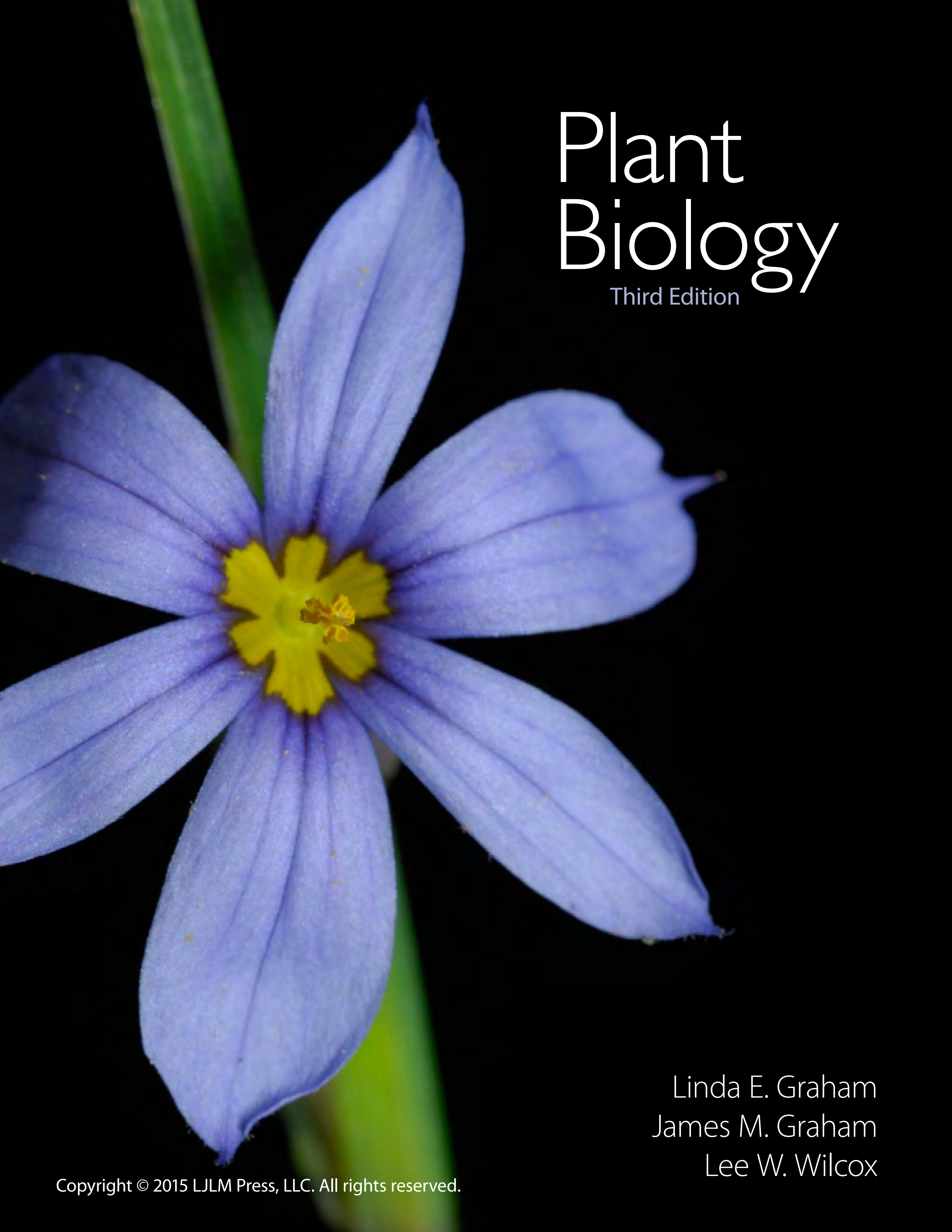

Plant Biology

Third Edition

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Aloe plant—Lee W. Wilcox

2

Plants and People

Our group of botanists and marine biologists was temporarily marooned on a remote island in the Bahamas without normally available air transport when one member of our group suddenly required medical attention. She had gone tuna fishing with a local crew and, distracted by the excitement of landing a trophy-sized fish, acquired an extremely painful and extensive sunburn. We were nowhere near a clinic where we could seek medical advice or a pharmacy or store where we could obtain a soothing lotion. Then, one of us remembered seeing *Aloe* plants growing in a nearby garden. We cut several of the sword-shaped leaves and smeared the sap over our colleague's sunburn, whereupon she experienced immediate relief from pain. Additional applications prevented itching and infection of her damaged skin. We were grateful for aloe's healing properties, which allowed us to return to our studies of tropical plants and coral reefs.

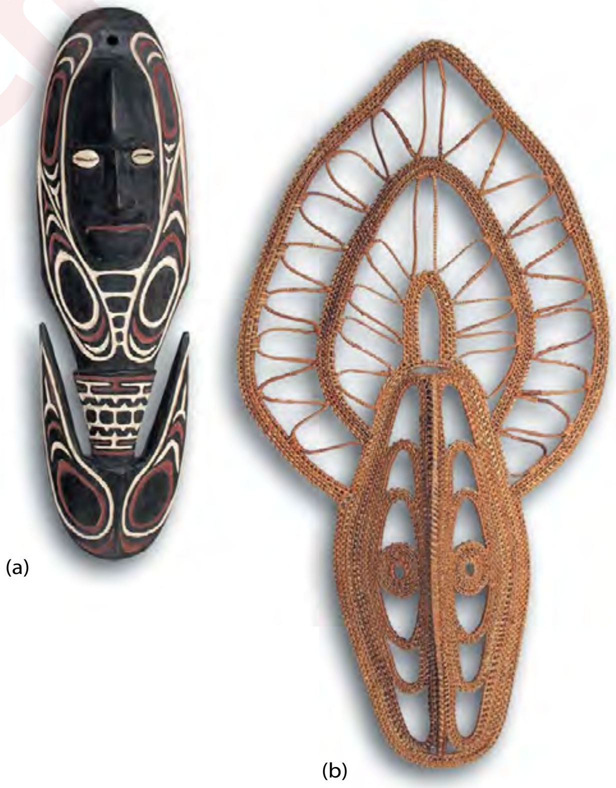
Aloe—an asparagus relative that is native to Africa—has been known since ancient times as the "burn plant" or "medicine plant" for its efficacy in treating burns, poison ivy rashes, fungal infections, and other skin problems. It is planted in home gardens in warm areas around the world as a source of treatment for skin conditions. Modern science has shown that the thick, mucilaginous sap of cut leaves contains many compounds that are beneficial to skin. For this reason, modern skin lotions often contain aloe extract and plantations have been established to supply the market demand.

Aloe is but one example of the many medicinal plants that were used in ancient times and continue to be valued today. Plants also provide us with food, beverages, spices, cosmetics, fibers, building materials, and many other products, explaining why plants have influenced the course of human civilizations. For example, successful cultivation of olive plants for oil production fueled the rise of Athens and, with it, Greek culture and the birth of Western civilization. In the 15th and 16th centuries, market demand for exotic spices stimulated voyages of discovery that connected diverse cultures. This chapter will explore how scientists study past human-plant interactions, including the origins of agriculture, the purposeful cultivation of plants. We will also see how diverse types of plant chemistry can explain the many uses of plants in modern society.

2.1 Ethnobotany and economic botany focus on human uses of plants

Learning Goals:

1. Provide an example of how ethnobotanists perform their work.
2. Provide an example of how economic botanists perform their work.



Lee W. Wilcox

FIGURE 2.1 Plants as components of material culture Artifacts produced by aboriginal peoples of northern New Guinea include (a) this carved and decorated wooden hook used to hang food out of the reach of animals, beautiful and utilitarian baskets, and (b) masks woven from plant fibers that decorate cultivated yams for ceremonial purposes. To these people, yams are valuable not only for their high food value and long-keeping properties but also because they symbolize male pride and are thought to have spirits that communicate underground.

