.) showing the five petals and the many stamens typical of the rosaceae. Mature fruits do not develop for another four months.

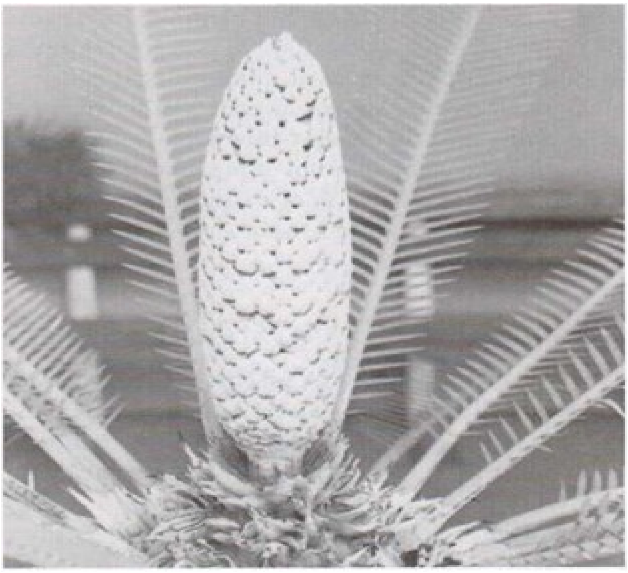

Figure 7-7

The inflorescence of a cycad (Dioon edule Lindl.) native to Mexico. The inflorescence is about 23 cm (9 in.) tall. The pinnate leaves might erroneously lead one to call this plant a palm.

Certain plant parts might not be available because they may not be in season—when needed to identify the plant. An example of this occurs in the simplified key in Table 7—1. In the family ROSACEAE (the second item), both flowers and fruit are needed to be certain of making the correct choice. In the case of strawberries, both fresh flowers and fruits can be obtained at the same time; however, it is not possible to have flowers and fruits at the same time for the apricot or the pear (Fig. 7-6). In such cases, it might be necessary to preserve flowers for future examination or simply describe them thoroughly in the spring when they are abundant, and then wait for the fruit to develop to accurately determine its characteristics. See Figures 7-7 through 17-10 for additional examples of hard-to-classify plants.

This simple key illustrates how choices are made between two characteristics-eliminating alternatives that are not pertinent to finally identify the plant in question. Much of the upper portion of the key can be ignored by a trained taxonomist or a good botany student because, to them, it is easy to identify a gymnosperm or an angiosperm. The family characteristics are determined by observing and studying certain flower characteristics. Sometimes it is difficult but necessary to distinguish between an inferior or superior ovary (the characteristic that divides the

Figure 7-8

The fruits ofTaxus baccata L. 'Lutea'. The single seed (arrow) is within the cuplike fruit, which is poisonous.

LILIACEAE from the AMARYLLIDACEAE families; see (Fig. 6-36), but one finds these determinations easier after some experience is gained. Once the family is known, the correct genus and species are identified by referring to taxonomic books with detailed keys.

Obviously one must be familiar with plant parts and structures (Chapter 6) to use a botanical key and determine the identity of the plant. Various plant parts and shapes are useful in illustrating plant identification.

ORIGIN OF CULTIVATED PLANTS

Most of the crop plants important today were cultivated in a primitive way long before recorded history. Agriculture began about 10,000 years ago when ancient peoples selected certain plant types they found growing about them and thus enlarged their food sources beyond hunting and fishing. Most of these early food plants are still cultivated but in much improved forms. Others that were unknown to early humans have been added over the centuries to make up our present-day selection of food plants. Then, much later, as people became more concerned about the aesthetics of their environment, they also added shade trees, shrubs, flowering plants, and lawn grasses to the list of cultivated plants.

Several botanists have brought together fascinating information on the subject of where and when the crops that now feed the world's peoples, their livestock, and other domestic animals originated. The Swiss botanist Alphonse DeCandolle wrote Origin of Cultivated Plants, first published in 1833. Later, the famous Russian plant geneticist Nikolai Vavilov also studied the origin of cultivated plants. The results of his studies were published in The Origin, Variation, Immunity, and Breeding of Cultivated Plants, translated from the Russian and published in English in 1951.

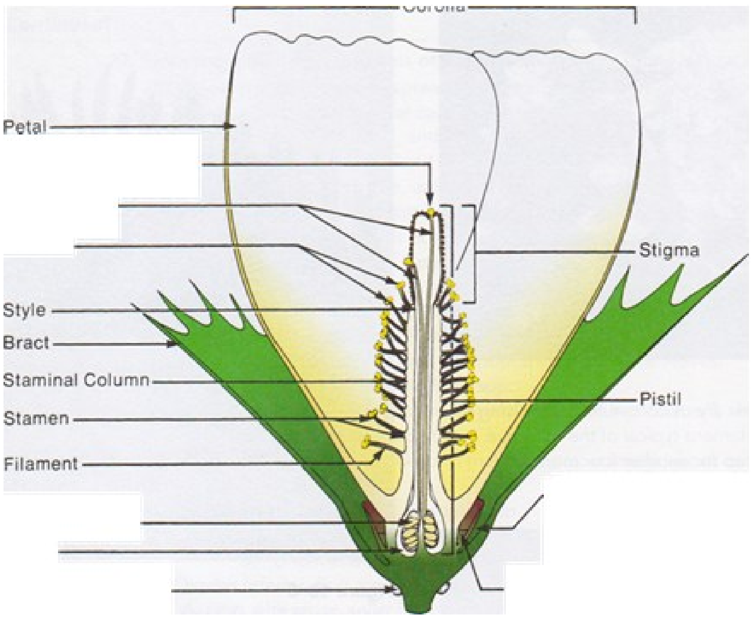

Figure 7-9

Cotton (Gossypium hirsutum L.) flower in a longitudinal section. Source: USDA.

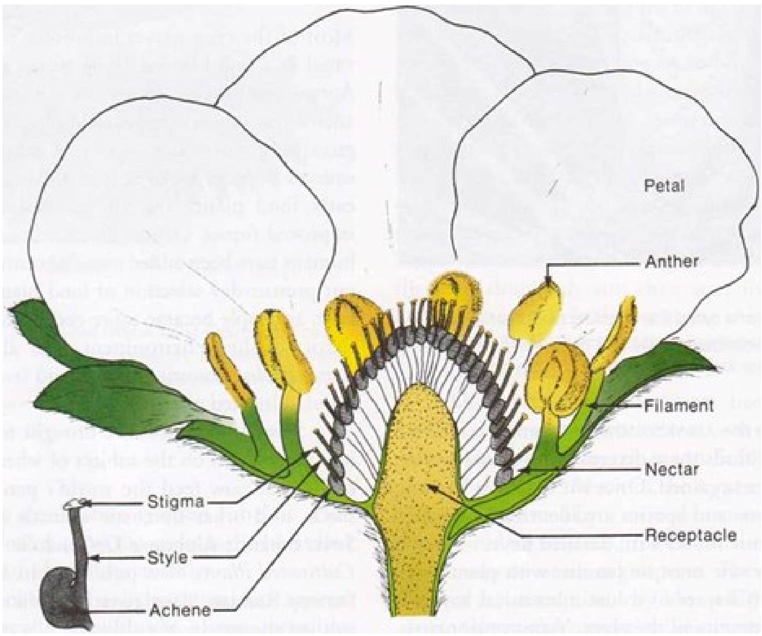

Figure 7-10

A strawberry flower in a longitudinal section. Also shown is an individual achene. Source: USDA.

More recent studies and theories on the origins and movements of the world's agricultural crops have been summarized by Carl Sauer in *Agricultural Origins and Dispersals* (1952), by Jack Harlan in *Crops* *and Man* (1975), by Jack Hawkes in *The Diversity of Crop Plants* (1983), by Barbara Bender in *Farming in Prehistory (1975),* and by Joseph Smartt and Norman Simmonds in *Evolution of Crop Plants* (1976).

Because breeding is most often accomplished between closely related species, many times plant breeders use close wild-type relatives of commercial plants to introduce or re-introduce desirable traits. One of the best regions to look for wild-types is in the region where a domesticated plant originated.

DOMESTICATION OF PLANTS

Toward the end of the Ice Age, about 11,000 to 15,000 years ago, when the glaciers were in full retreat and early humans were wandering about the earth, the stage was being set for the initiation of food production (Table 7-2). Before this time, tool-using hunter- gatherers had been on earth for about 4 million years. Then—only about 400 generations ago—there was a gradual transition to food-producing activities. This transition phase suggests several interesting questions, such as why it took so long for humans to become food producers and why such activities began in various parts of the world—southwest and southeast Asia, middle America, and western South America—at about the same time.

places in this area by at least 5000 to 6000 BCE. There is evidence from site excavations that einkorn wheat, emmer wheat, barley, lentil, chickpeas, oats, and vetch were being cultivated, as well as dates, grapes, olives, almonds, figs, and pomegranates. Excavations at Jarmo in Iraqi Kurdistan, at ancient Jericho in the Jordan Valley, and many other sites in the Fertile Crescent have supplied much of the evidence to support these conclusions.

An indigenous savanna type of agriculture apparently was developing from domesticated native plants about 4000 BCE in a belt across central Africa (Fig. 7-11). This area also was the first home of the human race, as we understand it now. The genus Homo originated here, where most of human evolution subsequently occurred. Some important world crops brought under cultivation in this area include coffee, sorghum, millet, cowpeas, yams, and oil palm.

The Chinese center of agricultural origins became important about 4000 BCE according to radiocarbon dating. Crops domesticated include millet, chestnuts, hazelnuts, peaches, apricots, mulberries, soybeans, and rice. The West did not learn of the all-important rice plant until about 350 BCE, and the peach was unknown outside China until about 200 CE.

A farming culture in southeast Asia and what is now Indonesia apparently had domesticated rice around 6000 BCE. Other important crops appearing later under cultivation in this area were sugar cane, coconut, banana, mango, citrus, breadfruit, yams, and taro.

In the New World, evidence from archeological sites shows agricultural beginnings in two areas. One is present-day southern Mexico and Central America, where plant cultivation began about 5000 to 7000 BCE. The plants grown were early forms of maize (corn), sweet potato, tomato, cotton, pumpkin, peppers, squash, runner beans, papaya, avocado, and pineapple.

The second American region is a broad "noncenter" of agricultural origins stretching from Chile northward to the Atlantic Ocean and eastward into Brazil. There is evidence that both the snap and lima beans were cultivated here by about 6000 BCE or earlier. Other important cultivated crops from this region are the potato, peanut, cacao, pineapple, cashew, papaya, avocado, Brazil nut, peppers, tobacco, guava, tomato, yam, cassava (manioc), and squash.

No major cultivated crop originated in the area of the present-day United States. Agriculture here relies in a large measure on introduced crops. There are, however, many minor native American fruit and nut crops, such as the American grapes and plums, the pecan,

Toward the end of the Ice Age, about 11,000 to 15,000 years ago, when the glaciers were in full retreat and early humans were wandering about the earth, the stage was being set for the initiation of food production (Table 7-2). Before this time, tool-using hunter- gatherers had been on earth for about 4 million years. Then—only about 400 generations ago—there was a gradual transition to food-producing activities. This transition phase suggests several interesting questions, such as why it took so long for humans to become food producers and why such activities began in various parts of the world—southwest and southeast Asia, middle America, and western South America—at about the same time.

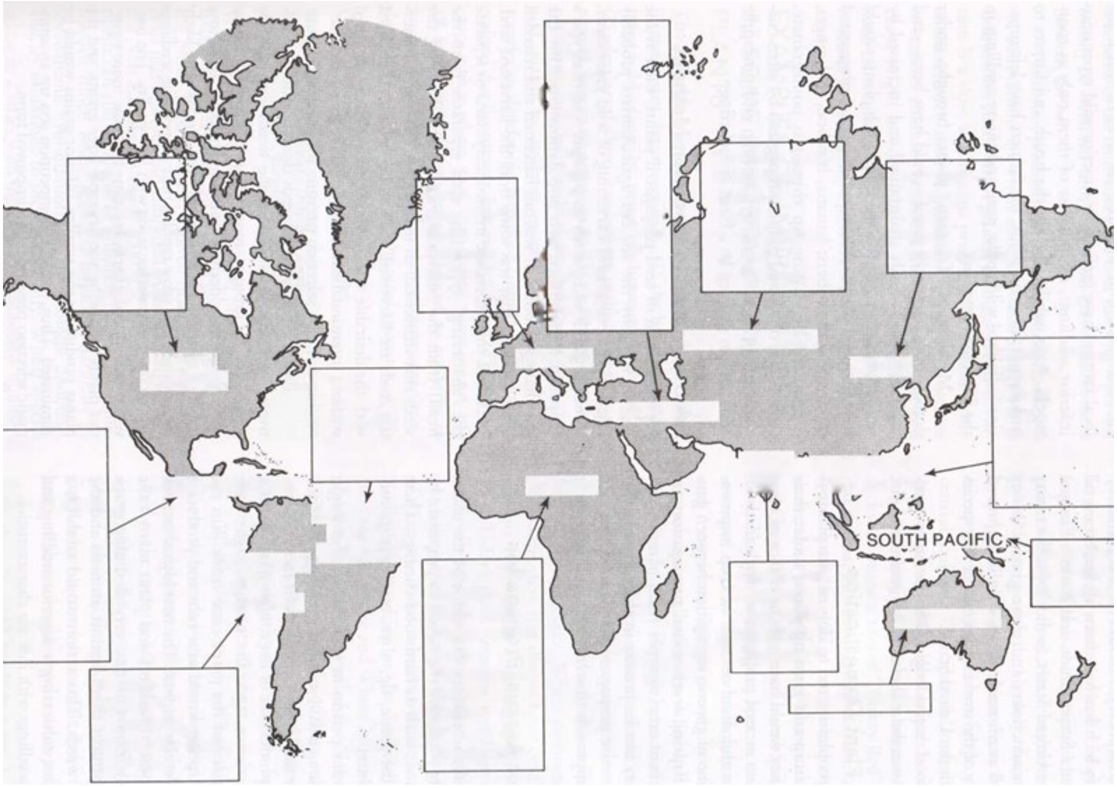

Figure 7-11

Regions of the world where major food crops were domesticated. Crops that apparently originated in several different areas are shown in parentheses. Question marks after the name indicate doubt about the location of origin.

