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Publisher’s Note

Magill’s Encyclopedia of Science: Plant Life is designed to meet the needs of college and high school students as well as nonspecialists seeking general information about botany and related sciences. The definition of “plant life” is quite broad, covering the range from molecular to macro topics: the basics of cell structure and function, genetic and photosynthetic processes, evolution, systematics and classification, ecology and environmental issues, and those forms of life—archaea, bacteria, algae, and fungi—that, in addition to plants, are traditionally studied in introductory botany courses. A number of practical and issue-oriented topics are covered as well, from agricultural, economic, medicinal, and cultural uses of plants to biomes, plant-related environmental issues, and the flora of major regions of the world. (Readers should note that, although cultural and medicinal uses of plants are occasionally addressed, this encyclopedia is intended for broad information and educational purposes. Those interested in the use of plants to achieve nutritive or medicinal benefits should consult a physician.)

Altogether, the four volumes of Plant Life survey 379 topics, alphabetically arranged from Acid precipitation to Zygomycetes. For this publication, 196 essays have been newly acquired, and 183 essays are previously published essays whose contents were reviewed and deemed important to include as core topics. The latter group originally appeared in the following Salem publications: Magill’s Survey of Science: Life Science (1991), Magill’s Survey of Science: Life Science, Supplement (1998), Natural Resources (1998), Encyclopedia of Genetics (1999), Encyclopedia of Environmental Issues (2000), World Geography (2001), and Earth Science (2001). All of these previously published essays have been thoroughly scrutinized and updated by the set’s editors. In addition to updating the text, the editors have added new bibliographies at the ends of all articles.

New appendices, providing essential research tools for students, have been acquired as well:

- a “Biographical List of Botanists” with brief descriptions of the contributions of 134 famous naturalists, botanists, and other plant scientists
- a Plant Classification table
- a Plant Names appendix, alphabetized by common name with scientific equivalents
- another Plant Names appendix, alphabetized by scientific name with common equivalents
- a “Time Line” of advancements in plant science (a discursive textual history is also provided in the encyclopedia-proper)
- a Glossary of 1,160 terms
- a Bibliography, organized by category of research
- a list of authoritative Web sites with their sponsors, URLs, and descriptions

Every essay is signed by the botanist, biologist, or other expert who wrote it; where essays have been revised or updated, the name of the updater appears as well. In the tradition of Magill reference, each essay is offered in a standard format that allows readers to predict the location of core information and to skim for topics of interest: The title of each article lists the topic as it is most likely to be looked up by students; the “Category” line indicates pertinent scientific subdiscipline(s) or area(s) of research; and a capsule “Definition” of the topic follows. Numerous subheads guide the reader
through the text; moreover, key concepts are italicized throughout. These features are designed to help students navigate the text and identify passages of interest in context. At the end of each essay is an annotated list of “Sources for Further Study”: print resources, accessible through most libraries, for additional information. (Web sites are reserved for their own appendix at the end of volume 4.) A “See also” section closes every essay and refers readers to related essays in the set, thereby linking topics that, together, form a larger picture. For example, since all components of the plant cell are covered in detail in separate entries (from the Cell wall through Vacuoles), the “See also” sections for these dozen or so essays list all other essays covering parts of the cell as well as any other topics of interest.

Approximately 150 charts, sidebars, maps, tables, diagrams, graphs, and labeled line drawings offer the essential visual content so important to students of the sciences, illustrating such core concepts as the parts of a plant cell, the replication of DNA, the phases of mitosis and meiosis, the world’s most important crops by region, the parts of a flower, major types of inflorescence, or different classifications of fruits and their characteristics. In addition, nearly 200 black-and-white photographs appear throughout the text and are captioned to offer examples of the important phyla of plants, parts of plants, biomes of plants, and processes of plants: from bromeliads to horsetails to wheat; from Arctic tundra to rain forests; from anthers to stems to roots; from carnivorous plants to tropisms.

Reference aids are carefully designed to allow easy access to the information in a variety of modes: The front matter to each of the four volumes includes the volume’s contents, followed by a full “Alphabetical List of Contents” (of all the volumes). All four volumes include a “List of Illustrations, Charts, and Tables,” alphabetized by key term, to allow readers to locate pages with (for example) a picture of the apparatus used in the Miller-Urey Experiment, a chart demonstrating the genetic offspring of Mendel’s Pea Plants, a map showing the world’s major zones of Desertification, a cross-section of Flower Parts, or a sampling of the many types of Leaf Margins. At the end of volume 4 is a “Categorized Index” of the essays, organized by scientific subdiscipline; a “Biographical Index,” which provides both a list of famous personages and access to discussions in which they figure prominently; and a comprehensive “Subject Index” including not only the personages but also the core concepts, topics, and terms discussed throughout these volumes.

Reference works such as Magill’s Encyclopedia of Science: Plant Life would not be possible without the help of experts in botany, ecology, environmental, cellular, biological, and other life sciences; the names of these individuals, along with their academic affiliations, appear in the front matter to volume 1. We are particularly grateful to the project’s editor, Bryan Ness, Ph.D., Professor of Biology at Pacific Union College in Angwin, California. Dr. Ness was tireless in helping to ensure thorough, accurate, and up-to-date coverage of the content, which reflects the most current scientific knowledge. He guided the use of commonly accepted terminology when describing plant life processes, helping to make Magill’s Encyclopedia of Science: Plant Life easy for readers to use for reference to complement the standard biology texts.
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About the Editor: Bryan Ness is a full professor in the Department of Biology at Pacific Union College, a four-year liberal arts college located atop Howell Mountain in the Napa Valley, about ninety miles north of San Francisco. He received his Ph.D. in Botany from Washington State University. His doctoral work focused on molecular plant systematics and evolution. In addition to authoring or coauthoring a number of scientific papers, he has contributed to The Jepson Manual: Higher Plants of California, The Flora of North America, a multivolume guide to the higher plants of North America, and more than a dozen articles for various Salem Press publications, including Aging, Encyclopedia of Genetics, Magill's Encyclopedia of Science: Animal Life, Magill’s Medical Guide, and World Geography. For four years he managed The Botany Site, a popular Internet site on botany. He is currently working on a book about plant myths and misunderstandings.

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**SUSTAINABLE FORESTRY**

**Categories:** Disciplines; economic botany and plant uses; environmental issues; forests and forestry

Sustainable forestry is a system of forest management that relies on natural processes to maintain a forest’s continuing capacity to produce a stable and perpetual yield of harvested timber and other benefits, including recreation, wildlife habitat, and forest-related commodities.

Forest management in the United States first became an issue in 1827 when the Department of the Navy and President John Quincy Adams saw the need for a continuous supply of mature timber for ship construction. In the 1860’s, the American Association for the Advancement of Science first discussed the need for sustained-yield forestry. In 1878, the Cosmos Club, a Washington, D.C., club of intellectuals, proposed the wise use of natural resources for the greatest good, for the greatest number, and for the longest time, establishing the foundation for the conservation movement. The first national forest reserves were established by the U.S. government in 1891, and the first selective logging and marketing of U.S. government timber reserves occurred in 1897. Clear-cutting was the general method of timber harvesting. Continued clear-cutting during the twentieth century accelerated the deforestation of private and Forest Service lands, leading to concerns about soil erosion, water pollution, wildlife habitat loss, and the sustained availability of forest resources.

Management Systems

Forest science developed the high-yield forestry plantation tree farming system in the 1930’s. By the 1960’s, ecological concerns had led to restoration forestry, which emphasized human intervention to reconstruct forest ecosystems and return forests to baseline conditions that existed before clear-cutting or plantation planting. By the 1980’s, new understandings concerning the complexity of forest ecosystems led to an emphasis on perpetually sustaining existing forest resources rather than relying on human efforts to reconstruct forests.

Sustainable Alternatives

Sustainable forestry is an alternative to clearcutting, the standard logging practice. Clear-cutting removes all timber in one harvest that usually occurs no more than once every sixty to one hundred years. Both mature and immature trees are removed in one process. Logging roads are cut into the forest so heavy machinery can remove all trees from a large area, often about 100 acres at a time. Road construction and clear-cutting lead to soil erosion, topsoil and nutrient loss, silting and pollution of waterways, the loss of wildlife habitat, and the loss of recreational benefits. Repeated cycles of growth and clear-cutting erode soil nutrition, destroy plants, animals, and microorganisms in the ecosystem necessary for healthy forest growth, and reduce the value of future harvests.

Sustainable forestry is also an alternative to monoculture plantation forestry. Plantation forestry requires active human intervention to plant tree seedlings, control disease and pests, and nurture the timber stand to maturity. Plantations usually feature a grid planting of a single tree species, with all trees maturing simultaneously. The lack of species and age diversity makes tree plantations unsuitable for wildlife habitat or recreation and makes trees susceptible to disease and pests. Monoculture plantations also deplete species-specific minerals and other nutrients in the soil, reducing its future productivity.

Goals

Sustainable forest management techniques seek a perpetual high yield of timber and pulpwood while maintaining biodiversity and natural forest ecosystems and permitting forests to restore their vitality through natural processes, such as foliage decomposition and fire.

Sustainable forestry maintains a balance between natural environmental stresses and the human needs for timber, pulpwood, recreation, and a
variety of harvested forest products. In spite of the effort to maintain this balance, various sustainable forestry methods often tend to favor either ecosystem maintenance or high timber yields.

Sustainable forestry with an ecosystem emphasis is the discipline of repeated thinning of natural tree stands to sustain a mixed-age, mixed-species forest that is naturally perpetuated by seeds from the mature trees. The forest is periodically thinned, usually every twenty years, to provide a steady income to the forest owners, permit the remaining trees to reach their full maturity, and provide space for new seedlings to grow. When the timber stand reaches full sustainable maturity, immature trees are continuously harvested for pulpwood, and mature trees over one hundred years of age are continuously harvested for high-quality lumber. Natural processes promote the health of the forest and revitalize the forest soil. Diversity in both age and species makes the forest a suitable habitat for a variety of forest-dwelling species and human recreation. The forest is able to recover quickly from natural disasters, fires, or drought.

Sustainable forestry with an emphasis on timber yield divides the forest into subplots, then manages each subplot to produce two sequential high-yield plantation crop cycles of eighty years each before permitting the plot to grow to maturity in a third four-hundred-year cycle. The third cycle permits the forest soil to restore its vitality and produces an old-growth forest suitable for wildlife and eventual timber harvesting. Once fully implemented, this system ensures that each forest has subplots at each stage of growth and harvesting, from newly planted plots to old-growth plots with trees at or near four hundred years of age.

Gordon Neal Diem
See also: Deforestation; Forest and range policy; Forest management; Forests; Logging and clear-cutting; Monoculture; Rangeland; Reforestation; Sustainable agriculture; Timber industry; Wood and timber.

Sources for Further Study
Berger, John. Understanding Forests. San Francisco, Calif.: Sierra Club, 1998. Various forestry techniques, including clear-cutting, sustainable forestry, and restoration forestry, are described here.

SYSTEMATICS AND TAXONOMY

Categories: Classification and systematics; disciplines

Systematics deals with evolutionary, or phylogenetic, relationships among organisms, whereas taxonomy is more involved with the classification, naming, and description of organisms. In practice, the two terms are often used interchangeably to refer to the study of relationships among organisms, which in turn often derives from their description and drives their naming.

The history of the disciplines of systematics and taxonomy has shifted with the evolution over the years of the state of knowledge about living organisms, their origins, and their relationships. There has been a historical shift from an emphasis on classification (simply naming and identifying organisms) to the study of phylogenetic (evolutionary) relationships. Classification traditionally focused on defining the relationships among organisms based primarily on their overall similarity in morphology and appearance. Phylogenetics is now the more common approach in studying the relationships among organisms and involves constructing phylogenies, or evolutionary trees, using evidence from evolutionary relationships. In addition, the advent of genetics and DNA research has significantly changed the way many biologists approach classification, leading in some cases to reconsideration of former taxonomic relationships.

Ancient World and Middle Ages
The roots of taxonomy go back to Greeks, most notably the philosopher Theophrastus in the third century B.C.E., who wrote two treatises on plants, Peri phyton histories (also known as Historia plantarum; “Enquiry into Plants,” 1916) and Peri phyton aition (also known as De causis plantarum; English translation, 1976-1990). Theophrastus’s system and many other early classification systems grouped plants into herbs, undershrubs, shrubs, and trees. Classification of plants, beyond this more or less simplistic approach, was not attempted until the latter part of the sixteenth century, when Andrea Cesalpino published De plantis libri (1583). Between the time of the Greeks and Cesalpino, most botanical work was done in the name of medicine, and numerous plants were described because of their usefulness as herbs.

Naming of plants was haphazard, at best. Colloquial names were used by some, and Latin phrases
not only were used to describe a plant but also served as official names. There was no accepted length for Latin phrase names, and the names carried little information about how a particular plant might be related to others.

**Linnaeus and the Birth of Modern Taxonomy**

In 1753 Carolus Linnaeus published his *Species plantarum*, which quickly brought simplicity and order to the naming of organisms, including plants. Linnaeus introduced *binomial nomenclature*, which standardized the naming of all organisms by using two Latin words, which together were referred to as the *species* name. The first word in the species name was the *genus*, which immediately identified how an organism fit into the classification system.

In addition to improving the system of naming, Linnaeus revolutionized the classification system by introducing a hierarchical approach. Similar species were grouped together into genera. Similar genera were grouped into families. In turn, families were grouped into orders, orders into classes, classes into phyla, and phyla into kingdoms, the most inclusive of the categories. Although his classification of organisms implied no evolutionary relationships, it was useful for bringing some order to taxonomy. All of these hierarchical categories are used for all types of organisms, including plants, although in plants the name *division* is sometimes used instead of the phylum.

According to Linnaeus, the turnip, *Brassica rapa*, which is the name Linnaeus gave to this species, is in the same genus as black mustard, *Brassica nigra*. The genus *Brassica* is in the mustard family, *Brassicaceae*, along with related genera such as *Raphanus* and *Arabis*. The family *Brassicaceae* is in the order *Capparales*, along with related families like *Capparaceae* and *Resedaceae*. *Capparales* is a member of the class *Eudicotyledones*, which includes all the other orders commonly referred to as dicots or dicotyledons. Class *Eudicotyledones* belongs to the division *Anthophyta*, along with class *Monocotyledones*. *Anthophyta*, along with all other green plants in divisions like *Coniferophyta* (the gymnosperms) and *Pteridophyta* (the ferns), belongs in kingdom *Plantae*. Each of these categories has a standard suffix, such as -*phyta* for divisions, -*opsida* for classes, -*ales* for orders, and -*aceae* for families, so that the rank of a name is immediately apparent. Rare exceptions to these rules exist.

In addition to the main categories in the hierarchy, many subdivisions are used. For example, between the levels of kingdom and division, there is subkingdom, which would contain within it one or more divisions. The *sub-* prefix can be used before any of the categories, so that there are subclasses, subfamilies, and even subspecies. The prefix *super-* can also be used to define additional ranks. For example, a superfamily contains one or more related families, and a superorder contains one or more related orders.

**Classification Since Linnaeus**

Linnaeus’s binomial nomenclature and hierarchical classification system have been used ever since, but when particular taxa have been added, the classification system has undergone great change. The placement of taxa by Linnaeus was done in what is called an artificial manner. He grouped taxa into categories based on the organisms’ overall similarities and the possession of particular physical characteristics. Linnaeus’s system is called an *artificial classification system* because he made no attempt to group taxa based on evolutionary relationships. Although other plant taxonomists since Linnaeus have also produced artificial classifications, after evolution became more generally accepted in science, many attempts were made to produce a “natural,” or phylogenetically based, classification that would reflect, as much as possible, the evolutionary relationships of the taxa.

One of the first, and still highly respected, phylogenetic classifications of plants was published in 1892 by Adolf Engler. It was actually a revision of an earlier classification by August Wilhelm Eichler. With the help of Karl Prantl and others, the system continued to be elaborated until 1911 and became a twenty-volume work called *Die natürlichen Pflanzenfamilien* (1887-1911; the natural families of plants). The families and genera, instead of being ordered alphabetically, were ordered within their taxonomic ranks, from most evolutionarily primitive to most advanced. It was so influential that plant specimens stored in many herbaria are still organized by what is now referred to as the Engler and Prantl system.

As more and more sophisticated phylogenetic studies have been done, many other plant taxonomists have attempted to improve on Engler and Prantl’s system. Some of the more notable plant taxonomists of the twentieth century have included John Hutchinson, Armen Takhtajan, Arthur Cron-
quist, Robert F. Thorne, and Rolf M. T. Dahlgren. The differences among the systems proposed by these various taxonomists are mainly due to different opinions about which plant taxa should be considered most primitive and which most advanced. The identification of what the first land plants, first seed plants, and first flowering plants were like is still uncertain, leaving ample room for speculation. Consequently, a number of competing classification systems exist today. Modern information from DNA analysis and cladistics continues to sharpen taxonomists’ understanding of how plants should be classified, but more work remains to be done.

Naming Rules: The Genus and Below

The rules for naming plants are very specific. The International Code of Botanical Nomenclature (ICBN) contains authoritative rules on the correct way to name plants, as well as groups such as algae and fungi, which have traditionally been considered plants in a broad sense. Rules for naming fossil plants are also covered. Revisions to the code take place on a regular basis.

For a plant name to be accepted, it must be validly published. For any new species (or genus) described before 1953, “validly published” could mean anything from publication in a newspaper or catalog to publication in a respected scientific journal or other professional work. Since 1953, all new names must be published in accepted scientific publications. In addition, all new species (or genus) descriptions must include a complete description in Latin, often called the Latin diagnosis.

 Sometimes two or more plant taxonomists inadvertently describe the same species, giving it different names. When this happens, the earliest validly published name is given priority and is considered the correct name; any other names are called synonyms. May 1, 1753, the date Linnaeus published Species plantarum, is considered the starting date for determining priority, and any names published before this date are not considered.

In addition to being validly published, a type specimen must be identified. A type specimen is a preserved plant specimen that is designated by the author as the best representative of the new species. An author can define more than one type, in which case the first designated specimen is the holotype and duplicates are called isotypes. Each of these is placed in an established herbarium so other plant taxonomists can examine it.

All names of taxonomic groups are treated as Latin, regardless of their source. Proper names and non-Latin words must be Latinized, following specific rules in the ICBN. Species names always comprise the genus name, with the first letter capitalized, followed by the species epithet, which is not capitalized. Both names must be either italicized or underlined to denote the name as a species name. A complete species name is also followed by the name of the author who named it. Author names are often abbreviated, and many author names have official abbreviated forms. An example of a species named by Linnaeus is Brassica rapa L. (the L. stands for Linnaeus). The author’s name should not be italicized or underlined. Once a genus has been referred to in a scientific paper, later references to species within the genus can then be written with the genus abbreviated to just the first letter and the author’s name is left off: for example, Brassica rapa L. becomes B. rapa.

In a species with a lot of variability, subspecies and varieties can also be described. Some plant taxonomists consider subspecies to be of higher taxonomic rank than varieties, whereas others treat them as equivalent. Often particular taxonomists will use only one of these ranks to describe taxa below the species rank. Any species can be split into two or more varieties or subspecies. The variety or subspecies that contains the type specimen is always considered the typical variety or subspecies. For example, the species Abies magnifica Andr. Murray (California red fir) has been divided into two varieties. The typical variety is A. magnifica var. magnifica, and the other variety is A. magnifica var. shastensis Lemmon. Notice that the word “variety” is abbreviated as “var.” and is not italicized or underlined and that the name of the author of the variety follows the variety name (except for the typical variety, where the author is assumed to be the author of the species). The word “subspecies” is abbreviated as “ssp.” and is also not italicized or underlined.

For the sake of simplicity, italics are now often used for taxonomic groups higher than the genus, all the way up to the phylum. However, strictly speaking, only the genus and species names are italicized.

How Names Are Chosen

Names can be chosen for a variety of reasons and can be derived from anything, as long as the source word is Latinized, if it is not already in Latin. One of
the most common name choices is one that describes some obvious characteristic of the plant. For example, the genus name *Trillium* nicely describes the fact that essentially all the plant parts are in three’s (tri- meaning “three”), and the species epithet for *T. albidum* nicely describes the striking white petals of this species.

Names can also be derived from the geographic location where the plant is found. These kinds of names are most commonly found in species epithets, such as *Juniperus californica* (California juniper) or *Carex norvegica* (Scandinavian sedge). In rare cases, a genus will be named after a place, as in *Idahoa*, a mustard genus found in Idaho and elsewhere in the western United States.

Another popular approach is to name a plant after someone famous, as in the genera *Darwinia* (after Charles Darwin) and *Linnaea* (after Carolus Linnaeus). Species epithets are often given the name of the person who collected the plant. Examples of this type include *Pseudotsuga menziesii* and *Iris douglasii*.

Some species are named with less originality, using very common Latin epithets. For example, *Juncus ambiguus*, meaning ambiguous, not only is nondescriptive but also leaves some doubt about what the author intended. Then there is *Fritillaria affinis*, where the epithet *affinis* simply means “like.” Like what? In case these like cases, it may be necessary to refer to the original publication where the species is described to understand why the name was given.

Naming Rules: Above the Genus

Above the genus the type concept is used to determine correct names. All family names must be derived from a genus name within the family. For example, the rose family is called *Rosaceae*, which is derived from the genus *Rosa*, and the lily family is called *Liliaceae*, which is derived from the genus *Lilium*. Exceptions to this rule are only allowed when acted upon by the International Botanical Congress. In 2001, there were only eight exceptions to the family naming rules. These are referred to as conserved family names and are of long-standing usage. These *conserved names* can be used, but each also has a name derived according to the rules, and the names can be used interchangeably. The eight conserved names, and their alternatives (in parentheses) are *Palmae* (*Arecales*); *Gramineae* (*Poaceae*); *Cruciferae* (*Brassicaceae*); *Leguminosae* (*Fabaceae*); *Guttiferae* (*Clusiaceae*); *Umbelliferae* (*Apiaceae*); *Labiateae* (*Lamiaceae*); *Compositae* (*Asteraceae*).

Two common ranks between the family and genus are subfamily and tribe. Names for these should also follow the type concept, with their name being derived from a genus within them. The proper suffixes for subfamilies and tribes are *-oideae* and *-inae*, respectively.

Ranks above the family level can be chosen either by the type concept or by using a common characteristic of members of the taxon. Standard suffixes for these higher ranks are mentioned above. Using the type concept, the flowering plants, or angiosperms, are phylum *Magnoliophyta* (based on the genus *Magnolia*), but a common alternative name is *Anthophyta*. Likewise, the gymnosperms are phylum *Pinophyta* (after the genus *Pinus*), but are also commonly called *Coniferophyta*. In each of these cases, both names are valid and are used preferentially by different plant taxonomists.

Sometimes, not only the names will differ, but even the suffixes may not follow the standards. For example, using the type concept, the class names for the monocots and dicots (the two major groups of flowering plants) are *Liliopsida* and *Magnoliopsida*, respectively. Alternative names, in common use, are *Monocotyledones* and *Eudicotyledones*, respectively.

Why Names Change

Some common reasons that names change are the result of changes in taxonomic opinion, the discovery that the current name is not the oldest published name, or the discovery that it has some other technical problem. Although such name changes can be annoying and unpopular to some people, they are essential if the ICBN is to be followed. If plant taxonomists and others were to be free to ignore the rules, then confusion would result.

Plant taxonomists are continually studying relationships among plants, and as new discoveries are made, they are incorporated into the classification system. Sometimes it is discovered that a species needs to be split into two species, in which case the plants that include the holotype retain the original name, and the remaining plants are given a new name. On the other hand, separate species are sometimes found to be so similar that they are reclassified as belonging to the same species, in which case all the plants from both original species are given the name that was published first. These
same rules must be applied to all taxonomic levels whenever taxonomic conclusions warrant splitting or joining of taxa.

Changes in classification at the genus level can also affect species names. For example, if two genera are found to be so similar that they end up being combined into one genus, or some of the species from one genus are found to be more related to members of another genus and are therefore moved into it, species names will be affected. When this happens, the new species name will carry two authors' names after it (the original author of the old species name and the author of the new species name), and it is considered a new combination. The species does not have to be redescribed, but the change must be validly published. Thus, the species *Castilleja exserta* (A. A. Heller) Chuang & Heckard used to be in the genus *Orthocarpus* and was called *Orthocarpus exsertus* A. A. Heller. Note that the author of the original species name appears in parentheses. Also note, in this case, that the ending of the species epithet had to be changed slightly to follow proper rules of Latin grammar. Similar rules are followed when a taxon changes from a species to a variety (or some other lower rank) or vice versa. For example, *Potentilla breweri* S. Watson was later determined to be so closely related to the *P. drummondii* Lehm. that it was changed to a variety of this species, *P. drummondii* var. *breweri* (S. Watson) B. Ertter.

Sometimes a simple study of the published names of taxa in a particular plant group reveals that a currently used name is invalid according to ICBN rules. For example, it may be discovered that the same species name has been published twice, by different authors who have also identified different holotypes. In this case the current name is considered illegitimate and cannot be used, and the name must be changed to the next oldest validly published name. Alternatively, it may be discovered that a currently used species name is not actually the oldest validly published name, in which case the name must be changed to the older name. Such changes can be controversial, especially when the species is very common and is used by many people who are not plant taxonomists themselves. Nontaxonomists do not often understand the reasons for such changes. A notable example of this problem is for the species *Pseudotsuga menziesii* (Mirb.) Franco. The name *P. douglasii* Carr. was used for many years and led to the use of the common name Douglas fir. This species is extremely important to foresters, and when the name had to be changed, many resisted the name *P. menziesii*. With the change in scientific name, the common name should probably be Menzies fir, but it remains Douglas fir.

**Future of Plant Taxonomy**

Plant taxonomy is a field that has completely embraced modern methods and uses data from molecular genetics, biochemistry, and electron microscopy to gain greater insights into plant evolutionary relationships. The use of computers to perform detailed phylogenetic and cladistic analyses has also revolutionized the field. A greater emphasis on evolutionary relationships and processes has led to a much better understanding of species concepts and relationships but has led others to consider doing away with the species concept as currently used. Continuing studies using modern approaches should lead to ever better classification systems that better reflect the evolutionary history of plants.

**See also:** Angiosperm evolution; Biochemical co-evolution in angiosperms; Cladistics; Coevolution; Competition; Evolution: convergent and divergent; Evolution: gradualism vs. punctuated equilibrium; Evolution of plants; Fossil plants; Molecular systematics; Reproductive isolating mechanisms; Selection; Species and speciation; Systematics: overview.

**Sources for Further Study**


Hoek, C. Van Den, D. G. Mann, and Hans M. Jahns. *Algae: An Introduction to Phycology*. New York: Cambridge University Press, 1996. This is a college textbook and is one of the few sources for basic and detailed information on algal taxonomy. It takes into account many
of the recent re-evaluations of algal systematics based on molecular genetics and electron microscopy.


Woodland, Dennis W. *Contemporary Plant Systematics*. 3d ed. Andrews University Press, 2000. This is a college textbook intended for use in plant systematics or plant taxonomy courses. Covers all aspects of plant systematics with a good treatment of the history of the field. Focuses on higher plants with no mention of algae or fungi.

**SYSTEMATICS: OVERVIEW**

*Categories:* Classification and systematics; disciplines

Systematics is the description and study of the diversity exhibited by living organisms. The goal of systematics is classification, or assigning an organism to a particular category within a logical scheme that accurately reflects underlying patterns of evolutionary relationships. The evolutionary history of an organism—its patterns of ancestry and descent through time, on which systematics and classification are largely based—is the organism’s phylogeny.

In a formal scientific sense, systematics is the study of the diversity exhibited by living organisms and their evolutionary history. It involves the accurate and precise description of organisms and their diagnostic features, the use of a uniform system for assigning names to organisms, and the development of an appropriate classification scheme to reflect the evolutionary relationships among the organisms being considered.

Systematics itself can be subdivided into several phases. The first phase of systematics, identification, involves the determination of whether an unknown plant belongs to a known, previously named group of plants. This is often achieved by examination of a diagnostic manual for plant identification, consultation with reference collections of plants (termed herbaria), and collaboration with an authority who possesses expertise with a particular group. The uniform system for naming organisms is referred to as nomenclature and typically involves using a Latin binomial (a genus name followed by a species name) to designate a particular organism’s species name. The use of a uniform nomenclature is arrived at through consensus and greatly facilitates communication among scientists when discussing organisms.

The final, and perhaps most elusive goal of systematics, classification, entails assigning an organism or group of organisms to a particular category in a logical hierarchical scheme that accurately reflects underlying patterns of natural (that is, evolutionary) relationships. This hierarchical scheme typically consists of large inclusive groupings (such as classes and orders) containing less inclusive, progressively nested groups (such as families, genera, and species). A group of organisms at any hierarchical level can be abstractly referred to as a taxon.

In a strict sense, taxonomy can be defined as the science of assigning names to groups of organisms. The major difference between systematics and taxonomy is evolutionary, in that systematics encompasses all that taxonomy strives for and also attempts to re-create or elucidate the evolutionary history of the organisms under investigation. In essence, the ultimate goal of systematics is the accurate description of the evolutionary history of organisms.

**Homologous Versus Analogous Characters**

Those diagnostic features of an organism that are used in its identification and subsequent classification are termed characters. The different manifestations of the characters are character states. Characters can involve any aspect of morphology, anatomy, biochemistry, and the genetic composition of an or-
ganism. The more reliable characters used for systematics must have a genetic basis; that is, they must be inherited in a predictable and reliable fashion and be subject to a minimal amount of variation by nongenetic factors. Superficial characters, which should be excluded from consideration, are subject to environmental modification or lack a predictable genetic basis. For example, the height of a plant or overall size of leaves typically are not good characters, as a number of environmental factors, such as nutrients, water availability, or soil depth and texture, readily influence these traits.

One difficulty faced by systematists is in determining the true nature of character similarities among different groups of organisms. Homologous characters have a direct evolutionary relationship (that is, a common origin). An example of such characters is the placentation of the ovaries in different taxa of the superorder Caryophyllales. Placentation is the arrangement of the placentas (the structures to which the ovules are attached) in the ovary. All Caryophyllales have free central placentation, basal placentation, or some form in between. It is presumed this kind of placentation arose first in the common ancestor to all members of this superorder.

In contrast, analogous characters have different origins but are similar due to convergent evolution. An example is the presence of the succulent habit (fleshy stems and highly reduced, absent, or modified leaves) in members of two families of different evolutionary origins, the Euphorbiaceae of the Old World and the Cactaceae (cactus family) of the New World. For an evolutionarily sound classification scheme, one needs to emphasize homologous characters and be extremely cautious in using analogous characters.

Evolution and Classification

Some previous classification schemes were highly artificial, in that they did not reflect true evolutionary relationships but rather grouped different organisms together on the basis of superficial similarities. One example of this is the classification of plants based on their growth form, such as grouping all woody plants together, all herbaceous plants in a separate group, and shrubs in yet a third group. The publication of Charles Darwin’s On the Origin of Species by Means of Natural Selection in 1859 prompted systematists to revise their thinking and cast their efforts at classification in an evolutionary context. This has been manifest in the efforts of systematists to elucidate the phylogeny of related groups of organisms.

In its essence, phylogeny refers to the evolutionary history of a group of organisms. This evolutionary history entails an understanding of the genealogy of a group or groups of organisms, their patterns of ancestry and descent through time. This conceptual approach is analogous to reconstructing a person’s family tree or genealogy from often fragmentary and indirect evidence.

Phylogenetic Systematics

Phylogenetic systematics focuses on evolutionary processes and speciation events as core components of classification. The objective is to describe the results of speciation events (the species themselves) and to document the events and processes that have led to the present state of biological diversity. Classification is an attempt to reflect the evolutionary history of the living organisms and their lineages. A group of organisms that resemble one another and have a common evolutionary origin is termed a lineage. This concept often includes the ancestral population that first gave rise to this group of organisms and all individuals, both extant and extinct, that are members of that particular group. To achieve this goal, systematists rely on observable features and traits of the organisms and distinguish between the different means by which these characters might arise in different groups of organisms.

Most systematists use character similarities as a basis for grouping organisms together, but this can cause some difficulty in terms of homologous versus analogous characters. However, not all homologous characters are of an identical nature in terms of origin and persistence through time. This problem of distinguishing the true nature of character similarities has been taken to a higher level by phylogenetic systematists through a methodology termed cladistics. In this framework, the nature of homologous characters is further distinguished. Character states that are present in the evolutionary ancestor or ancestral population of a particular organism or set of organisms are referred to as ancestral. Character states that are absent in the ancestor but present in descendants are referred to as derived. Ancestral states that are shared by both ancestral and descendant, or derived, organisms are termed symplesiomorphic. Derived character states not pres-
ent in the ancestral organisms but shared by two or more lineages are termed *synapomorphic*. A novel character state that is present in only one lineage, and therefore has little use in classification outside that lineage, is termed *autapomorphic*.

A key tenet of phylogenetic systematics is that only *monophyletic* taxa should be formally recognized. A monophyletic group consists of an ancestral taxon and all its descendant taxa. A *polyphyletic* group is composed of two or more ancestral taxa and their descendant taxa and is not an evolutionarily appropriate grouping. Some traditional classifications use polyphyletic groups, and there is much discussion regarding the scientific validity and utility of such schemes.

**Phylogenetic Trees**

A common way of communicating phylogenetic relationships or patterns is through *phylogenetic trees*, which are diagrammatic representations of the genealogy of taxa or patterns of relationships. Typically, a decision is made as to which taxa or character states are of recent origin and which occurred in the past. The origin of the tree is referred to as the *root*, and the character changes across the tree (from ancestral to derived taxa) are given a directionality (ancestral versus derived) that is termed *polarity*. In general, phylogenetic trees are rooted (and therefore the directionality of evolutionary change determined) using a near-relative taxon, termed the *outgroup*, of the group under consideration.

Ideally, all aspects of the phylogenetic tree should be testable, as with any sound scientific hypothesis. Great progress has been made in evaluating the evolutionary relationships of the flowering plants through phylogenetic systematics. Undoubtedly, with the use of new characters and the development of improved methods of data analysis, further progress in this rapidly changing field is certain.

*Pat Calie*

See also: Angiosperm evolution; Biochemical co-evolution in angiosperms; Cladistics; Coevolution; Evolution: convergent and divergent; Evolution: gradualism vs. punctuated equilibrium; Evolution: historical perspective; Evolution of plants; Flower types; Fossil plants; Molecular systematics; Systematics and taxonomy.

**Sources for Further Study**


TAIGA

Categories: Biomes; ecosystems; forests and forestry

“Taiga” derives from a Russian word for the forests of cone-bearing, needle-leaved, generally evergreen trees of northern Eurasia and North America. “Coniferous forest” and “boreal forest” are other names given to this biome. Some botanists include the temperate rain forests along the Pacific Coast of North America and the coniferous forests in the western mountains in the taiga.

While the term “coniferous forest” can be applied to temperate rain forest and coniferous forest biomes in the western mountains, the terms “taiga” and “boreal forest” should be restricted to the northern forests. “Taiga” is also sometimes used in a more restricted way, to mean a subdivision of the boreal forest.

Components
The dominant plants in the taiga are cone-bearing, needle-leaved, evergreen trees, such as pines, spruces, and firs. North American taiga is dominated by two species of spruce: black spruce (Picea mariana) and white spruce (Picea glauca). Jack pine (Pinus banksiana), balsam fir (Abies balsamea), and eastern larch (Larix laricina, a deciduous conifer) are also important in parts of the taiga. A few deciduous flowering trees are also important components. Quaking aspen (Populus tremuloides, the most widespread tree species in North America) and paper birch (Betula papyrifera) are two examples. Eurasian taiga is dominated by related species of spruce and pine and has the same character.

Determinants and Adaptations
Taiga occurs in a broad band across Canada, Alaska, Siberia, and Europe; essentially, this band is interrupted only by oceans. This pattern suggests that climate plays a major role in determining the distribution of the taiga. Average temperatures are cool, and precipitation is intermediate, but evaporation is low because of the cool temperatures. Hence, moisture is generally available to plants during the growing season. The growing season is short, and winters are long. Permafrost is present in the northern part of the taiga, and wetlands are common because drainage is often deficient. These physical conditions are primarily determined by the high latitude at which taiga occurs, but why taiga develops under these conditions is not entirely clear.

The length of the growing season may help explain why the dominant taiga trees are evergreen. Because they retain their leaves through the winter, these trees can carry out some photosynthesis on mild winter days. More important, they avoid the energetic expense of replacing all their leaves at one time. Deciduous trees put tremendous amounts of energy into leaf replacement each spring and must replace those energy stores as well as produce energy for growth during the growing season. Deciduous forests generally occur south of the taiga, where the growing season is longer. However, some deciduous trees are successful in the taiga, so other adaptations must also be important.

Asexual reproduction probably contributes to the success of taiga trees, especially in severe environments. Black and white spruce reproduce by layering, the growth of a new tree from a lower branch which makes contact with the ground. Most deciduous trees of the taiga can sprout from the roots or other underground parts if the aboveground part of the tree is damaged or killed. Both strategies allow new trees to develop using the resources of the parent tree. In contrast, some plants growing from seed do not have sufficient resources to survive.

Fire is an important environmental factor in the taiga. Many of the conifers produce at least some cones which open and release their seeds only after they have been heated intensely, as in a forest fire. Jack pine responds to fire this way, as does black spruce to a lesser extent. Most deciduous trees send up new stems from undamaged underground parts after a taiga fire. White spruce does not employ ei-
ther of these strategies but does have efficient seed dispersal and so can move into a burned area fairly quickly. Similar adaptations make Eurasian taiga species fit for life in northern environments. Apparently, no single suite of adaptations suits a tree species for taiga life; instead various combinations of characteristics are employed by the different species.

Adjacent Zones

The taiga is bordered by tundra to the north, and the meeting place between the two biomes is a broad transition zone often called the “taiga-tundra,” or forest-tundra. This ecotone is composed of a mixture of forest and tundra plants, with trees becoming fewer and smaller from south to north until conditions become so harsh that trees can no longer grow.

The southern boundary of the taiga is often adjacent to deciduous forest, grassland, or parkland. These are also broad, transitional ecotones. In eastern North America, the northern hardwood forest region is such a transition zone and is composed primarily of a mixture of trees from the deciduous forests and the taiga. The aspen parklands in the west are also transitional. Quaking aspen from the taiga and grasses from western grasslands mix in this zone between the taiga and grassland biomes.

Environmental Concerns

Human activities may have less impact on the taiga than on many other biomes, primarily because the taiga occurs in a harsh environment less accessible to humans than many other biomes. Still, there are serious concerns. Acid rain became a problem for the taiga in eastern Canada in the late twentieth century. These forests are northeast of the industrial centers in the United States, and the prevailing southwesterly winds move nitrogen and sulfur oxides into eastern Canada, where they precipitate on plants and soil. Both oxides interact with water to produce acids, thus acidifying the soil and plant leaves. Many ecologists believe that acid precipitation has seriously damaged the taiga of both North America and Eurasia.

Global warming is a second and perhaps more insidious threat to the taiga. The taiga will almost certainly be negatively impacted by changes in temperature, the length of the growing season, fire frequency and intensity, and precipitation patterns. Taiga itself may play a role in carbon storage and mitigation of the greenhouse effect. This possibility, its role as a source of timber, and the inherent value of the biome and its component species make it imperative that the taiga be conserved.

Carl W. Hoagstrom
See also: Acid precipitation; Arctic tundra; Biomes: definitions and determinants; Biomes: types; Community-ecosystem interactions; Conifers; European flora; Forest fires; Forest management; Forests; Greenhouse effect; Gymnosperms; North American flora; Old-growth forests; Sustainable forestry; Timber industry; Tundra and high-altitude biomes.

Sources for Further Study

TEXTILES AND FABRICS

Categories: Agriculture; economic botany and plant uses

Cotton, flax, ramie, hemp, jute, and other cellulosic fiber plants are all sources capable of producing textiles and fabrics that can be used to create knitted, woven, or nonwoven cloth material or fiber and yarn intended for fabric production.

All textiles are made through the use of fibers, thin strands of natural or artificial material. A fiber is a threadlike strand, usually flexible and capable of being spun into yarn. About forty different fibers are of commercial importance. While textiles are primarily made from yarn, they are also made by felting, which is the process of pressing steamed fibers together to make cloth. All knitted and woven textiles are made from yarn, while fibers alone are used to produce nonwoven cloth. The invention of the spinning machines and weaving machines during the Industrial Revolution greatly increased production and boosted the demand for fibers.

The textile industry has created a tremendous diversity of products available for use in clothes, home furnishings, and industrial and special applications. These products are fabricated from natural resources such as animals, plants, and minerals, as well as from synthetic compounds. The major classifications of fibers by source are natural and artificial. Natural fibers are those fibers found in nature such as those from animals and plants.

About 5000 B.C.E., in Egypt’s Nile Valley, the flax plant was grown and processed into a cloth which was used to wrap mummies of Egyptian rulers. By about 3000 B.C.E., people in Switzerland, India, and Peru were using cotton. The trade in textiles as an international commodity began around 1700 B.C.E. as cotton manufacture became more developed in China, Egypt, India, Iraq, and Africa. In more recent history, the Industrial Revolution had a profound effect on the making of textiles, and textile manufacturing was established by the early 1900’s as an industry in many countries of the world.

Plant Fibers
A major plant fiber source is the cellulose from plants. Cellulosic fiber can be found in a plant’s leaves, stems or stalks, seed pods, or fruit, as applicable. Pina, from the pineapple plant, is an example of a leaf fiber. Flax, jute, ramie, and hemp are fibers taken from a plant’s stem or stalk, also known as bast fibers. Cotton and kapok are examples of seed pod and fruit fibers. Azlon fibers are produced from proteins found in soybeans and corn. Cotton and flax are the major plant fibers. One plant source which is not cellulosic is sap from the rubber tree, which can be processed into yarn.

Fiber Makeup
The textile fabric that one can see and touch is composed of many individual fibers. The differ-
ences between fibers is determined by their chemical
composition and individual unique structure.
Molecular combinations of different elements are
called compounds. Any particular (molecular)
compound always contains the same type and
number of elements and their atoms. This gives
each compound unique characteristics that deter-
mine its particular end use as a textile. When many
molecules making up a compound are connected to
one another in a line, they form a linear molecule. If
this linear molecule is very long, it is called a poly-
mer. Animal hair, the living matter of plants, and
some synthetic compounds all contain polymers.
These long-string linear molecular compounds are
the building blocks of fibers, which can then be
made into fabrics. When polymers are formed syn-
thetically, the process is called polymerization.

Only a few elements, in different combinations,
make up all the natural and artificial fibers in tex-
tiles. For example, carbon, hydrogen, and oxygen,
in various combinations, make up all the plant cel-
lulosic fibers. The protein fibers contain nitrogen
as well. Chlorine, fluorine, silicon, and sulfur are
other elements found in some fibers. Artificial fi-
ers may be constructed from natural polymers
that have been reshaped or from synthesized poly-
mers made through chemical processes.

Artificial Fibers from Plant Sources

After their early beginnings in the late 1800’s,
there was wide-ranging development of artificial
fibers in the 1900’s. There are two subgroups of arti-
ficial fibers: reconstituted or altered fibers made
from natural sources, and fibers made from chemi-
cal compounds. Artificial fibers are produced from
compounds having a wide range of chemical com-
position and internal structure. However, this range
of products can be broken down into groups of fibers
that have similar composition and structure. A ge-
neric name is given to each of these groups. For nat-
urally occurring materials there are six generic fam-
ilies: acetate/triacetate, azlon, glass fiber, metallics,
rayon, and rubber. All these fam-
ilies are legally defined and iden-
tified. Manufacturers making any
of these products register a trade-
mark name (or trade name) for
their particular fiber.

Developed as a substitute for
silk, the first artificial fiber was
named rayon around 1925. Wood
pulp is the major cellulose source
of raw material used to produce
rayon fiber. Cotton linters (a by-
product of cotton production) is
another source. These sources are
chemically processed to extract
and purify the cellulose. In re-
generating cellulose into rayon,
the purified cellulose undergoes
several chemical and mechanical
treatments before being forced
through a spinneret machine. Ac-
etate and triacetate are two other
artificial fibers that are based on
cellulose as a raw material.

Cotton, one of the major plant fibers worldwide, is an example of a seed pod fiber.
Yarn
Yarn is generally defined as a continuous strand of fibers spun together as a group which can then be used to make fabrics. In practice, the majority of yarns are made in one of four ways: twisting a number of (short) fibers together, twisting a number of (long) filaments together, laying a number of (long) filaments together without twist, or twisting or not twisting a single (long) filament to produce a mono-filament (thread).

Yarn should be strong, flexible, and elastic so that it can be braided, knotted, interlaced, or looped as it is processed by various methods into a fabric. A system of producing tightly twisted yarns results in worsted yarn that is firmer and smoother than regular yarn. Yarns are often made by blending two or more different fibers to combine the strong points of each. When a manufactured yarn is texturized the long, plain, uniform yarn is changed to exhibit bulk, loft, and three-dimensional appearance. Stretchability may also be included. Yarns are curled, crimped, and twisted when texturized.

Textile Production
The major textile production methods are weaving and knitting. Minor methods produce braids, nets, lace, tufted carpets, and other products. The only fabrics made which do not use yarn are those nonwoven fabrics made directly from fibers before they are processed into yarn. Felt is the traditional nonwoven product. Textiles can be classified by their weave or structure. The value of a textile depends on many factors, primarily the quality of the raw material; the characteristics of the fiber/yarn; smoothness, hardness, and texture; fine, medium, or coarse fibers/yarn; density of yarn twist and density of weave; dyes/colors and pattern; and finishing processes.

A major method for producing fabrics is weaving, in which yarns are interlaced at right angles to each other. This method was used by the ancient Egyptians. Weaving continued to be done by hand as a manual labor task until machines were developed during the Industrial Revolution. The invention of the flying shuttle and the steam-powered loom in the 1700’s were major contributors to automating the weaving process.

Three basic types of weaves are plain, twill, and satin. There can be variations within each of these three weaves. Besides the type of weave and the yarn types used, another variation of the weaving process is how close together the yarns are interlaced.

Knitted fabrics are formed by continuously interlooping one or more yarns. The knitting process may have been used to make fabrics as early as the first century. Knitting remained a hand labor skill until the eighteenth century, when powered knitting machines were developed.

Various knitting processes within the basic weft knit type include plain knit, purl knit, rib knit, and interlock stitch. Weft knits are produced by machine and by hand. For another basic method, the warp knitting process uses a machine in which many parallel yarns are interconnected simultaneously to form loops in the lengthwise direction. Within the basic warp type process, tricot knitting and raschel knitting are two methods used. Special processes that are variations of the two basic methods, sometimes in combination with special yarns, produce double knits, high pile knits, Jacquard knits, full-fashioned knits, textured knits, stretch knits, and bonded knits.

Finishes
Finishes are the treatments given to fibers, yarns, or fabrics to improve their basic characteristics. The three types of finishes employed are mechanical treatments, heat treatments, and chemical treatments. It is common for one or more of these treatments to be applied to practically every fabric produced. They change the appearance of the product, as in its look or feel, or add a functional characteristic such as waterproofing or flameproofing. Brushes, rollers, and hammers may be used in mechanical treatments. Heat-setting of thermoplastic material is a common heat treatment. Chemicals such as acids, bases, bleaches, polymers, and reactive resins are used to chemically change the characteristics of a material.

The aesthetic finishes, by process name, include bleaching, brushing and shearing, calendering, carbonizing, crabbing, decating, fulling, glazing, mercerizing, napping and shearing, scouring, singeing or gassing, sizing, and tentering. The functional type finishes make textiles abrasion-resistant, antibacterial, antisoil and antistain, antistatic, durable press (permanent press), flame/fire retardant/resistant, moth repellent, permanently crisp, shrink resistant, waterproof, water repellent, or wrinkle resistant.
Fabric Design

The major elements of fabric design are the visual (how it looks) and the tactile (how it feels). Solid colors or shades of black, white, and all colors can be applied in an unending combination of patterns and designs. The feel of the fabric can be varied by the types of yarn used, the fabrication method, how the color pattern is applied, and the types of finishes used. Dyeing and printing are two major methods of applying a pattern, color, or both, to a fabric. Dyes can be applied to fiber, yarn, or fabric. Color can be applied by at least three methods: directly, the discharge method, and the resist or reserve method. Printing is typically done by methods such as roller printing, block printing, toiles de Jouy, stencil, screen printing, spray printing, electroplating, and by hand.

The Textile Industry

The textile industry is dynamic, with new processes, techniques, and methods constantly being developed. Sometimes they add to, and sometimes they replace, previous ways of operating. The idea of evolution and change can be applied to all parts of the industry, such as raw material and fiber development, yarn production technique, fabrication method, finishing technology, and the printing, dyeing, and design processes. The primary goal of all research and development is to sell a product attractive to consumers. Consumer research is an important factor in determining what the public wants, thereby helping to drive and focus the technology in particular directions. Federal laws govern textile labeling and product advertising, and the industry has developed voluntary self-regulating product quality and testing standards.

Robert J. Wells

See also: Agriculture: history and overview; Australian agriculture; Biopesticides; Bromeliaceae; Cacti and succulents; Cycads and palms; Farmland; Fertilizers; High-yield crops; North American agriculture; Plant domestication and breeding; Plants with potential; Soil degradation; Timber industry.

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THIGMOMORPHOGENESIS

Categories: Movement; physiology

Thigmomorphogenesis refers to the influence of mechanical stimuli on plant growth and development. Many plants respond to stimuli such as wind or touch, intentionally by human beings or unintentionally by farm machineries and animals.

Plants subjected to thigmomorphogenesis, or physical disturbances such as wind and touch, generally respond through reduction in the rate of stem elongation and shoot height, and they increase in stem diameter. All of these features result in the formation of short, stocky plants. This response is purely adaptive and allows individual plants to compensate for the different levels of stress that occur in their natural environment. The advantage of this is that shorter and stronger plants are less easily damaged by natural mechanical stresses (especially wind) than their taller, more slender counterparts. Inhibitory effects of mechanical stress on flowering of a few species have also been observed. Thigmomorphogenesis is common and may be as important to plants as their responses to light, temperature, water, and gravity.

Response Indoors

The indoor plant environment (greenhouses, sheds, and homes) influences the plants' hardiness with regard to mechanical stimuli. Unless deliberately altered, the indoor space is typically a calm, windless environment. Moving air causes a plant to lose moisture faster; in contrast, a windless environment encourages the development of a thin cuticle (waxy layer on outer epidermal walls, such as leaf surfaces). The absence of physical disturbance also promotes formation of long cells with thin cell walls. These modifications result in the development of slender stems, which are not adapted to the buffeting provided by the wind outside.