For most people on Earth today, and for most humans in the past, material culture has been based primarily on plants (Figure 2.1). The scientific study of past human uses of plants or present-day plant uses by traditional societies is known as **ethnobotany**. The root *ethno* refers to the study of people, and *botany* is the study of plants, otherwise known as plant science. **Economic botany** is concerned with the use of plants by modern industrialized societies. These two areas of plant science are closely related in that ethnobotanical work reveals much indispensable information to developed societies, including the recognition of previously unknown medicinal properties of plants. Economic botany often involves investigations into the history of cultivation of modern crop plants to identify their wild relatives. These wild relatives harbor genetic material that is useful in developing crops that are more resistant to disease, insect attack, or drought.

Ethnobotanical studies have revealed that indigenous people—those who follow traditional, nonindustrial lifestyles in areas they have occupied for many generations—often use trial-and-error methods closely resembling the processes of modern science. People might first try a small amount of plant material or extract to estimate potential harm or benefit, then observe multiple incidents of use to make conclusions about general utility. Use of such methods

Essay 2.1

Ethnobotany

Ethnobotanists work with indigenous societies and with materials from archeological sites to piece together the history of plant uses by human cultures. Their training combines the study of botany with anthropology, archeology, folklore, linguistics, psychology, chemistry, medicine, pharmacology, and ecology. To accomplish their work, ethnobotanists must also know something of diplomacy, economics, and political systems.

An ethnobotanical study begins with identification of an interesting problem, such as the uses of plants by a culture that has previously been inaccessible or incompletely studied or a search for new medicines. Ethnobotanists must first obtain the approval of the government of the country in which the study will be done; plant materials and artifacts cannot generally be removed from the country of origin without permission. The ethnobotanist must meet and establish rapport with tribal elders and healers. It is usually necessary to negotiate some kind of return of knowledge or other reward to the local population or national government. Information about plant uses is best obtained directly, requiring mastery of local dialects and culture. Ethnobotanists assume the roles of participant-observer, teacher, and friend; they learn how the people identify, collect, prepare, and use plant materials.

Eve Emshwiller (**Figure E2.1A**) of the University of Wisconsin-Madison is an ethnobotanist who focuses on the domestication of oca (*Oxalis tuberosa*), a tuber crop that was first domesticated in the Central Andes, as was the more familiar potato. Tubers are enlarged root or stem structures in which plants store food, which can then be harvested by people for use as food. Both potato and oca are tubers produced by underground stems, and should not be confused with root tubers such as sweet potato, cassava, or yam that are also used for food. Oca is an important food for modern Andean farmers because this crop is tolerant to harsh conditions and poor soils, and can be planted in rotation with potato. The tubers occur in a wide variety of attractive colors (**Figure E2.1B**), and are increasingly of interest as a food crop in other parts of the world. To better understand how ancient people first established oca crops, Emshwiller uses information from farmers about how they use oca, linguistics, as well as DNA sequencing to understand how different strains of oca are related to each other and to wild plants.

Farmers tell Emshwiller that they classify oca into two groups. The sweeter oca types, called wayk'u in the Quechua language, are cooked fresh after a few days in the sun. Other types, known as khaya in Quechua, are soaked in water for a month to remove bitter-tasting oxalic acid, then naturally freeze-dried for long-term preservation. Emshwiller has been comparing gene sequences from these and wild oca to determine how these plants are related and how the crop varieties originated from wild ancestors. Her studies will illuminate the processes by which humans domesticate food crops and disseminate knowledge of new agricultural and food-processing methods.


Armando Mamani Mamani

E2.1A Eve Emshwiller


Eve Emshwiller

E2.1B Oca

by ancient people led to the discovery that thousands of plants were useful as food, medicine, or construction materials. Modern industrialized societies owe enormous debts of gratitude to past and present indigenous cultures that over millennia have done the hard work of developing and preserving knowledge of plant uses. Ethnobotanists bridge the gap between folk wisdom and modern science, bringing to industrialized societies traditional knowledge that may otherwise have been lost (see Essay 2.1, "Ethnobotany: Buried Treasures").

Ethnobotany often interfaces with archeology, the study of past human activity. One fascinating example involves Cahokia, a large pre-Columbian site along the Mississippi River near modern St. Louis. Famous for large mounds and other imposing constructions that supported more than 15,000 people, Cahokia served as the administrative center for colonies extending northward into Wisconsin. Cahokia also traded with coastal societies to the south. Recent chemical analyses of residues absorbed into pottery cups that were found at Cahokia revealed a caffeine-rich substance typical of the holly plant *Ilex vomitoria*. The scientific name of this shrub, native to southern regions of the United States, reflects its emetic properties. Cahokians imported *I. vomitoria* to make Black Drink, a beverage that seems to have been as important in their everyday lives as coffee is to us today. People would consume Black Drink for stimulation and ritual cleansing of the body before important events such as religious rituals, political meetings, negotiations, sporting events, or warfare. To make Black Drink, holly leaves and small twigs were first toasted, then boiled with water, and finally agitated into a froth, much as a modern barrista might prepare a specialty coffee drink. Although Black Drink is not commonly consumed today, such knowledge helps us to understand how past humans used plants in ways similar to those of modern times.

Economic botany often interfaces with economics, the social science concerned with how people use resources. For example, economic botanists recently studied cacao (chocolate) cultivation in regions of Indonesia recognized for high natural biodiversity. The botanists aimed to determine the best way to preserve nature while also taking into account farmer preferences. The scientists observed that growing cacao trees beneath the shade of taller, native trees helps preserve many forest-loving species, but that farmers can obtain more profit by growing cacao in unshaded plots. By analyzing regional land use, surveying households, and determining plant and animal numbers, sizes, and types, the scientists discovered that a compromise situation was possible. Farmers' income can double when crops are grown under partial shade that maintains much natural biodiversity. Economic botanists also proposed that ecologically-concerned chocolate consumers might be willing to pay premium prices which, passed along to farmers, might encourage more farmers to grow cacao in more shaded conditions that preserve maximum levels of biodiversity. Understanding the tradeoffs that affect biodiversity and income are important to helping people earn a living while at the same time preserving as much of nature as possible.

The next section focuses on the origins of agriculture, arguably the most important scientific and cultural advance in human history. Agriculture is the purposeful cultivation of living things to sustain human life. Understanding how the first plant crops originated is a major goal of many ethnobotanists and archeologists because such efforts have yielded many useful lessons for modern societies.

2.1 Reviewing the Learning Goals

1. Ethnobotanists study the past and present uses of plants by traditional societies by combining procedures typical of natural sciences (such as botany and chemistry) with those used to study human cultures.
2. Economic botanists focus on the use of plants in modern industrialized societies by meshing techniques used in modern ecology with those of social sciences.

2.1 Testing Your Learning Goals

1. How does the natural science of botany interface with social sciences?
   - a. Ethnobotanists combine ways of understanding plants, such as plant chemistry, with analysis of human societies.
   - b. Economic botanists focus on how modern agricultural societies use plants.
   - c. Anthropologists, who focus on past human activities, often need to understand how past cultures used plants.
   - d. All of the above are correct.
   - e. None of the above is correct.

2.2 The origin of agriculture

Learning Goals:

1. List some sources of information that help scientists learn about the origin of agriculture.
2. Explain where, when, and why agriculture appears to have arisen.
3. Explain how the environments of wild ancestors of modern cereals and legumes influenced plant properties in ways that make these plants particularly useful to people.
4. Describe major differences between modern domesticated cereals and their wild relatives.
5. Describe the roles of mutation and selection in plant domestication.