Source: J. R. Harlan, "The Plants and Animals that Nourish Man," Scientific American *235, no. 3 (1976):88—97.*

There is definite evidence from archeological sites that agricultural villages existed about 8000 to 9000 BCE in the area of southwest Asia known as the Fertile Crescent. It extends from the alluvial plains of Mesopotamia (now Iraq) across Syria and down the eastern coast of the Mediterranean sea to the Nile Valley of Egypt. Radiocarbon dating suggests that plants and animals were being domesticated at several

EXAMPLES OF IMPROVEMENT IN SOME IMPORTANT CROP PLANTS[3]

The following examples illustrate patterns in plant improvement, beginning with: (1) the harvest of crops from wild plants by primitive humans, followed by (1) selection of superior types from prehistoric eras to the present time, and going on to (3) modern methods of plant breeding that can dramatically increase crop yield and quality by applying genetic principles and gene transfer to developing improved cultivars. It should be realized that the present, improved cultivars of important crops such as wheat, corn, rice, potato, sweet potato, and all fruit crops have been so adapted to conform to human cultural practices that they all now completely depend on our care for their continued existence.

Grains and Vegetable Crops

Wheat (Triticum aestivum and T. turgidum Durum group)

Wheat is the most widely cultivated plant in the world today, the chief cereal, and is used worldwide for making bread. Present wheats evolved from wild wheatlike grass plants found and cultivated by ancient humans in the Near East region about 7000 BCE. Native wheatlike plants can still be found in this area. Even in early prehistoric times, wheat probably improved naturally by spontaneous hybridizations, by chromosome doubling, and by mutations to increase fertility. Wheat species occur in a series with increasing chromosome numbers

(polyploidy): First is the small primitive diploid einkorn wheat (7 pairs of chromosomes); second is the much larger tetraploid emmer wheat (14 pairs of chromosomes); and third is the hexaploid bread wheats (21 pairs of chromosomes), the ones grown today. Humans probably had no role in this early advancement of wheat by polyploidy. From the Near East, these early wheat forms were taken into ancient Egypt, the Balkans, and central Europe. The Spanish brought wheat to the Americas; eventually, the United States, Canada, and Argentina became the world's largest wheat producers. A chance introduction of "Turkey Red" wheat into central Kansas, by a small group of Mennonite immigrants from Russia in 1873, established the basis for the tremendous hard red winter wheat industry of the central Great Plains area of the United States.

The two major wheat species today are Triticum aestivum, used for flour in making breads and pastries, and T. turgidum (Durum group), used for products such as macaroni, spaghetti, and noodles. In the twentieth century, plant breeders, through hybridization and selection, have produced perhaps a thousand cultivars of bread wheat alone designed for certain climates, high productivity, special milling and cooking properties, and particularly disease resistance. Wheat cultivars resistant to the devastating stem rust disease must continually be developed to cope with the mutating stem rust pathogen.

Today's plant breeders, too, have developed dwarf forms of wheat, which can produce high seed yields without falling over (lodging) when heavily fertilized. Some of these new dwarf cultivars were developed by Norman E. Borlaug, working at the Rockefeller Foundation's International Maize and Wheat Improvement Center in Mexico. Borlaug was awarded the Nobel Peace Prize in 1970 for his work. Certain of these cultivars have been so successful with fertilizers and irrigation in Pakistan and India that both countries have become exporters rather than importers of wheat.

Wheat plants are self-pollinated, allowing farmers to save their seeds for future planting. Fj hybrid wheat for increased plant vigor and yields has not been developed to the extent it has with corn, owing to difficulties arising from the wheat's flower structure. Wheat has perfect (bisexual) flowers, making cross pollination difficult, whereas corn has the male and female flowers separate on the same plant and is cross-pollinated easily.

Corn (Zea mays)

Corn (or maize) originated in the New World about 5000 to 6000 BCE, but its earliest history is still a mystery. Maize is known only as a domesticated plant.

There is no wild form except, apparently, teosinte, a close relative. The economic life of the ancient American civilizations—the Aztecs, Mayas, and Incas—depended on corn. At the time of Columbus's expeditions to the New World, corn was being grown by Indian tribes from Canada to Chile. Corn probably originated in several places in both Mexico and South America. An early form of corn is still growing in South America (Fig. 7-12).

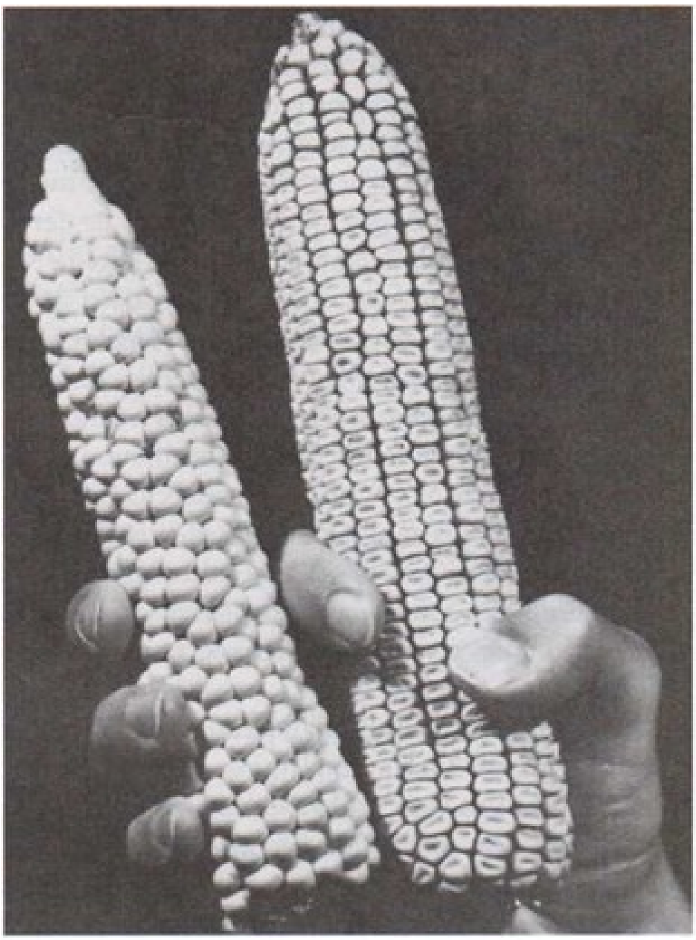

Figure 7-12

Improvement in corn (maize) from a primitive type (left) *still growing on the eastern slope of the Andes mountains in South America, to modern hybrid corn* (right). *The primitive type corn contains a valuable trait—multiple-aleurone layers in the grain—that is being transferred by plant breeders to modern dent corn. This example illustrates the need for maintaining the germplasm of seemingly worthless plant types.* Source: USDA.

Several hypotheses have been advanced to explain the origin of corn: (1) it developed from "pod corn," a type in which each individual kernel is enclosed in floral bracts—as in the other cereals; (2) it originated from teosinte, corn's closest relative, by gradual selection under the influence of harvesting by humans; (3) corn, teosinte, and Tripsacum (a perennial grass) descended along independent lines directly from a common ancestor; or (4) there is the tripartite theory that (a) cultivated corn originated from pod corn, (b) teosinte is a derivative of a hybrid of corn and Tripsacum, (c) the majority of modern corn cultivars are the product of an admixture with teosinte or Tripsacum, or both.

Corn, even today, is an extremely variable species, from the color of the grains to the size and shape of the grains and ears (Fig. 7-12). Corn mutates easily, forming new types. The Native Americans in Mexico must have made considerable conscious selections of corn for so many types to be introduced to European agriculture following the New World explorations.

The development of hybrid corn in the 1930s is one of the outstanding achievements of modern agriculture. High-yielding Fj corn hybrids were developed for different climatic zones. In 1935, percent of the corn planted in the United States was of the hybrid type. By 1970, almost all corn produced in the United States was of the hybrid type. The planting of hybrid cultivars, along with fertilizers, irrigation, and mechanization, dramatically improved production. Corn is now one of the world's chief food crops for both humans and domesticated animals.

The latest development in corn improvement is bioengineered germplasm, including the Bt® corn for corn borer resistance, and the Roundup Ready® and Liberty Link® corn for herbicide tolerance. Specialty corns—such as white, waxy, hard endosperm food grade, high oil, nutritionally enhanced, high amylase and high extractable starch corn—are being developed. Ethanol production from high-starch corn as a replacement for some petroleum fuels has become a major use of corn.

Rice (Oryza sativa)

Rice is the basic food for more than half the world's population and one of the oldest cultivated crops. It is believed to have originated in southeast Asia about years ago, or even earlier, and it spread to Europe and Japan by the second century BCE.

There are about twenty-five species of Oryza, but O. perennis, widely distributed throughout the tropics, is probably the one from which cultivated rice was developed. Primitive humans most likely collected seeds and cultivated the wild types. During cultivation of rice, mutations, plus hybridization with other Oryza species, probably occurred, leading to improved forms with larger grains and nonshattering fruit stalks. Rice was first cultivated in America along the coast of South Carolina about 1685. Four rice experiment stations were established by the US government in the early 1900s. Breeding work at US government rice experiment stations has resulted in many superior cultivars being introduced to the rice-growing areas of the United States.

Much of the rice harvested in Asia was from old, unproductive types grown under primitive conditions. The Ford and Rockefeller Foundations established the International Rice Research Institution (IRRI) in the Philippines in 1962, bringing together scientists from eastern and western nations for the purpose of improving rice culture. This group of researchers developed new early, high-yielding dwarf cultivars by hybridization that did not lodge when heavily fertilized and allowed up to three crops to be grown in the same field each year. These cultivars dramatically increased yields, and some are highly resistant to insects and disease pathogens native to the Far East, South America, and Africa. Hybrid rice is now commonly grown in China and other parts of Southeast Asia.

A genetically engineered rice has been developed that produces beta-carotene in its kernels, giving the rice a yellow color. Adding beta-carotene, a precursor for vitamin A (which is essential for human health), to rice increases the nutritional value of the rice significantly. It is predicted that the modified rice would help prevent blindness in millions of children in developing countries where rice is a dietary staple.

Soybean (Glycine max)

The soybean has risen spectacularly to prominence in the United States with an increase in production from metric tons (5 million bushels) in 1925 to about 75 million tons (3 billion bushels) in 2008. This great increase is due, in part, to the availability of more productive, disease-resistant cultivars. From about 1910 to 1950, large numbers of new strains and seed lots of soybeans were introduced into the United States from the Orient, its native home, largely by United States Department of Agriculture (USDA) plant explorers. From these diverse sources of germplasm, hybridization programs developed many superior cultivars. Much of this work was done at the USDA Regional Soybean Laboratory at Urbana, Illinois, in cooperation with various midwestern agricultural experiment stations. These cultivars give high yields, proper bean maturity for the particular area, strong erect plants that hold their seeds until harvest, and high disease resistance and bean quality. The soybean is particularly well adapted to the United States' Midwest corn belt and the southeastern states, which together account for about 40 percent of the world's soybean production (2008 data).

Sugar Beet (Beta vulgaris)

The modern sugar beet is a plant developed entirely by human efforts in plant breeding. It is our only major food crop that was not grown in some primitive form in ancient times. It was developed only about 250 years ago in Europe as a source of sugar to compete with the then very expensive cane sugar. Sugar beets and sugar cane contain the same kind of sugar. Breeding and selection increased the sugar content in the root from about 2 percent to about 16 to 20 percent.

In the early part of the nineteenth century, Napoleon encouraged the development and production of the sugar beet industry in France to free that country from the British monopoly on cane sugar. By the end of the nineteenth century, sugar beets were being grown in North America, and they have now become an important temperate zone crop in many areas of the United States and southern Canada, and even more so in other parts of the world. All production phases are now completely mechanized, permitting the sugar beet to compete favorably with the tropical sugar cane plant. To maintain profitable production, however, plant breeders have had to continue to develop sugar beet cultivars resistant to virus and fungus diseases.

Potato (Solanum tuberosum)

Potatoes are one of the big four crops that feed the world's population. Wild potato species are widespread in South America, particularly in the Andes Mountain region. Potatoes were probably cultivated by primitive peoples in this area more than 4,000 years ago, but they became a more productive crop over the years with selection of superior types. The potato was cultivated over the length of the Andes Mountain area at the time the Spanish explorers arrived. About 1575, they carried it back to the European continent, where today 90 percent of the world's potato crop is grown.

The potato plant produces pink, white, or blue flowers that develop into small green berries containing seeds. The seeds, when planted, produce new types of potato plants much different from the parent plant and from each other in many respects. In the early days of potato culture, the South American Indians undoubtedly selected superior plant types resulting from natural crosses. Once one single such superior plant was obtained, it could be perpetuated and increased in great numbers as a clone by tuber division. Some of these superior selections propagated by vegetative methods over the years became commercially successful cultivars. It was noted, however, that certain of these cultivars would degenerate after many generations of such asexual propagation and yield only weak unproductive plants. It was observed, too, that sowing seeds from such plants gave progeny plants with changed characteristics, including renewed vigor and productivity. It is now known that these clonal cultivars had become infected with viruses that passed along through the tubers to the new plants generation after generation. Such viruses did not pass through the seed to the new seedling plant, so that its growth was no longer inhibited by the virus.