Tall plants usually occur under indoor conditions where there is a relatively low light level and few physical disturbances. These morphologies are simply a response to the environment in which the plants are grown and, unless conditions change, these plants are well adapted to such an environment. Problems occur once the plants are transplanted outside because of the dramatic change in environment. On the other hand, plants in the wild are hardened by the wind, bright sunlight, lack of nutrients, and fluctuations in soil moisture and therefore show little further response to mechanical stress.

Response in Nature

Wind-tolerant and wind-intolerant genotypes exist within any population of plants. The plants that are capable of withstanding high levels of physical disturbances will respond by modifying their structures. They respond by growing more slowly and changing the way they build their cells. The cells that are produced are short and thick-walled, thereby making for short, sturdy plants. The decrease in elasticity also provides plants with a means of absorbing the strain within their structures. In trees, the response is usually increased taper, which is the result of a reduction in height or increase in radial growth. Increased radial growth confers bending stiffness and maintains a tree's vertical orientation in windy environments.

Location of Response

It has been shown that plants’ response to mechanical stimuli is localized and not whole-plant-based, as was previously thought. The more highly stressed areas of the plants, such as the base of the stem, are the areas that exhibit the greatest response. Most information available deals with the effects on aerial components of plants. Knowledge of the effects on roots is quite limited. To examine this, researchers have compared corn and sunflower plants that have been flexed with still ones. It was found that both species were able to change the morphologies and mechanical properties of their
roots in response to wind. Furthermore, mechanically stimulated plants were found to have more numerous, thicker, and stiffer roots than still plants.

**Perception of Stimuli**
How do plants perceive mechanical stimuli? Calcium ions have been implicated in mediating various growth responses including thigmotropism and thigmonasty (discussed below). Calcium may also be involved in thigmomorphogenesis. Differentially expressed genes have been isolated and are being identified to increase knowledge of the molecular and physiological responses of plants to increased mechanical stimuli. In *Arabidopsis*, mechanical stimuli appear to induce the expression of certain genes that encode proteins related to calmodulin, a calcium-binding protein. Calcium levels have also been reported to increase in stressed cells. Deformation of stressed cells may result in the opening of calcium channels in the cell membrane. Ethylene, a gaseous plant growth regulator, has also been implicated because mechanical stimulation results in increased ethylene production.

**Commercial Application**
Thigmomorphogenesis is especially important for vegetable producers who use automated crop transplanters in the field and where robustness of the seedlings is important. Scientists are aware that plants grown in greenhouses tend to be thin and limp as a result of high temperatures, low light levels, abundance of nutrients, and low wind speeds. Automated machinery easily damages these kinds of plants. To counter this problem, commercial agriculturists often resort to the use of chemical growth regulators, high concentrations of fertilizers, salts, and water-absorbent gels. They also reduce the amounts of nitrogen and phosphorus available to the seedlings.

By a simple technique of brushing or stroking plants several times a day, these problems may not only be overcome, but crop quality may also be significantly improved. Several kinds of plants have been shown to respond very well to mechanical stimulation. The technique of brushing or stroking seedlings has been shown to work on a variety of vegetable plants, such as cabbage, lettuce, tomatoes, cucumbers, and bedding plants including petunias, fuchsias, marigolds, and salvia. The effect of thigmomorphogenesis can also be used when planting trees. When short stakes are used instead of a long ones, the unsupported part of the stem can flex, making it stronger and tougher.

**Other Plant Responses**
Thigmomorphogenesis may be confused with thigmotropism and thigmonasty. In thigmotropism, the plant responds directly to the direction of the source of the stimulus. For example, contact of tendrils stimulates the coiling response caused by differential growth of cells on opposite sides of the tendril. In thigmonasty, the response is unrelated to the direction of the source of stimulus. An example of thigmonasty is the movement of the leaves of sensitive plants due to the rapid change in turgor pressure in specific cells at the base of leaflets. Thigmomorphogenesis is related to thigmonasty because the response is also not in the direction of the stimulus. However, thigmomorphogenesis involves alteration of growth pattern and is irreversible.

*Danilo D. Fernando*

**See also:** Heliotropism; Nastic movements; Tropisms.

**Sources for Further Study**


Timber Industry

Categories: Economic botany and plant uses; environmental issues; forests and forestry

The timber industry comprises a diverse group of companies and organizations using wood and fiber harvested from forests in the production of solid wood products (such as furniture and lumber), reconstituted wood products (such as particle board), pulp and paper, and chemicals.

Globally, about 3.8 billion cubic meters of wood were used for human consumption in 1995. The rate was increasing by 2.3 percent per year, faster than the rate of population growth. More than fifty thousand establishments in the United States are involved in the manufacture of forest products, and this industry contributed approximately 8 percent of the United States’ gross national product in 1980. In addition, many other commercial products are derived from forest resources, including types of fuel, medicine, and food, and specialty items such as Christmas trees. Globally, the Food and Agriculture Organization of the United Nations (FAO) estimated in 1992 that more than one-half of all harvested wood is used for fuel and that the majority of energy needs in many developing countries is met by fuel wood. The FAO found in 1995 that the global demand for wood was about 3.8 billion cubic meters per year and that this demand was increasing by about 86 million cubic meters per year.

Historical Significance

The development of the forest products industry parallels the development of Western civilization. From Robin Hood to Paul Bunyan, the utilization of forest products is ingrained in Western mythology and culture. Development of the first forest management techniques in the Middle Ages was motivated by security interests related to the continued availability of wood for shipbuilding. In North America, the westward movement of European culture was accompanied by, and in some cases motivated by, the development of the forest products industry. Eventually, first in Europe and then in North America, it was realized that natural forests could indeed be depleted and that it was necessary to develop techniques for regenerating and managing forest ecosystems to ensure a continued supply of wood products to meet human needs. This process is still occurring in many developing countries.

Old-Growth Forests

All ecosystems develop within the context of natural disturbance cycles. Whether the natural agent is fire, flooding, or windstorms, every hectare on the earth is subject to periodic disturbance even without the influence of human activity. The disturbance intervals may be very long in some systems; forests consisting of late-successional species that have not been disturbed in an extended interval are commonly referred to as old-growth forests.

The forest products industry developed through the utilization of these natural forests. As they became scarcer, forest management techniques were developed to ensure the restoration of forests following utilization. As old-growth forests containing large trees were depleted, manufacturing technology had to change to use smaller-sized material that could be harvested from second-growth forests. This led to the development of composite wood products such as oriented strand board, particle board, and laminated beams.

Sustained Yield

Humans obtained goods and services from natural forests for millennia before increasing population, the development of agriculture, and utilization technology begin to lead to the depletion of natural forests. Fear of the depletion of natural forests and an impending timber famine led to development of the sustained yield concept, which holds that forests should be managed to produce wood products at a rate approximately equal to the natural rate of biological growth. The development of the sustained yield concept was associated with the
belief that properly managed forests could produce a continuous, never-ending flow of wood and fiber. This concept is still evolving to include recognition that the continued survival of all species and the maintenance of ecosystem structure and function, as well as the production of goods and services, are of vital interest to human society.

Effects of Timber Harvesting

It is possible to harvest forest products in such a way as to mimic natural disturbance and to ensure the continued functioning and survival of all ecosystem components. Unfortunately, there are many examples of harvesting that have led to long-term disruption and alteration of ecological processes. Nutrient loss, erosion, and species loss following poorly designed or implemented harvesting operations can result in the loss of biodiversity and a reduction in long-term productive capacity.

The removal of forest canopy trees, whether through harvesting or natural disturbance, leads to increased soil temperature, increased decomposition, increased leaching of nutrients and soil carbon, and, if extreme, a reversion to an early-successional plant community. Removal of the canopy trees will usually lead to increased erosion, which, if harvesting is not properly implemented, can be severe and result in degradation of water quality and aquatic habitat. Programs promoting fire protection in the twentieth century resulted in the interruption of natural disturbance cycles in many ecosystems. In these cases, artificial disturbance through harvesting may be the only way to ensure the continued presence of early-successional species in the landscape. In many cases, these early-successional tree species are fast growing, straight, and relatively easy to artificially plant and regenerate. These early-successional forests are ideally suited for the production of pulp and paper, fuel wood, and such products as posts and poles. The challenge to industrial and public land managers is to develop the appropriate mix of all successional stages in the

In North America, the westward movement of European culture was accompanied by, and in some cases motivated by, the development of forest products and timber industries.
landscape in order to ensure the continued survival of all species and the maintenance of ecosystem structure and function, while allowing for utilization to meet the needs of the globally expanding human population.

David D. Reed

See also: Coal; Erosion and erosion control; Forest fires; Forest management; Forests; Logging and clear-cutting; Old-growth forests; Rain-forest biomes; Succession; Sustainable forests; Taiga; Wood and charcoal as fuel resources.

Sources for Further Study


**TRACHEOBIONTA**

Categories: Plantae; seedless vascular plants; taxonomic groups

Tracheobionta is the subkingdom of plants that contain vascular tissues, xylem and phloem. They are commonly known as the vascular plants.

Vascular plants are plants that have tissues called xylem and phloem as conducting tissues. *Xylem* is tissue composed of vessels, fibers, and tracheids responsible for upward conduction of water and dissolved minerals; it also functions as the supporting tissue of stems. *Phloem* is conducting tissue that is responsible for moving food manufactured in the leaves to other parts of the plant, including the roots. The botanical name for the vascular plants is *Tracheobionta*. This group of plants includes both seedless and seed plants, including the flowering plants (angiosperms).

Fossil forms of *Tracheobionta* are well represented, because the tough, lignified cell walls of xylem preserve well. Most vascular plants produce seeds and are classified as *Spermatophyta*, but the ferns and related groups are seedless. Tracheobionts are primarily terrestrial, although some are epiphytic or aquatic.

Life Cycle

The life cycle of vascular plants is characterized by alternation of a conspicuous diploid sporophyte generation with a reduced haploid gametophyte generation, termed alternation of generations. The sporophyte exists independently of the gametophyte and typically exhibits indeterminate growth. That is, a single sporophyte plant can live and continue to grow for many years due to the activity of its apical and lateral meristems. The gametophyte, although free-living and independent in the more primitive vascular plants, is dependent on the sporophyte in seed plants.

The spores produced by the sporophyte fre-
quently have a tough, well-defined wall hardened by the wall material sporopollenin. Some seedless vascular plants, including most ferns, are homosporous; they produce a single type of spore. The spore germinates and grows out of the spore wall to form an exosporic gametophyte. This free-living haploid plant produces both antheridia and archegonia. Antheridia are saclike sex organs with a thin jacket layer of cells surrounding a mass of sperm cells. In seedless plants, and even in some of the seed plants, the sperm are flagellated and motile. Archegonia are typically flask-shaped sex organs with a thin jacket layer of cells surrounding a large egg cell. Part of the jacket is an elongate neck that provides a passage through which the sperm can swim to fertilize the egg.

All of the seed plants, and some ferns and fern allies, are heterosporous; that is, they produce both small microspores and large megaspores. Microspores form male gametophytes that produce sperm, whereas megaspores form female gametophytes that produce eggs. In seedless plants, the microgametophytes produce typical antheridia; in seed plants, the microgametophytes are pollen grains. In all but flowering plants, the megagametophyte produces archegonia. In flowering plants, the megagametophyte is an embryo sac. Both the megasporangia and microgametophytes are endosporic; that is, they develop within the original spore wall.

Vegetative Structure

The sporophyte of vascular plants typically has three distinctive vegetative organs: roots, stems, and leaves. Each contains xylem and phloem in a specific, predictable pattern characteristic of the division. The vascular tissues of stems and roots are called a stele. All roots have
a simple stele with xylem forming a core in the center of the root, surrounded by phloem, either in a single sheath or in separate strands. In woody plants, multiple layers of xylem form in succession, pushing phloem and any external tissues outward. These layers of xylem are wood. Members of all divisions of vascular plants except psilotophytes form roots.

The stems of the simplest vascular plants have a stele similar to that of roots with a solid core of xylem in the center surrounded by phloem. In more specialized seedless plants, the pattern of xylem may be divided into separate bands surrounded by phloem. In stems of the most complex seedless plants, the pattern of xylem may be divided into separate bands surrounded by phloem. In stems of the most complex seedless plants, discrete vascular bundles form a ring around a core of parenchyma, the pith. In each bundle a core of xylem is surrounded by phloem; such stems are termed amphiphloic. Seed plants and horsetails have a similar arrangement, except that phloem is found only to the outside of xylem in each bundle; the stems are ectophloic. In woody plants, the ring of vascular bundles become connected by a vascular cambium that produces a succession of layers of new xylem, the wood. In monocot stems, the vascular bundles are distributed throughout the stem, rather than in a single ring surrounding a pith.

Leaves are characteristic of all divisions of vascular plants except some psilotophytes. The simplest leaves are small and scale-like and have a single vascular bundle forming a midrib. The vascular bundle in the leaf is a direct offshoot of the single vascular bundle in the stem. Such leaves are called microphylls. In plants with stems containing a pith, the leaves are supplied by one or more vascular bundles, which branch within the broadened blade of the leaf to form many veins. A gap is left in the stele where a leaf trace exits to supply the leaf. With a more extensive network of vascular tissue, these leaves are typically large and are termed megaphylls.

Sporangia

Sporangia are specific regions of the sporophyte body where meiosis occurs to produce spores. A single sporophyte can produce tens of millions of spores per year. The position, structure, and development of sporangia provide useful criteria for distinguishing the major groups of vascular plants.

In psilotophytes, two or three fused sporangia are located in the axils of leaves or leaflike appendages. In horsetails (Sphenophyta), sporangia terminate the main stem axis, forming a cone or strobilus. Lycophytes typically produce sporangia on the upper surface of leaves near their attachment to the stem. Depending on the group, these sporophylls may resemble vegetative leaves or may be concentrated into terminal cones. In ferns, sporangia also are typically localized on sporophylls. Frequently these sporangia are clustered in groups, called sori (singular “sorus”), on the edge or underside of the leaf. In gymnosperms, sporangia are concentrated in strobili, which can be quite large. Both the megasporangiate and microsporangiate cones of some cycads may approach a meter in length. In flowering plants, sporangia are localized in the flowers.

Among seedless vascular plants, two distinct sporangium types can be recognized based on structure and development. In the more primitive groups, a superficial layer of cells divides to form two layers. The outer layer forms the sporangium wall or jacket, while the inner layer becomes sporogenous tissue that undergoes meiosis to form spores. Eusporangia formed in this way have multiple-layered walls and frequently are at least partially embedded in vegetative tissue. In contrast, leptosporangia begin development from a single superficial cell. Following cell division, the inner of the two daughter cells forms a stalk that raises the sporangium above the vegetative tissue. The outer daughter cell eventually forms a single-layered jacket or capsule around a mass of sporogenous cells. Certain cells of the jacket layer differentiate to form an annulus, a specialized structure to open the sporangium and aid in spore dispersal.

Gametangia

Antheridia and archegonia are gametangia produced by the gametophyte. In vascular plants they are complex structures consisting of a sterile jacket layer of cells surrounding and protecting the gametes. Antheridia produce as few as four sperm (in Isoetes) to several thousand sperm in some eusporangiate ferns. All archegonia produce a single egg within a venter, the swollen base of the organ, which is usually embedded in gametophyte tissue. Extending out from the venter is an elongate neck, which becomes tubular when the neck canal cells degenerate to form an opening through which sperm can swim. At the base of the neck canal, adjacent to the egg, is a ventral canal cell.
The gametangia of seed plants are much reduced. The microgametophyte is a pollen grain, consisting of only two to four cells when it is released from the microsporangium. Depending on the group, zero, one, or two prothallial cells form, which represent the vegetative male gametophyte. The tube cell and generative cell may be interpreted as an antheridium. The generative cell divides to form two sperm. The megagametophyte of gymnosperms consists of a few thousand cells that typically form several archegonia, each consisting of four neck cells, a ventral canal cell, and a large egg. In flowering plants the entire megagametophyte, the embryo sac, typically contains only seven cells, one of which is the egg.

**Embryogeny**

In all plants with an archegonium, fertilization and the early stages of embryo development occur within the venter. This helps to establish a polarity with the first cell division. In all but the leptosporangiate ferns, the first cell division forms a new cell wall parallel to the surface of the gametophyte; one daughter cell faces inward, while the second faces out through the neck canal. In the horsetails and a few ferns, the apical cell, which will form the new sporophyte body, faces outward, a condition known as exoscopic. However, in most plants the apical cell faces inward (is endoscopic), and initially the embryo grows into the gametophyte tissue. As the embryo continues to grow, a shoot apex with leaf primordia forms at the apical end, and a root apex forms at the opposite pole.

**Phylogenetic Trends**

Some general evolutionary trends within the Tracheobionta are a reduction in the size and independence of the gametophyte generation and increasing dominance of the sporophyte. In the ferns and fern allies, the gametophyte may be photosynthetic and free-living, often resembling a very small liverwort in size and general shape. These are inconspicuous, however, compared to the large, leafy sporophytes. In seed plants, the larger megagametophyte is reduced to a countable number of cells, from a few thousand in gymnosperms to as few as seven in flowering plants. This gametophyte is retained within the sporangium and derives water and nutrients from the supporting sporophyte. This reduction is most dramatic in the microgametophyte, where the pollen grain consists of fewer than a handful of cells. Although the pollen of a few seed plants produces swimming sperm, in most cases a pollen tube grows to deliver sperm to the egg and free water is no longer required for fertilization.

In contrast to the reduction of the gametophyte, the sporophyte becomes increasingly larger and complex with development of the vascular tissues. Specialized organs, roots, stems, and leaves evolved for absorption of water and nutrients, to provide aerial support, and to increase photosynthetic surface area in a terrestrial environment. Development of vascular tissue provided the physical and physiological support required for the evolution of these structures.

Marshall D. Sundberg

**See also:** Angiosperms; Conifers; Cycads and palms; Evolution of plants; Ferns; Ginkgos; Gnetophytes; Gymnosperms; Horsetails; Lycophytes; Psilotophytes; Reproduction in plants; Seedless vascular plants; Spermatophyta.

**Sources for Further Study**

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As first proposed by Harlan Banks in 1968, the trimerophytes evolved from the rhyniophytes and then gave rise, either directly or indirectly, to all other groups of vascular land plants except the zosterophyllophytes and lycopods.

The trimerophytes appeared and diversified between 406 million and 401 million years ago, during the Devonian period. They evolved from the rhyniophytes (Rhyniophyta), and they share a number of characteristics with that group. Both groups branched by having an axis fork into two branches of equal size. Viewed from the side, the point of branching would appear like a capital Y. Both groups also bore elongate sporangia at the ends of some of these branches.

The chief feature that distinguished the two groups was size. The rhyniophytes were small plants, approximately 25 centimeters (10 inches) or less in height. The trimerophytes could reach heights in excess of 1 meter (1 yard). Because the trimerophytes were larger than the rhyniophytes, some species had a single main axis from which the lateral branches arose. Establishing a taxonomic group just because some of its members were bigger than other contemporary plants is unusual. Some researchers believe that the group is too broadly defined to be taxonomically useful. The two best-known genera, Psilophyton and Pertica, are more similar to early ferns and gymnosperms than they are to each other, supporting the belief that the trimerophytes are not a valid taxonomic group.

The smaller, herbaceous trimerophytes, such as Psilophyton, branched by forking into two branches of equal or unequal size and bore sporangia at the ends of some of these branches. Other trimerophytes, such as Pertica, were robust plants that probably reached the size of small shrubs. They had a large, central axis that gave rise to smaller lateral branches. In Pertica quadrifaria and P. dalhousii, the lateral branches forked synchronously from four to six times before ending in either sterile tips or elongate sporangia. The sporangia opened (dehisced) along one side by means of a longitudinal slit. Where known, the vascular tissue of the trimerophytes consisted entirely of primary phloem and xylem and seemed insufficient to support a plant more than a meter tall. The plants grew in dense clonal stands (a growth pattern called turfing), where the aerial axes could provide mutual support for each other.

At any site, about half of the trimerophytes present were fertile. The high proportion of fertile axes suggests plants that grew rapidly and reached reproductive maturity quickly. Since the sporangia all appear to be at the same stage of development, the aerial stems of the trimerophytes probably terminated their lives with a burst of reproduction. New growth would then arise from the perennial rhizomes or root systems when favorable conditions returned. The trimerophytes preferred to live near fresh water in habitats that were susceptible to flooding. At this time in earth history, size was more important for spore dispersal than for light interception to power photosynthesis.

Trimerophyton robustius

The trimerophytes are named for Trimerophyton robustius, a Canadian plant originally described as Psilophyton robustius by J. W. Dawson. The genus is based on a single specimen about 12 centimeters (5 inches) long. Trimerophyton’s central axis gave rise to spirally arranged lateral branches. Initially, the lateral branches were believed to fork twice to produce a total of nine axes. The first forking produced three new axes. The second forking of each new axis produced three more axes for a total of nine. When viewed from the side, the point of branching appeared similar to a tripod. Each of these nine branches forked into two branches from two to three more times. The ends of the branches were terminated by elongate sporangia that were all at the same stage of development. Reinterpretation of Dawson’s specimen indicates that the first divi-
sions in the lateral branches resulted in two rather than three new axes. If this interpretation is correct, 
*Trimerophyton* no longer possesses the diagnostic trait that names and identifies the trimerophytes. The stem of *Trimerophyton* was naked (lacked leaves or enations). Enations resemble leaves, but they lack vascular tissue and, therefore, have no veins. Both roots and rhizomes are unknown for *Trimerophyton*.

**Psilophyton**

At least nine species of *Psilophyton* are known. They range in size from small plants (*P. dapsile*) that lacked a central main axis to larger plants that had prominent central axes. The stems could be naked (*P. dapsile*, *P. dawsonii*, and *P. forbesii*) or variously cloaked with spiny or peglike enations (*P. crenulatum*, *P. princeps*, and *P. charientes*). The short species and the lateral branch systems of the larger species branched by forking to produce two new axes. The sterile branches end in blunt tips and the fertile ones in paired sporangia. The sporangia occur in dense clusters of thirty-two or more.

*Psilophyton princeps* was the first valid species described. Dawson named his Canadian fossils in 1859 but did not publish a reconstruction of the plant until 1870. As reconstructed by Dawson, the naked aerial stems arose from a rhizome (a stem that runs horizontally along the ground) and branched by forking. Sporangia were borne at the ends of the branches and hung down toward the ground (that is, the sporangia were pendant). Dawson also figured a spiny axis that he named *P. princeps* var. *ornatum*. This variety was subsequently found to have lateral sporangia and was redescribed as *Sawdonia ornata*. *Sawdonia* is classified as a zosterophyllophyte.

None of the parts (aerial stem, sporangia, or rhizome) of Dawson’s original *Psilophyton princeps* were found attached to each other. They were ultimately found to represent parts of three distinct plants. *Psilophyton princeps* itself was covered with short, peglike enations and bore clusters of terminal sporangia at the ends of some of its lateral branches. The naked axis bearing the pendant sporangia was named *Dawsonites arcuatus*. *Dawsonites* has remained in the *Trimerophytophyta* for convenience because scientists are not sure of its exact affinities. The rhizome was renamed *Taeniocrada dubia* and may belong in the *Rhyiophyta* (possibly in the genus *Stockmansella*). *Taeniocrada* is simply a long, naked axis that lacks any unique structural features.

**Pertica**

Plants of this genus (*P. quadri folia*, *P. dalhousii*, and *P. varia*) are the largest trimerophytes, reaching heights of a meter or more. The stem appears naked but is actually covered with small (0.4-millimeter) bumps call papillae. The strongly developed main axis gave rise to short lateral branches in groups of four. The lateral branches could fork into two or three new axes of equal size. These axes could be either sterile or fertile. The fertile branches were mixed in with the sterile branches. The fertile branches end in dense, spherical clusters of round to elongate sporangia, which opened by a slit down the side. If Dawson’s specimen of *Trimerophyton* did produce some lateral branches by forking into three axes, the specimen may actually represent a short segment of *P. varia* that branched in this fashion.

**Progeny**

The great majority of both fossil and living plants can trace their lineages back to the trimerophytes, specifically to the *Psilophyton-Pertica* complex. Derived groups include the ferns, horsetails, gymnosperms, and angiosperms. The trimerophytes are very similar to the early ferns and gymnosperms, most notably to the extinct progymnosperm *Tetraxylopteris*. The resemblance is so great that some researchers feel that the *Trimerophytophyta* is not a valid group. The trimerophytes are very different in appearance from the ferns, gymnosperms, and angiosperms that are alive today.

The groups that evolved from the trimerophytes had far greater impact on the global environment than their predecessors, the rhyiophytes, zosterophyllophytes, and trimerophytes, did together. These latter groups had a very narrow habitat range, had shallow rooting systems or rhizomes, and were not seed producers. Their successors had well-developed root systems, as seen in the increased thickness and horizontal zoning of fossil soils (paleosols). The development of seeds allowed the gymnosperms and angiosperms to escape from a dependence on moist, lowland habitats to ensure reproductive success and to colonize drier, upland habitats. The development of seeds allowed the spread of forests from 377 million to 362 million years ago. The spread of forests was followed by a worldwide increase in the deposition of black shale and the formation of coal. The organic material represented by these deposits re-
flected a significant loss of carbon dioxide from the atmosphere. The decrease in atmospheric carbon dioxide brought on a period of continental glaciation and caused a mass extinction of tropical marine invertebrates due to decreased water temperature. The tropical sea’s surface temperate cooled from 40 degrees Celsius (104 degrees Fahrenheit) about 345 million years ago to between 24 and 26 degrees Celsius (77 degrees Fahrenheit) about 280 million years ago.

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**TROPHIC LEVELS AND ECOLOGICAL NICHEs**

*Categories:* Classification and systematics; ecology; ecosystems

To be meaningful, classification of organisms based on divisions within the food pyramid, called trophic levels, often must be considered alongside the particular space, or place niche, occupied by an organism and its functional role in the community, the totality of the organism’s interactions and relationships with other organisms and the environment, or ecological niche.

For many years, ecologists referred to niche in terms of an organism’s place in the food pyramid. The food pyramid is a simplified scheme showing organisms’ interactions with one another while obtaining nourishment. The food pyramid is represented visually as a triangle, often with four horizontal divisions, each division being a different trophic level.

The base of the food pyramid is the first trophic level and contains the primary producers, photosynthetic plants. At the second trophic level are the primary consumers; these are the herbivores, such as deer and rabbits, which feed directly on the primary producers. At the third trophic level are the secondary consumers are the omnivores, which eat both plants and animals. The fourth trophic level contains the tertiary consumers, animals that eat only meat—carnivores such as the mountain lion. The members of the uppermost trophic level are the scavengers, such as hyenas and buzzards, and the decomposers, including fungi and bacteria. The organisms in this trophic level break down all the nutrients in the bodies of plants and animals and return them to the soil to be absorbed and used by plants.

All living things are dependent on the first trophic level, because plants alone have the capability to convert solar energy to energy found in, for example, glucose and starch. The food pyramid takes the geometric form of a triangle to show the flow of energy through a system. Because organisms lose a percentage of the energy they absorb
from the sun or consume by eating, less energy is found at each higher level of the pyramid. Because of this reduced energy, fewer organisms can be supported by each higher trophic level. Consequently, the sections of the pyramid get smaller at each higher trophic level.

Through the years, two concepts of niche have evolved in ecology. The first is the place niche, the physical space in which an organism lives. The second is the ecological niche, which encompasses the particular location occupied by an organism and its functional role in the community. The functional role of a species is not limited to its position within a food pyramid; it also includes its interactions with other organisms while obtaining food. Specific methods of tolerating climate, water or nutrient conditions, soil conditions, parasites, and other factors of the environment are part of its functional role. In other words, the ecological niche of an organism is its natural history: all the interactions and interrelationships of the species with other organisms and the environment.

**Niche Overlap**

The study of relationships among organisms has been the focus of ecological science since the 1960’s. Before that time, researchers had focused on the food pyramid and the effects of population changes of a single species upon predator-prey relationships. The goal of understanding how species interact with one another can be better accomplished by defining the degree of niche overlap, the sharing of resources among species. When two species use one or more of the same elements of an ecological niche, they exhibit interspecific competition. It was once believed that interspecific competition would always lead to survival of only the better competitor of the two species—that no two species can utilize the same ecological niche. It was conjectured that the weaker competitor would migrate, begin using another resource not used by the stronger competitor, or become extinct. It is now believed that the end result of two species sharing elements of ecological niches is not always exclusion.

Ecologists theorize that similar species do, in
fact, coexist, despite the sharing of elements of their ecological niches. Character displacement leads to a decrease in niche overlap and involves a change in the morphological, behavioral, or physiological state of a species without geographical isolation. The more specialized a species, the more rigid it will be in terms of its ecological niche. A species that is general in terms of its ecological niche needs will be better able to find and use an alternative for the common element of the niche. Because a highly specialized species cannot substitute whatever is being used, it cannot compete as well as the other species. Therefore, a specialized species is more likely to become extinct.

For example, some species of tropical orchids are so specialized that they rely on a single species of bee for pollination. The flowers so closely resemble female bees that male bees attempt to copulate with them, and in the process transfer pollen from flower to flower. If one of these species of bees were to become extinct, the associated orchid species, unable to reproduce, would soon follow. On the other hand, many species of daisies are freely pollinated by bees, flies, beetles, and a number of other insects. Even if a few of these pollinator species were to become extinct, daisies would be able to continue to reproduce using the remaining pollinator species.

Hence, species with specialized ecological niche demands (specialists) are more in danger of extinction than those with generalized needs (generalists). Although this fundamental difference in survival can be seen between specialists and generalists, it must be noted again that exclusion is not an inevitable result of competition. There are many cases of ecologically similar species that coexist.

When individuals of the same species compete for the same elements of the ecological niche, it is referred to as intraspecific competition. Intraspecific competition results in niche generalization, the opposite result from that of interspecific competition. In increasing populations, the first inhabitants will have access to optimal resources. The opportunity for optimal resources decreases as the population grows; hence, intraspecific competition increases. Deviant individuals may begin using marginal resources that are in less demand; those individuals will slowly come to use fewer optimal resources. That can lead to an increase in the diversity of ecological niches used by the species as a whole. In other words, the species may become more generalized and exploit wider varieties of niche elements.

**Why Study Niches?**

The shift in meaning and study from mere space and trophic level placement in the food pyramid to ecological niche has been beneficial for the field of ecology and for human activities. This focus on community ecology is much more productive for the goal of ecology, the understanding of how living organisms interact with one another and with the nonliving elements in the environment.

Perhaps more important is the attempt to describe niches in terms of community ecology, which can be essential for some of humankind’s confrontations with nature. One relevant function of community-oriented studies of ecological niches involves endangered species. In addition to having aesthetic and potential medicinal values, an endangered organism may be a keystone species, a species on which the entire community depends. A keystone species is so integral to keeping a community healthy and functioning that if it is obliterated the community no longer operates properly and is not productive.

Habitat destruction has become the most common cause of drastic population declines of species. To enhance the habitat of the endangered species, it is undeniably beneficial to know what conditions cause a species to favor its particular preferred habitat. This knowledge involves details of many of the dimensions of an ecological niche integral to specific population distribution. Danger to the survival of a species also occurs when an introduced organism competes for the same resources and displaces the native species. Solving such competition between native and introduced species would first involve determining niche overlap.

Researching and understanding all the dimensions of ecological niches can prevent environmental manipulations by humankind that might lead to species extinction. Many science authorities have agreed that future research in ecology and related fields should focus on solving three main problems: species endangerment, soil erosion, and solid waste management.

This focus on research in ecology often means that studies of pristine, undisturbed communities is the most helpful for future restoration projects. Although quantitative and qualitative descriptions of pristine areas seem to be unscientific at the time they are made, because there is no control or experimental group, they are often the most helpful for later investigations. For example, after a species has
shown a drastic decline in its population, the information from the observations of the once-pristine area may help to uncover what niche dimension was altered, causing the significant population decrease.

Jessica O. Ellison

See also: Animal-plant interactions; Competition; Community-ecosystem interactions; Ecology: concept; Ecosystems: overview; Ecosystems: studies; Endangered species; Food chain; Species and speciation; Succession.

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**TROPISMS**

**Categories:** Movement; physiology

*Tropisms are the means by which plants grow toward or away from environmental stimuli such as light, gravity, objects to climb, moisture in soil, or the position of the sun.*

Although plants appear not to move, they have evolved adaptations to allow movement in response to various environmental stimuli; such mechanisms are called tropisms. There are several kinds of tropism, each of which is named for the stimulus that causes the response. For example, gravitropism is a growth response to gravity, and phototropism is a growth response to unidirectional light. Tropisms are caused by *differential growth*, meaning that one side of the responding organ grows faster than the other side of the organ. This differential growth curves the organ toward or away from the stimulus. Growth of an organ toward an environmental stimulus is called a positive tropism; for example, stems growing toward light are positively phototropic. Conversely, curvature of an organ away from a stimulus is called a negative tropism. Roots, which usually grow away from light, are negatively phototropic. Tropisms begin within thirty minutes after a plant is exposed to the stimulus and are usually completed within approximately five hours.

**Phototropism**

*Phototropism* is a growth response of plants to light coming from one direction. Positive phototropism of stems results from cells on the shaded side of a stem growing faster than cells along the illuminated side; as a result, the stem curves toward the light. The rapid elongation of cells along the shaded side of a stem is controlled by a plant hormone called *auxin* that is synthesized at the stem’s apex. Unidirectional light causes the auxin to move to the shaded side of stems. The increased amount of auxin on the shaded side of stems causes cells there to elongate more rapidly than cells on the lighted side of the stem. This, in turn, causes curvature toward the light.

Only blue light having a wavelength of less than 500 nanometers can induce phototropism. The photoreceptors in this system are called *cryptochromes* and may alter the transport of auxin across cellular membranes, thereby facilitating its transport to the shaded side of the stem. Phototropism is important for two main reasons: It increases the probability of stems and leaves intercepting light for photosynthesis and of roots obtaining water and dissolved minerals that they need.

**Gravitropism**

*Gravitropism* is a growth response to gravity. The positive gravitropism of roots involves the root cap, a tiny, thimble-shaped organ approximately 0.5 millimeter long that covers the tip of roots. Decapped roots grow but do not respond to gravity, indicating that the root cap is necessary for root gravitropism. Gravity-perceiving cells, called *columella cells*, are located in the center of the root cap. Each columella cell contains fifteen to twenty-five amyloplasts (starch-filled plastids) which, under the influence of gravity, sediment to the lower side of columella cells. This gravity-dependent sedimentation of amyloplasts is the means whereby roots sense gravity, possibly by generating electrical currents across the root tip. These gravity-induced changes are then transmitted to the root’s elongating zone, located 3 to 6 millimeters behind the root cap. The differential growth that causes curvature occurs in the elongating zone.

When roots are oriented horizontally, growth along the lower side of the elongating zone is inhibited, thereby causing the root to curve downward. Among the first events that produce this differential growth is the accumulation of calcium ions along the lower side of the root tip. Calcium ions move to the lower side of the cap and elongating zone of horizontally oriented roots. This movement may be aided by electrical currents in the root. The accumulation of calcium along the lower side of the root causes the auxin to accumulate there as well.
Because auxin inhibits cellular elongation in roots, the lower side of the root grows slower than the upper side of the root, and the root curves downward. When the root becomes vertical, the lateral asymmetries of calcium and auxin disappear, and the root grows straight down.

Gravity-sensing cells in stems are located throughout the length of the stem. As in roots, the auxin and calcium ions in stem cells direct the negative gravitropism (in this case, upward curvature) of shoots. As auxin accumulates along the lower side, calcium ions gather along the upper side of horizontally oriented stems. The accumulation of auxin along the stem’s lower side stimulates cellular elongation there. Gravitropism increases the probability of two important results: Roots will be more likely to encounter water and minerals, and stems and leaves will be better able to intercept light for photosynthesis.

**Thigmotropism**

*Thigmotropism* is a growth response of plants to touch. The most common example of thigmotropism is the coiling exhibited by specialized organs called *tendrils*. Tendrils are common on twining plants such as morning glory and bindweed. Prior to touching an object, tendrils often grow in a spiral. This type of growth is called *circumnutation*, and it
increases the tendril’s chances of touching an object to which it can cling. Contact with an object is perceived by specialized epidermal cells on the tendril. When the tendril touches an object, these epidermal cells control the differential growth of the tendril. This differential growth can result in the tendril completely circling the object within five to ten minutes. Thigmotropism is often long-lasting. For example, stroking one side of a tendril of garden pea for only a few minutes can induce a curling response that lasts for several days. Thigmotropism is probably controlled by auxins and ethylene, as these regulate thigmotropic-like curvature of tendrils even in the absence of touch.

Growing tendrils touched in the dark do not respond until they are illuminated. This light-induced expression of thigmotropism may indicate a requirement for adenosine triphosphate (ATP), as ATP will substitute for light in inducing thigmotropism of dark-stimulated tendrils. Tendrils can store the sensory information received in the dark, but light is required for the coiling growth response to occur. Thigmotropism by tendrils allows plants to “climb” objects and thereby increases their chances of intercepting light for photosynthesis.

**Hydrotropism and Heliotropism**

Roots also grow toward wet areas of soil. Growth of roots toward soil moisture is called **hydrotropism**. Roots whose caps have been removed do not grow toward wet soil, suggesting that the root cap is the site of moisture perception by roots. Hydrotropism is probably controlled by interactions of calcium ions and hormones such as the auxins.

**Heliotropism**, or “solar tracking,” is the process by which plants’ organs track the relative position of the sun across the sky, much like a radio telescope tracks stars or satellites. Different plants have different types of heliotropism. The “compass” plants (*Lactuca serriola* and *Silphium laciniatum*) that grow in deserts orient their leaves parallel to the sun’s rays, thereby decreasing leaf temperature and minimizing desiccation. Plants that grow in wetter regions often orient their leaves perpendicular to the sun’s rays, thereby increasing the amount of light intercepted by the leaf. Heliotropism occurs in many plants, including cotton, alfalfa, and beans. Sunflowers get their name from the fact that the flowers follow the sun across the sky.

On cloudy days, leaves of many heliotropic plants become oriented horizontally in a resting position. If the sun appears from behind the clouds late in the day, leaves rapidly reorient themselves—they can move up to 60 degrees in an hour, which is four times more rapid than the movement of the sun across the sky. Heliotropism is controlled by many factors, including auxins.

**Growth, Survival, and Beyond**

Plants, like animals, are finely tuned to their environment; their growth and development are influenced strongly by that environment. Tropisms are rapid, while other responses such as flowering are long-term and are associated with changes of season. Regardless of their duration, most responses of plants to environmental stimuli are the result of growth and are controlled, at least in part, by hormones.

Tropisms account for many common examples of plant growth, including curvature of stems toward a window and the “climbing” of many plants up posts and fences. More important, tropisms help a plant to survive in its particular habitat, making use of separate systems for detecting and responding to environmental stimuli. Biologists are studying these systems in hopes of being able to mimic these detection and “guidance” systems. Scientists at the National Aeronautics and Space Administration (NASA) study how plants perceive and respond to gravity in hopes that this knowledge will help in the understanding of how to grow plants in deep space. NASA scientists also hope that understanding the gravity detection and guidance systems in plants will help people design more effective rockets which, like plants, must detect and respond to gravity to be effective.

*Randy Moore*

**See also:** Circadian rhythms; Heliotropism; Hormones; Nastic movements; Photoperiodism; Roots; Stems; Thigmomorphogenesis.

**Sources for Further Study**

diagrams illustrate experiments and results, and suggestions for further reading appear at the end of the chapter. Includes a glossary. College-level but suitable for high school students also.


Haupt, W., and M. E. Feinleib, eds. The Physiology of Movements. New York: Springer-Verlag, 1979. This college-level textbook provides much detailed information about tropisms. Includes an index, illustrations, and extensive bibliography.


**TUNDRA AND HIGH-ALTITUDE BIOMES**

**Categories:** Biomes; soil

Regions where no trees grow because of frozen soil or extreme water runoff due to steep grades (at high altitudes) are known as tundra. High altitude biomes have similar limitations on the growth of plant life.

Tundra landscapes appear where long, cold winters, a permanently frozen subsoil, and strong winds combine to prevent the development of trees. The resulting landscapes tend to be vast plains with low-growing forbs and stunted shrubs. Vast areas of this biome encircle the northernmost portions of North America and Eurasia, constituting the Arctic tundra. Climatic conditions atop high mountains at all latitudes are similar; these small, isolated areas are called the alpine tundra.

**Permafrost**

The low temperatures of the tundra regions cause the formation of a permanently frozen layer of soil known as permafrost. Characteristic of Arctic tundra, permafrost, which varies in depth according to latitude, thaws at the surface during the brief summers. As the permafrost below is impenetrable by both water and plant roots, it is a major factor in determining the basic nature of tundra.

The alternate freezing and thawing of soil above the permafrost creates a symmetrical patterning of the land surface characteristic of Arctic tundra. Perhaps the best known features of the landscape are stone polygons that result when frost pushes larger rocks toward the periphery, with smaller ones occupying the center of each unit. This alteration of the tundra landscape, called cryoplanation,
is the major force in molding Arctic tundra landscapes.

In contrast, alpine tundra generally has little or no permafrost. Even though alpine precipitation is almost always higher than for Arctic tundra, steep grades result in a rapid runoff of water. Alpine soils are, therefore, much drier, except in the flat alpine meadows and bogs, where conditions are more like those of Arctic areas.

Vegetation

Both Arctic and alpine tundra regions are composed of plants that have adapted to the same generally stressful conditions. Biodiversity of both plants and animals—the total number of species present—is low compared to most other ecosystems. Plant growth is slow because of the short growing seasons and the influence of permafrost. Most tundra plants are low-growing perennials that reproduce vegetatively rather than by seed. Often they grow in the crevices of rocks that both shelter them in the winter and reflect heat onto them in summer.

Common plants of the low-lying Arctic tundra sites include various sedges, especially cottongrass, and sphagnum moss. On better-drained sites, biodiversity is higher, and various mosses, lichens, sedges, rush species, and herbs grow among dwarfed heath shrubs and willow. The arrangement of plants within a small area reflects the numerous microclimates resulting from the peculiar surface features.

Alpine plants possess many of the features of Arctic plants. However, because strong winds are such a prominent feature of the alpine environment, most of the plants grow flat on the ground, forming mats or cushions.

Below alpine tundra and south of Arctic tundra,
there is the boreal (also known as taiga) biome, dominated by coniferous forest. Between the forest and tundra lies a transitional zone, or ecotone. This ecotone is characterized by trees existing at their northern (or upper) limit. Especially in alpine regions, stunted, gnarled trees occupy an area called krummholz. In North America, the krummholz is much more prominent in the Appalachian Mountains of New England than in the western mountains.

Conservation

Like all world biomes, tundra regions are subject to degradation and destruction, especially as a result of human activities. Because of low human population density and their unsuitability for agriculture, tundras generally are less impacted by humans than are grasslands and forests. However, tundra ecosystems, when disturbed, recover slowly, if at all. As most tundra plants lack the ability to invade and colonize bare ground, the process of ecological succession that follows disturbances may take centuries. Even tire tracks left by vehicles can endure for decades. The melting of permafrost also has long-lasting effects.

The discovery of oil and gas in tundra regions, such as those of Alaska and Siberia, has greatly increased the potential for disturbances. Heavy equipment used to prospect for fossil fuels and to build roads and pipelines has caused great destruction of tundra ecosystems. As the grasses and mosses are removed, the permafrost beneath melts, resulting in soil erosion. The disposal of sewage, solid wastes, and toxic chemicals poses special problems, as such pollutants tend to persist in the tundra environment longer than in warmer areas.

Animals of the Arctic tundra, such as caribou, have been hunted by the native Inuit, using traditional methods for centuries without an impact on populations. The introduction of such modern inventions as snowmobiles and rifles has caused a sharp decline in caribou numbers in some areas.

Although efforts at restoring other ecosystems, especially grasslands, have been quite successful, tundra restoration poses difficult problems. Seeding of disturbed Arctic tundra sites with native grasses is only marginally successful, even with the use of fertilizers. In alpine tundra, restoration efforts have been somewhat more successful but involve transplanting as well as seeding and fertilizing. A recognition of natural successional patterns and long-term monitoring is a necessity in such efforts.

Thomas E. Hemmerly

See also: Arctic tundra; Asian flora; Biomes: definitions and determinants; Biomes: types; European flora; Forests; Lichens; North American flora; Rangeland; South American flora; Taiga.

Sources for Further Study


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ULVOPHYCEAE

Categories: Algae; microorganisms; Protista; taxonomic groups; water-related life

One of four classes in the phylum Chlorophya, the green algae, the ulvophytes (Ulvophyceae) include both freshwater and marine species of green algae classified in six orders. Members of this class display varying shapes and range in size from a few cells to long filaments, sheets, or coenocytic masses of cells. Two of the more familiar species are the green, leafy sea lettuce, Ulva lactuca, and the egg-shaped Ventricaria.

The name Ulvophyceae is derived from a Latin word designating plants that live in marshes. Carolus Linnaeus referred to algae with the taxonomic term Ulva in his Species plantarum (1753). In 1978 Kenneth D. Stewart and Karl R. Mattox identified Ulvophyceae, or the ulvophytes, as a distinct phyletic line in the division Chlorophyta. The classification of Ulvophyceae was modified as botanists gained new insights into its ultrastructure. Using electron microscopes, botanists detected that Ulvophyceae algae exhibit unique flagellar apparatus and root systems. Ulvophyceae taxonomy was developed according to these physical characteristics. During the 1980’s, botanists assigned six orders to class Ulvophyceae: Ulotrichales, Ulvales, Cladophorales, Dasycladales, Caulerpales, and Siphonocladales.

By 1990 cladistic analysis of Ulvophyceae genetic material caused researchers to reconsider the evolutionary relationships and lineages of Ulvophyceae orders. Molecular comparisons suggest that ulvophytes might be basal to (evolutionary predecessors of) those green algae classified in Chlorophyceae and Pleurostrophyceae. Investigations continue to advance comprehension of Ulvophyceae’s role in plant evolution.

Structure

The ultrastructure of species of Ulvophyceae usually is radially symmetrical and consists of motile cells with flagella, basal bodies positioned in a counterclockwise rotation, cruciate microtubular roots, and persistent mitotic spindles that do not collapse during telephase. Many ulvophytes are macroscopic and appear as filamentous or as flat sheets of cells. Others are microscopically small. Some are scaly or slippery. The sea lettuce (Ulva) and Ventricaria are the most familiar representatives of Ulvophyceae.

In the order Ulotrichales, species in the genus Ulothrix consist of single-nucleus cells arranged to form unbranched filaments. A cell at each filament’s basal end is a rootlike holdfast that adheres plants to surfaces. Plants in the order Siphonocladales often resemble bubbles and are found on shells or stones in tropical waters. The plants in order Ulvales have a flat or hollow thallus (body). Members of Enteromorpha in this order consist of tubular strands that can attain widths of 5 centimeters (2 inches). Some species in the genus Ulva are as large as 65 centimeters (25.6 inches). Members of Codium magnum in order Caulerpales sometimes reach lengths of 8 meters (26.25 feet). Order Cladophorales includes both branched and unbranched filamentous algae. Members of Cladophora (also sometimes classified in the order Siphonocladales) have branching filaments, which often grow tightly together and are formed by multinucleate cells with thick walls. Some members of order Dasycladales are extinct. Fossils indicate that these ulvophytes first lived during the Middle Silurian period, about 420 million years ago.

Sexual reproduction in Ulvophyceae is significant because ulvophytes are the only members of Chlorophyta that reproduce by an alternation of generations, with haploid and diploid thalli. Instead of zygotes, spores are the site of meiosis. Species also form dense stands as a result of vegetative reproduction of fragments, which usually sink instead of float. Temperature and sunlight regulate the rate of growth.
Distribution
Ulvophytes are usually found in marine environments, especially along coasts and in harbors, although freshwater species thrive in shallow parts of lakes and streams. Other habitats include rocks and soil. These algae live primarily in small clumps but occasionally form mats near the water surface as dense as five thousand fronds per square meter (11 square feet). They occasionally live at maximum depths of 10 meters (33 feet), although some species have been discovered as deep as 99 meters (325 feet). Ulvophytes prefer still, clear water but can survive in brackish and polluted environments.

Plants in class Ulvophyceae are indigenous to tropical regions in the Pacific, Indian, and Atlantic Oceans and the Red Sea. Some species are unintentionally transported on ships to other regions. If conditions are suitable, ulvophyte colonies multiply by as much as 28 percent daily, invading territory and competing with native plants. In 1984 Caulerpa taxifolia was discovered in the Mediterranean Sea. By 1996 that species had spread from covering an area of one square meter (11 square feet) to invading 3,096 hectares (7,647 acres) in seventy-seven places in the Mediterranean. Ulvophytes often adapt to new environments by deviating from their original characteristics—for example, lengthening and increasing the number of fronds to adjust to lower water temperatures.

Uses and Cultural Impact
Several Ulvophyceae species are valued by humans for their nutritional qualities, texture, and flavor. Rich in vitamins and minerals, especially iron and iodine, Ulva are sources of protein, sugar, starch, and roughage. Ulva lactuca, commonly called sea lettuce, is collected for salad, soup, and sauce ingredients. Ulva is also cultivated as livestock feed and fish bait.

Many ulvophytes have medicinal characteristics and are able to soothe burns. Soaps, oils and shower gels, and nutritional supplements often include ingredients from ulvophytes. Some animals symbiotically rely on Ulvophyceae. For example, sea slugs gather chloroplasts from Codium, which continue to undergo photosynthesis in the slugs’ respiratory chambers, enhancing their oxygen supply. Ulva is cultivated to absorb nitrogen and phosphorus in water at abalone farms. Ulvophytes indicate environmental quality and are used to detect metal contamination and eutrophication, because they quickly accumulate in areas where large amounts of polluting substances cause those conditions.

Ulvophytes also can be toxic. Caulerpa taxifolia emits terpene caulerpenyne, which discourages predators from eating algae. Cephaleuros causes red rust, a fungus that can be economically disastrous for tea, pepper, and citrus growers. Sometimes considered a pest or pollutant, filamentous algae can destroy water quality necessary to sustain life, interfere with commercial and recreational uses, and deplete oxygen, causing fish kills. Codium can destroy oyster beds. Algae decomposition, especially when plants wash onto beaches and rot, results in unbearable stenches caused by the ulvophytes’ sulfur content. Green tides resulting from an overabundance of ulvophytes thriving on nutrients in agricultural effluent are problematic. These thick clumps of algae prevent other plant and animal organisms from having access to sufficient quantities of crucial sunlight and oxygen.

Elizabeth D. Schafer

See also: Agriculture: marine; Algae; Animal-plant interactions; Aquatic plants; Culturally significant plants; Eutrophication; Green algae; Marine plants.

Sources for Further Study
**USTOMYCETES**

**Categories:** Fungi; taxonomic groups

The Ustomycetes are a group of the basidiosporic fungi that includes about a thousand species. These fungi all produce spores in a sorus, a mass of spores that is produced on the surface of a plant host. Ustomycetes are all parasites of plants, and some are serious pathogens. Most produce hypertrophy (excessive cell growth) in plant tissues.

