Pearson New International Edition

Hartmann & Kester's Plant Propagation
Principles and Practices

Hartmann Kester Davies Geneve

Eigth Edition

ALWAYS LEARNING

PEARSON

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PEARSON

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Table of Contents

General Aspects of Propagation

Plant propagation not only describes procedures originating thousands of years ago, but also the application of recent scientific advances. Plant propagation can be described as *the purposeful act of reproducing plants.* It has been practiced for perhaps the past 10,000 years, and its beginning probably marks the start of civilization. The traditional concept of a propagator is a skilled technician who loves plants and who acquired the art from traditional skills learned by experience, or whose knowledge was handed down from one generation to another. Today, propagation may be carried out by an array of general and specialized industries that produce plants to feed the world; to provide fiber, building materials, and pharmaceuticals; and to enhance the world's beauty.

How Plant Propagation Evolved in Human Society

How Plant Propagation Evolved in Human Society

learning objectives

- Describe the evolution of plant propagation during human history.
- Describe aspects of modern plant propagation activities.

"And the earth brought forth grass, and herb yielding seed after his kind, and the tree yielding fruit, whose seed was in itself, after his kind: and God saw that it was good."

Genesis 1:12.

"Man has become so utterly dependent on the plants he grows for food that, in a sense, the plants have 'domesticated him.' A fully domesticated plant cannot survive without the aid of man, but only a minute fraction of the human population could survive without cultivated plants."

from: J. R. Harlan, *Crops and Man*, 2nd edition. Madison, WI: Amer. Soc. of Agron. 1992.

INTRODUCTION

agriculture The deliberate practice of propagating and growing plants for human use.

The propagation of plants is a fundamental occupation of humankind. Its discovery began what we now refer to as civilization and initiated human dominion over the earth. Agriculture began some 10,000 years ago when ancient peoples, who lived by hunting and gathering, began to cultivate plants and domesticate animals. These activities led to stable communities where people began to select and propagate the kinds of plants that provided a greater and more convenient food supply, as well as other products for themselves and their animals (21, 35). Once this process began, humans could remain at the same site for long periods of time, thus creating centers of activity that eventually would become cities and countries.

Agriculture is the deliberate cultivation of crops and animals for use by humans and involves five fundamental activities:

1. Plant selection—selecting and (or) developing specific kinds of plants.
2. Plant propagation—multiplying plants and preserving their unique qualities.
3. Crop production—growing plants under more controlled conditions for maximum yield.
4. Crop handling and storage—preserving crop products for long-term usage and transport to other areas.
5. Food technology—transforming and preserving crop products for food or other uses (e.g., making bread, pressing oil, preparing wine, dehydration, etc.).

STAGES OF AGRICULTURAL DEVELOPMENT

The pivotal role of plant propagation in the evolution of human society can be seen in terms of particular stages of agricultural development.

Hunting and Gathering

Most of the millions of years of human existence as hunters and gatherers were related to the presence of specific food resources including seeds, fruits, roots, and tubers, as well as animals that fed on the plants. The distribution and the characteristics of plant species were determined by the environment; that is, both the physical world (climate, soil, topography) and the biological interactions of plant, animal, and human populations (21, 32, 35). Humans have existed for millions of years, spreading from their presumed place of origin in western Africa into Asia, Europe, and, eventually, into North and South America. Food supplies were abundant in the native vegetation, although quite variable in different parts of the world. Apparently, early humans were quite effective in searching out those that were useful, as well as in developing processes to utilize and preserve them.

What motivated humans to begin to propagate and grow specific kinds of plants near their homes has been the subject of much scientific debate (21, 35). It is clear that the development of agriculture forever changed the relationship between humans and their surrounding environment. This event occurred in separate areas of the world, more or less simultaneously within a relatively short period of a few thousand years nearly 10,000 years ago. These areas included the Near East fertile crescent of Southwest Asia and Northeast Africa, extending from the valley of the Euphrates and Tigris Rivers along the coasts of Syria, Turkey, and Israel to the Nile Valley of Egypt; China, including a northern and a tropical southern area; and Central and South America, including areas in Mexico, and the coastal lowlands and highlands of Peru (21, 23).

The key activity bringing about this change must have been the deliberate selection and propagation and cultivation of specific kinds of plants that were particularly useful to humans. As a result, a larger and more stable population could be supported, which evolved into cities and countries. Human organization changed from subsistence existence, where everyone participated in the production of food and other items, to a division of labor between agricultural and non-agricultural segments of the population, and even to specialization within the agricultural segment. In this context, the plant propagator, who possessed specific knowledge and skills, had to assume a key role.

Domestication

domestication The process of selecting specific kinds of wild plants and adapting them to human use.

Early civilization developed with relatively few domesticated plant species, determined both by their usefulness in the primitive economy and the ease with which they could be propagated. The lists differed in the separate areas of the world where human societies evolved (21, 32, 34, 35). In the Near East, the earliest domesticated food crops included wheat, barley, peas, and lentil. In the Far East, millet appears to be the first domesticated crop, followed by rice. In Central and South America, the first food crops domesticated were apparently squash and avocado, followed by such important modern-day food crops as corn, bean, pepper, tomato, and potato. Many of the early food crops were seed plants (cereals, such as wheat, barley, rice), which provided carbohydrates, and legumes (beans, peas), which provided protein. These seed-propagated plants could be subjected to genetic selection in consecutive propagation cycles for such agricultural characteristics as high yield, "non-shattering," large seed size, and reduced seed dormancy. These species were maintained more or less "fixed" because of their genetic tolerance to inbreeding. Highly desirable single plants of certain species, such as grape, fig, olive, pomegranate, potato, yam, banana, and pineapple (39) could be selected directly from wild populations and "fixed" through vegetative propagation. Domestication of fruit plants, such as apple, pear, peach, apricot, citrus, and others occurred with the discovery of grafting methods. By the time of recorded history (or that which can be reconstructed), most of the basic methods of propagation had been discovered. During domestication, crop plants had evolved beyond anything that existed in nature.

The establishment of specific crops and cropping systems resulted in some side effects that have continued to create problems (21). As the fields used to grow plants near human sites were disturbed and became depleted, certain aggressive plant species also were spontaneously established in these sites. These so-called weedy species have become a part of the agricultural system and more or less evolved along with cultivated plants.

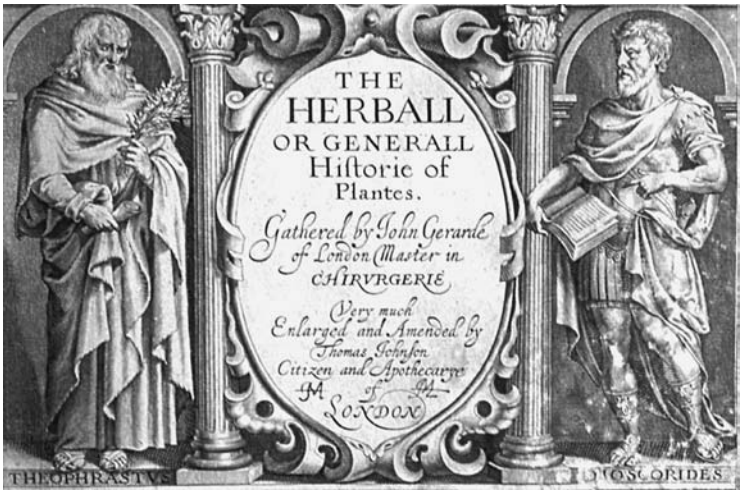


Figure 1
Theophrastus (300 BC) was an important influence on Renaissance agriculture, as indicated by his being depicted and commemorated on the front page of John Gerard's influential herbal, published in 1597. His image is in the left panel opposite his Greek counterpart Dioscorides (1 AD), renowned as an authority on the medicinal use of plants.

ORGANIZATION OF HUMAN SOCIETIES

Ancient (7000 BC)

The initial phases of domestication probably involved plant selection, plant propagation, and plant production. With an increase in food supply, a larger population could be supported and division of labor began to occur. Classes of individuals may have included laborers, manufacturers, artisans, government bureaucrats associated with irrigation systems, religious groups, and soldiers, as well as farmers and herdsmen. Historical records of early civilizations in Egypt and the Middle East (as well as archaeological investigations) have shown that the agricultural sector was well organized to produce food (cereals, vegetables, fruits, dates), fiber (flax, cotton), and other items for the non-agricultural components of society (25). Early Chinese writings indicate the knowledge of grafting, layering, and other techniques, although rice and millet were the principal food sources. In the Americas, seed-propagated crops (maize, beans, cucurbits, squash), as well as vegetatively propagated crops (potato, cassava, sweet potato, pineapple), were developed and grown.

Greek and Roman (500 BC to AD 1000)

Early writings described the agricultural world in detail with accounts of propagation techniques much as we know them today. Control of land and agricultural surplus was the key to power and wealth (35). Small and large farms existed. Olive oil and wine were exported, and grains were imported. Vegetables were grown near the home as were many fruits (fig, apple, pear, cherry, plum). Not only were food plants essential, but Romans developed ornamental gardening to a high level (21).

Some of the earliest references to plant propagation come from Theophrastus, a Greek philosopher (circa 300 BC) and disciple of Aristotle (Fig. 1). He described many aspects of plant propagation including seeds, cuttings, layering, and grafting in his two books *Historia de Plantis* and *De Causis Plantarum* (36, 37). An example from the translation of *De Causis Plantarum* (37) illustrates his understanding of propagation: "while all the trees which are propagated by some kind of slip seem to be alike in their fruits to the original tree, those raised from the fruit . . . are nearly all inferior, while some quite lose the character of their kin, as vine, apple, fig, pomegranate, pear."

Additional information on propagation can be seen in surviving works from Romans Pliny the Elder and Columella (circa 1 AD). For example, Pliny recommends that cabbage seeds be soaked in the juice of houseleek before being sown so that they will be "immune to all kinds of insects" (30), and Columella describes taking leafless, mallet stem cuttings in grape (12).

Medieval Period (AD 750 to 1500)

Society was organized around large estates, manor houses, and castles with landlords providing protection. Large areas of forest were kept as game preserves. Equally important were the monasteries that acted as independent agricultural and industrial organizations and preserved a great deal of the written and unwritten knowledge (Fig. 2). In both kinds of institutions, a separation developed among those involved in the production of cereals, fibers, and forages grown extensively in large fields (agronomy); vegetables, fruits, herbs, and flowers grown in "kitchen gardens" and orchards near the home (horticulture); and woody plants grown for lumber, fuel, and game preserves (forestry) (25).

Figure 2
The monastic garden was an enclosed area of medicinal and edible plants. The Cloisters in New York has several representative enclosed period gardens.

The end of the medieval period and the beginnings of modern Europe brought a shift from a subsistence existence to a market economy and the emergence of land ownership (35). In Western Europe, both large landowners and owners of smaller individual plots emerged. In Eastern Europe, the shift was toward large wealthy estates with the populace being largely serfs.

Through these periods, the specific skills and knowledge of the plant propagator were possessed by specific individuals. These skills, considered "trade secrets," were passed from father to son or to specific individuals. Often this knowledge was accompanied by superstition and, sometimes, attained religious significance.

EXPLORATION, SCIENCE, AND LEARNING

Plant Exchanges

The plant material exchange from the area of origin to other countries of the world has been one of the major aspects of human development. Not only did the range of plants available for food, medicine, industrial uses, and gardening expand, but plant propagation methods to reproduce them were required. Early movement of useful plants often followed military expansion into different countries when the invading soldier brought plants from his home country into a new land. Conversely, returning soldiers introduced to their homelands new plants they found while on a military campaign. There are numerous examples of this type of exchange taking place during the Roman conquests of northern Europe. Similarly, Islamic expansion in the 9th Century introduced citrus and rice to southern Europe, along with new concepts of cultivation and the use of irrigation. The voyages of Columbus opened the world to exploration and the interchange of plant materials from continent to continent. Such food staples as potatoes, tomatoes, beans, corn, squash and peppers all became available to Europe in the 16th and 17th centuries after voyages to the new world.

plant exchange The movement of plants from their place of origin to their place of use.

In addition to edible food crops, new and exotic plants were being sought out for introduction. Centers of learning in which scientific investigations began on all aspects of the biological and physical world were established in many countries. Linnaeus established the binomial system of nomenclature, and botanists began to catalog the plants of the world. Exploration trips were initiated where the primary mission was plant introduction, such as the voyages of Captain Cook in 1768, which included the plant explorers Sir Joseph Banks and Francis Masson who brought large numbers of exotic plants to England for the Royal Botanic Garden, established at Kew, outside of London (23, 31). Nathanial Ward, a London physician and amateur horticulturist, invented the Wardian case early in the 1800s to help preserve plant material on these long expeditions (Fig. 3) (38).

Wardian case A glazed wooden cabinet designed to keep high humidity inside and salt water spray outside the case on long sea voyages.

Plant-collecting trips continued throughout the world: from Europe (David Douglas, Joseph D. Hooker,

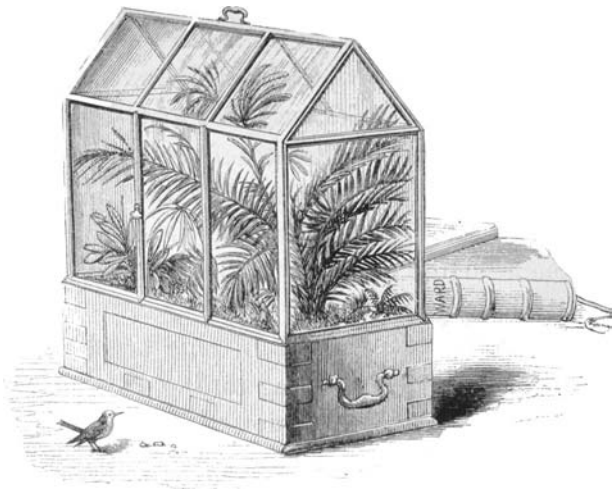


Figure 3
The Wardian case was invented by N. B. Ward in the early 19th Century to use when transporting plants over long ocean voyages.

Figure 4
Herbals were produced soon after the invention of the printing press to describe the utility of local and introduced plants. Plants such as this pea in Matthioli's herbal (*Commentarii*, 1564) were depicted from woodcuts on blocks.

Robert Fortune, George Forrest, Frank Kingdon Ward) and from the United States (David Fairchild, Frank Meyer, Joseph Rock, Charles Sargent, Ernest Wilson) (13, 18, 23, 31). Significant ornamental species that are mainstays of modern gardens were collected: from the Orient (rhododendron, primula, lily, rose, chrysanthemum), Middle East (tulips, many bulb crops), and North America (evergreen and deciduous trees and shrubs). "Orangeries" and glasshouses (greenhouses) were expanded to grow the exotic species being collected from India, Africa, and South and Central America.

Scientific and Horticultural Literature

The first important written works on agriculture, plant medicinal uses, and propagation that shaped western society came from the early Greek, Roman, and Arab writers between 300 BC and AD 2. Although many works were undoubtedly lost, many survive today because they were preserved in Arab libraries and passed on though medieval monasteries. Following the invention of the printing press in 1436, there was resurgence in the production of books called herbals (Fig. 4) describing and illustrating plants with medicinal properties. Much of the information came from older first century Greek literature, especially Dioscorides (Fig. 2). These early works were written in Latin, but eventually works began to appear in local languages (2), making plant information available to a wider audience.

The Renaissance heralded the appearance of scientific enquiry that relied heavily on meticulous observation of plant morphology and behavior. This is wonderfully shown in the illustrations from Marcello Malpighi (29) on plant anatomy in 1675 (Fig. 5).

In the late 1800s, the concepts of natural selection and genetics made a big impact on scientific advancement. Charles Darwin and his *Origin of Species* (14) as well as its important contemporary *The Variation of Animals and Plants Under Domestication* (15) introduced the concept of evolution and set the stage for the genetic discoveries following the rediscovery of Mendel's papers in 1900. The subsequent explosion in knowledge and application provided the framework on which present-day plant propagation is based, as did the increase in knowledge of plant growth, anatomy, physiology, and other basics of biological science (31).

Books and articles on gardening and propagation began to appear (16). The first book on nurseries, *Seminarium,* was written by Charles Estienne in 1530. Later, Charles Baltet, a practical nurseryman, published a famous book, *The Art of Grafting and Budding,* in 1821, describing 180 methods of grafting (see Figs. 6 and 7) (11). A book by Andrew J. Fuller—*Propagation of Plants*—was published in 1885 (19).

The Morrill Act

Morrill Act An act of Congress in 1862 that established land-grant universities for scientific study and teaching of agriculture and mechanical arts.

The passage of the Morrill Act by the United States Congress in 1862 was a landmark event that established land-grant colleges and fostered the scientific investigation of agriculture and mechanical arts. Departments of agronomy, horticulture, pomology, and related fields were established, which became centers of scientific investigation, teaching, and extension. Liberty Hyde Bailey (33), a product of this system, published his

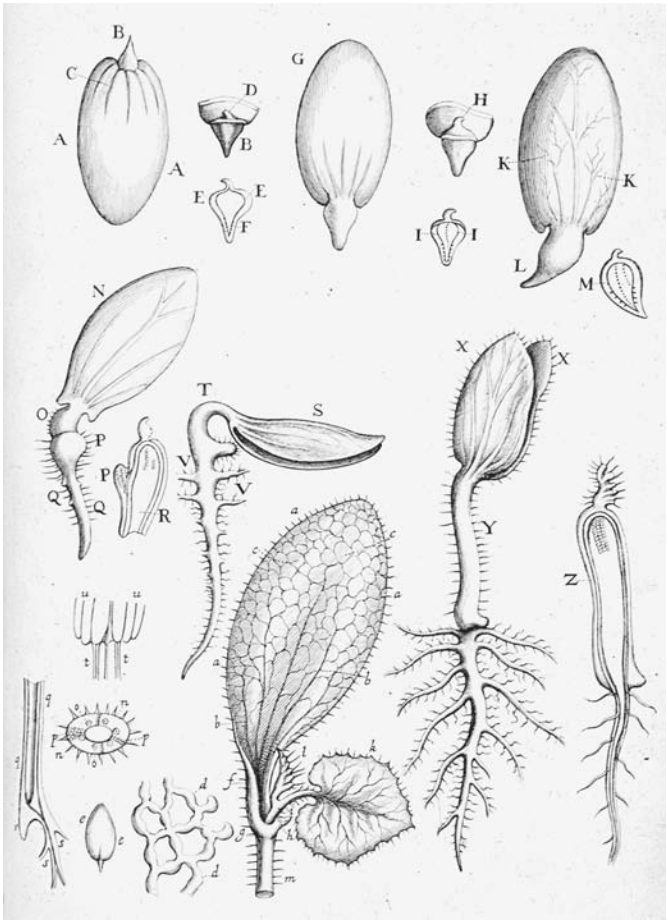


Figure 5
With the Renaissance, there was a resurgence in scientific inquiry. Malpighi was a keen observer of plants, as seen in his depiction of this germinating cucumber in his wonderfully illustrated *Anatome Plantarum*, 1675.

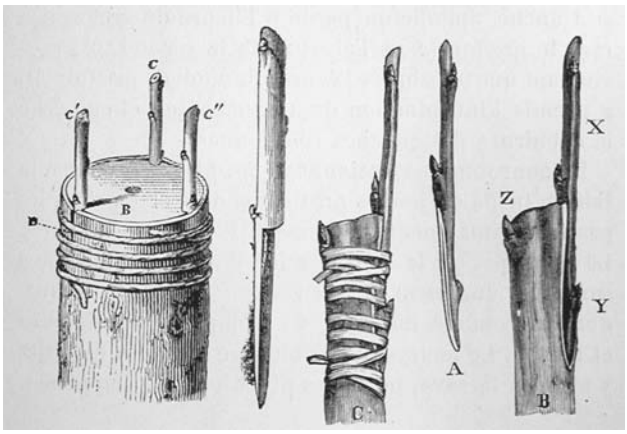


Figure 6
Bark grafting as illustrated in *The Art of Grafting and Budding* (1910) by Baltet.

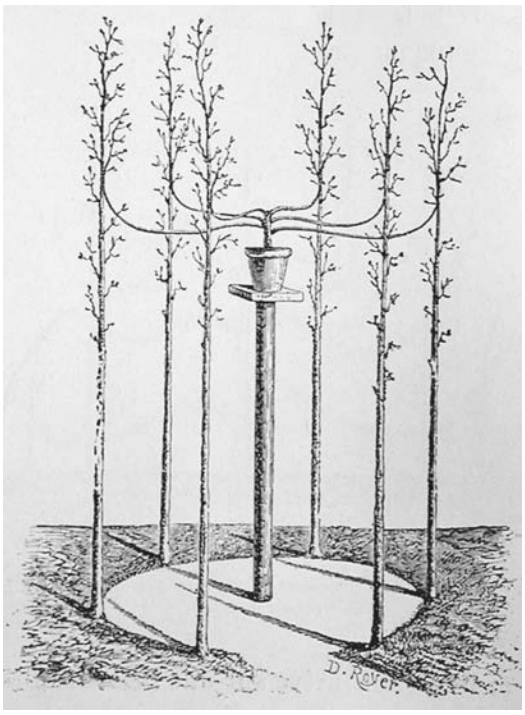


Figure 7
Approach grafting was a more important propagation technique before the introduction of mist propagation (11).

first edition of *The Nursery Book* (3) later revised as the *Nursery Manual* in 1920 (6), which cataloged what was known about plant propagation and the production of plants in the nursery (Fig. 8). His *Cyclopedia of American Horticulture* (4) in 1900–1902, *Standard Cyclopedia of Horticulture* (5) in 1914–1917, *Hortus* (7) in 1930, *Hortus Second* (8) in 1941, and *Manual of*

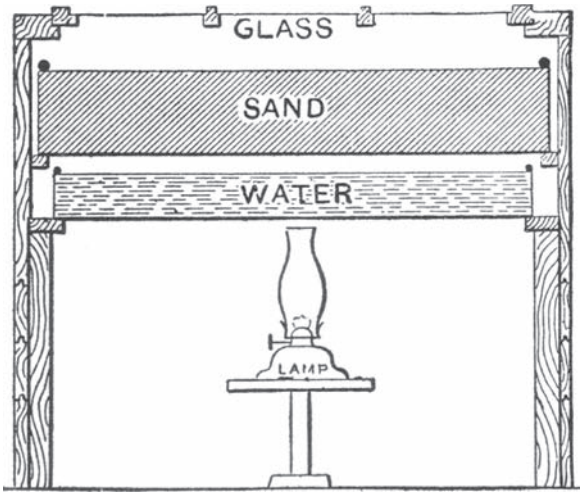


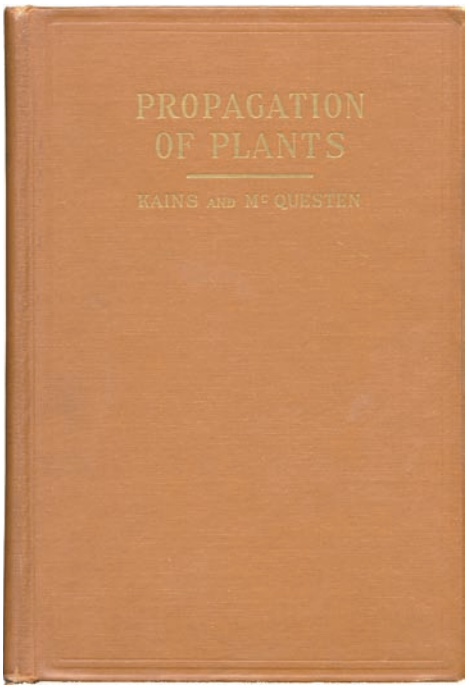
Figure 8
Liberty Hyde Bailey is considered the Father of American Horticulture (Seeley, 1990). He provides an interesting version of bottom heat for germination and cutting propagation in the *Nursery Book* (3), one of his 63 published books on horticulture.

Cultivated Plants (9) in 1940 and 1949 described the known plants in cultivation. An update, *Hortus Third* (10), is a classic in the field.

M. G. Kains of Pennsylvania State College and, later, Columbia University in New York, published *Plant Propagation* (26), later revised by Kains and McQuesten (27), which remained a standard text for many years (Fig. 9). Several other books were written during this period including titles by Adriance and Brison (1), Duruz (17), Hottes (24), and Mahlstede and Haber (28). The first edition of *Plant Propagation: Principles and Practices* (22) was published in 1959 and has continued through eight editions.

THE DEVELOPMENT OF NURSERIES

The concept of the nursery, where plants are propagated to be transplanted to their permanent site either as part of the agricultural unit or to be sold to others, has likely been a part of agriculture since its beginning. Nevertheless, the development of commercial nurseries is probably something that has developed largely within the recent era (16). Most agronomic crops (wheat, corn, etc.) and many vegetables were grown by seed. A portion of the seed was retained each year to supply the seed for the next cycle. In regions with cold winters, starting vegetables and flowers in protected structures



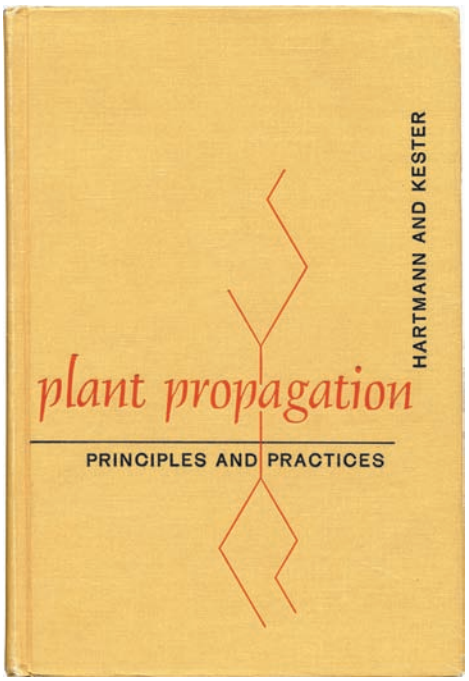


Figure 9
Early books for students and nursery professionals include *Propagation of Plants* by Kains and McQuesten (1938) and the first edition of *Plant Propagation: Principles and Practices* by Hartmann and Kester (1959).

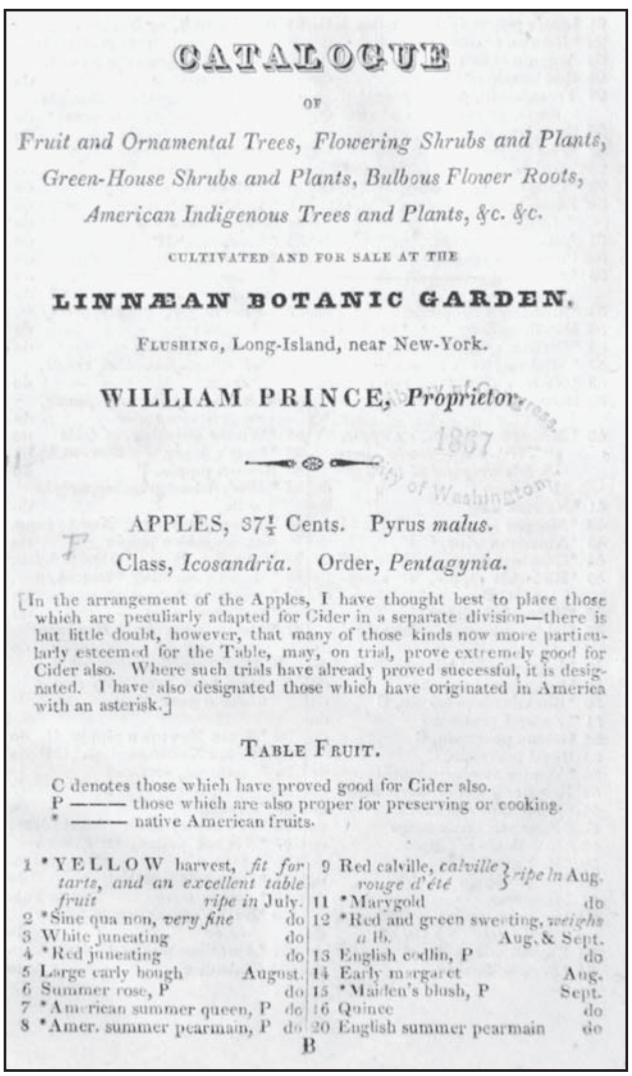
(cold frames, hotbeds) and later transplanting them to the open was an important part of production, because doing so extended the length of the growing season.

A number of important nurseries existed in France during the 16th and 17th centuries and, eventually, throughout Europe (17). Ghent, Belgium, had a gardener's guild as early as 1366. The first glass house (greenhouse) was built in 1598. The Vilmorin family established a seed house and nursery business in 1815, which was maintained through seven generations.

Early plant breeding was often combined with a nursery, as exemplified by Victor Lemoine (1850) who specialized in tuberous begonias, lilies, gladiolus, and other garden flowers. Nickolas Hardenpont and Jean Baptiste van Mons specialized in fruits, particularly pears. The Veitch family started a major nursery in England in 1832. Thomas Andrew Knight, a famous hybridizer of fruits, established the Royal Horticultural Society in 1804.

Early colonists brought seeds, scion, and plants to the United States from Europe, and Spanish priests brought material to the West Coast. John Bartram is credited with providing a major impetus with his Botanical Garden in Philadelphia in 1728. The first nursery, however, was credited to William Prince and Son in 1730 on Long Island (Fig. 10). These were followed by the expansion of nurseries throughout the eastern United States during the 19th Century. To a large extent, the early nurseries specialized in selecting and grafting fruit trees, although ornamentals and forest trees also began to be produced.

David Landreth established a seed company, and the seed industry in the Philadelphia area, in 1784. He offered seeds internationally and later distributed seeds collected during the Lewis and Clark expedition. In 1906, Bernard McMahon produced the American Gardener's Calendar, which was reprinted through



CATALOGUE

OF

Fruit and Ornamental Trees, Flowering Shrubs and Plants, Green-House Shrubs and Plants, Bulbous Flower Roots, American Indigenous Trees and Plants, &c. &c.

CULTIVATED AND FOR SALE AT THE

LINNÆAN BOTANIC GARDEN.

Flushing, Long-Island, near New-York.

WILLIAM PRINCE, *Proprietor.*

APPLES, 37½ Cents. Pyrus *malus.*

Class, *Icosandria.* Order, *Pentagynia.*

[In the arrangement of the Apples, I have thought best to place those which are peculiarly adapted for Cider in a separate division—there is but little doubt, however, that many of those kinds now more particularly esteemed for the Table, may, on trial, prove extremely good for Cider also. Where such trials have already proved successful, it is designated. I have also designated those which have originated in America with an asterisk.]

TABLE FRUIT.

C denotes those which have proved good for Cider also.
P ——— those which are also proper for preserving or cooking.
* ——— native American fruits.

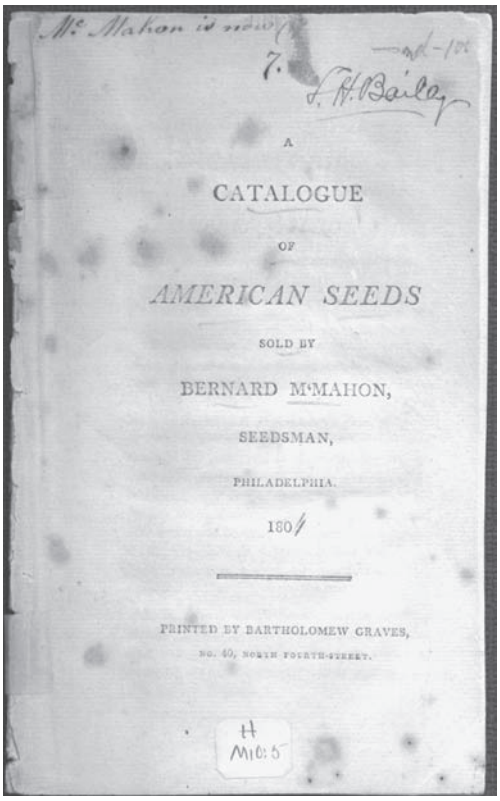
1 *YELLOW harvest, *fit for tarts, and an excellent table fruit* *ripe in* July.
2 *Sine qua non, *very fine* do
3 White juneating do
4 *Red juneating do
5 Large early bough August.
6 Summer rose, P do
7 *American summer queen, P do
8 *Amer. summer pearmain, P do
9 Red calville, *calville rouge d'été* *ripe in* Aug.
11 *Marygold do
12 *Red and green sweeting, *weighs a lb.* Aug. & Sept.
13 English codlin, P do
14 Early margaret Aug.
15 *Maiden's blush, P Sept.
16 Quince do
20 English summer pearmain do

B

TO BE SOSD, BY
WILLIAM PRINCE,
At FLUSHING-LANDING, 1771
On *LONG-ISLAND*, near NEW-YORK,
A large Collection of Fruit Trees, as follows,

NEW-YORK: Printed by H. GAINE, in HANOVER-SQUARE.

Figure 10
The first established nursery in the United States was begun in New York in 1730 by William Prince.



(a)

(b)

Figure 11
Seeds were offered through the mail by placing orders through seed catalogs. (a) Liberty Hyde Bailey's copy of Bernard McMahon's *Catalogue of American Seeds*. (b) The Shakers from Mount Lebanon, New York, pioneered the use of retain seed packets.

eleven editions. His Philadelphia seed house sold over 1,000 species of plants (Fig. 11a). The Shakers in Mount Lebanon, New York, began packaging seeds in individual envelopes for local retail sales in the early 1800s (Fig. 11b). The first seed catalog in color was produced in 1853 by B. K. Bliss. At the turn of the 20th Century, these mail order catalogs became wonderful lithographic works of art (Fig. 12).

Figure 12
The seed business was competitive, so companies produced colorful mail order seed catalogs to attract potential customers.

BOX 1 **GETTING MORE IN DEPTH ON THE SUBJECT**

PLANT PROPAGATION ORGANIZATIONS

American Seed Trade Association (ASTA) This organization of seed companies has been serving the industry since 1883. ASTA holds a general meeting each year and sponsors conferences on specific crops. It publishes a newsletter, an annual yearbook, and proceedings of individual conferences. It participates in regulatory activities that affect the seed industry. (http://amseed.com)

American Society for Horticultural Science (ASHS) This organization has a membership of public and private scientists, educators, extension personnel, and industry members with an interest in horticulture. The organization holds annual national and regional meetings and publishes scientific reports in the *Journal of American Society for Horticultural Science, HortScience,* and *HortTechnology.* It includes working groups in all propagation areas. (http://www.ashs.org)

Association of Official Seed Analysts, Inc. (AOSA) Membership is seed laboratories, both private and governmental, mostly in the continental United States. The association holds an annual meeting and publishes the *Journal of Seed Technology.* They provide numerous handbooks on the rules for seed testing, seed sampling, purity analysis, etc. They also provide a seed technologist's training manual. (http://www.aosaseed.com/)

Association of Official Seed Certifying Agencies (AOSCA) Originally organized in 1919 as the International Crop Improvement Association, membership includes United States and Canadian agencies responsible for seed certification in their respective areas. These agencies maintain a close working relationship with the seed industry, seed regulatory agencies, governmental agencies involved in international seed market development and movement, and agricultural research and extension services. (http://aosca.org/)

International Fruit Tree Association This organization is for members interested in fruit tree rootstocks and propagation but also includes cultural aspects. An annual meeting is held, and the proceedings are published in *Compact Fruit Tree.* (http://www.ifruittree.org/)

International Plant Propagators Society (IPPS) The society was organized in 1951 to recognize the special skills of the plant propagator and to foster the exchange of information among propagators. The organization has expanded to include Eastern, Western, and Southern Regions of the United States; Great Britain and Ireland; Australia; New Zealand; Japan; and a Southern African Region. Each region holds an annual meeting, and their papers are published in a *Combined Proceedings.* (http://www.ipps.org)

International Seed Testing Association (ISTA) This is an intergovernmental association with worldwide membership accredited by the governments of 59 countries and involving 137 official seed-testing associations. The primary purpose is to develop, adopt, and publish standard procedures for sampling and testing seeds and to promote uniform application of these procedures for evaluation of seeds moving in international trade. Secondary purposes are to promote research in all areas of seed science and technology, to encourage cultivar certification, and to participate in conferences and training courses promoting these activities. They hold an annual conference and publish the *Seed Science and Technology* journal, as well as a newsletter, bulletins, and technical handbooks on seed testing. (http://www.seedtest.org/en/home.html)

International Society for Horticultural Science (ISHS) This organization is an international society for horticultural scientists, educators, extension, and industry personnel. It sponsors an International Horticultural Congress every four years as well as numerous workshops and symposia. Proceedings are published in *Acta Horticulture.* A newsletter, *Chronica Horticulturae,* is published four times per year. (http://www.ishs.org)

American Nursery and Landscape Association (ANLA) Organized in 1875 as the American Association of Nurserymen, this association is a national trade organization of the United States nursery and landscape industry. It serves member firms involved in the nursery business—wholesale growers, garden center retailers, landscape firms, mail-order nurseries, and allied suppliers to the horticultural community. (http://www.anla.org/)

Society for In Vitro Biology (SIVB) This organization is composed of biologists, both plant and animal, who do research on plant cellular and developmental biology, including the use of plant tissue culture techniques. The organization publishes the journal *In Vitro Cellular and Developmental Biology—Plant* and holds an annual meeting. (http://www.sivb.org/)

Southern Nursery Association (SNA) An organization of nurseries in the southeastern United States, this trade organization has annual conferences and publishes newsletters and conference proceedings. (http://www.sna.org)

The establishment of the nursery industry in the Pacific Northwest was a unique accomplishment (17). In the summer of 1847, Henderson Lewelling of Salem, Iowa, established a traveling nursery of grafted nursery stock growing in a mixture of soil and charcoal in boxes on heavy wagons pulled by oxen, which crossed the Great Plains, covering 2,000 miles to Portland, Oregon. The 350 surviving trees were used to establish a nursery at Milwaukee, Oregon.