In modern commercial potato growing however, pieces of tubers called seed tubers or seed potatoes are planted to maintain clonal uniformity. Seed potatoes are produced under carefully observed conditions in regions where any viruses can readily be detected and the infected stock discarded. Growers who plant only "certified" stock can be reasonably sure that their fields will not be infected with viruses or other pathogens and will be true to type. In the United States, certified "seed" potatoes are produced by commercial growers in the northern states and are strictly inspected by state government agencies. This is also true for many other, but not all, countries.

Many potato cultivars now being grown have been developed by plant breeders who have introduced superior characteristics into an existing cultivar. An example is resistance to Phytophthora infestans (late blight)—from Solanum demissum, a wild potato species, obtained from collections in Mexico. Many cultivars are being grown today for different purposes and for different climatic zones. New cultivars are constantly being introduced by plant breeders and older ones are being discarded.

Tomato (Lycopersicon esculentum)

The cultivated tomato originated from wild forms in the Peru-Ecuador-Bolivia area of the Andes Mountains in South America. Prehistoric Indians carried it to Central America and Mexico. Early explorers introduced the tomato to Europe about 1550, and it was brought back west, to the Carolinas in North America, about 1710. Thomas Jefferson grew tomatoes on his plantation around 1780. In those days, most people considered the tomato poisonous, but in the United States it started gaining acceptance as a food plant about 1825. The early Indians undoubtedly improved the tomato by planting seeds taken only from the best fruits on the most productive plants. This selection process continued in the early days of tomato culture in Europe and the United States. Early cultivars introduced by US seed companies were 'Stone' and 'Globe' in 1870. In the early 1900s, the USDA and the state experiment

stations began breeding tomato cultivars to include specific characteristics. 'Marglobe' was introduced by the USDA in 1925 and 'Rutgers' by New Jersey in 1934. Some tomato cultivars, more recently introduced, carry resistance to fusarium wilt, verticillium wilt, and nematodes. Cultivars developed especially for machine harvesting have firm-fleshed fruits that all ripen at one time. Vigorous, highly productive Fj hybrids, marketed both as seeds and as bedding plants, are recent developments by seed companies.

Fruit Crops

The major fruit crops are all heterozygous. They do not "come true" when propagated by seed, so vegetative propagation must be used to maintain an improved seedling selection. In ancient times, most kinds of fruit—other than those very easily propagated vegeta- tively, such as bananas, grapes, figs, pomegranates, and olives—were probably seed propagated and the variability in offspring accepted by farmers. Later, however, as more sophisticated methods of vegetative propagation were developed, such as budding and grafting, it would have been found that certain superior individual fruit plants could be maintained and increased by these methods. Nevertheless, considerable seed propagation of fruit species was undoubtedly practiced in the early days of fruit growing.

Apple (Malus pumila)

The early US colonists planted many seedling apple trees probably because it was easier to bring seeds taken from their favorite apple trees in their native homes rather than material for grafting. As a result, they continued to increase their apple orchards by planting seedlings. In these early days, much of the apple crop was preserved as cider, for which fruit from seedling trees was quite satisfactory. Certain individual seedling trees, no doubt, were much superior to the others and formed the starting point for vegetative propagation and the origin of the many hundreds of apple cultivars grown in the United States up to the early part of the twentieth century. These numbers dwindled, however, until the 1980s, when only fifteen cultivars accounted for over 90 percent of the apples produced in the United States. Important cultivars are 'Delicious,' 'Golden Delicious,' 'McIntosh,' 'Rome Beauty,' 'Jonathan,' 'Winesap,' 'York,' 'Stayman,' 'Cortland,' and 'Granny Smith.' Although apple breeding programs have been conducted by the USDA and by some state agricultural experiment stations, all the major apple cultivars now being grown originated as chance seedlings many

years ago. For example, the 'McIntosh' apple was found growing as a seedling tree near Dundela, Ontario, Canada by John McIntosh in 1796. The 'Delicious' apple started as a single chance seedling near Peru, Iowa, about 1870. The 'Golden Delicious' also originated as a chance seedling in Cass County, West Virginia, about 1910. Most of the preceding cultivars remain popular, but more have been added, among them ‘Jonagold,’ ‘Fuji,’ ‘Gala,’ and ‘Braeburn.

Pear (Pyrus communis)

In pears, too, cultivars originating as chance seedlings have dominated the markets. The ‘Bartlett’ (Williams Bon Chretien) originated in England as a chance seedling in 1796 and has been the world’s leading pear cultivar ever since. Other leading pear cultivars in the United States, such as ‘Beurre d’Anjou’ and ‘Beurre Bose,’ originated in Belgium as open-pollinated seedlings of cultivars then grown there. No pear cultivar from a controlled breeding program in the United States has become commercially important, although European pear breeders have developed several superior cultivars that produce well in France, Italy, and Belgium.

Peach and Nectarine (Prunis persica)

In contrast to the apples and pears, the important peach and nectarine cultivars grown today are the products of public and private plant breeding programs. Plant breeders have provided the consuming public with truly outstanding peaches and nectarines, in contrast to the small-fruited, nonproductive cultivars of earlier days that got their start as chance seedlings.

Strawberry (Fragaria x Ananassa)

Today’s garden strawberry first originated in France about 1720 as a natural hybrid between two native American Fragaria species. From this and subsequent hybridizations, a number of cultivar selections were made and maintained vegetatively by runners in the early days of strawberry culture in Europe. However, many of these early cultivars were susceptible to viruses, verticillium wilt, and other diseases and were low in productivity, so that around 1945 the entire US strawberry industry was falling into a precarious position.

Since World War II, a parade of new strawberry cultivars has been replacing older ones, coming from USDA and several state strawberry breeding programs and from similar programs in other countries. New cultivars have been developed for specific climatic regions and

for characteristics such as adaptability of fruits to be used for freezing or for fresh shipping, resistance of plants to viruses and fungi and to winter cold, fruit appearance and flavor, and extended fruit-producing period.

PLANT IMPROVEMENT PROGRAMS

From the time of Neolithic humans up to the early 1900s, sexual plant improvement mostly consisted of selecting seeds from those individual plants in a mixed population that had the desired characteristics. The seed was planted and from that population seeds were again taken from the most desirable plants, and so on. While improvements resulted, this method offered no way to transfer desirable characteristics from one line to another.

Evolution and Darwinism Charles Darwin, the great English naturalist working in the middle of the nineteenth century, provided scientific explanations of how evolution occurred, published in his monumental work (1859), On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life. Darwin's concept of evolution, generally accepted today, is:

Variation exists in an initial population of plants or animals.

Environmental stresses place certain individuals at an advantage.

Because certain individuals survive and reproduce more successfully, they leave more offspring, which then carry the same genetic traits.

The abundance of the advantageous traits increases in this way in every generation, but variation still persists.

In Darwin's time, nothing was scientifically known about heredity. Darwin, in his proposals, had great difficulty in accounting for a sufficient supply of variation. But the discoveries by the Austrian monk Gregor Mendel, in the 1860s, demonstrated the genetic mode of plant inheritance and developed the foundation for the science of genetics. His published works lay unappreciated in an obscure journal for thirty-four years, but in 1900 his papers were discovered independently by three European botanists. The discoveries of Mendel provided exactly the mechanisms needed by Darwin, and removed his difficulties in explaining variation. The integration of Darwinian selection and Mendelian genetics are now generally accepted as the proper explanation of evolution.

Many crop scientists have discovered patterns of evolution in various crop genera, primarily from two points of view: (1) relationships between crops and their related wild and weedy species, and (2) adaptive variation in geographical races. Plant breeders have made fascinating and useful applications of this knowledge in terms of collecting and utilizing many germplasm resources. In fact, all of the processes of evolution in native plants have direct analogues in breeding methods. For example, induced mutations and hybridization follow natural sources of novel variation; selection and cycles of recombination in hybrid materials provide the genetic changes in both natural and breeders' populations.

Based on Mendel's work and utilizing the expertise of trained geneticists, modern breeding programs have produced an array of new cultivars for many crops. These have been bred for characteristics such as resistance to disease, insects, and cold, and for productivity, flavor, and nutritive value. Today's breeding programs have been called directed and accelerated evolution.

Since the start of the twentieth century, public and private plant breeding programs have had a tremendous beneficial impact on our food supply and range of ornamental plants. These programs have produced a great many new superior cultivars for almost all cereal, vegetable, forage, fruit, and ornamental crops. The USDA and most state agricultural experiment stations in the United States maintain such programs. Most other countries also have plant breeding programs, often specializing in certain crops. Private plant breeding has mostly been done by seed companies producing new agronomic, vegetable, and flower cultivars.

Innovations by plant breeders include the development of Fj hybrid corn and new vegetable and flower cultivars. Most of the new vegetable and flower lines are far superior to previous cultivars in vigor and in insect and disease resistance; the new vegetable cultivars are also superior in flavor, appearance, and productivity.

By developing plants that show strong resistance to insects and disease, plant breeders are reducing the need for insecticides and fungicides. This, in the long run, would be the best method of pest control. For example, potato cultivars have been developed that are resistant to the late blight disease (Phytophthora infes- tans), which was responsible for the nineteenth-century Irish potato famine. Other potato cultivars have been developed that are resistant to the golden nematode, permitting potatoes to be produced in soils infested by these worms without expensive soil fumigation. Wheat breeders must continually develop new wheat cultivars resistant to stem rust (Puccinia graminis tritici) because this fungus continually changes to attack formerly resistant cultivars.

Plant breeders have a useful procedure for obtaining improved plant forms by spontaneous or induced mutations resulting from chromosome or gene changes. These changes can be induced by chemical treatment with colchicine or by irradiation with gamma or X-rays.

In one instance, plant breeders have gone beyond just improving native plants. They have created a new humanmade cereal, triticale, by hybridizing the ancient grains, wheat and rye. The name triticale derives from the generic names of these two grains: Tritium and Secale. The hybrid combines the high yield and protein content of wheat with the winter hardiness of rye. The triticale plant is disease-resistant and thrives in some unfavorable soils and climates.

THE MECHANISM OF EVOLUTION

Evolution, as accepted today, can be explained as follows:

Genes, in the chromosomes, are largely responsible for the structure, metabolism, and development of plants and animals.

The complement of genes does not remain constant because mutations occur that modify the metabolism and structure of the individuals that contain them.

Mutations, which may cause considerable change, may kill or greatly weaken the plant because they can upset the equilibriums that exist between the plant and its environment.

Hybrids differ from their parents because of the resulting new combinations of genes.

If the variants, as developing from mutations or by hybridization, are better adapted to the existing environment than the parent plants, then the parent plants may be replaced by the new forms.

As the earth's surface and climate change, or as plants' habitat may be changed in other ways, those plants best adapted to the new environment replace those poorly adapted.

Evolution thus results from slow changes in the environment, variations occurring in plants and animals, and adjustments taking place between the changes in the environment and changes in the living organisms.

SEARCHING FOR AND MAINTAINING NEW GERMPLASM

There is no assurance that we are at present cultivating all the useful food and ornamental plants in existence on earth, or that all the germplasm containing useful genes has been found. Germplasm is the protoplasm of the sexual reproductive cells containing the units of heredity (chromosomes and genes). Plant explorers have long roamed the world and they continue their searches. They have found many plants that have subsequently made a major impact on the world's agriculture, often in different parts of the world from the plants' native regions. Accessible plants have always been moved about over the world by explorers on land and sea, armies, immigrants, and travelers. Plants moved into a new region often perform much better than they did in their original home. For example, the coffee plant (Coffea arabica) is native to the Ethiopian area of eastern Africa. It never developed into much of a crop there, but when moved to Brazil and Colombia in South America, the coffee tree prospered so well that these countries now produce the bulk of the world's coffee supply.

Several prominent plant explorers have contributed much to the wealth of available plant materials. Many of the early plant collecting trips were less than successful because the plants did not survive the long trip back. A London physician who was an amateur horticulturist, Nathanial Ward, invented the Wardian case early in the 1800s. The case was a small glass-enclosed box containing soil in the bottom. Plants kept in the Wardian case could survive long sea voyages, permitting the importation of species never before received alive. Large, magnificent, ornate glasshouses were built in England about this time to house the many tropical and subtropical plants brought back by the plant hunters.

Many plant explorers from the United States brought back plants that would later be the foundation for several crops grown in the United States. Colonel Agoston Haraszthy (wine grapes), N. E. Hansen (cold-resistant fruit and cereal plants), Mark Carleton (hard red winter wheat), David Fairchild, Frank Meyer, and others brought back many different species that have become the genetic basis for many of our edible and ornamental crops.

Plant-collecting trips to the native homes of certain desirable plant types are still being made by plant explorers. Plant explorers may be looking for an entirely new plant species to serve as a crop in a particular climatic region of their own country. Safflower came to the northern Great Plains of the United States this way, and it has proven most profitable. Plant explorers may also be searching for new germplasm for existing crops. Closely related types can be used by plant breeders to introduce, for example, genes for insect or disease resistance or improved vigor or quality into cultivars already being grown.

International Conventions Relating to Plant Genetic Resources, Conservation, and Utilization

Currently, two international conventions relating to the promotion of conservation and protection of biological diversity are in effect. The Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), which came into operation in 1975, helps to ensure that international trade in specimens of wild animals and plants does not threaten their survival. CITES has about 28,500 species of plants listed under protec-tion, and this list is growing as more and more plant habitats are damaged. For example, many of the orchids are on this list. Further information on CITES can be found at http://www.cites.org/. The second is the Convention on Biological Diversity (CBD) which is an outcome of the 1992 United Nations Environment Programme's Earth Summit in Rio de Janeiro, Brazil, and became effective in 1993. Its objectives are the conservation of biological diversity, the sustainable use of its components and the fair and equitable sharing of the benefits arising out of the utilization of genetic resources, including appropriate access to genetic resources and appropriate transfer of relevant technologies, taking into account all rights over those resources and to technologies, and appropriate funding.