One of three main classes of Basidiomycota, the ustomycetes include several different orders. Cryptobasidiales is a small order of fungi found in tropical areas of South America and Africa. The only species in the Cryptomycocolacales is a parasite of ascomycetes. The Exobasidiales produce galls on leaf tissue of plants in the Ericaceae and Commerlinaceae families. The Graphioales produce black sori on the leaves of Palmae. The Platyglaeiales produce small gelatinous to waxy basidiocarps and are saprophytes or mycoparasites. The Sporidiales are yeastlike saprophytic fungi. The remaining order, the Ustilaginales contains almost all of the fungi of the ustomycetes.

**Reproduction**

The reproduction of the ustomycetes begins when a haploid hypha from a germinating basidiospore combines with a compatible hypha from another germinating spore. The resultant dikaryotic hypha then ingresses into the plant host. The hypha begins to parasitize the host, allowing the fungus to increase in mass. The fungus needs actively growing tissue to be able to reproduce. After the fungus has gained sufficient energy, the hypha begins to fragment into small cells, which become thick-walled chlamydospores. These spores are dark in color and form the sorus.

The chlamydospores undergo genetic change, and a diploid nucleus is produced. The nucleus then undergoes meiosis and produces haploid nuclei. The chlamydospore germinates, forming a small length of hypha called a metabasidium. The nuclei migrate into the metabasidium, and small basidiospores are produced. The basidiospores often form a yeastlike phase as they reproduce by cell division. This mechanism is unique among the fungi, as most spores, once formed, are unable to divide into two new units. Ustomycetes also have a yeastlike phase when they are grown in axenic culture. Spore release is passive.

**The Smuts**

The ustomycetes in the order Ustilaginales are important plant parasites, known commonly as smuts, and can affect most meristematic areas of plants. Some of these cause considerable economic damage to plants. The smuts cause hypertrophy (excessive growth) of growing tissues. Infection is by dikaryotic hyphae that can penetrate into the meristems of ovaries, leaves, and even roots of plants. The resultant mass of cells can produce a large growth that is unsightly.

The Ustilaginales are divided into two families based on the location at which the basidiospores are produced on the metabasidium. In the Tilletiaceae, the spores are located terminally, while in the Ustilaginaceae, the spores are located laterally. One of the more visible smuts is caused by Ustilago maydis, which infects corn. Corn smut has been recorded for thousands of years and is depicted in Mayan and Incan drawings of corn. The fungus infects the developing ovum by penetrating the silk at the time of pollination. Pollination does
not occur, but rather the fungus becomes established and fungal tissue begins to grow in place of the developing ovum. A mass of fungal tissue forms under the seed coat. The resulting gall can become more than an inch in length. These are often found on ears of corn as large gray or black growths. Thousands of years ago, it was believed that these growths were divine in origin, and any infected ears were separated. The infected ears were then used as offerings in religious ceremonies. The smut galls were often consumed by the religious leaders. This practice may have preserved corn for future generations. Seed corn can become coated with chlamydospores at the time of harvest. These spores can germinate at the time of planting and infect the germinating seed. Death of the seedling is possible.

Other kinds of smut include bunt and stinking smut, which infect wheat. With bunt, the seed becomes infected but does not show any symptoms. The mycelium of the fungus remains dormant in the seed. The following year, as the seed germinates, the mycelium remains associated with the meristem. When the wheat plant produces its inflorescence, the fungus causes sori to be produced instead of ovaries. With stinking smut, the chlamydospores are transmitted on the surface of the seeds. Basidiospores are produced, and the mycelium infects the developing plant. When the inflorescence is produced, the ovaries appear enlarged, and the “seed” produced will have a sorus occupying the entire interior. The sori have a distinctive dead fish odor, accounting for the name.

While many smuts attack ovaries, some smuts cause sori to be formed on leaves. Striped smut occurs on some turf grasses, while other smuts can cause spots on leaves of plants.

Most inflorescence smuts occur only once a year and do not affect more than about 5 percent of the seeds. They are disseminated by wind. They can be more damaging, however, if crops are staggered in the same growing season.

*J. J. Muchovej*

**See also:** Basidiomycetes; Basidiosporic fungi; Diseases and disorders; Fungi; Rusts.

**Sources for Further Study**


Vacuoles are receptacles within plant cells that hold water, enzymes, acids, waste products, pigments, or other substances that serve the plant.

Vacuoles are the largest organelles in most mature plant cells. Frequently constituting more than 90 percent of the volume of a cell, the vacuole presses the rest of the protoplasm against the cell wall. Vacuoles are surrounded by a single fragile membrane called the vacuolar membrane, or tonoplast. The contents of the vacuole, referred to as vacuolar sap, is 90 to 98 percent water. The vacuole of a typical plant cell occupies approximately 500,000 cubic micrometers. It would take approximately two million of these vacuoles to equal the volume of a sugar cube.

Almost all plant cells contain vacuoles. Not all mature cells of plants, however, contain a single vacuole. For example, the cells of the tissue that produces the wood and bark of trees contain many small vacuoles during winter, when the tissue is dormant. When the tissue becomes active in spring and summer, these small vacuoles fuse into single, large vacuoles.

Storage Reservoirs

Vacuoles were discovered in 1835 and were thought to have relatively little function. It is now known that vacuoles are versatile organelles that have many important functions, including that of storage reservoirs. Vacuoles store waste products that would be dangerous if they accumulated in the cell’s cytoplasm. Many of these waste products, such as nicotine, other alkaloids, and cyanide-containing compounds, are poisons that help protect the plant against predators. Vacuoles are also temporary, controlled repositories for useful materials such as potassium, chloride, and calcium ions. Ions such as sodium (Na+) and chloride (Cl−) are moved across the tonoplast by active transport, an energy-dependent means of transport in cells. These ions are important for cellular metabolism. For example, absorption or release of calcium from vacuoles regulates calcium-dependent enzymes in the cell’s cytoplasm.

Vacuoles store many economically important products. For example, proteins are stockpiled in vacuoles of storage cells in seeds. Latex is stored in vacuoles of rubber plants. Vacuoles of many plants store large amounts of amino acids, which are used as a reservoir of nitrogen. Vacuoles of beet roots and sugarcane store large amounts of sugar. Large amounts of salt are also accumulated in vacuoles. The sap in most vacuoles has concentrations of salts similar to that of seawater. In marine algae and plants that grow in the salty soils of deserts and ocean shores, vacuoles often accumulate salts, such as potassium chloride and sodium chloride, to levels several thousand times greater than that of the soil or brackish water in which the plants grow.

Sometimes the concentration of a particular salt in the vacuole is so great that it precipitates as crystals. For example, calcium oxalate crystals are common in vacuoles of many plants such as dumb cane (Dieffenbachia), which has toxic levels. Organic acids such as oxalic acid and malic acid are also accumulated. These acids make vacuoles slightly acidic. For example, the typical pH of a vacuole is near 5.5, while that of the cytoplasm is near 7.5. (A pH of 7.0 is neutral.) The vacuoles in citrus fruit contain large amounts of citric acid. Consequently, these vacuoles are very acidic, thus accounting for the tart, sour taste of the fruit.

Water Management

When vacuoles absorb salts, they also absorb water. This water swells the vacuole, much as air inflates a tire. The water entering the vacuole creates a pressure inside the vacuole called turgor pressure and presses the surrounding layer of cytoplasm against the edge of the cell. Turgor pressure is what makes nonwoody plant tissue firm. When the vacuole loses water, the turgor pressure is lost, and the tissue wilts. Thus, leaves of plants that lack water wilt, while those of well-watered plants remain firm.
The turgor pressure generated in vacuoles is important for cell growth because it stretches the cell wall of the plant. During cell growth, cells secrete protons into their cell walls. These protons weaken chemical bonds in the cell wall and can stretch it to a larger size. Plant hormones, such as auxins, control the secretion of protons. This type of pressure-driven growth by plant cells is energetically “inexpensive,” because it involves little more than absorbing water. This contrasts sharply with the growth of animal cells, which lack vacuoles. Animal cells must expand by making energy-rich cytoplasm, including large amounts of proteins and lipids.

Plant Movement and Gas Exchange

Vacuoles are important for the movements of many plants. For example, leaf movements in the sensitive plant (*Mimosa pudica*) and Venus’s flytrap (*Dioneae muscipula*) are based on the tonoplast’s ability to absorb or lose water quickly. Cells in specialized regions of the leaves quickly transport salts out of their cells. When they do, water from the cells’ vacuoles also leaves the cells. This “deflates” the cells, and the tissue shrinks, thus moving the leaf.

Gas exchange in the leaves is also influenced by vacuoles. Pores through which gases enter and exit leaves are called *stomata*, and they are bordered by specialized cells called *guard cells*. When the vacuoles of these cells absorb water, the cells become turgid and bow apart, thereby creating a pore through which gases move. Thus, water uptake by vacuoles of guard cells correlates with stomatal opening and gas exchange. When water leaves the vacuoles of guard cells, the cells wilt and the pore closes, which stops gas exchange. Gas exchange is crucial because it brings carbon dioxide into the leaf for photosynthesis and releases oxygen into the atmosphere. Many factors control water absorption by guard cells, including light, wind, temperature, and water availability.

Digestive Centers

Vacuoles function as digestive centers of cells: They contain a variety of digestive enzymes, such as phosphatases and esterases, that can degrade (break down) many different kinds of molecules. Vacuoles use these enzymes to degrade and recycle the parts of damaged or old, unneeded organelles. Small vacuoles fuse with old or damaged organelles and, by means of enzymes, digest the organelles. The parts of the digested organelle are then recycled by the cell.

Pigment Holders and Pumps

Many cells have vacuoles that contain water-soluble pigments called *anthocyanins*. These pigments are responsible for the red and blue colors of many vegetables (turnips, radishes, and cabbages), fruits (cherries, plums, and grapes), and flowers (geraniums, roses, delphiniums, peonies, and cornflowers). Anthocyanins help attract pollinating insects to the flowers. Sometimes these pigments are so bright that they mask the chlorophyll, as in the ornamental red maple. The red color of garden beets is caused by another vacuolar pigment, called betacyanin.

Many protozoa and unicellular algae contain specialized vacuoles called *contractile vacuoles*. These vacuoles pump excess water from cells. As a result of this secretion, pressure does not build inside the cells. Contractile vacuoles are rare in marine algae and are absent in terrestrial plants.

Growth, Development, and Transport Models

Vacuoles perform many functions that are critical to plant growth and development. For example, the cellular expansion that produces leaf movements and *tropisms* results largely from water uptake by vacuoles. Similarly, the absorption and loss of water by vacuoles of guard cells regulates photosynthesis, the process that fuels life on earth.

Vacuoles are increasingly used as tools for studying transport across membranes. Ions and sugars move quickly across the tonoplast; this movement makes isolated vacuoles a model system for studying transport of materials across membranes. The movement is controlled by specific proteins that transport each ion or sugar across the membrane.

Many economically important chemicals, including drugs, dyes, spices, and other materials, such as rubber, are contained in vacuoles. Biologists are trying to understand how plant cells make and package these chemicals in vacuoles. Biotechnologists hope to use this knowledge to increase production of these chemicals. Far from being the inert structures they were once believed to be, vacuoles are critical to many aspects of plant life.

Randy Moore and Joyce A. Corban

See also: Cytoplasm; Leaf anatomy; Plant cells: molecular level; Plant tissues; Respiration; Tropisms.
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VEGETABLE CROPS

Categories: Agriculture; economic botany and plant uses; food

Vegetables are plant products, either fruits or other fleshy parts of the plant, consumed in human diets. Although the word itself has no precise taxonomical significance, agriculturally vegetables constitute a significant sector of world food crops.

Although most of the world’s people consume “vegetables” daily, the word itself has no precise botanical or scientific meaning. Various vegetative (nonreproductive) parts of plants are eaten as vegetables, but reproductive parts of plants such as cucumbers and tomatoes, which are technically fruits, are also consumed as “vegetables.”

Vegetative “vegetables” include the stems of celery, the tubers Irish (white) potatoes, and asparagus shoots. Other vegetables commonly consumed include roots: sweet potatoes, carrots, parsnips, and radishes, among others. Leaves eaten as vegetables include lettuce, spinach, collards, and cabbage.

Reproductive plant parts that are considered vegetables include broccoli (flower buds); cauliflower (flowers); green beans, squash, and tomatoes (fruits); and green peas and lima beans (seeds). Many more vegetables can be identified for each of those categories of reproductive parts.
The plant crops discussed here include those that are generally eaten along with meat as a part of the main course of a meal, as opposed to the fruits, which are generally sweet and are consumed as desserts. Interestingly, whereas many fruits are commonly referred to as vegetables, most foods commonly referred to as “fruits” tend also, in the strict botanical sense of the word, to be fruits.

Origins

Early humans during the Neolithic (Stone) Age were hunter-gatherers who foraged wild plants and ate them both raw and cooked. Gradually, the plants that were most useful were domesticated. Domesticating these plants involved both the selection of superior plants and improving the conditions under which they are grown. Improvements included loosening the soil and applying various materials as fertilizers. Nearly all the vegetable crops now cultivated are known to have been domesticated more than two thousand years ago.

Knowledge about the origins of agriculture, including the domestication of plants, comes from a variety of sources. Before the birth of Christ, the Greek botanist Theophrastus in the third century B.C.E. listed in his *Peri phyton historias* (also known as *Historia plantarum*; “Enquiry into Plants,” 1916) crops known to have been grown at that time. A few centuries later, the Roman Pliny the Elder made similar observations. In modern times, two economic botanists summarized the accumulated knowledge relating to economic plants, including vegetable crop plants. The Swiss Alphonse de Candolle wrote *Origine des plantes cultivées* (1882; origin of cultivated plants). Nikolai I. Vavilov, a Russian, gained fame as a result of his work (translated into English as *The Origin, Variation, Immunity, and Breeding of Cultivated Plants*, 1951). Among the conclusions reached by Vavilov, Candolle, and others is that agriculture originated not in a single region, as previously thought, but more or less simultaneously in widely separated “centers of origin” on several of the world’s continents.

Vegetables meet the variety of nutritional needs of humans. In addition to providing varying amounts of carbohydrates, fats, and proteins, they supply needed vitamins and minerals so necessary in the diet. Also, vegetables supply the insoluble fiber, or “roughage,” that is essential in maintaining intestinal regularity and preventing colon cancer.

**Root Crops**

A “root crop” in the commercial/agricultural sense includes any plant crop in which an underground part is dug from the soil and eaten as a vegetable. Botanically, the edible part may be a root, rhizome (underground stem), corm (compressed underground stem surrounded by dry scales), or bulb (short underground stem covered by fleshy leaf bases). The objective is to harvest these plant parts soon after carbohydrates and other nutrients have been stored there for the future use of the plant.

Most root crops have larger amounts of carbohydrates and less protein and oil than grains (cereals) or legumes. Because of their bulk, root crops cost more to ship than do grains and most other food crops. Therefore, root vegetables tend to be consumed locally. Nevertheless, measured in tons, root crops are comparable to grain crops on a worldwide basis. The most important root crops are the...
Irish (white) potato, the sweet potato, and cassava. These three are to root crops what maize, wheat, and rice are to grain crops. They, together with root crops of secondary importance, are discussed below. The common name of each crop plant is followed by its scientific name and family name.

### White Potato

The common potato, *Solanum tuberosum* (family *Solanaceae*), is the most important nongrain food item of the world. However, it has been known outside the Americas for only a few centuries. Spanish explorers of the sixteenth century found potatoes growing in what is now the nation of Colombia in South America. It had long been grown by Native Americans in the cool, high elevations of the Andes Mountains south to the present country of Chile. Soon after discovery by Europeans, the potato was introduced into Spain and from there into other parts of Europe, including the British Isles. Throughout many of these regions, it became an important staple in the diets of most citizens.

When a fungal disease, potato late blight, wiped out most of the potato crop in Ireland in the mid-1840’s, a severe famine (the Irish Potato Famine) resulted, causing large numbers of people to emigrate to the United States, Canada, and other countries. As a result, the popularity and cultivation of potatoes spread in North America, and the potato became known as the Irish potato, to distinguish it from the sweet potato.

The potato is a crop of cool regions. Potato plants are grown from sections of the tuber cut into segments, each containing an “eye” (bud). The resulting plants produce tubers that are harvested, usually by digging machines, later the same growing season. Principal potato-growing regions of the United States include Idaho, Maine, and New York. Many potatoes are also grown in northern Europe.

The potato is an economical source of starch used for both food and industrial purposes. Protein content is only about 2 percent. Purchases of whole potatoes declined throughout the later decades of the twentieth century, but that decline was offset by the increased consumption of processed potato products such as potato chips, ready-mix mashed potatoes, and frozen french fries.

### Cassava

*Manihot esculenta* (Euphorbiaceae), also called manioc and tapioca, is an important root crop and a staple item in the diets of more than 500 million people of tropical regions. The starch storage roots are produced by the perennial plant, which is native to tropical America. It is believed to have been domesticated in Brazil, where it is known to have been grown around 2000 B.C.E. In addition to Latin America, it is important in Africa and other tropical regions.

There are several advantages to growing and using cassava as a food plant. After clearing the land, farmers can plant stem sections. Storage roots can be harvested in only eighteen months or can be left in the ground and dug up later. In addition to providing high yields per acre, cassava has the advantage of being resistant to diseases. Furthermore, it survives in poor soil and both dry and wet tropical climates.

One of the disadvantages of cassava is its low protein and vitamin content. Thus, an overdependence on cassava often results in severe nutritional deficiencies. Also, the roots often contain poisonous cyanide-type compounds that must be removed before consumption. As the amounts of these compounds vary with the variety of cassava and the conditions under which they are grown, processes for removal of the toxins can be problematic. Traditionally, in Brazil, the shredded roots are ground by hand, after which the pulp’s mass is dried over fires to yield a subsistence product known as *farinha*. Also, a large, round flatbread is made by spreading the pulp on a griddle. In Africa, roots are produced from “sweet” varieties (in which only small quantities of toxins are present). There, the roots are peeled, boiled, dried, and eaten as a lumpy, starchy vegetable with little flavor. In temperate regions, a product called *tapioca*, made from processed roots, is used for puddings.

### Sweet Potato

*Ipomoea batatas* (Convolvulaceae), or the sweet potato, a relative of the morning glory, is a trailing tropical vine. Unlike those of the cassava, the edible parts of the sweet potato are true roots. Evidence indicates that it is a native of South America, but it is known to have been cultivated more than a thousand years ago in Polynesia. It was also known in New Zealand before Europeans had ships that could cross the oceans. How the sweet potato was carried across the Pacific remains a mystery.

The sweet potato is cultivated today around the world, in the tropics as a perennial, and in temper-
ate regions as an annual. In the latter case, the stem sections of the vine are planted in the spring, and the roots are dug up later the same season.

Sweet potatoes contain much more protein than either white potatoes or cassava; also, they have significant amounts of vitamin A. However, sweet potatoes do not store as well as cassava and are not grown in as high a quantity. In the United States, they are prepared much like white potatoes. Large amounts are also fed to animals or used as sources of industrial products. China is the leading producer of sweet potatoes.

Other Root Crops
Perhaps the most important world root crop, after those listed above, is the yam, *Dioscorea alata* (family Dioscoreaceae). Not to be confused with sweet potatoes, which are often called “yams” in the southern United States, the true yam is, like the white potato, a tuber. Also like potatoes, yams are propagated using sections of tubers with the buds. The resulting plants are deep-rooted climbing vines. One problem in harvesting them is the large amount of labor required to dig the tubers. However, yams are well adapted to tropical rain forests. Yams are prepared as are white potatoes and have a similar nutritional value. In addition to *Dioscorea alata*, native to China, several other *Dioscorea* species are cultivated as root crops.

Several plants of the arum family, *Araceae*, are grown as root crops. The most important is taro, *Colocasia esculenta*. Taro is believed to have originated in southern Asia; it spread from there to India and also through the islands of the South Pacific. Later it was introduced into the Mediterranean, tropical Africa, and the West Indies. The plant is closely related to “elephant ear,” which is grown as an ornamental. The edible portions include both tubers and corms. Visitors to Hawaii are familiar with the viscous preparation poi, which made from taro.

Onions and their close relatives of the genus *Allium* (family Liliaceae) have a long and esteemed reputation in the culinary arts. Native to Central Asia and the Near East, they have long been cultivated. The bulbs, after being dug, can be consumed directly or stored. Onions (*A. cepa*) produce a single large bulb; garlic (*A. sativum*), several smaller ones. The bulb of the leek (*A. ampeloprasum*) is continuous with the leaf blade above.

Stem and Leaf Crops
Cole crops include cabbage and its close relatives, all of the species *Brassica oleracea* (family Brassicaceae), along with other plants of this family. There is evidence that from cabbage, native to northern Europe, each of the cole vegetables has resulted from a different modification of the stems or leaves. Cabbage has long been an important crop in Germany, where it is used to make sauerkraut. Other vegetables of this group include brussels sprouts, cauliflower, kohlrabi, broccoli, and kale.

The aster family (*Asteraceae*) also includes several plants grown as vegetables. Lettuce (*Lactuca sativa*) is believed to have been derived from a plant native to the Mediterranean region. It has been grown for centuries and used for salads, much as it is today. Selection has resulted in numerous varieties including leaf lettuce and romaine lettuce. In the United States, iceberg lettuce is the familiar, popular type seen in supermarkets. Plants known as endive and chicory are also used as salads. Both are cultivars of *Cichorium intybus*.

Several other common vegetables, of various families, are grown for their edible stems or leaves. The principal edible parts of celery, *Apium graveolens* (family Apiaceae), are the stalks or leaf petioles. Spinach, *Spinacia oleracea* (family Chenopodiaceae), is used raw in salads and as a cooked vegetable. Asparagus, *Asparagus officinalis* (family Liliaceae) is a perennial from which young shoots are cut each spring.

Thomas E. Hemmerly

See also: African agriculture; Agricultural revolution; Agriculture: traditional; Agriculture: world food supplies; Asian agriculture; Australian agriculture; Central American agriculture; European agriculture; Fruit crops; Fruit: structure and types; Green Revolution; Horticulture; Legumes; North American agriculture; Plant domestication and breeding; Plant tissues; Roots; South American agriculture.

Sources for Further Study
VESICLE-MEDIATED TRANSPORT

**Categories:** Cellular biology; physiology; transport mechanisms

Large substances such as proteins, some amino acids, and polysaccharides are transported into and out of plant cells by vesicle-mediated transport, which involves interaction with and fragmentation of the cell membrane to create a membrane-bound vesicle for internal distribution or external export. Once formed, the vesicle can be transported to its destination within the cell.

Plant cells use several methods to transport ions, polar molecules, and macromolecules through the cell membrane. Some of these can permeate the membrane via osmosis. Small substances, mostly ions, can diffuse through pores composed of transmembrane proteins. Other substances, however—such as glucose, glycogen, and some amino acids—must be transported by membrane-bound carrier molecules in a process called vesicle-mediated transport.

Also called *bulk transport*, vesicle-mediated transport is an active process that involves the cell membrane (plasma membrane) and consumes energy. Vesicle-mediated transport also provides a mechanism that enables a cell to “hoard” needed nutrients against a concentration gradient. The product of vesicle-mediated transport is a saclike vesicle, typically about 0.05-0.1 micrometer in diameter, comprising a fragmented portion of the cell membrane that bounds and contains the substances being transported. Vesicle-mediated transport of substances into plant cells is called *endocytosis* (*endo* means “within”; *cytosis*, “cytosol” or “cytoplasm”), and movement of substances out of cells is called *exocytosis*. The three forms of endocytosis are pinocytosis, phagocytosis, and receptor-mediated endocytosis.

**Pinocytosis**

*Pinocytosis* is called “cell drinking” because during the process fluids and dissolved solutes are taken into the cell. Pinocytosis involves the formation of membrane-bound vesicles at the cell membrane surface, called pinocytic vesicles, which are then taken into the cell interior and released. Under certain circumstances, pinocytosis enables a cell to take in fluid at a much faster rate than during normal osmosis. Pinocytosis may augment osmosis or may function entirely independently; cells in an isosmotic solution, for example, can acquire large volumes of additional fluid via pinocytosis.

Studies of plant cell uptake of heavy metals such as lead have clarified much of the processes involved in pinocytosis. Pinocytosis occurs in special depressions in the cell membrane. Each depression, or *pit*, consists of one or more proteins called clathrin. Clathrin is a complex protein that consists of three large and three small polypeptide chains bound together to form a tripodlike configuration called a *triskelion*.

During pinocytosis, clathrin-coated pits form around a droplet of extracellular fluid as well as any ions contained within the fluid droplet. The membrane-bound droplet then invaginates via a deep groove through the membrane, pinching off within the interior as a minute, fluid-filled vesicle. The whole process takes only a few seconds.

**Phagocytosis**

*Phagocytosis* is called cell eating (*phage* for “eating,” and *cytosis* meaning “cell”) and refers to the cellular intake of large and generally insoluble molecules and macromolecules that cannot be taken into the cell using other membrane transport mechanisms. Phagocytosis differs from pinocytosis in that little fluid is taken into the cell.
Many small single-celled organisms such as amoebae feed by phagocytosis. Some of the more specialized forms of phagocytosis in plants include uptake of food by slime molds and the intake of nitrogen-fixing bacteria such as *Rhizobium* into the root nodules of legumes as they form.

The products of phagocytosis are typically solid substances rather than fluid and are contained within a vesicle called a phagosome. Some examples of phagocytosis involve extensions of the plasma membrane called pseudopodia, which surround the substance. The ends of the pseudopodia fuse to encircle the substance, which is then transported through the membrane and budded off into the cytoplasm. Inside the cell at least some phagocytic vesicles bind with one or more structures within the cytoplasm for further processing. Others are transported and their contents emptied into cell vacuoles or other cytoplasmic organelles.

**Receptor-Mediated Endocytosis**

Receptor-mediated endocytosis is an efficient process whereby nutrients and other essential macromolecules are taken into the cell. During receptor-mediated endocytosis, specific receptor sites located on the plasma membrane bind to target molecules in the extracellular fluid medium. Most of the receptor sites in plant cell membranes are glycoproteins which bind to specific sites on the target macromolecules, called ligands. Some receptor sites are located throughout the cell membrane, but others are found in clathrin-coated depressions or pits in the membrane. During receptor-mediated endocytosis, the receptor sites located in membrane depressions selectively bind with target substances to form a receptor-ligand complex. Following this, several receptor-ligand complexes may combine to form clusters around which a portion of the cell membrane encircles, producing a vesicle that invaginates inward to pinch off as a coated vesicle. Once inside, changes in the acidity (pH) within the cytoplasm separate the substance from the protein coating. The substance diffuses or is dissolved within the cytoplasm, and the protein coating is recycled back to the cell membrane.

**Exocytosis**

Exocytosis is the reverse of endocytosis. During exocytosis a vesicle-bound substance is transported through the membrane from the interior to the exterior of the plant cell. Exocytosis represents the method by which plant cells secrete or excrete substances out of the cell by means of membrane-bound sacs. A common example found in most plant cells during initial growth involves exocytosis of precursor molecules that will form the cell wall. During the process, the precursor molecules bind to the interior of the plasma membrane, then evaginate into the region where the cell wall is developing.

Exocytosis begins in the cytoplasm when a substance or a membrane-bound substance in the cytoplasm migrates to and fuses with the cell membrane. A pit or groove evaginates outward through the cell membrane, and the membrane-bound substance is transported to the cell surface. In some examples of exocytosis, the membrane opens at the cell surface and the interior substance diffuses into the extracellular fluid. In other cases, the vesicle is secreted or excreted as a membranous sac into the extracellular fluid.

Plant hormones, other secretory products, and waste are the most common substances removed from the cell by exocytosis. Following exocytosis, the vesicle generally dissolves, and the substance diffuses into the extracellular fluid.

Dwight G. Smith

**See also:** Active transport; Cells and diffusion; Endocytosis and exocytosis; Liquid transport systems; Membrane structure; Osmosis, simple diffusion, and facilitated diffusion; Plasma membranes; Water and solute movement in plants.

**Sources for Further Study**


Viruses and viroids • 1045

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**VIRUSES AND VIROIDS**

*Categories:* Cellular biology; diseases and conditions; medicine and health; microorganisms

Viruses are extremely small parasites that have none of the structures characteristic of living cells. Many viruses are little more than a protein-coated and particle-containing DNA or RNA. The protein coat is specifically adapted for breaching the plasma membranes of host organisms. Viroids are even simpler parasites comprising small, single-stranded molecules of RNA with no protein coat. They are the smallest known agents of infectious disease.

The concept of a virus dates back to the late nineteenth century investigations of the mosaic disease of tobacco by Dmitri Iosifovich Ivanovsky in Russia and Martinus Willem Beijerinck in Holland. They found that the agent that caused a mosaic pattern of light and dark green areas on tobacco leaves was smaller than a bacterium, being able to pass through a filter known to exclude bacteria. Subsequently, similarly small agents were shown to cause disease in animals.

**Particle Components**

As their extremely small size suggests, virus particles do not contain everything needed to reproduce themselves. They can multiply only within the cells of living organisms. Virus particles, also known as *virions*, universally contain one or more deoxyribonucleic acid (DNA) or ribonucleic acid (RNA) chains. Encoded in the sequence of nucleotides of the DNA or RNA is all information needed for virus reproduction. Virions also contain one or more types of capsid proteins, which protect the nucleic acid from destruction by the environment. Virions of some viruses contain additional coatings, including membranes derived from cell membranes containing distinctive, virus-encoded proteins.

Despite their simplicity and small size, viruses are not the smallest infectious agents of plants. That title belongs to viroids: small, circular RNA molecules with extensive secondary structures. They do not encode proteins and are not encapsulated. Viruses are classified based on the type of nucleic acid strands contained in virions, their mode of replicating the strand or strands, and the shape of virions.

Viruses may have RNA or DNA as genetic material. These nucleic acids may be single-stranded or double-stranded. If single-stranded, the instructions for making protein may be on the packaged strand (*positive sense*), on its complement (*negative* or *antisense*), or on both strands (*ambisense*). The genome of the virus may be in one nucleic acid strand or distributed among several. The sizes of plant viral genomes vary from about four kilobases (kb) to about twenty kb. Exceptions are the phycoenaviruses of algae whose DNAs are over three hundred kb. Virions may be roundish in shape (in actuality an intricate geometrical form called an icosahedron), rod-shaped, or filamentous.

**Replication and Evolution**

Most known plant viruses have positive sense RNA as genetic material. However, examples of negative sense and ambisense virion RNAs are known. Virus-encoded RNA replicase enzymes make strands complementary to the virion strands and then use the complements to make strands for packaging in progeny virions. The single DNA strands of begomoviral virion DNA are made by host-encoded DNA polymerases. Spanning the
RNA and DNA worlds, the virion DNA of plant equivalents of retroviruses is copied into RNA by host enzymes. The RNA is then copied into DNA by a virus-encoded enzyme.

Mistakes in viral replication are so frequent, and replication so prolific, that the population of viral genomes in an infected organism is a collection of many different sequences, called a quasispecies. Quasispecies allow viruses to evolve rapidly when novel environments act on them, to select a better adapted variant. The study of bacteriophages, viruses that infect bacteria, has contributed to understanding how plant viruses evolve and function.

Viral genomes are collections of gene modules, each with a different purpose. Viruses also evolve by exchanging modules. A reassortant arises when a novel mixture of RNA or DNA strands is packaged, while a recombinant arises by exchange of only part of one strand. Therefore, one virus may have multiple origins, one for each module. Relationships that have not been obscured by evolutionary divergence suggest modules themselves have multiple origins.

Viral Gene Function

Gene modules are classified into those coding for structural (virion-associated) proteins and those coding for nonstructural proteins. Structural proteins are those that can be found in virus particles, including capsid and envelope proteins and, in some viruses, include replication proteins. Plant viruses are unique in having a module required for movement of infection from one cell to the next. Indeed, an insect-infecting virus can spread in plants engineered to make a movement protein of a plant virus. Movement proteins alter plasmodesmatal connections between cells, but how they allow virus movement from cell to cell is still under intensive study. Movement of some viruses may depend on an as-yet-undetermined pathway for intracellular RNA movement.

Viruses also move from the infected leaves to other leaves. This movement follows the phloem pathway used by the plant to transport sucrose, with the infection moving from source leaves to sink leaves. Some viruses require the coat protein for long-distance movement. A few viruses move in the xylem. Movement of a virus from one plant to another requires a vector (another organism that assists in transmission); numerous insect species, nematodes, and fungi can transmit specific viruses. Specific viral proteins interact with a host-component to assure transmission specificity. Some viruses, such as tobacco mosaic virus, and viroids are transmitted only mechanically, by contact with animals or farm equipment.

Disease and Control

Viruses first grabbed scientists’ attention because they cause disease. In plants, symptoms associated with virus infection include leaf discoloration, foliar distortion, and fruit blotches. It is now known, however, that many viral infections are unapparent. Specifically what causes symptoms is not known.

Most plants are not susceptible to most viruses. A virus may be unable to replicate in cells of the plant species. The plant may mount a hypersensitive response in which it kills its own cells at the site of infection, to limit the infection. Overproduction of RNA, such as occurs during RNA virus infection, can lead to induction of an RNA destruction mechanism. Some viruses have evolved suppressors of that defense pathway. Systemic acquired resistance

Viruses, such as this Ebola virus shown at 108,000 × magnification, are extremely small parasites that have none of the structures characteristic of living cells. Many are little more than a protein-coated and particle-containing DNA or RNA.
is a pathogen-nonspecific state of resistance induced by infection with any kind of pathogen.

Infection of crop plants by viruses causes large agricultural losses. Control methods have been developed. Culling is the removal of infected plants. Controlling vectors with pesticides can limit the spread of viral outbreaks. Breeding genes from resistant plant species or varieties into the crop variety is a standard approach. Such resistance may break down as viruses evolve to overcome the new genes. In cross protection, plants are purposely inoculated with a mild strain of the virus and become resistant to other strains. Cross protection led to the biotechnological pathogen-derived resistance, in which protection comes from a viral DNA element incorporated into the plant chromosome.

*Ulrich Melcher*

**See also:** Bacteriophages; Cell-to-cell communication; DNA in plants; Plant biotechnology; Plant diseases and disorders; Proteins and amino acids; RNA; Viral genetics; Viral pathogens.

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**WATER AND SOLUTE MOVEMENT IN PLANTS**

**Categories:** Physiology; transport mechanisms

Plants have two separate transport systems for conducting essential nutrients and water into and through the plant. These take the form of two types of vascular tissue. One, for water and minerals, the xylem, originates in the root and moves water and minerals upward. The second, the phloem, moves dissolved carbohydrates out of the leaves to other plant parts in which they are used for growth or stored.

Vascular plant tissue is designed to meet the nutritional transport needs of land plants. Xylem tissue has two types of transport cells; both are nonliving when functional. The smaller in diameter is the **tracheid**. These have a narrow bore and tapering, overlapping ends. These tapered ends have numerous **pits**, which are narrow passages to adjacent cells. Water passes through the cell to the next cell through these pits. Because of the narrow openings from one cell to the next, the flow of water tends to be rather small.

The second cell type in the xylem is the **vessel element**. These cells have a much larger diameter than the tracheids and have endwalls that rarely overlap and are totally open. This second type is very much like a section of water pipe, with no endwalls at the end of each section to restrict the flow of water. The structure of the phloem is similar to that of the xylem in that two cell types are found. Unlike the cells in the xylem, however, only one of the phloem cells, called the **sieve element**, actually transports fluids; the other is called the **companion cell** and seems to be involved in unloading the phloem.

**Water Movement in the Xylem**

One of the early explanations for water and mineral movement in plants was “root pressure.” The water in the xylem in the root contains ten to fifteen times the mineral content of the soil water, an accumulation that cannot be explained by diffusion or osmosis. Botanists now realize that the root hairs, those fingerlike outgrowths of the epidermal cells that expand the surface area of the roots to hundreds of square meters, and the cells of the cortex are able to use energy to collect mineral ions, such as magnesium ions, which are then transported into the xylem in the root.

As mineral ions accumulate in the root’s xylem, water diffuses into the root as well. This accumulation of mineral ions and water creates a type of pressure called **turgor pressure**. This pressure is identical to the pressure in the water pipes of a house. Any time a faucet is opened, water moves toward the opening. This movement is called bulk flow or **convective movement** or **hydraulic lift**.

Root pressure is generally limited by two factors. The first is the large amount of energy needed to accumulate mineral ions from the soil. The second is the problem associated with the narrow passages between tracheids. As a result, root pressure is generally limited to plants of a few meters in height or less. While root pressure is easily demonstrated in the laboratory, it is clearly not able to move water to the tops of trees, which may reach a height of 130 meters (400 feet) or more.

**Cohesion-Adhesion Theory**

The means whereby nutrients and water are transported through large plants and trees is explained by the **cohesion-adhesion theory**. Leaves are the primary sites of photosynthesis in most plants. During photosynthesis atmospheric carbon dioxide is required to make glucose, which is converted to sucrose for transport. As a result the leaves’ surface is covered by small openings called **stomata**. As carbon dioxide is entering the leaf, water is evaporating from the leaf in a process called **transpiration**. Transpiration is driven by the much lower water content of the atmosphere compared to the water content of the leaf.

Transpiration generates a **tension**, from 0.1 to 5 megapascals in the xylem of the leaf. This tension is transmitted through the solid water columns of the xylem to the roots and increases the uptake of water.
in the root. At the more negative part of this range, water should exist as a gas rather than a liquid. That, however, is not the case, because the cell wall, with its massive number of -OHs, stabilizes the water via adhesion—that is, by forming hydrogen bonds with water molecules, which are also hydrogen bonded to each other via cohesion. One might expect the water column to break under its own weight (called cavitation), but that does not occur either. Lyman Briggs (1950) demonstrated that a small column of water requires at least 25 megapascals before it will cavitate. For example, as oil in an oil lamp is used in the burning end of the wick (transpiration), more oil is pulled (via adhesion and cohesion) up the wick (similar to a stem or root) from the oil in the base of the lamp (similar to the soil). The moving stream, called the transpiration stream, transports water, mineral ions, and sometimes other materials from the roots to the leaves.

Evidence for the Cohesion-Adhesion Theory

Evidence to support the cohesion-adhesion theory was provided by Per Scholander (1965). He reasoned that if the xylem were under tension when a twig is cut from the plant, the water columns in the xylem would pull back to a position that could be supported by atmospheric pressure. If this twig were placed in a closed chamber with the cut surface exposed and the pressure were increased gradually in the chamber, it should be possible to force the water columns out to the cut surface of the twig. The pressure would be a direct measure of the tension in the xylem but of opposite sign, that is if 2 megapascals were necessary to get the water out to the cut surface the twig, it must have been under -2 megapascals, since tension is a negative pressure.

Scholander built a small aluminum chamber with an associated pressure gauge and gas supply, called the Scholander Pressure Chamber. He then traveled about and measured the tension in numerous parts of many trees, under a variety of environmental conditions. He and many others since have reported tension in the -0.1 to -5 megapascals range for leaves, twigs stems, and roots, with the values becoming more negative as one takes samples higher on the same plant.

The Problem of Transpiration

Transpirational water loss is a major loss to the plant. As much as 95 percent of all the water entering the roots is lost by transpiration. Transpiration is under environmental control. Stomatal opening is controlled by the carbon dioxide level of the interior of the leaf; as carbon dioxide inside decreases, the stomata open. With the stomata open, a drop in humidity, an increase in temperature, an increase in air currents, or all these conditions will cause an increase in transpiration and the tension in the xylem.

Water moves into plants through roots but can rise only so far by means of “root” pressure or turgor pressure. The cohesion-adhesion theory has been used to explain water movement in larger plants and trees.
Transpiration will continue until darkness or until the water in the plant is so reduced that the plant wilts.

When the xylem is under tension, air bubbles may enter the water columns; these are called embolisms. When a water column is broken by an embolism, it will not transport water. Thus, water transport is reduced. There is some evidence that these embolisms may be repaired.

Movement in the Phloem

Movement of materials in the phloem—again, the conducting tissue that is responsible for moving food manufactured in the leaves to other parts of the plant, including the roots—is driven by pressure rather than by tension. The leaves are the primary sites for photosynthesis and thus its product sucrose; leaves, therefore, may be called the source. These carbohydrates are loaded into the phloem in the leaf, up to 1.2 moles per kilogram of water. With more solute in the phloem, water diffuses into the phloem from the xylem. This loading of sucrose and influx of water generate pressure, which is transmitted throughout the phloem. Any site in the plant, known as a sink, which is actively using carbohydrates for the production of new cells in fruits or the storage of starch in the roots, relieves the pressure, and the assimilate stream, as the fluid in the phloem is called, will move in the direction of the relief, much like a dripping faucet. This assimilate flow will continue as long as carbohydrates are being consumed in an area. As a result of high levels of carbohydrates in the source and the use of carbohydrates in the sinks, the rate and direction of flow of materials in the phloem are controlled. Sinks may change from hour to hour during the day, sometimes sending materials to the roots, other times sending materials to the flowers or even developing leaves.

Evidence for Pressure in Phloem Transport

Evidence for pressurized phloem transport is easily collected using aphids. Aphids have sharp, hollow snouts, which they are able to insert into sieve cells very accurately. To investigate phloem transport, scientists have allowed aphids to infest a plant. Once they are settled, it is fairly easy to sever the snouts from the bodies of the aphids. These snouts will continue to “bleed” phloem sap for several days. Bleeding could not occur if the phloem were under tension, which supports the theory of pressurized phloem transport.

Additional evidence for pressurized phloem transport was provided by Ernst Munch in 1927 as a laboratory model. He attached two dialysis bags together by way of a glass tube. Into one of the bags he placed a sucrose solution (the source), and water was placed in the other (the sink). When both bags were placed in water, the water diffused into the sucrose solution. This generated a pressure that was transmitted via the tube to the other bag and caused water to flow out of the second bag. Thus, the materials in the sucrose bag were transported to the other bag.

James T. Dawson

See also: Active transport; Angiosperm cells and tissues; Cells and diffusion; Endocytosis and exocytosis; Liquid transport systems; Osmosis, simple diffusion, and facilitated diffusion; Plant tissues; Root uptake systems; Roots; Leaf anatomy; Shoots; Stems; Tracheobionta; Vesicle-mediated transport.

Sources for Further Study


WETLANDS

Categories: Ecosystems; water-related life

Wetlands, transitional areas between aquatic and terrestrial habitats, are home to a variety of flood-tolerant and salt-tolerant plant species.

Wetlands represent one of the most biologically unique and productive of all natural habitats. In their unaltered state, these water-influenced areas are used by a variety of wildlife species. These habitats also have the ability to take up and store water during floods, and their soils and plants have the ability to remove nutrients and heavy metals from water. The recognition of these values helped to slow the rate of wetlands loss to such uses as agricultural development and urban expansion. A desire to protect remaining wetland acres has led to a significant movement for wetlands preservation.

Definition of Wetlands

Ecologists recognize wetlands as a type of ecotone. Ecotones are unique areas that represent a transition from one type of habitat to another. Often, these transitional areas have characteristics of both habitats. Wetlands are areas located between aquatic, water-based habitats and dry land. Because they are located at the edge of an aquatic habitat, wetlands are always influenced to some degree by water. They are not always underwater, as are aquatic habitats, and they are not always dry, as are terrestrial habitats.

The most important environmental factor in wetlands is the periodic or frequent occurrence of water. This presence of water influences both the nature of the soil and the flora and fauna of a region. Soils which experience periodic coverage with water become anoxic, develop a dark color, and give off an odor of hydrogen sulfide. These soil characteristics differ from those of upland soils and give wetland soils their unique hydric nature. In these soils influenced by water, only flood-tolerant hydrophyte species can exist. Hydrophytic plants vary in their tolerance to flooding from frequent (such as bald cypress) to infrequent (such as willows).

In defining a particular area as a wetland, often all three of the components listed above are used: water, hydric soils, and hydrophytic plants. However, the presence of water is not always a reliable indicator because water rarely covers a wetland at all times. Often, a wetland is dry during a period of low river flow or during a low tide. For this reason, only hydric soils and hydrophytic plants should be used as reliable indicators of a wetland.

Classification of Wetlands

The broadest classification of wetlands includes two categories: freshwater and saltwater wetlands. Freshwater wetlands occur inland at the edges of rivers, streams, lakes, and other depressions that regularly fill with rainwater. Saltwater wetlands occur along the coast in bays, where salt water and fresh water mix and wave energy is reduced.

Of the two categories, freshwater wetlands are by far the most common. Freshwater wetlands are subdivided into two categories: tree-dominated types and grass-dominated types. Tree-dominated freshwater wetlands include areas that are frequently covered with water (such as cypress swamps) and those that are only occasionally covered with water (such as bottomland forests). Grass-dominated types include freshwater marshes, prairie potholes, and bogs.

While freshwater marshes are widespread, prairie potholes and bogs occur regionally in the United States. Prairie potholes are located in the central portion of the United States, while bogs are found in the Northeast and Great Lakes regions.

Saltwater wetlands are also subdivided into tree-dominated and grass-dominated types. Tree-dominated types include tropical mangrove swamps. Grass-dominated types can be further subdivided into salt marshes and brackish marshes. Salt marshes occur in bays along the coast where salt
water and fresh water mix in almost equal proportions. Brackish marshes occur farther inland than salt marshes do; their mix contains less seawater and more fresh water. Both grass-dominated types are common in bays along the Gulf of Mexico and the East Coast of the United States.

The Biota of Wetlands
The most noticeable feature of all wetlands is the abundance of plant life. A variety of plant species thrive in wetlands, but each occurs only in a particular kind of habitat. Freshwater wetlands that are frequently flooded provide a favorable habitat for water-tolerant trees, such as bald cypress and water tupelo, and water-tolerant herbaceous plants, such as cattail, arrowhead, bulrush, spike rush, water lily, and duckweed. Less frequently flooded freshwater areas support trees such as willow, cottonwood, water oak, water hickory, and red maple. Seawater areas in tropical bays favor the development of mangroves, while temperate bays favor the development of cordgrass.

Wetland plants provide a habitat for a variety of animals. Cypress swamps and cattail marshes support a large assortment of animals, including alligators, ducks, crayfish, turtles, fish, frogs, muskrat, wading birds, and snakes. Likewise, mangrove prop roots provide attachment sites for a variety of invertebrates and shelter for numerous small fish, while upper branches provide roosting and nesting sites for birds. In salt marshes, mussels live among cordgrass roots, while snails, fiddler crabs, oysters, and clapper rails live among plant stalks. When water covers cordgrass at high tide, plant stalks shelter small fish, crabs, and shrimp seeking refuge from large predators.

The Value of Wetlands
The amount of plant material produced in wetlands is higher than that produced in most aquatic and terrestrial habitats. This large amount of plant material supports an abundance of animal life, including commercially important species such as crayfish, ducks, fish, muskrat, shrimp, and crabs.

The biotic value of wetlands is well recognized, but it represents only a part of their total value. Wet-
lands provide “services” for other areas that often go unrecognized. For example, freshwater wetlands are capable of storing large amounts of water during periods of heavy rainfall. This capability can be important in minimizing the impact of flooding downstream. Saltwater wetlands along coastlines are an effective barrier against storms and hurricanes. These natural barriers hold back the force of winds, waves, and storm surges while protecting inland areas. Wetlands are also capable of increasing water quality through the trapping of sediment, uptake of nutrients, and retention of heavy metals. Sediment trapping occurs when moving water is slowed enough by grass and trees to allow suspended sediment particles to settle. Wetland plants take up nutrients, such as nitrates and phosphates, from agricultural runoff and sewage. For this reason, wetlands are used as a final treatment step for domestic sewage from some small cities. Wetland soils are capable of binding heavy metals, effectively removing these toxic materials from the water.

Wetlands Loss and Preservation

It is estimated that the United States once contained more than 200 million acres of wetlands. Less than half this amount remains today. Once considered wastelands, wetlands were prime targets for “improvement.” Extensive areas of freshwater wetlands and prairie potholes have been drained and filled for agricultural development. Saltwater wetlands have been replaced by urban or residential development and covered with dredge spoil. Wetlands loss rates have slowed, but an estimated 300,000 acres continue to be lost each year in the United States. The loss of wetlands habitat threatens the survival of a number of animal species, including the whooping crane, American crocodile, Florida panther, manatee, Houston toad, snail kite, and wood stork.

Since the 1970’s the rate of wetlands loss has slowed for several reasons. One is the passage of federal and state laws designed to protect wetlands; another is the efforts of conservation organizations. At the federal level, the single most effective tool for wetlands preservation is Section 404 of the Clean Water Act. Section 404 requires that a permit be issued before the release of dredge or fill material into U.S. waters, including wetlands. At the state level, Section 401 of the Clean Water Act allows states to restrict the release of dredge or fill material into wetlands. There are several conservation organizations that support wetlands preservation, including Ducks Unlimited, the National Audubon Society, the National Wildlife Federation, and the Nature Conservancy. These organizations keep the public informed regarding wetlands issues and are active in wetlands acquisition.

Steve K. Alexander

See also: Aquatic plants; Biomes: types; Ecosystems: studies; Halophytes; Pacific Island flora; Peat; Rice.

Sources for Further Study
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a valuable examination of how cultural attitudes shape the physical world. Provides a compelling understanding of environmental conflicts.


## WHEAT

**Categories:** Agriculture; economic botany and plant uses; food

*Wheat (Triticum sativum) is the world’s most important grain crop, serving as a natural food source for much of the world’s population. The wheat grain is easily refined to raw foods such as flour, which can be used in countless recipes.*

Throughout the world, large portions of agricultural land are devoted to the production of wheat. Wheat is the national food staple for more than forty nations and provides 20 percent of the total food calories for the world’s population; it is the major staple for about 35 percent of the people of the world. In the United States, wheat constitutes a large part of the domestic economy, makes up a large part of the nation’s exports, and serves as the national bread crop.

The cultivation of wheat is older than the written history of humankind. Its place of origin is unknown, but many authorities believe that wheat may have grown wild in the Tigris and Euphrates Valleys and spread from there to the rest of the Old World. Wheat is mentioned in the first book of the Bible, was grown by Stone Age Europeans, and was reportedly produced in China as far back as 2700 B.C.E. Wheat was brought to the New World by European settlers and was being grown commercially in the Virginia Colony by 1618.

**Botany and Classification**

Wheat is an annual grass, but its structural morphology varies considerably, depending on the type. The wheat flowers and subsequently the seed are borne on spikes originating from the top of the plant. Wheat is widely adapted throughout the world and can grow in many climates. It can be found growing from near the equator to 60 degrees north latitude. About the only places wheat does not grow are those with climates that continually stay hot and moist.