THE MODERN PLANT PROPAGATION INDUSTRY

The present-day plant propagation industry is large and complex, and involves not only the group that multiplies plants for sale and distribution, but also a large group of industries that provides services, sells the product, is involved in regulation, provides consultation, carries on research, or is involved in teaching. The key person within this complex is the plant propagator who possesses the knowledge and skills either to perform or to supervise the essential propagation task for specific plants. In 1951, the Plant Propagator's Society was established to provide the nursery profession with knowledge and research support.

DISCUSSION ITEMS

Modern day plant propagation is a complex, many faceted industry that represents a synthesis of different skills. Underlying these skills is a love and appreciation for the rich history and importance plant propagation has played in agriculture development.

1. Discuss how the relationship between the domestication of plants has been symbiotic with human development.
2. Discuss the relationship between plant selection and domestication with methods of plant propagation.
3. The number of plant species used for food is relatively small. Speculate on some of the reasons why.
4. The terms "agriculture," "forestry," and "horticulture" became distinct disciplines during the medieval period of human history. What do you see as the differences in these disciplines that led to their separation in medieval times, and does this relate to our modern views of these disciplines?
5. Why do you think the "modern" nursery developed and how did the period of plant exploration relate to nurseries?
6. Visit the web site of a professional organization and discuss why you think membership would be important to a person working in plant propagation or horticulture.

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Biology of Plant Propagation

Biology of Plant Propagation

learning objectives

- Describe the basic life cycles of plants as related to sexual (seed) and asexual (vegetative) propagation.
- Explain the rules for naming plants.
- Describe how ownership of cultivars can be controlled.
- Explain the difference between mitosis and meiosis.
- Describe how genes and gene expression impact plant growth and development.
- Identify plant hormones and their role in plant development.

INTRODUCTION

The natural world is covered by populations of many different kinds of plants that have evolved over eons of time. We identify these as **species,** although there are other divisions that will be described in this text. These populations can more or less maintain themselves from generation to generation because of their natural genetic characteristics. If not, they evolve into other variants or become extinct.

In agriculture and horticulture, on the other hand, propagators primarily deal with special kinds of plants, which are defined as **cultivars (varieties)** (9). We buy 'Thompson Seedless' grapes and 'Elberta' peaches for our table, grow 'Queen Elizabeth' roses and 'Bradford' pear trees in our landscape, and plant 'Hybrid Yellow Granex' onion seed and 'Marquis' wheat in our fields. All of these represent populations of plants that are unique and only exist in cultivation. These plants would likely change drastically, or disappear altogether, if not maintained by genetic selection during propagation.

Plant propagation and plant breeding both involve genetic selection. The role of the plant breeder is *to recreate patterns of genetic variation in its many forms from which to select new kinds of plants useful to humans.* The role of the plant propagator, on the other hand, is *to multiply these selected cultivars and to do it in such a manner as to maintain the genetic characteristics of the original population.* To do both requires an understanding of genetic principles and procedures.

BIOLOGICAL LIFE CYCLES IN PLANTS

Plant Life Cycles

In natural systems, plant life cycles can be described based on their life span and reproductive pattern. Therefore, they are referred to as annuals, biennials, or perennials:

1. **Annuals** are plants that complete the entire sequence from germination to seed dissemination and death in one growing season. Technically, annuals are monocarpic, meaning that they die after reproducing. However, "annuals" also refers to plants that may be perennial in mild climates but are not winter hardy, and so die after the first growing season due to cold temperatures.

2. **Biennials** are plants that require two growing seasons to complete their life cycle. During the first year, the plants are vegetative and grow as low clumps or a rosette of leaves. These plants usually need a period of cold weather for **vernalization** of the shoot meristem before they can become reproductive. During the second season, biennial plants bolt, producing a fast-growing flowering spike, flower, produce seeds, and then die. Although the terminology is confusing, winter annuals fit into this category. Seeds germinate in late summer, forming a seedling with numerous rosette leaves that hug the ground. After winter vernalization, the meristem bolts, flowers, sets seeds, and dies before summer (less than 12 months).
3. **Perennials** are plants that live for more than 2 years and repeat the vegetative-reproductive cycle annually. Perennial cycles tend to be related to seasonal cycles of warm-cold (temperature climates) or wet-dry periods (tropical climates). Both herbaceous and woody plants can be perennial:
   a. **Herbaceous perennials** produce shoots that grow during one season and die back during the winter or periods of drought. It may take herbaceous perennials several growing cycles before they become reproductive, and they may not flower every year, depending on the plant's accumulation of resources during the growing cycle. Plants survive during adverse conditions as specialized underground structures with roots and crown that remain perennial. Geophytes (bulbs, corms, rhizomes, tubers) are included in this group.
   b. **Woody perennials** develop permanent aboveground woody stems that continue to increase annually from apical and lateral buds with characteristic growth and dormancy periods. Woody perennials are trees and shrubs.

clonal propagation
A group of plants originating from a single source plant by vegetative propagation.

In horticultural systems, plant life cycles can also be described based on their propagation methods. Here they can be described based on the seedling, **clonal,** and **apomictic** life cycles.

Life Cycles of Seedling Cultivars

In propagation, an individual plant that develops from a seed is referred to as a **seedling** whether it is an **annual, biennial, herbaceous perennial,** or **woody perennial.** During the **life cycle of a seedling,** the sequence of growth and development is separated into four broad **phases** (Fig. 1a) (10, 25, 29, 46).

seedling life cycle
Growth and development of a plant when propagated from a seed.

Phase I Embryonic This phase begins with the formation of a zygote. This cell grows into an **embryo,** which receives nourishment from the mother plant through physiological stages of development. At first, growth involves cell division of the entire embryo as it increases in size. Later, growth potential develops with a polar orientation as the embryo develops its characteristic structure.

Phase II Juvenile Seed germination initiates a dramatic change from the embryonic pattern to the developmental pattern of the young seedling. Vegetative growth is now polar, extending in two directions via the shoot and root axis. Cell division is concentrated in the root tips, shoot tips, and axillary growing points. Subsequently, the extension of the root and shoot is accompanied by an increase in volume. New nodes are continually laid down as leaves and axillary growing points are produced. Lateral growing points produce only shoots that are not competent to flower. The juvenile period is the growth stage where plants cannot flower even though the inductive flowering signals are present in the environment (33, 61).

Phase III Transition The vegetative period at the end of the juvenile phase and prior to the reproductive stage is marked by subtle changes in growth and morphology. Growth tends to decrease as the plants enter the reproductive period when flowering occurs. The important point is that the developmental potential of the growing points is sensitive to particular signals, partly internal, although often dictated by cues from the environment such as changes in day length and chilling.

Phase IV Adult (or Mature) During this phase, shoot meristems have the potential to develop flower buds, and the plant produces flowers, fruits, and seeds.

The duration and expression of these phases represent fundamental variation in plant development, which is analogous to comparable phases in animal development. The most conspicuous expression of phases occurs in long-lived perennial plants, such as trees and shrubs, where conspicuous differences in juvenile and mature traits may be observed in the same plant. Nevertheless, phase changes have been

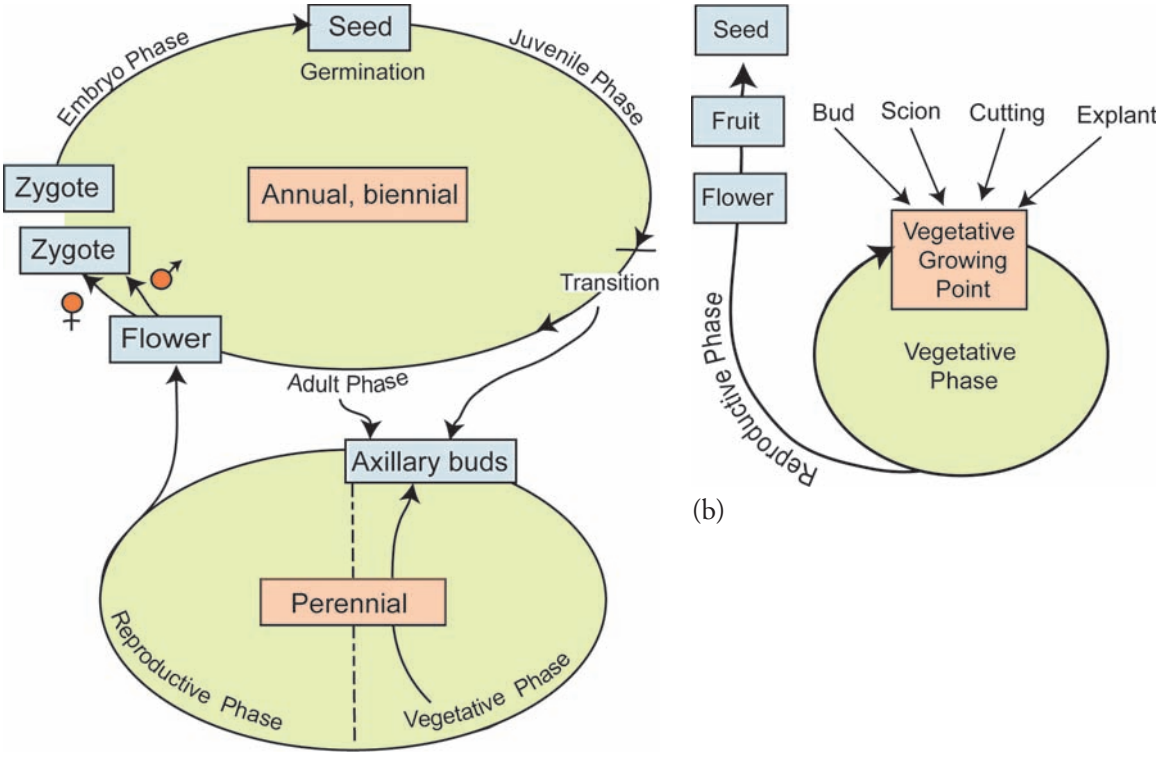


Figure 1
Seedling and clonal life cycles. (a) Seedling cycle in plants. Model illustrates epigenetic changes involving embryo development, juvenile, transition, and adult phases. In the annual or biennial, the apical meristem progresses more or less continuously through one (*annual*) or two (biennial) growing seasons (*top circle*). In herbaceous and woody perennials (*bottom circle*), the adult vegetative meristem is renewed continuously by seasonal cycles of growth and development. (b) A clonal life cycle results when a plant originates by vegetative propagation. The type of growth, time to flower, and other characteristics may vary among different propagules depending on the location on the seedling plant from which the propagule was taken. With continued vegetative propagation, the clone is stabilized at its mature form by characteristic consecutive vegetative and reproductive phases.

identified in annual plants, such as maize (61), and must be recognized as a fundamental aspect of all plant development.

The following characteristics of plant development are associated with phase change:

- *Time of flowering* (52, 79, 85). The age when flowering begins is the most characteristic aspect of phase change. Time of first flowering varies from days to a few months in some annuals to as much as 50 years in some perennials (Table 1). Usually, flowering begins in the upper and peripheral parts of the tree where shoots and branches have attained the prerequisite phase.
- *Morphological expression of leaves and other structures.* Leaf form in the juvenile phase sometimes differs radically from that of the adult phase (Fig. 2). English ivy is a classic example of phase change, as illustrated in Figures 3 and 4. Juvenile parts of apple, pear, and citrus seedlings may be very thorny, although the trait disappears in the adult phase (33, 80).
- *Potential for regeneration* (34, 80). Each phase tends to have a differing potential for regeneration. For instance, cuttings taken from the juvenile phase usually have a higher potential for rooting than do cuttings from the adult phase.

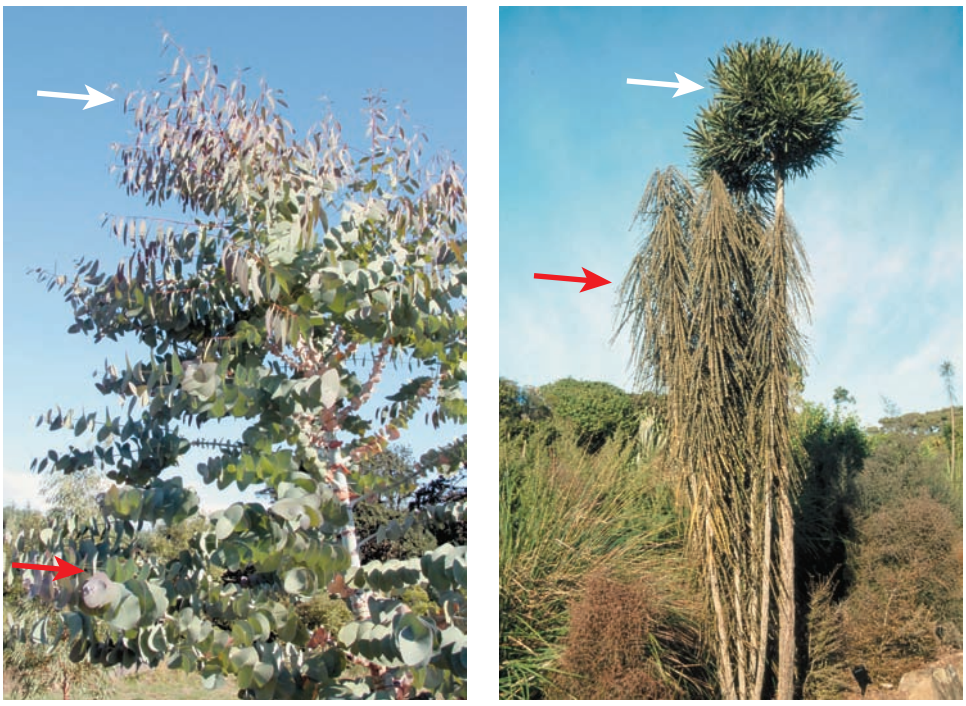
Life Cycles of Apomictic Cultivars

Apomixis is a natural reproductive process possessed by some species of plants in which the embryo develops directly from specific vegetative cells of some part of the reproductive structure that has not undergone meiosis (50). The result is that an asexual process has replaced the normal sexual process.

apomixis Reproduction in which vegetative cells in the flower develop into zygotes to create seeds by a clonal reproduction process.

Table 1
AGE OF FLOWER DEVELOPMENT IN SOME WOODY PLANTS

Species	Length of juvenile period
Rose (*Rosa* spp.)	20–30 days
Grape (*Vitis*)	1 year
Stone fruits (*Prunus* spp.)	2–8 years
Apple (*Malus* spp.)	4–8 years
Citrus (*Citrus* spp.)	5–8 years
Scotch pine (*Pinus sylvestris*)	5–10 years
Ivy (*Hedera helix*)	5–10 years
Birch (*Betula pubescens*)	5–10 years
Sequoia (*Sequoia sempervirens*)	5–10 years
Pear (*Pyrus* spp.)	6–10 years
Pine (*Pinus monticola*)	7–20 years
Larch (*Larix decidua*)	10–15 years
Ash (*Franxinus excelsior*)	15–20 years
Maple (*Acer pseudoplatanus*)	15–20 years
Douglas-Fir (*Pseudotsuga menziesii*)	20 years
Bristlecone pine (*Pinus aristata*)	20 years
Redwood (*Sequoiadendron giganteum*)	20 years
Norway spruce (*Picea abies*)	20–25 years
Hemlock (*Tsuga heterophylla*)	20–30 years
Sitka spruce (*Picea sitchensis*)	20–35 years
Oak (*Quercus robur*)	25–30 years
Fir (*Abies amabilis*)	30 years
Beech (*Fagus sylvatica*)	30–40 years



(a) (b)

Figure 2
In some woody plants, there is a dramatic change in leaf shape (foliar dimorphism) that accompanies the change from juvenile (red arrows) to mature phase (white arrows). (a) *Eucalyptus*; (b) *Pseudopanax*.

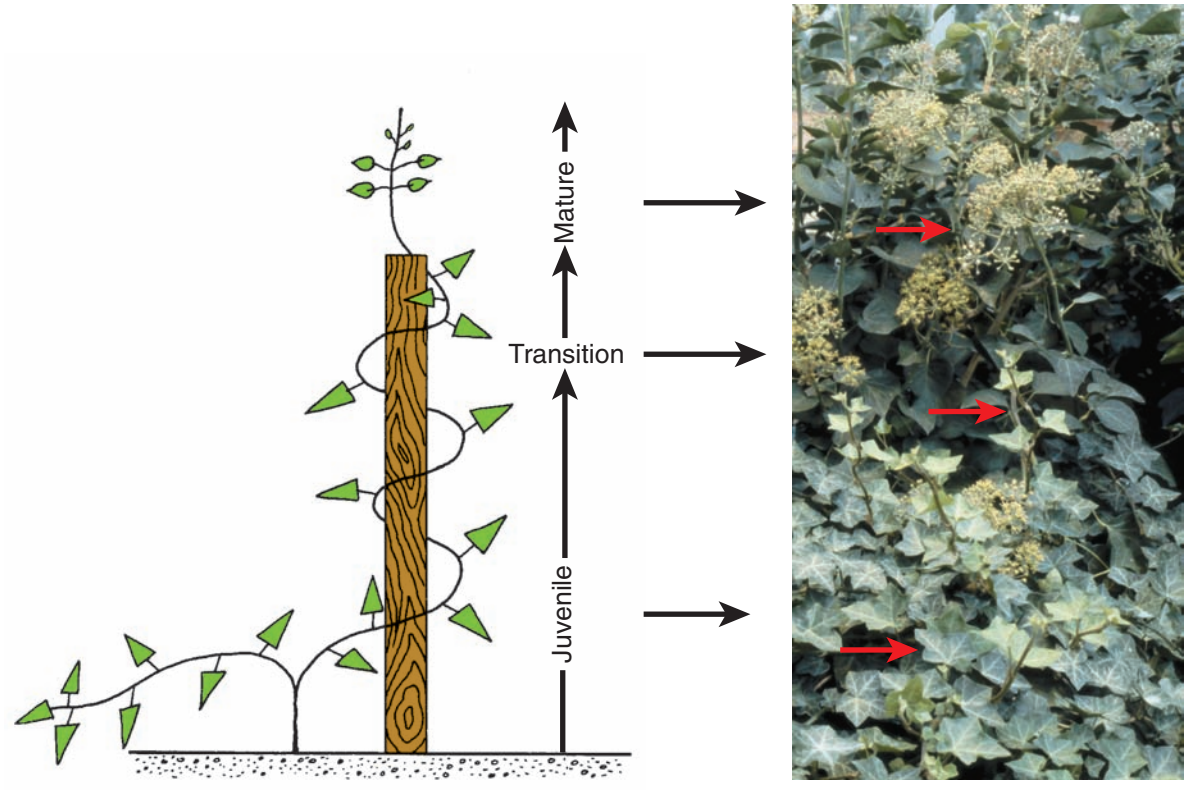


Figure 3
Phase change in Ivy (*Hedera helix*) in which the *juvenile* (non-flowering) phase is a vine which, as it grows into a vertical form, undergoes a *transition* into the *mature* (adult) flowering and fruiting phase.

apomictic life cycle
Growth and development of a plant when propagated from an apomictic embryo.

Different types of these phenomena are described in Chapter 4. The **apomictic life cycle** (not shown) is the same as the seedling cycle, except that the embryo is essentially a clone since it is produced as a result of mitosis and is asexual. Plants of the apomictic cycle go through the same phase changes as the sexual life cycle.

Life Cycles of Clonal Cultivars

clonal life cycle Growth and development of a plant when propagated vegetatively from a particular propagule of an individual plant.

Two essential aspects characterize **clonal life cycles** (Fig. 1b) (46):

- A clone originates by vegetative propagation from an individual plant using various types of **vegetative propagules.** The basic kinds are bud, scion, cutting, layer, bulb, corm, tuber, and explant. Depending on their history and origin, each of these propagules may represent a different phase of the seedling cycle.
- The phase-potential of the propagule is maintained during vegetative propagation such that the progeny plants may vary significantly in their morphological characteristics. For instance, Figure 4 compares the appearance of a plant propagated from the juvenile and mature phase of English ivy and *Chamaecyparis.*

TAXONOMY

Organisms are named in a hierarchical system described as their taxonomy. A sample hierarchy is provided for apple (Table 2).

The basic system for naming plants was introduced by Linnaeus (Fig. 4) as the Latin system of binomial nomenclature using a **genus** and **species** name for each plant (each of which are italicized). The genus describes a group of plants that are similar in morphological, biochemical, and genetic properties. The species is used to designate a

species The natural grouping of plants that have common characteristics in appearance, adaptation, and breeding behavior (i.e., can freely interbreed with each other).

(a) (b) (c) (d)

Figure 4
The juvenile or mature phase may be retained by vegetative propagation. (a) Juvenile and (b) mature forms of English ivy (*Hedera helix*). The juvenile form is a vine, while the mature form is a three-foot shrub with terminal inflorescences. (c) Mature and (d) juvenile foliage forms of false cypress (*Chamaecyparis*).

Table 2
THE TAXONOMIC HIERARCHY FOR APPLE

Classification
Kingdom: Plantae
Division: Spermatophyta
Subdivision: Angiospermae
Class: Dicotyledonae
Order: Rosales
Family: Rosaceae
Genus: *Malus*
species: *domestica*

population of plants within a genus that can be recognized and reproduced as a unit (51). The rules for naming plants are maintained by the International Association of Plant Taxonomists under the longstanding International Code of Botanical Nomenclature (http://ibot.sav.sk/icbn/main). In nature, individuals within one species normally interbreed freely but do not interbreed well with members of another species. Geographical isolation or some physiological, morphological, or genetic barrier prevents gene exchange between them. A true species can usually be propagated and maintained by seed but may require some control during propagation.

Cultivated plants may also be designated by binomial name even though they may be a complex hybrid rather than a distinct "natural" species (51, 72). For example, peach cultivars are variations within a recognized species *Prunus persica* L., but the European prune (*Prunus domestica* L.) is a complex hybrid that apparently developed in cultivation. **Cultivars** may also be derived from repeated vegetative propagation of an initial desirable mutation. The rules for naming cultivated plants are spelled out in the *International Code of Nomenclature for Cultivated Plants* (9).

cultivar A group of plants that have originated in cultivation, are unique and similar in appearance, and whose essential characteristics are maintained during propagation.

Eastern redbud illustrates the various subgroups occurring in selected or natural populations within a species (Fig. 6):

Genus and species: *Cercis canadensis* L.

Subspecies: *Cercis canadensis* subsp. *texensis*.

(a) (b)

Figure 5
Linnaeus was important in championing the binomial system for naming plants. (a) Portrait as a young man in Sweden. (b) The Linnean system grouped plants based on the number of male and female parts of the flower as illustrated in this old plate, "The Sexual System of Linneaus." Ehret, 1736.

Botanical variety (*varietas* in Latin): *Cercis canadensis* var. *alba*

Cultivar: *Cercis canadensis* cv. Forest Pansy or 'Forest Pansy'

In some cases, breeders have been able to make genetic crosses between different species or even between genera. Interspecific hybrids within a genus are designated with an "*x*" between the genus and species (i.e., *Viburnum xburkwoodii,* which is a hybrid between *V. carlesii* and *V. utile*). Intergeneric hybrids are formed between genera within a family and are designated with an "*x*" before the new genus name, which is a contraction of the two genera names (i.e., *xFatshedera lizei* is an intergeneric hybrid between *Fatsia japonica and Hedera helix*).

There are a number of web sites that provide information on current taxonomy for plant names:

International Plant Names Index	http://www.ipni.org/index.html
USDA PLANTS database	http://plants.usda.gov/
USDA Germplasm Resources Information Network (GRIN) Taxonomy for Plants	http://www.ars-grin.gov/cgi-bin/npgs/html/index.pl
eFloras.org	http://www.efloras.org/index.aspx
World checklist of plant families	http://www.kew.org/ (choose Scientific Research & Data, and in the search box enter World Checklist of Selected Plant Families)

(a) **Genus and species:** *Cercis canadensis* L. The authority indicates who is responsible for giving this plant its name. In this case "L." is for Linnaeus.

(b) **Botanical variety:** *Cercis canadensis* var. *alba* (white-flowered eastern redbud). A botanical variety is considered a variant that occurs in the wild, but its differences from the species are less distinct compared to a subspecies.

(c) **Subspecies:** *Cercis canadensis* subsp. *texensis*. A subspecies is a group of variants that occur consistently in nature. They can be viewed as the beginning of a new species. They are often geographically isolated from the main species.

(d) **Cultivar:** *Cercis canadensis* cv. Forest Pansy or 'Forest Pansy'. A cultivar (cultivated variety) can be set off from the species by the "cv." abbreviation or by single quotes.

Figure 6
Major categories for naming plants include Genus, species, botanical variety, subspecies, and cultivar.

Names for new plants should be registered with the proper registration authority. The International Society for Horticultural Sciences provides a home for the Commission for Nomenclature and Cultivar Registration (http://www.ishs.org/sci/icra.htm). They provide a link to individuals or organizations that maintain the registry for a single genus or group of plants. For example, the registry for English ivy (*Hedera*) is maintained by the American Ivy Society, while woody plants without specific registries are handled by the American Public Gardens Association.

LEGAL PROTECTION OF CULTIVARS

In modern agricultural and horticultural industries, individual cultivars and breeding materials have commercial value and, according to law, are entitled to legal protection as is any invention made by humans (17, 40, 42, 59). The right to propagate specific cultivars that are developed through controlled selection and/or breeding programs can be protected by a number of legal devices. These allow the originator to control their distribution and receive monetary awards for their efforts. Legal protection has been available in the United States with the passage of the Townsend-Purnell Act in 1930, which added vegetatively propagated plants to the general patenting law for inventions. Protection was provided to seed-propagated cultivars by the 1970 Plant Variety Protection Act, revised in 1994 (4). Many countries of the world have legal systems that grant protection to patents and breeders' rights, and a large network of such programs have developed. Guidelines have been produced by the International Union for the Protection of New Varieties of Plants (http://www.upov.int/index_en.html) in 1961, 1972, 1978, and 1991 (77) and the Food and Agriculture Organization of the United Nations (38). Propagators need to be aware of the rights and obligations under these particular conditions (see Box 1).

GENETIC BASIS FOR PLANT PROPAGATION

The life cycle of plants begins with a single cell known as a **zygote.** This cell is the result of the union of male and female gametes. From this initial cell, additional cells

BOX 1 **GETTING MORE IN DEPTH ON THE SUBJECT**

LEGAL PROTECTION OF CULTIVARS

Patent A **plant patent** is a grant from the United States Patent and Trademark Office, which extends patent protection to plants. Exclusive rights are given to the inventor of a "distinct and new" kind of plant (cultivar) for a 20-year period. Only vegetatively propagated cultivars are covered—not tuber-propagated plants. A plant growing wild is not considered patentable. There is no necessity to prove that the cultivar is superior, only that it is "new and different." To obtain information, contact the United States Patent and Trademark Office, Washington, DC 20231 (http://www.uspto.gov).

plant patent Legal protection of a vegetatively propagated cultivar (except tuber) granted by the United States Patent and Trademark Office to allow the inventor of the plant to control its propagation.

Plant Variety Protection The United States **Plant Variety Protection Act (PVPA)** extends plant patent protection to seed-propagated cultivars that can be maintained as "lines," including F_1 hybrids. Tuber-propagated plants are also protected. The new cultivar must be novel, distinctive, and stable. A plant-breeding certificate allows breeders propagation protection for many agricultural and horticultural crops propagated by seed, including such crops as cotton, alfalfa, soybean, and marigolds. The length of time is 20 years for most plants, but 25 for trees, shrubs, and vines. These rights may be sold or licensed. To obtain information, contact the Plant Variety Protection Office, USDA National Agricultural Library Building, Room 500, 10301 Baltimore Blvd., Beltsville, MD 20705, USA. It is also available at the USDA's web site in PDF form (http://www.ams.usda.gov/AMSv1.0/; Type "Plant Variety Protection Act" in the Search box, choose the link for "Plant Variety Protection Act [PDF])

plant variety protection Legal protection granted by the United States Plant Variety Protection Act for a seed-propagated cultivar; a plant-breeding certificate allows the inventor of the plant to control its propagation.

Trademarks A registered trademark offers protection for a name that indicates the specific origin of a plant (or product). The trademark is any word, symbol, device, logo, or distinguishing mark. It is granted for 10 years but can be renewed indefinitely as long as it remains in use. The trademark is distinct from the cultivar name and both identities should be provided. Unfortunately, the ways nurseries are using trademark names can confuse and even mislead consumers. For example, *Acer rubrum* 'Franks Red' is the cultivar name for the popular Red Sunset® maple, although most consumers assume Red Sunset is the cultivar name. The owner of the Red Sunset trademark has every right to use that name for a different red maple cultivar if he chose to make that change because the trademark is a company mark that is not permanently linked to *Acer rubrum* 'Frank's Red'. There are also examples where the same cultivar is being sold under numerous trademark names by different companies. This is the case for *Loropetalum chinensis* 'Hines Purple Leaf' that is being sold under the trademark names Plum Delight and Pizzaz even though they are the same plant.

Utility Patents This protection is under the general patent law, which uses the criteria of novelty and utility. An application requires the same full description as a plant patent. It may include more than one claim that involves specific uses of the plant. Utility patents are used by commercial biotechnology and engineering firms to control the use of specific genes and technologies.

Other Methods *Contracts* can be used to control the propagation of specific plants as well as the selling of their fruit or other products. Enforcement comes under contract law. Trade secrets are protected by law and can provide some protection for disclosure of certain technology. This may include information that is not disclosed to the public, or temporary protection prior to disclosure for patent application. *Copyrights* have the purpose of preventing unauthorized reproduction or copies of printed material. Although this device could apply to plant materials, copyrights are usually used to control reproduction of pictures or printed material about the plant that is used in brochures or catalogs.

multiply and develop the body of the plant. Living plant cells contain a **nucleus** embedded within the **cytoplasm,** all enclosed within a **cell wall** (Fig. 7). The nucleus contains the genetic material that directs growth and development by determining when particular **RNAs (ribonucleic acid)** and proteins are made by a cell. **Chromosomes** within the nucleus contain **DNA (deoxyribonucleic acid)** that forms the genetic blueprint for heredity. DNA is present in two other structures of the cell—**chloroplasts** and **mitochondria.** Individual characteristics and traits are associated with sequences of DNA nucleotides coded on the chromosome as **genes.** Genetic information is passed along from cell to cell during cell division.

chromosome Structures within the nucleus of a cell that contain the genes.

DNA (deoxyribonucleic acid) The basic biochemical compound that makes up the gene.

Gene Hereditary unit of inheritance now known to be composed of specific arrangements of nucleotides to make up a genetic code.

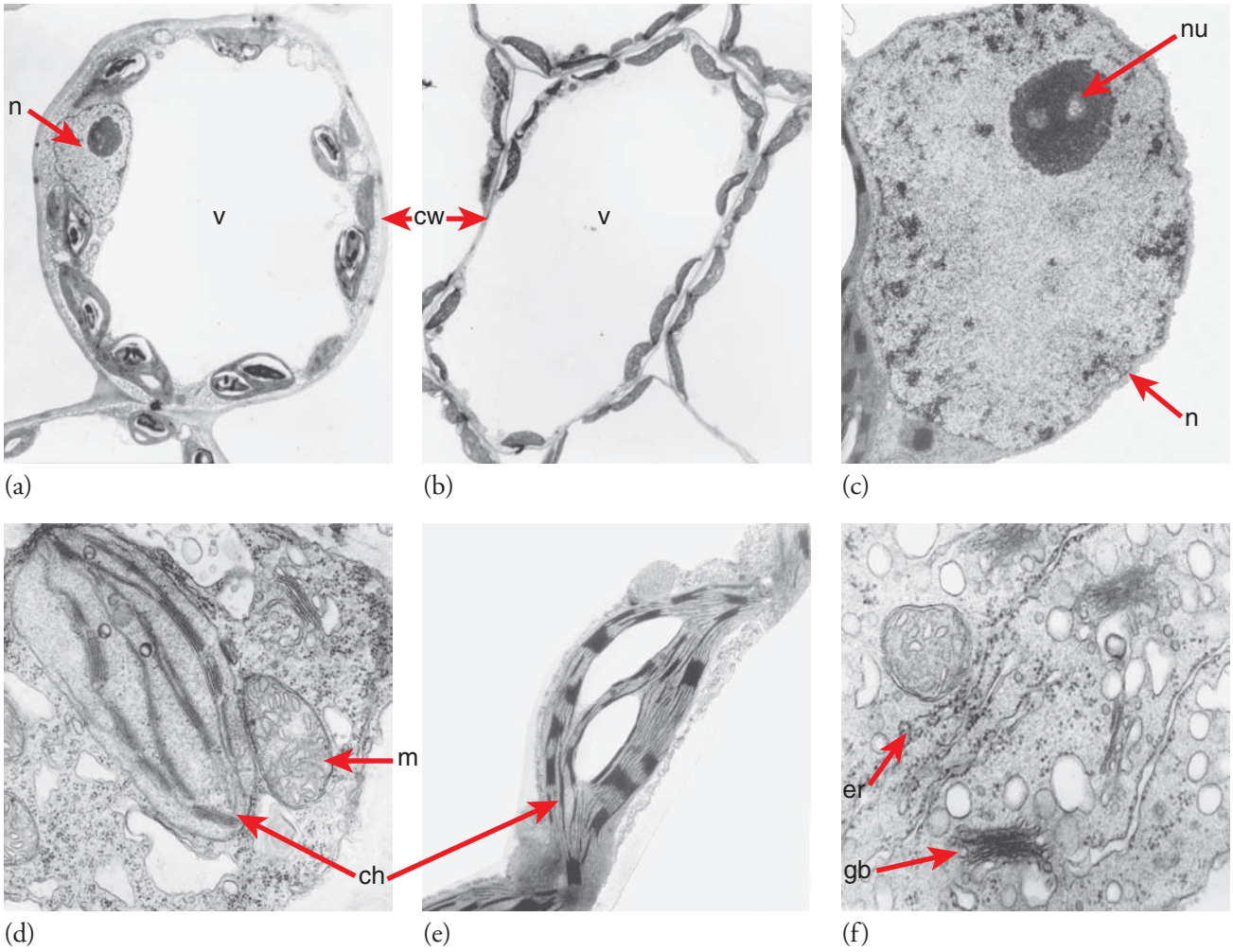


Figure 7
Electron micrographs of cells and cell components. (a) A mesophyll cell; (b) parenchyma cell with a large central vacuole and cytoplasm and organells pushed against the cell wall; (c) nucleus and nucleoli; (d) chloroplast and mitochondria; (e) mature chloroplast with starch; (f) Golgi body and endoplasmic reticulum. Abbreviations: n—nucleus; nu—nucleolus; cw—cell wall; ch—chloroplast; m—mitochondria; gb—Golgi body; er—endoplasmic reticulum; v—vacuole.