This also means that plant germplasm becomes a country's natural resource, and the use of a germplasm by another country now requires prior official consents, collection permits, and specific material transfer agreements, including benefit sharing when a germplasm is commercialized. Annually, an estimated $500 to $800 billion of genetic resources derived products is traded globally. In the past, plant germplasm was shared and exploited globally as common properties of humankind. Thus, CBD can be seen as a response of germplasm-rich countries to the intellectual property rights protection systems in place in the world to protect developed germplasm. The International Treaty on Plant Generic Resources for Food and Agriculture (ITPGRFA), a Food and Agriculture Organization (FAO) of the United Nations initiative, is the first endeavor to create a common multilateral agreement to ensure the conservation of sixty-four food and feed crops in harmony with CBD for sustainable agriculture and food security. It covers approaches in germplasm exploration and conservation, measures to induce sustainable germplasm uses, recommendations on international cooperation, measures to uphold farmers' rights, sovereign rights of contracting states, a standard material transfer agreement, benefit sharing, and so on. To implement ITPGRFA, a $260 million endowment-the Global Crop Diversity Trust - was instituted to provide the necessary funds for protect-ing and conserving the most threatened and valuable collections of crop diversity. Detailed information on CBD is available at http://www.cbd.int/

Moving plant materials about the world can also introduce devastating insect or disease pests into a country where they have never before appeared. For example, the chestnut blight fungus (Endotbia parasitica) was inadvertently introduced on imported plant material to the New York area from the Orient in the late 1800s. By about 1935, this fungus had practically eliminated all varieties of the beautiful native American chestnut trees (Castanea dentata) from the eastern United States. To guard against the introduction of such pests, most countries have set up elaborate inspection, fumigation, and quarantine procedures. The 1997 International Plant Protection Convention (https://www.ippc.int/), an international treaty under the auspice of FAO and signed by 127 governments in 2004, helps to harmonize and standardize the rules and procedures, and agreements in plant quarantine to prevent the spread and introduction of pests of plants and plant products, and to promote appropriate measures for their control in the world. Where appropriate, storage places, packaging, conveyances, containers, soil, and any other organism, object, or material capable of harboring or spreading plant pests are included, particularly where international transportation is involved. As a result, regional plant protection organizations, for example, the North American Plant Protection Organizations (NAPPO), were established to promote the development and use of relevant international standards for phytosanitary measures, and to encourage interregional cooperation in promoting harmonized phytosanitary measures for controlling pests and in preventing their spread and or introduction.

Plant material can be introduced as seeds, bulbs or corms, rooted cuttings, or as scions or budwood for grafting or budding onto related growing plants. Seeds are the easiest to ship and pose the least danger of carry-ing pathogens. Rooted plant parts with soil particles around the roots are particularly suspect because the soil may contain nematodes or soil-borne diseases.

Vegetative plant material coming into the United States is usually fumigated, then held under post-entry quarantine for as long as two years before distribution to nurseries is permitted.

Shipment of plant material is now easy and highly successful because of specialized packing materials, refrigeration, and frequent worldwide air flights. This contrasts to earlier days when only slow ship transport, often through hot tropical seas, was possible.

Preservation of Desirable Germplasm

A concerted worldwide effort is needed to ensure the survival of the earth's endangered plant species and thus preserve genetic diversity. International germplasm networks operate under the auspices of the Consultative Group on International Agricultural Research (CGIAR) and the World Conservation Union (IUCN). These networks interact with, and are supplemented by, many national seed banks and agricultural centers. In 1998, FAO estimated that 6.1 million accessions of primary food, forage, and industrial crops had been collected and conserved globally. Such gene pools are needed for developing improved crops in the future, for introducing ben-eficial genes into existing crops from close relatives, for maintaining attractive plants and trees valued for their aesthetic purposes, and for keeping plants intact as part of ecosystems where their presence is necessary to the survival of other plant and animal species. The genetic diversity of plants, as well as animals and microbes, is of fundamental importance to our survival on earth. Food and other agricultural crops are derived from the genetic diversity of natural plant populations.

To help prevent eradication of many plant species, the US Congress in 1973 passed the Endangered Species Act, which directed the Smithsonian Institution to prepare a list of endangered plant species and to rec-ommend measures for saving them. As many as one in ten plant species is now extinct or endangered because of the encroachment of agricultural operations, the removal of rare plants by plant collectors, and the general destruction of vegetation from various causes. Such endangered germplasm can be saved and stored for future use as seeds or as living plants in special protected locations.

The CGIAR international research centers, such as the International Rice Research Institute (IRRI) in the Philippines and the International Maize and Wheat Improvement Center (CIMMYT) in Mexico, have assem-bled one of the most comprehensive collections of our major food and forage crops. This endeavor is coordinated by its specialized plant germplasm conservation center, the International Plant Genetic Resources Institute (IPGRI). IPGRI also provides technical leadership to national gene bank programs. The IUCN has the mission "to influence, encourage and assist societies throughout the world to conserve the integrity and diversity of nature and to ensure that any use of natural resources is equitable and ecologically sustainable.” The focus of IUCN is the conservation of the whole ecosystem and the total biodiversity. It monitors the state of the world’s species in the IUCN Red List of threatened and endangered species (http://www.redlist.org/). This list is adopted globally by national governments, nongovernmental organizations, and scientific institutions in their biodiversity conservation efforts. An estimated 60,000 to plant species, representing about one-third of the world’s plants, are currently threatened or facing extinction in their native habitats. In 2002, the Global Strategy for Plant Conservation (http://www.cbd.int/ gspc/) was adopted by CBD and in 2004, the Global

Partnership for Plant Conservation (http://www.bgci .org.uk/files/2/786/GlobalPartnershipstatement.doc), consisting of international and national agencies and organizations active in plant conservation, was established to support the worldwide implementation of the strategy. The Botanic Gardens Conservation International (http://www.bgci.org/), founded in 1987, is one of such organizations that is taking the forefront in this attempt. Over 500 member institutions in 112 countries are working together to implement a worldwide botanic gardens conservation strategy for plant conservation. For example, the Royal Botanic Gardens, Kew, England, has established the collaborative Millennium Seed Bank Project to collect and conserve 24,000 plant species from around the world and protect them against extinction.

In the United States, the National Plant Germplasm System (NPGS) is a coordinated network of four main plant introduction stations in four geographic regions of the country, a long-term storage gene bank in Fort Collins, Colorado, and about twenty-three repositories and active collection sites. The functions of the repositories and active sites are to collect, introduce, maintain, characterize, evaluate, catalog, and distribute plant germplasm. Financial support comes from the USDA and from state agricultural experiment stations as well as from commercial plant breeding and seed trade organizations. The general mission of the system is to provide plant scientists with the germplasm needed to carry out their work, for example, in breeding new cultivars resistant to certain insects, diseases, smog, or high soil salinity. In 2002, more than 450,000 accessions are in conservation.

The activities of the National Plant Germplasm System are:

Introduction of plant materials into useful scientific channels is done by planned foreign and domestic exploration trips, by exchanges with foreign agencies, or by traveling scientists. There may also be useful domestic germplasm that should be maintained—for example, mutations, species hybrids, or germplasm resistant to a certain insect or disease—and may be valuable for future crop development. These, along with introduced foreign material, are eligible to enter the National Germplasm System.

Maintenance of this potentially valuable germplasm for future research programs is the responsibility of the regional and interregional plant introduction stations, the National Center for Genetic Resources Preservation, and the curators of collections of specific crops.

Characterization and evaluation of the plant genetic resources is done by initial screening and subsequent tests in the field, greenhouse, and laboratory by cooperating state, federal, and private scientists.

Distribution of plant germplasm is made free of charge to all qualified scientists and institutions requesting it, in sufficient amounts to enable them to initiate their research program.

The decentralized system is held together by a common web-based database management system, the Germplasm Resources Information Network (GRIN), which helps NPGS curators to handle both the plant and store inventory data. Another notable component of NPGS is about forty crop germplasm committees, which are made up of crop specific experts for each crop from USDA, universities, public institutions, and industry to advise on policy and coordinating activities to meet the immediate and long-term national goals of agriculture in the United States.

BROADENING THE BASE OF AGRICULTURAL PRODUCTION

The world's peoples are largely fed today by only about twenty crops. Reliance on so few crops could lead to a catastrophic famine if but a few of them were obliterated by insect or disease attacks or by climatic changes. The ravage of U.S. corn plantings by the corn blight disease in 1970 is an example of such a possibility.

In an attempt to broaden the base of agricultural plants in the tropics and to promote interest in neglected but seemingly useful tropical plants with economic potential, the U.S. National Academy of Science promoted a compilation of plants nominated by plant scientists around the world and published an account of thirty-six plants selected from the 400 proposed. Each plant was described along with its special requirements, research needs, selected readings, research contacts, and germplasm sources.

All thirty-six plants were thought to have considerable potential, but most have not been cultivated out of their own limited region of origin. Among the cereals, for example, the report cited an almost completely neglected grain species in the genus Amaranthus, native to Central America, that has very high levels of protein and the essential amino acid lysine, which is usually deficient in plant proteins. Among the vegetables studied, the wax gourd (Benicasa bispida) gives three crops a year of a large melonlike fruit that can be stored for twelve months without refrigeration.

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*8

Soil, Water, and Fertility Management

key learning concepts

After studying this chapter, you should be able to:

- Explain why and how land is prepared for growing plants.
- Describe how improper soil handling degrades soil and how improper handling improves soil.
- Explain the practices that improve degraded soil and prevent degradation and conserve soil.
- Discuss the basic principles and components of irrigation and drainage.
- Describe how plant nutrition is managed through fertility practices.

In earlier chapters you saw why soil, water, and nutrients are required for plant growth. Now you will learn how they can be managed to improve and manipulate the growth of plants using ecologically sound practices. Indeed, soil, water, and fertility management cannot be separated into distinct components. They are very tightly integrated and what you do in one area can dramatically impact the other two areas. When you choose the practices you will use with soil, water, and fertility management, you will have to consider these close relationships.

LAND PREPARATION

The first step in growing plants is preparing the soil where the plants are to be grown. Major purposes of land preparation are to:

1. Level the land where needed.
2. Incorporate crop residues, green manure, and cover crops.

3. Improve and maintain the tilth of the soil (tilth is a subjective term for the physical condition of the soil with respect to its capability to provide a good environment—aeration and porosity—for optimizing crop production)

4. Help control weeds, diseases, and insects.

5. Help control erosion where needed.

In general, tillage is defined as the mechanical manipulation of soil to provide a favorable environment for crop growth. Soil moisture condition at the time of tilling is a factor in the effectiveness of tillage. Unfavorable moisture conditions—too dry, too wet—will result in ineffective tillage and will damage soil structure. Effective tilling improves the moisture holding charac- teristics of the soil. Ideally, soils should hold enough water to maintain the plant for several days between irrigations yet allow enough air to reach the roots for sufficient root respiration. The "ideal" soil is often considered to consist of 50 percent solid and 50 percent open or pore space. Of the pore space, 50 percent is small enough to hold water by capillary force and 50 percent is large enough to drain by gravity.

Tillage is done with a wide variety of equipment and for various purposes. The soil should provide an environment conducive to rapid germination of seeds and good plant growth. For most crop plants, this means that the surface soil is loose and free of clods (Fig. 8-1).

The subsoil is permeable to air and water and has adequate drainage and aeration. It should not be water-logged or anaerobic (without oxygen).

Land Leveling

Land is leveled to permit water to flow and spread evenly over the soil surface without causing erosion. In considering the land's suitability for leveling, the land's productive capacity and the method of irrigation to be used are evaluated.

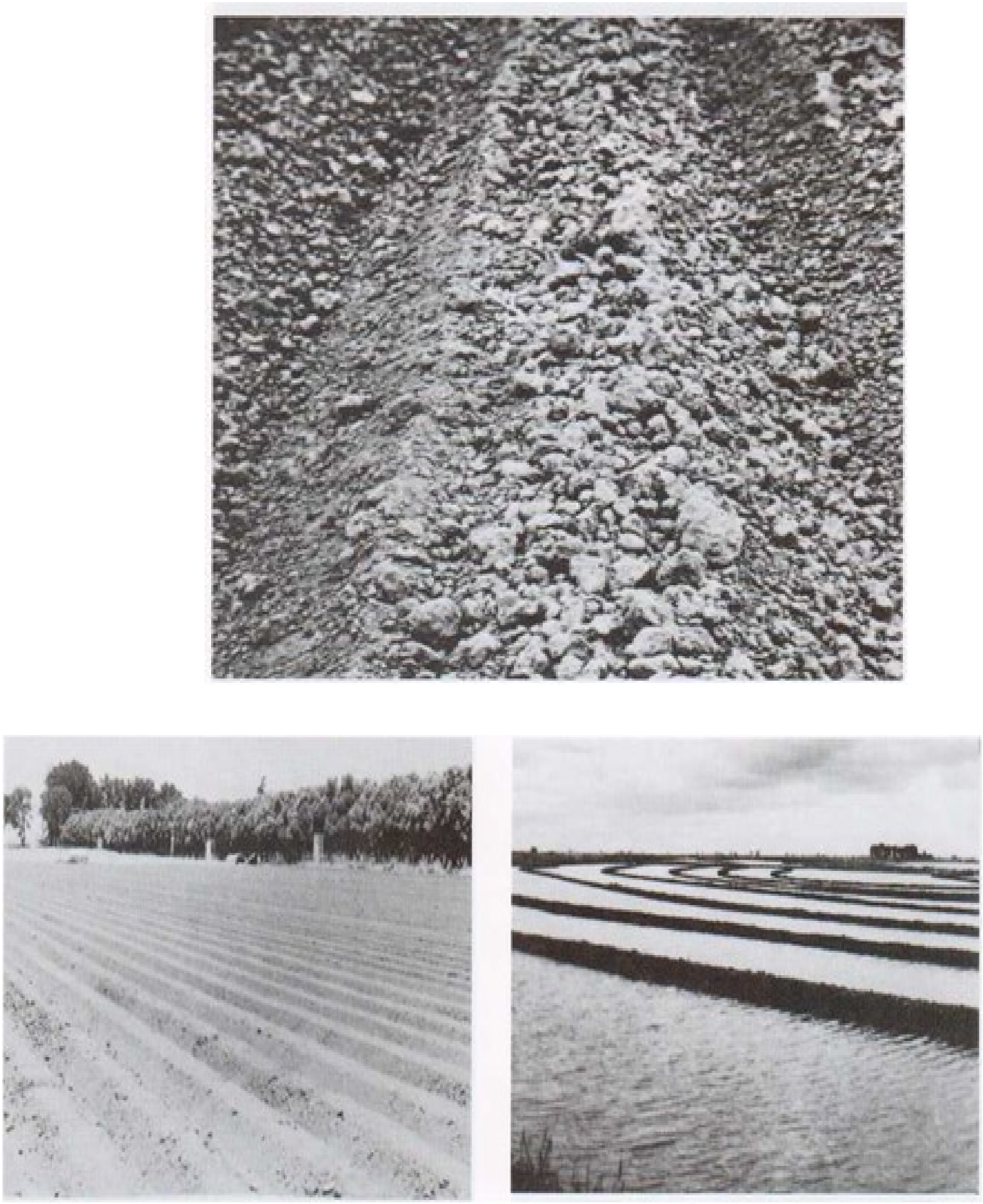

Figure 8-2

A rice field ready to be planted. The levees follow contour lines to allow uniform water depth within each paddy.