Most commercially grown wheats can be separated into either hard grain wheat or soft grain wheat. Hard wheat is usually dark in color and possesses no white starch, while the soft wheat is generally much lighter in color and shows a white starch. Both hard and soft wheat contain a protein...
called gluten, which enables leavened dough (dough after yeast has been added) to rise by trapping the gas bubbles produced during fermentation by the yeast, but hard wheat contains more gluten than does soft wheat. As a result, the hard wheats are much more desirable for making bread. The weaker flour produced by the soft wheats is preferred for making biscuits, crackers, pie crusts, and starchy breakfast foods. The most common types of commercially planted wheat are common wheats, durum wheat, and club wheat.

The common wheats include hard red winter wheat, grown in Texas and northward up through Kansas; hard red spring wheat, grown in the north central states (North and South Dakota, Idaho, Montana, and Minnesota); soft red winter wheat, grown in the east-central United States (Ohio, Michigan, Missouri, Illinois, and Indiana); and white wheat, grown around the Great Lakes and in the far West. Hard red winter wheat and hard red spring wheat are primarily used in making bread, while soft red winter wheat and white wheat are used chiefly for making cakes, cookies, pies, and other pastries. Durum wheat is a very hard wheat also grown in the north-central United States. Durum wheat is primarily used for making pasta such as macaroni and spaghetti. Club wheat, also grown in the far West, is used to make the starchy flours required for making pastries. Additional wheat types include poulard, emmer, spelt, polish, and einkorn; these types are of little importance in the United States.

Production and Harvest

Production begins with the selection of the seed. So that high yields can be obtained, extreme care is taken to select only the highest-quality seed. For winter wheat, the seed is planted in the fall, generally at the time of the average first frost. This timing allows the crop to make a stand before winter but is not so early that it begins rank growth or starts to send up tall shoots. Spring wheat is generally planted as early as is practical in the spring, which is usually early March in the areas where spring wheat is normally grown. In the United States, almost all wheat is planted by drilling the seed into the soil. Drilling provides for the best germination and the least amount of winter killing.

Harvest time for wheat is determined primarily by the moisture content of the grain. Most wheat in the United States is harvested with mechanical combines, and the ideal seed moisture for combine
harvest is 12 to 13 percent. After harvesting, the grain is taken to the mill. During the milling process, the grain is washed and scoured to remove fuzz and foreign material. The grain is then tempered by soaking in water to toughen the bran. After tempering, the grain is crushed by a series of corrugated rollers. The bran, produced primarily in the seed coat, is then separated from the starch. The milled flour is often chemically bleached to improve the color and baking quality and enriched with vitamins and minerals to replace those lost by removing the bran. The average flour yield is 70 to 74 percent of the weight of the grain.

D. R. Gossett

See also: Agriculture: world food supplies; Alternative grains; Corn; Grains; Grasses and bamboos; Green Revolution; High-yield crops; Rice.

Sources for Further Study

WOOD

Categories: Anatomy; economic botany and plant uses; forests and forestry

Wood is a fibrous plant tissue that functions in support and water conduction. It composes the bulk of stems and roots in the magnoliids and eudicots of the angiosperms (phylum Anthophyta), as well as in the conifers (phylum Coniferophyta). It is formed by thickening growth, which persistently adds new layers that accumulate as a cylinder of wood between the pith and the bark.

Secondary Xylem
Technically, wood is secondary xylem. The growth in girth that produces it is called secondary growth. This growth occurs after the stem or root segment has completed its increase in length, or primary growth. Secondary growth also yields, in much smaller amounts, secondary phloem, which becomes a part of the bark.

Secondary growth results from divisions of the cells in a layer called the vascular cambium, located between the bark and wood. Cambial cell divisions that are oriented toward the interior of the stem or root (that is, on the pith side of the cambium) result in a new layer of secondary xylem cells at the periphery of the layers formed previously. Cambial cell divisions oriented toward the exterior (on the bark side) of the stem or root add a new layer of secondary phloem to the inside of the bark. The angiospermous group Monocotyledones (the monocots) forms neither secondary xylem nor secondary phloem, because the fibrous conducting tissues are arranged in scattered bundles rather than in layers.

Wood Structure and Growth Rings
Wood is composed of cells arranged in two orientational systems. Most of the cells are oriented axially, in approximate alignment with the long axis of the stem or root. The rest are oriented radi-
ally, perpendicular to the long axis. The axial, or longitudinal, cellular system functions in both support and water conduction. In conifers, which include pines, spruces, and firs, this system is composed mainly of tracheids, with some parenchyma cells. In angiosperms, which include oaks, ashes, and elms, the axial system contains, in addition to tracheids and parenchyma, vessel members and fibers. Vessel members are one of angiosperm wood’s most distinctive features because they commonly enlarge greatly in diameter. The radial system in both gymnosperms and angiosperms is composed mainly of parenchyma cells. These are aggregated into rays, which conduct nutrients from the phloem to the interior of the stem or root. In temperate-zone trees, the vascular cambium usually lays down a single increment of secondary xylem each year, during the warm season. The wood formed early in the growing season, called earlywood, is less dense, and in some species has a different cell composition than the latwood. Because of the within-increment contrast in cell characteristics, the increments appear as annual growth rings on cross sections. Trees growing in relatively uniform tropical climates do not form annual rings because growth is not generally limited to a particular season.

Softwoods and Hardwoods
Angiosperm woods are often referred to as hardwoods and coniferous woods as softwoods. Although these terms are generally accurate, some hardwoods are actually softer than some softwoods. For example, the conifers known as “hard pines” are technically “softwoods,” and basswood is technically a “hardwood,” yet hard pines are much harder than basswood. Softwoods compose much of the commercial lumber in the Northern Hemisphere.

Sapwood and Heartwood
Because each new increment of wood is produced at the periphery of the preceding increment, the wood that is nearest the bark is the youngest. Eventually, the older wood, which is deeper within the tree, loses its capacity to function in conduction and storage. It accumulates oils, resins, tannins, and other substances. This darker, nonconducting, inner wood is called heartwood. The lighter, functioning, outer wood that surrounds it is called sapwood. The relative amounts of heartwood and sapwood, and the degree of their color contrast, vary with the species.

Reaction Wood
Leaning branches or trunks produce a specialized kind of wood, called reaction wood, that generally helps the stem return to a more vertical orientation. In conifers, reaction wood develops on the undersides of leaning branches or trunks and is called compression wood. In angiosperms, it develops on the upper sides and is called tension wood. In leaning conifer stems, the growth rings are much wider on the compression-wood side of the stem than in the ordinary wood on the opposite side.

Wood’s Appearance
Certain characteristics that affect wood’s appearance are quite variable. Color is one. For example, black walnut, widely considered North America’s finest cabinet wood, owes its aesthetic appeal largely to its heartwood, which is often a rich chocolate brown, in contrast to the much lighter heartwood of many other species. Grain, texture, and figure also affect the appearance of wood. Grain is considered straight if the longitudinal wood cells closely parallel the stem’s long axis. Deviations produce spiral, wavy, and interlocked grains. Texture, which refers to the sizes and proportional distribution of the various kinds of wood cells, may be coarse or fine. Figure, or distinctive markings and patterns on longitudinal wood surfaces, results from basic anatomical structure, irregular coloration, and defects or from irregular patterns as in “bird’s-eye maple.”

Knots
During the course of secondary growth, the bases of the branches that had formed when a tree was younger are typically buried within the trunk or within a larger branch, through addition of successive increments of woody tissue. That part of a branch that becomes overgrown by secondary growth is called a knot. Knots generally degrade the quality and value of lumber.

See also: Angiosperm cells and tissues; Angiosperms; Conifers; Dendrochronology; Forest and range policy; Forest management; Forests; Gymnosperms; Logging and clear-cutting; Petrified wood; Plant tissues; Stems; Timber industry; Wood and charcoal as fuel resources; Wood and timber.
WOOD AND CHARCOAL AS FUEL RESOURCES

Categories: Economic botany and plant uses; forests and forestry

Globally, the amount of wood and charcoal used for fuel exceeds the combined amount of wood used for all other purposes. Between 60 percent and 95 percent of the total energy needs of some developing countries are met by wood.

Wood is one of the oldest energy sources. Rough wood and bark may be burned directly for fuel, or wood may be converted into charcoal by charring in a kiln from which air has been excluded. According to the Food and Agriculture Organization of the United Nations, more than half of all the wood utilized in the world at the end of the twentieth century was used for energy production. Wood provides for as much as 60 to 95 percent of the total energy needs of some developing countries, but it provides less than 5 percent of the total energy required in most developed countries. As a rough estimate, around two billion people use wood for their cooking and heating. In some developing areas of the world, fuelwood demand is greater than the supply; particularly in parts of Africa, consumption significantly exceeds replacement of the stock of trees.

Wood fuel also finds some use in industry, as in the paper industry. Industries often burn waste material from other manufacturing processes. Bark removed from raw logs, sawdust, planer shavings, sander dust, edges, and trim pieces may all be burned to generate power while disposing of the unwanted material. Small wood particles such as sawdust and shavings may be compressed to produce briquets or “logs” for use as fuel.

Increasing numbers of forests are being planted and cultivated for the sole purpose of energy production. Entire trees are chipped and burned for energy production at the end of a rotation. These forests may be known as forest plantations, tree farms, or energy forests. This type of wood production and fuel use has the potential to reduce dependency on fossil fuels. Energy forests remove carbon from the atmosphere over their life span, then release this carbon in various forms during combustion for energy production.

Types of Combustion

The direct burning of wood occurs when the surface is intensively irradiated so that the temperature is raised to the point of spontaneous ignition, anywhere from 500 to more than 900 degrees Fahrenheit (260 to 500 degrees Celsius), depending on the conditions. More common is indirect combustion, in which the wood breaks down into gases, vapors, and mists, which mix with air and burn.
About 1.4 pounds (0.6 kilogram) of oxygen are required for the complete combustion of a pound of wood. At normal atmospheric concentrations, this implies that about 6 pounds (2.7 kilograms) of air are needed for the complete combustion of a pound of wood. During combustion, gases such as carbon dioxide and carbon monoxide, water vapor, tars, and charcoal are produced, along with a variety of other hydrocarbons. Dry wood or bark and charcoal burn relatively cleanly; wetter wood produces a larger amount of emissions. Collectors may be used to remove particulate matter from industrial sources. It is less feasible to reduce emissions from cooking stoves (either chemically or mechanically), however, and cooking stoves are a major source of human exposure to emissions from wood burning in much of the world.

**Charcoal**

Charcoal is lighter than wood and has a higher energy content. It takes approximately 3 pounds (1.4 kilograms) of wood to produce 1 pound (0.45 kilogram) of charcoal. The exact conversion ratio depends on the tree species, the form of wood utilized, and the kiln technology used. Charcoal is more efficient to transport than wood, and it can be burned at higher temperatures. It is used both for domestic purposes and, in some countries—Brazil is one—as an industrial fuel. In general, charcoal is considered a cleaner, less polluting fuel than wood in that its combustion produces fewer particulates. Charcoal was used extensively as an energy source for smelting and metalworking from prehistoric times into the Industrial Revolution, but coal eventually became the principal alternative energy source for these processes in areas where it was available. Today, petroleum and natural gas are major sources of energy for industrial processes.

**Energy Content**

The average recoverable heat energy from a pound of wood is about 8,500 British thermal units (Btu’s). The value ranges from 8,000 to 10,000 Btu’s per pound for different species. In some efficient
processes, 12,500 Btu's can be recovered from a pound of charcoal. If wood with a high moisture content is burned, some of the energy produced by combustion is absorbed as the moisture evaporates, reducing the recoverable energy.

**Impacts on Environment and Health**

Traditional uses of wood fuel for cooking and home heating utilize woody material obtained from tree pruning or agroforestry systems. These uses are sustainable and have relatively little environmental impact in areas with low human population levels, but they may be associated with serious air pollution problems as well as widespread deforestation and erosion if they are the major sources of energy for a large or concentrated population. In most of the areas that have deforestation problems, the problem is primarily attributable to changes in land use, particularly the opening of land for agriculture and grazing. Fuelwood is often recovered during such land-use changes, but the need for fuelwood production is often a secondary cause or by-product of deforestation.

Industrial power production that utilizes available technology to ensure high-temperature, virtually complete combustion minimizes hydrocarbon and particulate emissions and can be designed to meet most existing air quality standards. Less efficient domestic combustion may be associated with unacceptable levels of human exposure to airborne particulates, carbon monoxide, and other hydrocarbons produced by incomplete combustion. The health effects of exposure to domestic wood fires are difficult to determine, since they often occur along with other factors known to increase health risks.

David D. Reed

See also: Coal; Deforestation; Forest and range policy; Forest management; Peat; Reforestation; Sustainable forestry; Timber industry; Wood.

**Sources for Further Study**


**WOOD AND TIMBER**

**Categories:** Economic botany and plant uses; forests and forestry

*The use of products derived from woody plants, notably timber, takes advantages of wood’s insulating ability, strength, workability, and abundance as a construction and engineering material.*

No other material has all the advantages of wood. One material may equal wood in insulating quality but lack its abundance and low cost. Another may rival it in strength but fail on the point...
of workability. A third may rank with it in workability but fail to measure in durability. If wood were a newly discovered material, its properties would startle the world.

Since the human race first started to build crude shelters at the dawn of civilization, wood has been available as a construction material. Wood has long been used in the construction of buildings, bridges, and boats. As technology developed, wood also found a variety of less readily recognizable forms, such as paper, films, and pulp products, many of which are mainstays of daily life.

Woody material is produced in many plants, but its most useful manifestation is in the limbs and trunks of trees. There is a great diversity of tree species, and most climatic zones have at least one tree that has adapted to the prevailing conditions within that area. Thus, wood is available in most inhabited regions of the world. Wood has played a dominant role as a construction and engineering material in human society, yet humankind has lived with this material for so long that its significance is easily overlooked.

**Hardwoods and Softwoods**

Trees are broadly classified into hardwoods and softwoods. These terms can be misleading, as they are not connected to the actual hardness of the wood. Hardwoods are broad-leaved, deciduous trees. Softwoods, on the other hand, have narrow, needlelike leaves and are usually evergreens. Oak, birch, and basswood are common hardwood species, whereas longleaf pine, spruce, and cypress are softwoods. While some hardwoods (for example, oak) are really hard, many others (basswood) are nevertheless softer than the average softwood. In fact, balsa is classified as a hardwood, even though it is one of the softest woods in the world.

By far, the majority of timber used in building structures comes from the softwood category. Douglas fir, southern pine, and redwood are some of the important softwood species widely employed in structural applications. They are relatively strong and can be used in structural elements such as joists, beams, and columns. By comparison, the stronger hardwood species, such as oak, are relatively heavy, hard to handle, and hard to nail. As far as construction is concerned, their utility is limited; they are generally only used in flooring, cabinetry, and furniture.

**Supply and Disposal**

Wood is a renewable resource. It does not exist in finite quantities; rather, it is constantly produced in growing trees. If forests are carefully managed, timber can be harvested on a sustained-yield basis, year after year. Wood is also a reusable resource. The recycling of timber from old buildings is well documented. The ease with which wood can be cut, joined, and worked into various shapes permits the extension of its functional life beyond that of many other construction materials.

Wood is a biodegradable natural product: It can be reduced to its constituent carbohydrates and extractives through degradation. After wood has reached the end of its useful service, it can be disposed of with little damage to the environment. Unlike plastics or chemicals, timber has a very low pollution potential. A study quantified the pollution potential of various construction materials, finding that steel is five times more polluting than timber, while aluminum and concrete blocks are respectively fourteen and twenty-four times more polluting. From an environmental standpoint, timber is recognized as the most appropriate construction and engineering material.

**Logging**

Tremendous quantities of timber are consumed each year throughout the world. In the early and mid-1990’s, an average of about 3.5 billion cubic meters of timber was harvested annually. The majority of hardwood harvest is used for fuel, while softwoods are primarily used in construction and manufacturing. To produce the large quantities of timber needed annually, logging operations have become highly organized and technologically advanced. When trees are removed in harvest, steps are taken to provide for forest renewal and to prevent soil erosion. Such steps include leaving some trees to produce seeds, transplanting young trees, and other methods of reseeding.

Sometimes a “prelogging” operation is undertaken before the main harvest. In this phase, the small trees are removed for conversion into poles, posts, and pulpwod. During harvest, various types of machinery are used to cut trees close to the ground. The limbs are then removed from the fallen trees, and the trunks are bucked into various lengths and transported to sawmills for further processing. The remaining tree limbs are converted into chips for sale to pulp and paper mills. Fre-
quently, roads are built to facilitate the transportation of trunks and the deployment of heavy logging equipment. At the conclusion of harvest, refuse should be disposed of so that it will not interfere with the growth of new trees.

Owing to careful management of forests and improved efficiency of logging operations, the supply of timber in the United States currently renews itself at a higher rate than the removal level. It must be pointed out, however, that growth in world population will inevitably bring about an increase in timber consumption. The adequacy of timber supply will be a matter of concern in the future.

Physical Structure and Strength
As a material of botanical origin, wood is composed of hollow, elongated fibers. These fibers are usually arranged parallel to one another in the direction of the length of the trunk. They are cemented together by a substance known as lignin. The fibers in softwoods are longer than those in hardwoods. The length of the fibers, however, is not a criterion of the strength of the wood. Owing to the parallel arrangement of their fibers, wood possesses different mechanical properties in different directions and is said to be anisotropic. As an example, timber is five to ten times as strong in compression parallel to the grain as it is perpendicular to the grain. The varying strength of timber in different directions must be taken into consideration in construction design. By contrast, metals are isotropic and have the same characteristics in any direction.

The strength of timber is affected by its moisture content. Wood in a living tree typically contains more moisture than the surrounding atmosphere. When a piece of timber is cut from the log and exposed to air, its moisture content decreases to an equilibrium value determined by the temperature and relative humidity of ambient air. Should wood dry below a value called the fiber saturation point, it becomes stronger and stiffer. That is why higher design stresses are allowed for timber which is used under relatively dry conditions, such as a girder in a building, than for timber used under relatively moist conditions, such as in a waterfront house or in a bridge.

Wood has a very high strength-to-weight ratio. Compared with many other construction materials at the same weight, wood is stronger. For instance, in bending tests, Douglas fir has a strength-to-weight ratio which is 2.6 times that of low-carbon steel. Wood also has very high internal friction within its fibrous structure and is therefore a good absorber of vibrations. It has much greater damping capacity than other materials, particularly the metals. That explains why wood is the preferred material for construction of houses in earthquake-prone regions. Finally, timber structures can be designed to withstand impact forces that are twice as large as those they can sustain under static conditions. Materials such as steel and concrete do not permit such increase in the applied forces. This exceptional impact strength of wood is utilized in timber structures such as bridges or the landing decks of aircraft carriers.

Insulation and Fire Resistance
Due to its fibrous composition, wood has excellent insulating properties. At a low moisture content, wood is classified as an electrical insulator. This is what makes wood such a common material for high-voltage power-line poles and for tool handles. Wood is also an effective thermal insulator. The thermal conductivity of timber is only a fraction of that of metals and other common construction
materials. For example, bricks are about 6 times more conductive than timber, and glass and steel are respectively 8 and 390 times more conductive.

By using stud walls or layers of spongy materials, thermal insulation of timber structures can be further enhanced. In addition, timber structures may be designed to provide a very degree of acoustical insulation. (Sound is transmitted through vibration of air particles.) Because of its high vibration-damping capacity, wood is also a good acoustical insulator.

It is well known that wood is combustible. On the other hand, wood that is thick enough is also fire-resistant. Because of the low thermal conductivity of wood, the high temperatures of a fire cause a temperature rise for only a short distance into the wood from the surface exposed to the fire. This is the reason larger timber members may continue to support a structure in a fire long after an insulated steel member has collapsed because of elevated temperatures. In fact, buildings framed with large timber members have been given the highest rating by fire underwriters among all common buildings erected.

Fabrication and Workability
Wood may be cut and worked into various shapes with the aid of simple hand tools or with power-driven machinery. It therefore lends itself not only to conversion in a factory but also to fabrication on-site. It is the latter fact that principally keeps conventional wood-frame construction fully competitive with any method of prefabrication of houses yet employed.

Timber can be joined with nails, screws, bolts, and connectors, all of which require the simplest kinds of tools and produce strong joints. Timber may also be joined with adhesives, which can produce a continuous bond over the entire surface to which they are applied and develop the full shear strength of the solid timber. This use of adhesives provides a means of fabricating timber members of different shapes and almost unlimited dimensions. The prefabrication of large wood trusses, laminated beams and arches, and stress-skin panels has permitted wood to remain extremely competitive as a building and engineering material.

Durability
Wood is remarkably resistant to decay and is inert to the action of most chemicals. It is widely used in facilities for bulk chemical storage; the timber may be in direct contact with the chemicals. When wood is exposed to atmospheric conditions, it slowly erodes under the action of weather at a rate of about 0.25 inch per century. If properly used, wood lasts for a long time. Decay and insect damage are often significant problems, but these can be minimized by following sound methods of design in construction and by using properly seasoned timber. In situations where biological wood-destroying agents are difficult to control, the decay resistance of timber can be maintained by impregnation with suitable preservatives.

Significance of Wood
Wood has remained a primary construction material for thousands of years, essentially because no competitive material has all the advantages of wood. The importance of wood as a raw material for pulp and paper is also profound. No other natural substance can meet the increasing demands of modern society for paper and other pulp products. It is also unlikely that a synthetic material can be made economically to rival wood as a source of pulp, particularly in light of the limited supply and high cost of petroleum. On the other hand, methods for converting wood into various chemicals are continually being developed. There is potential for using wood as a raw material to produce chemicals that are now obtained from petroleum.

Future Prospects
Tremendous progress was made in the late twentieth century in transforming wood from a material of craftsmanship to one of engineering. Reliable structural grading, improved fastenings, efficient fabrication, and glue-laminating have all contributed to making wood a truly modern construction material. Timber connectors and other improvements in fastenings have permitted the use of small timber members for larger spans.

The increasing popularity of glue-laminated wood products is of particular significance. A glue-laminated timber member typically has greater strength than a solid sawed member of the same size. It may also have superior surface properties such as higher fire resistance. The laminated arches used in churches and buildings are common examples of this application. Other examples include the exterior waterproof laminations in such structures as bridges and ships.
See also: Asian agriculture; Conifers; Deforestation; Dendrochronology; European flora; Erosion and erosion control; Forest and range policy; Forest fires; Forest management; Forests; Logging and clear-cutting; North American flora; Old-growth forests; Petrified wood; Plant tissues; Rain-forest biomes; Reforestation; Savannas and deciduous tropical forests; Sustainable forestry; Taiga; Timber industry; Wood; Wood and charcoal as fuel resources.

Sources for Further Study


YEASTS

Categories: Economic botany and plant types; food; fungi; microorganisms; taxonomic groups

The term “yeast” does not refer to any recognized taxonomic name but instead describes fungi that are unicellular and usually reproduce asexually by budding. The term yeast is also used, more specifically, for those species in the genus \textit{Saccharomyces} that are used to leaven bread and ferment alcoholic beverages.

Among mycologists, there is some disagreement over what should be called a yeast. Many mycologists use the term to describe any fungus that has a unicellular budding form at any time in its life. They often use the term “monomorphic” to describe those that are always unicellular and the term “dimorphic” to describe those that can have both unicellular and filamentous growth. Others, however, reserve the name yeast for those species that are permanently unicellular and use the term “yeastlike” to describe those fungi that can alternate between mycelial and unicellular forms. Because some species that have traditionally been called yeasts have later been shown to have a mycelial form, the former broader definition will be used here.

Taxonomy
Yeasts are found in all three major fungal phyla, \textit{Zygomycota}, \textit{Ascomycota}, and \textit{Basidiomycota}, but the vast majority are ascomycetes. As in many fungi, the placement of some species in the proper phylum is made difficult by the lack of data on sexual reproduction. In others, the sexually reproducing, or telomorph, form and the asexually reproducing, or anamorph, form have been assigned different names. In addition, dimorphic fungi were often assigned different names for their yeast and mycelial phases. \textit{Mucor indicus} (synonymous with \textit{Mucor rouxi}) is a zygomycote yeast. Basidiomycete genera include \textit{Filobasidiella} (anamorph: \textit{Cryptococcus}), \textit{Rhodospiridium}, and \textit{Ustilago}. Some ascomycote genera are \textit{Saccharomyces}, \textit{Candida}, \textit{Blastomyces}, and \textit{Ajellomyces} (anamorph: \textit{Histoplasma}).

Reproduction
The most common reproductive mechanism seen in yeasts is budding. During this asexual process the nucleus divides, and a small section of the original cell containing one of the new nuclei begins to bulge from the original cell. The cell and the bud begin to separate by the formation of a new cell wall called, at this stage, the cell plate. The bud grows and, usually, separates from the original cell. In some species, buds do not separate and, after they have grown, may produce buds of their own. This pattern leads to a connected group of cells produced by sequential budding referred to as a pseudomycelium. Yeasts may bud new cells from any part of the original cell (called multilateral budding) or from just the tips of the cell (called polar budding). The release of a bud often leaves a bud scar, and the scarred area is usually not able to produce another bud.

Other methods of reproduction include fission, in which the original cell divides equally, and the production of various kinds of spores occurs both asexually and sexually.

Cells
Like all fungi, yeasts are eukaryotic organisms that can exist in haploid, diploid, and dikaryotic (two haploid nuclei per cell) states. Unlike filamentous fungi, in which the zygote is the only diploid cell, ascomycte yeasts such as \textit{Saccharomyces} can have a prolonged diploid state after the haploid nuclei of the dikaryote fuse. Cell components of yeasts are quite similar to those of filamentous fungi. One exception is that monomorphic yeasts have much lower levels of chitin in their cell walls, and the small amount that is present is found mainly in the bud scars.

Uses
Both brewing and bread making, which use various \textit{Saccharomyces} species, have existed for millen-
nia. Four-thousand-year-old tomb paintings in Egypt depict both, but only since the mid-1800’s has the involvement of yeast in these processes been studied. In both, complex carbohydrates are converted to glucose, and the yeasts ferment glucose, producing ethyl alcohol and carbon dioxide. *Saccharomyces cerevisiae* is the most common baker’s yeast, although *Candida milleri* is important in the production of sourdough breads. In beer brewing, the bottom-fermenting *Saccharomyces carlsbergensis*, which tolerates cold (10 degrees Celsius) is the most commonly used yeast. Wines, a few beers, and most ales use *Saccharomyces cerevisiae*, a top fermenter that requires higher temperatures (20-25 degrees Celsius).

Yeasts are also important in the development of flavor and texture in certain cheeses. Production of Limburger, Camembert, Brie, and Swiss cheeses all rely on yeast fermentation. Because of their high nutrient content, yeasts themselves are important foods and food additives. Yeasts have also been used in the production of various industrial chemicals and biochemicals, including glycerol, ethanol, B vitamins, and polysaccharides. With the advent of modern genetic techniques, yeasts are being engineered to produce many other useful products.

**Pathogens**

Many yeasts can cause disease in plants or animals. *Histoplasma capsulatum*, *Blastomyces dermatitidis*, and *Cryptococcus neoformans* are all dimorphic fungi that can cause systemic infection in humans when the fungi are in the yeast form. *Candida albicans*, also dimorphic, is an opportunistic human pathogen which is pathogenic in its filamentous form. Most *Candida* infections, such as vaginal yeast infections and thrush, are superficial, but systemic infections can occur in immunocompromised individuals. *Pneumocystis carini*, which causes respiratory infections in patients with acquired immunodeficiency syndrome, was originally classified as a protist but is now thought to be a dimorphic fungus. The dimorphic genera *Ustilago* and *Taphrina* both contain many plant pathogens.

*Richard W. Cheney, Jr.*

**See also:** Ascomycetes; Basidiomycetes; Basidiosporic fungi; Deuteromycetes; Ethanol; Eukaryotic cells; Extranuclear inheritance; Fungi; Genetically modified bacteria; Glycolysis and fermentation; Model organisms; Ustomycetes; Wheat; Zygomycetes.

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**Sources for Further Study**


A good introduction to basic fungus biology.


A comprehensive look at yeasts.

The Zosterophyllophyta are a phylum of extinct seedless vascular plants that have been recovered from fossils in the stratum ranging from the Early to the Late Devonian, approximately 408 million to 370 million years ago.

Today, scientists believe that zosterophyllophytes and lycopods arose at about the same time from a common but unknown ancestor. The zosterophyllophytes went extinct, but the lycopods have survived until today.

Characteristics
The Zosterophyllophyta evolved independently from the Rhyniophyta, but both groups shared a number of characteristics. Their aerial stems arose from a horizontal axis, the rhizome, when one of two branches formed by the forking rhizome turned and grew upward. Some of the zosterophyllophytes had no leaves, the common condition in the rhyniophytes. The two groups were distinguished by sporangial position and the presence or absence of a coiled stem that grew in length by unrolling like a New Year’s Eve noisemaker. In the rhyniophytes, the sporangia were borne at the branch tips. In the zosterophyllophytes, the sporangia were borne on short branches along the sides of the stem. Growth from a coiled stem is characteristic of most zosterophyllophytes but does not occur in the rhyniophytes (or lycopods).

The zosterophyllophytes formed dense stands that could cover hundreds of square meters. Most of the plants existed in a vegetative state (lacking reproductive organs) for most of their lives. Their ability to grow and reproduce asexually through K- and H-branching allowed them to spread and dominate an area (a characteristic known as turfing). H-branching occurred when the aerial stem forked twice in rapid succession. One of the two branches formed by the first forking was short and ran parallel to the ground. This short axis forked again, and one of the new branches turned upward, while the other returned to the ground. Viewed from the side, the pattern resembled a capital H. In K-branching, a short branch on the rhizome forked, giving rise to two new axes. The upper axis was coiled and became a stem. The lower axis was not coiled and became a root. Viewed from the side, the branching pattern resembled a capital K.

Taxonomy
Zosterophyllales contains two orders: the Zosterophyllales, whose members have completely naked stems, and the Sawdoniales (also called prelycopods), whose aerial stems bear flaps of photosynthetic tissue (enations) that lacked vascular tissue. Typical members of the Zosterophyllales are Zosterophyllum and Rebuchia. Members of the Sawdoniales include Bathurstia, Crenaticaulis, and Serrulacaulis.

Zosterophyllum
All members of this order have naked stems which bear clusters of oval to kidney-bean-shaped sporangia on short side branches at the stem tip. Depending on the species, the sporangia may be arranged either spirally, like the red line on a barber pole, or in two vertical rows. For most species of Zosterophyllum, only the aerial stems are known. The lower portions of these stems lack a cuticle (a surface covering secreted by the plant to retard water loss). Since a cuticle was absent, the lower portions of Zosterophyllum probably grew in standing water. Although the aerial stem normally branched by forking, occasionally H-branching also occurred. The oldest fertile specimens (Z. myretonianum and Z. fertile) are from 412 million to 406 million years old. In a specimen of Zosterophyllum, from Bathurst Island in Arctic Canada, the aerial stems grew from a horizontal rhizome that bore rootlike structures on its lower surface.

Rebuchia resembles Zosterophyllum in all features except sporangial position. The sporangia of Rebuchia are borne on short side branches at the
stem tip. They arise in two rows on opposite sides of the stem, but the stalks on which they are borne curve so that the sporangia all lie on the same side of the stem when mature.

**Sawdoniales**

Members of the *Sawdoniales* have spherical sporangia that are located on short side branches at various places along the stem. Flaps of photosynthetic tissue (enations) are present. These lack vascular tissue and do not influence the growth of the adjacent vascular tissue in the stem. The enations are arranged either randomly or in one or two rows. The sporangia are not associated with the enations. In the lycopods, the sporangia sit on the upper surface of vascularized leaves (called sporophylls), which are spirally arranged. *Bathurstia*, *Crenaticaulis*, and *Serrulacaulis* are typical sawdonialeans whose wedge-shaped enations lacked vascular tissue.

The enations of *Bathurstia* are arranged randomly on the stem. The sporangia are grouped together in two rows on opposite sides of the stem tip. *Bathurstia* exhibited K-branching. In *Crenaticaulis*, two rows of triangular, rounded (that is, crenate) enations were located on opposite sides of the stem. Subordinate branches, which were once thought to be rhizophores similar to those of *Selaginella*, are found just below each fork of the main axis. These subordinate branches are clearly stems, while rhizophores are rootlike. Therefore, the subordinate branches do not indicate a close relationship with the lycopods, as scientists once thought. *Sporangia* arose in two rows on opposite sides of the stem. Rootlike structures were found on some specimens of *Crenaticaulis*, and root hairs may be present. The gametophyte of *Crenaticaulis* was similar in appearance to *Sciadophyton*. In *Serrulacaulis*, two rows of triangular, pointed (that is, serrate) enations were located on opposite sides of both the aerial stem and rhizome. Sporangia occur alternately in two rows on one side of the stem. Rhizoids were seen coming from the rhizome.

**Herbivory**

The spinelike enations found on sawdonialeans were not adaptations to prevent insects from eating the plant (herbivory). All the known contemporary insect herbivores were too small to be affected by them. Wounds found on fossil plants are consistent with sap-sucking and not chewing insects. Insect coprolites (fossil fecal material) containing a mixture of vegetative plant cell types and spore masses are known but were produced by detritivores (animals that eat dead plant material). No evidence for any herbivore that chewed and digested living plant material has been found prior to 345 million years ago.

**Asteroxylon mackiei**

For some researchers, the most important member of the *Sawdoniales* (formerly *Asteroxylales*) was *Asteroxylon*, a plant from the Rhynia Chert of Scotland. The naked rhizome of *Asteroxylon* grew along the ground and branched by forking into two new axes. Because *Asteroxylon* was a large plant, its water and anchorage needs could not be met with rhizoids alone. Enationless, rootlike structures (possibly adventitious roots) depart from the rhizome and penetrate the soil. The aerial stem that arose from the rhizome had a single central axis from which the lateral branches arose. The aerial stem was densely covered with spirally arranged enations, which superficially resembled leaves but lacked vascular tissue. A vascular trace did leave the central vascular cylinder of the stem and traveled to the base of the leaf but did not enter it. Sporangia were found scattered among the enations. Each sporangium was borne on short stalk containing vascular tissue.

The sporangial position and overall appearance of *Asteroxylon* is very similar to that of the living lycopod, *Huperzia* (*Lycopodium*) *selago*. The sporangia of *Huperzia* are also scattered on short axes among the leaves of the stem. The enations of *Asteroxylon* lacked vascular tissue, a characteristic of the leaves (microphylls) of the lycopods, which initially prevented researchers from classifying *Asteroxylon* as a lycopod. By redefining a microphyll as a stem outgrowth which influences the growth of the adjacent vascular tissue in the stem, *Asteroxylon* can be classified as a lycopod because a vascular trace did run up to the leaf base although it did not enter the leaf. Vascular tissue might never have formed in the microphyll of *Asteroxylon*, or the vascular tissue that was once present might have been lost. *Asteroxylon* is now placed in the *Drepanophycales* along with *Drepanophycus* and *Baragwanathia*.

**Baragwanathia**

*Baragwanathia*’s stem is covered with long, thin microphylls, each with a single vein. The sporangia are borne on the stem among the microphylls and...
appear to be spirally arranged. *Baragwanathia* may be the oldest lycopod, although this statement does cause controversy. The age of oldest specimens from Australia has been disputed. Some researchers believe that they are more than 414 million years old, while others claim that the sediments in which *Baragwanathia* was found are less than 406 million years old. If the older age is accepted, *Baragwanathia* is older than the simpler rhyniophytes (*Aglaoiphyton*) and zosterophyllophytes (*Zosterophyllum*) and contemporaneous with the coxsonioids. An older *Baragwanathia* supports an evolutionary origin for the lycopods distinct from that of the rhyniophytes and prevents the zosterophyllophytes from being the direct ancestors of the lycopods. Therefore, the *Sawdoniales* are mistakenly called prelycops. The evolutionary development of microphylls through the sequence of naked stems, enations, and finally microphylls using *Asteroxylon* as an intermediate is also not possible. The similarity between the *Sawdoniales* and the lycopods is an example of convergent evolution.

Gary E. Dolph

See also: Adaptive radiation; Evolution of plants; Fossil plants; Lycophytes; Paleobotany; Plant tissues; Rhyniophyta; Shoots; Species and speciation; Stems; Trimerophytophyta.

Sources for Further Study


ZYGOMYCETES

Categories: Fungi; taxonomic groups

*Zygomycetes* are a group of fungi that constitute the phylum *Zygomycota*. Also called zygote fungi, *zygomycetes* include about 750 species. Most are saprobes, living on decaying plant and animal matter in the soil; some are parasites of plants, of insects, or of small soil animals; some cause the familiar soft fruit rot and black bread mold; and a few occasionally cause severe infections in humans and farm animals.

*Zygomycetes* share many common features with members of other phyla in kingdom *Fungi*. They are rapidly growing, nonphotosynthetic organisms that characteristically form filaments called hyphae. Hyphae are highly branched to form an interwoven network mass called mycelium. All *zygomycetes* are terrestrial and reproduce by means of spores. No motile cells are formed at any stage of their life cycle. The primary component of their cell wall is chitin, and the primary storage polysaccharide in the cytoplasm is glycogen. Most *zygomycetes* have coenocytic hyphae, within which the cytoplasm can frequently be seen streaming rapidly. Both sexual and asexual reproduction occurs in *zygomycetes*.

Members of *Zygomycota* play important roles both ecologically and economically. Some species (such as *Rhizopus stolonifer*) cause soft fruit rot, posing a problem for transport and storage of many fruits. The same fungi may also feed on bread and
other bakery foods, a potentially serious health hazard. Others, such as *Glomus versiforme*, may form intimate and mutually beneficial symbiotic associations with plant roots called mycorrhizae (literally, “fungus roots”).

Yet another group of zygomycetes, the *trichomycetes*, form a fascinating relationship with arthropods. Trichomycetes are found in the larvae of aquatic insects, millipedes, crayfish, and even crustaceans living at the bottom of the ocean near hydrothermal vents. They usually reside in the guts of these animals and are thought to provide vitamins to their hosts. Members of zygomycetes in the order of *Entomophthorales* have great ecological significance based on their parasitic relation with insects and other small pest animals. They are being increasingly used in the biological control of insect pests of crops.

**Reproduction and Life Cycle**

Even though by appearance all haploid hyphae of zygomycetes look identical, they are actually of two different mating types. When the two hyphae are in close proximity, hormones are released that cause an outgrowth near their hyphal tips to come together and develop into gametangia. Although some species are homothallic (self-fertilizing), most *Zycomycota* species are heterothallic, requiring a combination of + and – strains for sexual reproduction. The two strains “mate” sexually through the combination of two gametangia. In the process, the walls between the two touching gametangia dissolve, fusing their haploid nuclei to form diploid zygospores (hence the name *Zycomycota* for this phylum). Zygospores have very thick walls and thus are very hardy, able to tolerate extreme environmental conditions. Zygospores are dispersed through the air and can remain dormant until conditions are favorable for growth. Zygospores then undergo meiosis and germinate, producing structures on which sporangia (spore cases) are formed. The sporangia produce and disperse numerous haploid spores, marking the beginning of the asexual part of the reproductive cycle.

During asexual reproduction, haploid spores released by sporangia germinate on food such as fruits, bread, and dung, producing haploid hyphae. These hyphae in turn may produce more hyphae or additional spores within sporangia through mitosis, and the cycle begins again. Asexual reproduction via haploid spores of sporangia is universal among all species of zygomycetes. Two examples illustrate the important role of zygomycetes in human lives: *Rhizopus stolonifer* and *Glomus versiforme*.

**Rhizopus stolonifer**

This is one of the best-known and most familiar members of phylum *Zycomycota*. *Rhizopus stolonifer* is a black mold that forms cottony masses on the surfaces of moist, carbohydrate-rich foods and similar substances that are exposed to air. This organism is a serious pest for stored fruits and vegetables, bread, and other types of staple food. Many people are familiar with rotten fruits or aged bread that are covered by *R. stolonifer*.

The life cycle of *R. stolonifer* is similar to those of other species of *Zycomycota*. The mycelium of *R. stolonifer* is composed of several distinct types of haploid hyphae. Most of the mycelium consists of rapidly growing, coenocytic hyphae, which grow through the substrate (such as orange or bread), absorbing nutrients. From coenocytic hyphae, arching hyphae called stolons are formed. The stolons form rhizoids wherever their tips come into contact with the substrate. From each of these points, a sturdy, erect branch arises, which is called a sporangiophore. Each sporangiophore produces a spherical sporangium at its apex. A sporangium begins as a swelling sac, into which a number of nuclei flow. The sporangium is eventually isolated from other hyphae by the formation of a structure called a septum. The protoplasm within is cleaved, and a cell wall forms around each spore. The sporangium wall becomes black as it matures, giving the mold its characteristic color. Each mature spore, upon dispersal, is capable of germinating under adequate conditions to produce a new mycelium. Each year *R. stolonifer* causes an estimated loss of millions of dollars to farmers, fruit growers, and consumers.

**Glomus versiforme and Mycorrhizae**

As one of the most important groups of zygomycetes, *Glomus versiforme* and related genera grow in intimate associations with the roots of plants, forming mycorrhizae. Mycorrhizae not only dramatically increase the surface area of roots for absorption but also help convert nutrients in soil into forms usable by plants. For many forest trees, if seedlings are grown in a sterile nutrient solution and then transplanted to grassland soil, they grow poorly and may eventually die from malnutrition.
However, if a small amount of forest soil containing the appropriate fungi (including *G. versiforme*) is added to the soil around the roots of the seedlings, normal growth is restored. Studies have found that in forest soil *G. versiforme* and related fungi ensure the formation of mycorrhizae and restore the normal growth of seedlings.

Mycorrhizae occur in most groups of vascular plants. The fungal partner *G. versiforme* helps plant roots to absorb and transfer essential nutrients such as phosphorus, zinc, manganese, and copper. By extending several centimeters out from colonized roots in all directions, the plants are able to obtain nutrients from a much larger volume of soil than would be possible otherwise. In return, *G. versiforme* obtains carbohydrates from the host plants. Some fungi may simply attach to the outer surface of the root to form a sheath of hyphae around the root called ectomycorrhizae. In addition to surface extension, other fungi may penetrate into the root to form endomycorrhizae. Of the two major types of mycorrhizae, endomycorrhizae occur in about 80 percent of all vascular plants. The *G. versiforme* hyphae penetrate the cortical cells of the plant root, where they form either minute, highly branched, treelike structures called arbuscules or swellings called vesicles. Such endomycorrhizae are particularly important in the tropics, where soils tend to be positively charged and thus retain phosphates so tightly that this nutrient is available only in very limited supplies for plant growth. Since the impoverished farmers there are often unable to afford fertilizers, endomycorrhizae play a critical role in making phosphates available to crops in these regions. The commercial applications of endomycorrhizae to crops in other regions to reduce fertilizer use and increase yields appear to be an increasingly attractive possibility as well.

Yujia Weng

See also: Ascomycetes; Basidiomycetes; Basidiosporic fungi; Chytrids; Community-ecosystem interactions; Deuteromycetes; Diseases and disorders; Fungi; Lichens; Mycorrhizae; Nitrogen; Nitrogen fixation; Nutrient cycling; Nutrients; Oomycetes; Rusts; Ustomycetes; Yeasts.

Sources for Further Study

Christensen, C. M. *Molds, Mushrooms, and Mycotoxins*. Minneapolis: University of Minnesota Press, 1975. Well-organized and thoughtful discussions on some fungi and their ecological and economic importance.


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Adanson, Michel (1727-1806), French naturalist and African explorer. He collected biological specimens in Senegal, 1749-1753, and published *Histoire naturelle du Sénégal* (1757). He was the first to develop a natural classification of plants, in *Familles des plantes* (1763, 2 vols.), though he was strongly influenced by his studies with Bernard de Jussieu in developing his “natural method.” Many of his specimens and manuscripts still exist.

Albertus Magnus (c. 1200-1280), German natural philosopher. He was the most important medieval European student of plants, and he achieved such a prominent role both in the Church and in education (Thomas Aquinas was a student) that his *De vegetabilibus et plantus* (c. 1250) was highly regarded. In writing it, he was inspired by an uncritical *De Plantis* that was wrongly attributed to Aristotle, and he lacked access to the works of Theophrastus. However, his training in the authentic writings of Aristotle prepared him well for his task. Book 7 in *De vegetabilibus* is the best general work on agriculture since that of Lucius Columella.

Arber, Agnes Robertson (1879-1960), English botanist and historian of herbals. She studied under Ethel Sargent, who inspired her interest in comparative anatomy. She married the Cambridge University paleobotanist E. A. N. Arber. She published three anatomical monographs, *Water Plants* (1920), *Monocotyledons: A Morphological Study* (1925), and *Gramineae* (1934). She first published her study of early printed herbals in 1912, then largely rewrote a second edition (1938). She also published three books on her philosophical perspectives as a biologist (1950-1957). She was the first woman botanist elected a fellow of the Royal Society of London, and she received the Linnean Society’s Gold Metal in 1948.

Banks, Joseph (1743-1820), English botanist and science administrator. He inherited enough wealth to follow his interests, and his friendship with England’s King George III facilitated his activities on behalf of science. Although he entered Oxford University, its resources for botanical education were slight, and he left in 1766 in order to spend eight months exploring Labrador and Newfoundland. He returned with the beginnings of the renowned Banks Herbarium and was elected to the Royal Society of London. He also was a naturalist on the first voyage of Captain James Cook (1769-1771); this voyage made them both famous. From his presidency of the Royal Society (1778-1820), he dominated British science and exerted a broad influence in Europe. He was also influential in the early development of the Royal Botanic Gardens at Kew.

Bartram, John (1699-1777) and William (1739-1823), America’s most prominent early native botanists. John was the son of a farmer and became one himself, near Philadelphia. However, his fascination with plants extended far beyond utilitarian uses, and Philadelphia provided both the personal connections and books to study botany. His exploratory expeditions throughout the British colonies began in 1738, and he supported them by selling his collected plants and seeds to supporters in England and Europe. In 1753 he first took along his son, William, on a trip into the Catskill Mountains, and they collected plants in Florida in 1765. In recognition of his discoveries and shipments of plants to England, he was appointed botanist to the king in 1765. Both Bartrams published accounts of their explorations and botanical discoveries. William was a skilled illustrator of plants and animals, and his *Travels Through North and South Carolina, Georgia, East and West Florida* (1791) was widely read.

Bary, Anton de (1831-1888), German founder of mycology. He was the son of a physician who encouraged his early interest in fungi and algae. De Bary earned a medical degree at the University of Berlin (1853), with a dissertation on sexual reproduction of plants. He practiced medicine for a while, then taught botany and worked as Hugo
von Mohl’s assistant at the University of Tübingen. De Bary demonstrated in 1853 that rusts and smuts of cereals and other plants are not diseased cells but fungal parasites. In 1855 he succeeded Karl Nägeli as botanist at Freiburg im Breisgau. After the Franco-Prussian War, de Bary became rector of the University of Strasbourg. In 1858 he demonstrated sexual reproduction in fungi. In 1861 he began publishing his studies on the potato blight that had devastated Ireland. Although it seemed to have only one host, he later showed that wheat rust has a two-stage life cycle, its other host being common barberry. He coined the terms “mutualism” and “symbiosis” in his monograph, *Die Erscheinung der Symbiode* (1879). He also made important contributions to bacteriology.

**Bauhin, Jean (1541-1613) and Gaspard (1560-1624),** Swiss botanists. Their father was a prominent physician who fled France because of the persecution of Protestants. Jean studied botany in Zurich under Konrad Gesner and in 1560-1565 helped Gesner compile his *Historia plantarum*, which Gesner did not live to publish. The same fate befell Jean’s own *Historia plantarum universalis*, which describes and gives synonyms of 5,226 species. It appeared in three well-illustrated volumes in 1650-1651. Gaspard studied botany under his older brother, Jean, and traveled to Italy and France to study medicine. Gaspard’s two main botanical works, *Prodromos* (1620) and *Pinax theatri botanica* (1623), distinguished between genus and species and introduced binomial nomenclature for about six thousand species.

**Bawden, Frederick Charles (1908-1972),** English virologist and plant pathologist. An early interest in gardening and botany led him to obtain a Ministry of Agriculture scholarship to Cambridge University. Upon graduation, he became assistant to R. N. Salaman, director of the Potato Virus Research Station at Cambridge. Bawden and his collaborator, N. W. Pirie, discovered that plant viruses are nucleoproteins. This was an early step toward molecular biology. In 1940 he became head of the Plant Pathology Department at the Rothamsted Experimental Station. Later he became director of Rothamsted. His work carried him frequently to Africa and Asia as a consultant. He also served as president of several important organizations, including the Institute of Biology.

**Beijerinck, Martinus Willem (1851-1931),** Dutch botanist. His early interest was botany, but he majored in chemical engineering at the Delft Polytechnic School. Upon graduation in 1872, he taught botany while working on a doctoral degree in botany at Leiden, which he earned in 1877. In early 1880’s he became interested in tobacco mosaic disease (his father was a tobacco dealer) and attempted unsuccessfully to discover a bacterial cause. He became a bacteriologist at the Dutch Yeast and Spirit Factory and discovered a bacterium that lives in nodules on leguminous plants and converts atmospheric nitrogen into soil-fertilizing compounds. In 1895 he returned to the Delft Polytechnic School as professor of microbiology and discovered that the causative agent for tobacco mosaic disease can pass through a porcelain filter that traps bacteria. After determining that the cause was not a toxin, he concluded in 1898 that it was a molecule, which he called a “filterable virus,” and suspected was a liquid. American biochemist Wendell Meredith Stanley isolated tobacco mosaic virus in 1935.

**Benthem, George (1800-1884),** English botanist. He accompanied his father, a government official, to St. Petersburg (1805-1807) and while there learned Russian, French, German, and Latin. As an adult, he read botanical works in fourteen languages. By age seventeen, he and his family had moved to France and his mother’s enthusiasm for gardening had aroused his interest in botany. He borrowed her copy of Jean-Baptiste Lamarck and Augustin de Candolle’s *Flore francaise*, which awakened his lifelong interest in systematic botany. His first publication was in French, a catalog of the plants of the Pyrenees and Languedoc (1826), but it was only in 1833, after inheriting enough wealth to be independent, that he became fully committed to botany. He borrowed her copy of Jean-Baptiste Lamarck and Augustin de Candolle’s *Flore francaise*, which awakened his lifelong interest in systematic botany. His first publication was in French, a catalog of the plants of the Pyrenees and Languedoc (1826), but it was only in 1833, after inheriting enough wealth to be independent, that he became fully committed to botany. In 1854 he transferred his herbarium of 100,000 specimens and his library to the Royal Botanic Gardens at Kew, where he was given research facilities. His major work was coauthored with the gardens’ director, Joseph Hooker; their *Genera plantarum ad exemplaria imprimis in herbariis kewensis servata definita* (1862-1883, 3 vols.) was a monumental achievement.
Bessey, Charles Edwin (1845-1915), American botanist. The son of an Ohio schoolteacher, Bessey devoted his own career to teaching and research, but in higher education. He earned a bachelor’s degree at Michigan Agricultural College and then taught at Iowa’s College of Agriculture (1869-1884). In 1884 he became professor of botany at the University of Nebraska, where he remained for the rest of his career. He was equally prominent as an author and as a professor. His botany textbooks dominated the field from 1880 to 1915, but he was also influential as an investigator of the evolution of flowering plants. His evolutionary classification was founded upon the classifications of George Bentham and Joseph Hooker and of Adolf Engler and Ludwig Prantl. Bessey published “Evolution and Classification” in 1893, and his system achieved its final form in *The Phylogenetic Taxonomy of Flowering Plants* (1915). Although not an ecologist, he steered several students in that direction, most notably Frederic E. Clements.