Cell Division

There are two types of cell division in plants—mitosis and meiosis. **Mitosis** is cell division in vegetative tissue used for growth, while **meiosis** is a reductive division used during the sexual reproductive cycle to produce gametes.

mitosis The special kind of cell division that results in vegetative propagation.

meiosis The special kind of cell division that results in sex cells, which are utilized in sexual reproduction.

Mitosis The **cell cycle** (24) is the period from the beginning of one cell division to the next (Fig. 8). The cell cycle is divided into a two parts: interphase and mitosis. Interphase is composed of three phases: G_1, S, and G_2. During the G_1 (G stands for gap) phase, there are active biochemical processes that increase the internal contents of the cell as well as its size. Cells that are not

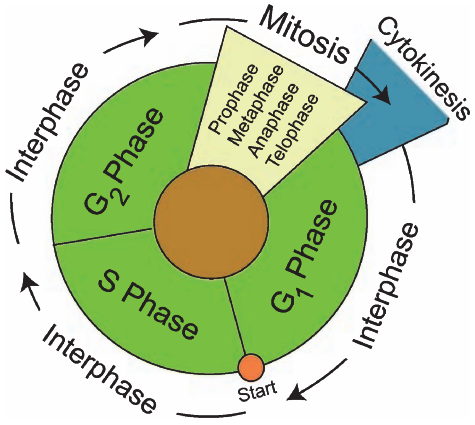


Figure 8
Cell cycle – see text for details.

preparing for cell division are arrested in the G_1 phase. In order for the cell cycle to proceed, there is a critical point referred to as the "start" where the cell commits to cell division. Progression through the cell cycle is controlled by proteins called cyclin-dependent protein kinases. The S (synthesis) phase involves DNA replication and synthesis. During the second gap phase (G_2), the cell, which now has replicated sets of chromosomes, prepares to partition these into two identical daughter cells during the cell division phase of mitosis.

Mitosis is separated into four phases (prophase, metaphase, anaphase, and telophase) related to the way the chromosomes appear within the dividing cell (Fig. 9). During ***prophase,*** chromosomes condense and appear as short, thickened structures with distinctive morphology, size, and number. The chromosomes exist as homologous pairs of chromatids attached together at their centers by centromeres. After the nuclear envelope disappears, **metaphase** spindle fibers form and the chromosomes migrate to the center of the cell. In **anaphase,** the mitotic spindle fiber microtubules attached to each chromosome pair at the centromere contract, pulling the chromosomes apart. The daughter chromosomes move to opposite ends of the cell in preparation for division. Nuclear envelopes reform around the separated daughter chromosomes during **telophase.** The phragmoplast forms at the cell's center. The phragmoplast is the initial formation of the cell plate, which will eventually form the new cell wall. The chromosomes again become less distinct within the nuclear matrix as the cell cycle proceeds from mitosis to interphase. Cell division ends with

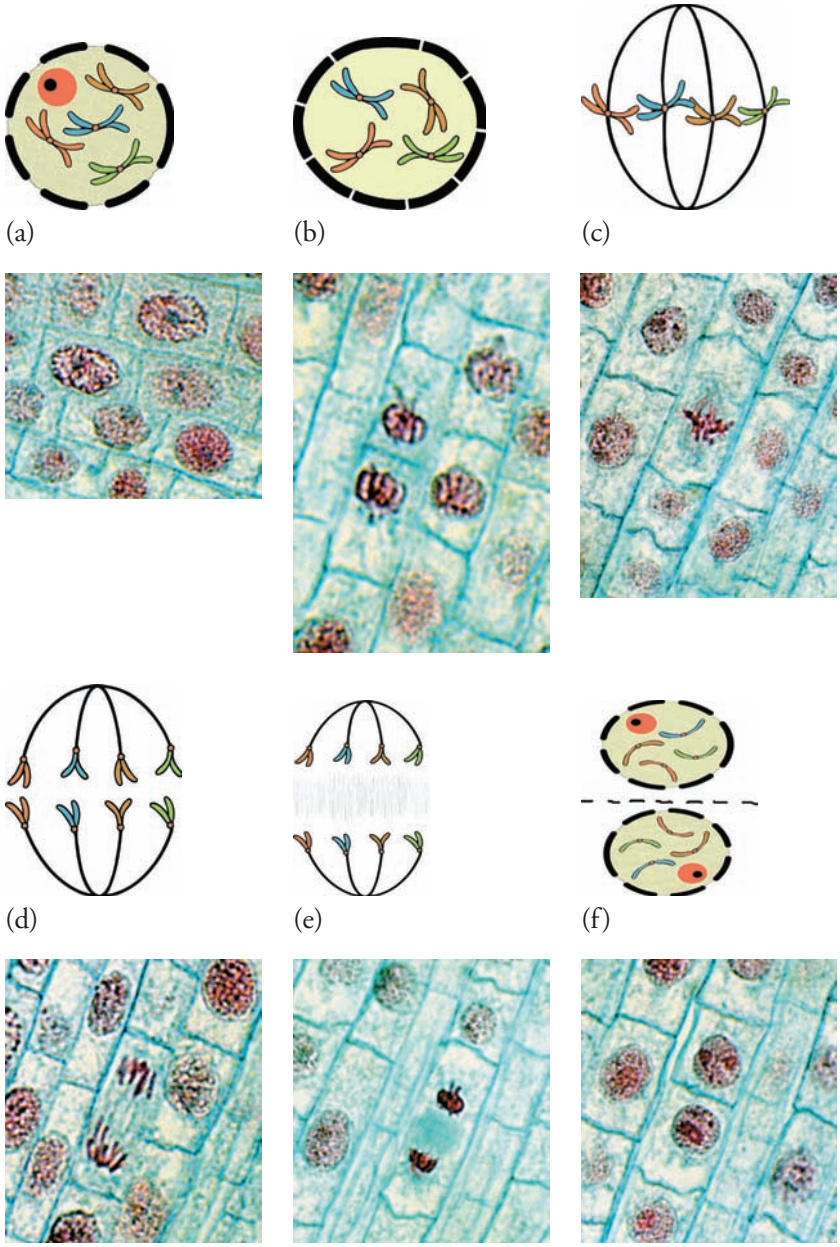


Figure 9
Stages in mitosis. (a) Early prophase, chromosomes begin to condense as nuclear envelope and nucleolus begin to deteriorate. (b) Prophase, chromosomes thicken and become conspicuous. (c) Metaphase, chromosomes line up across the center. (d) Anaphase, chromosomes separate. (e and f) Early and late Telophase, cell plate is laid down to produce two new cells.

cytokinesis, which is the division of the cytoplasm by the completed new cell wall. The result is the production of two new cells identical in genotype to the original cell.

Growth by mitosis increases the vegetative size of the plant. Cells may undergo enlargement, differentiation, and development into different kinds of cells (e.g., **parenchyma, collenchyma, fibers, and sclereids**) (Fig. 10). Parenchyma cells represent the basic living cell type. It is a living cell with a primary cell wall that is metabolically active and capable of differentiating into specific cell types. These may be for reserve storage as in endosperm cells or specialized for photosynthesis as the palisade and spongy mesophyll layers of the leaf. They may also develop into cells that provide structural support for stems and leaves or protective layers for seeds. These include collenchyma cells that are living cells with thickened primary cell walls. Collenchyma is usually found just below the epidermis in herbaceous and woody stems. Fibers and sclereids are examples of sclerenchyma cells that are nonliving at maturity. These have thick secondary walls that provide strength and structural support.

Eventually, cells differentiate into **tissues** (e.g., **xylem, phloem**) and **organs** such as stems, roots, leaves, and fruit (Fig. 11). Cells capable of dividing are referred to as **meristematic** and are located in primary or apical meristems (shoot and root tips) and secondary

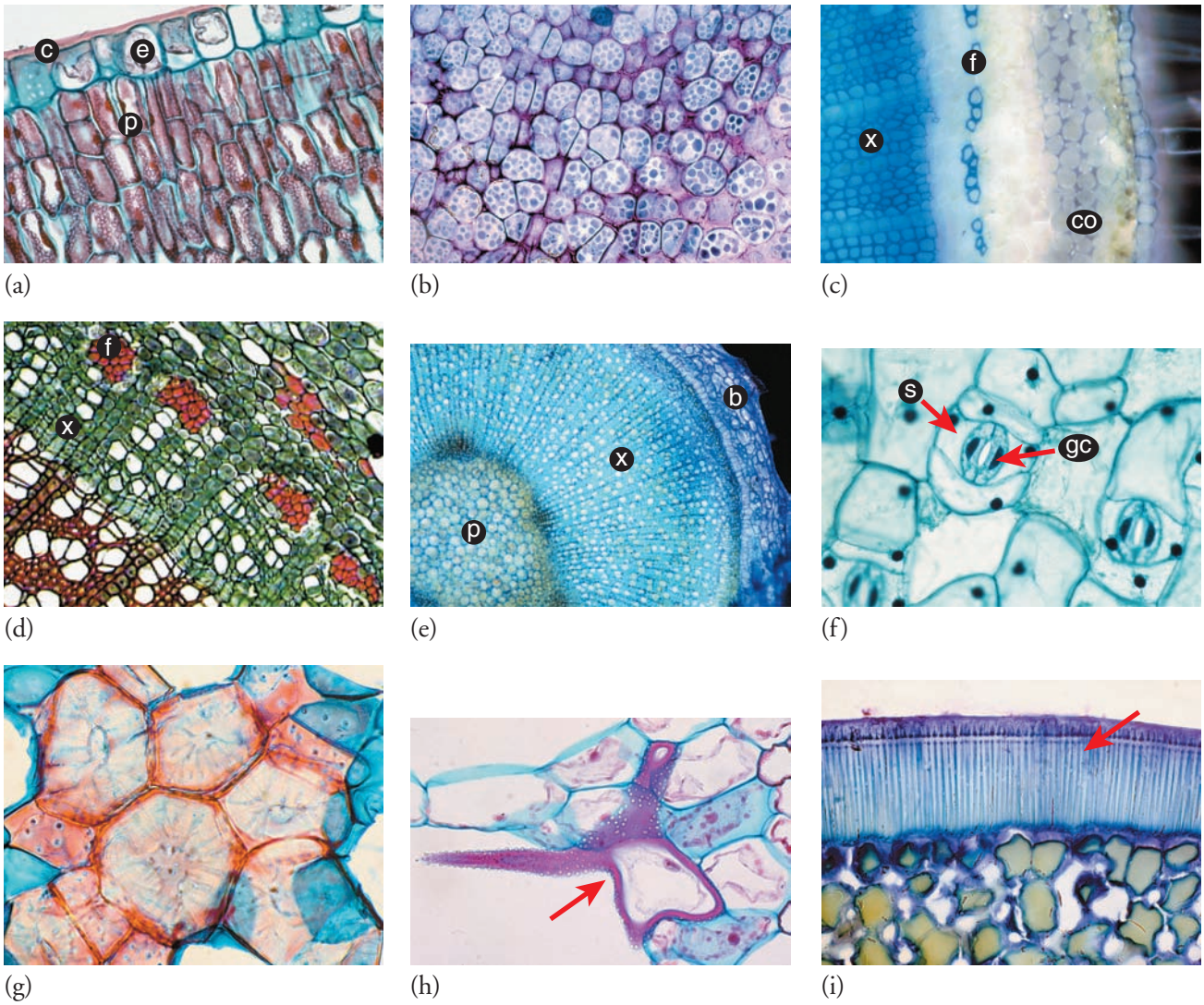


Figure 10
Different cell types in plants. (a) Cross-section of the adaxial portion of a leaf showing cuticle—c, epidermis—e, and palisade—p cells. (b) Parenchyma cells in an endosperm with storage bodies. (c) Cross-section of tomato stem showing xylem—x, phloem fibers—f, and collenchyma—co cells. (d) Cross-section of a woody plant stem showing xylem—x, and fibers—f. (e) Cross-section of azalea stem showing pith—p, xylem—x, and bark—b. (f) Lower (abaxial) surface of a leaf showing stomates with guard cells. (g, h, and i) Three types of sclereid cells: (g) brachysclereids, or stone cells, in pear fruit, (h) trichosclereids in water lily, (i) macrosclereids in a legume seed.

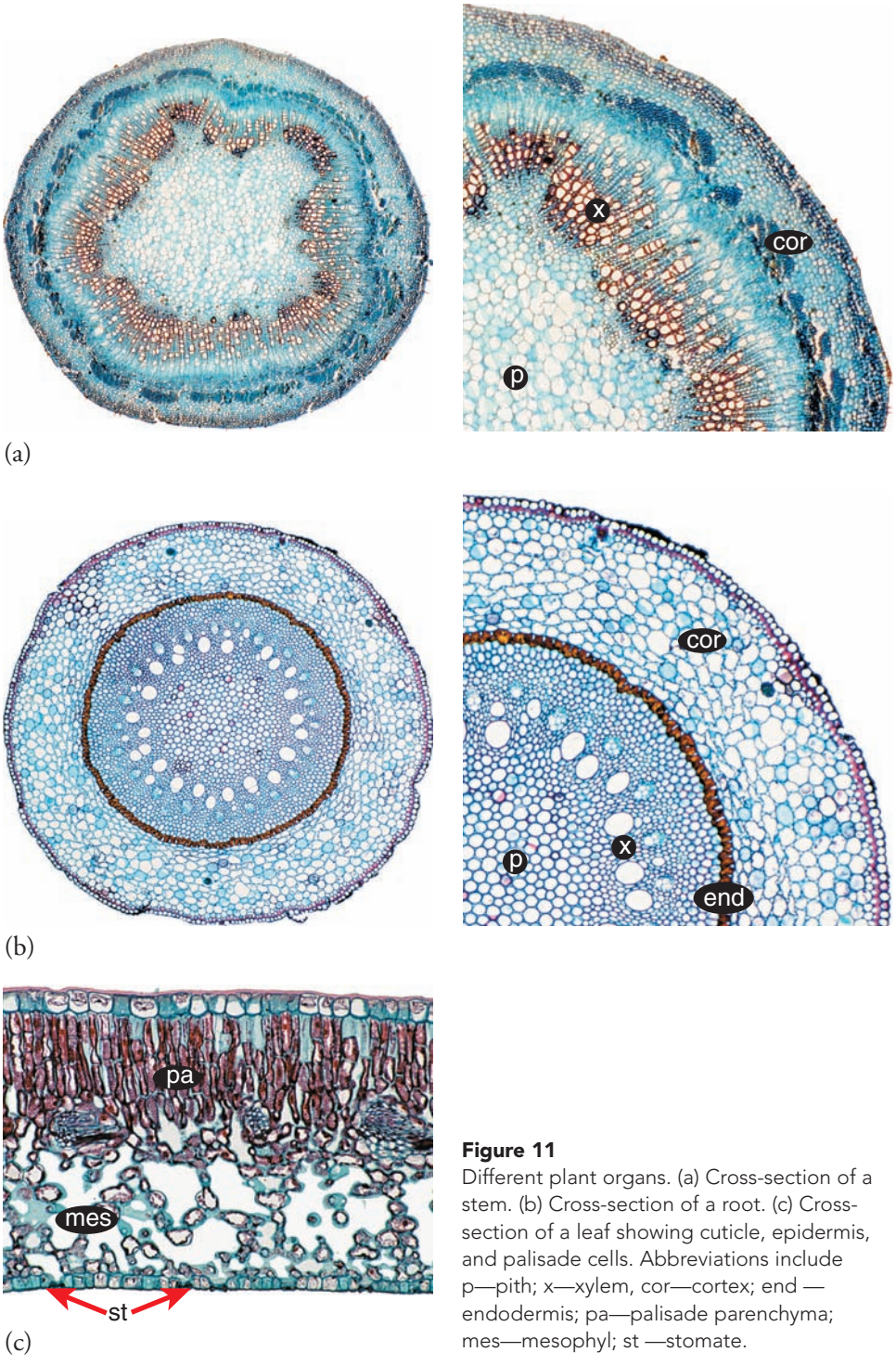


Figure 11
Different plant organs. (a) Cross-section of a stem. (b) Cross-section of a root. (c) Cross-section of a leaf showing cuticle, epidermis, and palisade cells. Abbreviations include p—pith; x—xylem, cor—cortex; end —endodermis; pa—palisade parenchyma; mes—mesophyl; st —stomate.

growing points (vascular cambium, cork cambium, leaf marginal meristems) (Fig. 12).

Meiosis The key feature of sexual reproduction is cell division through *meiosis* (64). Meiosis takes place within mother cells **(microspore mother cells** and **megaspore mother cells)** of the flower to produce **pollen** (male) and the **embryo sac** (female). Meiosis is the division of the nucleus that results in a reduction in the chromosome number by one-half, producing the haploid (1*n*) condition. Eventually, successful fertilization between haploid male and female gametes restores the diploid (2*n*) zygote leading to seed formation. Meiosis (Fig. 13) is separated into two parts: meiosis I and II. Each part of meiosis I and II includes prophase, metaphase, anaphase, and telophase stages.

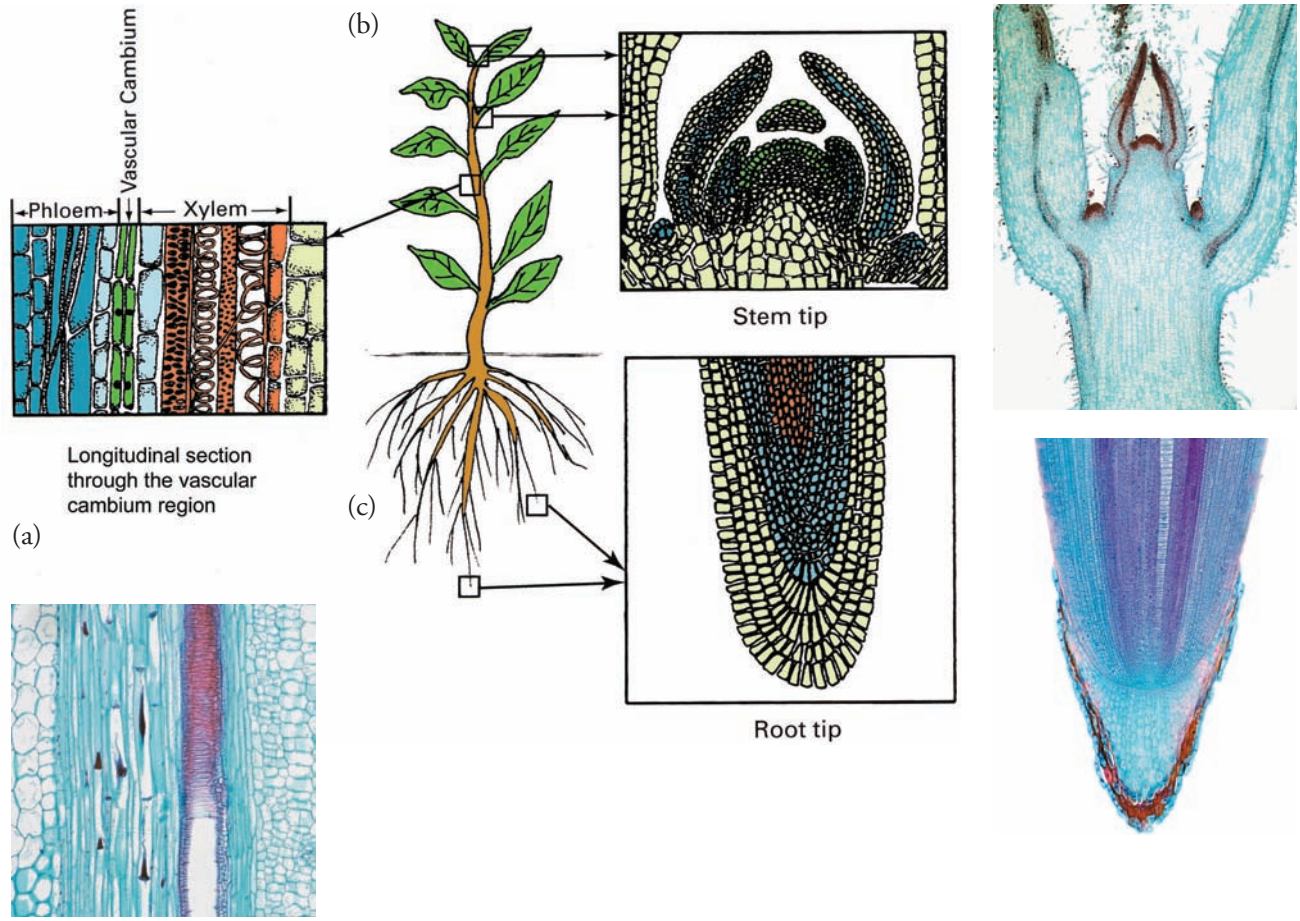


Figure 12
Location of growing points where meristematic cells occur and mitosis takes place. The points are located in the (a) cambium, (b) shoot tip, and (c) root tip.

Meiosis differs from mitosis in several important aspects:

1. Mitosis results in two genetically identical diploid cells, while meiosis results in four genetically different haploid cells.
2. There is only one division cycle for mitosis, while meiosis requires two division cycles.

Just as in mitosis, cells preparing for meiosis duplicate and double their chromosome number during interphase in preparation for division. During prophase I, the chromosomes become visible as centromeric chromatids and are arranged into homologous pairs. Then a remarkable process begins as the homologous chromosomes pairs exchange parts **(crossing-over)** of individual chromatids**.** Attached pairs of chromosomes then separate during metaphase, anaphase, and telophase to generate two new cells to complete meiosis I.

In meiosis II, each pair of chromosomes separates at the centromere and produces two daughter cells (four **gametes**), each with a haploid (*n*) number and genetically different from the parent cell and from each other. During sexual reproduction, a haploid gamete from a pollen unites with the haploid gamete from the embryo sac to produce a diploid zygote.

The consequence of meiosis is the creation of new patterns of genetic variation. Three opportunities for variation exist: (a) **crossing-over** (i.e., the interchange of genetic information during the early stages of meiosis I), (b) the **independent assortment** of the chromosomes during the later stages of meiosis II, and (c) the **recombination** of (haploid) male and female gametes in the creation of new zygotes during fertilization.

GENETIC INHERITANCE

Because of the exchange of genetic material during crossing-over, the independent assortment of chromosomes during meiosis, and the chance recombination during fertilization, patterns of genetic variation may appear in seedling populations that can be expressed in mathematical ratios of individual traits (see Figs. 14 and 15).

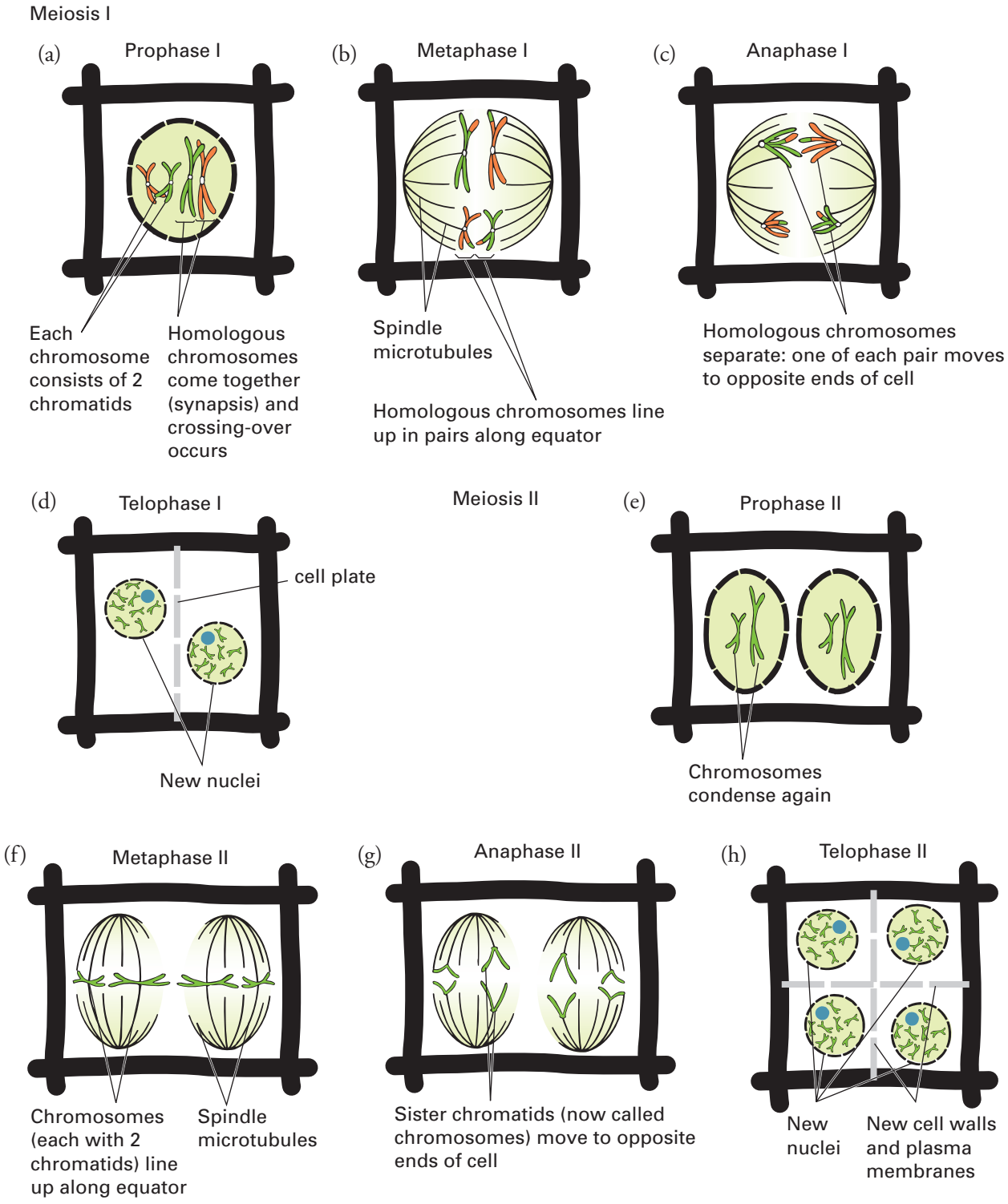


Figure 13

Stages of meiosis. **Meiosis I** - Interphase, in between divisions (not shown). However, chromosomes divide in preparation for division but remain attached at the centromere. (a) Prophase I, each shortened and conspicous chromosome has two chromatids attached at centromere. Chromosomes pair and exchange segments (crossing-over or synapsis). (b) Metaphase I, pairs line up along the center of the cell. (c) Anaphase I, pairs separate and move to opposite ends. (d) Telophase I, chromosomes disperse to form two nuclei. **Meiosis II -** (e) Prophase II, chromosomes again condense to form conspicuous pairs. (f) Metaphase II, chromosomes line up across the center of each cell. (g) Anaphase II, chromosomes separate into chromatids and move to opposite ends. (h) Telophase II, cell walls laid down to produce four haploid *(n)* gametes. Adapted from Linda R. Berg. 1997. *Introductory Botany.* Saunders College Publishing.

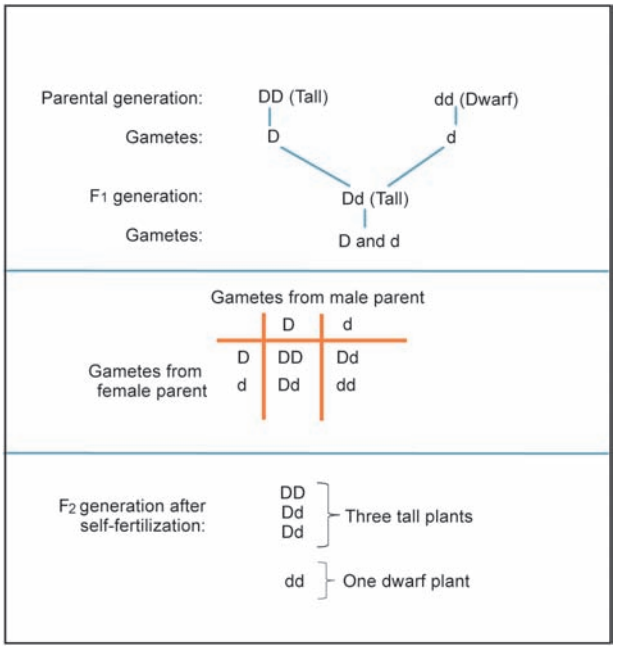


Figure 14
Inheritance involving a single pair of alleles in the gene controlling height in the garden pea. *Tallness* (D) is dominant over *dwarf* (d). A tall pea plant is either homozygous (DD) or heterozygous (Dd). Segregation occurs in the F_2 generation to produce three genotypes (DD, Dd, or dd) and the two phenotypes *tall* and *dwarf*.

These phenotypic distributions will be affected by whether the two genes are **dominant** or **recessive** and whether they are present as **homozygous** or **heterozygous** pairs. Many traits, however, are determined **quantitatively** by the interactions of a large number of genes that may be expressed uniquely in different environments (Fig. 16). In nature, seedling variability provides the opportunities for selection so that new genotypes can evolve that are adapted to specific environmental niches. Over time, genotypes tend to become more or less stabilized, or **"fixed,"** when grown over a long period in the same environment. This genotype–environment interaction is the basis for the origin of species (21, 70). In cultivation, seedling variation provides the opportunity for plant breeders to develop new kinds of plants that have special traits useful for humans but whose genotype must be maintained by special techniques of seed production. In general, plant breeding includes transferring genes from desirable parents to their offspring by crossing and then stabilizing (**fixing**) the genotype of the offspring population for propagation (1, 12, 37, 71).

"fixing" The process of genetically stabilizing the genotype so that the cultivar will breed true from seed.

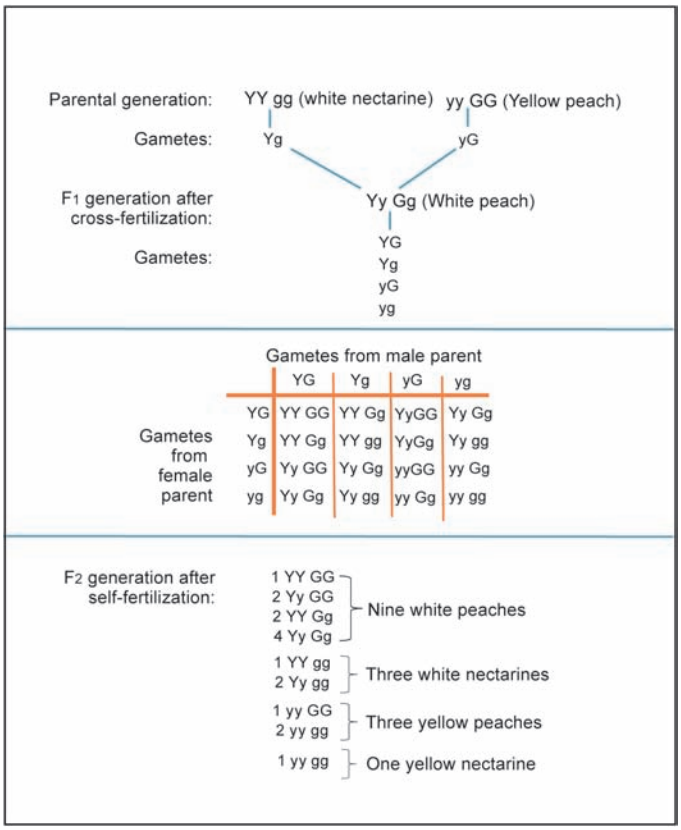


Figure 15
Simultaneous inheritance of two genes in a cross involving peach and nectarine (*Prunus persica*). *Fuzzy skin* (G) of a peach is dominant over the *smooth skin* (g) of a nectarine. *White flesh color* (Y) is dominant over *yellow flesh color* (y). In the example shown, the phenotype of the F_1 generation is different from either parent. Segregation in the F_2 generation produces nine genotypes and four phenotypes.

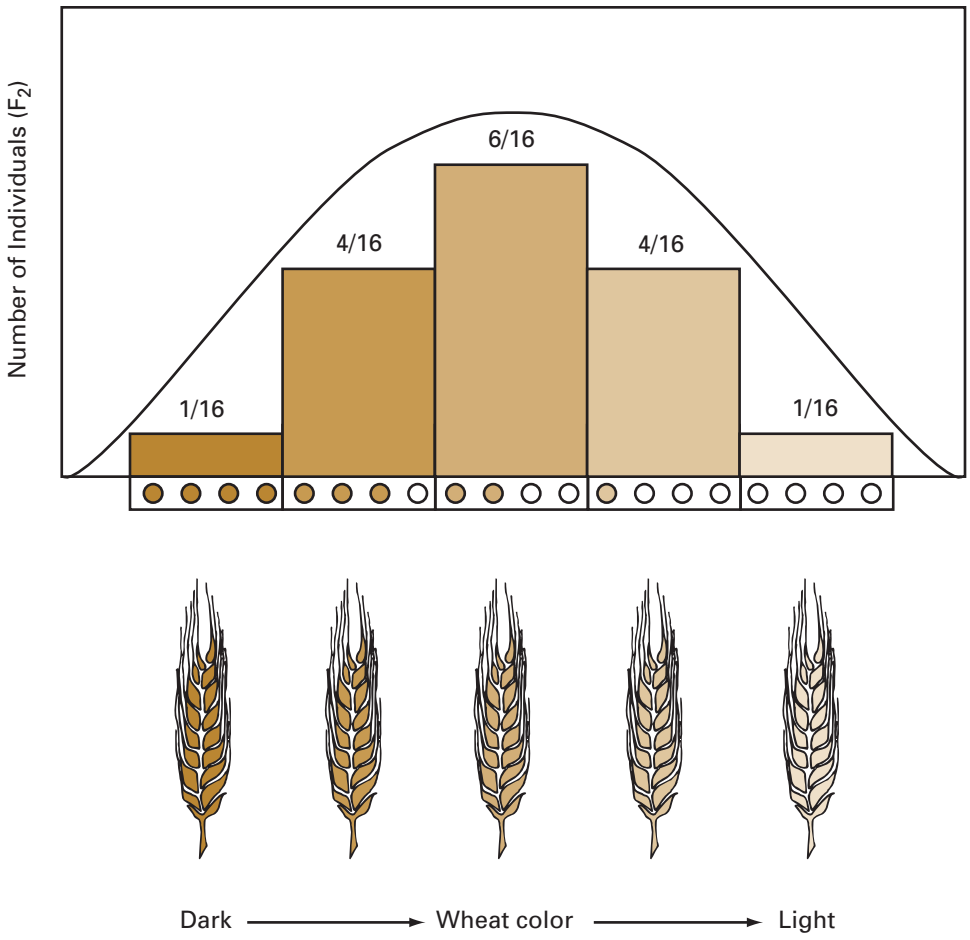


Figure 16
Quantitative genetic distribution is illustrated by the continuous varying pattern of wheat grain color. This makes a normal distribution curve, which indicates that many genes contribute to this phenotype. Adapted from Linda R. Berg. 1997. *Introductory Botany.* Saunders College Publishing.