Humans who first learned to cultivate food plants lived thousands of years ago, before the invention of writing. Thus, we have no written records of their monumental achievement. Yet it is possible to know a great deal about such ancient events from the unearthed remains of human activities that occurred thousands of years in the past. Sometimes pottery shards depict food or ceremonial plants or bear impressions of plant materials. Scientists also analyze seeds, grains, wood, pollen, and plant fibers that were preserved by being dried, charred in fires, or buried in lake sediments. Mineral crystals known as phytoliths (meaning "plant stones") are often produced within plant cells where they help protect plant tissues from being completely consumed by animals. The grittiness you experience while eating pears is caused by phytoliths. Such phytoliths do not decay when surrounding plant tissues do, and occur in different forms that are distinctive for particular plants (Figure 2.2). Starch grains that are stored in plant cells as nutritional reserves likewise occur in diverse shapes that are diagnostic of particular plant species (Figure 2.3). Starch grains can be found adhering to stone grinding tools or cooking utensils that are thousands of years old. For example, starch grains obtained from 105,000-year-old stone tools found in Mozambique reveal that ancient humans who lived there gathered and ate the seeds of wild grasses such as sorghum. A few modern cultures likewise lack agriculture and depend on foraging for food supplies, and so model aspects of early human hunter-gatherer societies. Learning how these cultures obtain and process plant foods helps anthropologists understand pre-agricultural phases of human life. Taken together, these varied sources of information provide a picture of when, why, where, and how agriculture began and its role in nurturing human civilizations.

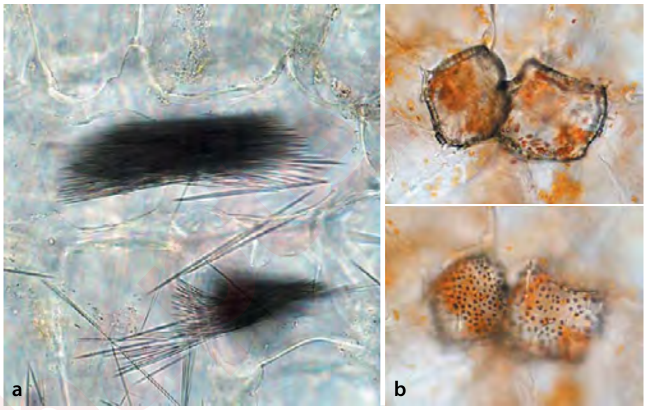


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FIGURE 2.2. Phytoliths In (a), thin crystals called raphides are shown, photographed in cells of a banana peel viewed with a microscope. In (b), thick-walled cells ("stone cells") from a pepper are seen with the microscope focused in two different planes.

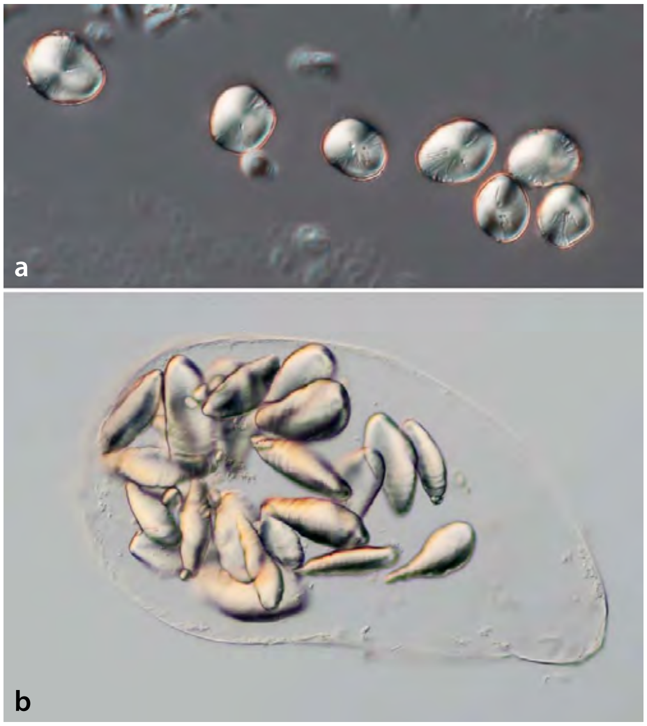

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FIGURE 2.3 Starch grains The size and structural features of starch grains varies among different plant species. Those shown here are from (a) popcorn (*Zea mays*), in which they were scraped from unpopped kernels, and (b) banana (*Musa* sp.), where they are still found within a cell.

When and why did agriculture rise?

Ancient human societies obtained food by hunting, fishing, and gathering wild plants until ~11,000 years ago, the earliest time period associated with deliberate plant cultivation. The shift from foraging to agriculture as a primary mode of food acquisition occurred gradually and apparently independently in several different regions around the world at about the same time. Many experts think that this agricultural revolution might be related to a worldwide climate change leading to warmer conditions at the end of the most recent ice age. This climate warming is also linked to a rise in atmospheric carbon dioxide levels that would also have increased the rate of plant photosynthesis. Scientists think that these environmental changes favored the growth of grasses, legumes, and other wild plants that were nutritious, easily stored, and otherwise suitable for transformation into crops, a process known as **domestication**.

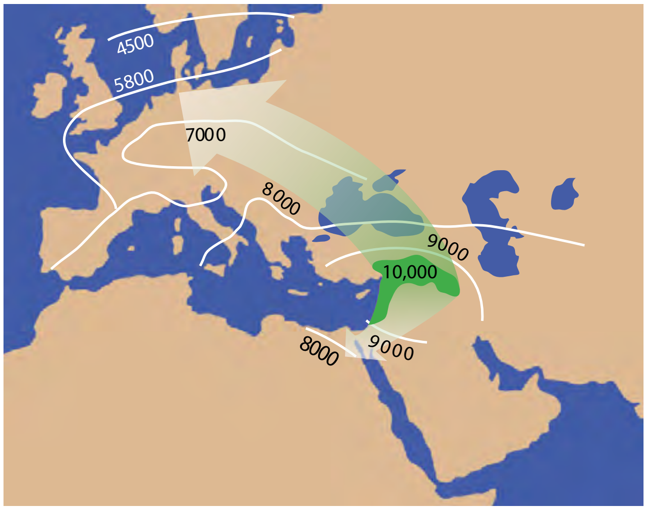
Domestication is an evolutionary process, guided by humans, that results in organisms having traits that differ in some useful way from those of wild relatives. Early farmers generated crop plants that differed from wild relatives by selecting plants having useful traits as the sources of seed for planting the next generation and continuing to perform this selection process over many years. As crop plants changed through time in ways that were beneficial to humans and humans domesticated farm animals, agriculture became more efficient, allowing human populations to increase.

Another boost for human populations came with the development of methods for food storage from year to year. Food storage reduces the risk that food supplies could suddenly and unexpectedly fail—an ever-present danger for the forager. Because agricultural food production does not require that everyone be involved, some people were freed to practice other pursuits, including the arts, architecture, philosophy, science, medicine, law, and commerce. Major human civilizations, past and present, were built on the foundation of a productive agricultural system.

Where were plants first domesticated?

Agriculture seems to have originated independently in multiple geographic locations, including the Near East, Far East, Mesoamerica, South America, and the Eastern United States. Among the oldest evidence for domesticated plants are remains of cultivated wheat and barley in 11,500 year-old deposits of southern Turkey and northern Syria, and domesticated figs in archeological sites in the Jordan Valley that are more than 11,000 years old. Legumes, domesticated relatively early in the Near East, are plants of the pea family named for their pod-shaped fruits. Like cereals, members of the grass family whose fruits are known as grains, legumes are valued as rich sources of protein in the human diet. Other modern crops that were first domesticated in various parts of the Near East include olives, grapes, figs, dates, pistachios, almonds, and pomegranates.

Agricultural knowledge spread rapidly from the Near East, reaching southern Europe by about 8,000 years ago, the Balkans and Central Europe by 7,500 years ago, and Scandinavia by 4,500 years ago (Figure 2.4). Europeans expanded the number of domes-



Re-drawn and modified from Diamond, J. (1997) Nov 14 278:1243. Location, location, location: the first farmers. © 1997 AAAS.

FIGURE 2.4 The spread of agriculture This map depicts the spread of agriculture from an origin in the Near East. Numbers represent thousands of years ago.