Source: USDA Natural Resource Conservation Service.

Figure 8-3

Heavy equipment such as tractors and implements can contribute to soil compaction especially when the soil is moist and the tires run over the same area several times.

Source: USDA-NRCS, http://photogallery.nrcs.usda.gov/

Irrigated land generally benefits from being level, especially if flood (Fig. 8-2) or furrow irrigation is used and row crops are grown. Land leveling can also be used to remove excess surface water from depressions that result in poorly drained fields. The use of GPS and laser technology is common when precision leveling is required. Heavy equipment may be necessary for leveling when the terrain is rough or soils are heavy (Fig. 8-3). Timing is important. Land should not be leveled when saturated or near saturation because leveling of wet soil subjects it to compaction.

Figure 8-4
A moldboard plow is used to turn the soil over and bury in surface vegetation.

Plowing

Often, the first step in land preparation after any necessary leveling is to plow the land. Plows invert the soil and bury the residues from the previous vegetation, but they often leave the soil in large linear lumps that must be reduced in size. When large amounts of residues are left on the field, they are often chopped with a disk or a rotary stalk cutter before plowing.

A farmer has the choice between two plow types, the moldboard or the disk plow, each adapted to certain soil characteristics. Moldboard plows range in size from a single moldboard, or bottom, to a gang (group) of plows that turns twelve furrows (twelve bottoms) simultaneously. Each moldboard shears and inverts a slice of so as it moves along, leaving the top of the slice at the bottom of the furrow (Fig. 8-4). Moldboard plows are used when the soil is sufficiently moist to allow the plow to pass through easily but not so wet as to cause the furrow slice to stick to the face of the moldboard and create a drag that requires excessive tractor power and causes poor results. The ideal moisture content for plowing loam soils is slightly less than field capacity.

Figure 8-5
Chisel plows dig a channel or trough through the soil.
Source: USDA-NRCS, http://photogallery.nrcs.usda.gov/

Figure 8-6
The disk plow accomplishes essentially the same objective as the moldboard plow. However, the disk plow can operate when soil conditions are either too wet or too dry for the moldboard plow. The disks rotate as the plow moves forward, rolling the furrow slice over.
Source: USDA-NRCS, http://photogallery.nrcs.usda.gov/

Two-way reversible plows (flip-over plows) are used to eliminate "dead" furrows (unfilled furrows). They are also used in hilly areas for contour plowing to reduce erosion and in irrigated areas where dead furrows hinder irrigation. These plows always throw the furrow slice in the same direction regardless of the direction the plow travels.

Chisel plows are primary tillage tools consisting of curved shanks spaced widely along a tool bar (Fig. 8-5). The shanks dig through the ground. They are normally operated at depths similar to those attained with moldboard plows, but they shatter rather than invert the soil in the plow layer. Chiseling can be done more quickly than moldboard plowing, disturbs the soil less, and leaves significant quantities of crop residue on the soil surface to provide erosion control. For these reasons, chisel plows are rapidly replacing moldboard plows as the primary tillage tool on many farms, particularly in the Midwest.

The disk plow (not to be confused with the disk harrow) consists of a series of large concave disks 60 to 75 cm (24 to 30 in.) in diameter that are set at an angle to the forward movement and cut into the soil while rotating as the plow moves forward (Fig. 8—6). There can be three to ten or more disks on a plow. Soil moisture conditions are less critical for disk plow operation.

Figure 8-7

A disk harrow cutting and covering crop residue near prior seedbed preparation. Source: Allis-Chalmers.

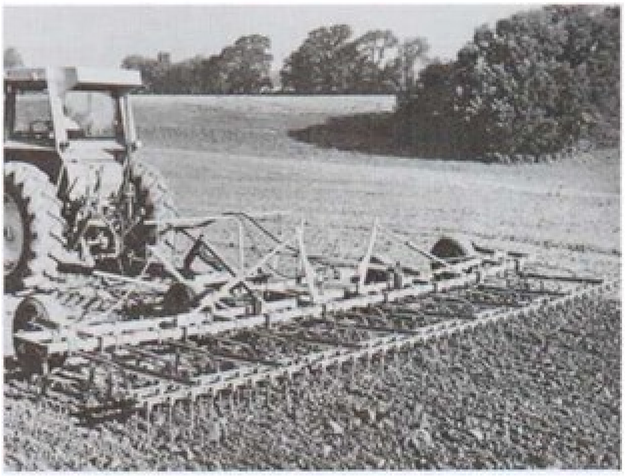

Figure 14-8

A spring-tooth harrow is sometimes used in seedbed preparation because it is effective in breaking up soil crusts, reducing clod sizes, and destroying small weeds. Source: Allis-Chalmers.

Disking

Disk harrows which are smaller in diameter than disk plows are used to reduce the size of larger soil clods by fracturing them with cleavage and pressure. Disking generally follows plowing, but under some conditions disking can substitute reasonably well for plowing.

half to the left. This forms a ridge of soil commonly about 20 to 25 cm (8 to 10 in.) high and of variable width at the base. Listers can be equipped with attachments to list, plant, and fertilize in one operation. Some farmers flatten the tops of the ridges with a roller, drag, or bed shaper before planting. For some crops at the same time the rows are listed, additional attachments lay irrigation lines and plastic or paper mulch on top of the beds (Fig. 8—9).

Cultivation

Cultivation is the tillage between seedling emergence and crop harvest. The main reason for cultivating is to control weeds, but other benefits are improved water

Figure 8-9

Irrigation lines under plastic mulch research plots. The irrigation lines can be seen ***as*** *faint stripes under the mulch. The raised objects in the beds are tensiometers to measure water content of the soil at various levels beneath the mulch. Source: Dennis Decoteau, The Pennsylvania State University.*

Figure 8-10

A multiple-row crop cultivator loosening soil and destroying weeds in this corn field. The enclosed driver cabs in modern tractors are air conditioned and many have CPS/GIS and other electronic devices to increase production efficiency and reduce environmental impact.

Source: USDA-NRCS, http.Y/photogallery .nrcs.usda.gov/

Figure 8-12

An example of a deep chisel (ripper) used to break deep compacted hardpans. This procedure is used only when justified because the high amount of energy required makes this an expensive operation. Source: William E. Wildman

infiltration and soil aeration on soils that crust, the conservation of soil moisture, loosening compacted soils, and in some cases help with insect control. Row- crop cultivators (Fig. 14-10), field cultivators, rotary hoes, and rototillers are types of cultivators as are handheld hoes.

Deep Tillage

Some farmers use deep tillage to improve problem soils especially when hardpans are present. Extra heavy equipment is used for deep tillage when the soil is dry. Different types include the slip plow (Fig. 14—11) and ripper or deep chisel (Fig. 14—12). The latter consists of one or several shanks that penetrate the soil from 60 to 120 cm (2 to 4 ft). It shatters hardpans best when the

Figure 8-11

The V-shaped blade of this slip plow is pulled horizontally well below the soil surface to break up hard soil layers.

Source: USDA Soil Conservation Service.

soil is dry. Deep tillage is expensive, and sometimes it does not materially increase crop yields. In established orchards, it can damage trees by severely cutting the roots. When deep tilling, the operator also has to be aware of drainage tile and any utility lines such as gas or electric that may be buried in the area.

Although the above practices were developed for field crops, the principles are applicable for most growing situations. Growers of vegetables and small fruits, landscapers, golf course superintendents and athletic field managers, nursery crop producers, all depend on working the land before growing their respective commodities. In these cases, the equipment they use is often modified for use on smaller areas or for very precise results, but the principles remain the same.

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*9

Forage Crops and Rangelands

Давид Баркерва Марк Сулс

key learning concepts

After reading this chapter, you should be able to:

- Describe the different types
- of forage and rangeland crops.
- Explain the principles of hay and silage growing, harvesting, and storage.
- Discuss rangeland ecology and the principles of rangeland management.
- Describe the diverse uses of rangelands.

Forage, browse, or herbage are the edible parts of plants, primarily the leaves and digestible stems that can be fed directly or following storage to livestock. Forage crops, pasture, meadows, prairie, grazing land, and range are a continuum of forage-producing grasslands (swards) that vary in characteristics such as their geographical location and intensity of production. Generically, all are termed grasslands and although they are usually dominated by grass (monocotyledonous) species, they also include dicotyledonous (legume and forb) species. Alfalfa is sometimes termed the queen of the forages. Forage crops and rangelands have unique and distinct characteristics compared to other crop systems:

1. Worldwide, more land is devoted to grasslands than to all other crops combined (8.4 vs. 3.7 billion acres) and totals 26.1 percent of the worlds land area (FAO statistics). Much of this land is too rocky, hilly, dry, or wet for growing other crops but is suitable for forage production (Fig. 18—1). Grasslands can also have environmental benefits such as

stabilizing land against erosion (Fig. 9-2), carbon sequestration, and providing wildlife habitat.

2. Most forage and rangeland species are perennial plants, and part of year-round production systems. Usually these production systems are required to support livestock for successive years. To be sustainable, management to ensure production in future years is a priority over maximizing production in any single year.

3. Forage crops and rangelands encompass tremendous diversity. Rangeland systems typically comprise five to fifty plant species, and worldwide more than 500 plant species are used for forage. These grasslands support a wide diversity of livestock. Forage crops and rangelands occur in every country of the world and on almost all soil types in the world. They encounter the range of climate within and between years and are employed by almost all the world's cultures.

4. Forage crops and rangelands have no immediate value to humans in terms of direct food products. It is only through consumption of the plant by live stock that biological and financial production can be captured from grasslands (Fig. 9-3). In the

Figure 9-1
This rangeland in Idaho is too rugged for farming most crops.
Source: USDA Natural Resource Conservation Service, http://photogallery.nrcs .usda.gov/

Figure 9-3

Worldwide, more land is devoted to grasslands than to all other crops combined. Grazing of perennial grasslands is productive and economic, and has many environmental and social benefits. Source: D. J. Barker, Ohio State University.

Figure 9-2

The grass and other plants in this pasture are protecting this hilly land from erosion. Source: USDA Natural Resource Conservation Service, http://photogallery.nrcs.usda.gov/

United States, the value of animal products is more than 25 percent of all farm cash receipts, and the value of the forage crops fed to animals is greater than any other single crop. It is often suggested that it would be more efficient for people to consume plants (e.g., grain) directly rather than having the plants fed to livestock and then consuming the meat and dairy products. However, most types of forage consumed by livestock are high-cellulose vegetative material that can't be digested by humans. Most areas of grasslands can only be converted to human food products by pasturing animals.

1. Animal access to pasture is a requirement for most organic livestock production systems.

UTILIZATION OF FORAGE CROPS

Forages in Traditional Confinement Systems

In the United States, livestock are usually housed in feed- lots (for beef) (Fig. 9-4) and milking barns (for dairy) and have all their rations brought to them. These rations usually contain forages as well as other high-energy concentrates and protein, such as by-products from other industries (e.g., distillers grains after ethanol fermentation, soybean meal after oil extraction) or cereal grains (e.g., corn). A specialized industry has developed around

Figure 9-4

The animals in this feedlot are feeding on the rations delivered by truck. **Source: USDA Natural Resource Conservation Service,** *http://photogallery.nrcs.usda.gov/*

the dedicated production of hay and silage by some farmers, and the blending of these crops into totally mixed rations (TMRs) by feed companies. Although these animals gain weight more rapidly and produce more milk, they could survive totally on- forage crops alone. Confinement systems are rare in New Zealand, Australia, South America, and South Africa, where livestock exclusively graze forages. Grazing systems usually have lower animal production than confinement livestock systems, but they are justified because the costs of production are proportionally lower, and proponents argue that they are more profitable. Regardless of the system, forage production is the basis of livestock production.

Grazing

Throughout the world, most forages are utilized by grazing. Ruminants (e.g., sheep, goats, and cattle) have four digestive chambers, the first of which (the rumen) is filled with microorganisms that digest and break down forage fiber (cellulose, hemicellulose, and pectin). Other groups of livestock, such as camelids (camels and llamas) and monogastrics (horses and pigs), can also thrive totally on forages but employ different digestive mechanisms.