GENE STRUCTURE AND ACTIVITY

Genes play a dual role in all organisms (6, 49, 64). First, they provide the physical mechanism by which individual traits and characteristics are reproduced from generation to generation both by seed (meiosis) or vegetative propagation (mitosis). Second, genes contain the specific directions for regulating the chain of morphological and physiological events that determine the expression of specific traits and characteristics of the phenotype. The central dogma of this process is that genetic information flows (with some exceptions) from deoxyribonucleic acid (DNA) to ribonucleic acid (RNA) to proteins through processes of transcription and translation.

Genes as Structural Units of Inheritance

Pre-Mendel The concepts and practices of plant (and animal) selection has a long and progressive history. Prior to 1900, plant breeders and plant propagators (often the same individual) carried on selection by visual inspection of specific traits and characteristics. That is, in seed propagation, the phenotypes of parents were compared with their seedling offspring; in vegetative propagation, the clonal source plant was compared with its vegetative progeny. Improvement was through mass selection in which the "best" phenotypes of one generation were chosen as parents for the next.

Mendelian Genetics The rediscovery in 1900 of Gregor Mendel's (56) paper published in 1866 marked the start of a new era in which selection became based on experimentally determined hereditary principles under the term *Mendelian genetics.* The concept of *gene* emerged as well as the term *genotype.* Chromosomes, which had been discovered about 50 years earlier, were found to be related to patterns of gene inheritance (20). Chromosomes were found to be composed of DNA and proteins. A basic question was whether proteins or DNA were responsible for inheritance. The answer obtained from studies with specific bacterial viruses called **bacteriophages** (39) showed that DNA was responsible for inheritance.

DNA-Based Genetics The studies of Watson and Crick published in 1953 on the structure of the DNA molecule (81) not only provided the biochemical model for DNA duplication during mitosis and meiosis but ushered in a new era of genetic research (Fig. 17). Subsequent

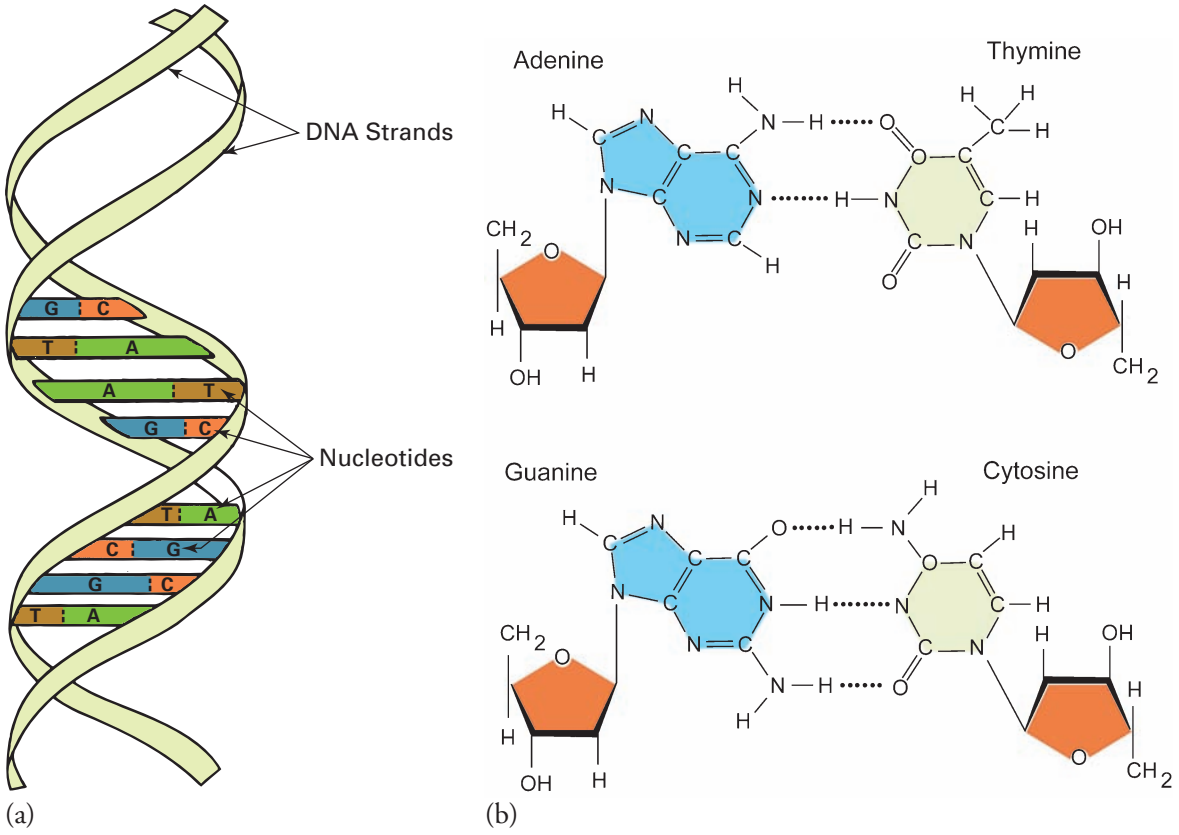


Figure 17
DNA structure. (a) Double helix of DNA strands made up of alternating sequences of ribose sugar joined by phosphate (PO_4) radicles. Nucleotides are made up of four possible bases—identified as A, T, G, C—that are joined at one end to a sugar molecule in the strand and loosely joined on the other to a complementary base (i.e., A with T, G with C). Combinations of base-pairs make up the genetic code. Adapted from Linda R. Berg. 1997. *Introductory Botany.* Saunders College Publishing. (b) Molecular structure of the binding pairs of nucleotide bases.

genetic code
Combinations of base pairs that create a code for different amino acids, whose combination in turn creates different proteins.

studies identified the **genetic code** used to translate genetic information into functional proteins. This universal code was first identified in bacteria and then confirmed as a universal code for all organisms. This identification of genetic code was accompanied by the elucidation of **gene regulation** through the processes of transcription and translation, which regulate the expression of individual genes.

The structure of a chromosome consists of two strands of DNA in combination with various structural proteins called histones. The essential components of the DNA structure are **nucleotides,** which are combinations of one of four possible chemical nitrogenous bases **(thymine, adenine, guanine, cytosine),** a five-carbon sugar molecule **(deoxyribose),** and **phosphate (PO_4)** (Fig. 17). Nucleotides are attached to long chemical strands made up of phosphate (PO_4^-) radicals that connect the 5′ (five-prime) position of one sugar molecule to the 3′ (three-prime) position on the next sugar molecule. A **base** is attached at one end to a sugar molecule and loosely attracted by a **hydrogen bond** to a different, but complementary, base on the other DNA strand. Guanine (G) pairs with cytosine (C), and adenine (A) with thymine (T). The result is a **double-helix** structure of long, double chains of repeating nucleotides. This structure gives DNA a unique capacity to replicate itself during mitosis and meiosis when catalyzed by the enzyme **DNA polymerase.** The specific sequence of nucleotide bases, i.e., **base pairs,** provides the genetic information that determines inheritance, establishes

nucleotide A component of the DNA molecule whose important component is one of the four bases identified as T, G, A, or C; particular combinations of the complementary bases on homologous chromosomes pair G with C, and A with T.

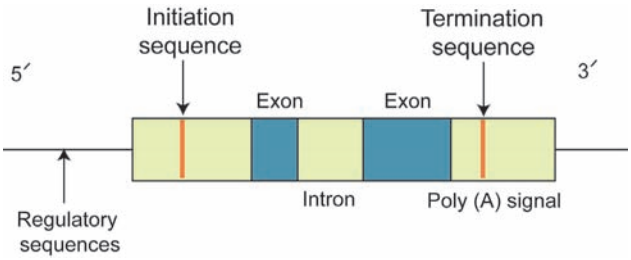


Figure 18
Schematic drawing of the structure of a gene. See text for details.

the specific genotype of the organism, and directs the pattern of gene expression. A coding unit consists of a specific sequence of three of the four bases and is known as a **codon.** Codons translate into one of twenty **amino acids** used to make proteins. From a molecular standpoint, a gene can be described as a linear piece of DNA (65), which includes the following: (a) coding regions, known as **exons,** that contain the genetic instructions, (b) noncoding regions known as **introns,** (c) an **initiation codon** (also known as a **promoter**), (d) a **termination codon,** and (e) a **regulator sequence** adjoining the gene on the 5′ end that determines when a gene is turned on and off (Fig. 18) (6, 64).

RNA (ribonucleic acid) Biochemical compound that functions to transcribe genetic code information from the chromosome to mRNA where it is translated into protein synthesis.

Gene Expression

Transcription Genetic information is copied from one of the strands of DNA onto similar macromolecules called **RNA (ribonucleic acid).** The structure of RNA differs from nuclear plant DNA in that it has only a single strand, a different sugar **(ribose),** and includes **uracil** instead of thymine. RNA exists in several forms. At the transcription stage it is called **messenger RNA** or **mRNA.** The process begins with a signal **recognition** process that involves various environmental, physiological, or hormonal cues to turn on the gene. This is followed by the initiation of **transcription** of specific DNA sequences to make single-stranded mRNA molecules. A specific enzyme **(RNA polymerase)** mediates transcription that results

transcription The process by which the genetic code of genes present in the DNA is enzymatically transcribed to a strand of RNA.

RNA polymerase An enzyme within the nucleus that mediates the transcription of DNA codes to tRNA.

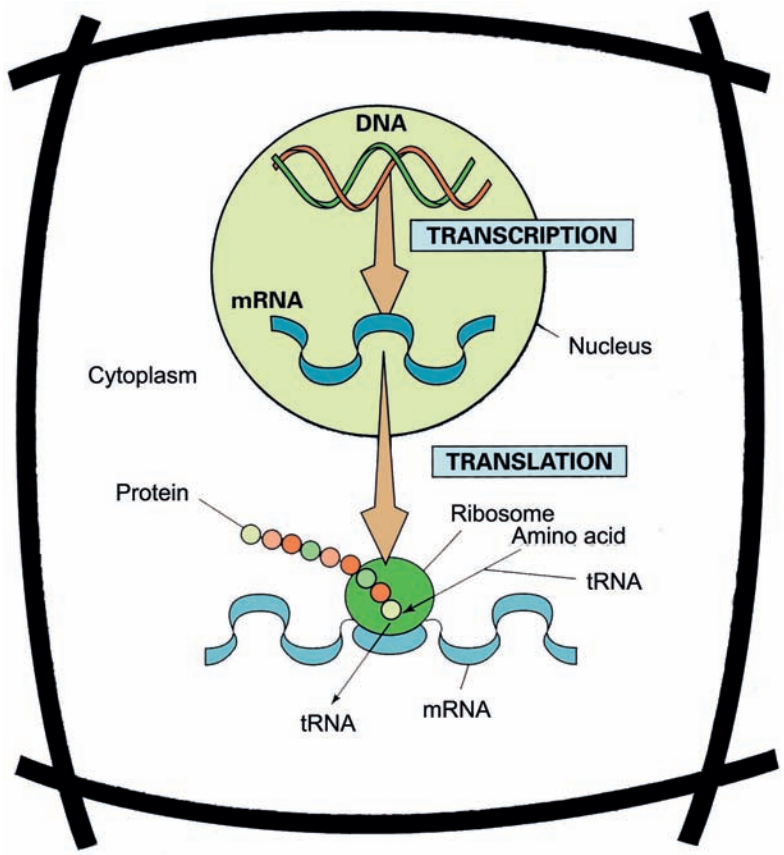


Figure 19
Transcription and translation. The diagram illustrates the fact that transcription is carried out in the nucleus in which mRNA transcribes the nucleotide sequences for a specific gene on one of the strands and then migrates to the cytoplasm. Here the message is used to manufacture specific proteins within the ribosomes with the help of tRNA and rRNA.
Adapted from Linda R. Berg. 1997. *Introductory Botany.* Saunders College Publishing.

translation The process by which the genetic code from genes is translated from mRNA by ribosomal RNA to combine amino acids to create peptides, polypeptides, and, eventually, proteins.

ribosome A structure within the cytoplasm composed of protein and ribosomal RNA (rRNA) within which translation takes place.

in the synthesis of mRNA molecules—which may vary from 200 to 10,000 nucleotides in size. These move from the nucleus across the nuclear membrane into the cytoplasm (Fig. 19).

Translation **Translation** is the process of building a protein based on the genetic code sequenced on the mRNA. Translation is a coordinated effort among mRNA, **ribosomes, transfer RNA (tRNA),** and amino acids. Proteins are made at the ribosome where the mRNA passes between the two ribosome subunits. Transfer RNA brings the appropriate amino acid to the ribosomal complex for translation into the protein called for by the codon on the mRNA. Amino acids become linked together in chains first as **peptides,** then **polypeptides,** and, eventually, specific **proteins.** Proteins expressed after translation can be visualized using gel electrophoresis (Fig. 20).

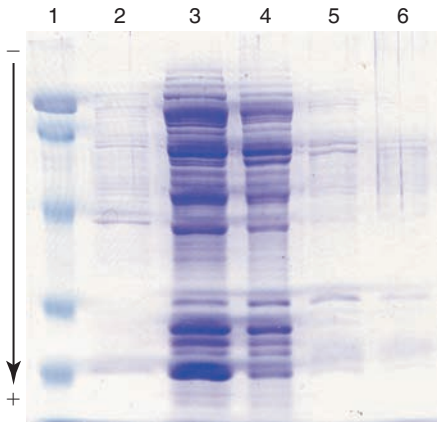


Figure 20
Gel electrophoresis showing the migration of proteins down the gel. Gel electrophoresis uses an electric current to move molecules from the top of the gel toward the base. Different sized molecules move at different rates. Gel electrophoresis can also be used to visually separate DNA and RNA. In this gel, proteins are stained with Coomassie blue to visualize the proteins. Lane 1 is a molecular weight ladder used as a reference. The five other lanes represent treatments with different protein level expression. Lanes 3 and 4 qualitatively have very similar protein profiles, but the treatment represented in lane 3 has more protein being expressed.

Regulating Gene Expression

Proteins are large, complex macromolecules, many of which function as enzymes that regulate the biochemical reactions controlling metabolic and developmental plant processes. The types and functionality of proteins produced by the cell determines plant growth and development. Therefore, regulation of gene transcription is an important component of determining a cell's developmental fate.

Regulation of gene transcription involves effector and repressor molecule interactions at the regulatory sequences found at the three-prime portion of the gene called the promoter region. This type of gene regulation can be illustrated by the repressor/de-repressor model for auxin action (Fig. 21) (83). The auxin responsive gene has a sequence in the promoter region called the auxin response element (AuxRE). The promoter protein called auxin response factor (ARF) physically interacts with this regulatory element to promote gene expression. However, when auxin is not present, the repressor molecule (AUX/IAA) interacts with ARF in such a way that it is unable to promote transcription. When auxin is present in the cell, auxin binds to its receptor moleculre (TIR1) to initiate degradation of the Aux/IAA repressor. This releases ARF from its repression by AUX/IAA to promote gene transcription. This type of repressor/de-repressor interaction seems to be a common mechanism controlling gene expression.

Gene expression can also be regulated after transcription is complete and mRNA is made. One example of this control is by small, nontranslating RNA molecules such as microRNAs. **MicroRNAs** function in translational repression and are important for controlling development in plants and animals. They are small ~22 nucleotide RNAs that are components of a RNA-induced silencing complex. MicroRNAs seek out complementary mRNA, bind to them, and target them for enzymatic degradation. Using auxin-induced gene expression again as an example, several microRNAs that are developmental regulated target ARF mRNA for silencing. These microRNAs prevent ARF mRNA translation, which, in turn, eliminates ARF as a promoter of auxin-responsive genes.

microRNA (miRNA) A small RNA molecule involved in post-translational control of gene expression.

Post-translational control is also an important regulatory mechanism for growth and development. Proteins made through the gene expression pathway may not have regulatory function until they are modified. A common protein modification is through phosphoroylation by kinase enzymes. This sets up "kinase

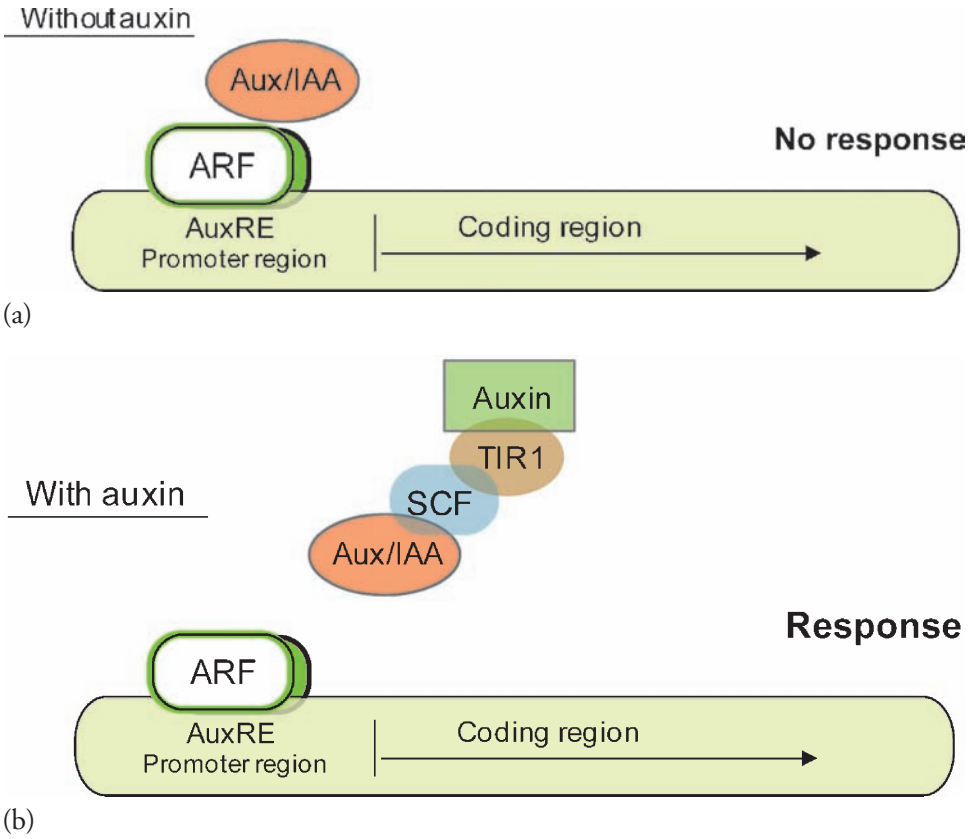


Figure 21
Presented is a model for auxin hormone action related to gene expression. (a) The gene being controlled by auxin as an auxin response element (AuxRE) in its promoter region. A transcription regulator called auxin response factor (ARF) is required for gene expression. It is available to bind the promoter region even in the absence of auxin; however, a repressor molecule (Aux/IAA) binds to ARF to inhibit gene expression. (b) When auxin is present, it binds to its receptor (TIR1) and initiates a ubiquitan-ligase complex (SCF) that targets AUX/IAA for destruction. With the repressor removed, ARF can initiate gene transcription.

cascades" that are important consequenses of hormone-receptor binding and downstream hormone activity.

Biotechnology

A long sequence of basic laboratory studies has led to a revolution in genetic research which is described under the umbrella term of **biotechnology.** These have begun to have far-reaching applications not only in propagation but across the whole range of applied biology.

Cell and Tissue Culture Technology This term refers to an array of concepts and procedures involving the propagation and culture of cells, tissues, and individual plant organs in aseptic closed systems. Among the culture systems developed are those for embryos, ovules, shoot apices, callus, protoplasts, and cell suspensions. These concepts and procedures are powerful tools that have revolutionized many aspects of plant physiology, genetics, and propagation. Some procedures are used commercially in nursery operations, others are primarily for genetic improvement, and others are for scientific investigations.

DNA-Based Marker Technology This category refers to the group of laboratory procedures that utilize the nucleotide sequences present on small DNA fragments produced artificially from chromosomes by specific enzyme treatments to identify and label specific locations in the **genome.** With appropriate procedures, the sequences on these segments can be used as **DNA markers,** which are visually observed as bands on an electrophoresis plate (Fig. 22). This technique

genome All of the genetic material (i.e., genes) present in the chromosomes of an organism; some DNA may be present in chloroplasts and mitochondria as well.

DNA markers Specific combinations of base pairs (bp) that are used to identify genes and genotypes in the laboratory.

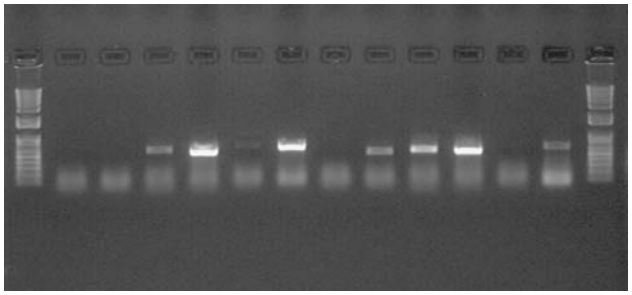


Figure 22
DNA visualization on an agarose electrophoretic gel. The first and last lanes are the DNA size markers. The DNA is visualized on an X-ray film taking advantage of the radiolabeled phosphorus that was added to mark the DNA during the PCR reaction.

makes it possible to identify specific genes and, eventually, to characterize whole genomes. Nucleotide sequencing techniques are used to monitor and predict variation during breeding operations (marker-assisted gene linkage maps) and to identify specific cultivars (DNA fingerprinting) (7, 78, 84). They also provide data to investigate botanical and evolutionary relationships by creating cladograms that show genetic similarities among members of a genus or plant family (23, 27, 63).

Recombinant DNA Technology This term includes a group of procedures in which the nucleotide sequences of the DNA molecule representing a gene can be isolated, cloned, and hybridized with other DNA fragments to produce what is known as **recombinant DNA.** These hybrid DNA clones can be used as **genetic probes** to identify and characterize gene expression. Also, by using appropriate methods, DNA from a donor organism can be introduced into cells of another organism to become part of its genome (19, 30, 44). Plants transformed using recombinant DNA techniques are called **transgenic** and are popularly

recombinant DNA The combination of DNA representing a particular gene cloned with other DNA fragments in the laboratory in order to be inserted into the genome of another organism.

BOX 2 **GETTING MORE IN DEPTH ON THE SUBJECT**

TECHNIQUES USED TO STUDY GENE EXPRESSION

DNA Marker Technology

Fragmentation Restriction Enzymes have been discovered in bacteria that cause chromosomal DNA to split into small fragments at specific nucleotide sequences and with different numbers of nucleotides. Under various laboratory procedures, large numbers of these **restriction fragments** can be generated, which, taken together, represent pieces of the entire genome of individual organisms. These fragments then become markers of specific segments of the genome representing specific genes and can be stored as **genomic libraries** in the laboratory. These fragments become the working tools of various procedures described in the subsequent text.

Amplification Treating DNA fragments with the bacterial enzyme **Taq polymerase** under appropriate temperature sequences causes single DNA strands to replicate (up to 1 million times in a few hours). The process known as **polymerase chain reaction (PCR)** is a form of cloning. As a result, large quantities of specific DNA clones can be produced.

polymerase chain reaction (PCR) DNA fragments can be caused to replicate in order to produce large amounts of a specific DNA clone.

Visualization and Separation DNA fragments are identified by the pattern of consecutive bands in the gel on an electrophoresis plate (Fig. 22). Mixtures of fragments are placed at one end of the gel and individual segments migrate to the other end in response to an electric current. The location of the segments differs primarily because of fragment size (i.e., numbers of base pairs). To visualize the pattern, the gel is treated by appropriate indicators (stains, ultraviolet light, radioactivity). The gel can be sliced into sections to isolate specific DNA fragments.

DNA Sequencing A DNA sample is divided into parts, each to be treated separately by different restriction enzymes, which recognize different nucleotide pairings. The samples are amplified (cloned) by the PCR reaction, electrophoresed, and analyzed for nucleotide sequences. The latter is done automatically by a DNA sequencing machine that utilizes different colored fluorescent dyes for visualization. Because the base-pair patterns of different fragments overlap, a complete "map" of an entire genome or individual gene location can be produced.

Molecular Genetics

Molecular genetics is the study of the function of genes at the molecular level. One important tool in the study of molecular genetics is to generate mutants impaired in an area of growth and development.

Mutant Generation and Analysis Mutant plants are usually generated by chemical (EMS) or radiation exposure. Mutagenesis directly impacts the DNA sequence, altering a gene's ability to be transcribed and translated into a viable protein. Mutant screens must be developed to visualize the few desired mutants in the thousands of treated seeds or plant parts. For example, seedlings germinated

(Continued)

in the presence of ethylene will develop a classical triple response (short, thickened stems growing horizontally). Mutant seedlings impaired for ethylene action were discovered because they grew as tall, upright seedlings seemingly immune to ethylene.

Transformation Technology (41). Foreign DNA can be introduced into a plant's genome using *Agrobacterium*-mediated transformation or particle bombardment. *Agrobacterium tumefaciens* is a bacteria that uses a circular piece of DNA called a plasmid to integrate a portion of its DNA into the plant's genome to create a plant tumor and facilitate bacterial replication (8). Researchers can modify this plasmid to replace bacterial genes with novel genes for plant improvement or basic plant science studies. Plant tissue cultures or intact flowers are exposed to the engineered bacteria for gene insertion (Fig. 23). A second transformation method is particle bombardment, sometimes called biolistics. This method uses microprojectiles (gold or tungsten particles) coated with DNA that are shot into plant tissue where they enter dividing plant cells and become integrated into the plant's genome (Fig. 23c). Following gene transfer, seedlings or plant tissue are placed on a selection medium where transformed individuals can be identified and raised into reproductive whole plants (Fig. 23d).

Plants are transformed to up-regulate a gene's activity, introduce a novel gene product (like herbicide resistance), or suppress or silence a gene (see later in this chapter). Plants may also be randomly transformed with short pieces of DNA that can insert into a gene to disrupt its activity; this is called tDNA insertional mutagenesis. Plants can be screened for activity in a similar way to mutants generated by chemicals or radiation. However, because the tDNA insertion has a known DNA nucleotide sequence, the disrupted gene can usually be more easily identified compared to other mutants.

Gene Silencing Technology

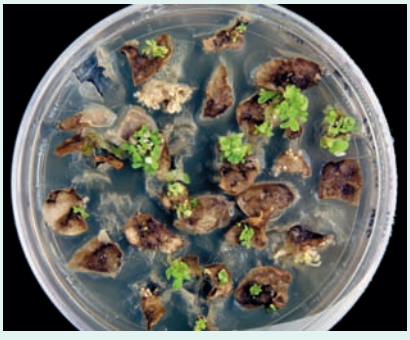
Once a gene is suspected of having regulatory properties, gene silencing technology can evaluate the importance of that gene in growth and development. Gene silencing significantly knocks down or eliminates the gene product (protein) from being produced and should impair the growth and development process being evaluated (like seed germination or flowering). Commercial plant cultivars can be developed so that a particular gene has been silenced in order to influence production of a biochemical product or slow a process like fruit ripening or flower senescence.

Antisense Technology (26) DNA consists of two complementary strands of nucleotides. Only one of these two strands of DNA serves as a template for mRNA formation and is called the **sense strand.** It is possible to reverse the order of a particular segment controlling a particular gene copy of the sense strand within the chromosome, which is

(a)

(b)

(c)



(d)

Figure 23
The most common forms of genetic transformation use *Agrobacterium*-mediated transformation or biolistics. (a) A solution of bio-engineered *Agrobacterium* designed to integrate new DNA into the plant's genome (b) *Arabidopsis* at the proper flowering stage to be dipped in the diluted *Agrobacterium* solution. (c) Technician placing a sample into the biolistics machine, which will shoot DNA-coated particles into the plant sample. (d) Leaf pieces on a selection medium after being transformed. Green, new shoots represent plants that were transformed, while non-transformed leaf pieces do not survive on the selection medium (i.e., antibiotic medium).

now called **antisense**. The nucleotides within the specific segment are not copied now, and in effect become nonfunctional, effectively turning off the gene associated with the segment. This antisense feature is then inherited like any gene.

RNA Interference (RNAi) Small RNA molecules (fewer than 20 nucleotides) have recently been discovered as important for plant defense (disease resistance) and for control of growth and developmental processes (43, 47). These include small interfering RNA (siRNA) and microRNA (miRNA). These small RNA molecules attach to complementary sequences on mRNA to prevent translation. These are natural processes of control in plants and animals. Researchers take advantage of this technology by inducing RNAi silencing of a gene of interest to investigate the gene's function.

Genome-Wide Gene Expression

Techniques have become available to do global gene expression profiling that measures the activity of thousands of genes at once. These techniques provide a huge amount of data that has lead to the development of a new field of study called bioinformatics, which aids in gene discovery experiments.

Transcriptome Analysis The transcriptome represents the mRNA being produced by a cell or plant tissue at a given time during growth and development. This is a measure of the gene expression at that particular developmental event in time (i.e. radicle protrusion during seed germination). The identification of these mRNA has been greatly enhanced by the availability of the gene sequences for entire genomes in plants such as *Arabidopsis*, poplar (*Populus*), rice, and *Medicago truncatula*. For plants like corn or tomato where genome sequencing is still under development, expressed sequence tag (EST) libraries have been developed that contain information about mRNA expression. Microarray (also called a gene chip) technology has been developed to measure global gene expression (Fig. 24). A microarray contains thousands of partial DNA sequences arranged on a slide or platform (62). These sequences will hybridize to cDNA (complementary DNA) synthesized from the mRNA extracted from the plant tissue. A positive interaction leads to a fluorescent label being activated that indicates the relative abundance of the mRNA signal.

Although microarray analysis reveals the different mRNAs being transcribed in the cell, that information does not necessarily give a full profile of the functional proteins being translated from those mRNA. Therefore, a second complementary technique called proteomics has been developed to measure all of the proteins made during that same developmental time.

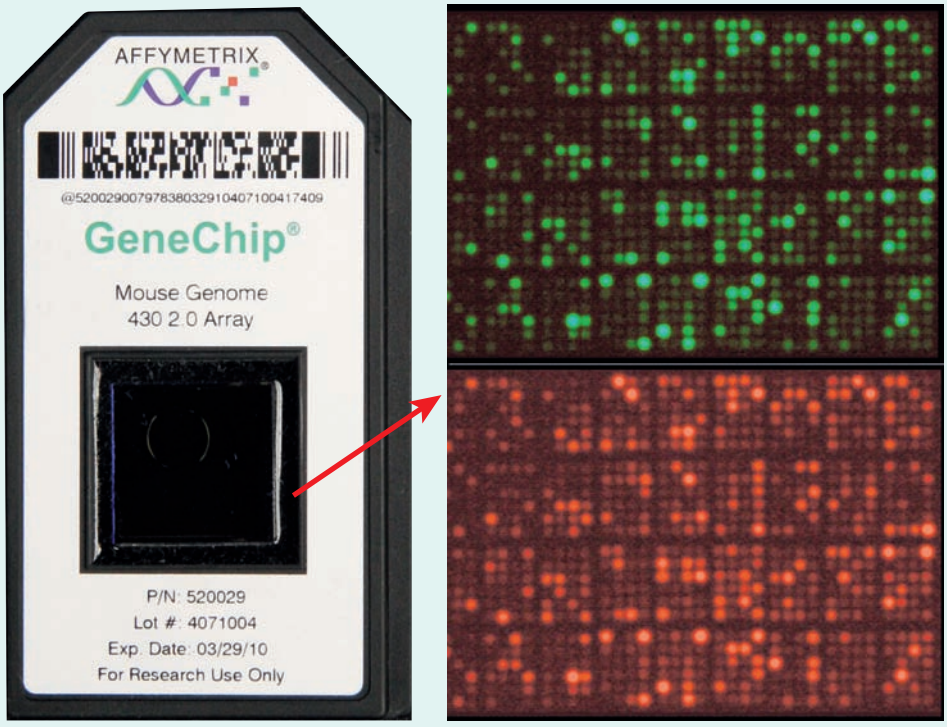


Figure 24
Microarray chips contain thousands of gene sequences as individual microscopic spots. They act as probes to visualize gene expression. Positive interactions can be seen by color and intensity on the chip.

known as **genetically modified organisms (GMOs).** Examples of economic traits being engineered include various seed components (13), flower longevity (31), and disease (53) and insect resistance (74).

PLANT HORMONES AND PLANT DEVELOPMENT

phytohormones (plant hormones) Organic chemicals that regulate growth and development.

Plant hormones (phytohormones) are naturally occurring organic chemicals of relatively low molecular weight, active in small concentrations. The classic definition of a hormone is that they are synthesized at a given site and translocated to their site of action; however, there are some exceptions for plant hormones. They are specific molecules involved in the induction and regulation of growth and development. The five major plant hormones are **auxin, cytokinin, gibberellin, abscisic acid,** and **ethylene.** Additional compounds considered hormones include **brassinosteroids, jasmonates, salicylic acid, polyamines,** and **peptide hormones.** Plant hormones have great importance in propagation because they not only are part of the internal mechanism that regulates plant function, but they also can induce specific responses such as root initiation in cuttings and dormancy release in seeds.

In addition to these substances, certain chemicals—some natural, others synthetic—show hormonal effects to plants. Both natural and synthetic types are classed together as **plant growth regulators (PGRs).** Table 3 lists the characteristics of important PGRs used in propagation. Their usage will be further described in subsequent chapters.

plant growth regulators (PGRs) Any natural and synthetic chemical that shows hormonal effects.

Here is a usual set of events that occurs during hormone-induced growth and development:

1. Biosynthesis of the hormone
2. Transport or distribution to its site of action

Table 3
CHARACTERISTICS OF IMPORTANT PLANT GROWTH REGULATORS AND HORMONES. THOSE MARKED WITH ASTERISK (*) OCCUR NATURALLY

Name	Chemical name	Mol. Wt.	Solvent	Sterilization[1]	Storage	
					Powder	Liquid
	A. Auxins					
IAA*	indole-3-acetic acid	175.2	EtOH or 1N NaOH	CA/F	–0°C	–0°C
IBA*	indole-3-butyric acid	203.2	EtOH or 1N NaOH	CA/F	0–5°C	–0°C
K-IBA	indole-3-butyric acid-potassium salt	241.3	Water	CA/F	0–5°C	–0°C
NAA	α-naphthaleneacetic acid	186.2	EtOH or 1N NaOH	CA	RT	0–5°C
2,4-D	2,4-dichloro-phenoxy-acetic acid	221.0	EtOH or 1N NaOH	CA	RT	0–5°C
	B. Cytokinins					
BA	6-benzyl-amino-purine	225.3	1N NaOH	CA/F	RT	0–5°C
2iP*	6(di-methyl-allyl-amino) purine	203.2	1N NaOH	CA/F	–0°C	–0°C
Kinetin		215.2	1N NaOH	CA/F	–0°C	–0°C
TDZ	Thidiazuron	220.2	DMSO or EthOH	CA	RT	0–5°C
Zeatin*		219.2	1N NaOH	CA/F	–0°C	–0°C
	C. Gibberellins					
GA_3*	gibberellic acid	346.4	EtOH	F	RT	0–5°C
K-GA_3	gibberellic acid potassium salt	384.5	water	F	0–5°C	–0°C
	D. Inhibitors					
ABA*	Abscisic acid	264.3	1N NaOH	CA/F	–0°C	–0°C

[1]CA = coautoclavable with other media; F = filter sterilize; CA/F = autoclavable with other components but some loss in activity may occur.

Source: Adapted from *Plant Cell Culture* 1993 catalog. Sigma Chemical Co., St. Louis, Mo.

3. Perception of the hormone signal by its cellular receptor
4. Signal transduction leading to downstream events often at the molecular (gene expression) level

It has become evident that many types of growth and development are not controlled by a single hormone; rather there is considerable interaction and "cross-talk" often between several hormones. Often there is one principle hormone controlling development with other hormones modifying its action (45). For example, abscisic acid's control over seed dormancy is modulated by gibberellin, cytokinin, ethylene, and brassinosteroid. Some of the plant hormones are present in active and conjugated forms. Conjugation is the addition of a sugar or amino acid to the chemical structure of the hormone. Conjugation may inactivate the hormone permanently, or enzymes can interconvert the hormone between conjugated and free forms through a process called homeostatic control.