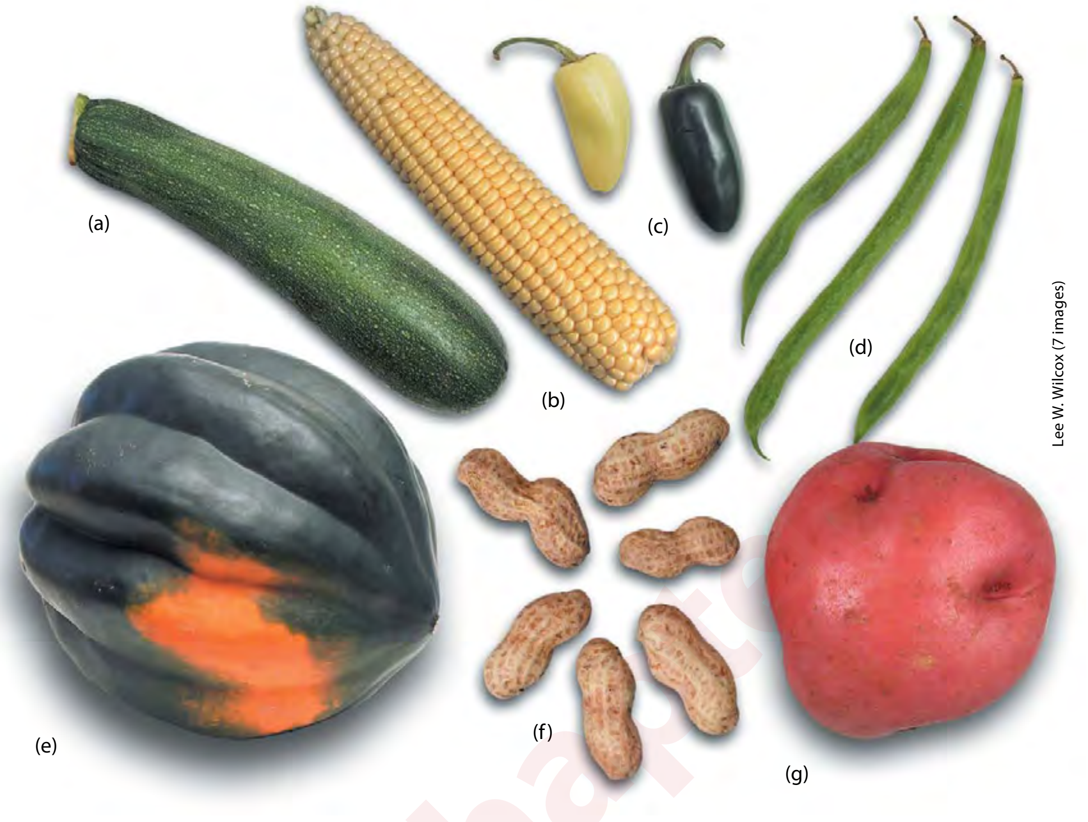


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FIGURE 2.5 Foods domesticated in Central and South America Ancient Americans domesticated (a) zucchini, (b) corn (cereal), (c) chilies, (d) beans (legume), (e) squash, (f) peanuts (legume), and (g) potato.

ticated plants to include such valued crops as oats, apples, pears, plums, and cherries. Some language experts, using techniques borrowed from evolutionary biologists, find evidence that a Proto-Indo-European language originated in large, Neolithic settlements in the same Near Eastern region associated with the origin of agriculture. Linguists think that this ancestral language eventually gave rise to nearly 150 distinct Eurasian languages (including English), which spread and diverged alongside agricultural knowledge. Archaeologists suspect that the advent of farming fostered the building of intriguing megalithic constructions at Stonehenge, Avebury, and other sites in Britain.

In the Far East, including sites along the Yellow and Yangtse River Valleys in China, people domesticated the cereal crops rice and millet, soybean (a legume), and hemp, whose fibers have been used in making cloth, paper, and rope for the past 5,000 years. Phytoliths and distinctive starch particles found stuck to the surfaces of stone tools indicate that bananas and taro (a starchy root crop from the plant *Colocasia esculenta*) were cultivated in New Guinea nearly 7,000 years ago. Coconut and sugar cane were also domesticated in tropical Southeast Asia.

Before the arrival of Europeans in the 15th century, Native Americans had domesticated more than 100 species of plants, including more than half the world's major modern crops. In addition to starchy oca (see Essay 2.1), crops first grown by people living in present-day North, Central, or South America include sunflower, squash, tomatoes, potatoes, maize, and several types of chili peppers. The protein-rich legumes peanut, common bean, and lima bean were also domesticated in the Americas (Figure 2.5).

Ecological adaptations are responsible for the useful features of cereals and legumes

A comparison of crops domesticated throughout the world (Table 2.1) reveals that most early agricultural societies cultivated both cereal and legume crops. This is no coincidence. Consumed together, cereals and legumes provide all of the amino acids needed in the human diet. For this reason, as most vegetarians know, a diet that includes both cereals and legumes can substitute for eating meat as a source of protein. In addition, cereal and legume harvests can be stored for long periods without spoiling. For ancient people, storehouses filled with these foods aided survival during stressful times. The nutritional and storage advantages of cereals and legumes arose as the results of adaptation to their environments by wild ancestors.

Cereals—named for the Roman goddess Ceres—that were domesticated early in human agricultural history include wheat, barley, rice, and corn (maize). As members of the grass family, cereals have in many ways become well adapted to grassland environments, which are typically drier than regions that support forests. Food production in cereals and other grasses is more efficient than in most other plants in dry conditions. Grass leaf structure and arranges fosters the absorption of sunlight for photosynthesis, grass stems resist damage by animals and fire, and grass roots are adept in absorbing minerals from deep soil sources (see Chapter 27). These features allow grass plants to store large amounts of carbohydrates and proteins in their one-seeded fruits (grains), and these reserves support the rapid growth of seedlings.

The high protein content of legumes arises from their ability to harness the biochemical properties of soil microbes. In response to low-nutrient soils, legume roots attract certain soil bacteria that are capable of producing nitrogen fertilizer from abundant nitrogen gas in air, a process that plants alone cannot perform. The bacteria multiply inside legume roots, nourished by food supplied by the plants, and, in return, provide needed nitrogen fertilizer to legume roots and the soils in which they grow. This partnership allows legume plants to produce more protein-rich seeds, increasing reproductive success. Like cereal grains, legume seeds are dry when mature, which is an adaptation to arid habitats. By collecting wild grains and legume seeds for food, humans learned to take advantage of the high productivity and nutritional content well before the origins of agriculture. That several types of cereals and legumes were domesticated relatively early and in diverse locations reflects their great value to humans.

Table 2.1 Some Crops Associated with Major Centers of Plant Domestication

Center	Uses	Common Name	Scientific Name
Near East	Cereal foods	Wheat	*Triticum monococcum, T. turgidum*
		Rye	*Secale cereale*
		Oats	*Avena sativa*
	Legume food	Lentil	*Lens culinaris*
	Legume forage	Alfalfa	*Medicago sativa*
	Other fruit	Fig	*Ficus carica*
	Fiber	Flax	*Linum usitatissimum*
China	Cereal food	Rice	*Oryza sativa*
	Legume food	Soybean	*Glycine max*
	Other fruits	Mulberry	*Morus alba*
		Orange	*Citrus sinensis*
	Fiber	Hemp	*Cannabis sativa*
New Guinea	Other fruit	Banana	*Musa spp.*
	Other food	Taro	*Colocasia esculenta*
Mexico and Central America	Cereal food	Corn	*Zea mays*
	Legume food	Common bean	*Phaseolus vulgaris*
	Other fruits	Avocado	*Persea americana*
		Squash	*Cucurbita pepo*
		Cacao	*Theobroma cacao*
		Red pepper	*Capsicum spp.*
	Other	Sweet potato	*Ipomoea batatas*
	Fiber	Cotton	*Gossypium hirsutum*
Central Andes	Legume food	Peanut	*Arachis hypogaea*
	Other fruit	Pineapple	*Ananas spp.*
	Other food	White potato	*Solanum tuberosum*
		Manioc (cassava)	*Manihot esculentum (M. esculenta)*
	Other	Rubber	*Hevea brasiliensis*