Biffen, Rowland Harry (1874-1949), English botanist and agronomist. He studied botany at Cambridge University and, after graduating, participated in an expedition to Brazil and Mexico to study rubber production. This experience turned his interests toward agriculture. He became a lecturer at Cambridge’s new School of Agriculture in 1899 and served as its professor of agricultural botany (1908-1931). He realized the importance of Gregor Mendel’s laws of genetics for improving crops, and in 1905 he bred a rust-resistant strain of wheat. He also directed the Plant Breeding Institute at Cambridge (1912-1936). He won the Royal Society’s Darwin Medal in 1920 and was knighted in 1925.

Blackman, Frederick Frost (1866-1947) and Vernon Herbert (1872-1967), English plant physiologists. Their father was a physician whose botany books attracted their interest. Although Frederick studied medicine, he became a plant physiologist at Cambridge University, where he studied plant respiration. He showed that stomata control gas exchanges between plants and their environment. His skills as both experimentalist and teacher attracted outstanding students who continued his studies. Vernon followed in his brother’s footsteps, studying medicine and then botany. He conducted cytological researches on the nucleus of *Pinus sylvestris* and on the *Uredineae*, demonstrating alternation of generations in rust fungi. He was the first professor of botany at Leeds University (1907-1915), after which he joined the Imperial College of Science, Technology, and Medicine in London, where he did agricultural research until he retired in 1942.

Blakeslee, Albert Francis (1874-1954), American botanist. He obtained a doctorate from Harvard University in 1904, with a dissertation on his discovery of sexual fusion in several species of fungi. In 1907 he joined the faculty of Connecticut Agricultural College (now the University of Connecticut), where he established a botanical garden and taught what was probably the first course in genetics in the United States. In 1915 he moved to the Carnegie Institution’s Station for Experimental Evolution and served as its director (1934-1941). In 1937 he discovered that the alkaloid colchicine, from the autumn crocus, produces polyploidy in plant chromosomes. In 1942 he became a professor at Smith College and founded its Genetics Experiment Station, funded initially by the Carnegie Institution. He was active in many national scientific organizations and served as president of five of them.

Borlaug, Norman E(rnest; 1914- ), American agronomist and plant pathologist. He received his bachelor’s (1937), master’s (1941), and doctoral (1942) degrees from the University of Minnesota, in plant pathology and forest management. The Rockefeller Foundation hired him to breed disease-immune crops that could grow in Mexico’s varied ecosystems. He developed a high-yield dwarf spring wheat. In response to German bacteriologist Paul Erhlich’s 1968 prediction that the world would soon face massive famine, Borlaug concluded that high-yielding crops could avert catastrophe. In 1963 the Rockefeller Foundation and Mexico established the International Maize and Wheat Center, which he headed. By 1968 he increased Pakistan’s wheat yield by 70 percent and ushered in the Green Revolution, which saved millions of lives and won him a Nobel Peace Prize in 1970. Controversy followed, however, because of the necessity of inorganic fertilizer and irrigation to achieve widespread results. He responded that
with higher production per acre, less land fell victim to slash-and-burn agriculture, more than offsetting the environmental stresses of his methods.

**Bose, Jagadis Chandra (1858-1934)**, Indian physicist and physiologist. He graduated from a Jesuit college in Calcutta, then went to Cambridge University, where he graduated in natural science in 1884. He then became professor of physics at Presidency College, Calcutta, where he remained until he retired in 1915. Early on, his research turned from the properties of radio waves to a comparison of the comparative responses of plant and animal tissues. Today he is seen as a pioneer in biophysics, but at the time, many viewed his researches as far-fetched. He was knighted in 1917 and became a fellow of the Royal Society of London in 1920. In 1917 he founded the Bose Research Institute, where he developed sensitive automatic recorders of plant growth.

**Brongniart, Adolphe-Théodore (1801-1876) and Alexandre (1770-1847)**, French paleontologists. Alexandre studied both geology and medicine and in 1794 became professor of natural history at École Centrale des Quatre-Nations. In 1820 he became professor of mineralogy at the Muséum d'Histoire Naturelle. He independently discovered the value of fossils to identify strata, though William Smith’s discussion of this was published before Brongniart’s. Alexandre trained his son, Adolphe, and they collaborated on important projects. Adolphe, however, focused more narrowly on botany and paleobotany at a time when most paleontologists studied fossil animals. His *Prodrome d’une histoire des végétaux fossiles* (1828) was an early synthesis of paleobotany, and his *Tableau des genres de végétaux fossiles* (1849) synthesized twenty-five years of research. Afterward, he devoted his research to the systematics of living plants, especially those from Neo-Caledonia.

**Brown, Robert (1773-1858)**, British botanist. Although he was primarily a taxonomist, he discovered the cell nucleus, protoplasmic streaming, and Brownian motion. Botany was only a hobby at first, as he trained and served as an army surgeon. However, in 1798 he attracted the interest of Joseph Banks, who arranged for him to accompany a naval expedition to Australia in 1801 under Matthew Flinders. Brown collected plants there and in Tasmania, Norfolk Island, and at the Cape of Good Hope. Upon returning to England, Banks arranged for the Admiralty to support Brown for five years while he described the more than four thousand plants he had collected. Brown became an officer of the Linnean Society of London and was its president (1849-1853). In 1820 he inherited Banks’s library, herbarium, an annuity, and the use of Banks’s Soho House. Brown gave the library and herbarium to the British Museum in exchange for its creation of a botany department under his directorship. He became one of Europe’s leading botanists.

**Brunfels, Otto (c. 1488-1534)**, German monk, physician, and botanist. He received a master of arts degree in 1508-1509 and then entered a monastery. However, he became swept up in the Protestant Reformation and left the monastery in 1521. He married in 1524, and his widow helped publish his manuscripts posthumously. His most important work was *Herbarium vivae eicones ad nature imitationem* (1530-1540, 3 vols.); a German version was titled *Contrafayt Kreüterbuoch* (1532-1540, 2 vols.). This work pioneered the transition from medieval herbalism to modern botany. Although his text drew heavily upon ancient and medieval sources, he added German names and illustrations drawn from live plants. Most of the approximately 230 species described were indigenous to the Strasbourg region and included more than 40 species not previously described.

**Burbank, Luther (1849-1926)**, American horticulturist. He was the son of a Massachusetts farmer and received a good education but did not go to college. In 1871 he bought land and became a truck-gardener for five years. In 1872 he bred a potato with attractive shape and white skin that became known as the “Burbank potato.” He sold sixty bushels of them to a seedsman and with the money moved to Santa Rosa, California, where he devoted his career to plant breeding. He introduced more than eight hundred new plants to gardeners and farmers. His breeding methods began well before the rediscovery of Gregor
Mendel’s genetic laws in 1900, and Burbank’s methods never caught up with the scientific techniques developed by university geneticists. Consequently, his credibility as a cereal breeder was questioned, but his empirical achievements were nevertheless impressive.

Calvin, Melvin (1911-1997), American plant physiologist. He trained in college as a chemist, and when he became a faculty member at the University of California at Berkeley in 1937, he joined an organic chemistry research group. During World War II he studied ways to produce oxygen. In 1946 he became director of the bio-organic chemistry group at the Lawrence Radiation Laboratory; in 1960 the group became the Laboratory of Chemical Biodynamics. Calvin’s work at the Lawrence Laboratory gave him the opportunity to use radioactive tracers, particularly carbon 14, to follow the complex steps in photosynthesis, for which he won the Nobel Prize in Chemistry in 1961. He identified eleven intermediate compounds plants create between the intake of simple ingredients and the formation of energy compounds. He also developed a theory on the chemical evolution of life.

Camerer, Rudolph Jakob (1665-1721), German botanist. He came from a long line of physicians and pharmacists. At a time when medicines were still made mainly from plants, it was natural for him to become director of the Tübingen Botanic Garden. He read Nehemiah Grew’s (1682) and John Ray’s (1686) comparisons of the stamen and pollen in flowers to male organs and semen of animals. Because Camerer’s microscopic studies indicated that these claims were plausible, he concluded that many species are hermaphroditic, while other flowers are monoecious or dioecious (though the latter terms came later). He then conducted experiments by removing male flowers from the vicinities of female flowers of mulberry. The female plants produced seeds, but none were fertile. This was the first important experiment in plant physiology. The results of his experiments over several years were published in 1694.

Candolle, Augustin Pyramus de (1778-1841) and Alphonse de (1806-1893), Swiss botanists. Augustin fell in love with the Swiss mountain flora at age fourteen. In 1796 he went to Paris to study medicine but became so excited about science from his contacts with Georges Cuvier, Jean-Baptiste Lamarck, and other scientists at the Muséum d’Histoire Naturelle that he abandoned medicine for botany. While in Paris, his many botanical publications earned him a professorship of botany in Montpellier (1808-1816). In 1816 his hometown, Geneva, established a professorship of natural history for him, where he spent the rest of his life. In 1820 he published an important, lengthy essay in a science encyclopedia, “Géographie botanique,” that went beyond Alexander von Humboldt’s perspectives by emphasizing the competition between species as an important factor influencing distribution. Augustin de Candolle’s most significant work was *Prodromus systematis naturalis regni vegetabilis* (1824-1873, 17 vols.), which is not limited to descriptions of plants but includes ecology, phytogeography, biometry, agronomy, and evolutionary allusions. Alphonse was born in Paris and lived in Montpellier until 1816, when the family returned to Geneva. He earned a bachelor’s degree in science in 1825, then a doctorate in law in 1829. His legal training facilitated his participation in Geneva’s civic life. He succeeded his father in 1835 as professor of botany and director of the university’s botanical garden. Alphonse’s greatest work is his *Géographie botanique raisonnée* (1855, 2 vols.), which is worldwide in scope. Two other notable works were his *Histoire des sciences et des savants depuis deux siècles* (1873) and *Origine des plantes cultivées* (1882; *Origins of Cultivated Plants*, 1884). Furthermore, he continued his father’s *Prodromus systematis naturalis regni vegetabilis* (1844-1873, vols. 8-17).

Carson, Rachel Louise (1907-1964), American marine biologist, author, and environmentalist. As an undergraduate at the Pennsylvania College for Women (now Chatham College), she was undecided about whether to major in English or biology. A professor persuaded her to choose biology, but she spent the rest of her life using both literary and scientific skills to persuade people to appreciate and preserve nature. She earned a master’s degree at Johns Hopkins University before joining the U.S. Fish and Wildlife Service as an author-editor. She published three best-
selling books on the sea (1941-1954), but enduring fame came with *Silent Spring* (1962), her eloquent and meticulous attack on the careless, widespread use of insecticides, especially DDT. Such sprays killed not only herbivorous insects, she showed, but also their predators and pollinating insects. She died of cancer before DDT was banned in the United States in 1972.

**Carver, George Washington** (c. 1864-1943), American agricultural scientist. He was born into slavery in Missouri, but emancipation enabled him to get a public education in Kansas and a college degree from Iowa State University in Ames in 1894. He joined its faculty and received a master’s degree in agriculture in 1896. He then became director of the agricultural experiment station at Tuskegee University in Alabama. He devoted his career to developing sustainable agriculture for the South, emphasizing peanuts and sweet potatoes as supplements or alternatives to cotton. He found new uses for peanuts and sweet potatoes, such as dyes, milk substitutes, and cosmetics.

**Cesalpino, Andrea** (1519-1603), Italian physician, botanist, and philosopher. He studied philosophy and medicine at Pisa University, received a doctorate in 1551, and in 1555 succeeded his teacher Luca Ghini as medical professor and director of the botanical garden. In 1592 he became physician to Pope Clement VIII and professor at Universita degli Studi “La Sapienza,” Rome. His *De plantis libri XVI* (1583), heavily influenced by Aristotle and Theophrastus, was the first true textbook of botany. He considered the fruit the most important part of the plant and made it the basis for his classification system of about fifteen hundred species, while still using of the Greek division of plants into trees, shrubs, shrubby herbs, and herbs. He denied the sexuality of plants. He first provided a system of plants based on a coherent set of principles, though his narrative (rather than an outline) presentation of it limited its influence.

**Clements, Frederic Edward** (1874-1945), American plant ecologist. A native of Lincoln, Nebraska, he attended the university there and studied under Charles Edwin Bessey, who ran the state’s phytogeographic survey. Clements collaborated with fellow student Roscoe Pound on the survey, developing methodologies which Clements used in his doctoral research. (Pound became a law professor.) Clements taught botany at Nebraska (1897-1906) and married his doctoral student Edith Schwartz, who was often his assistant or collaborator. They bought a cabin in a Pike’s Peak canyon that became a summer laboratory. Although he also taught botany at the University of Minnesota, 1907-1917, Clements was much more interested in research than teaching, and in 1917 he became a full-time research associate at the Carnegie Institution in Washington, D.C. *Plant Succession* (1916) was his most important book, which developed his main ecological ideas about discrete communities that are adapted to a climate; if disturbed, a community grows through a series of stages and returns to a climatic climax. He was the most productive publisher in plant ecology of his time, and his books were both influential and controversial, as his theories went beyond the supporting evidence.

**Cohn, Ferdinand Julius** (1828-1898), Polish botanist and bacteriologist. He came from Breslau’s Jewish ghetto but was allowed to attend the city’s gymnasium. He became interested in botany at Breslau University but was barred because of religion from taking the degree examinations. He transferred to the University of Berlin, where he was introduced to microscopic studies, and he received a doctorate at age nineteen. In 1849 he returned to Breslau (now Wroclaw) and in 1850 became a Privatdozent at Breslau University, working under Jan Purkinje in his Institute of Physiology. In 1850 Cohn began researches on unicellular algae and similarities to protozoa, and in 1855 he demonstrated sexuality in unicellular algae. About 1870 he turned to bacteria and soon developed a classification system that became accepted. However, he also studied bacterial physiology and proved that bacteria are killed at 80 degrees Celsius. Cohn became professor of botany in 1872. In 1887 the university provided him with an institute of plant physiology, and he received many international honors.

**Colonna, Fabio** (1567-1650), Italian jurist and botanist. He studied law but suffered from chronic epilepsy. Ancient pharmacists and physicians
had allegedly used a medicinal plant to cure epilepsy, but it was uncertain to which species the ancient name applied. Colonna’s efforts to determine its identity drew him into botany. He departed from Andrea Cesalpino’s classification of plants by fruits, believing that flowers provide better evidence of relationships. He was the first botanist to make comparative studies of flowers and to establish plant genera based on his findings. His two books, *Phytobasanos* (1592) and *Ecphrasis* (1616), first used illustrations engraved on copper plates rather than on wood, enabling him to achieve greater floral detail than before.

Columella, Lucius Junius Moderatus (early first century c.e.), a Roman from Cadiz, Spain, and author on agriculture. His is the third and most detailed Latin agricultural treatise, which includes information on the cultivation of many different kinds of food plants. He explained grafting techniques and knew that both manure and legumes improve soil fertility. His *De re rustica* (*De re rustica*, 1968-1979, 3 vols.) is published in a modern Latin-English edition.

Cordus, Euricius (1486-1535), German teacher, physician, and botanist, and Valerius (1515-1544), pharmacist and botanist. Euricius, the youngest of thirteen children, adopted his nickname, “Cordus” (last-born), as a surname. He became a schoolmaster, but because his income did not adequately support his own family, he went to Italy in 1519 and studied medicine. In 1523 he became a municipal physician, and in 1527 he became professor of medicine at the new Protestant University of Marburg. While Martin Luther reformed religion, Cordus attempted to reform the understanding of names of medicinal plants, in his *Botanologicon* (1534). Valerius studied at Marburg under his father and after receiving a bachelor’s degree in 1531 went to Leipzig to study pharmacy. Next, he went to Wittenburg, where he wrote a *Dispensatorium*, which was published posthumously (Nuremberg, 1546); it was Germany’s earliest city-sponsored pharmacopoeia, which discussed about 225 medicinal plants and minerals. With later editions, its use spread far beyond Germany. More purely botanical were his *Annotationes in Dioscoridis de materia medica libros* (1549), *Historiae stirpium libri IV* (1561), and *Stirpium descriptionis liber quintus* (1563), which describe about five hundred species. His descriptions were based on his own studies and are presented in an organized, thorough fashion.

Correns, Karl Franz Joseph Erich (1864-1933), German botanist and geneticist. He studied botany at the University of Munich under Karl Nägeli and married Nägeli’s niece. He did graduate work at Berlin and Tübingen and then taught at several universities. When the Kaiser-Wilhelm Institut für Biologie was founded in 1913, he became its director. His fame came from his rediscovery in 1899 of Gregor Mendel’s laws of heredity. Correns followed Hugo de Vries’s example of publishing his own findings, while acknowledging Mendel’s priority. He devoted the rest of his career to testing and refining these laws.

Cowles, Henry Chandler (1869-1939), American plant ecologist. He studied science at Oberlin College, and when he went to the University of Chicago as a graduate student in 1895, his main interest was in geology. However, in 1896 Professor John Merle Coulter persuaded him to switch to botany. Cowles read Johannes Warming’s introduction to plant communities (1895) and decided to study the vegetation of the Lake Michigan sand dunes. His main publications were based on his doctoral dissertation, “The Ecological Relations of the Vegetation of the Sand Dunes of Lake Michigan” (1899) and “The Physiographic Ecology of Chicago and Vicinity” (1901), showing that while habitat influences the type of vegetation, vegetation can also influence the character of habitat. Although his publications (1899-1911), were well received, he eventually focused his career on effective teaching at the University of Chicago.

Crick, Francis (1916–), English molecular biologist. He earned a bachelor’s degree in physics in 1937, and his graduate education was interrupted by World War II. He became interested in biology in 1946 upon reading Erwin Schrödinger’s *What Is Life?* In 1947 Crick began working at Cambridge University and soon undertook doctoral research on protein structure, using X-ray diffraction. When James Watson came to the Cavendish Laboratory, he and Crick collaborated on an attempt to discover the struc-
ture of deoxyribonucleic acid (DNA). With advice and data from various colleagues, they were successful in 1953 and won the Nobel Prize in Physiology in 1962. Their work was a major component of a new science, molecular biology, to which Crick continued making contributions in his subsequent career.

Curtis, John Thomas (1913-1961), American plant ecologist. He was a small-town boy who became friends with a curator at the Milwaukee Public Museum, who inspired him to study wild plants, especially orchids. Curtis attended the local Carroll College, majored in biology, and wrote a senior thesis on orchid seeds, germination, and growth. In 1934 he entered graduate school at the University of Wisconsin to study plant physiology, with a minor in plant pathology. His master’s thesis and doctoral dissertation were also on orchid seed germination. In 1937 he became an instructor in botany at the University of Wisconsin and in 1938 began teaching plant ecology. He had long been interested in the environments of different orchid species, and his ecological interests expanded after he became director of research at the university arboretum. During World War II he conducted a statistical study on the phytosociology of the tropical vegetation of Haiti, which changed the direction of his research. Back in Wisconsin in 1946, he embarked on a long-term study of its vegetation. He attracted a half-dozen outstanding graduate students to assist the project with doctoral dissertations, and he synthesized the findings in *The Vegetation of Wisconsin: An Ordination of Plant Communities* (1959). Besides being a valuable account of a state’s vegetation, this book is also his definitive account of his continuum concept, showing that the notion of distinct plant communities is often an illusion.

Darwin, Charles (Robert) (1809-1882) and Erasmus (1731-1802), English naturalists. Erasmus Darwin studied medicine at Cambridge and Edinburgh and became one of the most prominent physicians of his day. In 1766 he became a founding member of the Lunar Society, a group of amateur, radical scientists who met in Birmingham. Three of his four books were on botany; his earliest speculations on evolution were in *The Botanic Garden* (2 parts, 1789-1791), and he developed further those ideas in *Zoonomia* (1794-1796, 2 vols.) and *The Temple of Nature* (1803). When published, his evolutionary ideas fell on deaf ears, but Charles Darwin developed a high regard for his grandfather and read his books—initially, before developing his own ideas on evolution and again after he began searching for explanations of evolution. Charles attended the same universities as his grandfather but found himself unsuited to the medical profession. He was willing to go into the Anglican ministry because such a career would leave time for natural history, but he received an offer to sail as naturalist on a naval survey ship *Beagle*, which mapped the coastlines of South America (1831-1836). His contacts with science professors had prepared him for the task, and on the voyage he collected specimens and observations that turned him into an evolutionist in July, 1837. His early researches were in zoology and geology, and it was only in the final writing of *On the Origin of Species by Means of Natural Selection* (1859) that he shifted his emphasis to botany. That was partly because of his reliance on the judgment of Joseph Hooker and Hewett Watson. Today, Charles Darwin’s fame rests mainly on his 1859 work, but he wrote sixteen works—all highly regarded—seven of which are partly or wholly on plants.

De Duve, Christian (1917- ), Belgian cytologist and biochemist. He was born near London during World War I and grew up speaking four languages. He received his medical degree in 1941, and during World War II he was confined in a prison camp until he escaped. He studied the action of insulin on glucose uptake for his philosophy doctorate in 1945 and published his dissertation that year as a book. In 1947 he joined the faculty of Louvain University, and in 1962 he became a professor at Rockefeller University while still serving half-time at Louvain. His insulin studies led to enzyme research. He pioneered the use of the centrifuge and electron microscope in cytology and discovered two new organelles: lysosome and peroxisome, for which he shared a Nobel Prize in 1974.

Dioscorides, Pedanius (c. 50-70 C.E.), Greek physician-pharmacist who spent one or two years traveling with the Roman army, collecting me-
Dioscorides, Pedanius (c. 40-90), Greek physician and pharmacist. His pharmacopoeia is in Greek but is known by a Latin title, De materia medica (c. 78; The Greek Herbal of Dioscorides, 1934). It is organized by plant species and is the earliest known dictionary of plants, giving descriptions and locations for more than five hundred species. During the 1500’s and 1600’s De materia medica became one of the foundations of modern botany and was translated into English in 1655 (though not published until 1934).

Dodoens, Junius Rembert (1517-1585), Belgian botanist and physician. He studied medicine at the University of Louvain and served as a municipal physician in his hometown, Mechelin (1548-1574). He was inspired by the herbals published by Otto Brunfels, Jerome Bock, and Leonard Fuchs. His first brief botanical book, De frugum historia liber unus (1552), was on cereals, vegetables, and fodders. In 1554 he incorporated it into his own large Flemish herbal, Cruydeboeck (A New Herbal: Or, Historie of Plants, 1586). There were also Latin and French editions of his herbal, with new species being introduced into later editions. He described and illustrated for the first time about one hundred plants. He left his town to become physician to Emperor Maximilian II (1574-1580), and in 1782 he became professor of medicine at the University of Leiden.

Dokuchaev, Vasily Vasilievich (1846-1903), Russian geologist and soil scientist. From a family of priests, in 1867 he entered the St. Petersburg Ecclesiastical Academy but soon abandoned it for St. Petersburg University. In 1871 he received a master’s degree, with a thesis on the alluvial deposits of the Kachna River, near his birthplace. He remained connected to St. Petersburg University and that city’s other scientific institutions. He founded Russia’s first department of soil science. He received a doctorate in 1878 with his dissertation, “Methods of Formation of the River Valleys of European Russia.” He then studied the formation of topsoils, and he helped prepare a soil map of European Russia. A severe drought in 1891 turned his attention to steppe soils and farming methods. He believed soil science must incorporate the study of bedrock, climate, topography, and the influences of plants, animals, and humans.

Douglass, Andrew Elicott (1867-1962), American astronomer and dendrochronologist. His interest in astronomy and mathematics developed during high school and continued at Trinity College in Hartford, Connecticut. He graduated with honors in 1889 and became an assistant at the Harvard University Observatory, which sent him on an expedition to Peru for three years. In 1894 wealthy Bostonian Percival Lowell hired him to find a site for an observatory in Arizona Territory, which he did, west of Flagstaff. Douglass remained there in various occupations until he joined the University of Arizona faculty in Tucson in 1906. In 1916 an endowment established The Steward Observatory, which was completed in 1922. Douglass was interested in the influence of sunspots on weather and therefore studied tree rings as indicators of climate. Tree rings seemed to confirm an eleven-year cycle of sunspots. He also worked with archaeologists to develop a history of southwestern U.S. climate from tree rings extending from 11 c.e.

Dutrochet (René Joachim) Henri (1776-1847), French plant and animal physiologist. He was born into an provincial aristocratic family that lost its wealth and power in the French Revolution. He went to Paris, studied medicine, and then became an army surgeon. At age thirty-four he abandoned medicine for science and became interested in gas exchanges between the atmosphere and the tissues of plants and animals. He concluded that respiration is essentially the same in plants and animals. In 1831 he demonstrated that mushrooms are fruiting bodies of fungal mycelia.

Englemann, George (1809-1884), German-American botanist. His parents ran a girls’ school in Frankfurt and encouraged his interest in plants, which developed when he was fifteen. He received a medical degree in 1831 from the University of Würzburg, with a thesis on plant and animal monstrosities. In 1832 he immigrated to a relative’s farm 20 miles from St. Louis as a base for studying American botany, and in 1836 he began keeping meteorological observations which he continued until his death. In 1840 he
Flemming, Walther (1843-1905), German cytologist. He studied at three other universities before taking his medical degree at the University of Rostock (1868). He also did research at several universities before becoming professor of anatomy at Kiel University in 1876, where he remained, living with his sister Clara. By 1879 he had investigated all stages of mitotic cell division and published his results in three famous articles (1879-1881). In 1880 he coined the term “chromatin” for the stainable threads (chromosomes) in the cell nucleus. He concluded that the heads of spermatozoa are composed entirely of chromatin. In 1887 he described meiotic cell division in spermatozoa but did not fully distinguish it from mitosis. He also developed two new staining methods.

Fritsch, Felix Eugen (1879-1954), English algologist. He earned a bachelor’s degree in botany from London University in 1898 and a philosophy doctorate at Munich in 1899. He appreciated the German emphasis on physiology and ecology, in contrast to English emphasis on anatomy and morphology. In 1901 he worked at the Jodrell Laboratory at Kew, and in 1902 he became assistant lecturer at University College, London. He began his long-lasting studies on periodicity in phytoplankton. In 1905 he earned a science doctorate at London and became assistant professor at University College. In 1911 he took charge of botany at Queen Mary College, where he collaborated with assistant lecturer Edward Salisbury on five widely used textbooks (1914-1928). In 1927 Fritsch published a revised, rewritten edition of G. S. West’s Treatise of the British Freshwater Algae and urged formation of a freshwater biological station. In 1929 the Freshwater Biological Association was formed, with him serving as chairman until his death. A biological station at Wray Castle was also established in 1929. Fritsch was elected fellow of the Royal Society of London in 1932 and received its Darwin Medal in 1950. He published his greatest work, The Structure and Reproduction of Algae, in two volumes (1935-1945). He retired in 1948 and thereafter worked at the Botany School, Cambridge University. He was president of the Linnean Society of London (1949-1952) and received its gold medal in 1954. He was president of the International Association of Limnology and the Institute of Biology in 1953.

Fuchs, Leonhard (1501-1566), German physician and botanist. While a child, his grandfather, Johann Fuchs, taught him the names of flowers and evidently imparted a lasting interest in them. In 1517 Leonhard graduated from the University of Erfurt and opened a school. He became a Lutheran and was influenced by religious reformism in his scientific outlook. In 1519 he enrolled at the University of Ingolstadt and received his master’s degree in 1521 and his medical degree in 1524. In 1526 he became professor of medicine at Ingolstadt but in 1528 resigned to become court physician to a Lutheran ruler. In 1533 he attempted to return to the Ingolstadt faculty but was prevented because of his religion. In 1535 he became professor of medicine at Ingolstadt but in 1528 resigned to become court physician to a Lutheran ruler. In 1533 he attempted to return to the Ingolstadt faculty but was prevented because of his religion. In 1535 he became professor of medicine at the University of Tübingen, where he remained. He published a popular medical textbook (1531) that he frequently republished in revised and enlarged editions. His lasting fame came from his pharmaceutical herbal, De historia stirpium commentarii insignes maximis impensis et vigiliis elaborati adjectis earundem vivis plusquam quingentis imaginibus, nunquam antea ad naturae imitationem artificiosius efictis & expressis (1542). Of 487 species and varieties included, more than 100 were recorded in Germany for the first time. Among the species that had never before been illustrated were foxglove and corn. His publications were marred, however, by plagiarism.

Gärtnner, Joseph (1732-1791) and Karl Friedrich von (1772-1850), German botanists. Joseph obtained a medical degree at the University of Tübingen in 1753 but never practiced medicine. He had broad scientific interests and turned to
botany after attending botanical lectures at Leiden in 1759. He was professor of botany and head of a botanic garden at St. Petersburg (1768-1770), and he explored the Ukraine, discovering many undescribed plant species. In 1770 he returned to live in his hometown, Calw, where he studied carpology. His *De fructibus et seminibus plantarum* (1788-1807, 3 vols.) describes fruits and seeds of 1,050 genera. Karl earned his medical degree from the University of Tübingen, but unlike his father, he did practice medicine, in Calw. However, in 1824 he became interested in plant fertilization and hybridization and devoted the rest of his career to that research. He believed in the stability of species. He published his findings in three major studies (1827-1838, 1844, 1849).

**Gesner, Konrad (1516-1565)**, Swiss physician, naturalist, and philologist. His early studies were in Protestant theology, but by 1535 he had become more interested in Greek, Latin, and Hebrew; then he switched to medicine and received his medical degree at Bern in 1541. Gesner had an early interest in natural history, and his encyclopedic works include not only his *Bibliotheca universalis* (1545-1555, 4 vols.) but also his *Historia animalium* (1551-1587, 5 vols.; history of animals). He did publish a few brief botanical works, but his *Opera botanica* (1751-1771; botanical works) was unfinished when he died during an epidemic of plague. He was the first botanist to emphasize the importance of flowers for determining kinship of species, but the unfortunate publishing history of his botany limited its influence.

**Ghini, Luca** (c. 1490-1556), Italian botanist. His hometown was near Bologna, and he received his medical degree from the University of Bologna in 1527. The following year he joined its faculty and in 1535 began teaching medical botany. From 1544 to 1554 he taught medical botany at Pisa but then rejoined the Bologna faculty. He collected the first herbarium, and the oldest surviving herbaria are those assembled by two of his students. The botanical garden he created at the University of Pisa is one of the two oldest. Andrea Cesalpino was one of his many students and was his successor as head of the Pisa botanical garden.

**Gleason, Henry Allan (1882-1975)**, American botanist. As a child he enjoyed playing in the woods, but at age thirteen he took a course in botany that focused his interest on the local flora. He earned his bachelor’s (1901) and master’s (1904) degrees at the University of Illinois and his doctorate (1906) at Columbia University. The writings of Frederic Clements inspired him to make a plant ecological study of the Ozark Mountains and prairies of southwestern Illinois, but he also developed a strong interest in taxonomic botany. In 1910 he became an associate professor at the University of Michigan. However, in 1919 he went to the New York Botanical Garden, where he remained through 1950. Clements had pioneered the use of quadrats and statistics in the study of vegetation but did not persist in this technique. Gleason, however, used the technique to study vegetation and concluded (1920) that species are not distributed in discrete communities, as Clements claimed. Gleason preferred the term “plant association” to “plant communities.” However, it was only in the writings of John Curtis and Robert Whittaker in the 1950’s that Gleason’s claims were taken seriously and gained widespread support.

**Goethe, Johann Wolfgang von (1749-1832)**, German author and naturalist. He obtained a law degree in 1771 but was soon so famous as a poet, novelist, and natural philosopher that he did not practice law. His theorizing in biology was influenced by Baruch Spinoza’s philosophy and George-Louis Leclerc de Buffon’s natural history. Goethe believed that related species are variations of an archetype and that biologists could gain an understanding of archetypes by comparative studies on species or genera that are its variants. The archetype of a major class has simple components that vary according to the species. For example, flowering plants have cotyledons, inflorescences, stamens, and pistils that are all variations of leaves. He developed this idea from studying the fan palm and explained the concept in *Versuch die Metamorphose der Pflanzen zu erklären* (1790). He also coined the term “morphology.” Although he believed that the environment plays a role in the modification of leaves into the variants found in different species, his system was an idealistic substitute for the idea of evolution.
Golgi, Camillo (1843-1926), Italian histologist and pathologist. The son of a Pavian physician, he earned his own medical degree from the University of Pavia in 1865, studying under its first professor of histology. Most of his research was on the histology of nerves. Little progress had been made in this field because of inadequate techniques. Golgi’s development of satisfactory techniques enabled him to make the important discoveries leading to his sharing the Nobel Prize in Physiology in 1906. In 1898 he examined the histology of an owl’s brain and discovered a small organelle in the cytoplasm of nerve cells, now called the Golgi body. It was not an important discovery at the time because he could not explain its function.

Gray, Asa (1810-1888), American taxonomic botanist. He was from upstate New York and studied medicine there but became more interested in the botany he studied than in medicine, in which he earned a degree in 1831. In 1832 he began assisting John Torrey, the United States’ leading botanist, to compile *Flora of North America*. By the time it appeared in 1836, Gray’s assistance was so significant that he became coauthor. In 1842 he became professor of natural history at Harvard University, where he remained. He was well positioned to receive specimens from botanical explorers of the West, and much of his time went into describing and organizing American systematic botany. However, in 1851 he traveled to England, where he met and became friends with Joseph Hooker and Charles Darwin. In the correspondence that followed, Darwin confided in Gray in 1857 key details of his theory of evolution. After the publication of Darwin’s *On the Origin of Species by Means of Natural Selection* (1859), Gray became Darwin’s staunch ally against Gray’s antievolution colleague Louis Agassiz. Gray collected the essays he had written on evolution over several years into *Darwiniana* (1876). Under Hooker and Darwin’s influence, Gray also became America’s leading phytogeographer.

Greene, Edward Lee (1843-1915), American botanist. His mother was a skilled gardener, and Greene at age six began reading her copy of Elmira Lincoln’s *Familiar Lectures on Botany* (1842). A neighbor in southern Wisconsin, the naturalist Thure Kumlien, encouraged Greene’s botanical interests. In 1859 Greene entered Albion Academy, but his education was interrupted by the Civil War, in which he was a Union Army private (1862-1865). He carried with him Alphonso Wood’s *Classbook of Botany* and sent specimens and seeds from his travels to his mother and Kumlien. Greene returned to Albion and graduated in 1866. He taught school for several years, became an Episcopal priest in 1873, and joined the Roman Catholic Church in 1885. He also was professor of botany at the University of California at Berkeley (1885-1895). Greene was a diligent explorer of western America, but he was also a controversial botanist because he published names of new species of plants that other botanists challenged. Nevertheless, he was elected president of the Madison Botanical Congress in 1893 and served as an associate of the National Museum, Smithsonian Institution (1904-1914). He ended his career by writing *Landmarks of Botanical History* (1983, 2 vols.), which defended his distinctive perspective.

Grew, Nehemiah (1641-1712), English plant anatomist. The son of a Nonconformist Protestant clergyman-schoolmaster, he was allowed to earn a bachelor’s degree at Cambridge University but could not remain there. He obtained a medical degree at the University of Leiden and returned to practice medicine at Coventry. In 1672 the Fellows of the Royal Society of London raised fifty pounds to enable Grew to move to London, where he continued practicing medicine while also investigating plant anatomy. Robert Hooke instructed him in the use of the society’s compound microscope. Grew had broader scientific interests than plant anatomy, but in this he excelled. His earlier studies were collected and expanded into *The Anatomy of Plants* (1682), which is well illustrated. He attempted to understand plant physiology by studying anatomy, but that proved to be very difficult. He had no students to continue his work.

Grisebach, August Heinrich Rudolph (1814-1879), German phytogeographer and taxonomist. As a youth he learned botany from his uncle, botanist Georg Friedrich Wilhelm Meyer. Grisebach studied medicine and natural history at Göttingen
and Berlin and eventually became professor of botany at Göttingen. From 1839 to 1840 he traveled through the Balkan States and Asia Minor on botanical explorations, and later he explored in Norway (1842), southern France, the Pyrenees (1850), and the Carpathian Mountains (1852). His taxonomic studies included monographs on the Malpighiaceae, Gramineae, and the genera Gentiana and Hieracium. He also studied the flora of southeastern Europe, Central America, and Argentina. In phytogeography he was strongly influenced by Alexander von Humboldt, and his own earlier studies culminated in his grand synthesis, *Die Vegetation der Erde nach ihrer klimatischen Anordnung* (1872), which emphasizes the influence of climate on composition and distribution of flora.

**Haberlandt, Gottlieb (1854-1945),** Hungarian-German botanist. His father was a professor of applied botany and taught him botany as a youth. Haberlandt studied at the University of Vienna and was greatly influenced by Julius von Sachs’s textbook of botany. He earned his doctorate in 1876 and then worked under Simon Schwendener at Tübingen, because Schwendener emphasized the combined study of anatomy and physiology. The outcome of Haberlandt’s investigations was *Physiologische Pflanzenanatomie* (1884; *Physiological Plant Anatomy*, 1914), which he later revised and enlarged through six editions. His text considered evolutionary and ecological aspects of plants. He also published on other topics, including a travel book, *Eine botanische Tropenreise* (1893), on his experiences in Ceylon and Java from 1891 to 1892.

**Hales, Stephen (1677-1761),** English plant and animal physiologist. He studied divinity at Cambridge University and was greatly influenced by Julius von Sachs’s textbook of botany. He earned his doctorate in 1876 and then worked under Simon Schwendener at Tübingen, because Schwendener emphasized the combined study of anatomy and physiology. The outcome of Haberlandt’s investigations was *Physiologische Pflanzenanatomie* (1884; *Physiological Plant Anatomy*, 1914), which he later revised and enlarged through six editions. His text considered evolutionary and ecological aspects of plants. He also published on other topics, including a travel book, *Eine botanische Tropenreise* (1893), on his experiences in Ceylon and Java from 1891 to 1892.

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**Hedwig, Johann (1730-1799),** Czech-German botanist. He had a childhood interest in plants, and although he studied medicine at the University of Leipzig (receiving his medical degree in 1759), while there he worked as an assistant to the professor of botany and continued to study plants while practicing medicine. His special interest was in mosses and liverworts, and during the 1770’s he studied their reproduction and published his findings in 1781. Despite some skepticism, his accounts withstood scrutiny, and he became professor of botany at the University of Leipzig.

**Hofmeister, Wilhelm Friedrich Benedict (1824-1877),** German botanist. His father, whose business was publishing and selling books on music and botany, was an amateur botanist. The son’s initial interest was in entomology, physics, and mathematics. However, he did not go to college and instead followed his father into music publishing, with botany as a hobby. He suffered from severe myopia, which inclined him toward microscopic studies. He was also influenced by Matthias Schleiden’s studies on life histories and cell structure, and his first scientific paper (1847) corrected Schleiden’s account of fertilization and embryo development in flowering plants. Hofmeister’s 1849 book expanded his findings to other species, and his most famous book (1851) generalized about the alteration of generations in plants. The University of Rostock was impressed by his achievements and awarded him an honorary doctorate in 1851. His 1851 book is now seen as the beginning of modern botany. In 1863 he became professor of botany at Heidelberg and in 1872 at Tübingen. In 1868 he published the first textbook on plant morphogenesis.

**Hooke, Robert (1635-1703),** English scientist. As a child he was fascinated by mechanical devices,
and as a teenager that fascination extended to Euclid’s geometry. He entered Oxford in 1653 and received a master’s degree in 1663. Oxford was the center of English science when he arrived, and he became Robert Boyle’s experimental assistant. In 1660 the Royal Society of London was founded, and in 1662 it appointed Hooke curator of experiments, expecting him to demonstrate three or four significant experiments per week. Although an impossible task, Hooke’s *Micrographia* (1665) records what he managed to achieve in a few years. He discovered “cells” in a slice of cork and also observed them in a variety of plants. In moss and mold fungus he observed “seeds” small enough to disperse in air, and therefore he doubted the possibility of spontaneous generation. He also concluded that fossils are the remains of living plants and animals; because they do not resemble living species, they represent either extinct species or species that had changed.

**Hooker, Joseph Dalton (1817-1911) and William Jackson (1785-1865)**, British botanists-administrators. William was from a prosperous family but did not attend college. His general interest in nature became focused on botany in 1804 when he discovered a moss that was previously unknown in Britain. Despite his young age, he soon knew Britain’s prominent botanists, and in 1809 Joseph Banks arranged for him to join a diplomatic mission to Iceland, where he was the first to botanize. Dawson Turner became his patron, and William married Turner’s eldest daughter. In 1820 Banks had him appointed professor of botany at Glasgow, where he was very popular with students and others. In 1841 William became first director of the Royal Botanic Gardens, Kew, where he was the first to botanize. Dawson Turner became his patron, and William married Turner’s eldest daughter. In 1820 Banks had him appointed professor of botany at Glasgow, where he was very popular with students and others. In 1841 William became first director of the Royal Botanic Gardens, Kew, where he remained. He was also a very productive botanical author and editor and made Kew into an important scientific and recreational institution. Joseph received a medical degree from Glasgow University but wanted a profession in botany. He followed the examples of Banks, Robert Brown, and Charles Darwin of serving as a naturalist on a naval expedition, 1839-1843, to the South Pacific. He became Darwin’s closest friend but resisted Darwin’s theory of evolution until he read *The Origin of Species by Means of Natural Selection*. He succeeded his father as a successful director of the Royal Botanic Gardens and outdid his father as a scientist. In both taxonomy and phytogeography, Joseph was a leading botanist of his time.

**Humboldt (Friedrich Wilhelm Heinrich) Alexander von (1769-1859)**, German scientist. He was from a wealthy family and attended the universities of Frankfurt and Göttingen and the Freiburg School of Mines. He studied botany under Karl Ludwig Willdenow and geology under Abraham Gottlob Werner. In 1792 Humboldt entered the Prussian mining service and made effective changes in equipment and the training of miners. He also conducted scientific research until 1798, when he went to Paris to arrange an expedition to Latin America, at his own expense. He and botanist Aimé Jacques Alexandre Bonpland reached Venezuela in July, 1799, and they departed from Cuba in April, 1804. Humboldt then lived in Paris until 1827 and published their findings in elaborate detail. The greatest private scientific expedition in history was documented in the greatest private expedition report in history. Taxonomic botany was greatly advanced, but Humboldt also founded phytogeography as a modern science. In 1829 he explored Siberia with naturalist Christian Gottfried Ehrenberg and mineralogist Gustav Rose. Humboldt achieved great fame both for his scientific and his popular science writings. Charles Darwin was among the many inspired by his works.


**Ibn al-Awwam (second half of 1100’s)**, Hispano-Arabic agricultural author. Nothing of his life is known except that he wrote or compiled the most important book on agriculture between the time of Columella and that of Albertus Magnus. *Kit b al-fil ha* discusses 585 plants and more than 50 fruit trees. He had access to Columella and
other ancient and medieval authors, and there seems little in his book that is original, but it was a reliable guide for the time. It was translated into Spanish (1802, 2 vols.) and French (1864-1867, 2 vols.).

Ingenhousz, Jan (1730-1799), Dutch-English physician and plant physiologist. He studied medicine in the universities of Louvain, Paris, and Edinburgh and became an expert on smallpox inoculation, even traveling to Vienna to inoculate the royal family. (He stayed on as court physician.) He was inspired by Joseph Priestley’s experiments, 1771-1779, on plant and animal gas exchanges under glass enclosures to undertake similar studies. Although Priestley found that plants can restore air exhausted by a candle or a mouse, he did not obtain consistent results because he did not discover that light is also essential for photosynthesis. That connection was established in Ingenhousz’s *Experiments upon Vegetables* (1779); he could account for Priestley’s inconsistent results by showing that plants produce carbon dioxide at night, just as animals do.

Ivanovsky, Dmitri Iosifovich (1864-1920), Russian botanist and microbiologist. He attended St. Petersburg University in 1883 to study science. In 1887 he and a student of plant physiology, V. V. Polovtsev, were sent to study tobacco blight at plantations in the Ukraine and Bessarabia. They concluded that it was a contagious disease, and Ivanovsky graduated in 1888 with a thesis, “On Two Diseases of Tobacco Plants.” In 1890 another disease appeared at tobacco plantations in the Crimea. Ivanovsky’s investigation of tobacco mosaic provided the first evidence of pathogenic viruses. In 1895 he earned his master’s degree with a thesis on yeast activity under aerobic and anaerobic conditions. He received a doctorate at Kiev in 1903 for his book *Mosaic Disease in Tobacco*, but because this research attracted little attention, he then researched photosynthesis at Warsaw University.

Jacob, François (1920- ), French microbiologist, geneticist, and physiologist. He studied medicine to become a surgeon, but Germany’s invasion of France in 1940 interrupted his education. He escaped to London and became a medical officer in the French Free Army. During the Normandy invasion in 1944 he was wounded severely while assisting an injured officer and was unable to train as a surgeon. He therefore turned to microbiology and received a Ph.D. under André Lwoff’s guidance, studying lysogenic bacteria. He then studied sexuality and genetics of bacteria with Elie Wollman; they showed that bacterial chromosomes are circular DNA molecules, with genes that can be mapped experimentally. Next, Jacob and Jacques Monod discovered messenger RNA, leading to their differentiation of ribosomal, messenger, and transfer RNA—all of which assist in protein synthesis. Jacob and Monod hypothesized that chromosomes are divided into “operon” units; an operon is composed of a regulatory gene, an operator site, and several structural genes. This concept helped them explain enzyme induction caused by a sudden increase in food. Lwoff, Jacob, and Monod shared the 1965 Nobel Prize in Physiology for their discoveries on genetic control of enzymes and virus synthesis.

Johannsen, Wilhelm Ludwig (1857-1927), Danish botanist and geneticist. Although Johannsen was a good student, his family could not afford to send him to college, and in 1872 he was apprenticed to a pharmacist. While working in pharmacy he taught himself botany and chemistry, and in 1881 he became an assistant in the new Carlsberg Laboratory. He investigated the metabolism of ripening, dormancy, and germination in fruits and seeds. In 1892 he became a lecturer in botany at the Copenhagen Agricultural College, and in 1893 he discovered a way to end dormancy of winter buds. Despite a lack of a university education, in 1905 he became professor of plant physiology at the University of Copenhagen and in 1917 became its rector. He began studying variability in relation to heredity in the 1890’s, improving Francis Galton’s statistical methods. He showed that selection for heavier or lighter seeds has no effect on pure strains of peas and beans, but it can affect impure strains. In 1909 he shortened Hugo de Vries’s “pangene” to “gene” as the name for the unit of heredity. In 1923 he wrote in Danish a history of genetics that went through four editions.

Jung (Jungius), Joachim (1587-1657), German natural philosopher, botanist, and mathematician.
He was the son of a professor at the Gymnasium St. Katharinen in Lübeck and studied there until he entered the University of Rostock in 1606. He studied mathematics and logic and then transferred to the University of Giessen, where he received his master’s degree in 1608. He taught there and elsewhere until 1616, when he reentered the University of Rostock to study medicine. He obtained an medical doctorate from Padua in 1619. During the following decade he practiced medicine and taught mathematics at Rostock. Finally, he became professor of natural science and rector of the Akademisches Gymnasium of Hamburg, where he remained for thirty years. In botany, he developed morphology based upon the writings of Theophrastus and Andrea Cesalpino. He developed a comprehensive terminology for describing precisely all plant parts and their relationships. This brought order to a developing quagmire. His botanical treatises appeared posthumously—\textit{Doxoscopiae Physicae Minores} in 1662 and \textit{Isagoge Phytoscopica} in 1679—but John Ray had access to a manuscript, \textit{Isagoge}, in 1660.

\textbf{Jussieu, Adrien-Henri (1797-1853), Antoine (1686-1758), Antoine-Laurent de (1748-1836), Bernard (1699-1777), and Joseph (1704-1779), French botanists.} Antoine, Bernard, and Joseph were sons of a Lyons apothecary, Laurent de Jussieu. Laurent’s fourth son, Christophe, was an amateur botanist and father of Antoine-Laurent, who, in turn, was father of Adrien-Henri. Antoine studied medicine and botany at Montpellier under Pierre Magnol, France’s first botanist to attempt a natural classification of plants and originator of the family concept in botany. Antoine received his medical degree in 1707 and went to Paris to study under Tournefort, who died the following year. In 1710 Antoine succeeded Tournefort as professor of botany at the Jardin du Roi, where he concentrated on developing the garden and training other botanists, including his brothers Bernard and Joseph. Bernard went to Paris in 1714 to finish his medical and botanical studies. In 1722 he became \textit{sous-démonstrateur de l’extérieur des plantes} at the Jardin du Roi. He was an effective teacher and was famous for his field trips. He arranged the garden at Trianon, near Versailles, to illustrate his natural system. Joseph also studied medicine and botany, but in addition, he was interested in engineering. In 1735 he joined a scientific expedition to Peru and did not return to Paris until 1771. The intervening years were spent exploring, botanizing, practicing medicine, and building a bridge at Potosí. Antoine-Laurent went to Paris to study medicine, receiving his medical degree in 1770, with a thesis comparing animal and plant physiology. He soon became deputy professor of botany at the Jardin du Roi and in 1774 published a paper on his uncle Bernard’s Trianon garden arrangement of plants, as adapted to the Jardin du Roi. Antoine-Laurent made a thorough study of genera and families of flowering plants for his epoch-making \textit{Genera Plantarum Secundum Ordines Naturales Disposita, Juxta Methodum in Horto Regio Parisiensi Exaratam, Anno 1774} (1789; \textit{Genera of Plants Arranged According to Their Natural Orders, Based on the Method Devised in the Royal Garden in Paris in the Year 1774}). In 1793 the Jardin du Roi was reorganized as the Muséum National d’Histoire Naturelle, and he became professor of botany. He established a herbarium which absorbed herbaria and libraries confiscated by France’s revolutionary armies. In 1800 he became director of the museum. Adrien-Henri followed family tradition, studying medicine and botany, and received a medical degree in 1824 with a thesis on \textit{Euphorbiaceae}. In 1826 he succeeded his father as professor of botany at the Muséum National d’Histoire Naturelle. He was a brilliant teacher, and his textbook went through twelve editions, 1842-1884. He also wrote taxonomic monographs, contributed articles on taxonomic theory, and built up a large herbarium.