Auxins

Auxin was the first plant hormone discovered by plant scientists. Phototropism, where uni-directional light altered the growth of plant coleoptiles, in grass seedlings was one of the first biological systems studied by botanists including Charles Darwin (22). Fritz Went, Kenneth Thimann (82), and a number of other researchers showed that these effects could be induced by plant extracts, which were subsequently shown to contain the chemical **indole-3-acetic acid (IAA).**

There are two biosynthetic pathways for IAA in plants (5). Primary auxin biosynthesis is via the amino acid L-tryptophan, but IAA can also be synthesized by a tryptophan-independent pathway. Most of the IAA in plant tissue is in the conjugated form using both amino acids and sugars for conjugation. Free, active IAA comprises approximately 1 percent of the total auxin content, with the remaining portion in the conjugated form. Primary sites of auxin biosynthesis include root and shoot meristems, young leaf primordia, vascular tissue, and reproductive organs including developing seeds (Fig. 25).

Auxin movement from cell to cell requires efflux carriers located on the plant membrane (Fig. 26) (83). They control polar auxin movement from plant tips (distal ends) to their base (proximal end). Cellular auxin movement and the subsequent polar gradient established between cells is important for normal development of the plant embryo as well as the shoot apical meristem (57).

Auxin has a major role for controlling phototrophism, inhibition of lateral buds by terminal buds (apical dominance), formation of abscission layer on leaves and fruit, activation of cambial growth, and adventitious root initiation. Auxin is the most widely used hormone in plant propagation because of its impact on adventitious rooting in cuttings and its control of morphogenesis during micropropagation.

IAA degrades in the light, and exogenously applied IAA is quickly degraded by the enzyme IAA-oxidase.

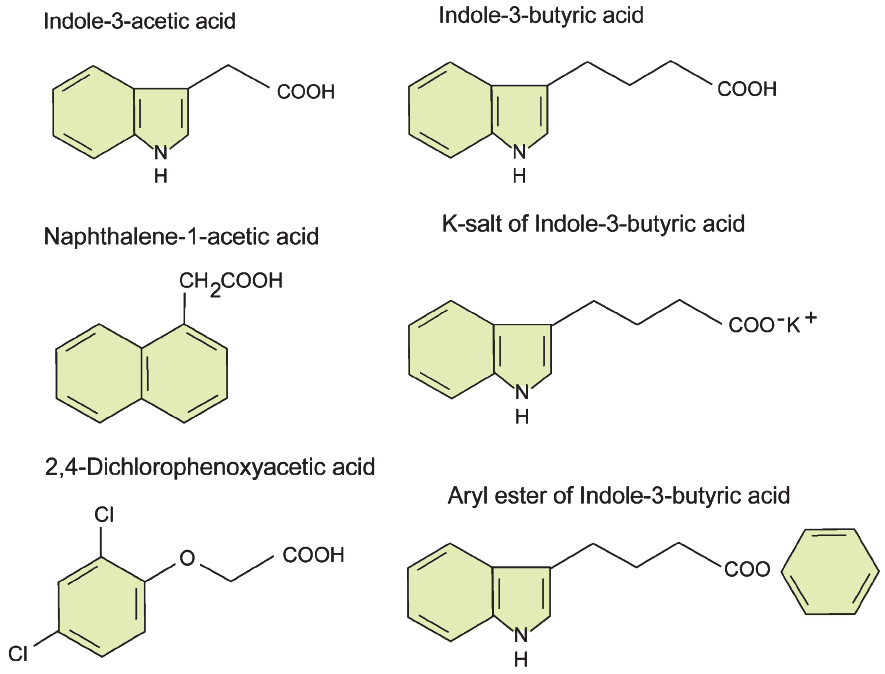


Figure 25
Chemical structures of various auxins.

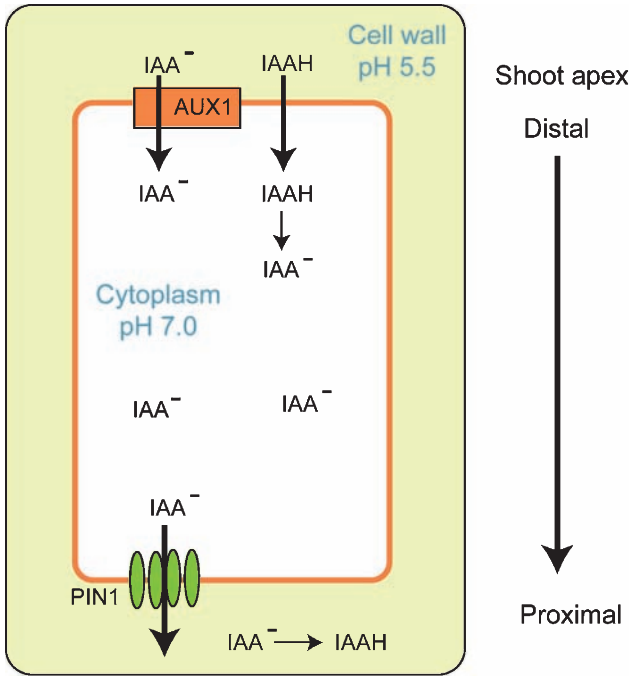


Figure 26
The chemiosmotic model for polar auxin transport. Auxin in the protonated form at the low cell wall pH can pass through the cell membrane or it may be transported by an influx carrier (AUX1). At the higher cytoplasmic pH, IAA dissociates. In this state, auxin can only move back into the cell wall by active transport using efflux carriers (PIN1). Since efflux carriers are only located at the base (proximal) end of the cell, auxin moves in a polar fashion from shoot to the root–shoot junction.

Synthetic auxins are less susceptible to IAA-oxidase degradation and are, therefore, used more often for commercial applications. The most useful synthetic auxins, discovered about 1935, are **indole-3-butyric acid (IBA)** and 1-**naphthalene acetic acid (NAA).** IBA has been subsequently found to occur naturally, but in less abundance compared to IAA. IBA must be converted by plant tissue into IAA to function. The herbicide, 2,4-D (2,4-dichlorophenoxyacetic acid) has auxin activity and is an important inducer of somatic embryogenesis in tissue culture. Various synthetic IBA conjugates (such as its aryl ester PITB—Fig. 25) have been developed with good auxin activity but are not widely available or used (35). Auxins are not readily dissolved in water and must be dissolved in a solvent (ethanol, DMSO) or a base (1N NaOH) before being quickly added to water. Potassium salts of IBA and NAA (K-IBA, K-NAA) are auxin formulations that easily dissolve in water and are available commercially.

Cytokinins

Cytokinins were discovered by Miller and Skoog at the University of Wisconsin in efforts to develop methods for growing plant cells in tissue culture (68). Through the 1940s and 1950s, researchers were frustrated because isolated plant cells and tissues grew poorly or not at all in tissue culture. At that time, tissue culture media supplemented with coconut milk (liquid endosperm) had the most stimulating effect on cell division compared to other compounds evaluated. Then Miller and Skoog inadvertently discovered that an extract from autoclaved fish sperm DNA yielded a compound that greatly stimulated cell division. This synthetic compound was called **kinetin** and the hormone class was called cytokinins because of their ability to stimulate cell division. Subsequently the naturally occurring cytokinins **zeatin** (isolated from corn endosperm) and **isopentenyladenine (2iP)** were found in seeds and other plant parts. These previously mentioned cytokinins along with the naturally occurring **dihydrozeatin** and the synthetic **benzyladenine (BA** or **BAP)** represent the aminopurine type cytokinins (Fig. 27). Another class of compounds—the dipheylureas—displays potent cytokinin activity but are structurally dissimilar to natural occurring cytokinins, including thiourea, diphenylurea, **thidizuron (TDZ),** and N-(2–chloro-4-pyridyl) n′-phenylurea (CPPU).

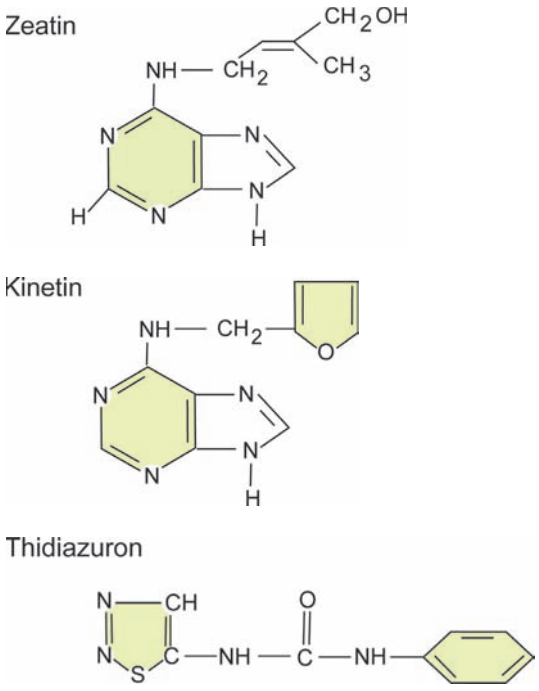


Figure 27
Chemical structure of cytokinin.

The major route for cytokinin biosynthesis is via the isoprenoid pathway with isopenteyltransferase (*ipt*) being the key regulatory enzyme (48). The root tip is a primary source of cytokinin, but biosynthesis also occurs in seeds (embryos) and developing leaves. In addition to free forms of cytokinin, conjugated derivatives include ribosides, ribotides, aminoacids and sugars—many of which freely interconvert. The major enzyme for cytokinin destruction is cytokinin-oxidase.

Cytokinins are thought to play a regulatory role in cell division, shoot initiation and development, senescence, photomorphogenesis, and apical dominance. Cytokinins play a key role in regulating various aspects of the cell cycle and mitosis. Transgenic plants over-expressing the *ipt* gene show elevated cytokinin levels, reduced height, increased lateral branching, and reduced chlorophyll destruction leading to a deep green color. Tissue infected with *Agrobacterium tumifaciens* grow and proliferate in tissue culture independent of growth regulator application. This is because it induces elevated cytokinin levels by inserting an *ipt* gene from its plasmid into the plant's genome.

The interaction of auxin and cytokinin is one of the primary hormonal relationships in plant growth and development as well as plant propagation. A high auxin:cytokinin ratio favors rooting, a high cytokinin:auxin ratio favors shoot formation, and a high level of both favors callus development.

Gibberellins

Gibberellins (69) were discovered before World War II by Japanese scientists trying to explain the abnormally tall growth and reduced yield of rice infected by the fungi *Gibberella fukikuori* (perfect stage) or *Fusarium moniliformne* (imperfect stage). An active ingredient was extracted from the fungus and its chemical structure was determined as gibberellins (named after the fungus). Subsequently, gibberellins were found to be naturally occurring hormones in plants. All gibberellins are cyclic diterpenoids and named for their structure not their activity. More than 100 forms of gibberellins have been found in plants but only a few are physiologically active. The most important naturally occurring active gibberellins include GA_1, GA_4, GA_7 (Fig. 28). Depending on the plant, they will tend to make either GA_1 or GA_4 as their primary gibberellin. Gibberellic acid (GA_3) is the gibberellin found in fungi and is the most important commercial product.

Biosynthesis of gibberellins (73, 76) starts with mevalonate (an important precursor for many secondary compounds in plants) and proceeds via the iosprenoid pathway. Its biosynthesis is a coordinated process involving the plastids, endoplasmic reticulum, and cytosol. Numerous enzymes are regulated during gibberellin biosynthesis, but GA_{20} oxidase appears to especially important. Active gibberellins are inactivated by GA_2 oxidase. Gibberellins can also be sugar conjugated as previous discussed with other hormones.

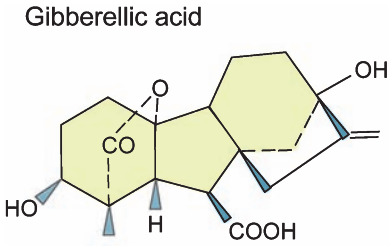


Figure 28
Chemical structure of gibberellic acid.

Gibberellins are made in developing seeds and fruits, elongating shoots, and roots. Gibberellins are the primary hormone controlling plant height. Gibberellin mutants impaired for gibberellin biosynthesis are dwarfed compared to wild type plants, demonstrating the importance of gibberellins for shoot elongation. Several commercially available gibberellin biosynthesis inhibitors, including ancymidol, cycocel, paclobutrazol (Bonzi), and uniconizole (Sumagic), are important plant growth regulators used to control plant height during greenhouse pot and bedding plant production. Gibberellins also play a role in plant maturation and in triggering flowering. Gibberellins are particularly important during seed germination, where the antagonistic interactions between gibberellin and abscisic acid are involved in dormancy release and germination.

Abscisic Acid (ABA)

Abscisic acid was originally discovered during the 1960s in studies searching for hormonal control of leaf abscission and bud dormancy (Fig. 29). These studies

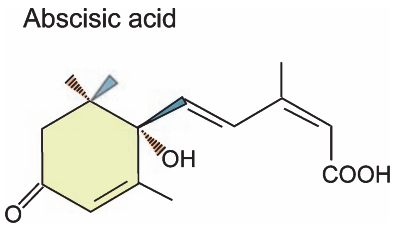


Figure 29
Chemical structure of abscisic acid (ABA).

suggested that ABA was involved in abscission, and the isolated compound was called "Abscisin II." Studies also suggested that ABA was involved in bud dormancy, and that compound was called "dormin." However, subsequent analyses determined that ABA was not a major factor in leaf abscission (2) but may be involved in bud dormancy. ABA's major role in plant growth and development is to modulate environmental stresses, especially water stress. ABA regulates stomatal opening and closure as an indicator of plant water status and promotes root growth under water stress. ABA's other major roles are as a major determinant of zygotic embryo growth during seed development and in maintaining seed dormancy. ABA mutants typically show reduced seed dormancy, increased precocious germination, and wilted leaves at the whole plant level.

ABA is a sesquiterpene synthesized directly from carotenoids (ß-carotene and zeaxanthin) rather than the usual mevalonate pathway observed for gibberellins. Biosynthesis occurs in coordination between enzymes in the plastids and cytosol (67). The ABA molecule has two isomeric forms, *cis* and *trans*. The trans form is the more active and common form in plants. The chemical structure also has a (+) and (–) form that cannot be interconverted. The (+) form is active and occurs in nature. Commercial products are mixtures of both (+) and (–) forms. Fluridone is a carotenoid biosynthesis inhibitor that chemically reduces ABA levels in plants. Cellular ABA concentrations are important for controlling ABA action. Important regulated enzymes in the biosynthetic pathway appear to be 9-*cis*-epoxy-carotenoid dioxygenase (NCED) and xeaxanthin epoxidase (ZEP) for increased ABA levels, while cytochrome P450 707A (CYP707A) is the major enzyme reducing ABA levels (28).

Ethylene

Dimitry Neljubow, a Russian scientist, is credited with the first report of the effects of ethylene on plants in 1901 (66). He demonstrated that ethylene was the agent from illuminating gas used in street lamps that caused plant damage. He also used etiolated pea seedlings to study the effects of ethylene on plant growth and identified the triple response in ethylene-treated seedlings. Seedlings displaying the triple respone show inhibition of stem elongation, increased radial swelling in the hypocotyl, and horizontal stem orientation to gravity.

Ethylene is a gas with a very simple hydrocarbon structure (Fig. 30). However, it can have profound effects on plant growth, including epinasty at high concentrations, senescence and abscission in leaves and

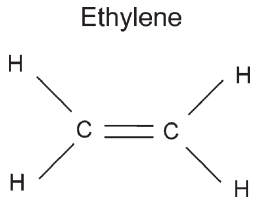


Figure 30
Chemical structure of ethylene.

fruit, flowering, apical dominance, latex production, and flower induction. In propagation, ethylene can induce adventitious roots, stimulate germination, and overcome dormancy. Wounding, stress, and auxin usually stimulate increased ethylene production. Naturally occurring ethylene is involved in the maturity of certain fruits and is widely used to induce ripening in commercial storage. Ethephon (2–chloroethylphosphoric acid) is absorbed by plant tissue where it breaks down to ethylene. It is used on some crops to promote ripening, to act as a thinning agent, to promote or reduce flowering, and to reduce apical dominance. Ethylene gas is a natural by-product of combustible fuels, and escaping fumes can cause damage in commercial storage and greenhouse production. Likewise, ethylene from ripening fruit causes damage to other plant material in common storage.

Ethylene is synthesized from the amino acid methionine via a pathway that includes S-adenosylmethionine and l-aminocyclopropane-l-carboxylic acid (ACC) as precursors. Key regulated enzymes in the pathway include ACC-synthase and ACC-oxidase. Ethylene inhibitors are used commercially to inhibit flower senescence and delay fruit ripening. Aminoethoxyvinylglycine (AVG; Retain) inhibits ethylene biosynthesis, while silver thiosulfate, silver nitrate, and 1-methylcyclopropene (MCP) inhibit ethylene action by altering ethylene's ability to bind to its receptor.

Additional Plant Hormones

Certain other naturally occurring substances are considered by some to show hormonal action. These include brassinosteroids, jasmonates, salicylic acid, polyamines, and peptide hormones.

Brassinosteroids Brassinosteroids were originally extracted from *Brassica napus* pollen and called "Brassins" (15). They were shown to have growth-regulator activity in seedling bioassays, and the active components were identified as brassinolide. Brassinosteroid's importance as a new plant hormone on plant growth was demonstrated when brassinosteroid-deficient mutants were discovered in *Arabidopsis* that showed extreme dwarf plant growth

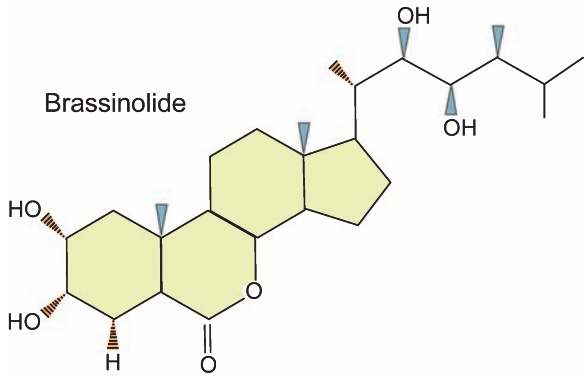


Figure 31
Chemical structure of brassinolide.

that was recovered to wild type growth with exogenous brassinosteroid application.

Brassinosteroids are a class of plant steroid hormones that include over forty members including brassinolide (Fig. 31). Biosynthesis of brassinosteroids is from plant sterols (cycloartenol, campestrol) derived from the mevalonate pathway. Brassinosteroid-deficient mutants show reduced shoot growth, reduced fertility, and vascular development. Brassinosteroids complement auxin and cytokinin for cell division, gibberellin for seed germination, and are involved in phytochrome-mediated photomorphogenesis.

Jasmonates Jasmonic acid and methyl jasmonate are collectively called jasomnates and are members of the oxylipins derived from the oxidation of fatty acids starting with membrane linolenic acid (Fig. 33) (11, 18). The name jasmonate is in reference to its first discovery as a component in *Jasminum grandiflora* oil. In the 1980s, jasmonate was found to naturally occur as a germination inhibitor in bean seeds, and was thought to have similar properties to ABA. However, their primary roles are in plant defense, abiotic stress, and plant developmental process like wounding and senescence. Jasmonate levels increase with wounding and are important for inducing systemic wound responses, and exogenous jasmonate accelerates senescence. They interact with salicylic acid and ethylene as part of regulatory systems involved in plant defense. Methyl-jasmonate is a volatile compound thought to move within and between plants as a form of communication that can induce defense genes and compounds in plants prior to being exposed to the invading organism.

Salicylic Acid Salicylic acid is a plant phenolic compound derived from the shikimic acid pathway. Its name comes from its discovery in willow (*Salix*) bark

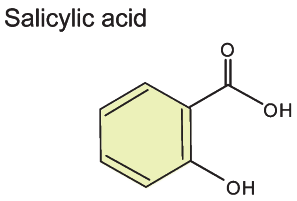


Figure 32
Chemical structure of salicylic acid.

(Fig. 32). It is a precursor to aspirin (acetylsalicylic acid). Salicylic acid has a major role in plant defense and is a critical component in systemic acquired resistance against pathogen attack (36). Salicylic acid may also be involved in plant growth via photosynthesis, flowering, and mineral nutrition. One interesting role for salicylic acid is as part of the heat-generating system found in thermogenic aroid and cycad plants. Application of salicylic acid to voodoo lily led to temperature increases of as much as 12°C. As previously indicated, salicylic acid interacts with jasmonates and ethylene for plant defense.

Polyamines Polyamines, (putrescine, cadaverine, spermidine, and spermine) are synthesized from the amino acids arginine and ornithine and are widespread in animals and plants (3). Polyamines are required for cell growth and can function to stabilize DNA. In 1678, Antoni van Leeuwenhoek using the recently invented microscope found stellate crystals in human semen, which were later identified and named spermine. Key enzymes in the pathway include ornithine decarboxylase, arginine decarboyxlase, spermine synthase, and spermidine synthase. Inhibitors are available for each of these enzymes. Spermine and spermidine synthase share S-adenosylmethionine as a precursor with the ethylene biosynthetic pathway. Competition for this precursor has been shown to be important for a number of plant processes, including seed germination, senescence, fruit ripening, and adventitious root formation. Additional processes where polyamines appear important or essential include seed development, somatic embryogenesis, flower initiation, and plant stress. Inclusion of polyamines in tissue culture systems has enhanced both of these processes.

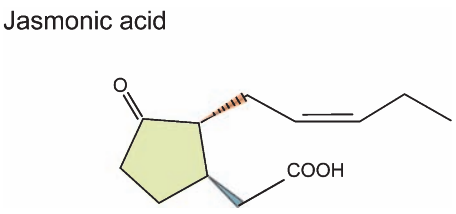


Figure 33
Chemical structure of jasmonic acid.

Flower initiation in thin layer culture systems of tobacco have been directly related to polyamines.

Plant Peptide and Polypeptide Hormones Peptide hormones have an established role in animal physiology, but it has only been recently that small peptide molecules have been discovered that influence plant growth in development (54). Systemin was the first peptide hormone discovered as an 18-amino acid peptide involved in long-distance communication in response to insect attack. Other peptide hormones include SCR/SP11, involved in pollen/stigma self-incompatibility; ENOD40, involved in *Rhizobium*-induced nodule formation in legumes; IDA, involved in flower petal abscission; and phytosulfokines, involved in cell proliferation during carrot tissue culture. **Florigen,** the long-sought-after factor promoting plant flowering, may be a polypeptide transcription factor called the FT (FLOWERING LOCUS T) protein (16, 75).

Plant Development, Competency, and Determinism

One of the principles in biology is that each living plant cell has the potential to reproduce an entire organism since it possesses all of the necessary genetic information in its genes to reproduce all the characteristics of the plant. This concept is known as **totipotency** (32).

totipotency The concept that a single cell has the necessary genetic factors to reproduce all of the characteristics of the plant.

The basic concepts of competency and determination for plant organ formation were developed from a series of experiments inducing shoot and root regeneration in field bindweed (*Convolvulus arvensis*) leaf explants (14). **Competency** was described as the potential of a cell(s) or tissue to develop in a particular direction; for example, the initiation of adventitious roots on a stem cutting or the change from a vegetative to a flowering meristem (55, 58, 60). At some point of development, the process becomes irreversible and the cells are said to be determined. Therefore, **determination** describes the degree to which cells are committed toward a specific organ formation. A general scheme for adventitious organ formation is shown in Figure 34.

competence The potential of a cell(s) to develop in a particular direction, such as forming adventitious roots.

determination The degree that a cell(s) is committed toward a given developmental direction at a given stage of development.

Development of competency into a particular kind of cell, tissue, or organ also may require a special signal. These may originate internally within the plant or externally as an environment signal. For example, the internal change in type of growing point, such as vegetative to flowering, may be associated with a shift in the activity of specific hormones. External parameters, including the application of specific growth regulators or the subjection of the plant to various environments, may bring about

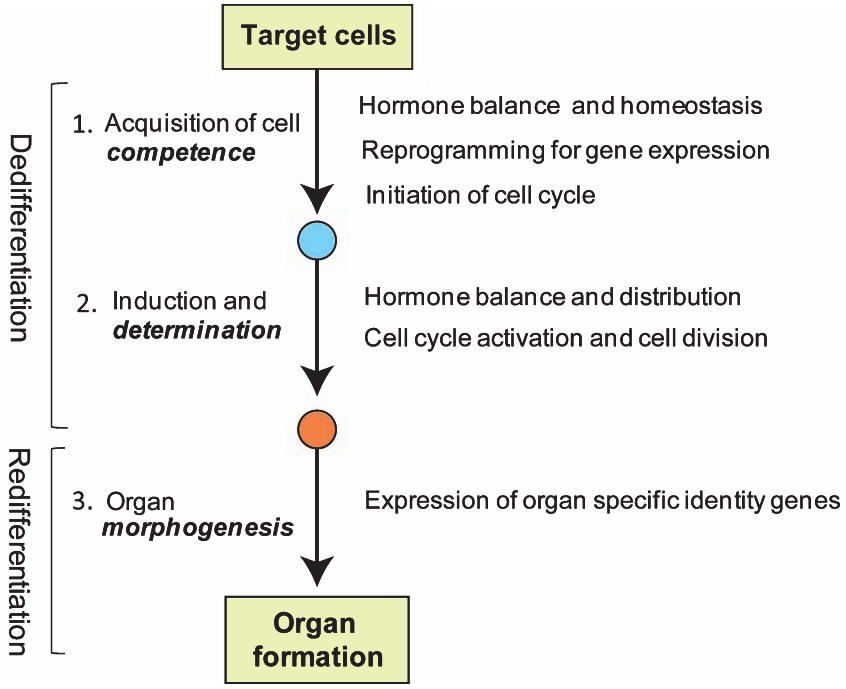


Figure 34
A generalized scheme for organ formation from target cells, such as parenchyma cells, during adventitious rooting or shoot formation. Target cells must acquire cell competency and become determined during dedifferentiation in order to redifferentiate into an organ (root or shoot).

changes. The signal may be applied exogenously, such as hormone application for the induction of adventitious roots, buds, shoots, or somatic embryos. These events take place if specific cells retain the potential for regeneration during development. In addition, specific cells can be induced to "dedifferentiate" and develop the capacity to regenerate. This potential to regenerate is the basis of propagation by cuttings, layering, specialized stems and roots, and tissue culture.

DISCUSSION ITEMS

This chapter covers areas of biology that are fundemantal to understanding plant propagation. These include plant nomenclature, plant life cycles, cell division, genes and gene expression, and plant hormones.

1. Compare and contrast mitosis and meiosis, and discuss how they function during sexual and asexual (vegetative) propagation.
2. How does phase change impact the seedling and clonal plant life cycles?
3. How do trademarks seem to be in contradiction to the rules for naming plants as set forward in the Botanical Code of Nomenclature for Cultivated plants?
4. Compare gene silencing used by the plant to regulate gene expression with gene silencing used as a biotechnology tool by the scientist.
5. How do plant scientists use mutants to understand growth and development? What kind of mutants might be important to better understand plant propagation?
6. What is hormone cross-talk, and why is it important for understanding plant propagation?

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The Propagation Environment

INTRODUCTION

Propagation can be done in the field, orchard, forest, outdoor raised beds, and in protected culture environments such as greenhouses, poly-covered houses, and tissue culture laboratories. The plant propagation period is generally a very narrow segment of a plant's life, ranging from several weeks for fast-growing herbaceous plants to one to two years for woody perennials. Following propagation, the rooted cuttings, seedlings **(plugs), layers,** or tissue culture produced plants are transplanted as **liner plants.** The liner plants are grown in small pots and then transplanted into larger containers or directly transplanted into field production. In other production systems plants may be propagated and produced in the same container or field location without going through a liner stage.

plugs Small seedling plants.

layers Plants produced asexually from layering, such as air layering or stooling.

propagule A plant structure used for regenerating plants, which can include cuttings, seeds, grafts, layers, tissue culture explants, and single cells.

microclimatic conditions Any environmental factors (relative humidity, temperature, light, gases, etc.) in the immediate vicinity of the propagule during propagation.

edaphic factors Any factors influenced by the soil or propagation medium (substrate).

To enhance the propagation of plants, commercial producers manipulate the environment of **propagules** (cuttings, seeds) by managing:

a. **microclimatic conditions** (light, water-relative humidity, temperature, and gases)
b. **edaphic factors** (propagation medium or soil, mineral nutrition and water), and
c. **biotic factors**—interaction of propagules with other organisms (such as beneficial bacteria, mycorrhizal fungi, pathogens, insect pests, etc.) (Fig. 1).

Unique ecological conditions exist during propagation. Commercial propagators may have to compromise to obtain an "average environment" in

learning objectives

- Identify the environmental factors affecting propagation.
- Describe the physical structures for managing the propagation environment.
- Describe the containers for propagating and growing young liner pots.
- Discuss the management of media and nutrients in propagation and liner production.
- Discuss the management of microclimatic conditions in propagation and liner production.
- Discuss the management of biotic factors—pathogens and pests—in plant propagation.
- Explain the post-propagation care of liners.

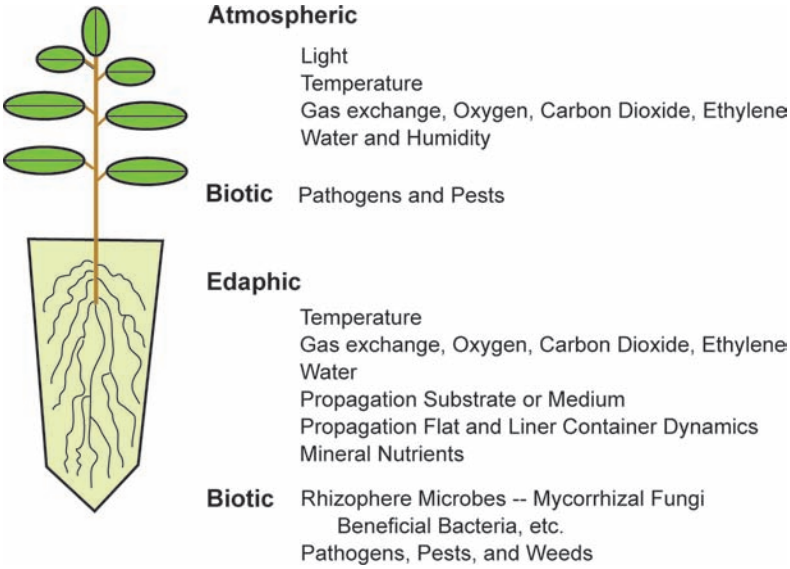


Figure 1
The propagation environment: Manipulation of microclimatic, edaphic, and biotic factors. Modified from Landis (69).

Shading Partial reduction of light to 100 percent light exclusion that can occur during stock plant manipulation and/or propagation

hardening-off The stress adaptation process or **acclimation** that occurs as a propagule, such as a cutting, is gradually weaned from a high to a low relative humidity environment during rooting; in **micropropagation** (tissue culture) acclimation is referred to as **acclimatization.**

which a whole range of species are propagated by cuttings, seed, and/or tissue culture explants (69). The environmental conditions that are optimum for plant propagation are frequently conducive for pests (pathogenic fungi, viruses, bacteria, insect, and mite development). Astute propagators not only manage the environment during propagation, but also manipulate the environment of **stock plants** prior to selecting propagules, such as **shading** and stooling to maximize rooting potential of a propagule; and post propagation—**hardening-off** (weaning rooted cuttings from the mist system and changing fertility regimes) to assure growth and survival of tender-rooted liner plants after propagation.

ENVIRONMENTAL FACTORS AFFECTING PROPAGATION

In propagating and growing young nursery plants, facilities and procedures are designed to optimize the response of plants to environmental factors influencing their growth and development, such as **light, water, temperature, gases,** and **mineral nutrition.** In addition, young nursery plants require protection from pathogens and other pests, as well as control of salinity levels in the growing media. The propagation structures, equipment, and procedures described in this chapter, if handled properly, maximize the plants' growth and development by controlling their environment.

BOX 1 **GETTING MORE IN DEPTH ON THE SUBJECT**
LINER PRODUCTION

A **liner** traditionally refers to lining out nursery stock in a field row. The term has evolved to mean a small plant produced from a rooted cutting, seedling, plug, or tissue culture plantlet. **Direct sticking** or **direct rooting** into smaller **liner pots** is commonly done in United States propagation nurseries. Seedlings and rooted cuttings can also be transplanted into small liner pots and allowed to become established during liner production, before being transplanted to larger containers **(upcanned)** or outplanted into the field.

BOX 2 **GETTING MORE IN DEPTH ON THE SUBJECT**

MEASUREMENT OF LIGHT

Irradiance is the relative amount of light as measured by radiant energy per unit area. Irradiance, intensity, and photon flux all measure the amount of light very differently; they are not interchangeable terms. **Photosynthetic photon flux (PPF)** is the best light measurement for plant propagation, since the process of photosynthesis relies on the number of photons intercepted, not light given off by a point source (intensity) or energy content (irradiance). **Photosynthetic active radiation (PAR)** is measured in the 400 to 700 nanometer (nm) waveband as PPF in micromoles of photons per unit area per time ($\mu mol\ m^{-2}s^{-1}$) with a **quantum sensor** or as watts per square meter (W/m^2) with a **pyranometric sensor.** Some propagators still measure light intensity with a **photometric sensor,** which determines foot-candles or lux (1 foot-candle = 10.8 lux). A photometric sensor is relatively insensitive to wavelengths that are important for plant growth; that is, it may record high light intensity from an artificial electric light source, but it does *not* take into account if the light source is rich in green and yellow, or poor in red and blue light—which would lead to poor plant growth. Quantum and radiometric (pyranometer) sensors can be purchased from instrument companies (i.e., LI-COR Biosciences, www.licor.com; or Apogee Instruments, Inc., www.apogee-inst.com). For determining **light quality** or **wavelength,** the spectral distribution is measured with a portable spectroradiometer, which is a very expensive piece of equipment.

Light

Light is important for photosynthesis as a source of radiant energy. Light also generates a heat load that needs to be controlled (i.e., too high a temperature can quickly desiccate and kill cuttings). The management of light can be critical for rooting cuttings, germinating seeds, growing seedlings, or shoot multiplication of **explants** during tissue culture propagation. Light can be manipulated by controlling *irradiance* (see Box 2), *light duration* (daylength, photoperiod), and *light quality* (wavelength). For a relative comparison of light units for propagation, see Box 3.

Irradiance While many propagators still measure light intensity, determining the photon flux of light is more accurate because the process of photosynthesis depends on the number of photons intercepted (*photosynthetic photon flux*), not just the light given off by a point source (*intensity*).

Daylength (Photoperiod) Higher plants are classified as long-day, short-day, or day-neutral, based on the effect of photoperiod on initiation of reproductive growth. **Long-day** plants, which flower chiefly in the summer, will flower when the **critical photoperiod** of light is equaled or exceeded; **short-day** plants, such as chrysanthemums, flower when the critical photoperiod is not exceeded. Reproductive growth in **day-neutral** plants, such as roses, is not triggered by photoperiod. The discovery of *photoperiodism* by Garner and Allard demonstrated that the dark period, not the light period, is most critical to initiation of reproductive growth, even though light cycles are traditionally used to denote a plant's photoperiod. In propagation, fresh seed collected in the fall from selected woody plant species, such as *Larix,* need long-day conditions to germinate. Dahlia cuttings need short-day conditions to trigger tuberous root formation.

Photoperiod can be extended under short-day conditions of late fall and early winter by lighting with incandescent lights, or high intensity discharge lights (HID) (Fig. 14). Conversely, photoperiod can be shortened under the long-day conditions of late spring and summer by covering stock plants and cuttings with black cloth or plastic that eliminates all light.