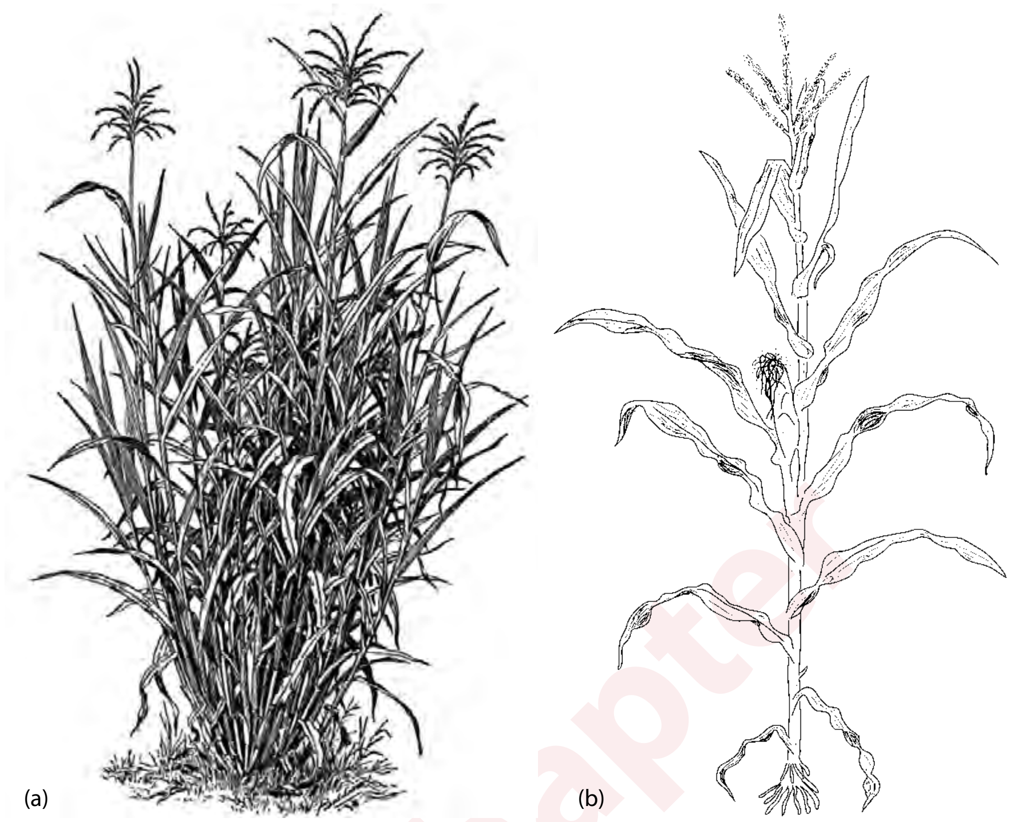
Today, wheat is widely used today for production of bread, pasta, and other food products. The average protein content of wheat is about 13%, higher than other cereals, and the whole grain contains iron and B-vitamins. Corn (maize) is a particularly versatile crop that can be used directly as human food (sweet corn and popcorn); to feed livestock (dent or field corn); to manufacture corn oil, corn meal, corn flour, corn syrup, and corn starch used in cooking and in processed foods; and to produce alcohol for use as a fuel and in beverages such as bourbon. Rice is a staple food for millions of modern people. Together, wheat, corn, and rice provide more than 50% of the calories that humans consume.

Modern food crops described as legumes include soybean, pinto bean, green bean, broad bean, garbanzo bean, peanut, green pea, lentil, and lima bean, as well as alfalfa, clover, lespedeza, and bird's-foot trefoil, which are used as livestock fodder. Soybean—probably the world's most widely planted legume—is also used in the production of such industrial products as paints, plastics, oils, and adhesives. The part of legume plants most frequently eaten by people is the seed, although we consume the entire fruit of green beans and pea pods. Livestock fodder includes most of the legume plant. Legume-derived foods are richer in protein than any other plant products. Legume crops are also valued because they enrich the soil where they are planted by adding nitrogen fertilizer. Farmers can rotate legumes with other crops that tend to deplete soil nitrogen levels in order to replenish soil nitrogen. This is of particular importance to farmers around the world who cannot afford to purchase and apply commercial nitrogen fertilizers.

How were cereals and legumes domesticated?

No one is quite sure how people first thought of deliberately planting the seeds of food plants. One possibility is that a few seeds remained in the unused parts of gathered food plants that were dumped in local trash heaps. These seeds later germinated, forming a dense growth that was more easily harvested than wild plants. Some enterprising person may have then tried scattering seed in a convenient location and soon realized how much easier it was to grow food plants nearby rather than to forage for them. In forested areas of the world, agriculture might have begun with human care of long-lived wild food plants in their natural environment. Repeated, tiring visits to prune, weed, and reap the harvest may have generated the idea to plant crops in plots closer to home.

When modern crops are compared to their wild relatives, differences are obvious. The grains of modern wheat are noticeably larger than those of wild relatives still growing in the grasslands of the Near East. Grains of wheat that accidentally fell into fires and became preserved as charcoal found at archeological sites show an increase in size over time. In addition, the fruit-bearing spike of modern cereal crops does not fall apart or shatter, as does that of the wild relatives. Shattering is advantageous to wild cereals because it helps spread the progeny of the parent plants as far apart as possible, which reduces competition for water, light, and



(a) USDA-NRCS PLANTS Database / Hitchcock, A.S. (rev. A. Chase). 1950. Manual of the grasses of the United States. USDA Miscellaneous Publication No. 200. Washington, DC.

FIGURE 2.6 Teosinte compared to a modern corn plant Teosinte (a) and modern corn (b). The dense, compact modern ear of corn represents an ear-bearing branch of teosinte that has been considerably shortened.

minerals. But shattering is disadvantageous to humans because it makes cereals more difficult to harvest. Scientists think that occasional mutations in wild cereals led to some plants having spikes that did not easily shatter. It is now known that change in a single DNA nucleotide in a gene called *sh4* was a mutation critical to rice domestication. The altered gene weakens the ability of rice spikes to shatter, but does not completely eliminate shattering. As a result, the grains stay on the plant long enough to be harvested, though grains can be easily separated by threshing. Similar mutations that reduced shattering occurred in wheat, barley, and corn (maize). Such variants, being more easily harvested by humans, would have been preferentially selected as sources of seed for planting new fields. Over many generations the non-shattering types would come to dominate the crop. Wild pea and lentil have fruits that open rapidly, which is beneficial for seed dispersal. But cultivated peals and lentils have fruits that open more slowly, facilitating human harvest. Similarly, humans repeatedly chose the largest cereal grains or legume fruits for seed, thereby contributing to a gradual increase in grain size.

Probably the most dramatic alteration that humans have achieved in food plants has been the transformation of a wild grass into modern corn (maize). Genetic (DNA) evidence has shown that the closest wild relative of modern corn is teosinte, a plant that grows in southern Mexico (Figure 2.6). The cobs of teosinte and modern corn are very different (Figure 2.7). Teosinte cobs bear only six to ten grains (also known as kernels), which are covered with a very hard, inedible casing. This hard fruit casing protects the seeds within from destruction by animals or microbes. The cobs of teosinte also lack a husk formed of leaves that, if present, would retard seed dispersal. In contrast, modern corncobs contain many more soft and edible grains, and a leafy husk encloses cobs, which increases ease of harvest and storage. Teosinte is much better adapted for survival in the wild than is cultivated corn.