\textbf{Kalm, Pehr (1716-1779), Swedish-Finnish naturalist.} He began his higher education at Abo, Finland, and in 1740 went to Uppsala University in Sweden, to finish under Carl Linnaeus. He went on several Scandinavian expeditions and in 1747 became professor of applied science at Abo. In 1748, at the urging of Linnaeus, the Royal Swedish Academy of Sciences sent Kalm to North America to find useful plants for Scandinavia. It was reasonable to travel mainly in Canada because of the similarity of climates, and he spent a few months there on two trips. However, he was attracted to the Philadelphia area, partly by the Swedish settlement in nearby New Jersey, where
he met his wife, and partly by the intellectual community, which included John Bartram. He reluctantly departed in 1751 with abundant living and pressed plants, fortunately leaving a set with Linnaeus in Uppsala before continuing on to Abo, where his own collection later was destroyed in a fire. His lasting fame comes from his En Resa til Norra America (1753-1761, 3 vols.), which also appeared in German, English, Dutch, and French translations. He was a popular teacher and devoted the rest of his life to Finnish botany, forestry, and agriculture.

Kämpfer, Engelbert (1651-1716), German geographer and botanist. Son of a Lutheran minister, he had a strong urge to travel that was manifested in his attending schools and universities in various places. He finally earned a master’s degree in Kraków in 1680 and then studied medicine at Königsberg, 1680-1681, and at Uppsala, Sweden in 1681. He became secretary and physician to the ambassador to Iran, and they left Stockholm in March, 1683, reaching Isfahan a year later. After the ambassador returned to Sweden in 1685, Kämpfer remained in Iran three more years as an employee of the Dutch East India Company. In 1688 he sailed on one of its ships to Southeast Asia and reached Nagasaki, Japan, in 1690, where he remained until November, 1692. He reached Holland in October, 1693, and received a medical degree from Leiden in 1694, with a dissertation on his foreign discoveries. He returned to his hometown, Lemgo, to practice medicine and prepare his journals for publication. He published one book, Amoenitatum exoticarum (1712), and after his death Hans Sloane bought his herbarium and manuscript history of Japan; the latter was translated and published in English. Kämpfer’s herbarium is in the British Museum, where Carl Peter Thunberg studied it.

Koch, (Heinrich Hermann) Robert (1843-1910), German bacteriologist. He earned a medical degree at Göttingen in 1866, having studied under Jacob Henle. After serving as a field physician in the Franco-Prussian War, he became a country doctor near Breslau. An anthrax epidemic in the area led him in 1876 to verify C.-J. Davaine’s contention that rodlike microorganisms found in sheep’s blood cause the disease. He learned to cultivate the bacterium in cattle blood at body temperature. He traced its life cycle, including spore formation and germination, and in 1876 took his work to Ferdinand Julius Cohn at the University of Breslau, who studied it and sponsored its publication. In 1877 Koch published Untersuchungen über die Aetiologie der Wundinfektionskrankheiten (Investigations into the Etiology of Traumatic Infective Diseases, 1880), in which he modified Henle’s criteria for determining contagion into “Koch’s postulates.” In 1880 he became adviser to the Imperial Department of Health in Berlin and had a laboratory with Friedrich Loeffler as an assistant. In 1881 at the International Medical Congress in London, Koch demonstrated in Joseph Lister’s laboratory his pure-culture methods, which Louis Pasteur praised. Returning to Berlin, Koch demonstrated the infectious properties of tuberculosis and was able to overcome great difficulties to isolate the bacterium. His 1882 lecture, “Über Tuberculose,” was sensational. He believed at the time that human and bovine tuberculosis was the same but later changed his mind. He went on to numerous other discoveries, becoming one of the main founders of bacteriology.

Kölreuter, Josef Gottlieb (1733-1806), German botanist. He graduated from the University of Tübingen in 1755 with a medical degree and then spent six years as keeper of natural history collections at the Imperial Academy of Sciences in St. Petersburg. There he began studies on plant fertilization and hybridization, continuing these experiments after moving to Karlsruhe as professor of natural history and director of the margrave’s gardens. His experiments continued until the death of his patroness, the margrave’s wife, in 1786. Despite publication of Rudolph Jakob Camerer’s experiments on plant sexuality (1694), doubts lingered among botanists. Kölreuter made thorough studies of pollen, stamen, and stigmas; he showed that many hermaphrodite flowers are not self-pollinating, as their stamens and stigmas ripen at different times. He successfully hybridized two species of tobacco and was pleased to report that the hybrids were infertile but later found he could produce fertile hybrids in the genus Dianthus. However, he continued to believe it impossible to produce new species by hybridization. Later hybridizers built upon his work.
Kramer, Paul Jackson (1904-1995), American plant physiologist. He grew up on an Ohio farm with a large library. The first scientific article he read was in the U. S. Department of Agriculture Yearbook for 1920, on photoperiodism. At Miami University he majored in botany and after graduating in 1926 worked for several summers for the Department of Agriculture. He entered graduate school at Ohio State University and studied ecology and physiology under E. N. Transeau. He received his Ph.D. in 1931, married fellow botany student Edith Vance, and accepted an instructorship at Duke University. At Duke’s School of Forestry Kramer researched and trained students in two related subjects—water absorption and woody plants. He synthesized his and his students’ findings in Plant and Soil Water Relationships (1949, 2d ed. 1969) and in Physiology of Trees (1960); the latter he coauthored with his former student Theodore T. Kozlowski. Neither subject had received much attention before Kramer’s researches, but when he retired, they were major components of plant science.

Krebs, Hans Adolf (1900-1981), German-English biochemist. He was son of a surgeon and studied medicine, receiving his medical doctorate at Berlin in 1925. He then practiced medicine and pursued biochemical research at the Kaiser Wilhelm Institute for Biology and at the University of Freiburg. In 1933, because he was Jewish, he lost his position at Freiburg and immigrated to England. In 1935 he became a lecturer in biochemistry at Sheffield University, and by 1945 he was chairman of a research unit in cell metabolism. His research focused on cyclic metabolic pathways. He had already discovered the urea cycle in 1930-1933, and by 1945 he was investigating the citric acid cycle that made him co-winner of a Nobel Prize in 1953.

Kunkel, Louis Otto (1884-1960), American plant virologist. He grew up on a Missouri farm and because of a need to earn a living was not able to enter the University of Missouri until 1906. His bachelor’s degree was in education, but he took a master’s degree in botany in 1911 and went to Columbia University for a philosophy doctorate in 1914, with a dissertation on fungus physiology. He became a pathologist with the U.S. Department of Agriculture (USDA) and studied diseases of potatoes and cabbage. In 1915-1916 he received a fellowship to study viral diseases of potatoes in Holland, Germany, and Sweden. In 1920 he left the USDA to become pathologist for the Hawaiian Sugar Planters’ Association. In four months he discovered that the virus causing cane mosaic was not transmitted by the sugar cane aphid but by another aphid whose usual host had been displaced by sugarcane. In 1923-1932 he was first a pathologist and later an administrator at the Boyce Thompson Institute for Plant Research and afterward at the Rockefeller Institute for Medical Research. Besides his own accomplishments in virology, Kunkel assembled a brilliant research team to study viruses, insect vectors, and disease eradication.

Lamarck, Jean-Baptiste (1744-1829), French botanist, zoologist, and evolutionist. He began his career as a soldier and fought in the Seven Years’ War; afterward, while on guard duty in eastern and southern France, 1763-1768, he became interested in French flora. After leaving the army he studied medicine and botany in Paris and published a highly regarded Flore française (1779 despite 1778 on title page, 3 vols.; reprinted in 1795 and revised by A. P. de Candolle in 1805). He developed a dichotomous key to the species that was easier to use than Linnaeus’s artificial system, and he adopted the natural system of classification being developed by Michel Adanson and the de Jussieus. He also wrote three and a half volumes of the eight-volume Dictionnaire de botanique (1783-1795). In 1779 he was elected to the Académie des Sciences as a botanist, and he was employed at the Jardin du Roi, 1788-1793. In 1793, when the Jardin du Roi was reorganized as the Muséum National d’Histoire Naturelle, he was not needed as a botanist and became professor of zoology to study the animals which he named “invertebrates.” It was while studying animals that he developed his theory of evolution, first published in 1800 and explained in detail in Philosophie zoologique: Ou, Exposition des considerations relative à l’histoire naturelle des animaux (1809, 2 vols.; Zoological Philosophy: An Exposition with Regard to the Natural History of Animals, 1914). However, he also introduced his evolutionary ideas into his Introduction à la botanique (1803, 2 vols.; introduction to botany).
Lawes, John Bennet (1814-1900), British agricultural chemist. He attended Oxford University and became interested in chemistry but left without a degree. In 1834 he inherited Rothamsted estate, where in 1836 he began adding acids to ground bone for fertilizer, and in 1843 he began manufacturing “superphosphate” fertilizer and used the profits to finance his experiments. He also hired chemist Joseph Henry Gilbert (1817-1901) as his assistant, and they collaborated for more than fifty years, making Rothamsted world famous. They devised a “chessboard” system of random plots for field trials. Work on agricultural use of sewage caused Lawes to be appointed a member of a Royal Commission in 1857. Because of Gilbert’s rigidity, in 1876 Lawes appointed Robert Warington as his personal assistant, which damaged his relationship with Gilbert. In 1889 Lawes put Rothamsted under a Lawes Agricultural Trust with endowment of 100,000 £; its work has continued to the present day.

L'Écluse (Clusius), Charles de (1526-1609), French-Low Countries botanist. He was from a wealthy Protestant family and was well educated in law. His interest in plants developed in 1551, after he went to Montellier to assist Guillaume Rondelet convert his notes on fish into a book. L'Écluse then became a translator of books, including a French edition of Junius Rembert Dodoens’s Crüjdeboeck and several books on the medicinal plants of exotic lands. He began publishing his own botanical discoveries in 1576 with a book on Spanish plants, followed by his flora of Austria-Hungary in 1583, Rariorum plantarum historia (1601) and Exoticorum (1605)—all important contributions to botany.

Leeuwenhoek, Antoni van (1632-1723), Dutch microscopist. He was from a prosperous family, but after his father died he was apprenticed to a cloth merchant in Amsterdam. After the apprenticeship he returned to his hometown, Delft, to live. He began as a shopkeeper, but in 1660 he became a municipal official. In 1671 he made a more powerful magnifying glass than cloth merchants used, to study minute objects from nature. He soon became an expert at making single-lens microscopes, which eventually were powerful enough to study sperm (his own) and bacteria. Initially, he was enchanted by minute animals; then he wondered how similar the minute structures of plants and animals are. He showed Dutch scientists his discoveries, and Reinier de Graaf put him in touch with the Royal Society of London, which proved very receptive to publishing Leeuwenhoek’s observations. He sent letters to it regularly for fifty years (1673-1723), which were translated into English and published in Philosophical Transactions. He also published his works in Dutch and Latin editions.

Linnaeus, Carl (1707-1778), Swedish botanist, zoologist, and physician. His father, a small-town Lutheran minister, was an enthusiastic gardener and introduced his son to botany. From the time he entered Latin School in 1716, Linnaeus was absorbed by natural history. A high school teacher insisted that he be allowed to study science and medicine, and his father reluctantly agreed. At Uppsala University Linnaeus wrote an essay defending the theory of sexuality in plants that so impressed a medical professor that he appointed Linnaeus lecturer in botany and tutor of his sons. In 1730 Linnaeus began working on a classification of plants based on the numbers of stamens and pistils, a later version of which appeared in the first edition of Systema naturae (1735; A General System of Nature Through the Three Grand Kingdoms of Animals, Vegetables, and Minerals, 1800-1801). His sexual system for flowering plants was easy to use, though artificial. In 1732 he received a grant from the Uppsala Scientific Society that supported his five-month exploration of Lapland. His discoveries were carefully recorded, though they were not published in an English translation until 1811. In 1735 he went to Holland to obtain a medical degree, to meet botanists, and to publish his manuscripts. He remained there for three very productive years. His basic ideas about classifying plants, animals, and minerals were developed and published there, with more emphasis on plants than on the other two kingdoms. He then practiced medicine in Stockholm until he became a professor of medicine at Uppsala in 1741. He soon turned it into a virtual professorship of botany. He developed a consistent system of binomial nomenclature that became widely accepted. In 1749 Linnaeus had a student defend one of his essays for a doctoral dissertation, on
This was the first attempt to organize an ecological science. The balance of nature concept, based on the fact that predatory animals usually have fewer offspring than their prey, had come down from antiquity, but Linnaeus added environmental studies to broaden the concept. It was translated into English and impressed Charles Darwin when he was developing his theory of evolution. In 1905 botanists agreed to take Linnaeus’s *Species plantarum* (1753; the species of plants) as the official starting point for scientific names, and zoologists chose the tenth edition of *Systema naturae* (1758) as the starting point for animal names.

L’Obel, Matthias (1538-1616), Flemish-English botanist. He was interested in medicinal plants by age sixteen; in 1565 he was studying medicine at Montpellier under Guillaume Rondelet, who left his botanical manuscripts to L’Obel when he died in 1566. L’Obel remained in Montpellier three more years in order to coauthor with Pierre Pena *Stirpium adversaria nova* (1570, enlarged ed. 1576) on more than twelve hundred plants that L’Obel had collected around Montpellier and elsewhere. In 1581 a Flemish translation appeared. L’Obel was interested in natural groupings of plants and was guided by the leaves.

McClintock, Barbara (1902-1992), American botanist and geneticist. She majored in botany at Cornell University, where she earned her bachelor’s degree (1923), master’s degree (1925), and philosophy doctorate (1927). She studied with Richard Goldschmidt in Germany in 1933, where she was shocked at Nazi behavior and left. Despite her outstanding research, Cornell would not give her faculty standing because she was a woman. In 1936-1941 she was an assistant professor at the University of Missouri but was not promoted. In 1941 she went to the Cold Spring Harbor Laboratory, where she remained. She investigated the genetics of corn (maize), especially the breakage, movement, and fusion of parts of chromosomes. She won the Nobel Prize in 1983 for research mostly conducted some forty years before.

Malpighi, Marcello (1628-1694), Italian physician and biologist. He was a native of Bologna and earned a medical degree at its university in 1653. He taught medicine at several universities until 1691, when he became chief physician to Pope Innocent XII. William Harvey’s two books on the circulation of the blood were convincing, as far as they went, but Harvey had worked before the development of adequate microscopes and had not discovered the links between arteries and veins. Malpighi mastered microscopic technique and sought the links in the lungs of frogs. He published his discoveries of capillaries in 1661. The Royal Society of London was impressed and began corresponding with him. In 1671 he sent the society his first study on plant anatomy, which he accomplished without knowledge of Nehemiah Grew’s first study, which the Royal Society had published a few months before. Several of Malpighi’s subsequent publications were published by that society, including his *Anatome plantarum* (2 parts, 1675 and 1679; plant anatomy). For nearly 150 years there were no significant advances in plant anatomy beyond what Malpighi and Grew had accomplished.

Manton, Irene (1904-1988), English botanist and cytologist. In 1923 she won a scholarship to Cambridge University to study cytology and genetics. She graduated in 1926 and spent 1927 studying cytology in Stockholm. She earned a Ph.D. at Cambridge in 1930 with a dissertation examining chromosomes of 250 plant species. During her lectureship in botany at Manchester, 1929-1946, she continued her chromosome studies. Her effective methodology and discoveries enabled her to obtain the botany chair at Leeds, 1946-1969. She began using the electron microscope in 1950 and was first to study plant cell organelles, including chloroplasts. She studied polyploidy and hybridization in ferns, and after retirement she went on collecting expeditions to obtain nanoplanckton from Denmark to South Africa and from Alaska to the Galápagos Islands, 1970-1974. She and her zoologist sister, Sidnie Milana Manton, were the first sisters to be elected to the Royal Society of London. Irene Manton won two medals from the Linnean Society and served as its president in 1973.

Mariotte, Edme (c. 1620-1684), French scientist. He was closely associated with the Académie Royale des Sciences from soon after its founding in 1666.
until his death. Nothing is known of his earlier life; he might have come from Chazeuil in Burgundy, where several Mariotte families lived. He moved from Dijon to Paris in the 1670’s. He was soon involved in controversy with Claude Perrault over the possible circulation of plant sap. His *De la végétation des plantes* (1679) went beyond that controversy to argue that plants take in water from their roots, but they make the different substances found in plants.

Mattioli, Pier Andrea (1501-1577), Italian physician and botanist. He was the son of a physician and earned a medical degree at the University of Padua in 1523. He had a very successful medical practice yet was also an industrious author. His books generally involved medicinal plants—at a time when virtually all species had medical uses. He began with commentaries on Pedanius Dioscorides’ *De materia medica* (1544) and by republishing enlarged and revised editions, he became the leading authority on the subject. He also provided many excellent illustrations of the plants discussed—more than five hundred in early editions and finally more than twelve hundred in the last editions.

Mendel, (Johann) “Gregor” (1822-1884), Czechoslovakian experimenter in genetics. His father was a farmer, and his mother was the daughter of a village gardener. He was not robust enough to become a farmer, though he helped his father graft fruit trees. He was determined to get a good education, and he entered the Augustinian monastery in Brno because it would enable him to complete college and become a teacher; he took the name “Gregor” when he entered in 1843. There, Matthew Klácel ran an experimental garden and studied variation, heredity, and evolution in plants, later putting Mendel in charge of the garden. Mendel also became a substitute teacher in a grammar school and did well; therefore, he took an exam for science teachers but failed. He was sent to the University of Vienna, 1851-1853, to broaden his knowledge. There he learned to apply mathematics to science, and he studied botany under the controversial Franz Unger, who taught that plants evolved over time. In 1855 Mendel retook the teacher’s exam and, being very nervous, failed again. In 1856 he began experiments on inheritance in peas, and the experiments he designed show that he had, in fact, mastered his science lessons. He was experimenting at a time when naturalists were not accustomed to thinking mathematically about biology. During ten years of research, he bred and tabulated at least twenty-eight thousand plants. By following the heredity of variable traits through at least three generations, he showed that traits such as height, flower color, and seed texture exhibit dominance and recessiveness and that hereditary patterns can be determined by statistical analysis of the offspring of breeding experiments. The scientific paper which he read at a meeting of the Natural Sciences Society of Brno in 1865 and published in its journal in 1866 is now judged to be clear and logical, but it was too advanced for a mathematically unsophisticated audience, and there was no response. Mendel did not give up but sought to expand his proofs to other species. In several species he did obtain the same type of results, but unfortunately he choose to study in detail the heredity of *Hieracium*, a genus that does not consistently reproduce sexually—reproducing also by apogamy. Since he never discovered this situation, his *Hieracium* results, which he reported in 1869 and published in 1870, failed to substantiate his findings of 1865. His work sank into obscurity until 1900, when three botanists—Karl Correns, Erich Tschermak, and Hugo de Vries—rediscovered and publicized it. 

Michaux, André (1746-1802) and François-André (1770-1855), French botanists. At age twenty-one, André succeeded his deceased father as manager of a royal farm. However, he became more interested in botany and horticulture than in farming and went to Paris to study under Bernard de Jussieu (1777) and botanize with Jean-Baptiste Lamarck in Auvergne and the Pyrenees (1780). He also explored Iran for three years before going to America in 1785, taking along his son. They lived in New Jersey and sent back to France five thousand trees and twelve packets of seeds. In 1787 they moved to South Carolina and purchased a plantation near Charleston to use as a nursery. They collected southward into Florida. In 1789 they collected in both the Bahamas and the Appalachian Mountains. In 1792 they spent eight months on a trip to Hudson Bay, Canada, and three months in Kentucky. In 1794
they collected in the southern Appalachians again and on the Illinois prairies. In 1796 they returned to France, and André wrote *Histoire des chênes de l’Amérique* (1801), on oaks, and *Flora boreali-americana* (1803), but he did not oversee their publication because he sailed to Madagascar in 1800, where he died. In 1801 François-André, who had learned botany from his father, returned to the nursery in South Carolina and then traveled extensively in the East until 1803; he returned to the United States for more collecting and exploring in 1806-1807. He published three works on his studies: *Voyage à l’ouest des monts Alleghany* (1804; *Travels to the Westward of the Alleghany Mountains*, 1805), *Mémoire sur la naturalisation des arbres forestiers de l’Amérique septentrionale* (1805), and *Histoire des arbres forestiers de l’Amérique septentrionale* (1810-1813, 3 vols.; *The North American Sylva: Or, A Description of the Forest Trees of the United States, Canada, and Nova Scotia*, 1819).

**Mirbel, Charles François Brisseau de (1776-1854),** French botanist. His education was interrupted by the French Revolution, and in 1796 he fled to the Pyrenees for two years, where he became interested in botany and mineralogy. In 1798 he obtained a post at the Muséum National d’Histoire Naturelle, where he initiated French studies on microscopic plant anatomy. He showed that seed and embryo characteristics are identical for species within natural families, laying the foundation for embryogenic classification. His numerous publications include *Traité d’anatomie et de physiologie végétales* (1802, 2 vols.) and similar, updated works in 1815 and 1832.

**Mohl, Hugo von (1805-1872),** German botanist. He had early interests in botany and optics and was able to combine those interests in his career. He earned a medical degree at Tübingen in 1828 with a thesis on plant pores (stomata), and in 1835 he became professor of botany there. He was a founder of *Botanische Zeitung* (1843; botanical newspaper) and published a manual on microscopy (1846). His encyclopedia memoir “Die vegetabilische Zelle” (1850; “The Vegetable Cell,” 1852) was an important synthesis of his and others’ researches during a crucial decade. He first used the term “protoplasm” in its modern sense.

**Nägeli, Karl Wilhelm von (1817-1891),** Swiss-German botanist. The son of a physician, he studied medicine in Zurich but left in 1839 to earn a Ph.D. in botany under Alphonse de Candolle in Geneva. In 1842 Nägeli went to Jena to work with Matthias Jakob Schleiden to investigate plant cells. Nägeli was influenced by German *Natur Philosophie*, and his careful research was sometimes undermined by his philosophical preconceptions. This was as true of his genetics as of his cytology. He made important discoveries, only to overinterpret them. This was unfortunate, because he achieved a position of eminence, as professor of botany at Munich. The most notorious example of his close-mindedness was his unwillingness to take seriously Gregor Mendel’s genetics paper of 1866. Mendel’s unfortunate choice of *Hieracium* as a subject for further hereditary studies was because of Nägeli’s interest in the genus.

**Oparin, Aleksandr Ivanovich (1894-1980),** Russian botanist and biochemist. He studied botany at the Moscow State University and was influenced by plant physiologist K. A. Timiryazev and by the writings of Charles Darwin. Graduating in 1917, he did research in botany and biochemistry under A. N. Bakh, and in 1922 he explained at a meeting of the Russian Botanical Society his hypothesis of primordial heterotrophic organisms arising in a brew of organic compounds. He argued that because organisms receive energy and materials from outside, they are not limited by the second law of thermodynamics. In 1935 he became the deputy director of the Bakh Institute of Biochemistry in Moscow and in 1946 became director. In 1957 he organized the first international meeting on the Origin of Life in Moscow, and in 1970 he was elected president of the International Society for the Study of the Origin of Life. Fame came with his *The Origin of Life on Earth* (1936, 3d ed. 1957), and he also published later works on this subject.

**Pasteur, Louis (1822-1895),** French chemist, crystallographer, microbiologist, and immunologist. His father was a veteran of Napoleon’s army and a tanner. Pasteur was only a mediocre student at the Collège Royal de Besançon, but he was able to enter the École Normale Supérieure in Paris and was inspired by chemistry professor Jean-
Baptiste Duman of the Sorbonne. He earned his Ph.D. in 1847 and remained at the École until 1848. His early research interests were in chemistry and crystallography, and in 1854 he became professor of chemistry at the new Faculty of Sciences at Lille. In 1855 he published an article showing that amyl alcohol, a by-product of industrial fermentation, is composed of two isomers, one optically active and the other not. In 1856 he began research on why a beetroot alcohol factory experienced variations in the quality of its product. He discovered that properly aged wine or beer contains spherical globules of yeast cells that produce alcohol, but sour wine or beer contains elongated yeast cells that produce lactic acid. This discovery undermined Justus von Liebig’s contention that fermentation is a purely chemical process not involving living organisms, and it led, in turn, to Pasteur’s opposition to the theory of spontaneous generation. Pasteur also discovered the existence of “anaerobic life” (his term). His search for ways to preserve wine led him to develop pasteurization (partial heat sterilization). In 1865 he began studying two silkworm diseases and devised ways to inhibit them. From 1877 until his death he studied anthrax, chicken cholera, swine erysipelas, and rabies. He was one of the main founders of microbiology.

Plinius (Pliny) Secundus, Gaius (c. 23-79 C.E.), Roman provincial administrator and author. He served as an army officer and naval administrator but was also a diligent compiler of a natural history encyclopedia in thirty-seven books. He drew upon both Greek and Roman authorities, and he discussed plants from agricultural, pharmaceutical, and botanical perspectives in books 12-27. Remarkably, his Natural History survived the decline of Rome and was an important resource during the Middle Ages; a modern Latin-English edition is in ten volumes.

Pringsheim, Nathanael (1823-1894), German botanist. His father wanted him to study medicine at the University of Breslau, where he was influenced by the great animal physiologist and histologist Jan Evangelista Purkinje. However, Pringsheim realized his true interest was botany, and he transferred to Berlin, where he was strongly influenced by Matthias Jakob Schleiden’s famous textbook on botany (1842-1843). He earned his Ph.D. in 1848 with a dissertation on the growth of cell walls. The dynamics of cell division was a thorny issue during the 1840’s and 1850’s, exacerbated by technical limitations in microscopy and cytology, and he challenged the explanations of both Schleiden and Hugo von Mohl. French botanist Gustave Adolphe Thuret’s discovery of sexual reproduction in the marine alga Fucus attracted Pringsheim’s interest in the study of sexual reproduction in algae. He established this as a general phenomenon in freshwater algae and corrected Thuret’s account of the fusion of sperm and egg. He also became involved in a long, inconclusive debate with Anton de Bary over whether the fungus Saprolegnia reproduces sexually. Pringsheim also encountered opposition to his account of alternation of generations in lower cryptogams. In 1864 he became Schleiden’s successor at Jena, but because of poor health and an inheritance, he resigned in 1868 and returned to a house in Berlin near the botanic garden. In 1874 he began research on photosynthesis, but his ideas on the role of chlorophyll won no converts. He was successful, however, in three organizational initiatives. In 1857 he founded Jahrbücher für wissenschaftliche Botanik (annals of scientific botany) and edited it until he died; in 1882 he was chief founder of the German Botanical Society and was its president until he died; and he helped establish a biological station on Helgoland island on the German coast. A museum was built there in his honor after he died.

Raunkiaer, Christen (1860-1938), Danish plant ecologist. Raunkiaer was Johannes Warming’s successor.

Ray, John (1627-1705), English naturalist. He acquired an interest in plants from his mother, a herbalist-healer. At Cambridge University he earned a bachelor’s degree in 1644 and a master’s degree in 1651. His teaching career at Cambridge ended in 1662, when he refused to take an oath required by a new Act of Uniformity. During the 1650’s Ray and his friends studied the flora of Cambridgeshire and published anonymously Catalogus plantarum circa Cantabrigiam nascentium (1660; Ray’s Flora of Cambridgeshire, 1975), listing 558 species, which was not superseded until 1860. After his exclusion Ray was
supported by a naturalist patron, Francis Willughby; they became close collaborators and traveled in Europe, 1663-1666. When Willughby died in 1672, Ray married and returned to live in his hometown, Black Notley. He developed his system of classification in *Methodus Plantarum Nova* (1682), and the revised edition of 1703 provided classification for nearly eighteen thousand species. His *Synopsis Stirpium Britannicum* (1690) was the first British flora—not superseded until 1762. His most important botanical work was his *Historia Plantarum Generalis* (1689-1704, 3 vols.), which contained an introduction to plant anatomy, morphology, and physiology and a classification and description of all known species, in some three thousand folio pages. It remained a leading authority for a century.

**Ruel, Jean (1474-1537)**, French physician and botanist. Little is known of his early years, but he received a medical degree in 1508 and in 1509 served as a physician to François I. His Latin translation of Pedanius Dioscorides’ *De materia medica* was published in 1516. His main work was his *De Natura Stirpium Libri Tres* (1536), with more than nine hundred pages of text and no illustrations. Because he gave full verbal descriptions of all species, he developed both terminology and definitions that became more widely known when they were appropriated by Leonhard Fuchs (1542).

**Sachs, Julius von (1832-1897)**, German plant physiologist. His father was an engraver, and both parents died within a year (1848-1849), which forced him to leave school, but he met the physiologist Jan Evangelista Purkinje, who took him to Prague as a draftsman. There, he finished school in 1851 and then entered the university. He found the botany and zoology lectures boring, but he did independent research, and after he had published eighteen scientific articles he received a Ph.D. in 1856. In 1859 he became assistant in plant physiology at the Agricultural and Forestry College near Dresden. In 1860 Hofmeister and Sachs began editing the *Handbuch der physiologischen Botanik* (1865). In 1861-1867 he taught at the Agricultural College in Poppelsdorf and in 1868 became professor of botany at Würzburg, where he remained. He was a brilliant lecturer and imaginative experimenter and became the foremost plant physiologist of the day. He studied metabolism, photosynthesis, mineral needs, etiolation, flower and root formation, and growth. However, his understanding of water and sugar transport was defective, and he spent his last years attacking Charles Darwin’s theory of natural selection as the cause of evolution. Sachs invented numerous laboratory techniques and devices, and his textbooks—*Lehrbuch der Botanik* (1868; textbook of botany) and *Vorlesungen über Pflanzenphysiologie* (2 editions, 1882, 1887)—were authoritative. He also wrote a history of botany, 1500-1860 (1875).

**Sargent, Charles Sprague (1841-1927)**, American botanist and arboretum administrator. He was from a prosperous Boston family and graduated from Harvard University in 1862 in classics. After serving in the Union Army during the Civil War, he toured Europe for three years. With only an amateur interest in horticulture and dendrology, he became director of the Arnold Arboretum at Harvard in 1873 and remained there. He was also appointed Arnold Professor of Arboriculture. Funds from the James Arnold estate were used to establish the arboretum on 150 acres of “worn-out farm,” which Sargent increased to a 250-acre world-class resource. The annual funds from the endowment were never enough to sustain the operations which he undertook, and he raised funds from wealthy friends and from his own finances. He had the benefit of advice from Asa Gray in planning and running the arboretum. In 1879 Sachs undertook a survey of the forests of the United States, and his six-hundred-page report became Volume IX of the “Tenth Census of the United States” (1880). He was a strong supporter of U.S. national parks and national forests and chaired a committee’s study and report on the latter for the National Academy of Sciences in 1896. At the urging of the Smithsonian Institution he undertook *Silva of North America* (1891-1902, 14 vols.), with 740 plates. It became the basis for his *Manual of North American Trees* (1905). He also edited the *Journal of the Arnold Arboretum* and the popular periodical, *Garden and Forest*, which encouraged forest conservation.

**Sargent, Ethel (1863-1918)**, English plant anatomist. She graduated from Cambridge University
in 1884 but never held a professional position. She next studied plant anatomy and laboratory techniques for a year at the Royal Botanic Gardens at Kew. In 1897 she visited several European laboratories, including Adolf Strasburger's at Bonn. She conducted her research in a home laboratory, and she had informal students who studied with her, most notably Agnes Arber. Her earliest research was on centrosomes in higher plants, followed by a study of oogenesis and spermatogenesis in *Lilium martagon*. She confirmed the existence of the synaptic stage in cell division at a time when some investigators dismissed it as an artifact of lab procedures. She concluded from her studies of monocots that the number and arrangement of vascular bundles (axial or lateral) are useful clues to evolution and discussed this in three important articles (1896-1902). She became a fellow of the Linnean Society of London and in 1913 was president of the Botanical Section at the meeting of the British Association for the Advancement of Science.

**Saussure, Horace Bénédict de (1740-1799) and Nicolas-Théodore de (1767-1845), Swiss scientists.** Horace’s father was an agricultural author, and his uncle was the prominent naturalist Charles Bonnet. Horace graduated from the University of Geneva in 1759 with a dissertation on transmission of heat by sun rays. In 1760 he traveled to the Chamonix mountains to collect plants for the physician-botanist Albrecht von Haller. He also dedicated to Haller his first botanical treatise, *Observations sur l’écorce des feuilles et des pétales des plantes* (1762). In 1767 he conducted experiments at Mont Blanc on heat and cold, the weight of the atmosphere, and electricity and magnetism. In 1768 he and his wife toured France and England and met many scientists. In 1774-1776 he was rector of the University of Geneva, and in 1776 he founded the Société des Arts and was its first president. His major work is *Voyages dans les Alpes, Précédés d’un essai sur l’histoire naturelle des environs de Genève* (1779-1796, 4 vols.). Nicolas-Théodore studied science under his father and assisted in his research. They spent several weeks in the summers of 1788 and 1789 conducting research on Swiss mountains. Nicolas-Théodore became interested in the chemistry of plant physiology and after seven years of research published his *Recherches chimiques sur la végétation* in 1804. It was translated into German in 1805 and became the foundation of phytochemistry science. He continued to publish specialized studies on the subject for the rest of his life. In 1815 he was a founding member of Société Helvétique des Sciences Naturelles.

**Schimper, Andreas Franz Wilhelm (1856-1901),** Franco-German botanist. His father was professor of natural history at the University of Strasbourg and director of the city’s museum of natural history. Schimper received a Ph.D. from the university in 1878, having studied under Anton de Bary. De Bary opposed his succeeding his father as museum director in 1880, and instead Schimper went to Johns Hopkins University to study starch formation. In 1881 he traveled in Florida and the West Indies and became interested in phytogeography. In 1883 he became lecturer in plant physiology at the University of Bonn, where he also taught phytogeography and other botany courses. In 1886 he traveled to Brazil to study salt concentration in mangroves and other littoral vegetation. He conducted similar studies in Ceylon and Java, 1889-1890. He published twenty-seven books and articles and is best remembered for his large *Pflanzengeographie auf physiologischer Grundlage* (1898; English translation, 1903).

**Schleiden, Matthias Jakob (1804-1881),** German botanist. The son of a prosperous physician, he earned a doctorate in law in 1827 and practiced law until 1833, when he decide to study science. He earned a Ph.D. in 1839, having worked in Johannes Müller’s laboratory, where he knew Theodor Schwann. Schleiden was a popular teacher and in 1850 he became professor of botany at Jena. In 1838 he published his ideas on cell formation, “Beiträge zur Phytogenesis,” which he had developed during conversations with Schwann. Schleiden accepted an idea that went back to Nehemiah Grew: that cells crystallize inside an amorphous primary substance. The clearest statement of his theory is in his *Grundzüge der wissenschaftlichen Botanik* (1842-1843, 3 vols.; *Principles of Scientific Botany: Or, Botany as an Inductive Science*, 1849). That textbook also displays his opposition to philosophical speculations that had damaged German science.
Schwann, Theodor Ambrose Hubert (1810-1882), German animal physiologist. In 1826 he entered a Jesuit college in Cologne to prepare for the priesthood but in 1829 transferred to the University of Bonn to study medicine and obtained a bachelor’s degree in 1831. He had studied under the physiologist Johannes Müller and later followed him to Berlin, where Schwann earned a medical degree in 1834 with a dissertation on the importance of air for chick embryo development. He also assisted Müller with his *Handbuch der Physiologie* (1834). In 1836 Schwann concluded that yeast causes alcoholic fermentation, but Cagniard de La Tour made the same discovery and got his article published that year, whereas Schwann’s appeared in 1837. Schwann explained in his *Mikroskopische Untersuchungen über die Übereinstimmung in der Struktur und dem Wachsthum der Tiere und Pflanzen* (1839; *Microscopical Researches into the Accordance in the Structure and Growth of Animals and Plants*, 1847) his cellular theory—all cells arise from other cells—though he misunderstood cell formation. In 1839, attacks on his theory of yeast producing alcohol caused him to lose interest in research. He became a professor at Louvain and later at Liège, teaching anatomy and physiology.

Sears, Paul Bigelow (1891-1990), American botanist, ecologist, conservationist. An Ohioan, he earned a bachelor’s degree in zoology from Ohio Wesleyan University (1913), a master’s degree in botany from University of Nebraska (1915), and a philosophy doctorate in botany from the University of Chicago (1922). He began teaching botany at Ohio State University in 1915 but was interrupted by Army service, 1917-1919. He later taught botany at the Universities of Nebraska (1919-1927) and Oklahoma (1927-1938) and Oberlin College (1938-1950). Much of his botanical research was on the history of postglacial American vegetation, and his first book, *Deserts on the March* (1935), was a popular account of the Dust Bowl based on that research. It explained how mismanagement of agricultural lands had been a major factor in that disaster and how proper management could restore the land. That book’s success reoriented his studies more toward conservation than botany, and he went to Yale University, 1950-1960, as professor and chairman of a new Master of Science Conservation Program—the first such program in the United States. His nine other books included *Life and the Environment* (1939) and *The Living Landscape* (1964). He won numerous awards, including Eminent Ecologist of the Ecological Society of America (1965), and was president of several societies, including the American Association for the Advancement of Science (1956).

Senebier, Jean (1742-1809), Swiss plant physiologist. Although he fulfilled his parents’ wish and became a Calvinist pastor, his interests lay in natural history. He served as a pastor for only four years before resigning in 1773 to become librarian for his native city, Geneva. In 1777 he began publishing a French translation of Lazzaro Spallanzani’s works and continued doing so until 1807. In 1779 he published *Action de la lumière sur la végétation*, the first installment on his voluminous *Traité de physiologie végétal* (1800, 5 vols.). This work displays his great experimental abilities; he also generalized upon that ability in his *Essai sur l’art d’observer et de faire des expériences* (1802).

Spallanzani, Lazzaro (1729-1799), Italian biologist. The son of a successful lawyer, he initially attended a Jesuit seminary in Reggio Emilia but left in 1749 to study law at Bologna. His cousin Laura Bassi was professor of physics and mathematics there, and she convinced him to study math and science. He received a Ph.D. in 1754 and a few years later became an ordained priest. In 1755 he began teaching languages and math at the University of Reggio Emilia, and in 1763-1769 he taught philosophy at Modena. He was professor of natural history at Pavia, 1769-1799. In 1761 he read the experiments of George Louis Leclerc Buffon and John Turberville Needham (1749) on the spontaneous generation of animalcules. In 1762 he obtained an adequate microscope and began repeating their experiments. His essay “Saggio di osservazioni microscopiche relative al sistema della generazione dei Signori Needham e Buffon” (1765; account of microscopic observations concerning Needham and Buffon’s system of generation) showed that animalcules only appeared when the organic infusions were either sealed inadequately or heated inadequately. However, Needham refused to accept these results, and Spallanzani returned to
the fray in 1770 and again in his Opuscoli di fisica animale e vegetable (1776; Tracts on the Nature of Animals and Vegetables, 1799). He was one of the most brilliant experimentalists of his century, and his works were translated into English, French, and German. Spallanzani was also director of the university museum in Pavia, and the need to collect specimens for it provided a welcome excuse for his many travels.

Stopes, Marie (Charlotte Carmichael; 1880-1958), British paleobotanist and advocate of birth control and sex education. Her father was an archaeologist-anthropologist who studied early humans. She earned a chemistry scholarship to University College, London, but went on to study botany in Cambridge, earning a bachelor’s degree in 1902 and a doctorate in 1905. She then went to Munich and earned a Ph.D. in 1909 with a dissertation on the morphology of cycad seeds. She published a paper on a fossil plant in 1903 and continued studying paleobotany for twenty years. She collected fossils in Japan, 1907-1909, and in 1910 published a popular book, Ancient Plants: Being a Simple Account of the Past Vegetation of the Earth. In 1911 she traveled in Canada and the United States to study Carboniferous fossils, and in 1913-1915 she published a Catalogue of the Mesozoic Plants in the British Museum (Natural History) in two volumes. Her evidence indicated the sudden rise of flowering plants early in the Cretaceous. Between 1919 and 1923 she published articles on the origins and petrography of coal; some of them were coauthored with R. V. Wheeler. In 1918 she married Humphrey Verdon-Roe, who was interested in birth control. They founded the Mother’s Clinic for Birth Control in London in 1921, the first of its kind in England, and she soon turned from paleobotany to family planning.

Strasburger, Eduard Adolf (1844-1912), Polish-German botanist-cytologist. He was born and raised in Warsaw to parents of German descent. After graduating from a Warsaw gymnasium in 1862, he studied for two years at the Sorbonne in Paris and then studied botany and microscopy at Bonn. Later, he became Nathaneal Pringsheim’s assistant in Jena. However, it was the enthusiasm of Jena’s zoologist, Ernst Haeckel, for Charles Darwin’s theory of evolution that turned Strasburger toward evolutionary research. He earned his Ph.D. in 1866, reporting on nuclear division during cell division in ferns. In 1867 he became Privatdozent at Warsaw University, but by 1869 he was back in Jena as professor of botany, and in 1873 he also became director of the botanical garden. His cytological investigations at Jena appeared in three editions of his Über Zellbildung und Zelltheilung (1880; on cell formation and cell division). He pioneered methods to fix and harden tissues in alcohol. In 1881 he became professor at Bonn, and his laboratory at the Botanical Institute—a former palace—became the most important center for cytological research in the world. In 1884 he in dependently concluded that hereditary material is in the filaments of the cell nucleus. He went on to study cell wall formation, the role of centrosomes, and protoplasmic connections among cells. He investigated the evolution of reproduction in plants, from algae and mosses to cryptogams and phanerogams (1894). His textbooks appeared in many editions and translations. He received two honorary degrees from universities and two medals from the Linnean Society of London.

Tansley, Arthur George (1871-1955), English plant ecologist. He studied botany at University College, London, and at Cambridge University, where he was friends with Bertram Russell. In 1902 he started the journal The New Phytologist as a forum for works in progress, and in 1904 he organized the British Vegetation Committee to survey the vegetation of the British Isles. He was stimulated by, but sometimes disagreed with, the publications of Frederic Clements on plant succession and climax communities. The two met in 1911 when Tansley organized an International Phytogeographical Excursion in the British Isles to bring together European and American ecologists. A reciprocal excursion was held in the United States in 1913. In 1913 Tansley also helped organize the British Ecological Society and was its first president. That society published The Journal of Ecology, which Tansley edited. In 1935 he attacked the Clementsian theory of a biological community being a superorganism in “The Use and Abuse of Vegetational Concepts,” and proposed the “ecosystem” as an alternative concept. A synthesis of his lifetime research was his British Isles and Their Vegetation (1939).
Theophrastus of Eresos (c. 371-c. 287 B.C.E.), Greek educator, botanist, philosopher. He was educated under Aristotle and succeeded him as head of the Lyceum at Athens. He wrote the two earliest treatises on botany, *Historia plantarum* (“Enquiry into Plants” in *Enquiry into Plants and Minor Works on Odours and Weather Signs*, 1916) and *De causis plantarum* (*De Causis Plantarum*, 1976-1990, 3 vols.), which were comparable to similar works on animals written at the Lyceum and attributed to Aristotle. These botanical treatises discuss more than five hundred species, are comprehensive in scope, and are available in modern Greek-English editions. Theophrastus classified plants as trees, shrubs, undershrubs, and herbs, and he distinguished among annuals, biennials, and perennials. He related the distribution of species to soil, moisture, and climate.

Thunberg, Carl Peter (1743-1828), Swedish botanist. At Uppsala University, where he earned a medical degree in 1770, Carl Linnaeus influenced him to pursue botany. A friend of Linnaeus arranged for Thunberg to go to Japan on a Dutch ship, but to do so he needed to learn Dutch, and for that he spent three years in South Africa, 1772-1775, where he collected and described more than three thousand plants, about one thousand being new to science. He then spent fifteen months in Japan, 1775-1776, and before returning home he studied Englebert Kämpfer’s Japanese plant collection in the British Museum. When Thunberg reached Sweden in 1779 he became botanical demonstrator at Uppsala University. His first major publication was his *Flora japonica* (1784). Linnaeus was succeeded as professor of botany by his son, but upon the son’s death in 1784 Thunberg succeeded to that professorship. He published his travel memoirs in Swedish (1788-1793, 4 vols.), and they were translated into English (1793-1795, 4 vols.), French, and German. He summarized his South African findings in *Prodromus plantarum capensium* (1794-1800), and the German botanist J. A. Schultes assisted him with the more detailed *Flora capensium* (1807-1823).

Tournefort, Joseph Pitton de (1656-1708), French botanist. Although educated in Jesuit schools and destined for the priesthood, at the University of Montpellier he studied botany under Père Magnol and gave up a clerical career. In 1683 he became a substitute professor of botany at Jardin du Roi and presumably would have become professor there had Guy-Crescent Fagon not outlived him. Tournefort traveled in western Europe collecting plants and meeting botanists in preparation for his *Éléments de botanique: Ou, Méthode pur connoître les plantes* (1694), which consists of one volume of his text and two volumes of Claude Aubriet’s illustrations. A Latin edition appeared in 1700. Tournefort did not accept the sexuality of plants, but he depended on corolla and fruit to determine genera. He was the first botanist to study plant genera specifically, of which he distinguished 725, the majority of which are still accepted, though Carl Linnaeus changed some of the names. He also explored in the Levant, 1700-1702, and his *Relation d’un voyage du Levant* (1717, 2 vols.; *A Voyage into the Levant*, 1718) appeared posthumously.

Tschermak (von Seysenegg), Erich (1871-1962), Austrian botanist-geneticist. His father was professor of mineralogy and a museum director at the University of Vienna, and his mother was daughter of the director of the Botanical Institute and Garden at the university. He studied botany in Vienna and agriculture at the University of Halle, where he earned his Ph.D. in 1895. In 1898 he studied hybridization of vegetables at Ghent, using Charles Darwin’s *The Effects of Cross and Self Fertilization in the Vegetable Kingdom* (1876) as a guide. This work led to Tschermak’s rediscovery of Gregor Mendel’s laws and of Mendel’s article (1866). Tschermak’s own article on this (1900) enabled him to become a lecturer at the Hochschule für Bodenkultur in Vienna, and in 1909 he became a full professor; he was also director of the Royal Institute for Plant Breeding. In 1909 he traveled to the United States to study Luther Burbank’s methods. Tschermak bred new varieties of rye, wheat, barley, oats, legumes, pumpkins, gillyflowers, and primroses. He also studied the xenia phenomenon in several species.

Tsvet, Mikhail Semenovich (1872-1919), Swiss-Russian plant physiologist and biochemist. Although his parents were Russian, he grew up in Geneva and did not move to Russia until he earned his Ph.D. from the University of Geneva in 1896. He continued his studies of plant anat-
omy and physiology at the St. Petersburg Biological Laboratory. Because foreign degrees were not recognized, he earned additional master's (1901) and doctoral (1910) degrees. In 1903 he moved to Warsaw and taught in several universities. In 1915 he moved to Moscow, and in 1917 he became professor of botany and director of the botanical garden at Yuryev (now Tartu) University but died two years later from war stress, overwork, and heart disease. He produced sixty-nine publications, 1894-1916, emphasizing cytophysiology. He showed that green pigment in chloroplasts is in the chlorophyll-albumin complex, which he called “chloroglobin.” He also showed that chlorophyll a and b differ in color, fluorescence, and spectral absorption. In order to separate pigments and other chemicals, in 1906 he developed “chromatography” and the law of adsorption replacement and explained how to use the technique in two articles. However, use of chromatography was rather limited until the 1930’s, when its value became apparent in studies on carotene and vitamin A.

Unger, Franz (1800-1870), Austrian botanist. He studied medicine at Vienna and Prague and earned his medical degree in 1827. He then practiced medicine until 1835, when he became professor of botany and zoology at Graz and director of the botanical garden at Johanneum. Finally, he accepted the new chair of plant anatomy and physiology at Vienna, 1849-1866. His Grundzüge der Botanik (1843, coauthored with Stephen Endlicher), made him famous because he opposed Matthias Jakob Schleiden’s erroneous ideas on cell origin; Unger argued that cells arise by division of preexisting cells. In 1851 he published a correlation between geological eras and paleobotany, and in 1852 he published newspaper articles advocating evolution; they were republished as a book, Botanische Briefe, which was violently attacked by the Catholic press. Calls for his resignation were drowned out, however, by student support. His Anatomie und Physiologie der Pflanzen (1855) synthesized his earlier writings. His teaching about cell theory and fertilization may have influenced the researches of his student Gregor Mendel.

Vavilov, Nikolai Ivanovich (1887-1943), Russian botanist-geneticist. He was from a prominent Moscow family, and his physicist brother Sergey became president of the Soviet Academy of Sciences. In 1906 Nikolai entered the Moscow Agricultural Institute and while there organized a science club that took field trips to various Russian regions. He won a prize for a thesis on garden slugs. He graduated in 1911 and taught for a year before entering the Bureau of Applied Botany at the Ministry of Agriculture. In 1913 the bureau sent him to England to study genetics. During World War I he was not drafted because of a defective eye, and he earned a master’s degree with a thesis on “Plant Immunity to Infectious Diseases.” In 1916 he led an expedition to Iran and the Pamir, and in 1917 he became a professor at Voronezh Agricultural Institute and at Saratov University. In 1920 he moved to Petrograd, and in 1923 he became director of the State Institute of Experimental Agronomy. In 1924 Vladimir Lenin agreed to his reorganization of the department of applied botany into the All-Union Institute of Applied Botany and New Cultures. During the 1920’s and 1930’s Vavilov led many botanical expeditions to many parts of the world, leading to his presidency of the U.S.S.R. Geographical Society, 1931-1940. His travel memoir, Five Continents, appeared posthumously in 1962. He amassed a collection of more than 250,000 specimens at the institute. His earliest research was on the genetics of plant immunity, published 1913-1919, followed by studies of variability. By 1924 he was also investigating centers of origin of cultivated plants. Alphonse de Candolle had investigated this using archaeological, historical, linguistic, and botanical evidence in 1882; Vavilov now added genetic and cytological evidence. In 1926 he identified five primary centers of origin, which coincided with early civilizations. By 1940 he had identified thirteen regions in seven centers. His main goal was to improve Soviet agriculture with new varieties of domesticates matched to particular environments. By 1931, however, he was being criticized for not achieving results fast enough. In contrast, T. D. Lysenko seemed to be making impressive achievements with his “vernalization” treatment of seeds before planting. Vavilov unwisely praised Lysenko’s method in 1935; Lysenko joined the attack on Vavilov’s methods. Lysenko’s political power steadily increased, while Vavilov’s declined. In 1939 Vavilov aban-
Vries, Hugo de (1848-1935), Dutch plant physiologist, geneticist, and evolutionist. He was descended from prominent scholars and statesmen on both sides of his family. Even before he entered the University of Leiden in 1866, he was assisting Professor Willem Suringar with the herbarium of the Netherlands Botanical Society. At the university he was inspired by Julius Sachs’s Lehrbuch der Botanik (1866) and Charles Darwin’s On the Origin of Species by Means of Natural Selection (1859) to study plant physiology and evolution, though the university was weak in instruction in both. Suringar was hostile to Darwin’s theory, and after de Vries earned a medical degree in 1870, they ceased interacting. De Vries went to Heidelberg and worked with Wilhelm Hofmeister, and in 1871 de Vries went to Würzburg and worked with Sachs. In September he began teaching at First High School in Amsterdam, but he returned to Würzburg in summers for research. In 1872 he studied tendril curling and other growth movements in plants, which Darwin praised (1876). In 1877 de Vries became instructor in botany at the new University of Amsterdam, and that summer he went to England to meet botanists, including Darwin. He became a professor in 1881. By 1885 he began changing his research from physiology to heredity and variation, as seen in his series of nineteen articles published in a Dutch agricultural journal: “Thoughts on the Improvement of the Races of Our Cultivated Plants” (1885-1887). His Intracellulaire pangenesis (1889; Intracellular Pangenesis, 1910) reviewed the hypotheses of Herbert Spencer, Darwin, Karl Nägeli, and August Friedrich Leopold Weismann before proposing his own “pangene” hypothesis. His studies during the 1890’s led to the rediscovery of Gregor Mendel’s laws (possibly in 1896) and discovery of mutations in Oenotheras lamarckiana. In 1900, while preparing to publish Die Mutationstheorie: Versuche und Beobachtungen über die Entstehung von Arten im Pflanzenreich (1901-1903, 2 vols.; The Mutation Theory: Experiments and Observations on the Origin of Species in the Vegetable Kingdom, 1909-1910, 2 vols.), he surveyed the relevant literature and discovered Mendel’s article of 1866. He, Karl Correns, and Erich Tschermak all published independently their rediscovery of Mendel’s work. De Vries distinguished between mutations in Oenotheras lamarckiana which seemed “progressive” and furthering of evolution and others which seemed “retrogressive” and not contributing to evolution. His later publications pursued these findings in greater detail. Others began studying the genetics of Oenotheras and challenged some of his conclusions.