Light Quality Light quality is perceived by the human eye as color, and corresponds to a specific range of wavelengths. Red light is known to enhance seed germination of selected lettuce cultivars, while far-red light inhibits germination. Far-red light can promote bulb formation on long-day plants, such as onion (*Allium cepa*). Blue light enhances in vitro bud regeneration of tomato (77). Using greenhouse covering materials with different spectral light-transmitting characteristics, researchers at Clemson University (97) have been able to control the height and development of greenhouse-grown plants, rather than relying on the chemical application of growth regulators for height control. This has application for plant propagation, liner production, and plant tissue culture systems. Red shade cloth shifts light quality towards the blue/green and is being used to enhance root development of cuttings (Fig. 11). Red shade cloth can also be used to increase leaf surface and branching, which is important in liner development (111).

BOX 3 **GETTING MORE IN DEPTH ON THE SUBJECT**

RELATIVE COMPARISON OF LIGHT UNITS FOR SOLAR RADIATION AND ARTIFICIAL LIGHTING (67, 72, 117)*

Light Source	Energy [Photosynthetic photon plux] (μmol $m^{-2}s^{-1}$)	Radiation [Irradiance] (watts m^{-2})	Illumination [Light intensity] (lux)	(ft-candles)
Solar Radiation				
Full sunlight	2,000	450	108,000	10,037
Heavy overcast	60	15	3,200	297
Artificial Light Source				
Metal halide (400 W) lamp @ 2 m height	19	4	1,330	124

* Photosynthetically active radiation (PAR): 400 to 700 nm. Conversions between energy, radiation, and illumination units are complicated and will be different for each light source. The spectral distribution curve of the radiant output must be known in order to make conversions.

Water-Humidity Control

Water management and humidity control are critical in propagation. Water management is one of the most effective tools for regulating plant growth. Evaporative cooling of an **intermittent mist** system can help control the propagation house microenvironment and reduce the heat load on cuttings, thereby permitting utilization of high light conditions to increase photosynthesis and encourage subsequent root development. A solid support medium, such as peat-perlite, is not always necessary to propagate plants; peach cuttings can be rooted under aeroponic systems, while woody and herbaceous ornamentals can be rooted in modified, aero-hydroponic systems without relying on overhead mist (108). Tissue culture explants are often grown in a liquid phase rather than on a solid agar media.

intermittent mist
A thin film of water produced through a pressurized irrigation system that cools the atmosphere and leaf surface of cuttings.

While leaf **water potential (Ψ_{leaf})** is an important parameter for measuring water status of seedlings and cuttings, and influences rooting of cuttings, **turgor (Ψ_p)** is physiologically more important for growth processes. The water status of seedlings and cuttings is a balance between transpirational losses and uptake of water. Later in this chapter the methods to control water loss of leaves of cuttings, seedlings, and containerized grafted plants are discussed.

BOX 4 **GETTING MORE IN DEPTH ON THE SUBJECT**

PLANT WATER MEASUREMENTS IN PROPAGATION

Water potential (Ψ_{water}) refers to the difference between the activity of water molecules in pure distilled water and the activity of water molecules in any other system in the plant. Pure water has a water potential of zero. Since the activity of water in a cell is usually less than that of pure water, the water potential in a cell is usually a negative number. The magnitude of water potential is expressed in megapascals [1 megapascal (MPa) = 10 bars = 9.87 atmospheres]. Propagators can determine water potential by using a pressure chamber (pressure bomb) manufactured by PMS Instrument Company (www.pmsinstrument.com) or Soil Moisture Corporation (www.soilmoisture.com). A psychrometer with a microvolt meter (LiCor, www.licor.com) can also be used. Estimation of **turgor (Ψ_p)** (or pressure potential) requires measurement of **water potential (Ψ_{water})** minus the **osmotic potential (Ψ_π),** which is based on the formula $\Psi_{water} = \Psi_p + \Psi_\pi$. Osmotic potential can also be determined by either a pressure chamber or a psychrometer. The matrix potential (Ψ_m) is generally insignificant in determining Ψ_{water} but is important in seed germination.

Temperature

Temperature affects plant propagation in many ways. Seed dormancy is broken in some woody species by cool-moist stratification conditions that allow the germination process to proceed. Temperature of the propagation medium can be suboptimal for seed germination or rooting due to seasonally related ambient air temperature or the cooling effect of mist. In grafting, heating devices are sometimes placed in the graft union area to speed up graft union formation, while the rest of the rootstock is kept dormant under cooler conditions.

It is often more satisfactory and cost-effective to manipulate temperature by bottom heating at the propagation bench level, rather than heating the entire propagation house (Fig. 2). The use of heating and cooling systems in propagation structures is discussed further in this chapter.

Gases and Gas Exchange

High respiration rates occur with seed germination and plug development, and during adventitious root formation at the base of a cutting. These aerobic processes require that O_2 be consumed and CO_2 be given off by the propagule. Seed germination is impeded when a hard seed coat restricts gas exchange. Likewise, gas exchange at the site of root initiation and subsequent rooting are reduced when cuttings are stuck in highly water-saturated propagation media with small air pore spaces. In leaves of droughted propagules, stomata are closed, gas exchange is limited, and suboptimal rates of photosynthesis occur. During propagation in enclosed greenhouses, ambient CO_2 levels can drop to suboptimal levels, limiting photosynthesis and propagule development. The buildup of ethylene gas (C_2H_4) can be deleterious to propagules during storage, shipping, and propagation conditions. Ethylene also plays a role in plant respiration, rooting of cuttings, and seed propagation.

Mineral Nutrition

To avoid stress and poor development during propagation, it is important that the stock plants be maintained under optimal nutrition—prior to harvesting propagules. During propagation, nutrients are generally applied to seedlings and plugs by **fertigation** (soluble fertilizers added to irrigation water) or with controlled-release fertilizers that are either

fertigation The application of soluble fertilizer during the irrigation of a seedling or rooted cutting.

(a) (b) (c) (d)

Figure 2
Propagation house heating systems. (a) Gas-fired infrared or vacuum-operated radiant heaters (arrow). (b) Forced hot air heating system. (c) Greenhouse, hot water boilers. (d) Heating below the bench for better control of root zone temperature.

preincorporated into the propagation medium or broadcast **(top-dressed)** across the medium surface. Cuttings are normally fertilized with a controlled-release fertilizer preincorporated into the propagation medium (which is discussed later in this chapter or with soluble fertilizer applied *after* roots are initiated. The development of intermittent mist revolutionized propagation, but the mist can severely leach cuttings of nutrients. This is a particular problem with cuttings of difficult-to-root species that have long propagation periods.

PHYSICAL STRUCTURES FOR MANAGING THE PROPAGATION ENVIRONMENT

Propagation Structures

Facilities required for propagating plants by seed, cuttings, and grafting, and other methods include two basic units. One is a structure with temperature control and ample light, such as a greenhouse, modified quonset house, or hotbed—where seeds can be germinated, or cuttings rooted, or tissue culture microplants rooted and acclimatized. The second unit is a structure into which the young, tender plants (liners) can be moved for hardening, which is preparatory to transplanting outdoors. Cold frames, low polyethylene tunnels or sun tunnels covered by Saran, and lathhouses are useful for this purpose. Any of these structures may, at certain times of the year and for certain species, serve as a propagation and acclimation structure. A synopsis of how structures are utilized in propagation is presented in Table 1.

Greenhouses

Greenhouses have a long history of use by horticulturists as a means of forcing more rapid growth of plants (11, 41, 55, 75, 122). Most of the greenhouse area in

Table 1
UTILIZATION OF PROPAGATION STRUCTURES

Propagation structure	Micropropagation	Cuttings	Seedlings/ Plugs	Grafting	Layering	Liner production and hardening-off
Micropropagation facilities (indoor)	Yes	No; except microcuttings	No	No; except micrografting	No	No
Greenhouses	Yes; during acclimatization	Yes	Yes	Yes	Yes; air layering	Yes
Closed-case propagation Hot frames (hotbeds) Heated sun tunnels	No	Yes	Yes	Yes	No	Yes
Closed-case propagation Cold frames Unheated sun tunnels	No; except acclimatization	Yes; hardwood and semi-hardwood cuttings	Yes	Yes	Yes	Yes
Lathhouses (shade houses)	No; except acclimatization	Yes; hardwood and semi-hardwood cuttings	Yes	Yes	Yes	Yes; used extensively for this
Miscellaneous closed-case propagation systems in greenhouses: (a) Propagating frames (b) Contact polyethylene systems	No; except acclimatization	Yes; hardwood and semi-hardwood cuttings	Yes	Yes; sometimes with bench grafting and acclimation	No	Yes

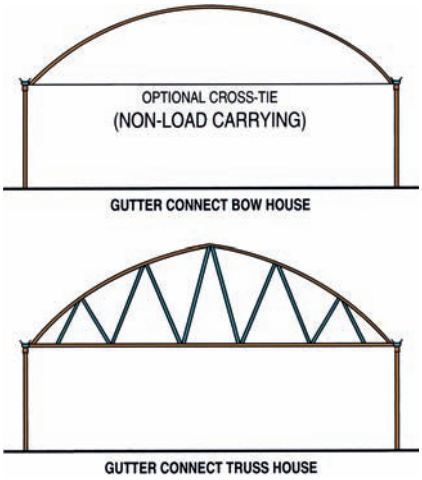
the United States is used for the wholesale propagation and production of floricultural crops, such as pot plants, foliage plants, bedding plants, and cut flowers; fewer are used for nursery stock and vegetable crops (104).

Greenhouse structures vary from elementary, home-constructed to elaborate commercial installations. Commercial greenhouses are usually independent structures of even-span, **gable-roof construction,** proportioned so that the space is well utilized for convenient walkways and propagating benches (55). In larger propagation operations, several single greenhouse units are often attached side by side, eliminating the cost of covering the adjoining walls with glass or polyethylene (Fig. 3). These gutter-connected houses, while more expensive to construct than independent ground-to-ground structures, allow easy access between houses and decrease the square footage (meters) of land needed for propagation houses. Heating and cooling equipment is more economical to install and operate, since a large growing area can share the same equipment (62). Greenhouses with double-tiered, moveable benches that can be rolled outside, and **retractable roof** greenhouses reduce energy costs (Figs. 4 and 5); they are being used in cutting and

gable-roof constructed greenhouse A unit that has more expensive, reinforced upper support for hanging mist systems, supplementary lights, or additional tiers of potted plants.

retractable roof greenhouse A unit with a roof that can be opened during the day and closed at night.

(a)



(b)

(c)

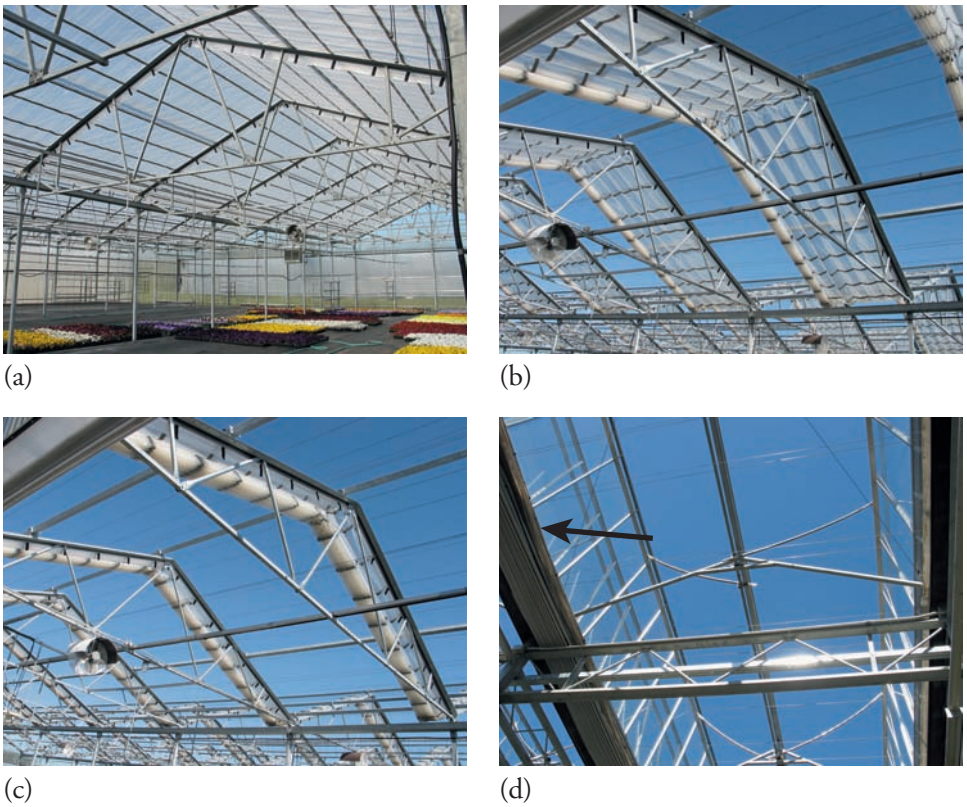
(d)

Figure 3
Gutter-connected propagation greenhouses. (a) A series of gutter-connected propagation houses. (b) The basic types of gutter-connected propagation greenhouses: bow or truss. Bows are less expensive, but offer less structural strength. Trusses make for a stronger house, while giving propagators the ability to hang plants and equipment, such as monorails, curtain systems, and irrigation booms. (c) Non—load-carrying bow propagation house. (d) Load-bearing, gutter-connected truss house (arrow).

(a) (b)

(c) (d) (e)

Figure 4
(a and b) Instead of a movable bench, propagation trays are placed on rollers; notice how all trays on rollers slant toward the middle of the propagation house for easier movement of materials. (c) Movable benches for seedling plug production. (d and e). Propagation house with retractable benches, which can be rolled from the greenhouse structure to the outdoors, have reduced energy costs. (d) Inside of house with double-tiered benches that can be brought in at night and during inclement weather. Benches slide through opening of greenhouse and can be left outside under full sun conditions.



(a) (b)

(c) (d)

Figure 5
(a, b, and c) Retractable roof greenhouse for reducing heat load during propagation and liner production, and (d) a top-vented Dutch-style glasshouse with thermal curtains (arrow) for shade and trapping heat during winter nights.

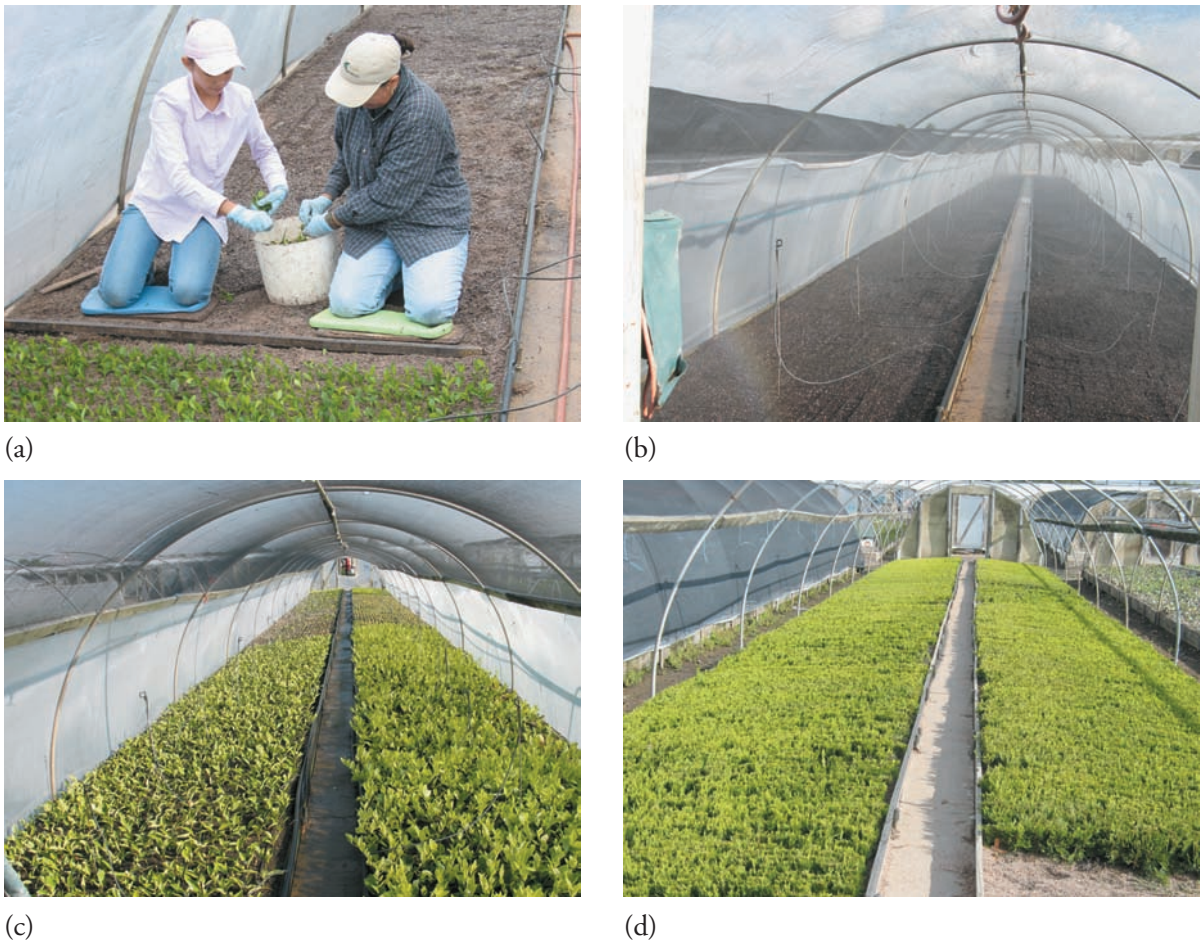
seed propagation, and seedling plug production. Since the liner seedlings are partly produced under full sun conditions, they are better acclimatized for the consumer (8).

Quonset-type greenhouse An inexpensive propagation house made of bent tubing or PVC frame that is covered with polyethylene plastic.

Quonset-type construction is very popular. Such houses are inexpensive to build, usually consisting of a framework of piping, and are easily covered with one or two layers of polyethylene (Fig. 6).

Arrangement of benches in greenhouses varies considerably. Some propagation installations do not have permanently attached benches, their placement varying according to the type of equipment, such as lift trucks or electric carts, used to move flats and plants. The correct bench system can increase production efficiency and reduce labor costs (124). Rolling benches can reduce aisle space and increase the usable space by 30 percent in a propagation greenhouse. The benches are pushed together until one needs to get between them, and then rolled apart (Fig. 4). With rolling benches, propagation work can be done in an ergonomically correct fashion, making workers more comfortable, efficient, and productive (118). Besides increased propagation production numbers, rolling benches allow other automation features to be added (Fig. 7). Conversely, to reduce costs, many propagation houses are designed not to use benches, but rather cutting flats or small liner containers are placed on the gravel or Saran-covered floor (Figs. 6 and 7). It all depends on the propagation system and units to be produced.

In an **floor ebb and flood system (flood floor),** greenhouse benches are eliminated and plants are produced with an automated floor watering and fertility system. There are below-ground floor-heating pipes and irrigation lines, a system of runoff-capturing tanks



(a) (b) (c) (d)

Figure 6
Versatility of a polyethylene, saran-shaded quonset house. (a) Propagators sticking cuttings into rooting media floor beds previously prepared and sterilized with methyl bromide. (b) Cuttings in small liner rooting pots under mist. (c) Rooted liner crop protected under saran shade with poly sidewalls, and (d) shade removed and rooted liner crop ready for transplanting and finishing off in larger container pots.

(a) (b) (c) (d)

Figure 7
For more efficient use of costly greenhouse propagation space, movable benches on rollers have been installed to reduce aisle space. (a and b) Hydraulic lift system (arrow) to pick up and move benches. (c) Movable benches for maintaining coleus stock plants. (d) To eliminate bench space, cuttings in liner pots are placed on the cement propagation house floor and intermittent mist is applied from mist nozzles suspended from the ceiling.

with filters, and computer-controlled return of appropriate levels of irrigation water mixed with soluble fertilizer to the floor growing area (9, 89). While this has received limited use in the propagation of plants, it does have application for liner stock plant production of seedling plugs, rooted cuttings, and tissue culture produced plantlets (Fig. 8). Flood floor systems are more efficient than conventional bench greenhouses. They are highly automated, require less labor, and are environmentally friendly—since irrigation runoff, including nutrients and pesticides, is recaptured and recycled. The drawback of these benchless systems is the potential for rapid disease spread.

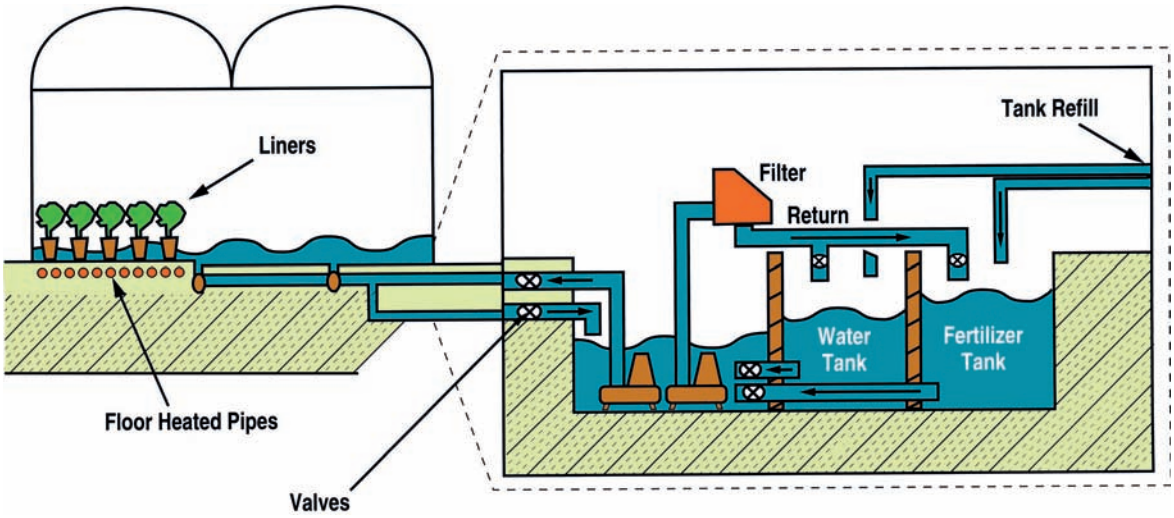
Greenhouse construction begins with a metal framework covered with polycarbonate, acrylic, glass, or poly (plastic) material. Gutter-connected greenhouses can be constructed as bow-style houses, which are less expensive and offer less structural strength, or as load-bearing truss-style houses, which give propagators the ability to hang mist and irrigation booms, install ceiling curtains for temperature and light control, and so on (Fig. 3). All-metal prefabricated greenhouses with prewelded or prebolted trusses are also widely used and are available from several manufacturers.

In any type of greenhouse or bench construction using wood, the wood should be pressure-treated with a preservative such as chromatid copper arsenate (CCA), which will add many years to its life (5). The two most common structural materials for greenhouses are steel and aluminum. Most greenhouses are made from galvanized steel, which is cheaper, stronger, lighter, and smaller than an aluminum member of equal strength. Aluminum has rust and corrosion resistance, and can be painted or anodized in various colors (62). With the high cost of

BOX 5 **GETTING MORE IN DEPTH ON THE SUBJECT**

SOURCES OF COMMERCIAL GREENHOUSES

For sources of commercial greenhouses, contact the National Greenhouse Manufacturers Association (www.ngma.com). A number of trade journals such as *GrowerTalks* (www.ballpublishing.com, choose the link for GrowerTalks) and *Greenhouse Beam Pro* (www.greenbeampro.com) list commercial greenhouse manufacturers and suppliers that include greenhouse structures, shade and heat retention systems, cooling and ventilation, environmental control computers, bench systems, and internal transport systems in greenhouses.



(a)

(b)

(c)

(d)

Figure 8
(a, b, and c) An ebb and flood or flood floor system. No benches are used and stock plants are produced with an automated floor watering and fertility system. There are below-ground floor heating pipes and irrigation lines, a system of runoff-capturing tanks with filters, and computer-controlled return of appropriate levels of irrigation water mixed with soluble fertilizer to the floor growing area. (a) Schematic of ebb and flood system with liner plants. (b and c) Flood floor system for maintaining stock plants. (d) Ebb and flood bench system.

lumber, fewer greenhouses are constructed with wood, and traditional wooden benches are being replaced by rigid plastics, metal benches, and other synthetic materials.

Greenhouse Heating and Cooling Systems

Ventilation, to provide air movement and air exchange with the outside, is necessary in all greenhouses to aid in controlling temperature and humidity. A mechanism for manual opening of panels at the ridge and sides or with passive ventilation can be used in smaller greenhouses, but most larger installations use a forced-air fan and pad-cooling ventilation system either regulated by thermostats or controlled by computer (42, 89).

Traditionally, greenhouses have been heated by steam or hot water from a central boiler through banks of pipes (some finned to increase radiation surface) suitably located in the greenhouse (Fig. 2). Unit heaters for each house, with fans for improved air circulation, are also used. If oil or gas heaters are used, they must be vented to the outside because the combustion products are toxic to plants (and people!), and ethylene gas generated can adversely affect plant growth. In large greenhouses, heated air is often blown into large—30 to 60 cm (12 to 24 in)—4-mil convection polyethylene tubes hung overhead. These extend the length of the greenhouse. Small—5 to 7.5 cm (2 to 3 in)—holes spaced throughout the length of these tubes allow the hot air to escape, thus giving uniform heating throughout the house. These same convection tubes can be used for forced-air ventilation and cooling in summer, eliminating the need for manual side and top vents.

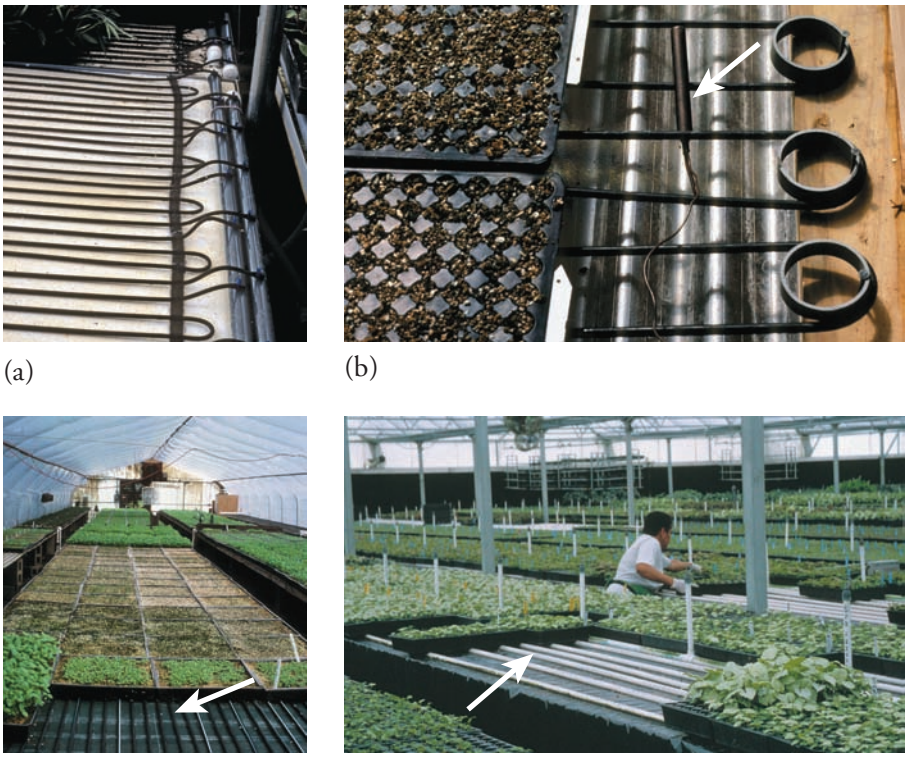
Gas-Fired Infrared Heaters **Gas-fired infrared heaters** are vacuum-operated radiant heaters that are sometimes installed in the ridges of greenhouses with the concept of heating the plants but not the air mass. Infrared heaters consist of several lines of radiant tubing running the length of the house, with reflective shielding above the tubes installed at a height of 1.8 to 3.7 m (6 to 12 ft) above the plants (Fig. 2). The principal advantage of infrared heating systems in greenhouses is lower energy use. Cultural practices may need to be changed because infrared heating heats the plant but not the soil underneath.

gas-fired infrared heaters Vacuum-operated radiant heaters installed in the ridges of greenhouses with the concept of heating the plants but not the air mass.

Root Zone Heating In contrast to infrared heating, root zone heating is done by placing pipes on or below the soil surface in the floor of the greenhouse, or on the benches, with recirculating hot water—controlled by a thermostat—circulating through the pipes. This places the heat below the plants, which hastens the germination of seeds, rooting of cuttings, or growth of liner plants. This popular system has been very satisfactory in many installations, heating the plants' roots and tops, but not the entire air mass in the greenhouse, yielding substantial fuel savings. It is also excellent for controlling foliage diseases. The majority of propagation (seed germination, rooted cuttings, and plug growing) is done with some form of root zone heat (Figs. 2 and 9) (55).

Solar Heating Conservation of energy in the greenhouse is important (83). In greenhouses, solar heating occurs naturally. The cost of fossil fuels has evoked considerable interest in methods of conserving daytime solar heat for night heating (50, 64). Conservation methods need to be developed and utilized; otherwise, high heating costs may eventually make winter use of greenhouses in colder regions economically unfeasible—relegating greenhouse operations to areas with relatively mild winters (89, 122).

Most heat loss in greenhouses occurs through the roof. One method of reducing heat loss in winter is to install sealed polyethylene sheeting outside over the glass or fiberglass covered structure, or to use two layers of polyethylene sheeting, as in a quonset house. This double-poly method of insulation is very effective. The two layers are kept separate by an air cushion from a low-pressure blower. Energy savings from the use of this system are substantial—more than 50 percent reduction in fuel compared to conventional glass greenhouses—but the greatly lowered light intensity with the double-layer plastic cover can lower yields of many greenhouse crops.



(a) (b) (c) (d)

Figure 9
Hot water, root zone heating of propagation flats. (a) Biotherm tubing heating root zone of the plug tray. (b) Notice the probe (arrow) for regulating temperature. (c) The flexible hot water tubing is hooked into larger PVC pipes at set distances to assure more uniform heating. (d) Cuttings in propagation flats placed over white PVC hot water tubing; in milder climates, the ground hot water tubing may be all that is used to control root zone temperature and the air temperature of the propagation house.

Figure 10
(a) Prop house with thermal and shade curtains (arrow) to reduce winter heating costs and reduce light irradiance and greenhouse cooling expenses during summer months. (b) Thermal screen for energy conservation, made of woven aluminized polyester fabric, covering for propagation house with 46 percent light transmission; (c and d) the fabric is placed on top of polyethylene propagation house the covered house.

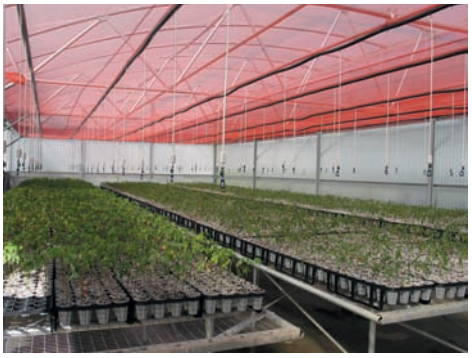
movable thermal curtains A device that reduces heat loss at night by creating a barrier between the crop and greenhouse roof and walls.

Another device that reduces heat loss dramatically is a **movable thermal curtain** (Fig. 10), which, at night, is placed between the crop and the propagation house roof and walls (119). Winter heating bills are reduced as much as 30 percent, since the peak of the propagation house is not heated (67). During summer, automated curtains also reduce heat stress on propagules and workers, and less energy is needed to run fans for cooling. Modified curtains can be used for light reduction during the day and **"black clothing"** for light exclusion during photoperiod manipulation of plants. Curtains range from 20 percent shade reduction to complete blackout curtains—ULS Obscura A + B (67). Curtain fibers are available in white, black, with aluminum coated fibers, and/or with strips of aluminum sewn in. Black shade cloth reduces light to the plants, but absorbs heat and emits heat back into the propagation house. Aluminum-coated curtain fabrics are good reflectors of light, but poor absorbers of heat (Fig. 10). Some curtain materials come with a top side for reflecting heat and reducing condensation and a bottom side for heat retention. Insulating the north wall reduces heat loss without appreciably lowering the available light. Heat reduction also occurs with red and blue shade cloth used for control of plant growth (Fig. 11).

black clothing A curtain that is drawn over plants to exclude light for manipulating photoperiod.

Greenhouses can be cooled mechanically in the summer by the use of large evaporative cooling units, as

(a)



(b)

(c)

Figure 11
(a and b) Propagation houses covered with red shade cloth for enhanced root initiation and development. The red netting increases the red, while reducing the blue and green spectra. (c) Shading seed propagation flats to reduce light irradiance and heat load.

pad and fan system
A system commonly used in greenhouse cooling to reduce the air temperature by raising the relative humidity and circulating air.

shown in Figure 12. The **"pad and fan" system,** in which a wet pad of material, such as special honeycombed cellulose, aluminum mesh, or plastic fiber, is installed at one side (or end) of a greenhouse with large exhaust fans at the other, has proved to be the best method of cooling greenhouses, especially in low-humidity climates (6). Fog can be used to cool greenhouses, but is more expensive than conventional pad and fan systems, and is inefficient in climates with high relative humidity (e.g., the Texas Gulf Coast).

(a)

(b)

Figure 12
Fully automated polycarbonate-covered greenhouse. (a) Air is pulled by exhaust fans (black arrows) to vent and cool. Components of both heating and cooling systems are electronically controlled via a weather monitoring station (white arrow) that feeds environmental inputs to computerized controls. (b) Cool cells (wettable pads) through which cooler, moist air is pulled across the propagation house by exhaust fans.

BOX 6 **GETTING MORE IN DEPTH ON THE SUBJECT**

ENVIRONMENTAL CONTROL EQUIPMENT

Environmental control equipment is available from such companies as Priva (www.priva.nl), Wadsworth Control Systems, Inc., (www.wadsworthcontrols.com), and HortiMaX USA Inc. (www.qcom-controls.com).

Greenhouses are often sprayed on the outside at the onset of warm spring weather with a thin layer of *whitewash* or a white cold-water paint. This coating reflects much of the heat from the sun, thus preventing excessively high temperatures in the greenhouse during summer. The whitewash is removed in the fall. Too heavy a coating of whitewash, however, can reduce the light irradiance to undesirably low levels. Aluminized polyester fabric coverings are used for reducing heat load and can be placed on top of polyethylene-covered propagation houses (Fig. 10).

Environmental Controls

Controls are needed for greenhouse heating and evaporative cooling systems. Although varying with the plant species, a minimum night temperature of 13 to 15.5°C (55 to 60°F) is common. Thermostats for evaporative cooling are generally set to start the fans at about 24°C (75°F). In the early days of greenhouse operation, light, temperature, and humidity were about the only environmental controls attempted. Spraying the greenhouse with whitewash in summer and opening and closing side and ridge vents with a crank to control temperatures, along with turning on steam valves at night to prevent freezing, constituted environmental control. Humidity was increased by spraying the walks and benches by hand at least once a day. Later, it was found that thermostats, operating solenoid valves, could activate electric motors to raise and lower vents, and to open and close steam and water valves, thus giving some degree of automatic control. Most environmental controllers of greenhouse environments are now analog or computerized systems.

Analog Environmental Controls Analog controls (i.e., Wadsworth Step 500) have evolved for controlling the greenhouse environment. They use proportioning thermostats or electronic sensors to gather temperature information. This information drives amplifiers and electronic logic (i.e., decision making) circuitry (55). Essentially, they combine functions of several thermostats into one unit (10). Analog controls cost more than thermostats, but are more versatile and offer better performance.