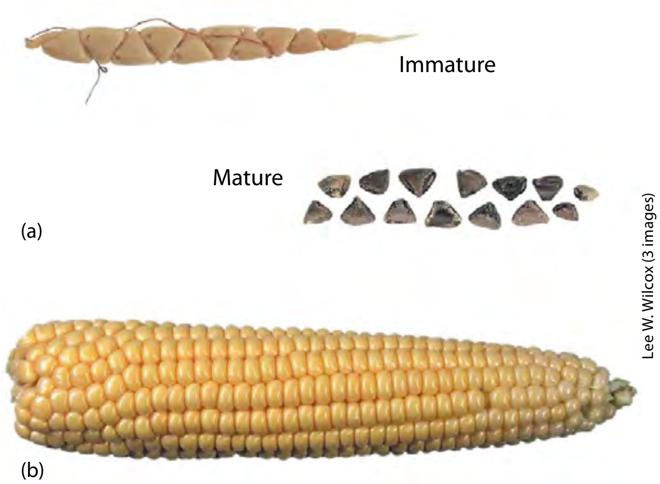


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FIGURE 2.7 Domesticated corn cobs differ from those of ancestral grasses Teosinte (a) has only a few, inedible grains per cob, in contrast to modern corn (b), which has many, edible grains per cob. Human (artificial) selection is responsible for these differences.

Some experts think that hunter-gatherers first began to grow teosinte as a sweet snack; they may have chewed the green ears and stalk pith much as Mexican children do today. Then ancient Americans may have noticed variants that had softer, edible kernel cases. People then began to cultivate the mutant teosinte for its grains. At least four other genetic changes occurred during the transition from teosinte to modern corn, explaining the dramatic difference in their appearance. Study of DNA extracted from cobs at least 4,300 years old, found in caves, has revealed that humans had already begun to alter the genetic structure of maize thousands of years ago. The many generations of Native Americans who transformed corn into its modern form accomplished an amazing feat of plant modification.

2.2 Reviewing the Learning Goals

1. Sources of information that scientists use to learn about the origins of agriculture include designs or impressions on constructed materials such as pottery, buried remains of plants, phytoliths, starch grains, and non-agricultural cultures that persist today.
2. Agriculture originated in several distinct centers at about the same period, starting ~11,000 years ago, when increased atmospheric carbon dioxide caused global warming, thereby changing human and plant environments.
3. The wild relatives of modern wheat, barley, and legumes adapted to arid environments by acquiring leaf, stem, root, and fruit features that make these plants unusually productive and nutritionally-rich sources of food for people. The wild relatives of modern legumes adapted to low-nutrient soils by forging partnerships with bacteria that are able to convert atmospheric nitrogen gas into nitrogen fertilizer.
4. Modern domesticated cereals produce spikes that do not readily shatter, whereas shattering is a common feature of wild relatives that fosters seed dispersal. Domesticated cereals also produce cobs with more and larger fruits (grains, kernels) that, in the case of corn (maize) are enclosed by a protective husk.
5. Mutations of DNA can alter plant features in ways that may not aid the success of wild plants but may benefit humans; in the past, observant humans selected seeds from these altered plants for cultivation. Over long time periods, human selection has generated domesticated crop plants.

2.2 Testing Your Learning Goals

1. In which of the following locations did agriculture arise independently thousands of years ago?
   a. Near East
   b. Far East
   c. Mesoamerica and South America
   d. Eastern United States
   e. all of the above
2. In what features does modern domesticated corn (maize) differ from its closest wild relative, teosinte?
   a. The cobs of modern corn bear many more kernels (grains, fruits) than do the cobs of teosinte.
   b. The grains of modern corn are soft, whereas those of teosinte have a hard, inedible coating.
   c. The cobs of modern corn are enclosed in a protective husk, whereas teosinte cobs lack a leafy enclosure.
   d. All of the above are correct.
   e. None of the above are correct.

2.3 Food plant genetic resources and traditional agricultural knowledge need to be preserved

Learning Goals:

1. Understand the processes of natural selection and artificial selection and how they affect plants.
2. Explain why farmers use monoculture or polyculture processes for growing crops in different latitudes.

Producing sufficient food has always been a challenge for the world's farmers and will continue to be a persistent problem in the future. These challenges arise from increases in human populations, global climate changes that foster pest populations and reduce water availability, and limits to fertilizer production. The development of new types of crops that are better adapted to resist pests and drought is viewed as a necessary goal of modern agriculture. Conservation of wild relatives of modern crop plants and their habitats, as well as traditional varieties of crop plants from around the world, is now recognized as essential for the development of new types of crops. Preservation of genetic material from crop plants and their wild relatives is essential to modern strategies for improving crops by classic genetic methods that generate new hybrids (Chapter 15) or genetic engineering (Chapter 16).

Obtaining and preserving information about ancient and traditional agricultural methods is likewise important to feed the world's people. This is because older cultures and modern people that still practice agriculture in traditional ways have invented clever ways to produce crops in diverse habitats or under difficult circumstances. By borrowing from cultivation practices of the past and traditional present, modern farmers may be able to cope with new challenges arising from population pressure and global environmental change.

For example, modern western agriculture typically involves planting large areas with a single type of crop (Figure 2.8), a practice known as **monoculture**. Farmers in a particular region will often use the same hybrid seed variety, typically bred for increased food production. The advantage of monoculture is relative ease of planting and harvesting. But a negative aspect of monoculture was dramatically revealed in the 1970s, when in some areas of the United States as much as 50% of the corn crop was lost and the total U.S. harvest was reduced by more than 15%. This disaster was caused by a fungal infection called southern corn leaf blight. Crop scientists (agronomists) knew that the widely planted hybrid was more vulnerable than other corn varieties to this disease, but no one expected such a rapid and extensive spread of the fungus. The pest's spread was favored by the absence of genetic variation in U.S. hybrid corn.

Agricultural experts now recognize that low genetic variation in modern crops is a widespread and serious problem. In response, crop scientists have collected and stored samples of crop varieties from around the world as sources of genetic material for plant breeding. They also collect wild relatives of modern crop plants, which have proven to be excellent sources of genes for pest and drought resistance. Such genes occur in wild plants because the presence of insect pests and microbial diseases, natural climate

Lee W. Wilcox (2 images)

FIGURE 2.8 Monocultured crops This cornfield (a) and soybean field (b) in Central Illinois are familiar examples of modern cereal and legume crops that are grown in large populations of uniform genetic composition.

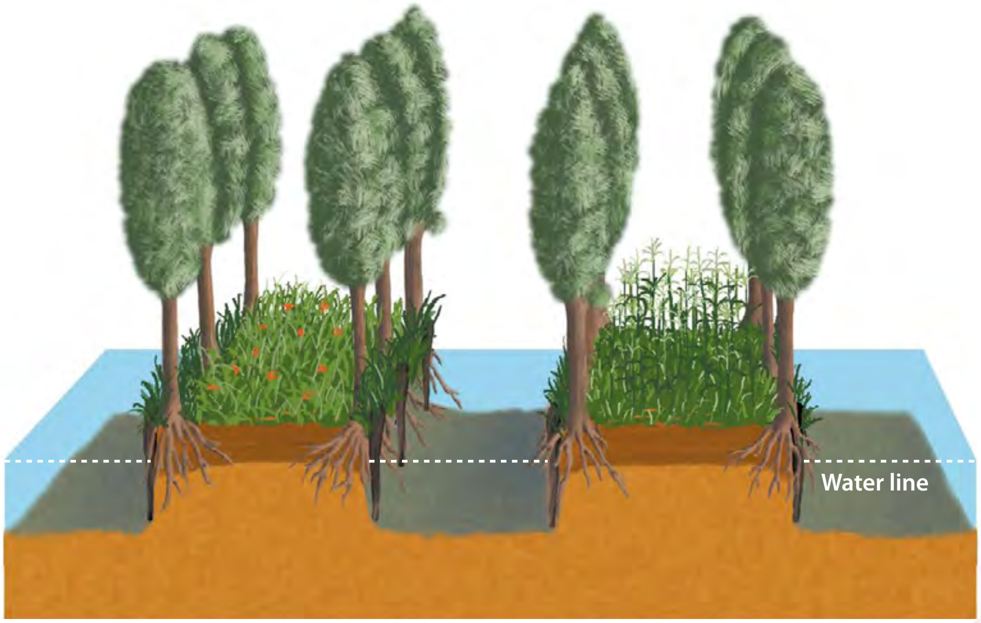

FIGURE 2.9 Diagram of chinampas agriculture Crops of several types are grown together on raised linear beds interspersed with water channels. This cultivation method reduces losses from insects and diseases and at the same time provides for irrigation.

variation, favors the survival of pest- or drought-resistant plants. The process by which wild plants become adapted to survive and reproduce despite environmental challenges is **natural selection**. Humans perform the similar process of **artificial selection** when they select plants having desirable traits for cultivation. People take advantage of natural selection by collecting potentially useful plants from nature and storing them in gene banks, seed banks, or germplasm repositories. In such banks, plants can be maintained for long periods and made available to scientists as needed.