Wallace, Alfred Russel (1823-1913), English naturalist and evolutionist. His formal education was rudimentary, but he became a diligent reader. In 1841 he bought a botany book to aid in making a herbarium, and he was soon reading the works of Alexander von Humboldt, Charles Lyell, Charles Darwin, Robert Chambers, and other science authors. In 1847 Wallace convinced a friend, Henry Walter Bates, to go to the Amazon to seek evidence of evolution. They supported themselves by collecting biological specimens to sell. Wallace returned to England in 1852 and published a well-received Narrative of Travels on the Amazon and Rio Negro (1853) and a smaller book on Amazon palms. Because most of his personal materials burned on the ship to England, he lacked evidence for an elaborate defense of evolution; he published only one provocative paper (1855), which caught the attention of Lyell and Darwin. Wallace went on another extensive collecting expedition to the Malay Archipelago, 1854-1862, and on March 9, 1858, he sent to Darwin his now-famous article “On the Tendency of Varieties to Depart Indefinitely from the Original Type,” which was read at a meeting of the Linnean Society along with extracts from Darwin’s writings on the same subject. Both of their contributions appeared in that society’s journal on August 20, 1858. After returning to England, Wallace published his highly praised travel
book, *The Malay Archipelago: A Narrative of Travel with Studies of Man and Nature* (1869). Wallace became a very productive author on diverse topics; his many books included *Contributions to the Theory of Natural Selection* (1870), *Island Life* (1880), and *Darwinism* (1889). He married Annie Mitten, daughter of botanist William Mitten. Wallace received numerous medals and other honors from scientific societies.

**Warming, Johannes Eugenius Bülow** (1841-1924), Danish botanist. He grew up on the Jutland coast, the ecology of which he later studied. He interrupted his university training in 1863-1866 to assist the vertebrate paleontologist Peter W. Lund in his Brazilian researches. While there, Warming thoroughly investigated the flora; his findings appeared in a Danish natural history journal (1867-1893), and those articles were the basis for his important book on the phytogeography of Lagoa Santa (1892). He earned his Ph.D. at the University of Copenhagen in 1871 and taught botany there until 1882. He became botany professor at the new University of Stockholm, 1882-1886, and then botany professor and director of the botanical garden at Copenhagen, 1886-1911. His botanical interests and publications were quite diverse, but he is best remembered for his *Plantesamfund* (1895), which was translated into English, German, and Russian. The English edition is titled *Oecology of Plants: An Introduction to the Study of Plant-Communities* (1909). He studied “Why each species has its own habit and habitat, why the species congregate to form definite communities and why these have a characteristic physiognomy.” Although Warming accepted a version of Lamarckism rather than Charles Darwin’s theory of natural selection, this book was nevertheless one of the main foundations for organized plant ecology.

**Watson, Hewett Cottrell** (1804-1881), English botanist. As a child, he became friends with the family gardener and developed a permanent interest in flowers. He studied medicine at Edinburgh, 1828-1831, but as his real interest was in botany, he left without a degree. While at Edinburgh, he became interested in phytogeography and wrote a prizewinning essay on it (1831). He was of independent means and settled near London to pursue botany and phrenology, though his interest in the latter declined about 1840. By 1834 he was a convinced transmutationist (before Charles Darwin was), and his botanical research emphasized the variability of British plants over their British distribution in hopes of documenting evolution. In 1842 William Hooker arranged for him to spend a few months collecting plants in the Azores, and he became interested in what those specimens might show about the dynamics of phytogeography and evolution. In 1845 Watson published a series of four brief articles in a popular botanical magazine on the evidence for plant evolution in Britain. A few years later, Joseph Hooker sent those and Watson’s articles on the Azores flora to Darwin, who found them all interesting. Watson began synthesizing his findings in species-by-species accounts in *Cybele Britannica* (1847-1859, 4 vols.), which were useful to Darwin. However, because Watson saved his main conclusions for the last volume, and because Darwin was preparing *On the Origin of Species by Means of Natural Selection* (1859) at the same time, Darwin sent Watson a series of questions, the answers of which were very helpful, as Darwin graciously acknowledged in his book. Watson became the earliest convert to Darwin’s theory, though he later had second thoughts about one aspect of it. Watson spent the rest of his life refining his species-by-species data, published in *Topographical Botany: Shewing the Distribution of British Plants* (1873-1874). In appreciation for what he accomplished, the Botanical Society of the British Isles named its journal *Watsonia*.

**Watson, James Dewey** (1928- ), American molecular biologist. He entered the University of Chicago at age fifteen and majored in biology. Graduating in 1947, he went to the University of Indiana to study genetics. He chose to write his doctoral dissertation under Salvador Luria, who was a member of an informal group that studied bacteriophages in summer at Cold Spring Harbor. Upon receiving his Ph.D. in 1950, Watson went to Denmark on a National Research Council Fellowship to learn biochemistry in order to understand genes. In the spring of 1951 he attended an international biological conference in Naples, where he realized he would rather do research on DNA in London under Maurice Wilkins. He was unable to persuade Wilkins to
invite him, but Luria was able to arrange for him to go to the Cavendish Laboratory at Cambridge University. There, he met Francis Crick, who was more interested in DNA as a way to understand genes than he was in X-ray diffraction of protein, on which he was to write a doctoral dissertation. Crick and Watson were congenial colleagues, and they were able to enlist the aid of many colleagues to answer various questions which they could not answer either in the laboratory or by consulting the literature. They were the only ones searching for an understanding of DNA who drew upon four areas of research—bacteriophage, biochemistry, X-ray crystallography, and stereochemical modeling—and they unraveled the mystery in spring, 1953. Their findings were published in Nature along with related findings by Maurice Wilkins, Rosalind Franklin, and their colleagues. In 1962 Watson, Crick, and Wilkins were jointly awarded the Nobel Prize in Physiology or Medicine for DNA discoveries. Franklin was not included because she had died. Their discovery was a major foundation for a new science, molecular biology, to which Watson continued to contribute. He taught at Harvard University, 1956-1976; later he became assistant director, then director, of the National Center for Human Genome Research, 1988-1992. His scientific memoir, The Double Helix (1968), was a sensation, and his Molecular Biology of the Gene (2d ed., 1970) has been a standard textbook.

Willdenow, Karl Ludwig (1765-1812), German botanist. He was the son of a Berlin apothecary interested in plants, who passed on that interest to his son. Willdenow studied first pharmacy, then medicine, earning his medical degree in 1789. He had already published a flora of Berlin (1787), and in addition to his medical and pharmaceutical practice, he taught botany informally; one of his students was Alexander von Humboldt, who became a friend and sometime colleague. Willdenow’s Grundriss der Kräuterkunde (1792) was the first textbook to supersede Carl Linnaeus’s Philosophia botanica (1751; The Elements of Botany, 1775), and it brought him membership in the Berlin Academy of Sciences in 1794. In 1798 he became professor of natural history at the Berlin Medical-Surgical College, and in 1801 he also became curator of the Berlin Botanical Garden. An important section of his textbook was on phytogeography, despite the fact that he had never traveled widely. This subject caught Humboldt’s interest, and in 1810 Willdenow traveled to Paris to help Humboldt with a scientific account of Humboldt’s vast botanical collection. However, Willdenow became sick and had to return to Berlin, where he died.

Frank N. Egerton

Sources for Further Study


PLANT CLASSIFICATION

Plants are classified, arranged, or ordered into a hierarchy of categories and ranks called taxa for scientific consistency, information retrieval, identification, and classification. This allows the scientist and the layperson alike to see and understand relationships between morphology and anatomy, simply and easily identify the plant they are studying, and begin to piece together the evolutionary history or phylogeny of plants and the groups to which they belong. The systems and methods used in plant classification historically have been either artificial, that is, based on any convenient trait without true regard to its connection with the biology of the plant, or natural, based on the present understanding of the biology, chemistry, and evolutionary history of the plant, with emphasis on those characteristics and traits that are quantitative or numerical and are thus quantifiable or mathematically described. The current trend is toward reflecting evolutionary relationships in classification systems.

Systematics

Simply naming an organism is the process of taxonomy, but distinguishing organisms involves classification. Taxonomy and classification both are included in the broad field of systematics. The three main schools of thought concerning systematics today are:

(1) analysis of primitive and derived characters to construct a phylogenetic branch or clade with a common ancestor and its derived line of organisms or species,

(2) clustering of organisms based on shared similarities without thought for any common origin or dependence, and

(3) the traditional stress on common ancestry and degree of structural difference in order to make a phylogenetic tree.

Groups

Historical work, current research, and present scientific thinking on plant classification indicate eight distinct groups, or taxa. The eight groups recognized most commonly, from largest to smallest, are domain, kingdom, phylum or division, class, order, family, genus, and species. These taxa and their uses are governed by rules set forth in the International Code of Botanical Nomenclature (ICBN). Scientific names for species are in Latin, and they are binomials (two names) composed of an uppercased genus name and a lowercased descriptive, or specific (species), epithet. The eighteenth century Swedish taxonomist Carolus Linnaeus is given credit for the consistent usage of this system of binomial nomenclature to name plant species. Historically, the nature of the organism’s cell walls formed the main criterion used to list a group as plant or plantlike. (However, see Plantae below.)

Domains

Research that looked at nucleotide base sequences for rRNA (ribosomal RNA) conducted by Carl Woese at the University of Illinois has revealed that all life-forms (including those that are plantlike) can be divided into three major super kingdoms or domains: Archaea, Bacteria, and Eukarya, suggesting that all organisms evolved from a common ancestor along three distinct lines. These three lines are called domains. The first two domains, Archaea and Bacteria, are what was traditionally the kingdom Monera. Both domains contain prokaryotes, that is, organisms made of cells with no true nucleus but rather a nucleoid where the DNA is “naked” in the cytoplasm (not surrounded by an envelope, with smaller ribosomes, and with plasmids). The domain Eukarya is composed of organisms made of eukaryotic cells, that is organisms whose cells have nuclei, membrane-bound organelles, and a cytoskeleton. Eukarya contains all “higher” forms of life, including those classified in the kingdoms Protista (also called Prototista), Fungi, Plantae, and Animalia (animals, including humans). The first three kingdoms are all of interest to the botanist, and typically the organisms in those kingdoms are addressed in the study of botany courses as well as in the general study of biology.
Archaea

The domain Archaea, sometimes referred to as the Archaeabacteria, contains unicellular prokaryotic life-forms and has varied, branched ether-linked lipids, with cell walls made not of peptidoglycan but of glycoproteins and polysaccharides, with no membrane-bound organelles (including no nuclear membrane), with RNA polymerase similar to that found in eukaryotic organisms, with the ability to metabolize methane, and with some introns (nucleotide base sequences in the DNA that do not translate into protein products).

The domain Archaea is placed within the kingdom Monera, which includes all prokaryotic organisms and consists of a single division or phylum, Mendosicutes or Archaebacteriophyta. Archaea live in

<table>
<thead>
<tr>
<th>Kingdom</th>
<th>Category</th>
<th>Species</th>
<th>Phylum</th>
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</thead>
<tbody>
<tr>
<td>Fungi</td>
<td></td>
<td>33,000</td>
<td>Ascomycota (ascomycetes)</td>
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<td></td>
<td></td>
<td>22,500</td>
<td>Basidiomycota (basidiosporic fungi)</td>
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<td></td>
<td>800</td>
<td>Chytridomycota (chytrids)</td>
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<td>1,000</td>
<td>Zygomycota (zygomycetes)</td>
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<td>Plantae</td>
<td>Bryophytes</td>
<td>100</td>
<td>Anthocerophyta (hornworts)</td>
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<td>9,500</td>
<td>Bryophyta (mosses)</td>
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<td>6,000</td>
<td>Hepatophyta (liverworts)</td>
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<td></td>
<td>Seedless vascular plants</td>
<td>1,000</td>
<td>Lycophyta (lycophytes)</td>
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<td></td>
<td></td>
<td>2 genera</td>
<td>Psilotophyta (psilotophytes)</td>
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<td>Pterophyta (ferns)</td>
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<td>70</td>
<td>Gnetophyta (gnetophytes)</td>
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<td>235,000</td>
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<td>Slime molds</td>
<td>700</td>
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<td></td>
<td></td>
<td>50</td>
<td>Dictyosteliumycota (cellular slime molds)</td>
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<td>Water molds</td>
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<td>Oomycota (water molds, oomycetes)</td>
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<td>Chlorophyta (green algae)</td>
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<td>200</td>
<td>Cryptophyta (cryptomonads)</td>
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<td>4,000</td>
<td>Dinophyta (dinoflagellates)</td>
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<td></td>
<td>1,000</td>
<td>Euglenophyta (euglenoids; photosynthetic algae)</td>
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<td></td>
<td>300</td>
<td>Haptophyta (haptophytes)</td>
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<tr>
<td></td>
<td></td>
<td>1,500</td>
<td>Phaeophyta (brown algae)</td>
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<tr>
<td></td>
<td></td>
<td>6,000</td>
<td>Rhodophyta (red algae; photosynthetic algae)</td>
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</tbody>
</table>
extreme environments thought to be similar to conditions present on the primitive earth: in extreme salinity, acidity, thermal, and anaerobic conditions.

**Bacteria**

The domain Bacteria, also placed within he kingdom Monera and sometimes referred to as the Eubacteria (or “true” bacteria), is unicellular and has unbranched lipids and phospholipids, cell walls with peptidoglycan, no membrane-bound organelles (including no nuclear membrane), and no introns (all the DNA translates into protein product).

The domain Bacteria includes three divisions or phyla characterized by their cell walls: division Gracilirutes contains gram-negative bacteria, division Firmicutes contains gram-positive bacteria, and division Tenericutes contains bacteria without cell walls.

Gracilirutes (prokaryotes with thin cell walls, implying a gram-negative type) is divided into three classes, one of which, Oxyphotobacteria, is important in plant science or botany because it contains the oxygen-producing photosynthetic bacteria. Oxyphotobacteria can be seen as divided into two other groups, either at the class or division level: the Cyanobacteria and the Chloroxybacteria. Both groups use chlorophyll a in photosynthesis, as do algae and plants proper. The cyanobacteria produce free oxygen as a by-product of photosynthesis, and forms such as Spirulina are commercially grown and marketed as high-protein dietary supplements. Chloroxybacteria also use chlorophyll b, which is restricted to plants and some algae otherwise.

**Eukarya**

The domain Eukarya (sometimes spelled Eucarya) has some unicellular and many multicellular forms, unbranched lipids and phospholipids, members both with cell walls (none of which is peptidoglycan but rather cellulose or chitin) and without cell walls, membrane-bound organelles (including the nuclear membrane), and introns. Sexual reproduction is common in this domain, and all kinds of types of life cycles are seen, including complex, haplontic, and alternation of generations.

Eukarya contains the kingdoms Protista, Fungi, and Plantae as well as Animalia (which is primarily the province of zoology). These three kingdoms are photosynthetic or heterotrophic by various means, including parasitism and saprotrophy (deriving nutrition from dead or decaying organic matter), and are of interest to the plant scientist because some members of Protista and all members of Fungi and Plantae have cell walls. Cell walls are the single most salient criterion distinguishing plants and plantlike organisms historically. All are nonmotile except for the Protista, which has members that move by flagella and cilia.

**Kingdoms**

In 1969 Dr. R. H. Whittaker, a plant ecologist, proposed the five-kingdom classification system followed by most scientists today. Until then—from the early Greek period and Aristotle until the mid-twentieth century—basically only two kingdoms of life were noted: animals, which were animated (that is, they moved), and plants, which were “planted” (did not move). With the development of light microscopy in the late 1600’s, however, it became possible to observe unicellular organisms, and a German scientist, Ernst Haeckel, proposed a third kingdom, the protists. Whittaker put all the work together, and he placed organisms into kingdoms based on whether or not they were prokaryotic or eukaryotic, whether they were unicellular or multicellular, and the types of nutrition. The five kingdoms in Whittaker’s system are the Monera (including the prokaryotic organisms in domains Archaea and Bacteria) and four kingdoms of eukaryotic organisms (domain Eukarya): Protista, Fungi, Plantae, and Animalia.

**Protista**

The kingdom Protista includes plantlike organisms of interest to the botanist: the slime molds, the water molds, and the algae. The following are divisions or phyla in Protista: Myxomycota (plasmodial slime molds), Dictosteliomycota or Acrasiomycota (dictyostelids, cellular slime molds), Oomycota (bilflagellate water molds), Euglenophyta (euglenoids), Cryptophyta (cryptomonads), Rhodophyta (red algae), Dinophyta or Pyrrophyta (dinoflagellates), Haptophyta (haptophytes), Chrysophyta (chrysophytes, or golden-brown algae), Bacillariophyta (diatoms), Phaeophyta (brown algae), and Chlorophyta (green algae).

**Slime Molds.** The slime molds and water molds can be classified into four divisions or phyla: Myxomycota, Dictosteliomycota, Oomycota, and Chytridiomycota. There is so much diversity within these four phyla that some taxonomists suggest
seven divisions instead of the usual four. The slime molds cannot photosynthesize, and they were long considered fungi (indeed, the Chytridiales are considered fungi in most recent taxonomic treatments; see below under Fungi). The cellular slime molds, Dictosteliomycota, have about 70 species, characterized by a phagotrophic mode of nutrition, glycogen storage product, cellulose cell walls, and amoeboid motility. The approximately 500 species of Myxomycota, or plasmodial slime molds, lack cell walls, and their motile cells have two whiplash flagella. Both slime molds live in terrestrial habitats.

Water Molds. Water molds, Oomycota and Chytridiales, absorb nutrients and have flagellated motile cells. These two phyla are distinguished by a single flagellum, as in the Chytridiales, or two flagella, as in the Oomycota. The uniflagellate water molds live in freshwater or marine habitats, store glycogen, and have cell walls of chitin or glucan. The biflagellate water molds prefer fresh water only, store glycogen or mycolaminarin (a glucose polymer), and have cell walls of cellulose, chitin, glucan, or a combination of any of these.

Euglenophyta. The 800 or so species of euglenoids and the 100 species of cryptomonads all lack cell walls, and instead their cells are surrounded by a flexible periplast (a plasma membrane with extra inner layers of proteins and with a grainy outer surface).

Rhodophyta. The 670 genera and 2,500 to 6,000 species of red algae, like the brown algae, are mostly marine organisms made up of microscopic filaments or macroscopic forms with complex, leafy branches. The red algae are characterized by the accessory photosynthetic proteinaceous pigments called phycobilins: phycoerythrin, phycocyanin, and allophycocyanins arranged in phycobilisomes. They have no flagella and no centrioles. Floridean starch is a storage product deposited free in the cytoplasm; cells have unstacked thylakoids in plastids and no chloroplast endoplasmic reticulum. Cell walls of red algae are cellulose and pectin mainly, but some form calcium carbonate, too. Photosynthesis in red algae depends on chlorophyll a; there is no chlorophyll b. Xanthophylls and carotenoids are also present.

Traditionally the red algae are divided into two classes, the Bangiophyceae and the Florideophyceae. Yet a single class, the Rhodophyceae and two subclasses, Bangiophycidae and Florideophycidae, are also used. The five orders of the red algae include the Cyanidiophyceae, Porphyridiales, Compsopogonales, Bangiales, and Florideophyceae. There are six families. Representative species include Kallymenia perforata and Gibsmithia hawaiiensis, both from the Philippines and members of Florideophyceae, and Porphyra carolinensis, from Masonboro Island, North Carolina, a member of the Bangiales. Red algae are ecologically significant as primary producers, providers of structural habitat, establishers and maintainers of coral reefs, and providers of food and gels, such as carrageenan from the Kappaphycus species, cultured in the Philippines.

Dinoflagellates of Pyrrophyta. The 2,000 species and 130 genera of dinoflagellates also usually lack a cell wall, but most species have armorlike cellulose plates interior to the plasma membrane. The cell-covering structure, the theca, clearly differentiates dinoflagellates from other algal groups, being either armored or not. Unarmored species have a membrane complex. Thecae can be smooth, simple, spiny, pored, grooved, or highly ornamental. Dinoflagellates have a distinctive flagellar arrangement among the unicellular algae, with two lateral flagella, one of which coils around the cell and undulates so the cell spins as it moves forward, and the other trailing like a rudder.

Dinoflagellates are highly varied in reproduction with primary asexual cell division, but some species reproduce sexually, and still others have complex, unusual life cycles. Nutrition is also varied, with autotrophic species (photosynthesis), heterotrophic (absorption of organic matter) species, and mixotrophic members (autotrophic cells engulf other organisms). Certain species of dinoflagellates produce neurotoxins.

Haptophyta. Haptophytes or Prymnesiophyta are unicellular and photosynthetic, with 500 species in 50 genera. Some are colonial. Haptophytes have a unique organelle called a haptonema (for which the phylum is named): a peglike structure where two flagella are attached. Reproductive and life histories are poorly understood. Some form toxic blooms, and some produce dimethyl sulfide (DMS). Pigments include diadinoxanthin and fucoxanthin. Genera include Phaeocystis and Emiliania.
**Chrysophyta.** Classes of Chrysophyta are Chrysophyceae (golden-brown algae) and Xanthophyceae (yellow-green algae). Chrysophytes are photosynthetic, unicellular organisms abundant in freshwater and marine environments. They have chlorophylls a and c, masked by the accessory pigment fucoxanthin, a carotenoid. Golden algae are in many ways very similar to the brown algae, storing food outside of the chloroplast in the polysaccharide laminarin or chrysolaminarin. Both brown algae and golden algae have unequal flagella of like form.

**Bacillariophyta.** Bacillariophyta, well known for their glasslike cell walls made of polymerized, opaline silica with ornate ridge patterns, are important components of the phytoplankton as primary sources of food for zooplankton in both marine and freshwater habitats. They are sometimes considered a class along with golden-brown and brown algae in a large, complex phylum called Heterokontophyta. Except for male gametes, diatoms lack flagella, but many can move by means of locomotion from secretions in response to outside physical and chemical stimuli. The overlapping shells, called frustules, can be used to identify diatom species and have accumulated over millions of years to form the fine, crumbly substance known as diatomaceous earth used in filtration and insulation.

Bacillariophytes number 250 genera and 1,500 species and have brownish plastids with chlorophylls a and c as well as fucoxanthin. Primary reproduction is asexual, by cell division. Most diatoms are autotrophic, but some must absorb organic carbon because they lack chlorophyll. Some few lack the characteristic frustules and live in symbiosis in large marine protozoa, giving organic carbon to their host.

**Phaeophyta.** Almost entirely marine, the almost 2,000 species of Phaeophyta are common along rocky shores in cold and temperate waters around the globe. The brown accessory pigment fucoxanthin gives the colors to the brown algae from pale beige to yellow-brown to very dark. Phaeophytes store mannitol and a glucose polymer called laminarin. Alginic acid is in the cellulosic cell wall, and motile cells have two lateral flagella. Brown algae are included in the class Phaeophyceae with four orders.

Products like ice cream are stabilized with an emulsifier from large kelps. Kelps are also used in fertilizers and are a vitamin-rich food source. *Macrocystis pyrifera*, the giant kelp, makes seaweed forests off the west coast of North America, providing habitat and shelter for many organisms. Genera such as *Sargassum* and *Turbinaria* may dominate in tropical waters, though there are fewer species of brown algae there. *Sargassum* is unique in that it is free-floating, requiring no bottom attachment. Brown algae range in size from microscopic filaments to several meters in length.

**Chlorophyta.** There are approximately 8,000 species of green algae, with pigments including chlorophylls a and b, carotenoids, and xanthophylls. These algae appear more than a billion years ago in the fossil record. Like plants, they store starch plants inside plastids, contain cellulose in their cell walls, and have motile and nonmotile cells with anywhere between one and about 120 flagella at or near the apex of the cell. *Chlorophyta* can be unicellular, multicellular, or colonial. Most chlorophytes are aquatic, but some live on the surface of snow, on tree trunks, or symbiotically with protozoans, hydras, or lichen-forming fungi.

*Halimeda* species (calcified green algae) are important contributors of marine sediments, and the clean white sand beaches of the Caribbean Sea and other areas around the world are made up of the calcium-carbonate remains of green algae. An interesting member of this group is the fleshy alga *Johnson-sea-linkia profunda* (Littler et al., 1985), found on bedrock at a depth of 157 meters off the Bahamas.

The class Chlorophyceae comprises predominantly freshwater algae that undergo mitosis in a persistent nuclear envelope. The class Ulvophyceae comprises predominantly marine organisms that undergo cell division by forming a phragmoplast like that of plants. The class Charophyceae includes mostly freshwater species whose nuclear envelopes disintegrate, as do those of plants, as mitosis proceeds.

**Fungi**

The kingdom Fungi is composed of mushrooms, rusts, smuts, puffballs, truffles, morels, molds, and yeasts. These organisms are usually filamentous, eukaryotic, and spore-producing. They generally lack chlorophyll and have a terrestrial origin. Fungi have nonmotile bodies, called thalli, made up of apically elongating walled filaments, *hyphae*, which as masses are referred to as mycelia (singular, myce-
lrium). The life cycle includes both a sexual and an asexual component. Haploid thalli result from zygotc meiosis. The cell walls are made up of chitin with other complex carbohydrates, including cellulose. The main storage carbohydrate of the fungi (unlike plants) is glycogen, and all species of fungi are either saprobes (deriving nutrition from dead and decaying organic matter) or symbionts (living with other organisms). Symbionts may be parasitic on a host, provide a benefit to the host, or be parasitized.

The following divisions or phyla in Fungi are distinguished by reproductive differences: Chytridiomycota (uniflagellate water molds), Zygomycota (such as black bread mold, dung fungi, and parasites of amoebas, nematodes, and small animals), Ascomycota (such as bread molds, truffles, morels, and ergot), Basidiomycota (mushrooms, stinkhorns, puffballs, jelly fungi, smut and rust diseases of plants), Deuteromycota, sometimes referred to as "fungi imperfecti" (penicillin mold, root-rot fungus, vaginal yeast fungus, and athlete's foot fungus), and Myxomycota, or lichens (a division created by L. Margulis and K. V. Schwartz to separate all the organisms with a fungal body or thallus that host green algae or cyanobacteria or both). Yeasts are not a formal taxon but rather are unicellular fungi that reproduce via budding, as seen in Zygomycota, Ascomycota, or Basidiomycota. Lichens are assumed to be mutualistic symbionts with a fungal (mycobiont) and green-algal (photobiont) component. They may be the dominant vegetation in Nordic environments and have been placed in their own division, or phylum, by Margulis and Schwartz, called Myxomycophyta.

Mortality-associated human diseases caused by fungi include Pneumocystis (a type of pneumonia affecting those with a suppressed immune system), Coccidioides (valley fever in the southwestern United States), Ajellomyces (blastomycosis and histoplasmosis), and Cryptococcus (cryptococcosis). However, fungi are also vital for ecosystems, and they help to flavor and process foods such as baker's yeasts and penicillia in cheese making, as well as producing antibiotics and organic acids. Fungi produce secondary metabolites such as aflatoxin, a potent toxin and carcinogen, and coumadin, which is an anticoagulant used to treat people with heart and arterial diseases.

While at least 100,000 species of fungi are recognized, new species (more than 1,000) are described every year. It is commonly believed by biologists that more than half of all extant fungi have yet to be discovered and named, and estimates of total numbers suggest that 1.5 million species may exist. Fungi are the primary decomposers in the varied natural habitats in which they are found.

**Zygomycota.** The Zygomycota, characterized by zygospores, are in two classes, Zygomycetes and Trichomycetes, and include about 1,100 species. Conjugation or fusion of morphologically similar gametangia (gametangia arising from hyphae to make zygosporangia with a thick wall supported on either side by the former gametangia, which are then named suspensors) is distinctive in most members of the phylum Zygomycota, although by no means universal.

Class Zygomycetes has seven orders, thirty families, and about 900 species. Four of those orders are Mucorales with thirteen families, fifty-six genera, and 300 species; Entomophthorales (as its name implies, these fungi often prey on insects and are of interest for their obvious potential in biological control of insect pests); Kickxellales (named after a mycologist named Kickx); and Glomales (fungi living in the soil and tentatively identified with the Zygomycota, since most do not form the characteristic zygosporangia but have hyphae that enter about 90 percent of all living higher plant root cells, making mutualistic symbioses named mycorrhizae). Included among the zygomycetes are the species Rhizopus stolonifer (familiar to most biology students as the ubiquitous bread mold) and the genus Mucor.

**Trichomycetes** is a rather offbeat class of Zygomycota in that members of this class live attached to the inner linings of the guts of living arthropods. Though members of this class have the suspensors mentioned above, they do not otherwise resemble the zygomycetes.

**Ascomycota.** The Ascomycota have spore-containing sacs called asci with ascospores and include about 30,000 species. An example of an ascomycete human pathogen is Coccidioides immitis, endemic to parts of the southwestern United States. Another ascomycete, Aspergillus flavus, produces the aflatoxin that contaminates nuts and stored grains.

**Basidiomycota.** The Basidiomycota produce spores on basidia (club-shaped structures where nuclear
fusion and meiosis occur and where the haploid basidiospores are made) and include about 25,000 species. The most conspicuous and familiar basidiomycetes are those that produce mushrooms. Basidiomycetes benefit plants by engaging in symbiotic relationships with their roots, called mycorrhizae, allowing the plant to have increased capabilities to acquire nutrients such as phosphorus. An interesting example of a basidiomycete is *Rigidiorpus ulmaris*, with the largest basidiocarp in the world located at the Royal Botanic Gardens in Kew, Surrey, England.

Distinguishing characteristics of *Basidiomycota* are their unique formation of ballistospores (forcibly discharged spores), the club-shaped basidia mentioned above, their dikaryotic mycelia (two nuclei put together in mating, without fusion in the thallus but instead separate, side-by-side, in every cell), their multilayered cell walls, their clamp connections (hyphal branches made while a division of two nuclei occurs in the apical cells), and their positive diazonium blue B reactions (which cause a color change in o-dianisidine, or diazonium blue B, which is not totally unique to the *Basidiomycota* but is nevertheless noted). *Basidiomycota* is divided into three lines or classes: the *Urediniomycetes*, the *Ustilaginomycetes*, and the *Hymenomycetes*.

**Deuteromycota.** The *Deuteromycota*, which include about 15,000 species, are an artificial group; that is, they form a group on the basis of characteristics other than their evolutionary relationships. They all produce spores asexually or are species not yet classified by sexual reproductive features. An example of a deuteromycete of historical importance is *Penicillium chrysogenum*, known for its production of the antibiotic penicillin, and *Candida albicans*, the cause of thrush, diaper rash, and vaginal yeast infections. Recent comparison of nucleic acid sequences combined with nonsexual phenotypic characters have caused many workers to integrate the asexual fungi into the *Ascomycota*.

**Plantae**

The kingdom *Plantae* includes multicellular eu- karyotes with cellulose-rich walls, chloroplasts with chlorophyll *a* and *b* and carotenoids, and starch as the main food reserve. Most plants reproduce sexually, with alternation of generations. Plants have sporophytes, which make haploid spores via meiosis that grow into gametophytes, which produce gametes that fuse to form the sporophyte again. This cyclic process is termed alternation of generations and is a key characteristic of plants.

The main divisions or phyla of *Plantae* are *Hepatophyta*, *Anthocerotophyta*, *Bryophyta*, *Psilophyta*, *Lycophyta*, *Sphenophyta*, *Pterophyta*, *Cycadophyta*, *Ginkgophyta*, *Coniferophyta*, *Gnetophyta*, and *Antho- phyta* or *Magnoliophyta* (the angiosperms). Algae and fungi are *Thallophyta*, as opposed to *Plantae*’s nonvascular bryophytes (which include liverworts, hornworts, and mosses) and vascular plants, or *Embryophyta*. Other terms used, although not formally, are phanerogams (plants with flowers) and cryptogams (plants without flowers).

**Hepatophyta.** About 9,000 species of hepatophytes, or liverworts, have been named, and they range in size from tiny, leafy filaments smaller than 0.5 millimeter in diameter to plants with a thallus more than 20 centimeters wide.

Hepatophytes have unicellular rhizoids (hairlike extensions that anchor the thallus to a substrate), no cuticle, no specialized conducting tissue (no water-conducting xylem or sugar-conducting phloem), and no stomata (no epidermal pores for gas exchange). Liverworts are the simplest of all living plants, classified in one class, divided into seven orders and twenty-six families.

**Anthocerotophyta.** Only about 100 species of anthocerotophytes, or hornworts, exist, in six genera, divided between two families in the same class and order. The horn-shaped sporophyte of hornworts (with a diploid structure producing haploid spores via meiosis) gives the name to this division or phylum. An intercalary meristem seeming capable of indefinite growth is associated with the sporophyte, and it has stomata, too. The gametophyte (haploid thallus with sex organs) is thallose (not leafy) and has no specialized conducting tissue and stomata-like structures.

**Bryophyta.** The bryophytes, or mosses, comprise more than 10,000 species, and they thrive on soil, tree trunks, and shady rock walls. Some mosses have a central strand of conducting cells functionally equal to xylem and phloem, so bryophytes do have a simple type of vascular tissue. Like the hornworts and liverworts, mosses are homosporous (producing only one type of spore). Mosses have leafy gametophytes, multicellular rhizoids, and sporo-
Psilotophyta. The psilotophytes (whiskferns, from the genera Psilotum and Tmesipteris, in one family, the Psilotaceae) are primitive. Psilotum has no roots or leaves, similar to the fossil genus Rhynia. Tmesipteris has aerial shoot structures that are leaflike or foliar. Both genera have compound sporangia (structures that make spores) called synangia, three-parted in Psilotum. Both genera have no roots, but the underground stems, the rhizomes, are infected with fungi (mycorrhizae). Dichotomous branching is obvious, especially in the aerial branches of Psilotum, and leaflike extensions called enations are seen.

Lycophyta. Club mosses, or lycophytes, come in three families: the Lycopodiaceae, the Selaginellaceae, and the Isoetaceae. They have true leaves, roots, and stems with vascular tissues. The leaves are microphylls (with one vein, not associated with a leaf gap), a defining characteristic of this group. Roots are adventitious. All members of the group are herbaceous except Isoetes, which has some secondary growth. Extinct Lycophyta are easily seen in the fossil record and apparently made up a large portion of the flora in Carboniferous swamp forests. These nonseed plants are either homosporous or heterosporous (two different types of spores).

Sphenophyta. Horsetails, or Sphenophyta, have only one living family, the Equisetaceae, and only one genus, the Equisetum. Fifteen living species, including Equisetum arvense (field horsetail), are known. Horsetails are characterized by shoots with nodes (where leaves come off) and internodes (spaces between nodes), strobili made up of a central axis with spore-bearing structures called sporangia, and spores with elators (strands of tissue attached to the spore itself that allow for dispersal of the spores as they spread when they dry). Sphenophyta is seen in the Devonian fossil record, and the order Equisetales can be dated from the Upper Devonian. Members of the living genus Equisetum and extinct members of the Equisetales share many anatomical features.

Pterophyta. Ferns are a group of nonseed plants with a fossil record going back to the Lower Devonian. There are about 11,000 living species. They are varied, with true leaves, roots, and stems. Leaves are macrophylls, and many members demonstrate circinate vernation, a pattern of unfolding of a crozierlike structure because of unequal growth. Both heterosporous and homosporous representatives are evident. Spore structure, sporangia, and sori (special structures on the underside of the leaf, or frond, or leaflets or pinnae containing the sporangia) are all important taxonomic features. Examples of families in the Pterophyta are Adiantaceae (the maidenhair family), Aspleniaceae (spleenworts), Ophioglossaceae (adder’s-tongues), Polypodiaceae (the polypodium family), and Osmundaceae (the cinnamon fern family).

Cycadophyta. Cycads are seed plants with only three living families: the Cycadaceae, the Stangeriaceae, and the Zamiaceae. They are prominent among Mesozoic fossils, however. They are found in tropical or subtropical climates around the world. Their leaves are pinnately compound and palmlike. There is secondary growth, but no large amounts form. Roots enclose mutualistic cyanobacteria that fix nitrogen. Plants are dioecious (with male and female sex organs appearing on different individuals), and they bear strobili made up of megasporophylls with ovules or microsporophylls with pollen sacs. Pollen makes a pollen tube that is haustorial (parasitic), delivering flagellated sperm to an egg in an archegonium of the female gametophyte.

Ginkgophyta. The ginkgos form a phylum of seed plants represented by only one living species, Ginkgo biloba, whose native habitat is restricted to China, where it is probably extinct in the wild. Represented well during the Mesozoic with worldwide distribution, Ginkgo biloba is planted ornamentally today and seems tolerant of pollution. The ginkgo is a deciduous tree, shedding leaves all at once in the fall in temperate zones, with fan-shaped leaves and branches that have spur shoots bearing the reproductive structures. Stems have extensive secondary xylem. The ginkgos are dioecious trees, with the megasporangiate (“female”) trees bearing two ovules at the end of a stalk. Only one ovule usually develops into a mature seed. There is an inner, stony seed coat and an outer, fleshy, fruitlike tissue. Micro-
sporangiate ("male") trees bear reduced strobili or cones that release pollen, or microgametophytes, that are wind-borne. Pollen makes a haustorial tube that delivers flagellated sperm to an egg in an archegonium of the female gametophyte.

**Coniferophyta.** The conifers are seed plants that produce woody stems. The fossil record shows them from the Upper Carboniferous. There are about 550 species, arranged in seven families: Pinaceae, Taxodiaceae, Cupressaceae, Araucariaceae, Podocarpaceae, Cephalotaxaceae, and Taxaceae. Some treatments place the conifers in the division Pinophyta, or gymnosperms, but as a class, Pinatae.

The conifers are noted for their abundant secondary xylem. They grow as trees or shrubs. Trachiary elements in the xylem of conifers include only tracheids, and sieve elements in the phloem include only sieve cells. The leaves of conifers are macrophylls but in most species are reduced as needles or scales.

Conifers are either dioecious or monoecious plants. Microgametophytes (pollen) are produced in microsporangiate strobili (pollen cones), with pollen sacs located on the lower surface. Sperm are not flagellated and are carried directly to egg via pollen tube. All species are wind-pollinated.

**Gnetophyta.** This phylum has three extant families—the Ephedraceae, the Gnetaceae, and the Welwitschiaceae—and four genera, such as Ephedra (Mormon tea). The plants grow as trees, shrubs, lianas, or stumps. Leaves are simple, opposite or whorled, straplike in the genus Welwitschia, angiosperm-like in the Gnetaceae, or scalelike in the genus Ephedra. Flowers are normally dioecious with compound stobili. Female flowers have an erect ovule, a nucellus of two or three coats, and a micropyle projecting as a long tube. The male cone is associated with bracts. Fertilization occurs through pollen tubes with two male nuclei. Some double fertilization is recorded, as in the angiosperms, but this double fertilization is not exactly homologous. Insect pollination is encouraged as a result of cone exudations.

**Anthophyta or Magnoliophyta.** The phylum or division Anthophyta, also referred to as the Magnoliophyta and commonly as the angiosperms, comprises the flowering plants and consists of about a quarter of a million species. The angiosperms constitute by far the largest phylum of plants and have traditionally been divided into two main classes. The class Magnoliopsida, the dicots, consists of about 180,000 species with two seed leaves, or cotyledons; netted venation in the leaves; flower parts in fours and fives and multiples thereof; primary vascular bundles in a ring in the stem; and a vascular cambium to produce true secondary growth in many species. The class Liliopsida, the monocots, consist of about 80,000 species with one seed leaf, or cotyledon, parallel venation, flower parts in threes, primary vascular bundles scattered in the stem, and no vascular cambium to produce true secondary growth. However, this division into two classes, monocots and dicots, is challenged now. Recently, the angiosperms have been divided into the eudicots ("true" dicots, or Dicotyledones) and the monocots (or Monocotyledones), with a small number of species (about 3 percent) relegated to the category of magnoliids.

Land plants date back in the fossil record only to the early Cretaceous period, and Magnoliophyta is now the dominant plant group in most biomes (biogeographic groups shaped by climate, topography, and soils). This dominance is due to vegetative and reproductive structures and functions uniquely adapted to a terrestrial existence.

**Vegetative Characteristics.** Members of the Magnoliophyta, or Anthophyta, vary in size from tiny aquatic duckweed to extremely large forest trees. Flowering plants have many *habits* (forms) and *niches* (lifestyles) and are annuals, biennials, perennials, woody trees and shrubs, herbaceous plants, vines, carnivorous plants, parasites, epiphytes, succulents, and saprophytes. Vessel elements making up the xylem are common in this phylum, and leaves are broad and have complex venation patterns.

**Reproduction.** True flowers are interpreted as a modified shoot or a reduced compound strobilus. Floral elements are sepals, petals, stamens, pistils, and carpels. Ovules within megasporophylls are fused into an ovary (carpels). Pollination (movement of microgametophyte or pollen to a receptive surface of pistil or stigma) can be effected by wind, water, gravity, animal vectors (such as insects, birds, and bats), but self-pollination and asparthenogenesis (fruit production without fertilization) are also common. Double fertilization is evident in all members of this group: Two sperm nuclei are present in the pollen, one fusing with the egg to
form the new embryo and the other fusing with the embryo sac nuclei to form the endosperm. The endosperm is the stored food tissue for the embryonic plant until it can photosynthesize or obtain food on its own through saprophytic or parasitic (haustorial) means. Seeds are distributed by all sorts of fruits (developed ovary tissue), such as follicles, berries, drupes, capsules, and legumes.

F. Christopher Sowers

See also: Plantae; Systematics and taxonomy; Systematics: overview.

Sources for Further Study


Most people use common names for plants. Common names are usually easier to spell, pronounce, and remember than are the more precise and standardized binomial scientific genus and species names. However, there are no rules for the use of common plant names, and that leads to some problems. Many plants have more than one common name in different parts of the country, in different parts of the world, and sometimes between next-door neighbors. Another problem with common plant names is that some are so convenient, they are used inaccurately to describe more than one type of plant. The third problem with common plant names is that they are given to plants that people find interesting, useful, or familiar; many unfamiliar plants therefore do not receive common names. Therefore, some plants have too many common names, and some common names are used too often, whereas some plants do not have common names.

The following table lists, in alphabetical order by common name (left-hand column), some of the more common organisms studied by scientists, including not only plants (kingdom **Plantae**) but also some of the more important members of the kingdoms **Archaea**, **Bacteria**, **Fungi**, and **Protista**. Where more than one very common name exists, the organisms below are listed under both or all common names. To learn more about the taxonomy and special characteristics of a plant, please look it up under its scientific name in the appendix that follows this one, titled “Plant Names: Scientific-to-Common.” Those interested in the taxonomic arrangement of organisms may also wish to consult the appendix in this volume headed “Plant Classification.”

*William B. Cook*

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1118 • Plant Names: Common-to-Scientific
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<td>Feather mosses</td>
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## Common Name | Scientific Name
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Fennel, florentine | Foeniculum vulgare
Fenugreek | Trigonella foenum-graecum
Fern, Australian tree | Cyathea cooperi
Fern, bird’s-nest | Asplenium nidus-avis
Fern, Boston | Nephrolepis exaltata
Fern, bracken | Pteridium aquilinum
Fern, Christmas | Polystichum acrostichoides
Fern, cinnamon | Osmunda cinnamomea
Fern, climbing | Lygodium japonicum
Fern, clover-leaf | Marsilea spp.
Fern, deer | Blechnum spicant
Fern, grape | Botrychium spp.
Fern, Hawaiian tree | Cibotium glaucum
Fern, lady | Adiantum capillus-veneris
Fern, licorice | Polypodium glycyrrhiza
Fern, lip | Cheilanthes spp.
Fern, maidenhair | Blechnum spicant
Fern, staghorn | Platycerium bifurcatum
Fern, Tasmanian tree | Dicksonia antarctica
Fern, walking | Asplenium rhizophyllum
Fescue, tall | Festuca arundinacea
Fiddle-leaf fig | Ficus lyrata
Field bindweed | Convolvulus arvensis
Fig, common | Ficus carica
Fig, fiddle-leaf | Ficus lyrata
Fig, Florida strangler | Ficus aurea
Fig, weeping | Ficus benjamina
Filbert | Corylus maxima
Finger banana | Musa acuminata
Fir, Douglas | Pseudotsuga menziesii
Fir, grand | Abies grandis
Fir, noble | Abies procera
Fir, subalpine | Abies lasiocarpa
Fir, white | Abies concolor
Fir moss | Huperzia lucidula
Fireweed | Epilobium angustifolium
Fishtail palm | Caryota urens
Flamboyant tree | Delonix regia
False Solomon’s seal | Smilacina racemosa
Flax | Linum usitatissimum
Florentine fennel | Foeniculum vulgare
Florida silverpalm | Cocothrinax argentata
Florida strangler fig | Ficus aurea
Flowering dogwood | Cornus florida
Flowering maple | Abutilon hybridum
Fly agaric | Amanita muscaria
Flytrap, Venus’s | Dionaea muscipula

## Common Name | Scientific Name
---|---
Foolish seedling pathogen | Gibberella fujikuroi
Forget-me-not | Myosotis alpestris
Forsythia, weeping | Forsythia suspensa
Four-o’clock | Mirabilis jalapa
Foxglove | Digitalis purpurea
Foxtail millet | Setaria italic
Frankincense | Boswellia carteri
Fuchsia | Fuchsia hybrida
Fungus, aflatoxin | Aspergillus flavus
Fungus, bird’s-nest | Cruciifolium laeve
Fungus, bunt | Tilletia caries
Fungus, hemlock varnish shelf | Ganoderma tsugae
Fungus, lasso | Arthrobotrys anchonaria
Fungus, mycorrhizal | Glomus panshihalos
Fungus, nematicidal | Dactylaria candida
Fungus, stinking smut | Tilletia caries
Garden geranium | Pelargonium hortorum
Garden pea | Pisum sativum
Garden verbena | Verbena hybrida
Garlic | Allium sativum
Gaura | Gaura lindheimeri
Gayfeather | Eustoma exaltatum
Geranium, garden | Pelargonium hortorum
Gherkin | Cucumis anguria
Giant blue iris | Iris gigantaicaerulea
Giant kelp | Macrocystis pyrifera
Giant protea | Protea cynaroides
Giant pumpkin | Cucurbita maxima
Giant sequoia | Sequoiadendron giganteum
Gilia | Ipomopsis rubra
Ginger | Zingiber officinale
Ginkgo | Ginkgo biloba
Ginseng, American | Panax quinquefolius
Glinging bacterium | Cytophaga hutchinsonii
Globe amaranth | Amaranthus globosa
Globe artichoke | Cynara scolymus
Gloriosa lily | Gloriosa rothschildiana
Gloxinia | Sinningia speciosa
Goathead | Tribulus terrestris
Goat’s beard | Tragopogon dubius
Golden brown algae | Chrysosoma spp.
Golden brown algae | Dinobryon spp.
Golden brown algae | Paraphysomonas spp.
Golden brown algae | Uroglena spp.
Golden chain tree | Laburnum anagyroides
Golden waxy cap | Hygrophorus flavescens
Goldenseal | Hydrastis canadensis
Golden currant | Ribes aureum
Gooseberry | Ribes grossularia
Grand fir | Abies grandis
Granite mosses | Andreae spp.
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PLANT NAMES: SCIENTIFIC-TO-COMMON

The following table lists, in alphabetical order by genus and species name (far-left column), some of the more common organisms studied by scientists, including not only plants (kingdom Plantae) but also some of the more important members of the kingdoms Archaea, Bacteria, Fungi, and Protista. Arranged alphabetically by genus, organisms from these different kingdoms are intermixed in this table. Those interested in the taxonomic arrangement of organisms should refer to the appendix in this volume headed “Plant Classification.” Useful articles, also in these volumes, are “Cladistics,” “Molecular Systematics,” “Systematics and Classification,” “Systematics: Overview,” and the various articles filed under “evolution.” To find the scientific name for a common plant name, consult the appendix titled “Plant Names: Common-to-Scientific.”

Scientific names for plants are created according to rules set forth in the International Code of Botanical Nomenclature (ICBN). The ICBN describes how names are to be constructed, but it does not indicate which names are correct, or best. The ICBN specifies a two-word naming system called binomial nomenclature. Each plant is given a two-word name (a binomial), and all scientists agree to use this name exclusively. As a result of this naming system, the confusion caused by the common plant names that most people use (such as “bluebells”) is avoided. Occasionally, a scientific name must be changed, usually because the rules for naming a plant were not followed correctly. Normally, however, the scientific name is very stable.

In addition to the binomial, which names a plant’s species, each plant has a name for each higher-level group to which it belongs. Each plant belongs to a genus, each genus to a family, each family to an order, each order to a class, each class to a phylum, each phylum to a kingdom, and each kingdom to one of the three domains of life: Archaea, Bacteria (both made up of microorganisms formed by prokaryotic, or nucleus-free, cells), and Eukarya. The domain Eukarya, made up of organisms with cells that have nuclei, contains four kingdoms of life: Protista (protists, mainly molds and algae), Fungi (mainly nonphotosynthetic organisms), Plantae (plants, both nonvascular and vascular), and Animalia (animals).