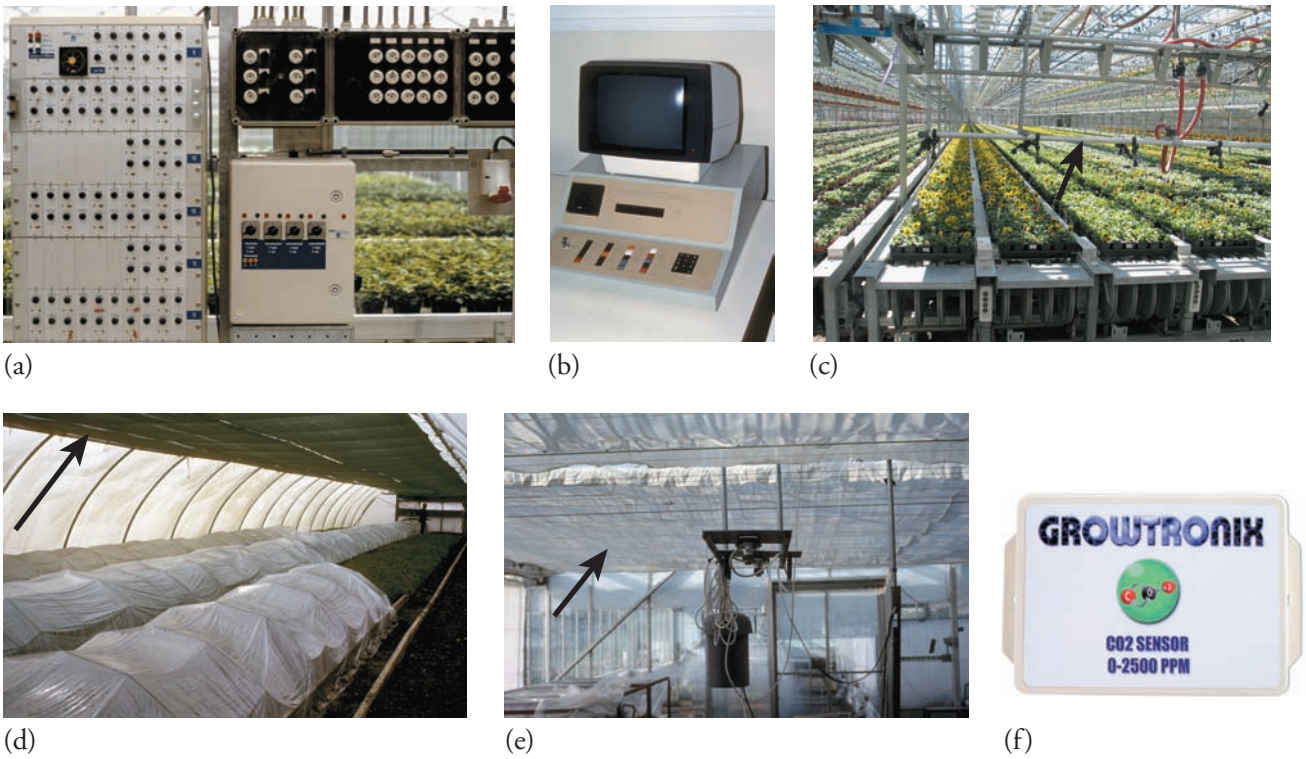
Computerized Environmental Controls The advent of computer technology (i.e., Wadsworth EnviroSTEP) has replaced the amplifiers and logic circuits of an analog control with a microprocessor "computer on a chip" (Figs. 13 and 14). Computer controls are quicker and more precise in combining information from a variety of sensors (temperature, relative humidity, light intensity, wind direction) to make complex judgments about how to control the propagation environment. Computers can be utilized as zone controllers or in more expensive integrated computer systems (10, 55).

Although more costly than thermostats or analogs, computer controls offer significant energy and labor savings and improved production efficiency in propagation. Not only can temperature, ventilation, and humidity be controlled, but many other factors, such as propagating bed temperatures, application of liquid fertilizers through the irrigation system, daylength lighting, light-intensity regulation with mechanically operated shade cloth (and thermal sheets or curtains), operation of a mist or fog system, and CO_2 enrichment—all can be varied for different times of the day and night and for different banks of propagation units (7, 47, 56, 124). Computers can be programmed so that alarms are triggered or propagators paged by phone if deviations from preset levels occur—such as a heating failure on a cold winter night or a mist system failure on cuttings on a hot summer day. Some of these operations are shown in Figures 12, 13, 14, and 15. Most importantly, the computer can provide data on all factors being controlled for review to determine if changes are needed. This makes it easier for the propagator to make management decisions based on factual information (42).

Greenhouse Covering Materials

Common greenhouse covering materials include (54, 103):

- Glass
- Flexible covering materials
- Rigid covering materials



(a) (b) (c)

(d) (e) (f)

Figure 13
(a and b) Computer-controlled environmental manipulation of propagation facilities including (c) a mechanized traveling mist boom for irrigating flats on moveable benches. (d and e) Automated shade material programmed to close along the top of the propagation house when preset radiant energy levels are reached; this system works well with contact polyethylene propagation systems for rooting cuttings. (f) Automated metering system for monitoring CO_2 injection in propagation house.

Glass Glass-covered greenhouses are expensive, but for a permanent long-term installation under low-light winter conditions, glass may be more satisfactory than the popular, low-cost polyethylene (poly)-covered houses. Due to economics and the revolution in greenhouse covering materials from polyethylene to polycarbonates, glass greenhouses are no longer dominant. Glass is still used, due in part to its superior light transmitting properties and less excessive relative humidity problems. Glass "breathes" (the glass laps between panes allow air to enter), whereas polyethylene, acrylic, and polycarbonate-structured sheet houses are airtight, which can result in excessive humidity and undesirable water drip on the plants if not properly controlled. This problem can be overcome, however, by maintaining adequate ventilation and heating. Some of the newer greenhouse covering materials are designed to channel condensation to gutters, avoiding water dripping onto plant foliage. Control of high relative humidity is a key cultural technique to manage plant pathogens, since water can both disseminate pathogens and encourage plant infection. See the section on cultural controls in propagation under integrated pest management, later in the chapter.

Flexible Covering Materials are Categorized as Follows

polyethylene (poly)
A plastic covering used to cover propagation greenhouses.

Polyethylene (Polythene, Poly). Over half of the greenhouse area in the United States is covered with low-cost **polyethylene (poly),** most with inflated double layers, giving good insulating properties. Poly is the most popular covering for propagation houses. Several types of plastic are available, but most propagators use either single- or double-layered polyethylene. Poly materials are lightweight and relatively inexpensive compared with glass. Their light weight also permits a less expensive supporting framework than is required for glass. Polyethylene has a relatively short life. It breaks down in sunlight and must be replaced after one or two years, generally in the fall in preparation for winter. The new polys, with ultraviolet (UV) inhibitors, can last three to four

Figure 14
Manipulating the propagation environment. (a) Greenhouse sensors that are connected to an analog or computer-controlled environmental system. (b) Analog-type controller. (c) High vapor pressure sodium lighting for propagating plants during low-light conditions. (d and e) Lighting to extend photoperiod, which encourages (e) Japanese maple cuttings to avoid dormancy.

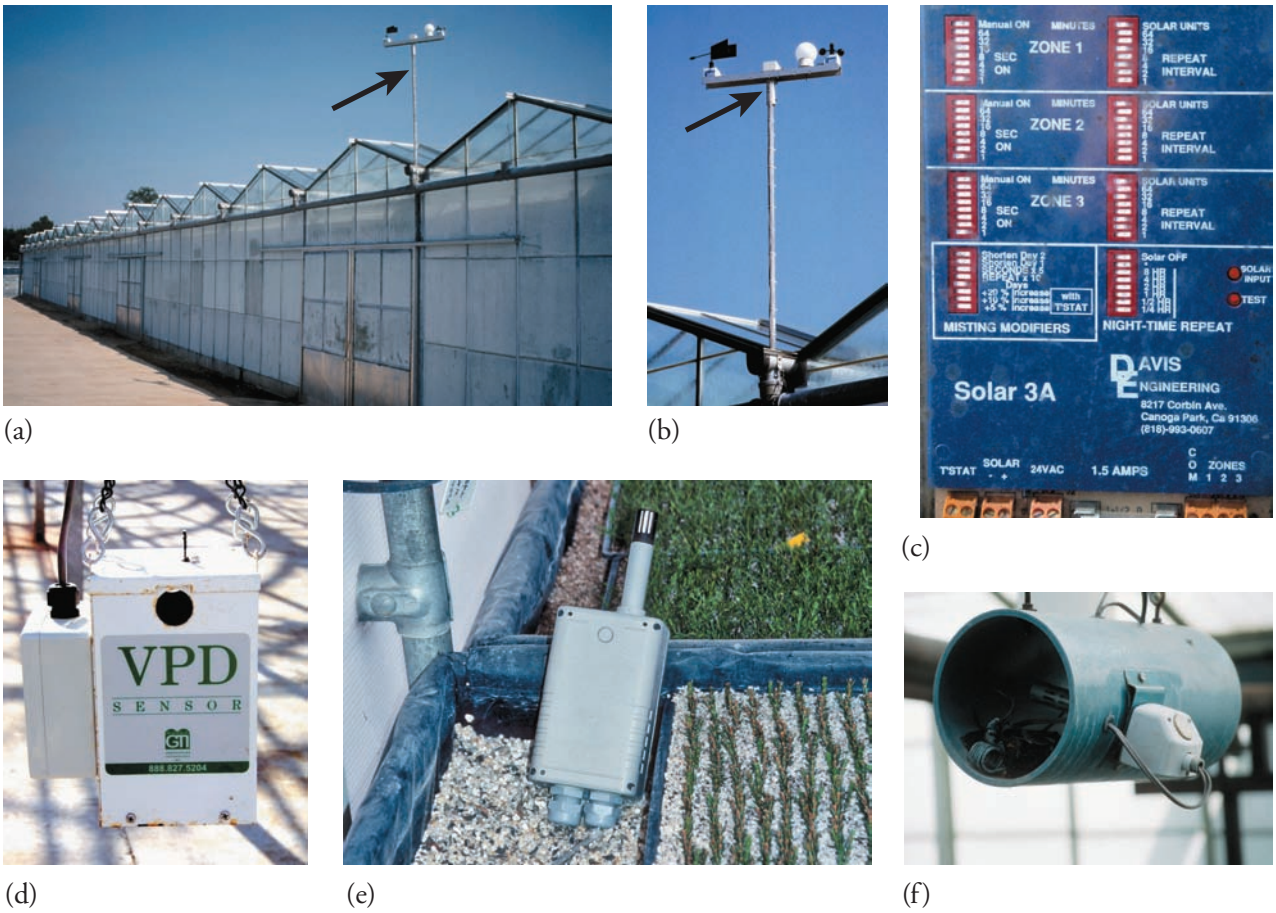
years, but in the southern United States where UV levels are higher, poly deteriorates more quickly and propagation houses need to be recovered more frequently.

A thickness of 4 to 6 mils (1 mil = 0.001 in) is recommended. For better insulation and lowered winter heating costs, a double layer of UV-inhibited copolymer material is used with a 2.5-cm (1-in) air gap between layers, kept separated by air pressure from a small blower.

Single-layer polyethylene-covered greenhouses lose more heat at night or in winter than a glass-covered house since polyethylene allows passage of heat energy from the soil and plants inside the greenhouse much more readily than glass. There are some newer infrared reflective polys, which save fuel but have lower light penetration than regular poly. Glass traps most infrared radiation, whereas polyethylene is transparent to it. However, double layer poly-covered greenhouses retain more heat than glass because the houses are more airtight and less infrared radiation escapes.

Only materials especially prepared for greenhouse covering should be used. Many installations, especially in windy areas, use a supporting material, usually welded wire mesh, for the polyethylene film. Occasionally, other supporting materials, such as Saran cloth, are used.

Polyethylene transmits about 85 percent of the sun's light, which is low compared with glass, but it passes all wavelengths of light required for plant growth. A tough, white, opaque film consisting of a mixture of polyethylene and vinyl plastic is available.



(a) (b) (c) (d) (e) (f)

Figure 15
Environmental sensors for propagation. (a and b) A propagation house with a weather station for detecting light intensity, wind speed and direction, external temperature; this helps regulate temperature control and the fog propagation system. (c) Measurement of solar light allows for better mist control. (d, e, and f) Relative humidity sensors are needed to determine vapor pressure deficit (VPD) for critical fog propagation control.

This film stays more flexible under low winter temperatures than does clear polyethylene, but is more expensive. Because temperature fluctuates less under opaque film than under clear plastic, it is suitable for winter protection of field-bed or container-grown, liner plants (Fig. 16). Polyethylene permits the passage of oxygen and carbon dioxide, necessary for the growth processes of plants, while reducing the passage of water vapor.

For covering lath and shade structures, there are a number of satisfactory plastic materials prepared for the horticultural industry. Some commercially available materials include UV-treated cross-woven polyethylene and polypropylene fabric that resists ripping and tearing, and knitted high-density UV polyethylene shade cloth and Saran cloth that is strong and has greater longevity.

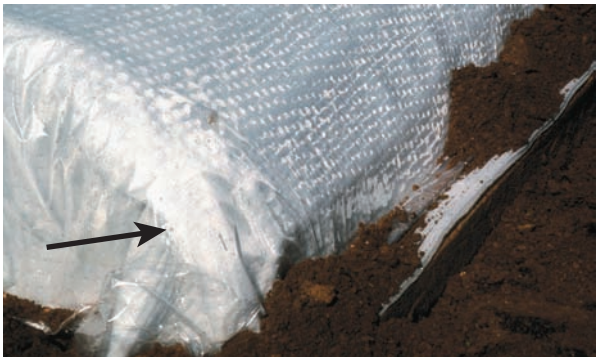
Rigid Covering (Structured Sheet) Materials Rigid Covering (Structured Sheet) Materials are Categorized as Follows

Acrylic (Plexiglass, Lucite, Exolite). Acrylic is highly weather resistant, does not yellow with age, has excellent light transmission properties, retains twice the heat of glass, and is very resistant to impact, but is brittle. It is somewhat more expensive and nearly as combustible as fiberglass. It is available in twin-wall construction which gives good insulation properties, and has a no-drip construction that channels condensation to run down to the gutters, rather than dripping on plants.

Polycarbonate (Polygal, Lexan, Cyroflex, Dynaglas). Polycarbonate is probably the most widely used structured sheet material today (55). Similar to acrylic in heat retention properties, it allows about 90 percent of

(a)

(b)



(c)

Figure 16
Low polyethylene tunnel or sun tunnel that is covered with polyethylene. (a) Sometimes a white poly material is used to avoid the higher temperature buildup and temperature fluctuation of clear poly. Propagation flats are placed on top of hot-water tubing or electric heating cables (b) Saran shade cloth can be used to cover the poly to reduce the heat load. (c) Winterization of sun tunnels can be done with white microfoam insulation covered with a clear poly or opaque poly (see arrow).

the light transmission of glass. Polycarbonate has high impact strength—about 200 times that of glass. It is lightweight, about one-sixth that of glass, making it easy to install. Polycarbonate's textured surface diffuses light and reduces condensation drip. It is available in twin-wall construction, which gives good insulation properties. Polycarbonate can be cut, sawn, drilled, or nailed, and is much more user-friendly than acrylic, which can shatter if nails or screws are driven into it. It is UV stabilized and will resist long outdoor exposure (some polycarbonates are guaranteed for ten years), but will eventually yellow with age (11, 90).

Fiberglass. Rigid panels, corrugated or flat, of polyester resin reinforced with fiberglass have been widely used for greenhouse construction. This material is strong, long-lasting, lightweight, and easily applied, and comes in a variety of dimensions (width, length, and thickness), but is not as permanent as glass. Only the clear material—especially made for greenhouses and in a thickness of 0.096 cm (0.038 in) or more and weighing 4 to 5 oz per square foot—should be used. New material transmits about 80 to 90 percent of the available light, but light transmission decreases over the years due to yellowing, which is a serious problem. Since fiberglass burns rapidly, an entire greenhouse may quickly be consumed by fire, so insurance costs can be higher. Fiberglass is more expensive than polyethylene, and is not as widely used as it once was.

The economics of using these greenhouse covering materials must be considered carefully before a decision is made. New materials are continually coming onto the market.

Closed-Case Propagation Systems

Hot Frames (Hotbeds) and Heated Sun Tunnels The **hot frame (hotbed)** is a small, low structure used for many of the same purposes as a propagation house. Traditionally, the hotbed is a large wooden box or frame with a sloping, tight-fitting lid made of window sash. Hotbeds can be used throughout the year, except in areas with severe winters where their use may be restricted to spring, summer, and fall. Another form of a hotbed is a **heated, low polyethylene tunnel or sun tunnel** that is made from hooped metal tubing or bent PVC pipe, which is covered with polyethylene (sometimes a white poly material is used to avoid the higher temperature buildup and temperature fluctuations of clear poly) (Fig. 16).

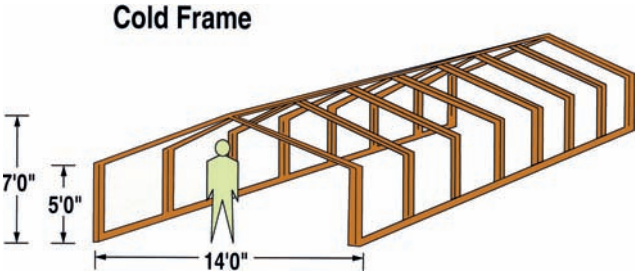
hot frames (hotbeds)
Propagation structures that are covered with poly and heated in the winter.

Traditionally, the size of the frame conforms to the size of the glass sash available—a standard size is 0.9 by 1.8 m (3 by 6 ft) (Fig. 17). If polyethylene is used as the covering, any convenient dimensions can be

(a)

(b)

(c)



(d)

Figure 17
Traditional cold frames were used for propagating tender plants. Frames are opened after protection is no longer required. (a) Older commercial use of glass-covered cold frames in propagating ground cover plants by cuttings. (b) Wood sash used for liner production in a cold frame. Glass and lath coverings are rarely used due to the high labor costs in moving the heavy sash. Plastic coverings are more suitable. (c and d) Today a cold frame is most commonly a very low cost, budget, unheated poly-covered hoop or galvanized steel bow house.

used. The frame can be easily built with 3-cm (1-in) or 6-cm (2-in) lumber nailed to 4-by-4 corner posts set in the ground. Decay-resistant wood such as redwood, cypress, or cedar should be used, and preferably pressure-treated with wood preservatives, such as chromated copper arsenate (CCA). This compound retards decay for many years and does not give off fumes toxic to plants. Creosote must not be used on wood structures in which plants will be grown, since the fumes released, particularly on hot days, are toxic to plants.

Plastic or PVC tubing with recirculating hot water is quite satisfactory for providing bottom heat in hotbeds. The hotbed is filled with 10 to 15 cm (4 to 6 in) of a rooting or seed-germinating medium over the hot-water tubing. Alternatively, community propagation flats or flats with liner pots containing the medium can be used. These are placed directly on a thin layer of sand covering the hot-water tubing.

Seedlings can be started and leafy cuttings rooted in hotbeds early in the season. As in the greenhouse, close attention must be paid to shading and ventilation, as well as to temperature and humidity control. For small propagation operations, hotbed structures are suitable for producing many thousands of nursery plants without the higher construction expenditure for larger, walk-in propagation houses (60).

Cold Frames and Unheated Sun Tunnels A primary use of **cold frames** is conditioning or hardening

cold frames Propagation structures covered with poly, lath, or other covering material and which are not heated in the winter.

rooted cuttings or young seedlings (liners) preceding field, nursery-row, or container planting. Cold frames and unheated sun tunnels can be used for starting new plants in late spring, summer, or fall when no external supply of heat is necessary (129). Today, cold frames include not only low polyethylene-covered wood frames or unheated sun tunnels that people cannot walk within (Fig. 17), but also low-cost, poly-covered hoop houses (Fig. 17). The covered frames should fit tightly in order to retain heat and obtain high humidity. Cold frames should be placed in locations protected from winds, with the sash cover sloping down from north to south (south to north in the Southern Hemisphere).

Low-cost cold frame construction (Fig. 17) is the same as for hotbeds, except that no provision is made for supplying bottom heat. With older-style cold frames, sometimes a lath covering with open spaces between the lath boards is used to cover the cold frame. This does not prevent freezing temperatures from occurring, but does reduce high and low temperature fluctuations.

In these structures, only the heat of the sun, retained by the transparent or opaque white polyethylene coverings, is utilized. Close attention to ventilation, shading, watering, and winter protection is necessary for success with cold frames. When young, tender plants are first placed in a cold frame, the covers are generally kept tightly closed to maintain a high humidity, but as the plants become acclimated, the sash frames are gradually raised or the ends of the hoop house or sun tunnels opened to permit more ventilation and drier conditions.

The installation of a mist line or frequent irrigation of plants in a cold frame is essential to maintain humid conditions. During sunny days temperatures can build up to excessively high levels in closed frames unless ventilation and shading are provided. Spaced lath, Saran or poly shade cloth-covered frames, or reed mats are useful to lay over the sash to provide protection from the sun. In areas where extremely low temperatures occur, plants being overwintered in cold frames may require additional protective coverings.

Lathhouses Lathhouses or shade houses (Figs. 6 and 11) provide outdoor shade and protect container-grown plants from high summer temperatures and high light irradiance (50). They reduce moisture stress and decrease the water requirements of plants. Lathhouses have many uses in propagation, particularly in conjunction with the hardening-off and acclimation of liner plants prior to transplanting, and with maintenance of shade-requiring or tender plants. At times a lathhouse is used by nurseries simply to hold plants for sale. In mild climates, they are used for propagation, along with a mist facility, and can also be used as an overwintering structure for liner plants. Snow load can cause problems in higher latitude regions.

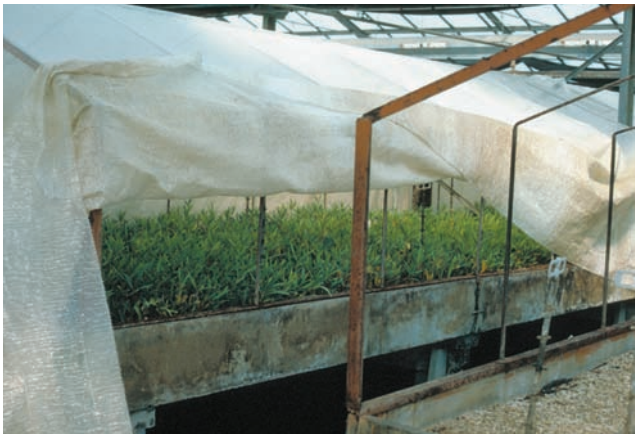
Lathhouse construction varies widely. Aluminum prefabricated lathhouses are available but may be more costly than wood structures. More commonly, pipe or wood supports are used, set in concrete with the necessary supporting cross-members. Today, most lathhouses are covered with high-density, woven, plastic materials, such as Saran, polypropylene fabric, and UV-treated polyethylene shade cloth, which come in varying shade percentages and colors. These materials are available in different densities, thus allowing lower irradiance of light, such as 50 percent sunlight, to the plants. They are lightweight and can be attached to heavy wire fastened to supporting posts. The shade cloth is resistant to ripping, and has an optimum life of 10 to 15 years, depending on climate and quality of material. For winterization in less temperate areas, producers will cover the shade cloth with polyethylene. Sometimes shade is provided by thin wood strips about 5 cm (2 in) wide, placed to give one-third to two-thirds cover, depending on the need. Both sides and the top are usually covered. Rolls of snow fencing attached to a supporting framework can be utilized for inexpensive construction.

Miscellaneous Closed-Case Systems There are a number of closed-case propagation systems that are used in the rooting of cuttings, acclimatization and rooting of tissue culture microcuttings, and propagation of seedlings. Besides the sun tunnels or cold frames previously described, closed-case propagation systems include nonmisted enclosures in glasshouses or polyhouses (shading, tent and contact polyethylene systems, wet tents, inverted glass jars).

Propagating Frames. Even in a greenhouse, humidity is not always high enough to permit satisfactory rooting of certain kinds of leafy cuttings. Enclosed frames covered with poly or glass may be necessary for successful rooting (see Fig. 18). There are many variations of such devices. Small ones were called Wardian cases in earlier days. Such enclosed frames are also useful for graft union formation of small potted nursery stock, since they retain high humidity.

Sometimes in cool summer climates (as far south as Virginia in the United States), when fall semi-hardwood cuttings are taken, a layer of very thin (1 or 2 mils) polyethylene laid directly on top of a bed of newly prepared leafy cuttings in a greenhouse or lathhouse will provide a sufficient increase in relative humidity to give good rooting. This is sometimes referred to as a **contact polyethylene system**. Good shade control to reduce light irradiance is essential for this system.

(a)



(b)

(c)

(d)

Figure 18
(a and b) Polyethylene-covered beds used in a greenhouse to maintain high humidity surrounding the cuttings during rooting. Propagation flats can be placed on beds or cuttings stuck directly into the mist beds and covered with poly. (c) Using shade (arrow) for light/temperature control. (d) Partially vented polycovered mist-bed under a quonset house for shade.

On a more limited scale, bell jars (large inverted glass jars) can be set over a container of unrooted cuttings or freshly grafted containerized plants to speed up graft union formation. Humidity is kept high in such devices, but some shading is necessary to control temperature.

In using all such structures, care is necessary to avoid the buildup of pathogenic organisms. The warm, humid conditions, combined with lack of air movement and relatively low light intensity, provide excellent conditions for the growth of various pathogenic fungi and bacteria. Cleanliness of all materials placed in such units is important; however, use of fungicides is sometimes necessary (see the section on **integrated pest management** later in the chapter).

Enclosed Poly Sweat Tent—Hydroponic System. An Australian producer of chrysanthemums uses a modified nutrient film technique (NFT) for growing greenhouse stock plants and propagating cuttings (58). Unrooted cuttings are stuck in Oasis root cubes and placed in mist propagation benches containing a reservoir of water, maintained with a float valve. The system is initially enclosed in a clear poly sweat tent. Once root initiation takes place, the mist is turned off and the poly tent lifted. Cuttings are then supplied with nutrient solution in the NFT system on the propagation bench and later transplanted with the roots intact and undisturbed in the root cube. Stock plants are also maintained in the NFT system and supported in root cubes, thus allowing more precise nutritional control and reduction in environmental stress to the stock plant.

CONTAINERS FOR PROPAGATING AND GROWING YOUNG LINER PLANTS

New types of containers for propagating and growing young liner plants are continually being developed, usually with a goal of reducing handling costs. Direct sticking

of unrooted cuttings into small liner containers, as opposed to sticking into conventional propagation trays, saves a production step and later avoids root disturbance of cuttings, which can lead to transplant shock (Figs. 19, 20, and 21) (31).

Flats

Flats are shallow plastic, Styrofoam, wooden, or metal trays, with drainage holes in the bottom. They are useful for germinating seeds or rooting cuttings, since they permit young plants to be moved easily. In the past, durable kinds of wood, such as cypress, cedar, or redwood, were preferred for flats. The most popular flats are made of rigid plastic (polyethylene, polystyrene) and come in all shapes and sizes. The 28 × 53 cm (11 × 21 in) *1020* plastic flats are the industry standard. The number of cells or compartments per tray may range from 1 cell for a community rooting flat or seed germination tray, to 18 or more cells for a rooted liner tray, to 100 to 400 cells for a seedling plug tray. Trays also can be fitted with removable sheet inserts containing the cells. Plastic flats will nest, and thus require relatively little storage space. The costs of producing plastic for flats and containers and for disposing of used plastic have led to increased plastic recycling programs in horticulture and biodegradable paper tube liner pots (Fig. 19).

Plastic Pots

Plastic containers, round and square, have numerous advantages: they are nonporous, reusable, lightweight, and use little storage space because they will nest. Some types are fragile, however, and require careful handling,

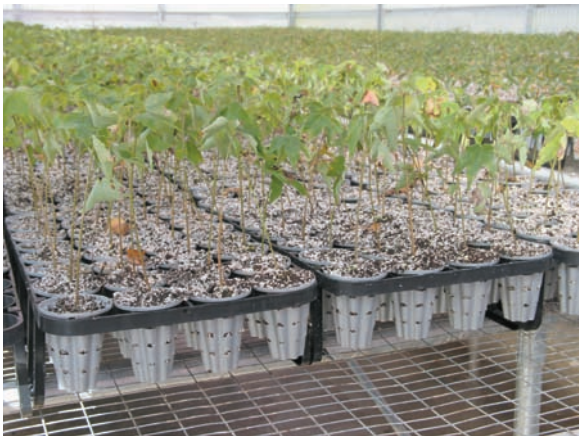
(a)

(b)

(c)

(d)

Figure 19
(a and b) A paper pot system direct sticking (direct rooting) liner plants in paper tubes filled with peat-lite media. (b) Paper pot sleeve liner (arrow) inserted in plastic tray. (c) Rooted poinsettia in paper sleeve tube. (d) Plastic rooting tray with ribs (arrow) to reduce root circling of poinsettias during propagation and rooted liner development.



(a)

(b)

Figure 20
(a) Air-root pruning system for direct sticking (direct rooting) tree liners to minimize root circling, encourage more fibrous root development, and increase root surface area. (b) Direct rooting poinsettia cuttings in paper sleeves inserted in ribbed plastic liner pots.

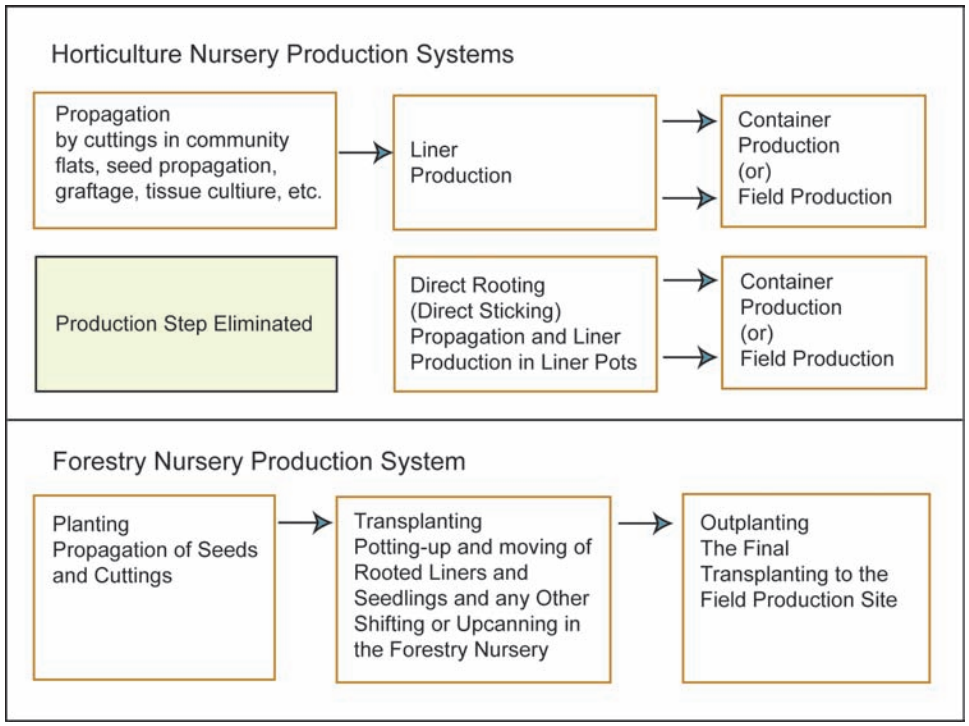
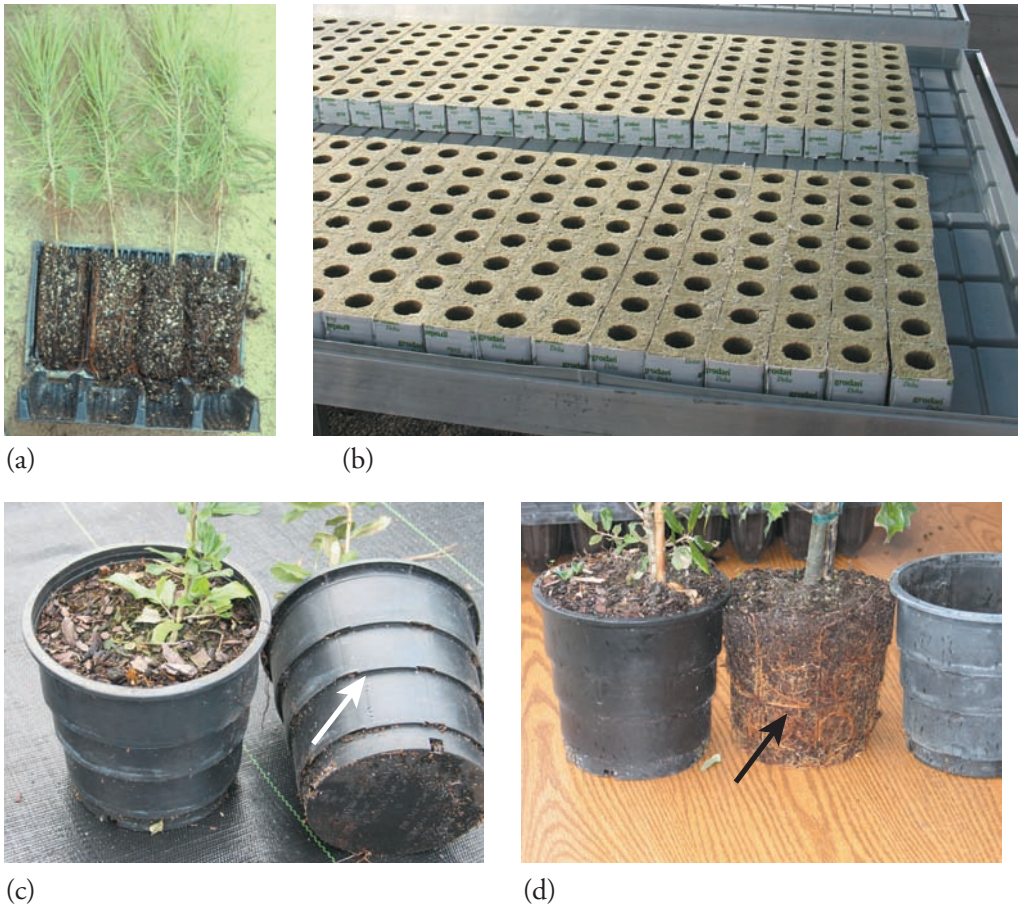


Figure 21
Flow diagram of a Horticulture Nursery Production System starting with propagation by rooted cuttings, seedlings, graftage, or tissue culture-produced plantlets—followed by transplanting into liner pots and final transplanting into larger containers or into nursery field production. Direct rooting (direct sticking) eliminates a production step, since both propagation and liner production occur in the same liner pot. A Forestry Nursery Production System of planting, transplanting, and outplanting is also described.



(a) (b) (c) (d)

Figure 22
(a) Plastic (Roottainer) container made of preformed, hinged sheets for propagating seedling liners. (b) synthetic fiber media (Rockwool) blocks for inserting seedling plugs and growing in greenhouse. (c and d) ridged containers for minimizing root circling.

although other types, made from polyethylene, are flexible and quite sturdy. Small liner pots for direct rooting of cuttings, seedling propagation, and tissue culture plantlet acclimatization and production have gained considerable popularity.

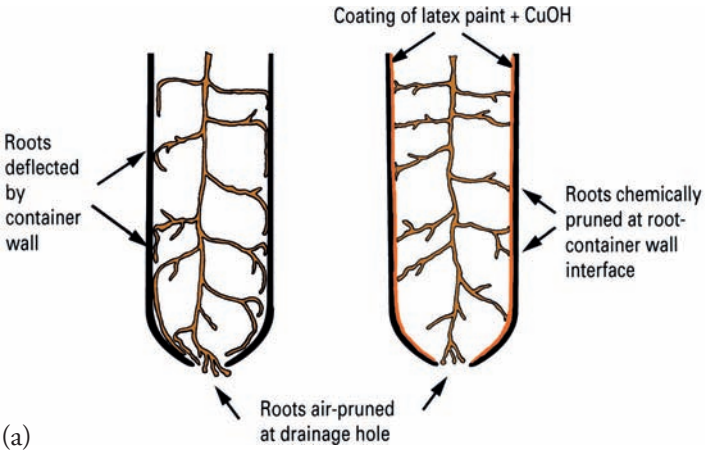
Many of these small containers have rib-like structures to redirect root growth and prevent girdling (Figs. 19, 20, and 22). In forestry seedling production, ribbed book or sleeve containers are used, which consist of two matched sections of molded plastic that fit together to form a row of rectangular cells (Fig. 22). The inner walls of small propagation containers and liner pots can also be treated with chemical root pruning agents, such as copper hydroxide ($CuOH_2$), which chemically prune liner roots at the root-wall interface (71). The chemically pruned lateral roots become suberized but will begin to grow again after transplanting, which results in a well-distributed root system that helps minimize transplant shock (Fig. 23) (71).