Unfortunately, loss of the natural habitats of the wild relatives of modern crop plants is a worldwide problem. Natural areas are often lost to agricultural development, which involves destruction of the native vegetation. Farmers may replace traditional crops of greater genetic variation with commercial crops of lower genetic variation. Also, farmers sometimes destroy wild relatives of commercial crops to prevent interbreeding. Preservation of natural habitats that harbor wild relatives of modern crops and traditional crop varieties has become an essential measure for improving food security for the world's population.

Another modern agricultural problem is the loss of knowledge about traditional methods for growing crops, especially techniques developed in tropical areas. Monoculture methods, which can work well in temperate areas once occupied by extensive grasslands and consequently climatically suited for cultivation of cereal crops, often do not work well in the moist tropics. This difference arises from a variety of climate and biological factors, including more rapid reproduction of pests and weeds in the tropics (Chapter 28). Furthermore, tropical farmers typically cannot afford to use chemicals for crop protection. Over the centuries, traditional farmers in the tropics have developed a variety of creative agricultural techniques that are well adapted to their local environments. One example is **chinampas** cultivation (Figure 2.9), invented by the ancient inhabitants of the Tehuacan Valley of Mexico 2,000 years ago in response to the challenge of farming swampy land. These farmers created raised, linear soil beds where they grew a mixture of corn, beans, squash, and other crops. This practice of growing several crops together, known as **polyculture**, is particularly well suited to the tropics because it reduces the ability of pests to find and entirely destroy any one crop. Crop beds were interspersed by water channels that provided a constant water supply to crops while also facilitating transport of the harvest using boats. The method was so successful that it formed the economic basis for the Aztec civilization that existed until 1519. Modern Mexican farmers continue to use the chinampas technique in areas having persistently wet soil because it also has low reliance on fossil fuels and chemical application. Many other locally adaptive agricultural techniques are being discovered through the study of traditional cultures.

Yet another reason for studying traditional agriculture is that new types of food crops may be revealed. Of the several hundred plants that have been domesticated, only 12 crops—primarily wheat, rice, corn, and potatoes—form the basis of most of the world's agriculture. A comparison of the diets of people in industrialized countries reveals that they eat fewer types of plants than those in non-industrialized countries, and some experts think that reliance on just a few crop plants is a dangerous dependency.

2.3 Reviewing the Learning Goals

1. Preservation of wild genetic resources by protecting natural habitats and the plants that rely upon them is essential to classical plant breeding programs that generate hybrid seed and genetic engineering to produce new crops that are better adapted to cope with environmental change and the needs of humans.
2. Learning about successful agricultural practices of the past and those performed by modern traditional cultures offers opportunities to improve modern agriculture.

2.3 Testing Your Learning Goals

1. True or false? Artificial selection is the process by which humans select plants having desirable characteristics for cultivation, thereby gradually changing the features of plants over time.
2. True or false? Natural selection is the process by which nature selects plants having traits that foster survival and reproduction in particular habitats, thereby gradually changing the features of plants over time.

2.4 Natural plant products are useful to humans as medicine and in other ways

Learning Goals:

1. Explain how secondary compounds differ from primary compounds.
2. Explain how secondary compounds benefit plants and are also useful to humans.
3. Describe the natural roles of psychoactive compounds produced by plants.
4. Explain why compounds such as caffeine, nicotine, and cocaine affect humans.

Crop plants are valued primarily because they are sources of minerals, vitamins, and primary compounds—carbohydrates, lipids (fats and oils), and proteins. These plant materials are important as major components of plant structure or as part of the chemical reactions that take place in plant cells. Primary compounds, minerals, and vitamins also explain the value to humans of plants as food. However, people also use plants as sources of medicines, herbal dietary supplements, and psychoactive drugs, as well as poisons, stimulating beverages, spices, perfumes, oils, waxes, gums, resins, fibers, and dyes. These non-food uses are based on the presence in plants of organic compounds known as **secondary compounds** (or **secondary metabolites**) that help protect or strengthen plants or aid in reproduction. Together, plants produce about 100,000 different kinds of secondary compounds. The chemical makeup of secondary compounds differs from that of primary compounds (see Chapter 4).

The roles of secondary compounds in plants include defense against plant-eating animals (known as herbivores) and disease-causing microbes. Because plants cannot run away, they depend on chemicals for defense; consequently, they have become experts at chemical warfare. Plants are surrounded in nature by voracious herbivores, including swarms of ravenous insects, and deadly microbes—yet still they flourish. This is a testament to the ability of plants to defend themselves chemically. Well-defended plants live to produce more descendants; thus, natural selection explains the presence of secondary compounds in plants. Individual plants also cannot move, so they often use animals to transport reproductive cells to accomplish mating or seeds to accomplish dispersal to new locations. Secondary compounds are involved in producing flower and fruit colors and fragrances that entice animals to perform these transport roles (see Chapter 25).

Plants contain mixtures of many types of secondary compounds and may differ considerably in the amount of secondary chemicals that they contain. To deal with their many enemies, plants require many different types of chemical defenses. Plants growing in tropical rain forests, where the diversity of insect pests and disease microbes is very high, typically have more defensive chemicals than plants living where the defensive challenges are fewer. As a result, plants differ in their usefulness to humans as beverages, spices, or medicines, as well as in their toxicity or psychoactivity—influence on the animal nervous system. For this reason, new medicinal compounds are often sought in tropical plants, and traditional healers in the tropics are often the focus of ethnobotanists' attention.

Plants are sources of medicine and dietary supplements

Among the common medications used in developed countries, more than one-quarter include plant-derived ingredients. One example is ipecac, used to induce vomiting in poisoning cases. Ipecac is derived from the plant *Cephaelis ipecacuanha*, native to South America. Cancer drugs originating from plants include podophyllin produced by the North American mayapple (*Podophyllum peltatum*) (Chapter 28), leukemia drugs from the Madagascar periwinkle (*Cantharanthus roseus*), and taxol from the Pacific yew (*Taxis brevifolia*) (Chapter 8).

In some other parts of the world, people often rely primarily on medicines derived from plants collected directly from nature.