The most important objective in grazing is to match the supply of forage production to the nutritional requirements of livestock. Many management strategies achieve this balance; however, the most important issue is to match stocking rate to forage production. Short-term deficits in forage production (e.g., during drought or over the winter) are usually met by feeding forage that has been conserved and stored (see later in this chapter) during a period of surplus (e.g., spring). Long-term deficits in forage production (i.e., overstocking or overgrazing) result in deterioration of the forage and soil resource.

There are many strategies for forage utilization by grazing; however, these can usually be simplified to variations of either rotational stocking or of continuous stocking. Rotational stocking is the movement of livestock between pastures according to a prescribed strategy. Most rotational stocking employs frequent (daily to weekly) movement of livestock; however, an infinite number of more and less frequent rotations exist. Once all pastures have been grazed, livestock return to the first pasture grazed, which has had suffi-cient time to regrow to a harvestable mass (Figs. 18—5, 18-6, and 18-7), thus completing the rotation. Rotational stocking is usually achieved with temporary electric fences that can be easily moved and replaced to allow livestock access to the correct area of pasture. Continuous stocking involves the allocation of

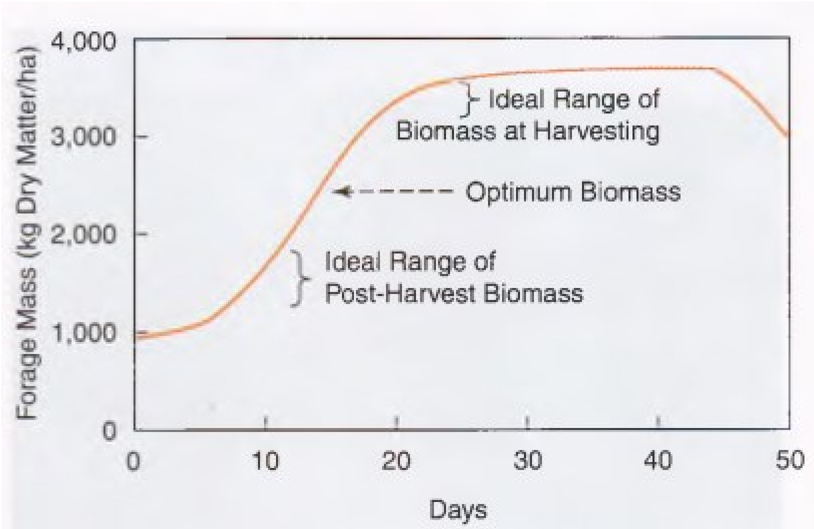

Figure 9-5

Generalized growth curve for forage production. Forages show slow initial growth, a period of high-growth rate, and a period of reducing growth rate. After long regrowth periods, forage mass can decrease as leaves low in the canopy wither and fall off. Source: David Barker, The Ohio State University.

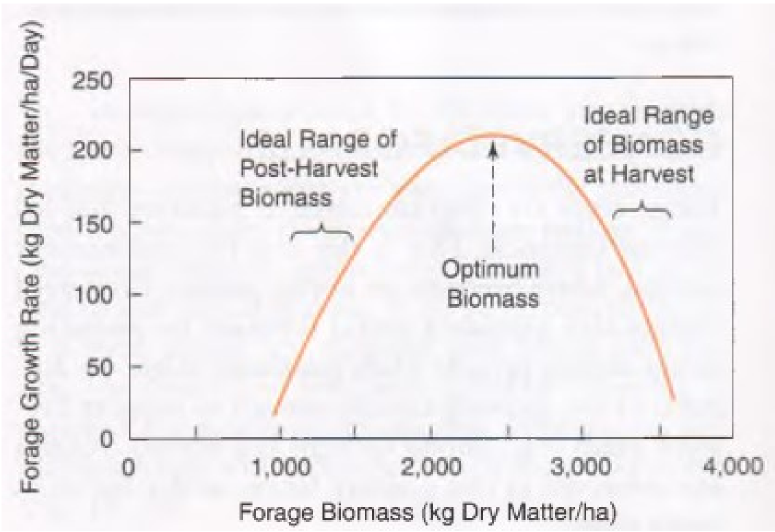

Figure 9-6

The data in Figure 18-5 is redrawn to show the relationship between forage growth rate and forage mass.

Source: David Barker, The Ohio State University.

livestock to a fixed area for a prolonged period. In a carefully managed situation, sufficient mass and growth rate of the forage crop support the livestock for the required period. As a generalization, intensive (high population of animals on relatively small amount of land) grazing systems use rotational stocking, while extensive grazing systems (few animals on a large area of land) use continuous stocking. Many grazers claim higher forage production from rotational stocking; however, it is difficult to identify the precise mechanisms for the response. For example, in addition to different patterns of forage removal compared to continuous stocking, rotational stocking also includes factors such as more regular livestock inspection, ease of herding livestock, more uniform manure dispersal, and less selective grazing.

Figure 9-7

The cattle on the left are grazing on a rotational field and will soon be moved to the adjacent field or another field in the rotation where the forage has had time to re-grow.

Source: USDA Natural Resource Conservation Service, http://photogallery.nrcs .usda.gov/

is made from grasses (meadow hay). One technology— as of 2009—still awaiting approval for use in the United States is Roundup Ready®, genetically modified alfalfa. Roundup® is a broad-spectrum herbicide, and Roundup® Ready varieties have been artificially created that have a resistance gene to Roundup®. Thus, Roundup® Ready alfalfa has the potential for easier weed control when treated with Roundup® herbicide.

In general, the best time to harvest hay for maximum yield and still maintain acceptable quality is just prior to the heading (seed development) stage. Hay fields can often be harvested several times during a growing season. Some forage crops, such as timothy, give only one or two harvests during the growing season, while others, such as alfalfa, give three to ten harvests depending on the region.

Hay quality is determined by plant maturity, leafiness, color, odor, and amount of foreign material. During harvest and transportation, every effort should be made to retain as much leaf as possible because most of the protein is in the leaves. High-quality hay has a fresh green color, a good aroma, and a pliable texture. It is nutritious, digestible, and palatable. Detrimental foreign material includes weeds, poisonous or thorny plants, spiny seeds, and objects such as wire, nails, rocks, and soil. Effort should be made to eliminate these from the hay.

Hay may be stored loose, chopped, baled, or pressed into cubes, pellets, or wafers. Harvesting is now highly mechanized. Many specialized machines are available for handling hay. The hay is cut, and laid down into windrows (Fig. 9-8), dried over two to

CONSERVED FORAGE

Forage crops are often conserved or preserved and fed later to livestock. This is the case for confinement systems, where livestock are not on pasture. Conserved forages also provide a useful function by providing forage during periods when grasslands might be dormant or not growing rapidly enough to support livestock needs (e.g., during drought and winter). Forages are conserved in two primary forms: as dry hay or as moist silage.

Hay Hay is defined as the shoots and leaves—and in some cases, the flowers, fruits, and seeds—of forage plants that are preserved by field drying, harvested, and stored for future feeding to livestock. Hay usually consists of grasses, legumes, or a combination of the two. The harvested material is dried to a moisture level of 15 to 20 percent. Proper dehydration is important to preserve quality and to prevent barn fires that result from spontaneous combustion of wet hay as it decomposes. Hay is the most important type of stored forage and provides considerable flexibility in animal feeding operations. Properly dried and stored, it can be kept for several years with minimal loss of nutritive qualities. In severe- winter regions, it permits feeding livestock a nutritious bulk of material when outside pastures are not growing and are covered with snow or ice. Hay is a cash commodity that can be bought and sold, whereas the value of pasture can be converted only by animal feeding.

The best quality hay in the United States is usually made from alfalfa, however the greatest quantity of hay

Figure 9-8

The hay is this field has been cut and raked into windrows to dry to the proper moisture level to preserve quality and reduce the risk for spontaneous combustion in storage.

Source: USDA Natural Resource Conservation Service, http://photogallery .nrcs.usda. gov/

Figure 9-9

In spring, forage growth exceeds the requirements of livestock. Surplus forage production can be made into hay and sold or used later during periods of deficit. Round bales suit mechanical manipulation better than the traditional small, rectangular bales. Source: R. M. Sulc, The Ohio State University.

Figure 9-10

Forages can be conserved by several methods. Here, alfalfa has been wilted to reduce its water content. It is being blown into a wagon and will be transported to a silo to be made into silage. Source: R. M. Sulc, The Ohio State University.

five days, and baled by mobile machinery (Fig. 18—9). This saves considerable labor over earlier methods of hauling hay to stationary machines. Most hay in the United States is now stored as small rectangular bales (14 X 18 X 38 in., 40 to 60 lbs), large rectangular bales (3 to 4 x 3 to 4 x 7 to 8 ft, 900 to 1,800 lbs), or round bales (4 to 6 ft diameter, 850 to 1,900 lbs). These bales are a commodity that can be bought, sold, or stored for later distribution.

Hay can also be chopped, green or dry, in the field into particles small enough to be blown in an air stream into trucks. The hay is then transported to feeding areas to be fed green to livestock or to dehydration equipment for processing.

Hay can be cubed, pelleted, or wafered and these practices are more common in regions of the United States where summers have low humidity, such as California, Arizona, New Mexico, and eastern Washington. In these areas, hay can be field-cured down to 12 percent moisture.

Silage The feeding of silage to livestock is an ancient practice from Europe dating back many hundreds of years, although the first silo was not constructed in the United States until 1876. Silage is moist forage, preserved by bacterial fermentation under anaerobic conditions. The corn plant is used most often for making silage, but almost any other forage species can be used, alone or in mixtures. Some commonly used species are oats, cereal rye, triticale, sorghum-sudangrass, smooth bromegrass, Italian ryegrass, orchardgrass, timothy, alfalfa, and red clover.

In silage fermentation by the direct cut method, the green chopped forage material—at 60 to 70 percent moisture—is blown into the silo. This is the procedure used for corn silage. A variation of this is haylage or hay crop silage: when the green forage is cut and laid in the field to wilt until it is about 45 to 50 percent moisture. It is then picked up, chopped, and blown into the silo. The practice of field wilting before chopping is required for perennial grasses and legumes, or any standing forage with moisture content above 70 percent.

Silos for silage must be airtight structures and are either vertical or horizontal. They may be made of concrete or glass-coated steel plates; they may be large, plastic, baglike containers, or they may be mere trenches in the ground. After the oxygen in the mass of tightly packed chopped material is used up by plant respiration (or aerobic bacteria if spoilage occurs), anaerobic bacteria multiply and act on the carbohydrates in the plant tissue to form lactic acid, which essentially ferments the plant material. The pH drops to 4.2 or below, inhibiting spoilage bacteria and enzyme action, thus preventing deterioration. The fermentation process is completed in two to three weeks. Silage can be kept in good condition for several years if air is kept out, moisture stays high, and the pH remains below 4.2.

Modern silage preparation is highly mechanized. It starts with cutting the corn plants (or other forage material) by special harvesters that chop and blow the particulate material into trailers for hauling to the silo. At the silo, it is mechanically unloaded and blown intovertical silos, or bags are spread and packed down in bunker silos.

Baleage With the advent of bale-wrapping technology in the mid-1990s, farmers have the option of replacing silos with individual plastic-wrapped bales. A variation of this technique is wrapping many round bales within a continuous plastic tube in a single row. Wrapped bales have the advantage of being weather resistant (as long as the wrap is not broken), thus allowing a shorter drying period in the field compared to hay, and they can be transported. Typically, the fermentation process is similar, although less efficient than in silos because more air (O2) is usually present in bales than in a well-packed silo. Baleage has become popular on small to medium-size farms in the humid areas of the United States such as the East Coast and southern states, where drying times in excess of three days increase the risk of rainfall damaging traditional hay crops. The additional cost of plastic, disposal issues with the plastic, and the costs of the wrapping machinery make this method less popular in western states of the United States, where field-dried hay is easier to make.

Integrated Systems (Crop Rotations with Cereals, Hay, or Livestock)

The diversity of forage production systems also includes many options for integrating forages into other types of production systems. Forage crops are often included as short-term components within a more complex crop rotation. This technique can work in many situations:

1. Various options for double cropping can be used. When a cereal crop is harvested early (e.g., winter wheat, or silage corn), a short-term annual forage crop might be planted to provide forage for livestock in the period until the main crop is replanted the subsequent year. Forage species that can be used in this situation include warm-season annuals such as sudangrass or

cool-season annuals such as cereal rye, oats, annual ryegrass, forage triticale, and brassica species (e.g., turnips, kale, and rape).

2. Forages can be used as part of a rotation with cereal crops. Legume species within grasslands build organic soil nitrogen that can be used by subsequent cereal crops. A possible rotation might include several years in forage crops, followed by several years of grain crops.

3. Hay and grazing systems are often integrated into a single production system. Although examples of grazing-only and hay-only systems are common, these are more generally integrated. Forage growth usually exceeds livestock requirements in There are also situations when livestock can graze crop residues remaining after grain harvest (Fig. 18-11).

Расм. 9-11

the spring, so farmers usually conserve this excess for other periods of the year when livestock demand exceeds supply. These periods include the short (one- to two-month) period of summer drought, and a longer (up to four-month) period of cold during winter when forage growth is slow or zero.

FORAGE QUALITY

Although the single largest influence on the profitability of forage systems is total production (or yield), the next most important factor is forage quality. The quality of forage is affected primarily by the amount of fiber it contains and its digestibility. Fiber in forage can be present as pectin and hemicellulose (moderately digestible by livestock), cellulose (poorly digestible by nonruminant livestock), and lignin (indigestible). Total fiber is measured in the laboratory using neutral detergent fiber (NDF) digestion. Digestibility can be measured directly in animals as the proportion of digested forage compared to total forage consumed (the difference being forage excreted); however, this procedure is time-consuming and expensive. Digestibility can also be predicted following incubation of a ground forage sample in rumen fluid in a laboratory and is currently considered the best available laboratory method for estimating forage digestibility.