Plastic pots (and flats) cannot be steam sterilized, but some of the more common plant pathogens can be controlled by a hot water dip, 70°C (158°F), for 3 minutes followed by a rinse in a dilute bleach solution (i.e., Clorox, Purex, etc.). Ultraviolet light inhibitors are sometimes incorporated in the plastic resin to prevent UV degradation of plastic pots under full sun conditions (Fig. 24).

Fiber Pots

Containers of various sizes, round or square, are pressed into shape from peat plus wood fiber, with fertilizer added. Dry, they will keep indefinitely. Since these pots are biodegradable, they are set in the soil along with the plants. Peat pots find their best use where plants are to be held for a relatively short time and then put in a larger container or in the field. During outplanting in the field, any portion of the fiber pot transplanted above the surface of the soil will act like a wick and quickly dry out the transplant.

During production, small peat pots with plants growing in them eventually deteriorate because of constant moisture, and may fall apart when moved. On the other hand, unless the pots are kept moist, roots will fail to penetrate the walls of the pot and will grow into



(a)

(b)

(c)

Figure 23
Chemical root pruning involves treating the interior container wall with a growth-inhibiting chemical such as copper hydroxide. This causes the lateral roots to be chemically pruned at the container wall. A well-branched root system occurs, which enhances transplant establishment. (a) Schematic of nonpruned versus chemically pruned seedling container roots. (b) Copper hydroxide-treated container. (c) Copper hydroxide-treated *Acalpha hispida* (see arrow) without visible surface roots. Photo courtesy of M. Arnold.

an undesirable spiral pattern. Units of 6 or 12 square peat pots fastened together are available. When large numbers of plants are involved, using peat pots results in time and labor savings.

Paper Pots

Paper pots or paper tube pots are more popular with seed plug and cutting propagation of ornamentals, vegetable and forestry species. They allow for greater mechanization with pot-filling machines, automatic seeders, and wire benches that allow air pruning of the root system. Typically, paper pots consist of a series of interconnected paper cells arranged in a honeycomb pattern that can be separated before outplanting (71). An advantage of the paper pot system is that pots are biodegradable, and the seedling plug can be planted intact into a larger container or into the ground without disturbing the root system. Some papier-mâché

(a)

(b)

Figure 24
(a) Colorful, labeled, rigid-plastic containers are used for growing and merchandising landscape and garden plants. Frequently, inhibitors are incorporated with the plastic resin to prevent ultraviolet breakdown of the containers under full sun conditions. (b) Flexible poly container bags are used for nursery production in Europe, England, and Australia, where petroleum-based products are more costly than in the United States.

pots (paper, wax, asphalt) come treated with copper hydroxide, which enhances root development and retards deterioration of the pot.

In Europe and the United States, paper tube pots with predictable degradation rates are produced by machine (39). The propagation medium is formed into a continuous cylinder and wrapped with a length of paper or cellulose skin that is glued and heat sealed (Fig. 19).

Peat, Fiber, Expanded Foam, and Rockwool Blocks

Blocks of solid material, sometimes with a prepunched hole (Fig. 22), have become popular as a germinating medium for seeds and as a rooting medium for cuttings, especially for such plants as chrysanthemums and poinsettias. Sometimes fertilizers are incorporated into the material. One type is made of highly compressed peat which, when water is added, swells to its usable size and is soft enough for the cutting or seed to be inserted. Such blocks become a part of the plant unit and are set in the soil along with the plant. These blocks replace not only the pot but also the propagating mix.

Synthetic rooting blocks (oasis, rockwool) are becoming more widely used in the nursery industry (and forestry industry for seed propagation), and are well adapted to automation (Fig. 22). Other advantages are their light weight, consistent quality, reproducibility, and clean condition. Watering must be carefully controlled to provide constant moisture, while maintaining adequate aeration.

Plastic Growing Containers for Post-Liner Production

Many millions of nursery plants are grown and marketed each year in 3.8-liter (1-gal) and—to a lesser extent—11-liter (3-gal), 19-liter (5-gal), and larger containers. They are tapered for nesting and have drainage holes. Heavy-wall, injection-molded plastic containers are used extensively in the United States. Machine planters have been developed utilizing containers in which rooted cuttings or seedlings can be transplanted as rapidly as 10,000 or more a day. See the horticulture and forestry nursery production flow diagrams (Fig. 21). Plants are easily removed from tapered containers by inverting and tapping. Some plastic containers are made of preformed, hinged plastic sheets that can be separated for easy removal of the liner (Fig. 22).

In areas with high summer temperatures, use of light-colored (white or silver) containers may improve root growth by reducing heat damage to the roots, which is often encountered in dark-colored containers that absorb considerable heat when exposed to the sun. However, light-colored containers show dirt marks (as opposed to black or dark green containers) and must be cleaned prior to shipping. More and more colorful, labeled containers are being used for growing and merchandising landscape and garden

plants (Fig. 24). A pot-in-pot system, in which a containerized plant is inserted into a hole in the ground lined with a plastic sleeve pot, helps moderate both high and low rootball temperatures (Fig. 25).

Polyethylene Bags and Plant Rolls

Polyethylene bags are widely used in Europe, Australia, New Zealand, and in less developed countries in the tropics—but rarely in North America—for growing rooted cuttings or seedling liners to a salable size. They are considerably less expensive than rigid plastic containers and seem to be satisfactory (Fig. 24), but some types deteriorate rapidly. They are usually black, but some are black on the inside and light-colored on the outside. The lighter color reflects heat and lowers the root temperature. Polybags do not prohibit root spiraling or allow air pruning, which is a drawback to their use in propagation and liner production; however,

Figure 25
Alternatives to traditional field production. (a) In-ground fabric containers or grow bags. (b) The pot-in-pot (P&P) system with individual pot, drip irrigation. (c) Copper-treated wall of outside sleeve containers (arrow) to prevent root penetration from the inner pots. (d and e) P&P containers. (f) The roots of the inside containers are very susceptible to heat stress when they are removed from the field. Here they are wrapped with an insulating packing fabric for shipping.

(a)

(c)

(b)

Figure 26
(a) Redwood containers used for large nursery specimen tree production. (b) Wood containerized tree and heavy equipment required to lift it. (c) A large, 8- to 9-year-old specimen tree produced in a 183 cm (72-in) box, weighing in excess of 3700 kg (8100 lbs). The enormous weight of the rootball will require a crane for lifting at the landscape site. The box is easier for landscapers to handle than heavy-duty plastic container that would need to be cut up.

poly tubes are open-ended, which reduces girdling problems. After planting, they cannot be stacked as easily as the rigid containers for truck transportation—the polybags often break, and the root system of the plant is more easily damaged.

A low-cost method of propagating some easy-to-root species is with a polyethylene plant roll. The basal ends of the cuttings are inserted in damp peat moss or sphagnum and rolled into the doubled-over plastic sheeting. The roll of cuttings is then set upright in a humid location for rooting. Polyethylene starter pouches with an absorbent paper inserted in the pouch are used for germinating selected seed lots.

Wood Containers

Large cedar-wood containers or boxes are used for growing large specimen trees and shrubs to provide "instant" landscaping for the customer. Some of the specimen trees are 8 to 9 years old and weigh up to 3700 kg (8100 lbs). Heavy moving equipment is required for handling such large nursery stock (Fig. 26).

MANAGEMENT OF MEDIA AND NUTRITION IN PROPAGATION AND LINER PRODUCTION

Media and Mixes for Propagating and Growing Young Liner Plants

Various substrates and mixtures of materials are used for germinating seeds and rooting cuttings. For good results, the following characteristics of the medium are required (51):

- The **medium must be sufficiently firm and dense** to hold the cuttings or seeds in place during rooting or germination. Its volume must be fairly constant when either wet or dry; excessive shrinkage after drying is undesirable.
- It should be **highly decomposed and stable** (preferably with a 20C:1N ratio) to prevent N immobilization and excessive shrinkage during production.
- It must be **easy to wet** (not too hydrophobic) and retain enough moisture to reduce frequent watering.

- It must be **sufficiently porous** so that excess water drains away, permitting adequate penetration of oxygen to the roots—all containers produce a perched water table that creates a zone of saturated growing medium at the bottom of the container.
- It must be **free from pests:** weed seeds, nematodes, and various pathogens.
- It must have a **low salinity** level.
- It should be **capable of being steam-pasteurized or chemically treated** without harmful effects.
- It should have a **high cation exchange capacity (CEC)** for retention of nutrients that may be applied preincorporated and/or in a supplementary soluble and/or controlled-release fertilizer program.
- It should be of **consistent quality** from batch to batch, and reproducible.
- It should be readily **available,** and **economical.**

Propagation media used in horticulture and forestry consist of a mixture of organic and inorganic components that have different but complementary properties. The **organic component** generally includes peat, softwood and hardwood barks, or sphagnum moss. Sawdust and rice hulls should be avoided since they oxidize readily and compact easily, which decreases pore space and aeration, and they have a high C:N ratio, which can result in nutritional problems for the propagule. A **coarse mineral component** is used to improve drainage and aeration by increasing the proportion of large, air-filled pores. A variety of mineral components include sand (avoid fine particle sands), grit, pumice, scoria, expanded shale, perlite, vermiculite, polystyrene, clay granules, and rockwool.

There is no single, ideal mix. An appropriate propagation medium depends on the species, propagule type, season, and propagation system (i.e., with fog, a waterlogged medium is less of a problem than with mist); cost and availability of the medium components are other considerations. The following media components can be used in propagation systems.

Soil A mineral soil is composed of materials in the solid, liquid, and gaseous states. For satisfactory plant growth, these materials must exist in the proper proportions. The solid portion of a soil is comprised of both inorganic and organic components. The inorganic part consists of the residue from parent rock after decomposition, resulting from the chemical and physical process of weathering. Such inorganic components vary in size from gravel down to extremely minute colloidal particles of clay, the texture of the soil being determined by the relative proportions of these particle sizes. The coarser particles serve mainly as a supporting framework for the remainder of the soil, whereas the colloidal clay fractions of the soil serve as storehouses for nutrients that are released and absorbed by plants. The organic portion of the soil consists of both living and dead organisms. Insects, worms, fungi, bacteria, and plant roots generally constitute the living organic matter, whereas the remains of such animal and plant life in various stages of decay make up the dead organic material. The residue from such decay (termed **humus**) is largely colloidal and assists in holding water and plant nutrients.

The liquid part of the soil, the soil solution, is made up of water that contains dissolved salts in various quantities, along with dissolved oxygen and carbon dioxide. Mineral elements, water, and some carbon dioxide enter the plant from the soil solution.

The gaseous portion of the soil is important to good plant growth. In poorly drained, waterlogged soils, water replaces the air, thus depriving plant roots as well as certain desirable aerobic microorganisms of the oxygen necessary for their existence.

The **texture** of a mineral soil depends upon the relative proportions of sand (0.05 to 2 mm particle diameter), silt (0.05 to 0.002 mm particle diameter), and clay (less than 0.002 mm particle diameter). In contrast to soil texture, which refers to the proportions of individual soil particles, **soil structure** refers to the arrangement of those particles in the entire soil mass. These individual soil grains are held together in aggregates of various sizes and shapes.

Propagation in commercial horticulture is generally done with flats, containers, and/or pot systems using ***"soilless" media.*** Some exceptions to this are field budding and grafting systems, stooling and layering systems, field propagation of hardwood cuttings without intermittent mist, direct seeding of crops, and utilizing outdoor seedbeds. With the greater reliance on containerized systems for propagation, mineral soils are either unsuitable or must be amended with other components to improve aeration and prevent the compaction that occurs with the structural changes of mineral soils in a container.

Sand Sand consists of small rock particles, 0.05 to 2.0 mm in diameter, formed as the result of the weathering of various rocks. The mineral composition of sand depends upon the type of rock. Quartz sand, consisting chiefly of a silica complex, is generally used for propagation purposes. Sand is the heaviest of all rooting media used, with a cubic foot of dry sand weighing about

(a)

(b)

(c)

(d)

Figure 27
Propagation medium. (a) Various types of propagation media components and mixes. (b) Sphagnum peat moss—excellent quality, but expensive. (c) A specialized azalea propagation mix composed of peat, bark, and perlite. (d) Media in bins used to fill propagation and liner flats inside the propagation house.

45 kg (100 lb). Preferably, it should be fumigated or steam-pasteurized before use, as it may contain weed seeds and various harmful pathogens. Sand contains virtually no mineral nutrients and has no buffering capacity or cation exchange capacity (CEC). It is used mostly in combination with organic materials. Sand collected near the ocean (beach sand) may be too high in salts. Calcareous sand will raise media pH and should be tested prior to mixing with vinegar or a dilute acid.

Peat Peat consists of the remains of aquatic, marsh, bog, or swamp vegetation that has been preserved under water in a partially decomposed state. The lack of oxygen in the bog slows bacterial and chemical decomposition of the plant material. Composition of different peat deposits varies widely, depending upon the vegetation from which it originated, state of decomposition, mineral content, and degree of acidity (82).

There are three types of peat as classified by the United States Bureau of Mines: moss peat, reed sedge, and peat humus. *Moss peat* (usually referred to in the market as **peat** or **peat moss**) is the least decomposed of the three types and is derived from sphagnum or other mosses. It varies in color from light tan to dark brown. It has a high moisture-holding capacity (15 times its dry weight), has a high acidity (pH of 3.2 to 4.5), and contains a small amount of nitrogen (about 1 percent) but little or no phosphorus or potassium. This type of peat generally comes from Canada, Ireland, or Germany, although some is produced in the northern United States. *Peat moss is the most commonly used peat in horticulture, the coarse grade being the best* (Fig. 27).

When peat moss is to be used in mixes, it should be broken apart and moistened before being added to the mix. Continued addition of coarse organic materials such as peat moss or sphagnum moss to greenhouse media can initially cause a decrease in wettability. Water will not penetrate easily, and many of the peat particles will remain dry even after watering. There is no good method for preventing this nonwettability, although the repeated use of commercial wetting agents, such as Aqua-Gro, can improve water penetration (12). Peat is not a uniform product and can be a source of weed seed, insects, and disease inoculum. Peat moss is relatively expensive so it is used less in nursery propagation and production mixes. It is gradually being replaced by other components, such as pulverized or shredded bark. However, peat is still the main organic ingredient in propagation and greenhouse mixes.

Sphagnum Moss Peat Commercial sphagnum moss peat or sphagnum peat is the dehydrated young residue or living portions of acid-bog plants in the genus *Sphagnum,* such as *S. papillosum, S. capillaceum,* and *S. palustre.* It is the most desirable peat for horticultural purposes, but its high cost limits its commercial use. It is relatively pathogen-free, light in weight, and has a very high water-holding capacity, able to absorb 10 to

20 times its weight in water. This material is generally shredded, either mechanically or by hand, before it is used in a propagating or growing media. It contains small amounts of minerals, but plants grown in it for any length of time require added nutrients. Sphagnum moss has a pH of about 3.5 to 4.0. It may contain specific fungistatic substances, including a strain of *Streptomyces* bacteria, which can inhibit damping-off of seedlings (2, 63).

Vermiculite Vermiculite is a micaceous mineral that expands markedly when heated. Extensive deposits are found in Montana, North Carolina, and South Africa. Chemically, it is a hydrated magnesium-aluminum-iron silicate. When expanded, vermiculite is very light in weight [90 to 150 kg per cubic meter (6 to 10 lbs per cubic foot)], neutral in reaction with good buffering properties, and insoluble in water. It is able to absorb large quantities of water—40 to 54 liters per cubic meter (3 to 4 gal per cubic foot). Vermiculite has a relatively high cation-exchange capacity and, thus, can hold nutrients in reserve for later release. It contains magnesium and potassium, but supplementary amounts are needed from other fertilizer sources.

In crude vermiculite ore, the particles consist of many thin, separate layers with microscopic quantities of water trapped between them. When run through furnaces at temperatures near 1090°C (1994°F), the water turns to steam, popping the layers apart and forming small, porous, spongelike kernels. Heating to this temperature provides complete sterilization. Horticultural vermiculite is graded to four sizes: No. 1 has particles from 5 to 8 mm in diameter; No. 2, the regular horticultural grade, from 2 to 3 mm; No. 3, from 1 to 2 mm; No. 4, which is most useful as a seed-germinating medium, from 0.75 to 1 mm. Expanded vermiculite should not be compacted when wet, as pressing destroys its desirable porous structure. Do not use nonhorticultural (construction grade) vermiculite, as it is treated with chemicals toxic to plant tissues.

Perlite Perlite, a gray-white silicaceous material, is of volcanic origin, mined from lava flows. The crude ore is crushed and screened, then heated in furnaces to about 760°C (1400°F), at which temperature the small amount of moisture in the particles changes to steam, expanding the particles to small, spongelike kernels that are very light, weighing only 80 to 100 kg per cubic meter (5 to 6.5 lbs per cubic foot). The high processing temperature provides a sterile product. Usually, a particle size of 1.6 to 3.0 mm (1/16 to 1/8 in) in diameter is used in horticultural applications (Fig. 27). Perlite holds three to four times its weight of water. It is essentially neutral with a pH of 6.0 to 8.0 but with no buffering capacity. Unlike vermiculite, it has no cation exchange capacity and contains no mineral nutrients. Perlite presents some problems with fluoride-sensitive plants, but fluoride can be leached out by watering heavily. It is most useful in increasing aeration in a mix. Perlite, in combination with peat moss, is a very popular rooting medium for cuttings (85). Perlite dust is a respiratory irritant. Perlite should be moistened to minimize dust, and workers should use respirators.

Calcined Clay and Other Aggregates Stable aggregates can be produced when minerals such as clay, shales, and pulverized fuel ash are heated (calcined) at high temperatures. They have no fertilizer value, are porous, are resistant to breakdown, and absorb water. The main purpose of these materials is to change the physical characteristics of a propagation or liner potting mix. Examples of commercial materials made from clay include Leca, Terragreen, and Turfice. Haydite is a combination of clay and shale, while Hortag (used in the UK) is made from pulverized fuel ash (16). Clay-type kitty litter is also a calcined clay, but contains perfumes that are not desirable for propagation.

Pumice Chemically, pumice is mostly silicon dioxide and aluminum oxide, with small amounts of iron, calcium, magnesium, and sodium in the oxide form. It is of volcanic origin and is mined in several regions in the western United States. Pumice is screened to different-size grades, but is not heat-treated. It increases aeration and drainage in a propagation mix and can be used alone or mixed with peat moss.

Rockwool (Mineral Wool) This material is used as a rooting and growing medium in Europe, Australia, and the United States (Figs. 22 and 27). It is prepared from various rock sources, such as basalt rock, melted at a temperature of about 1600°C. As it cools, a binder is added, and it is spun into fibers and pressed into blocks. Horticultural rockwool is available in several forms—shredded, prills (pellets), slabs, blocks, cubes, or combined with peat moss as a mixture. Rockwool will hold a considerable amount of water, yet retains good oxygen levels. With the addition of fertilizers it can be used in place of the Peat-Lite mixes. Before switching from more traditional media mixes, it is best to initially conduct small-scale propagation trials with rockwool and other new media components as they become commercially available (51).

Shredded Bark Shredded or pulverized softwood bark from redwood, cedar, fir, pine, hemlock, or various hardwood bark species, such as oaks and maples, can be

used as an organic component in propagation and growing mixes and are frequently substituted for peat moss at a lower cost (89, 91, 102, 112, 128). Before it is used as a growing medium, pine bark is hammer-milled into smaller component pieces, stockpiled in the open, and often composted by turning the piles and watering as needed. Fresh barks may contain materials toxic to plants, such as phenols, resins, terpenes, and tannins. Composting for 10 to 14 weeks before using reduces phenolic levels in bark and improves its wettability as media, and the higher bark pile temperatures help reduce insect and pathogen levels (16). Because of their moderate cost, light weight, and availability, barks are very popular and widely used in mixes for propagation and container-grown plants (Fig. 27). Wetting agents and gels increase available water content in pine bark and may play a greater role in helping propagators reduce irrigation frequency or the volume of water required during each irrigation (12).

Coconut Fiber/Coir Coconut fiber (coir) is an economical peat substitute that can be mixed with a mineral component as propagation media. It is derived from coconut husks.

Compost In some countries, compost is synonymous with container media for propagation and plant growth; however, we define *compost* (composting) as the product of biological decomposition of bulk organic wastes under controlled conditions, which takes place in piles or bins. The process occurs in three steps:

a. an initial stage lasting a few days in which decomposition of easily degradable soluble materials occurs;
b. a second stage lasting several months, during which high temperatures occur and cellulose compounds are broken down; and
c. a final stabilization stage when decomposition decreases, temperatures lower, and microorganisms recolonize the material.

Microorganisms include bacteria, fungi, and nematodes; larger organisms, such as millipedes, soil mites, beetles, springtails, earthworms, earwigs, slugs, and sowbugs, can often be found in compost piles in great numbers. Compost prepared largely from leaves may have a high soluble salt content, which will inhibit plant growth, but salinity can be lowered by leaching with water before use.

In the future, with dwindling landfill sites and environmental pressures to recycle organic scrapage materials, the use of composted yard wastes, chicken and cow manure, organic sludge from municipal sewage treatment plants, and so on will play a greater role as media components in the propagation and production of small liner plants. Many nurseries recycle culled, containerized plants and shred the plant and soil as compost or as a medium component to be mixed with fresh container medium. Composted sewage sludge not only provides organic matter, but nearly all the essential trace elements, and a large percentage of major elements needed by plants in a slowly available form (53). Mixes should always be analyzed for heavy metals and soluble salt levels. The usual recommended rate is that compost not comprise more than 30 percent of the volume of the mix (16).

Suggested Mixes—Media and Preplant Granular Fertilizers for Container Growing During Propagation and Liner Production

Following propagation, young seedlings, rooted cuttings, or acclimatized tissue culture plantlets (liners) are sometimes planted directly in the field but frequently are started in a blended, soilless mix in some type of container. Container growing of young seedlings and rooted cuttings has become an important alternative for field growers. In the southern and western United States, more than 80 percent of nursery plants are container produced (35). For this purpose, special growing mixes are needed (99, 128). It is sometimes more economical for a propagator to buy bags or bulk forms of premixed media. Typically, they are composed of a peat or peat-vermiculite, peat-perlite, hammer-milled and composted bark, rockwool, and other combinations. Preplant amendments in these mixes normally include dolomitic limestone, wetting agents (surfactants) to improve water retention and drainage of the peat or bark, starter fertilizers, trace elements, and sometimes gypsum and a pH buffer.

In preparing container mixes, the media should be screened for uniformity to eliminate excessively large particles. If the materials are very dry, they should be moistened slightly; this applies particularly to peat and bark, which, if mixed when dry, absorb moisture very slowly. In mixing, the various ingredients may be arranged in layers in a pile and turned with a shovel. A power-driven cement mixer, soil shredder, or front-end loader is used in large-scale operations. Most nurseries omit mineral soil from their mixes. The majority of container mixes for propagation and liner production use an organic component such as a bark or peat, which solely or in combination is mixed with mineral components such as sand, vermiculite, or pumice, depending on their availability and cost.

Preparation of the mixture should preferably take place at least a day prior to use. During the ensuing 24 hours, the moisture tends to become equalized throughout the mixture. The mixture should be just slightly moist at the time of use so that it does not crumble; on the other hand, it should not be sufficiently wet to form a ball when squeezed in the hand (44). With barks and other organic matter and supplementary components, particularly rice hulls and sugarcane begasse, it is necessary to compost the material for a period of months before using it as a container medium component.

Container mixes require fertilizer supplements and continued feeding of the plants until they become established in their permanent locations (132). For example, one successful mix for small seedlings, rooted cuttings, and bedding plants consists of one part each of shredded fir or hammer-milled pine bark, peat moss, perlite, and sand. To this mixture is added **preplant fertilizers**—gypsum, dolomitic limestone, microelements and sometimes controlled-release fertilizer. **Postplant fertilizers**—soluble forms of nitrogen, phosphorus, and potassium—are added later to the irrigation water (*fertigation*), or as a top dressing of controlled-release fertilizer, such as Osmocote or Nutricote.

preplant amendments/fertilizers Mineral nutrients that are applied to or incorporated in the propagation or container production media, prior to propagating propagules or transplanting liner plants into containers or into the field.

postplant amendments/fertilizers Mineral nutrients that are applied as a broadcast or liquid application during propagation or production of a containerized or field-grown plant.

In summary, nurseries have changed from loam-based growing media, as exemplified by the John Innes composts developed in England in the 1900s, to soilless mixes incorporating such materials as finely shredded bark, peat, sand, perlite, vermiculite, and pumice in varying proportions. The trend away from loam-based mixes is due to a lack of suitable uniform soils, the added costs of having to pasteurize soil mixes, and the costs of handling and shipping the heavier soils compared with lighter media materials. Much experimentation takes place in trying to develop other low-cost, readily available bulk material to be used as a component of growing mixes such as spent mushroom compost, papermill sludge (21, 26), composted sewage sludge (53), and other materials.

The Cornell Peat-Lite Mixes

The Cornell Peat-Lite mixes, like the earlier University of California (UC) potting mixes, are soilless media. First developed in the mid-1960s, they are used primarily for seed germination and for container growing of bedding plants, annuals, and flowering potted plants. The components are lightweight, uniform, readily available, and have chemical and physical characteristics suitable for the growth of plants. Excellent results have been obtained with these mixes. It may be desirable, however, to pasteurize the peat moss before use to eliminate any disease inoculum or other plant pests. Finely shredded bark is often substituted for the peat moss.

The term **peat-lite** refers to peat-based media containing perlite or vermiculite.

Peat-Lite Mix C (for germinating seeds): To Make 0.76 m^3 (1 cubic yard):

- 0.035 m^3 (1.2 ft^3) shredded German or Canadian sphagnum peat moss
- 0.035 m^3 (1.2 ft^3) horticultural grade vermiculite No. 4 (fine)
- 42 g (1.5 oz)—4 level tbsp ammonium nitrate
- 42 g (1.5 oz)—2 level tbsp superphosphate (20 percent), powdered
- 210 g (7.5 oz)—10 level tbsp finely ground dolomitic limestone

The materials should be mixed thoroughly, with special attention to wetting the peat moss during mixing. Adding a nonionic wetting agent, such as Aqua-Gro [(28 g (1 oz) per 23 liter (6 gal) of water)] usually aids in wetting the peat moss.

Many commercial ready-mixed preparations, based on the original Cornell peat-lite mixes, are available in bulk or bags and are widely used by propagators and producers. Some mixes are prefilled into cell packs, seed trays, or pots that are ready to be planted. Some soilless proprietary mixes are very sophisticated, containing peat moss, vermiculite, and perlite, plus a nutrient charge of nitrogen, potassium, phosphorus, dolomitic limestone, micronutrients, and a wetting agent with the pH adjusted to about 6.5.

Proprietary micronutrient materials, such as Esmigran, FTE 503, or Micromax, consisting of combinations of minor elements, are available for adding to growing media. Adding a controlled-release fertilizer such as Osmocote, MagAmp, Nutriform, Nutricote, or Polyon to the basic Peat-Lite mix is useful if the plants are to be grown in it for an extended period of time.

BOX 7 **GETTING MORE IN DEPTH ON THE SUBJECT**

SOME SUPPLIERS OF COMMERCIAL MIXES IN NORTH AMERICA

Sun Gro Horticulture (www.sungro.com)

Premier Horticulture (www.premierhort.com)

Scotts Professional Horticulture Solutions (www.scottspro.com)

Ball Horticultural Company (www.ballhort.com)

Managing Plant Nutrition with Postplant Fertilization During and After the Propagation Cycle

Developing an *efficient fertilizer program* for container plants for the 21st Century depends on (a) minimizing the loss of fertilizer from the production area and (b) increasing the amount of fertilizer utilized or taken up by the plant (133, 134). Suggested levels of *preincorporated* (*preplant*) granular fertilizers were discussed in the previous section on container media for propagation and small linear production. This section discusses some general fertilization practices for management of plant nutrition during **propagation and liner production** (Fig. 21). Both soluble and slow-release fertilizers are utilized.

Liquid Fertilizers For large-scale greenhouse and nursery operations, it is more practical to prepare a liquid concentrate and inject it into the regular watering or irrigating system by the use of a proportioner—**fertigation.** The most economical source of fertilizers to be applied through the irrigation water is from dealers who manufacture soluble liquid fertilizer for field crops. It is no longer recommended to use superphosphate in soilless mixes with outdoor container production because of the phosphorus leaching that occurs. Hence, more efficient, soluble forms of phosphorus are used, such as phosphoric acid or ammonium phosphate, in liquid feed programs. Potassium is typically applied as potassium chloride, or potassium nitrate, and nitrogen as Uran 30 (15 percent urea, 15 percent NH_4NO_3) or ammonium nitrate in the liquid concentrate.

An example of a liquid fertilizer system for production of containerized plants is the Virginia Tech System (VTS). With the VTS, all nutrients are supplied to the container by injecting liquid fertilizers into the irrigation water (131, 132). A 10N-4P_2O_5-6K_2O analysis liquid fertilizer is applied five times per week, 1.3 cm (0.5 in) each irrigation at an application rate of 100 to 80 ppm N, 15 to 10 ppm P, and 50 to 40 ppm K. Sometimes higher nitrogen levels are applied (200–300 ppm N), depending on the time of the year, plant growth conditions, or plant species. It is critical to regularly monitor soluble salt levels of the medium prior to fertigation. Supplemental micronutrients are also applied in a liquid form but from separate tanks and with separate injectors to prevent fertilizer precipitation. It is best to monitor soluble salt levels of the irrigation water by measuring electrical conductivity (EC) with a conductivity meter; that is, to apply 100 ppm N, the injector is set so that the conductivity of the irrigation water—minus the conductivity of the water before the fertilizer was injected—reads 0.55 mS/cm (millisiemens per cm or dS per m are the same units of measure) (132–134).

Controlled-Release Fertilizers (CRF) Controlled-release fertilizers (CRF) provide nutrients to the plants gradually over a long period and reduce the possibility of injury from excessive applications (127). There has been a long-term trend of nurseries in the southern United States incorporating CRF in propagation, liner and production media, and spot-fertilizing via liquid fertilizer (fertigation) or top-dressing with CRF. CRFs are some of the most cost-effective and ecologically friendly ways to fertilize plants because fertilizer is applied directly to the pots. In contrast, overhead fertigation with rainbird sprinkler-type systems is only about 30 percent efficient, and greater fertilizer runoff occurs from the container production area. Examples of CRF include Osmocote, Phycote, Nutricote, and Polyon, and some are available with micronutrients incorporated in the pellets. As previously described, for both cutting and seed propagation, a low concentration of macro and micro CRF can be included in the propagation mix, so the newly formed roots can have nutrients available for absorption (37). This is particularly important with mist propagation where nutrients can be leached out from both the plant and the medium.

Two types of CRF include coated water-soluble pellets or granules and inorganic materials that are slowly soluble, while slow-release, organic fertilizer includes organic materials of low solubility that gradually

decompose by biological breakdown or by chemical hydrolysis.

Examples of the resin-coated-type pellets are (a) Osmocote, whose release rate depends on the thickness of the coating, and (b) Nutricote (105), whose release rate depends on a release agent in the coating. After a period of time the fertilizer will have completely diffused out of the pellets (130). Another kind of controlled-release fertilizer is the sulfur-coated urea granules, consisting of urea coated with a sulfur-wax mixture so that the final product is made up of about 82 percent urea, 13 percent sulfur, 2 percent wax, 2 percent diatomaceous earth, and 1 percent clay conditioner.

An example of the slowly soluble, inorganic type CRF is MagAmp (magnesium ammonium phosphate), an inorganic material of low water solubility. Added to the soilless mix, it supplies nutrients slowly for up to 2 years. MagAmp may be incorporated into media prior to steam pasteurization without toxic effects. On the other hand, steam pasteurization and sand abrasion in the preparation of mixes containing resin-coated, slow-release fertilizers, such as Osmocote, can lead to premature breakdown of the pellets and high soluble salt toxicity.

An example of the slow-release, organic, low-solubility type is urea-formaldehyde (UF), which will supply nitrogen slowly over a long period of time. Another organic slow-release fertilizer is isobutylidene diurea (IBDU), which is a condensation product of urea and isobutylaldehyde, having 31 percent nitrogen.

Fertilizer Systems for Propagation Commercial propagators often apply moderate levels of controlled-release macro and micro elements to the propagation media—preincorporated into the media—prior to sticking cuttings and starting seed germination and seedling plug production. During propagation, supplemental fertilizer is added by top dressing (broadcasting) with controlled-release fertilizer or by injecting gradually increasing concentrations of liquid fertilizer (fertigation). These supplementary nutrients do not promote root initiation (30, 66) in cuttings, but rather enhance root development after root primordia initiation has occurred. Hence, supplementary fertilization is generally delayed until cuttings have begun to root. Propagation turnover occurs more quickly and plant growth is maintained by producing rooted liners and plugs that are more nutritionally fit.

Some recommended levels of CRF for propagation are:

- 3.6 kg/m^3 (6 lb/yd^3) 18-6-12 Osmocote (or comparable product)
- 0.6 kg/m^3 (1 lb/yd^3) Micromax or other trace element mixtures—Perk, Esmigran, or FTE 503
- For unrooted cuttings, fast-germinating seeds, and tissue culture liners, CRF are preincorporated in the propagation media. For slower rooting or seed-germinating species, use Osmocote 153 g/m^2 (0.5 oz/ft^2).
- Nutricote and others are top-dressed on the media after rooting or seed germination starts to occur. Determining optimum levels of fertilization for propagation depends on the propagule system, and needs to be determined on a species basis (30).

Fertilizer Systems for Liner Production Soilless mixes must have fertilizers added (107, 132). Irrigation water and the container medium should be thoroughly analyzed for soluble salts, pH, and macro- and microelements before a fertility program can be established. It is always wise to conduct small trials before initiating large-scale fertility programs during propagation and liner production.

A satisfactory feeding program for growing liner plants is to combine a slowly available dry, granular fertilizer (preplant) in the original mix, with a (postplant) liquid fertilizer applied at frequent intervals during the growing season or with CRF added as top dressings, as needed (49).

Of the three major elements—nitrogen, phosphorus, and potassium—nitrogen has the most control on the amount of vegetative shoot growth. Phosphorus is very important, too, for root development, plant energy reactions, and photosynthesis. Potassium is important for plant water relations and enhanced drought resistance (40).

Nitrogen and potassium are usually supplied by CRF or fertigation—*100 to 80 ppm nitrogen* and *50 to 40 ppm potassium* are optional container medium levels when the Virginia Tech Extraction Method (VTEM) is used (134).

Negatively charged ions, such as phosphorus, leach from soilless media, so small amounts of phosphorus must be added to the media frequently. Past research indicates that *15 to 10 ppm phosphorus* should be maintained in container medium as determined by the saturated paste or VTEM (131, 132). Phosphorus from superphosphate leaches rapidly; so in order to maintain 10 ppm in the medium, CRF is used or small amounts of phosphorus in soluble form are applied.

Calcium and magnesium are supplied as a preplant amendment in dolomitic limestone and may naturally be supplied by irrigation water. Limestone is primarily added to adjust the pH of the media. It is important to have the irrigation water checked to determine the level of dolomitic limestone needed, if any. VTEM levels of