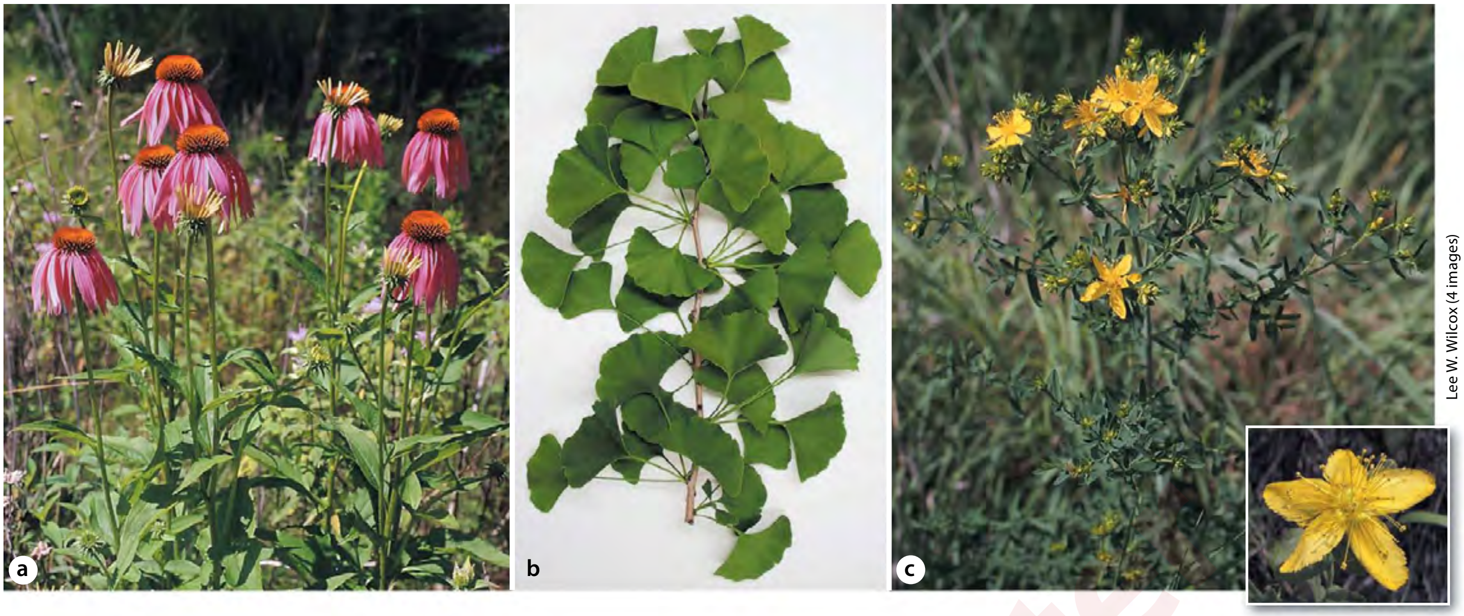

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FIGURE 2.10 Plants used in herbal preparations (a) Purple coneflower (*Echinacea purpurea*) roots and underground stems were used by Native Americans to treat wounds, and extracts are now marketed as treatment for colds and other infections. (b) *Ginkgo biloba* (the maidenhair tree) is a nonflowering seed plant (gymnosperm) whose dried leaves and seeds are used in herbal preparations that purport to improve memory. Extracts of whole St. John's Wort c. (*Hypericum perforatum*) plants are sold as preparations that are supposed to relieve depression. *Echinacea* and *Ginkgo* are also valued in gardens and streetside plantings.

Aloe barbadensis' widespread use as a skin treatment was described at the beginning of this chapter, and willow bark has long been chewed for pain relief, as it contains an active compound similar to commercial aspirin. The poppy *Papaver somniferum*, native to Eurasia, has been used since ancient times to relieve pain. Poppy contains more than 26 active compounds, including the habit-forming morphine, but also non-habit-forming codeine—used in cough medicines—and papaverine—used in the treatment of intestinal spasms.

People have long used herbs as dietary supplements and as a source of perceived health benefits. In recent years, commercial preparations from such plants as St. John's Wort, ginseng, garlic, *Ginkgo biloba,* goldenseal, saw palmetto, and *Echinacea* (Figure 2.10) have become popular in industrialized countries. The market for such products—termed herbs, nutriceuticals, or phytochemicals—is worth billions of dollars annually in the United States alone. Typically, plants are supplied in dried form, as in teas, or as extracts packaged in capsules; the active ingredients are not isolated. However, because (as previously mentioned) plants contain mixtures of many types of secondary compounds, commercial preparations made from plants typically contain mixtures of compounds that can influence human health. Secondary compounds commonly vary in relative proportions from one harvest to another. Researchers report substantial variation in the ingredient content of commercial herbal products, and also variations in patient responses to herbal supplements. Consequently, the consumption of herbal preparations is considered to be a human health issue.

It is important for human health that decisions about herbal supplements are based on scientific evidence. Experts recommend that responsible governmental regulation and certification would encourage the supplement industry to invest more in high-quality nutrition research. In the United States, the National Institutes of Health (NIH) Center for Complementary and Alternative Medicine is a federal agency that supports scientific research on the medical efficacy of herbal treatments. The NIH is a unit of the Public Health Service, which in turn is part of the U.S. Department of Health and Human Services. The NIH also supports an Office of Dietary Supplements, enabled by the 1994 Dietary Supplement Health and Education Act. This office is concerned with the development of reliable methods for analyzing chemical components of herbal supplements.

Plants are sources of psychoactive drugs

Some plants contain psychoactive compounds that help protect plants against animal herbivores by altering attackers' nervous system function. When herbivores consume these compounds, the animals may experience behavior changes that decrease feeding or increase vulnerability to their own predators. Since the human nervous system is similar to that of other animals, psychoactive plant compounds also affect humans. Depending on their effects on humans, psychoactive plant compounds are classified as stimulants, depressants, hallucinogens, or narcotics. Psychoactive compounds affect humans in a dose-dependent way; low doses may be stimulatory, but high doses can be dangerous—even lethal. Some psychoactive plant compounds are habit-forming (addictive) in humans, whereas others are not. Stimulants include cocaine, derived from the Coca plant; caffeine, derived from *Coffea*; and nicotine, derived from tobacco (*Nicotiana*). Plants that have been used for their hallucinogenic (psychedelic) properties include *Cannabis* (marijuana), native to Asia; belladonna (*Atropa belladonna*), native to Europe; as well as *Datura* and the peyote cactus (Figure 2.11), both native to the U.S. desert southwest and other world regions.

The National Institute on Drug Abuse is a U.S. Health and Human Services Department unit that deals with habit-forming plant compounds. This institute publishes bulletins on the specific health impacts of drugs of abuse, including the addictive substances nicotine, heroin, and cocaine, all derived from plants. Nicotine is only one of more than 4,000 components of tobacco smoke, but it is the major one that acts on the brain. Heroin, processed from morphine that occurs in poppy plants, acts in many places in the brain and nervous system. One effect is to depress breathing, sometimes to the point of death. Cocaine—though sometimes used medicinally—interferes with normal chemical communication among brain cells. Long-term cocaine use can generate full-blown paranoid psychosis, heart attack, breathing failure, and stroke. Knowledge of the beneficial and harmful effects of these and other plant secondary compounds is essential to maintaining good personal health and is vital for making sound societal policy decisions.


Claudia Lipke

FIGURE 2.11 **The peyote cactus, *Lophophora williamsii***

2.4 Reviewing the Learning Goals

1. Primary compounds are carbohydrates, lipids, and proteins that perform basic cell functions in all living things and are useful as food, whereas secondary compounds serve other functions in plants and are useful to people in diverse ways.
2. Secondary compounds occur in many different types and help protect or strengthen plants as well as aid in reproduction, and humans use these materials for stimulants and medicines and many other purposes.
3. Psychoactive compounds affect the nervous systems of animals that attack plants, thereby helping to protect plants from consumption by plant-eating animals.

4. Plant-produced alkaloids often affect humans because our nervous systems function much like those of other animals.

2.4 Testing Your Learning Goals

1. Which of the following medicinal materials is derived from plants?
   a. ipecac
   b. podophyllin
   c. taxol
   d. codeine
   e. all of the above
2. Which of the plants listed below has been used in traditional human societies for psychoactive effects?
   a. *Cannabis*
   b. *Datura*
   c. *Atropa*
   d. All of the above
   e. None of the above

Chapter Wrap-up

Examine and Discuss

Self Test

1. Describe three major regions in which plants were first domesticated and describe a legume and a cereal crop associated with each region.
2. What are the special advantages of cereals and legumes as food crops?
3. Provide an example of the role of artificial selection in the domestication of a food crop.
4. Explain how monoculture differs from polyculture and the advantages and disadvantages of each.
5. Explain why plants, particularly those of tropical regions, produce so many types of secondary compounds.
6. Why might physicians be concerned about people's casual use of herbal preparations?

Applying Concepts

1. If you were an archeologist who had discovered a previously unknown ancient human habitation, how could you decide from the plant remains uncovered in your excavation and a survey of the surrounding vegetation whether the ancient people who live there merely collected native plants for use or had developed agriculture?
2. If you were lost in a remote area with little prospect for immediate rescue and needed to eat wild plants, how might you deduce what kinds of plant foods might be least poisonous and most palatable?
3. If you were an agronomist (crop scientist) working in a non-industrialized country, what might you advise local farmers to grow to feed farm animals if the soil were low in nitrogen and the farmers could not afford commercial fertilizer?