Digestibility of a forage sample is commonly predicted by laboratories from empirical equations based on chemical composition of the forage (such as NDF and lignin).

Protein content, nutrients, and vitamins also affect overall forage quality. In most cases, these are present in sufficient quantities that they have less effect on forage value than does fiber content and digestibility. The main plant factors affecting forage fiber and other quality factors are listed below:

Forage species. Forage species vary in their amount of fiber and the chemical composition of that fiber. Generally, grasses have more fiber than legumes, and although grass fiber is generally more digestible (more hemicellulose) than are legumes, it can be insufficient to compensate for the higher amount of fiber. The result is that legumes generally produce better quality forage than grasses. Variation exists among grasses as well, and species such as perennial ryegrass and timothy are higher quality than orchard- grass and tall fescue.

Leaf-to-stem ratio. Almost without exception, stems have higher fiber (lower quality) than leaves. Vegetative grasses do not have true stems; their pseudostem is actually leaf sheaths wrapped together. Nonetheless, grass pseudostem, the true stems of legumes such as alfalfa, and the reproductive stems of grass all have higher fiber and lower quality than leaves. Good forage management aims to reduce these components in forage and to maximize leaf content.

Maturity. As forages mature, yield increases but quality declines. Stem yield increases dramatically with advancing maturity in most forage species. Flowering initiates developmental changes in all forage species that include higher amounts of fiber. Furthermore, the fiber produced (i.e., lignin) is less digestible. Although one component of this loss in quality is the prevalence of grass seed heads and flowering structures, leaves also have more fiber in flowering forages. Good harvesting strategy is to harvest forages prior to or right as flowering occurs. One field recommenda-tion for obtaining the best balance of yield and quality in a forage crop is to harvest at 10 percent bloom.

Antiquality components. Almost every forage species can contain antiquality components with varying toxicity to livestock. The list of potential toxic components is lengthy but some important compounds follow:

Leaf sap onins. Most legumes contain saponins that can produce a foam complex that causes bloat.

Ergot alkaloids (e.g., ergovaline). These are produced by fungal endophytes of some grass species. Levels vary with heat and drought. In most years, they cause subclinical growth retardation in young livestock, and in extreme cases, can result in animal death.

Nitrates. Many C4 annual species have the potential to accumulate nitrates that can be toxic to livestock. The greatest risk occurs with the flush of forage regrowth that can follow a temporary drought.

High protein. Livestock cannot digest protein in excess of 20 percent and forages with levels higher than this can result in impaired livestock growth and even abortion. High-protein forages should be diluted with low protein sources.

Natural estrogens. Some legume species (e.g., red clover and subterranean clover) can produce natural estrogens that can impair reproductive performance of sheep and cattle. Modern varieties have been selected to avoid this problem.

ESTABLISHMENT

Forage establishment is a necessary component of a forage management and forage improvement program. The many forage establishment methods can be reduced to three main options:

Full cultivation. The most expensive and most reliable establishment option of forage crops involves destruction of the existing vegetation by mechanical (plowing) or chemical means, a mechanical operation to bury this vegetation (disking or plowing), mechanical treatment of the soil to establish a fine and firm seedbed (by disking and rolling).

No-till planting. As implied in its name, no-till planting involves pasture establishment without tillage of the soil. In most cases, existing pasture land already has desirable physical characteristics (e.g., high porosity, infiltration, and organic matter), and only the pasture species need to be changed.

Frost seeding. Also called broadcast seeding and oversowing, frost seeding applies seed directly to existing vegetation (or, if applicable, to the soil surface). This method has the lowest success rate but is very inexpensive.

PLANT DIVERSITY IN GRASSLANDS

Forages and rangelands typically comprise a mixture of five to fifty species. One important aspect is the benefit that this diversity (biodiversity) provides to the pattern of forage production. The benefits include better tolerance of environmental stresses, a more uniform forage growth pattern, increased stand persistence, and fewer losses of nutrients to streams and groundwater. Biodiversity can be considered at various levels, and one theory is that biodiversity is maximized by adding species with different and unique functions rather than adding forage species that are essentially similar to those already present (Fig. 9—12). There are many methods or systems for grouping species; however, some common functional groups for grasslands are listed below:

C3—cool season grasses. This is the largest and most important group of forages and includes species such as perennial ryegrass, orchardgrass, timothy, Kentucky bluegrass, tall fescue, reed canary grass, crested wheat-grass, and smooth bromegrass (Fig. 9-13). These species can be characterized by typically higher quality for livestock, moderate to poor drought tolerance, good spring and autumn production, and moderate to low tolerance of low fertility. The name for this functional group results from the photosynthetic pathway these species use for fixing CO_2; that is, the first step for fixing CO_2 involves 3-carbon molecules and the enzyme ribulose bisphosphate carboxylase (RUBISCO).

Legumes. Legumes are species of the plant family FABEACEAE and are vital components of most forages and rangelands. Examples of legume species include alfalfa, red clover, white clover, birdsfoot trefoil, and lespedeza. Legumes provide many useful

characteristics such as nitrogen fixation by Rhizobium bacteria, high-digestibility forage, high-protein concentration, and often a growth pattern complementary to their companion grass species (Fig. 9-14 on page 408).

C4—warm-season grasses. This group of forages includes species such as Bermuda grass, big bluestem, switchgrass (Fig. 19-15 on page 409), indiangrass, lim- pograss, and paspalum. These species can be characterized by excellent tolerance of drought and heat, and high water use efficiency. In addition, many of these species are native prairie species and can have both conservation and productive value. Disadvantages of these species include their difficult establishment and lower forage quality. The name for this functional group results from the photosynthetic pathway these species use for fixing CO_2; that is, the first step for fixing CO_2 involves 4-carbon molecules and the enzyme phospho-enol pyruvate (PEP) carboxylase (see Chapter 11).

Forbs. This is a largely maligned group of species often regarded as weeds in pastures. We now realize that these species might provide useful functions including filling vacant spaces, protecting bare soil, and providing forage (often with high nutrient value) to livestock (Fig. 18-16 on page 409). Two species relevant to mention are chicory and plantain (also called buckthorn) (Fig. 9—17 on page 409), which have been selected for forage production and are being used in forage mixtures. In many extensive pastures, other forb species can provide unique characteristics to livestock products such as unique (niche) flavors to meat and dairy products.

Figure 9-12

(A) This healthy pasture is a mix of grasses and legumes. (B) This prairie grassland is being restored. The addition of forbs to the ecosystem is intended to stabilize and strengthen the system. Source: USDA Natural Resource Conservation Service, http://photogallery.nrcs .usda.gov/

Figure 9-13

Some grass species forage crops. Above (left to right): smooth bromegrass, orchardgrass, tall fescue. Below (left to right): timothy, bluegrass, western wheatgrass.

Figure 9-14

Examples of legume species forage crops, trefoil, lespedeza, bur clover. Above (left to right): alfalfa, sweet clover, red clover. Below (left to right): birdsfoot

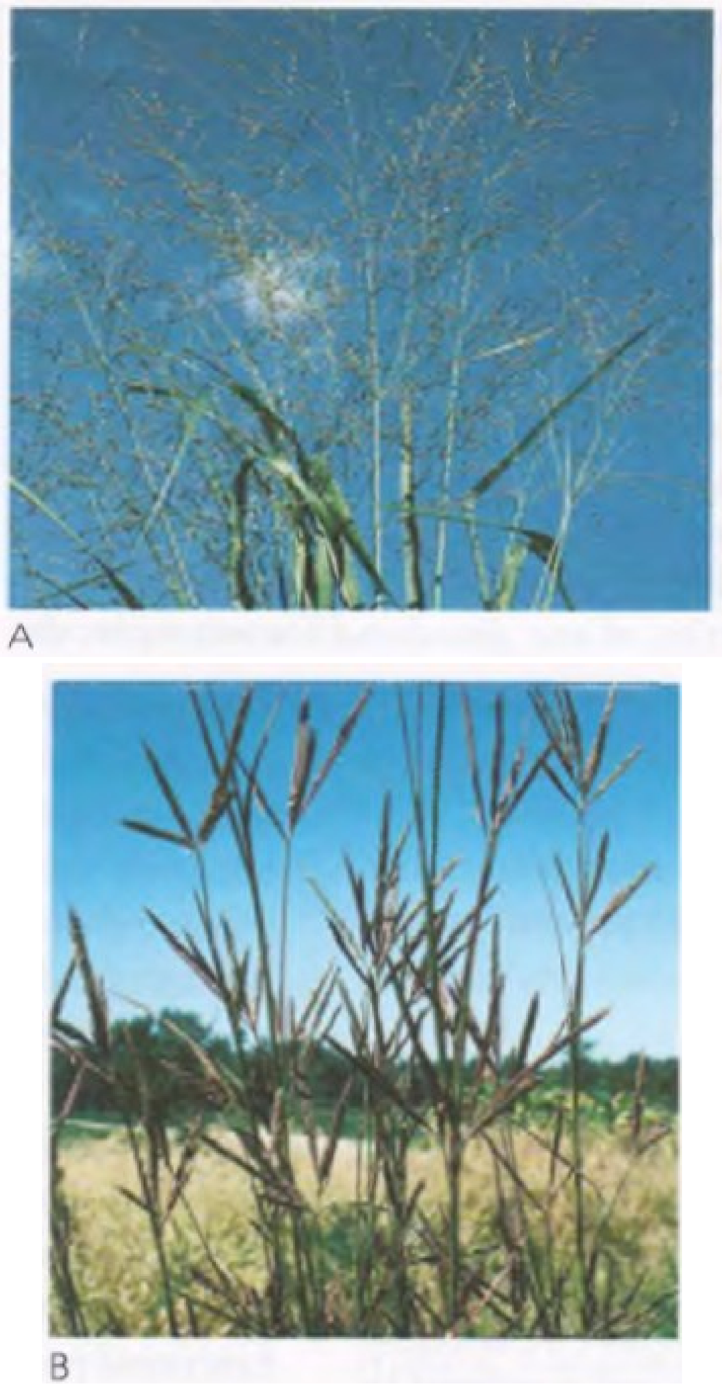

Figure 9-15

(A)Switchgrass with seed heads. (B) Big bluestem seed heads. Source: (A) USDA Agricultural Research Service Image Gallery, http://www.ars.usda.gov/is/ graphics/photos/(B) USDA Natural Resource Conservation Service, http://photogallery.nrcs

Figure 9-17
(A) Chicory and (B) plantain are two forbs that though usually considered to be weeds are now being used in some forage mixes to give stability to the forage ecosystem. Source:

SYMBIOSIS WITH MICROORGANISMS

Many forage species form symbiotic relationships with other microorganisms that are important and vital for the success of these plants.

Rhizobia are bacteria that form a symbiosis with legumes, in the form of nodules on the roots. The species of bacteria are unique for each species of legume. The bacteria benefit from a protective host which provides a source of energy and nutrition, while the plant benefits from a source of nitrogen. The nitrogen is fixed from the air and converted by the bacteria into a useful form in the plant. This symbiosis is described in greater detail in Chapter 13.

Mycorrhiza comprise a broad class of fungi that form various relationships (mutualistic, symbiotic) with a range of grass, legume, and forb species. In general, the mychorrhiza are more efficient at the uptake of essential nutrients, especially phosphorus, and can aid plant survival in low-fertility soil. In the case of most prairie grasses such as big bluestem and indiangrass, the presence of the appropriate native mychorrhizal species is essential to the persistence of the grass.

Endophytes are a classic seed-borne fungi that form a symbiosis in the intercellular spaces of grass leaves, stems, and seeds. Although there are about fifty fungi species infecting 200 grass species, most interest focuses on the genus Neotyphodium, and the grass species tall fescue and perennial ryegrass. When growing in the grass host, fungi produce various alkaloids that are feeding deterrents to both insects and livestock. The symbiosis has the ecological benefit of providing to the host increased production, persistence, insect resistance, and drought/heat tolerance, but it has the practical disadvantage of being toxic to livestock. To avoid the toxic alkaloid effects, the forage seed industry has developed mechanisms for the supply of endophyte-free seed. Since 2001, a new endophyte option has become commercially available. Nontoxic endophyte is a fungal isolate identical in all respects to the toxic endophyte except that it does not produce the toxic alkaloids. Pastures established with nontoxic endophyte have the benefits resulting from the fungus being present, but without the toxic effect of the alkaloid to animals.

FURTHER EXPLORATION

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GLOSSARY

abaxial	Away from the axis or central line; turned toward the base, dorsal.
abscisic acid	A plant hormone involved in abscission, dormancy, stomatal closure, growth inhibition, and other plant responses,
adaptation	The process of change in structure or function of an individual or population caused by environmental changes,
Biocide	A combination of a bactericide and a fungicide used for cut-flower-keeping solutions, or used as a sterilant in horticultural operations.
biological control	The use of natural predators or pathogens to control plant pests.
biomass	The solid part of living organisms. Sometimes called dry matter.
biodiversity	The term used to describe the genetic diversity within and among all species.
biome	Large terrestrial ecosystem characterized by specific communities, usually named after the predominant vegetation found there, e.g., temperate forest.
blade	The thin and often flat part of a leaf.
bolting	Rapid production of flower stalks in some herbaceous plants after sufficient chilling or a favorable photoperiod,
botany	The science of plants, their characteristics, functions, life cycles, and habits.
bourse shoot	Shoot arising from the mixed bud on a fruiting spur of apple. Bourse shoots terminate growth by forming floral or vegetative buds.
cure	To prepare crops for storage by drying. Dry onions, sweet potatoes, and hay crops are examples. Dehydration of fruits for storage is not considered curing.
cuticle	An impermeable surface layer on the epidermis of plant organs.
cutin	A clear or transparent waxy material on plant surfaces that tends to make the surface waterproof.
damping off	A pathogenic disorder causing seedlings to die soon after seed germination.
daylength	Number of effective hours of daylight in each twenty- four-hour cycle.
day-neutral plant (DNP)	Plant capable of flowering under either long or short daylengths.
domain	Broadest category of taxonomic classification that separates life forms into three categories: prokaryotes, eukaryotes, and archaea bacteria.
ecology	The study of life in relation to its environment.
endemic	Species native to a particular environment or locality.
endocarp	Inner layer of the fruit wall (pericarp).
epiphyte	A plant that grows upon another plant yet is not parasitic.
erosion	The wearing away of the surface soil by wind, moving water, or other means.
essential element	Any mineral that is required for proper growth and development of an organism.
eukaryotic cells	Cells that have a nucleus.
fallow	Cropland left idle for one or more seasons for any number of reasons, such as to accumulate moisture, destroy weeds, and allow the decomposition of crop residue.
family	In plant taxonomy, a group of genera.
fascicle	A bundle of needle-leaves of gymnosperms such as the pines.
fatty acid	Organic compound of carbon, hydrogen, and oxygen that combines with glycerol to make a fat.
fermentation	An anaerobic chemical reaction in foods, such as the production of alcohol from sugar by yeasts.
fertigation	Practice of adding fertilizer to irrigation water,
filament	Stalk portion of a stamen. *See also* anther; stamen.
food chain	The path along which food energy is transferred within a natural plant and animal community (from producers to consumers to decomposers).
forage	Vegetation used as feed for livestock, such as hay, pasture, and silage. The material is fed green or dehydrated.
forcing	A cultural manipulation used to hasten flowering or growing plants outside their natural season.

forb	Flowering herbaceous plants that are not grasses, sedges, or rushes.
fossil	Any impression, natural or impregnated remains, or other trace of an animal or plant of past geological eras that has been preserved in the earth's crust.
fungi.	A thallus plant unable to photosynthesize its own food (exclusive of bacteria).
furrow	Small V-shaped ditch made for planting seed or for irrigating.
furrow irrigation	A method of irrigation by which the water is applied to row crops in ditches.
genetics	The science or study of inheritance,
genotype	The genetic makeup of a nucleus or of an individual,
genera.	A group of structurally or phylogenetically related species.
geotropism	Growth curvature in plants induced by gravity,
herbicide	Any chemical used to kill plants; an herbicide may work against a narrow or wide range of plant species,
herbivore	Animal that subsists principally or entirely on plants or plant products.
heredity	The transmission of morphological and physiological characteristics from parents to their offspring,
hermaphrodite flower	A flower having both stamens (male) and pistils (female).
hygroscopic water	Water that surrounds and is tightly held by soil particles, making the water unavailable to plants.
hypha Plural: **hyphae.**	A filament that forms mycelial growth of a fungus.
hypocotyl	Portion of a stem that is located above the root and below the cotyledon.
hypogeal germination	In dicots, a type of seed germination in which the cotyledons remain below the soil surface. Peas are one example.
hypothesis	A proposition or supposition provisionally adopted to explain certain facts. Once proven by ultimate scientific investigation, it becomes a theory or a law.
imbibition	The absorption of liquids or vapors into the ultrami- croscopic spaces in materials like cellulose.
immobilization	The conversion of inorganic nitrogen to organic nitrogen.
immune	Free from attack by a given pathogen; not subject to the disease.
imperfect flower	A flower lacking either stamens or pistils,
impervious	Resistant to penetration by fluids or by roots,
inbred line	A pure line usually originating by self-pollination and selection.
inceptisol	A developing soil that is usually wet or moist and shows alterations in horizons.
internode	The region of a stem between two successive nodes.
interspecific cross	A cross, natural or intentional, between two species.
in vitro	Latin for *in glass.* Living in test tubes; outside the organism or in an artificial environment.
in vivo	Latin for *in living.* In the living organism.
jasmonate	A compound recently identified as a plant hormone involved in plant response to insect attack.
juvenile phase	A growth phase in plants characterized by the inability to flower and reproduce.
lamina	Blade or expanded part of a leaf.
lateral bud	A bud that grows out from the leaf axil on the side of a stem.
latex	A milky secretion produced by various kinds of plants,
layering	A form of vegetative propagation in which an intact branch develops roots as the result of contact with the soil or another rooting medium.
leach	To remove soluble materials from soil or plant tissue with water.
leaf mold	Partially decayed leaves useful for improving soil structure and fertility.
leggy	Weak-stemmed and spindly plants with sparse foliage caused by too much heat, shade, crowding, or overfertilization. *See* etiolation.
lenticel	An opening made up of loosely arranged cells in the periderm that permits passage of gases,
liane	A climbing or twining plant, usually woody.
lifecycle	The stages that an organism goes through during its lifetime.
line	Group of individuals from a common ancestry; When propagated by seed, it

	retains its characteristics. A type of cultivar.
liners	Young plants that are grown in a nursery until they are big enough for transplanting.
lipid	Any of a group of fats or fatlike compounds insoluble in water but soluble in certain other solvents.
loam	A textural class for soil with prescribed amounts of sand, silt, and clay.
locus	The fixed position of location of a gene on or in a chromosome.
long-day plant	A plant that flowers when the light period is greater (dark period is shorter) than a critical duration.
Lucerne	A name for alfalfa used in Europe, Australia, and other regions.
macronutrient	A chemical element, like nitrogen, phosphorus, and potassium, necessary in large amounts (usually greater than 1 ppm) for the growth of plants.
male sterility	A condition in some plants in which pollen either is not formed or does not function normally, even though the stamens may appear normal.
meristematic tissue	Region of actively dividing and differentiating cells.
mesocarp	Middle layer of the fruit wall (pericarp).
mesophyll	Parenchyma tissue in leaves found between the two epidermal layers.
mycelium	The mass of hyphae forming the body of a fungus.
Mycology	A branch of botany dealing with the study of fungi.
mycorrhiza	The association, usually symbiotic, of fungi with the roots of some seed plants.
necrosis	Death associated with discoloration and dehydration of all or some parts of plant organs.
nectary	Flower part that secretes nectar.
nematodes	Unsegmented roundworms abundant in many soils; they are important because many species of them attack plants or animals.
neutral soil	A soil in which the surface layer is neither acid nor alkaline in reaction.
night-break lighting	Low intensity lighting used in the middle of the night to change the photoperiod.
nitrification	The conversion of ammonium ions into nitrates through the activities of certain bacteria.
nitrogen assimilation	The incorporation of nitrogen into organic cell substances by living organisms.
nucellus	A tissue originally making up the major part of the young ovule, in which the embryo sac develops.
nucleic acid	An acid found in .all nuclei; all known nucleic acids fall into two classes, DNA and RNA.
nucleus	A dense body in the cytoplasm essential for cellular development and reproduction.
nut	A dry, indehiscent, single-seeded fruit with a hard, woody pericarp (shell), such as the walnut and pecan,
nutrient	Element essential to plant growth used in the elaboration of food and tissue.
obligate parasite	An organism that must live as a parasite and cannot otherwise survive.
obligate saprophyte	An organism obliged to live only on nonliving animal or plant tissue.
oedema	Intumescence or blister formation on leaves.
organelle	A specialized region in a cell, such as mitochondria, that is bound by a membrane.
palatability	Term used to describe how agreeable or attractive feed stuff is to animals or how readily they consume it.
palisade parenchyma cells	The cell layer in leaves immediately below the upper epidermis; it is packed with chloroplasts. Found in dicots but not in monocots.
pathogen	An organism that causes disease.
peat	Any unconsolidated soil mass of semicarbonized vegetable tissue formed by partial decomposition in water. An example is sphagnum peat moss.
pectin	Polysaccharide from the middle lamella of the plant cell wall; jelly-forming substance found in fruit,

pedicel	Individual flower stalk of an inflorescence.
peduncle	Flower stalk that is borne singly. Also, the main stem of an inflorescence.
percolation	The downward movement of water through soil,
pheromone	Any of a class of hormonal substances secreted by an individual and stimulating a physiological or behavioral response from an individual of the same species.
phospholipid	Lipids that contain a phosphorus molecule. Important in the structure and function of cellular and subcellular membranes
photomorphogenes is	Plant shape determined by light quality particularly through relative amounts of red, far-red, and blue light,
photomorphogenic response	The reaction of non-shade- adapted plants when they do not receive enough light at the correct red:far-red ratio.
line	Group of individuals from a common ancestry; When propagated by seed, it retains its characteristics. A type of cultivar.
liners	Young plants that are grown in a nursery until they are big enough for transplanting.
lipid	Any of a group of fats or fatlike compounds insoluble in water but soluble in certain other solvents.
Loam	A textural class for soil with prescribed amounts of sand, silt, and clay.
locus	The fixed position of location of a gene on or in a chromosome.
Lucerne	A name for alfalfa used in Europe, Australia, and other regions.
macronutrient	A chemical element, like nitrogen, phosphorus, and potassium, necessary in large amounts (usually greater than 1 ppm) for the growth of plants.
male sterility	A condition in some plants in which pollen either is not formed or does not function normally, even though the stamens may appear normal.
Mediterranean climate	A climate characterized by cool, wet winters and warm, dry summers.
meiosis	Two successive nuclear divisions, in the course of which the diploid chromosome number is reduced to the haploid and genetic segregation occurs.
metabolism	The overall physiological activities of an organism.
plant growth	An irreversible increase in size (biomass) of a plant,
plant growth regulators	Natural and synthetic chemicals that influence plant growth and development,
plant hormone	*See* hormone.
plant pathology	The scientific study of plant diseases and their causal organisms.
plasmalemma	Membrane that surrounds a plant cell,
plasmodesmata	Strand that forms a cytoplasmic connection between two plant cells.
plant growth regulators	Natural and synthetic chemicals that influence plant growth and development,
plant hormone	*See* hormone.
plant pathology	The scientific study of plant diseases and their causal organisms.
plasmalemma	Membrane that surrounds a plant cell,
plasmodesmata	Strand that forms a cytoplasmic connection between two plant cells.
pollinator	An agent (such as an insect) that pollinates flowers.
polyembryony	The presence of more than one embryo in a developing seed.
polyploidy	A condition in which a plant has somatic (nonsexual) cells with more than 2n chromosomes per nucleus.
receptacle	The enlarged tip of a stem on which a flower is borne,
recessive gene	A gene that does not express itself in the presence of the contrasting (dominant) gene.
recombination	The mixing of genotypes that results from sexual reproduction.
sdereid	A short, thickened cell that provides support or protection in plants. *See also* sclerenchyma tissue.
sclerenchyma tissue	Supporting or protective tissue in which the cells have hard lignified walls.
seed bank	The reserve of seeds in the ground.
seed potatoes	Pieces of potato tubers or whole tubers that are planted to produce new plants

	and subsequent commercial crops.
sexual reproduction	Development of new plants by the processes of meiosis and fertilization in the flower to produce a viable embryo in a seed.
shoot meristem	*See* apical meristem.
short-day plants (SDP)	Plant that initiates flowers only under short-day (long-night) conditions.
sidedressing	Applying fertilizer on a soil surface close enough to a plant that cultivating or watering carries the fertilizer to the plant's roots.
silo	A structure for making and storing silage.
silt	A soil textural class consisting of particles between 0.05 and 0.002 mm in diameter.
simple fruit	A fruit derived from a single pistil.
simple leaf	Leaf that is not divided into distinct leaflets. *See also* compound leaf.
soil salinity	The amount of soluble salts in a soil, expressed as parts per million, millimho/cm, or other convenient ratios,
soil series	The basic unit of soil classification; a subdivision of a family, comprising soils that are essentially alike in all major profile characteristics.
solute	A substance dissolved in a solvent.
solution	A homogeneous mixture; the molecules of the dissolved substance (the solute) are dispersed among the molecules of the solvent.
solvent	A substance, usually a liquid, that can dissolve other substances (solutes).
somatic tissue	Nonreproductive, vegetative tissue. Tissue developed through mitosis that will not undergo meiosis.
source leaf	Leaf that is producing and exporting more photosyn- thates than it requires for its own use.
spadix	An inflorescence with sessile flowers on a fleshy stalk, for example, *Spathiphyllum,* or peace lily.
sperm	A male gamete.
spermatophyte	A seed-bearing plant.
spike	An inflorescence that has a central axis on which sessile flowers are borne. Examples are some grasses, gladioli, and snapdragons.
spiroplasma	Helical prokaryote organisms that lack rigid cell walls and infect plants.
spodosol	A soil that is highly leached, has low fertility, and retains little water.
sprigging	Vegetative propagation by planting stolons or rhizomes (sprigs).
spring ephemerals	Small flowering plants that grow in deciduous forests that start and complete their annual lifecycle in a very short time in the spring before trees leaf out.
spur-bearing	A term describing a plant that predominandy bears fruit on fruiting spurs.
square	An unopened flowerbud in cotton with its accompanying bracts.
stamen	The male reproductive structure of a flower. The stamen produces pollen and is composed of a filament on which is borne an anther.
staminate (male) flower	A flower having stamens but no pistils.
starch	A complex polysaccharide carbohydrate. The form of food commonly stored by plants.
stele	The vascular tissue and closely associated tissues in the axes of plants. The central cylinder of the stem.
stem	The main body of a giant, usually the ascending axis, whether above or below ground in opposition to the descending axis or root. Stems, but not roots, produce nodes and buds.
stigma	In a flower, the portion of the style to which pollen adheres.
stipule	Appendage at the base of a leaf where it attaches to the stem.
stock	*See* rootstock.
stolon	A slender, prostrate above-ground stem. The runners of white clover, strawberry, and Bermuda grass plants are examples of stolons.