Names for the higher-level plant groups, or taxa, are all created according to rules of the ICBN. The rules for naming higher-level groups do not indicate which names are best or most correct. Unlike the binomial genus-species names, on which scientists generally agree, the best name for the higher-level groups to which these genera belong can sometimes be controversial. Therefore, some of the higher-level groups have more than one proposed name. Neither of the names is necessarily more correct than the other. Usually the different names reflect different ideas about how the higher-level groups are related to each other. In some cases, the higher-level names that are listed were selected from several proposed names. Other sources may classify some of these genera under slightly different higher-level group names, as a result of the ongoing studies, discussions, and controversies over classification. The binomial genus-species name, however, will nearly always be the same. The existence of more than one name for some of the higher levels of plant classification is simply a reminder that botanists are constantly learning new things about plants and occasionally change their ideas about how plants should be named.

Each of the organisms (bacteria, fungi, and plants) listed in this appendix is alphabetized by its binomial scientific name (far left-hand column); the most often used common name appears in the middle column. Finally, the far-right column identifies the kingdom (k.), phylum (p.), class (c.), order (o.), and family (f.) in which the species is commonly classified, along with some notable characteristics. All organisms can be assumed to belong to the domain Eukarya unless one of the other domains (either Archaea or Bacteria) is identified. The abbreviation g., for “group,” indicates a group name that is “artificial”—that is, not based on evolutionary relationships but rather on some common characteristics that have made it convenient for researchers to regard these organisms as a group. The abbreviation spp. stands for “species” (plural).

William B. Cook

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<table>
<thead>
<tr>
<th>Scientific Name</th>
<th>Common Name</th>
<th>Taxonomy and Characteristics</th>
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</thead>
<tbody>
<tr>
<td>Acer negundo</td>
<td>Box elder</td>
<td>k. Plantae, p. Anthophyta, c. Eudicotyledones, o. Sapindales, f. Aceraceae. Tree with leaves divided into three leaflets; fruit a pair of winged seeds.</td>
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<tr>
<td><em>Acetobacter</em> spp.</td>
<td>Acetobacter</td>
<td>d. Bacteria, k. Eubacteria, p. Proteobacteria, c. Alphaproteobacteria, o. Rhodospirillales, f. Rhodospirillaceae. Gram-negative cell producing acetic acid; one species is used to make vinegar; others spoil alcoholic beverages.</td>
</tr>
<tr>
<td><em>Aconitum napellus</em></td>
<td>Monk’s hood</td>
<td>k. Plantae, p. Anthophyta, c. Eudicotyledones, o. Ranunculales, f. Ranunculaceae. Tender plant with dark blue flowers, one petal forming a hood over the others; seeds and roots are poisonous.</td>
</tr>
<tr>
<td><em>Aesculus hippocastanum</em></td>
<td>Horse chestnut</td>
<td>k. Plantae, p. Anthophyta, c. Eudicotyledones, o. Sapindales, f. Hippocastanaceae. Tree with large lobed leaves; upright clusters of ivory flowers marked with yellow; glossy red-brown seeds in soft-spiny husks.</td>
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<tr>
<td><em>Ailanthus altissima</em></td>
<td>Tree of heaven</td>
<td>Plantae, p. Anthophyta, c. Eudicotyledones, o. Sapindales, f. Simaroubaceae. Tree with divided leaves; fruit a twisted wing with seed in its center, produced in dense clusters; invasive weedy plant.</td>
</tr>
<tr>
<td><em>Alectoria sarmentosa</em></td>
<td>Witches’ hair</td>
<td>Fungi, g. lichen, f. Alectoriaceae. A dangling, stringy form of lichen found on tree branches.</td>
</tr>
<tr>
<td><em>Aleurites fordii</em></td>
<td>Tung oil tree</td>
<td>Plantae, p. Anthophyta, c. Eudicotyledones, o. Euphorbiales, f. Euphorbiaceae. Tree whose fruits are pressed to collect oil used in paints and varnishes.</td>
</tr>
<tr>
<td><em>Alnus rubra</em></td>
<td>Red alder</td>
<td>Plantae, p. Anthophyta, c. Eudicotyledones, o. Fagales, f. Betulaceae. Tree whose roots are associated with soil microorganisms that convert (fix) nitrogen from the air to a form used by plants.</td>
</tr>
<tr>
<td><em>Alnus sinuata</em></td>
<td>Sitka alder</td>
<td>Plantae, p. Anthophyta, c. Eudicotyledones, o. Fagales, f. Betulaceae. Spreading shrub or small tree found in alpine or subarctic areas.</td>
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<tr>
<td><em>Aloe vera</em></td>
<td>Aloe vera</td>
<td>k. Plantae, p. Anthophyta, c. Monocotyledones, o. Liliales, f. Aloaceae. Clusters of soft, fleshy leaves patterned with dark and light green; slimy leaf contents used to treat ailments of the skin and other organs.</td>
</tr>
<tr>
<td><em>Alternaria brassicicola</em></td>
<td>Dark leaf spot pathogen</td>
<td>k. Fungi, g. deuteromycetes, c. Hyphomycetes, o. Moniliales, f. Dematiaceae. Causes disease on members of the cabbage family; carried by seeds.</td>
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<tr>
<td>Arachis hypogaea</td>
<td>Peanut</td>
<td>k. Plantae, p. Anthophyta, c. Eudicotyledones, o. Fabales, f. Fabaceae. Tender plant; seed pods mature underground after flowering; seeds are processed for many foods; stems and leaves are used as fodder, pods for industrial energy production.</td>
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<tr>
<td>Arbutus menziesii</td>
<td>Pacific madrone</td>
<td>k. Plantae, p. Anthophyta, c. Eudicotyledones, o. Ericales, f. Ericaceae. Tree with evergreen, leathery leaves; red bark peels from trunk and branches; flowers are urn-shaped.</td>
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<tr>
<td>Areca catechu</td>
<td>Betel nut palm</td>
<td>k. Plantae, p. Anthophyta, c. Monocotyledones, o. Arecales, f. Areaceae. Tall tree with featherlike leaves and orange or scarlet fruit; seed chewed with leaves of Piper betel for stimulant and narcotic effects.</td>
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<tr>
<td><em>Arthrobotrys anchonia</em></td>
<td>Lasso fungus</td>
<td>k. Fungi, g. deuteromycetes, c. Hyphomycetes, o. Moniliales, f. Monilicae. Traps roundworms (nematodes) with loops that tighten around them.</td>
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<tr>
<td><em>Artocarpus altilis</em></td>
<td>Breadfruit</td>
<td>k. Plantae, p. Anthophyta, c. Eudicotyledones, o. Urticales, f. Moraceae. Tree producing each spherical or cylindrical, yellow-green, starchy fruit from an entire flower cluster; fruit is roasted, boiled, or fried and eaten and is a staple crop on Pacific islands.</td>
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<tr>
<td>Betula nigra</td>
<td>River birch</td>
<td>Plantae, p. Anthophyta, c. Eudicotyledones, o. Fagales, f. Betulaceae. Tree found along river banks; bark on mature trees is dark and scaly.</td>
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<tr>
<td>Brassica oleracea</td>
<td>Cabbage family</td>
<td>k. Plantae, p. Anthophylla, c. Eudicotyledones, o. Capparales, f. Brassicaceae. Green flowering stalk harvested while flowers are in bud, eaten raw or cooked; includes broccoli, brussels sprouts, cabbage, cauliflower, collards, kohlrabi.</td>
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<tr>
<td>Camellia japonica</td>
<td>Camellia</td>
<td>k. Plantae, p. Anthophylla, c. Eudicotyledones, o. Theales, f. Theaceae. Shrub or small tree producing glossy leaves and large showy flowers; Alabama state flower.</td>
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<tr>
<td><em>Campanula medium</em></td>
<td>Canterbury bell</td>
<td>k. Plantae, p. Anthophyta, c. Eudicotyledones, o. Campanulales, f. Campanulaceae. Pink, blue, purple or white flowers are bell- or urn-shaped.</td>
</tr>
<tr>
<td><em>Candida albicans</em></td>
<td>Thrush pathogen</td>
<td>k. Fungi, g. deuteromycetes, c. Blastomycetes, o. Cryptococcales, f. Cryptococcaceae. Causes human infections when the immune system is weak or normal bacteria are depleted.</td>
</tr>
<tr>
<td><em>Cannabis sativa</em></td>
<td>Hemp, marijuana</td>
<td>k. Plantae, p. Anthophyta, c. Eudicotyledones, o. Urticales, f. Cannabaceae. Shrub with fanlike divided leaves; stem fibers used for rope, rough cloth; leaves and flowers contain a psychoactive compound.</td>
</tr>
<tr>
<td><em>Capsicum annuum</em></td>
<td>Pepper</td>
<td>k. Plantae, p. Anthophyta, c. Eudicotyledones, o. Solanales, f. Solanaceae. Produces a hollow berry; varieties differ in fruit size, shape, color, flavor; includes sweet and chili peppers.</td>
</tr>
<tr>
<td><em>Carica papaya</em></td>
<td>Papaya</td>
<td>k. Plantae, p. Anthophyta, c. Eudicotyledones, o. Violales, f. Caricaceae. Treelike plant with large, deeply lobed leaves; many thick, fleshy fruits grow from stem (trunk); seeds in center in a slimy envelope.</td>
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<tr>
<td><em>Ceiba pentandra</em></td>
<td>Kapok</td>
<td><em>k. Plantae, p. Anthophyta, c. Eudicotyledones, o. Malvales, f. Bombacaceae.</em> Tall tropical tree; silky, cottonlike fibers surrounding seeds are used to make mattresses, life preservers.</td>
</tr>
<tr>
<td><em>Centaurea cyanus</em></td>
<td>Bachelor’s button</td>
<td><em>k. Plantae, p. Anthophyta, c. Eudicotyledones, o. Asterales, f. Asteraceae.</em> Flower heads have lobed segments in shades of pink, blue, or white.</td>
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<tr>
<td>Cinnamomum camphora</td>
<td>Camphor tree</td>
<td>k. Plantae, p. Anthophyta, g. magnoliids, o. Laurales, f. Lauraceae. Tree with shiny yellow-green leaves and many clusters of tiny yellow flowers; source of commercial camphor.</td>
</tr>
<tr>
<td>Cinnamomum zeylanicum</td>
<td>Cinnamon</td>
<td>k. Plantae, p. Anthophyta, g. magnoliids, o. Laurales, f. Lauraceae. Tall tree; grown for its bark, which is scraped off and used whole or ground to powder for use as a cooking spice.</td>
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<tr>
<td>Citrus limon</td>
<td>Lemon</td>
<td>k. Plantae, p. Anthophyta, c. Eudicotyledones, o. Sapindales, f. Rutaceae. Small tree with glossy leaves producing a very acidic yellow fruit used for juice or candied rind.</td>
</tr>
<tr>
<td>Citrus sinensis</td>
<td>Navel orange, sweet orange</td>
<td>k. Plantae, p. Anthophyta, c. Eudicotyledones, o. Sapindales, f. Rutaceae. Evergreen tree with glossy leaves; fruit has juicy segments and peelable rind; eaten fresh or pressed for juice; blossom is Florida state tree.</td>
</tr>
<tr>
<td>Cladonia cristatella</td>
<td>British soldiers</td>
<td>k. Fungi, g. lichen, f. Cladoniaceae. Small, erect, light-colored stalks with red knobs on top.</td>
</tr>
<tr>
<td>Cladonia rangiferina</td>
<td>Reindeer lichen</td>
<td>k. Fungi, g. lichen, f. Cladoniaceae. Gray-green and darkening with age; grows in thick cushions in tundra.</td>
</tr>
<tr>
<td>Cladonia subtenuis</td>
<td>Reindeer moss</td>
<td>k. Fungi, g. lichen, f. Cladoniaceae. One of several lichens in the diets of reindeer and other Arctic mammals.</td>
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<tr>
<td><em>Cocos nucifera</em></td>
<td>Coconut palm</td>
<td>k. Plantae, p. Anthophyta, c. Monocotyledones, o. Arecales, f. Areaceae. Tree with large, featherlike leaves; fruit is three-sided and one-seeded, with a fibrous husk; seed contains white solid “meat” and thin white liquid “milk.”</td>
</tr>
<tr>
<td><em>Coffea canephora</em></td>
<td>Coffee</td>
<td>k. Plantae, p. Anthophyta, c. Eudicotyledones, o. Rubiales, f. Rubiaceae. Tree producing small fruits harvested for seeds (beans) inside husk; ground seeds are used for coffee.</td>
</tr>
<tr>
<td><em>Conocephalum conicum</em></td>
<td>Liverwort, thalloid</td>
<td>k. Plantae, p. Hepatophyta, c. Marchantiopsida, o. Marchantiales, f. Conocephalaceae. Found on moist sand or acidic rock surfaces; pores on lobes are surrounded by distinct hexagonal pattern.</td>
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<tr>
<td>Convallaria majalis</td>
<td>Lily of the valley</td>
<td>k. Plantae, p. Anthophyta, c. Monocotyledones, o. Liliales, f. Liliaceae. Small, fragrant, waxy, white, drooping, bell-shaped flowers on a stalk with two broad leaves; all parts are poisonous.</td>
</tr>
<tr>
<td>Cornus florida</td>
<td>Flowering dogwood</td>
<td>k. Plantae, p. Anthophyta, c. Eudicotyledones, o. Cornales, f. Cornaceae. Small tree; small flowers surrounded by four showy, petal-like white or pink bracts; fruits bright red; state tree of Virginia, Missouri; state flower of Virginia, North Carolina.</td>
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<tr>
<td>Crocus sativus</td>
<td>Saffron crocus</td>
<td>k. Plantae, p. Anthophyta, c. Monocotyledones, o. Liliales, f. Iridaceae. Cluster of small grasslike leaves from underground stems (corms); dried orange-red stigmas of flowers are the source of the spice saffron.</td>
</tr>
<tr>
<td>Cucurbita pepo</td>
<td>Zucchini</td>
<td>k. Plantae, p. Anthophyta, c. Eudicotyledones, o. Violales, f. Cucurbitaceae. Trailing stem or bushy plant; cylindrical or spherical fruit harvested when immature and used fresh, cooked, or in baking.</td>
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<tr>
<td>Cyperus papyrus</td>
<td>Paper rush</td>
<td>k. Plantae, p. Anthophyta, c. Monocotyledones, o. Cyperales, f. Cyperaceae. Tall stems topped by clusters of threadlike green stringers; found in standing water; ancient form of writing paper was made from pith and stems.</td>
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<tr>
<td>Dactylaria candida</td>
<td>Nematicidal fungus</td>
<td>k. Fungi, g. deuteromycetes, c. Hyphomycetes, o. Moniliales, f. Moniliaceae. Captures very small worms (nematodes) with sticky knobs or loops.</td>
</tr>
<tr>
<td>Daucus carota</td>
<td>Carrot, Queen Anne’s lace</td>
<td>k. Plantae, p. Anthophyta, c. Eudicotyledones, o. Apiales, f. Apiaceae. Root varies by variety from short to long, always swollen; eaten raw, cooked, or juiced.</td>
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<tr>
<td><em>Dianthus caryophyllus</em></td>
<td>Carnation</td>
<td>k. Plantae, p. Anthophyta, c. Eudicotyledones, o. Caryophyllales, f. Caryophyllaceae. Fragrant, showy, frilled, white, pink, or red flowers; Scarlet carnation is Ohio state flower.</td>
</tr>
<tr>
<td><em>Dieffenbachia amoena</em></td>
<td>Dumbcane</td>
<td>k. Plantae, p. Anthophyta, c. Eudicotyledones, o. Arales, f. Araceae. Ornamental plant with broad green and white leaves; all parts contain sap that numbs skin on contact.</td>
</tr>
<tr>
<td><em>Digitalis purpurea</em></td>
<td>Foxglove</td>
<td>k. Plantae, p. Anthophyta, c. Eudicotyledones, o. Scrophulariales, f. Scrophulariaceae. Tall plant with hairy gray-green leaves clustered at base and tubular, white or purple, dangling flowers along mature stem; source of digitalis used as heart medicine.</td>
</tr>
<tr>
<td><em>Dioscorea alata</em></td>
<td>Yam</td>
<td>k. Plantae, p. Anthophyta, c. Monocotyledones, o. Liliales, f. Dioscoreaceae. Climbing vines with heart-shaped leaves; one of several species grown in tropics for the starchy tuber; not related to sweet potato (which is sold as both “yams” and “sweet potatoes” in the U.S.).</td>
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<tr>
<td><em>Dodecatheon meadia</em></td>
<td>Shooting star</td>
<td>k. Plantae, p. Anthophyta, c. Eudicotyledones, o. Primulales, f. Primulaceae. Tender plant; bare stalk with several drooping flowers; pale blue petals bent back, other flower parts pointed forward.</td>
</tr>
<tr>
<td><em>Duchesnea indica</em></td>
<td>Indian mock strawberry</td>
<td>Small spreading plant producing dry, insipid, seedy fruit resembling a strawberry.</td>
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<tr>
<td><em>Elaeis guineensis</em></td>
<td>Oil palm</td>
<td>k. Plantae, p. Anthophyta, c. Monocotyledones, o. Arecales, f. Areaceae. Tall tree with feather-shaped leaves and large clusters of small coconut-like fruits; palm oil and palm kernel oil are extracted for commercial uses.</td>
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<tr>
<td><em>Elettaria cardamomum</em></td>
<td>Cardamom</td>
<td>k. Plantae, p. Anthophyta, c. Monocotyledones, o. Zingiberales, f. Zingiberaceae. Tall, leafy, grasslike relative of ginger; seeds used as cooking spice, as flavoring, and in perfumes.</td>
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<tr>
<td><em>Fallugia paradoxa</em></td>
<td>Apache plume</td>
<td>Shrub with flaky bark producing flowers like single white roses followed by feathery fruits.</td>
</tr>
<tr>
<td><em>Festuca arundinacea</em></td>
<td>Tall fescue</td>
<td>Coarse bunchgrass used for pasture, drought-resistant lawns, and erosion control.</td>
</tr>
<tr>
<td><em>Ficus aurea</em></td>
<td>Florida strangler fig</td>
<td>Tree-sized plant; seedlings grow on trunk of host tree and eventually surround it with stems and roots.</td>
</tr>
<tr>
<td><em>Ficus benjamina</em></td>
<td>Weeping fig</td>
<td>Evergreen tree; small, thin, leathery, glossy leaves on drooping branches; popular houseplant.</td>
</tr>
<tr>
<td><em>Ficus carica</em></td>
<td>Common fig</td>
<td>Tree or shrub with deeply lobed leaves; purple-red flowers in a flask-shaped chamber; each fruit is a ripened chamber and flower cluster.</td>
</tr>
<tr>
<td><em>Ficus elastica</em></td>
<td>India rubber plant</td>
<td>Shrub or small tree; leaves large, leathery, glossy; wounds weep white latex; popular houseplant.</td>
</tr>
<tr>
<td><em>Ficus lyrata</em></td>
<td>Fiddle-leaf fig</td>
<td>Tree with large, rigid, glossy leaves shaped like violins.</td>
</tr>
<tr>
<td><em>Flammulina velutipes</em></td>
<td>Velvet foot mushroom</td>
<td>Sticky tan cap, pale gills, velvety-brown stalk; grows in clusters.</td>
</tr>
<tr>
<td><em>Foeniculum vulgare</em></td>
<td>Florentine fennel</td>
<td>Swollen, enlarged leaf bases eaten raw or cooked for aniselike flavor.</td>
</tr>
<tr>
<td><em>Forsythia suspensa</em></td>
<td>Weeping forsythia</td>
<td>Graceful, drooping branches produce bright yellow spring flowers.</td>
</tr>
<tr>
<td><em>Fortunella margarita</em></td>
<td>Kumquat</td>
<td>Produces small fruits with edible rinds and tart flesh; candied or used in jelly.</td>
</tr>
<tr>
<td><em>Fouquieria splendens</em></td>
<td>Ocotillo</td>
<td>Tall, stiff, whiplike stems covered with stout thorns; small, fleshy leaves appear only after heavy rain.</td>
</tr>
<tr>
<td><em>Fragaria virginiana</em></td>
<td>Wild strawberry</td>
<td>Small mound of divided leaves producing creeping stems; fruits are swollen red flower bases with tiny, scattered, crunchy seeds.</td>
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<tr>
<td>Graphis scripta</td>
<td>Pencil marks lichen</td>
<td>k. Fungi, g. lichen, f. Graphidaceae. Thin, smooth, white crustose body bears dark fruiting bodies that resemble pencil marks.</td>
</tr>
<tr>
<td>Gutierrezia dracunculoides</td>
<td>Broomweed</td>
<td>k. Plantae, p. Anthophyta, c. Eudicotyledones, o. Asterales, f. Asteraceae. Many-branched plant used by pioneers as broom; can cause skin rash and eye irritation in humans.</td>
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<tr>
<td><strong>Hibiscus esculentus</strong></td>
<td>Okra</td>
<td>k. Plantae, p. Anthophyta, c. Eudicotyledones, o. Malvales, f. Malvaceae. Tall plant producing five-sided pods that are cooked alone or in soups and sauces.</td>
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<tr>
<td><em>Huperzia lucidula</em></td>
<td>Fir moss</td>
<td>k. Plantae, p. Lycophyta, c. Lycopsida, o. Lycopodiaceae. Horizontal stems belowground produce branches with green leaves; no cone is formed.</td>
</tr>
<tr>
<td><em>Ipomoea batatas</em></td>
<td>Sweet potato</td>
<td>k. Plantae, p. Anthophyta, c. Eudicotyledones, o. Solanales, f. Convolvulaceae. Trailing or climbing vines; tuberous roots vary in size, color of skin, and color of flesh; boiled, baked or candied; not related to true yams.</td>
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<tr>
<td>Isoetes melanopoda</td>
<td>Quillwort</td>
<td>k. Plantae, p. Lycophyta, c. Lycopsida, o. Isoetales, f. Isoetaceae. Short underground stem with tuft of upright or curved stiff leaves; found in water or wet ground.</td>
</tr>
<tr>
<td>Jasminum sambac</td>
<td>Arabian jasmine</td>
<td>k. Plantae, p. Anthophyta, c. Eudicotyledones, o. Scrophulariales, f. Oleaceae. Shrub with glossy leaves and powerfully fragrant white flowers; flowers are used in perfumery, jasmine tea, and Hawaiian leis.</td>
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<tr>
<td><em>Juniperus virginiana</em></td>
<td>Eastern red cedar</td>
<td>Tree with scalelike leaves or, at branch tips, stiff, prickly awl-like leaves; cones blue and fleshy.</td>
</tr>
<tr>
<td><em>Kalanchoe daigremontiana</em></td>
<td>Maternity plant, mother of thousands</td>
<td>Tender plant producing small plantlets on toothed edges of full-sized leaves.</td>
</tr>
<tr>
<td><em>Kalmia latifolia</em></td>
<td>Mountain laurel</td>
<td>Shrub or tree with leathery leaves and clusters of pink, starlike flowers; state flower of Connecticut, Pennsylvania.</td>
</tr>
<tr>
<td><em>Kigelia africana</em></td>
<td>Sausage fruit</td>
<td>African tree producing fleshy, red flowers followed by thick, sausagelike fruits hanging from ropelike stalks.</td>
</tr>
<tr>
<td><em>Laburnum anagyroides</em></td>
<td>Golden chain tree</td>
<td>Small tree producing long, dangling clusters of bright yellow flowers.</td>
</tr>
<tr>
<td><em>Lactarius indigo</em></td>
<td>Indigo milky</td>
<td>Indigo-colored mushroom turns green when bruised.</td>
</tr>
<tr>
<td><em>Lactobacillus spp.</em></td>
<td>Lactic acid bacteria</td>
<td>Gram-positive cells ferment sugars to lactic acid; produce foods like yogurt and sour cream but spoil other foods.</td>
</tr>
<tr>
<td><em>Lactuca sativa</em></td>
<td>Lettuce</td>
<td>Dense leafy heads are used in salads.</td>
</tr>
<tr>
<td><em>Larix laricina</em></td>
<td>Tamarack</td>
<td>Needle-leaf tree; drops needles in fall.</td>
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<tr>
<td><strong>Laurus nobilis</strong></td>
<td>Laurel, bay laurel</td>
<td>k. Plantae, p. Anthophyta, g. magnoliids, o. Laurales, f. Lauraceae. Evergreen tree or shrub; dark green leaves used as cooking herb.</td>
</tr>
<tr>
<td><strong>Letharia vulpina</strong></td>
<td>Wolf moss</td>
<td>k. Fungi, g. lichen, f. Parmeliaceae. Bright yellow-green tufted body; once used to poison wolves.</td>
</tr>
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<tr>
<td><strong>Linum usitatissimum</strong></td>
<td>Flax</td>
<td>k. Plantae, p. Anthophyta, c. Eudicotyledones, o. Linales, f. Linaceae. Tender plants with narrow leaves and blue flowers; grown for fibers used in linen and oil from seeds (linseed oil).</td>
</tr>
<tr>
<td><strong>Liriodendron tulipifera</strong></td>
<td>Tulip tree, yellow poplar</td>
<td>k. Plantae, p. Anthophyta, g. magnoliids, o. Magnoliales, f. Magnoliaceae. Tall tree with four-lobed leaves and tulip-shaped flowers; state tree of Indiana, Tennessee.</td>
</tr>
<tr>
<td><strong>Litchi chinensis</strong></td>
<td>Lychee</td>
<td>k. Plantae, p. Anthophyta, c. Eudicotyledones, o. Sapindales, f. Sapindaceae. Evergreen tree producing round, red fruits with warty rinds; fleshy, edible sac surrounding single seed is eaten fresh or dried to make lychee nuts.</td>
</tr>
<tr>
<td><strong>Lobaria pulmonaria</strong></td>
<td>Lung lichen</td>
<td>k. Fungi, g. lichen, f. Parmeliaceae. Resembles a limp, uninflated lung.</td>
</tr>
<tr>
<td><strong>Lodoicea maldivica</strong></td>
<td>Seychelles palm</td>
<td>k. Plantae, p. Anthophyta, c. Monocotyledones, o. Arecales, f. Arecaceae. Large tree with fanlike leaves, native to the Seychelles Islands; produces the largest known seed, sometimes called the double coconut.</td>
</tr>
<tr>
<td><strong>Luffa cylindrica</strong></td>
<td>Loofa sponge plant</td>
<td>k. Plantae, p. Anthophyta, c. Eudicotyledones, o. Violales, f. Cucurbitaceae. Tender vine producing cylindrical gourds with fibrous interiors that can be used as sponges.</td>
</tr>
<tr>
<td><strong>Lunaria annua</strong></td>
<td>Money plant</td>
<td>k. Plantae, p. Anthophyta, c. Eudicotyledones, o. Capparales, f. Brassicaceae. Tall stems with clear, circular membranes left when seeds are shed; used in dried arrangements.</td>
</tr>
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<tr>
<td>Lycopersicon esculentum</td>
<td>Tomato</td>
<td>k. Plantae, p. Anthophyta, c. Eudicotyledones, o. Solanales, f. Solanaceae. Straggling bush grown for fleshy, juicy, seedy, yellow to red fruits of various sizes and shapes, used raw, cooked, or processed.</td>
</tr>
<tr>
<td>Lycopodium complanatum</td>
<td>Ground cedar</td>
<td>k. Plantae, p. Lycopophyta, c. Lycopsida, o. Lycopodiales, f. Lycopodiaceae. Horizontal stems belowground produce upright branches with four relatively short leaves; cones on short branches from long, nearly leafless stalks; perennial plants produce yearly growth marks.</td>
</tr>
<tr>
<td>Magnolia grandiflora</td>
<td>Southern magnolia</td>
<td>k. Plantae, p. Anthophyta, g. magnoliids, o. Magnoliales, f. Magnoliaceae. Evergreen tree; leaves large, leathery, glossy green; white flowers large, showy, fragrant; reddish, hairy fruit with exposed red seeds; Mississippi state tree; state flower of Mississippi, Louisiana.</td>
</tr>
<tr>
<td>Malus angustifolia</td>
<td>Southern crabapple</td>
<td>k. Plantae, p. Anthophyta, c. Eudicotyledones, o. Rosales, f. Rosaceae. Tree with small applelike fruits; ornamental or fruits pickled or used in jelly.</td>
</tr>
<tr>
<td>Malus x domestica</td>
<td>Apple</td>
<td>k. Plantae, p. Anthophyta, c. Eudicotyledones, o. Rosales, f. Rosaceae. Tree with crisp, fleshy fruit; many cultivated varieties used fresh or processed; blossom is state flower of Arkansas, Michigan.</td>
</tr>
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<tr>
<td><strong>Mangifera indica</strong></td>
<td>Mango</td>
<td>Plantae, Anthophyta, Eudicotyledones, Sapindales, Anacardiaceae. Tree with thin evergreen leaves; large single-seeded fruit with yellow or orange flesh used fresh or cooked.</td>
</tr>
<tr>
<td><strong>Manihot esculenta</strong></td>
<td>Cassava, manioc, tapioca</td>
<td>Plantae, Anthophyta, Eudicotyledones, Euphorbiales, Euphorbiaceae. Tall tropical shrub with swollen roots; important source of starch in tropical diet.</td>
</tr>
<tr>
<td><strong>Manilkara zapota</strong></td>
<td>Sapodilla</td>
<td>Plantae, Anthophyta, Eudicotyledones, Sapindales, Sapotaceae. Evergreen tropical tree; edible pulpy fruit; sap collected for chicle.</td>
</tr>
<tr>
<td><strong>Maranta leuconeura</strong></td>
<td>Prayer plant</td>
<td>Plantae, Monocotyledones, Zingiberales, Marantaceae. Small leafy plant; leaves pale along veins; brown spots near edges; leaves fold upward at night.</td>
</tr>
<tr>
<td><strong>Marasmius oreades</strong></td>
<td>Fairy ring mushroom</td>
<td>Fungi, Basidiomycota, Tricholomataceae. Forms rings of mushrooms in grassy areas; easily confused with poisonous look-alikes.</td>
</tr>
<tr>
<td><strong>Marchantia polymorpha</strong></td>
<td>Liverwort, thalloid</td>
<td>Plantae, Hepatophyta, Marchantiopsida, Marchantiales, Marchantiaceae. Large pores and gemma cups on lobes; used extensively in laboratory studies.</td>
</tr>
<tr>
<td><strong>Marrubium vulgare</strong></td>
<td>Horehound</td>
<td>Plantae, Anthophyta, Eudicotyledones, Lamiales, Lamiaceae. Common weed around old fences and buildings; used as a flavoring in candies.</td>
</tr>
<tr>
<td><strong>Marsilea spp.</strong></td>
<td>Clover-leaf ferns</td>
<td>Plantae, Pterophyta, Marsileopsida, Marsileales, Marsiliaceae. Leaf blade floating or above water surface, divided into four segments like four-leaf clover.</td>
</tr>
<tr>
<td><strong>Matteuccia struthiopteris</strong></td>
<td>Ostrich fern</td>
<td>Plantae, Pterophyta, Filicopsida, Filicales, Dryopteridaceae. Cluster of dark green, head-high, plumelike leaves arise from ground level.</td>
</tr>
<tr>
<td><strong>Medicago sativa</strong></td>
<td>Alfalfa</td>
<td>Plantae, Anthophyta, Eudicotyledones, Fabales, Fabaceae. Tender plant with blue-purple flower clusters; used as high-quality animal fodder.</td>
</tr>
<tr>
<td><strong>Melampodium leucanthum</strong></td>
<td>Blackfoot daisy</td>
<td>Plantae, Eudicotyledones, Asterales, Asteraceae. Rounded mounds covered with white, daisylike flower heads.</td>
</tr>
<tr>
<td><strong>Melampsoridium betulinum</strong></td>
<td>Birch rust</td>
<td>Fungi, Basidiomycota, Uredinomycetes, Uredinales, Melampsoraceae. Infects birch and larch leaves.</td>
</tr>
<tr>
<td><strong>Melanophyllum chinatum</strong></td>
<td>Red-gilled agaric</td>
<td>Fungi, Basidiomycota, Basidiomycetes, Agaricales, Agaricaceae. Mushroom with dark red gills.</td>
</tr>
<tr>
<td><strong>Melia azedarach</strong></td>
<td>China berry</td>
<td>Plantae, Anthophyta, Eudicotyledones, Sapindales, Meliaceae. Tree with divided leaves; fleshy yellow fruits in clusters.</td>
</tr>
<tr>
<td><strong>Melilotus albus</strong></td>
<td>White sweet clover</td>
<td>Plantae, Anthophyta, Eudicotyledones, Fabales, Fabaceae. Bushy plant with small white flowers and exotic scent.</td>
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<tr>
<td></td>
<td>Spanish lime</td>
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</tr>
<tr>
<td><em>Mesembryanthemum crystallinum</em></td>
<td>Ice plant</td>
<td>k. Plantae, p. anthophyta, c. eudicotyledones, o. caryophyllales, f. aizoaceae. Fleshy spreading plant covered with transparent blisters that glitter in the sun.</td>
</tr>
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</tr>
<tr>
<td>Monilinia fructicola</td>
<td>Brown rot pathogen</td>
<td>Fungi, g. deuteromycetes, c. Hyphomycetes, o. Moniliales, f. Moniliaceae. Causes decay of stone fruits such as peaches, cherries, and plums.</td>
</tr>
<tr>
<td>Monstera deliciosa</td>
<td>Split leaf philodendron</td>
<td>Plantae, p. Anthophyta, c. Monocotyledones, o. Arales, f. Araceae. Vine with large, divided, glossy leaves; climbs on trees or other supports; fruit edible.</td>
</tr>
<tr>
<td>Morus rubra</td>
<td>Red mulberry</td>
<td>Plantae, p. Anthophyta, c. Eudicotyledones, o. Urticales, f. Moraceae. Tree; leaves unlobed or with two or three lobes; each blackberry-like fruit formed from entire cluster of small flowers.</td>
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<tr>
<td><em>Myristica fragrans</em></td>
<td>Mace, nutmeg</td>
<td>k. Plantae, p. Anthophyta, g. magnoliids, o. Magnoliaceae, f. Myristicaceae. Fleshy, netted seed; coating is dried and powdered to flavor pickles and ketchup.</td>
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<tr>
<td>Nephelium lapaceum</td>
<td>Rambutan</td>
<td>k. Plantae, p. Anthophyta, c. Eudicotyledones, o. Sapindales, f. Sapindaceae. Small tree producing yellow or red fruits; husks covered with soft spines; seeds surrounded by edible, fleshy sac; eaten fresh.</td>
</tr>
<tr>
<td>Olea europea</td>
<td>Olive</td>
<td>k. Plantae, p. Anthophyta, c. Eudicotyledones, o. Scrophulariales, f. Oleaceae. Small evergreen tree producing fruit with thin skin, fleshy pulp, and stony center; used for oil or table olives, ripe (black) or green.</td>
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<tr>
<td><strong>Paeonia spp.</strong></td>
<td>Peony</td>
<td>k. Plantae, p. Anthophyta, c. Monocotyledones, o. Dilleniales, f. Paeoniaceae. Shrubs; dark green foliage and large, showy, pink, red or white flowers grow from a thick rootstock; Indiana state flower.</td>
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<tr>
<td><em>Phaseolus lunatus</em></td>
<td>Lima bean</td>
<td>Climbing vine producing pods harvested for edible seeds, cooked or ground for flour.</td>
</tr>
<tr>
<td><em>Phaseolus vulgaris</em></td>
<td>Kidney bean, string bean</td>
<td>Most widely grown bean; young pods (string beans) eaten fresh or cooked; dried seeds cooked.</td>
</tr>
<tr>
<td><em>Philadelphus coronarius</em></td>
<td>Mock orange</td>
<td>Shrub or small tree producing white, fragrant flowers.</td>
</tr>
<tr>
<td><em>Philadelphus lewisii</em></td>
<td>Syringa</td>
<td>Arching plant producing large, fragrant, satiny flowers; Idaho state flower.</td>
</tr>
<tr>
<td><em>Phleum pratense</em></td>
<td>Timothy</td>
<td>Bunchgrass used for pasture or hay, especially for horses.</td>
</tr>
<tr>
<td><em>Phlogiotis helvelloides</em></td>
<td>Apricot jelly</td>
<td>Apricot-colored, rubbery, funnel-shaped cap with stalk attached near edge of cap.</td>
</tr>
<tr>
<td><em>Phoenix dactylifera</em></td>
<td>Date palm</td>
<td>Tall tree with featherlike leaves; fruits surround seeds with soft, sugary, fleshy edible pulp.</td>
</tr>
<tr>
<td><em>Phoradendron sertinum</em></td>
<td>Mistleoe</td>
<td>Parasitic shrub growing from branches of host tree; white berries ripen in winter, used as holiday decoration; Oklahoma state flower.</td>
</tr>
<tr>
<td><em>Photinia serrulata</em></td>
<td>Chinese photinia</td>
<td>Shrub or small tree with stiff, prickly-edged leaves; white flowers, then red berries, in flat-topped clusters.</td>
</tr>
<tr>
<td><em>Phragmidium violaceum</em></td>
<td>Violet rust</td>
<td>Causes violet leaf spots on bramble hosts.</td>
</tr>
<tr>
<td><em>Phycopeltis spp.</em></td>
<td>Green algae</td>
<td>Circular body grows on surface of many tropical plants.</td>
</tr>
<tr>
<td><em>Phyllitis scolopendrium</em></td>
<td>Hart’s tongue</td>
<td>Undivided leaves in a star-shaped cluster from a hardy base.</td>
</tr>
<tr>
<td><em>Physalis ixocarpa</em></td>
<td>Tomatillo</td>
<td>Tender plant producing a large berry surrounded by a lanternlike husk.</td>
</tr>
<tr>
<td><em>Physarum polycephalum</em></td>
<td>Plasmodial slime mold</td>
<td>Travels as a thin mass of protoplasm; divides into small mounds to reproduce.</td>
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<tr>
<td><em>Pistacia vera</em></td>
<td>Pistachio</td>
<td>Plantae, p. Anthophyta, c. Eudicotyledones, o. Sapindales, f. Anacardiaceae. Tree; shells of fruits split before harvest; nuts with green seeds eaten alone or added to foods.</td>
</tr>
<tr>
<td><em>Pisum sativum</em></td>
<td>Garden pea</td>
<td>Plantae, p. Anthophyta, c. Eudicotyledones, o. Fabales, f. Fabaceae. Tender vine producing seeds in pod; seeds used fresh, dried, or ground to flour; vines used as livestock fodder.</td>
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<tr>
<td>Prunus persica</td>
<td>Peach</td>
<td>k. Plantae, p. Anthophyta, c. Eudicotyledones, o. Rosales, f. Rosaceae. Small tree producing fruit with hairy skin, stony center, and juicy flesh; used fresh, canned, processed; blossom is Delaware state flower.</td>
</tr>
<tr>
<td>Prunus spinosa</td>
<td>Sloe</td>
<td>k. Plantae, p. Anthophyta, c. Eudicotyledones, o. Rosales, f. Rosaceae. Shrub with thorny branches; blue-black, plumlike fruit with sour green flesh used to make sloe wine or gin.</td>
</tr>
<tr>
<td>Ptelea trifoliata</td>
<td>Common hop tree</td>
<td>k. Plantae, p. Anthophyta, c. Eudicotyledones, o. Sapindales, f. Rutaceae. Tree with leaves divided into three leaflets; fruits round with paper-thin wing around the edge.</td>
</tr>
<tr>
<td>Pteridium aquilinum</td>
<td>Bracken fern</td>
<td>k. Plantae, p. Pterophyta, c. Filicopsida, o. Filicales, f. Dennstaedtiaceae. Large, upright, pale green leaves; grows in extensive stands.</td>
</tr>
<tr>
<td>Pueraria lobata</td>
<td>Kudzu</td>
<td>k. Plantae, p. Anthophyta, c. Eudicotyledones, o. Fabales, f. Fabaceae. Aggressive trailing or climbing vine; leaves divided into three leaflets; fruit a hairy pod.</td>
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<tr>
<td>Punica granatum</td>
<td>Pomegranate</td>
<td>k. Plantae, p. Anthophyta, c. Eudicotyledones, o. Myrtales, f. Punicaceae. Shrub or small tree producing fleshy flower and spherical fruit with leathery skin and many fleshy, juicy seeds; juice used in drinks, syrups, and wine production.</td>
</tr>
<tr>
<td>Pyrus communis</td>
<td>Pear</td>
<td>k. Plantae, p. Anthophyta, c. Eudicotyledones, o. Rosales, f. Rosaceae. Tree; fruits with thin skin, juicy, soft flesh surrounding seed compartments; used fresh, stewed, canned, or dried.</td>
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<tr>
<td><em>Quercus stellata</em></td>
<td>Post oak</td>
<td><em>k. Plantae, p. Anthophyta, c. Eudicotyledones, o. Fagales, f. Fagaceae.</em> Tree; leaves with rounded or blocky lobes; fruit an acorn.</td>
</tr>
<tr>
<td><em>Quercus virginiana</em></td>
<td>Live oak</td>
<td><em>k. Plantae, p. Anthophyta, c. Eudicotyledones, o. Fagales, f. Fagaceae.</em> Tree; evergreen, elliptical leaves; fruit an acorn; Georgia state tree.</td>
</tr>
<tr>
<td><em>Ramalina menziesii</em></td>
<td>Lace lichen</td>
<td><em>k. Fungi, g. lichen, f. Ramalinaceae.</em> Yellow-green, netlike growth, often in thick curtains dangling from trees.</td>
</tr>
<tr>
<td><em>Rhizocarpon geographicum</em></td>
<td>Map lichen</td>
<td><em>k. Fungi, g. lichen, f. Rhizocarpaceae.</em> Most common of several lichens with the common name; black lower layer bears yellow fruiting bodies.</td>
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<tr>
<td>Rubus spp.</td>
<td>Blackberry</td>
<td>k. Plantae, p. Anthophyta, c. Eudicotyledones, o. Rosales, f. Rosaceae. Prickly climbing plant producing stems that radiate from the rootstock; fruit a cluster of small, juicy globes containing seeds; eaten fresh or used in pies or jam.</td>
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<tr>
<td><em>Salix discolor</em></td>
<td>Pussy willow</td>
<td>k. Plantae, p. Anthophyta, c. Eudicotyledones, o. Salicales, f. Salicaceae. Shrub or small tree; male and female on different trees; male flowers in soft, silky clusters.</td>
</tr>
<tr>
<td><em>Salix interior</em></td>
<td>Sandbar willow</td>
<td>k. Plantae, p. Anthophyta, c. Eudicotyledones, o. Salicales, f. Salicaceae. Shrub or small tree; typically found along waterways.</td>
</tr>
<tr>
<td><em>Sanguinaria canadensis</em></td>
<td>Bloodroot</td>
<td>k. Plantae, p. Anthophyta, c. Eudicotyledones, o. Papaverales, f. Papaveraceae. Tender plant with grayish lobed leaves and white, spring flowers; cut stems and root bleed orange or red juice.</td>
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<tr>
<td><em>Sapindus saponaria</em></td>
<td>Soapberry</td>
<td>k. Plantae, p. Anthophyta, c. Eudicotyledones, o. Sapindales, f. Sapindaceae. Small tree with divided leaves producing yellow or orange berries; fruit flesh has been used as a soap substitute.</td>
</tr>
<tr>
<td><em>Sargassum spp.</em></td>
<td>Kelp</td>
<td>k. Protista, p. Phaeophyta, c. Phaeophyceae, o. Fucales, f. Sargassaceae. Large kelps that gave the Sargasso Sea its name; includes edible species.</td>
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<tr>
<td><em>Sassafras albidum</em></td>
<td>Sassafras</td>
<td>k. Plantae, p. Anthophyta, g. magnoliids, o. Laurales, f. Lauraceae. Small tree; leaves unlobed, or with two or three lobes; small, egg-shaped blue fruits; oils used in soaps.</td>
</tr>
<tr>
<td><em>Satureia hortensis</em></td>
<td>Summer savory</td>
<td>k. Plantae, p. Anthophyta, c. Eudicotyledones, o. Lamiales, f. Lamiaceae. Aromatic herb used to flavor a variety of meat and bean dishes.</td>
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<tr>
<td><em>Smilacina racemosa</em></td>
<td>False Solomon’s seal</td>
<td><em>k. Plantae, p. Anthophyta, c. Monocotyledones, o. Liliales, f. Liliaceae.</em> Tall, arching stalks with two rows of pale green leaves; cluster of white flowers on top stalk.</td>
</tr>
<tr>
<td><em>Solanum melanogena</em></td>
<td>Eggplant</td>
<td><em>k. Plantae, p. Anthophyta, c. Eudicotyledones, o. Solanales, f. Solanaceae.</em> Small, tough, short woolly plant producing a thick, fleshy, white, yellow or purple fruit; eaten cooked.</td>
</tr>
<tr>
<td><em>Sorbus aucuparia</em></td>
<td>European mountain ash, rowan</td>
<td><em>k. Plantae, p. Anthophyta, c. Eudicotyledones, o. Rosales, f. Rosaceae.</em> Tree with clusters of red or orange fruits; ornamental; fruits processed for use in jam.</td>
</tr>
<tr>
<td><em>Sorbus domestica</em></td>
<td>Service tree</td>
<td><em>k. Plantae, p. Anthophyta, c. Eudicotyledones, o. Rosales, f. Rosaceae.</em> Tree producing apple or pear-shaped fruit used for jam; must be allowed to half-rot before it is palatable.</td>
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<tr>
<td><em>Taxodium distichum</em></td>
<td>Bald cypress</td>
<td>Tree often found in standing water surrounded by woody “knees” above water surface; needles drop in fall; nearly spherical cones disintegrate at maturity; Louisiana state tree.</td>
</tr>
<tr>
<td><em>Taxus brevifolia</em></td>
<td>Pacific yew</td>
<td>Evergreen needle-leaf shrub or small tree; original source of substance used to make anticancer drug, paclitaxel (for Taxol).</td>
</tr>
<tr>
<td><em>Tectona grandis</em></td>
<td>Teak</td>
<td>Tropical tree; hard, heavy, durable wood is prized for furniture making and ship building.</td>
</tr>
<tr>
<td><em>Tetragonia expansa</em></td>
<td>New Zealand spinach</td>
<td>Leaves fleshy, shallow-lobed, triangular; leaves eaten as a substitute for spinach.</td>
</tr>
<tr>
<td><em>Thalassiosira pseudonana</em></td>
<td>Diatom</td>
<td>Marine cells used as a food source for commercial production of oysters and other shellfish.</td>
</tr>
<tr>
<td><em>Theobroma cacao</em></td>
<td>Cocoa</td>
<td>Tropical tree producing football-shaped fruits on trunk and branches; source of cocoa.</td>
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<tr>
<td><em>Thermoplasma acidophilum</em></td>
<td>Thermoplasma</td>
<td>Very small cell that does not produce a cell wall.</td>
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<tr>
<td><em>Thermus aquaticus</em></td>
<td>Taq</td>
<td>Grows in very hot water and produces the enzyme first used in automated polymerase chain reaction (PCR).</td>
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<tr>
<td><em>Thiobacillus ferrooxidans</em></td>
<td>Iron bacterium</td>
<td>Gains energy by converting iron from one form to another.</td>
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<td><em>Thuidium spp.</em></td>
<td>Feather mosses</td>
<td>Highly branched plants with a feathery appearance.</td>
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<td><em>Thuja occidentalis</em></td>
<td>Northern white cedar</td>
<td>Tree with flat twigs of scalelike leaves; small cones upright on twigs.</td>
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<tr>
<td><em>Thuja orientalis</em></td>
<td>Chinese arbor-vitae</td>
<td>Tree with flat, vertical twigs of scalelike leaves; small cones upright on twigs.</td>
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<tr>
<td><em>Thuja plicata</em></td>
<td>Western red cedar</td>
<td>Tree with flat, vertical twigs of scalelike leaves; small cones upright on twigs.</td>
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<tr>
<td><em>Tribulus terrestris</em></td>
<td>Goathead, puncture vine</td>
<td>k. Plantae, p. Anthophyta, c. Eudicotyledones, o. Sapindales, f. Zygophyllaceae; noxious weed of bare ground or lawns; produces a stony, five-headed fruit able to puncture tires or bare feet.</td>
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<tr>
<td>Urtica dioica</td>
<td>Stinging nettle</td>
<td>k. Plantae, p. Anthophyta, c. Eudicotyledones, o. Urticales, f. Urticaceae. Tall plant; stems and leaves covered with tiny hairs that produce a sharp, persistent sting when touched; leaves can be boiled and eaten like spinach.</td>
</tr>
<tr>
<td>Usnea alpina</td>
<td>Old man’s beard lichen</td>
<td>k. Fungi, g. lichen, f. Usneaceae. Bushy body hanging from tree branches; one of many lichens bearing the common name.</td>
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<tr>
<td>Vicia faba</td>
<td>Fava bean</td>
<td>k. Plantae, p. Anthophyta, c. Eudicotyledones, o. Fabales, f. Fabaceae. Tender plant; seeds in pods; immature seeds or whole pods cooked; dried seeds eaten or used as livestock fodder.</td>
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<td>Vigna unguiculata</td>
<td>Black-eyed pea, cowpea</td>
<td>k. Plantae, p. Anthophyta, c. Eudicotyledones, o. Fabales, f. Fabaceae. Climbing vine; very long pods harvested for edible seeds; white seeds with single black spot are black-eyed peas.</td>
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<tr>
<td>Vitis vinifera</td>
<td>Grape</td>
<td>k. Plantae, p. Anthophyta, c. Eudicotyledones, o. Rhamnales, f. Vitaceae. Woody vine producing a juicy berry; many cultivated varieties are used fresh or are processed for juice.</td>
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TIME LINE

c. 1800 B.C.E.  Hand pollination of date palms is mentioned in the Code of Hammurabi, king of Babylon.

c. 323-286 B.C.E.  In Athens the philosopher Theophrastus of Eresos, a student of Aristotle and Plato, publishes numerous works about plants, including the nine-volume *Peri phyton historias* (also known as *Historia plantarum*; translated into English as “Enquiry into Plants,” in *Enquiry into Plants and Minor Works on Odours and Weather Signs*, 1916), which describes the external and internal structures and habitats of plants, and the six-volume *Peri phyton aition* (also known as *De causis plantarum*; translated into English 1976-1990), discussing the physiology of edible and medicinal plants. He is regarded as the father of botany.

c. 235-150 B.C.E.  *De agri cultura* (*On Agriculture*, 1913), the earliest surviving treatise on farming, is written by the Roman statesman Marcus Porcius Cato (Cato the Elder).

c. 60-65 C.E.  Lucius Junius Moderatus Columella, a Roman citizen born in Spain, completes the twelve-volume *De re rustica* (*On rural matters*; translated in *Of Husbandry*, 1745) that lists plants and collects practical information about agriculture and *De arboribus* (“on trees,” also in *Of Husbandry*).

c. 77  The Roman philosopher Pliny the Elder publishes the encyclopedic *Historia naturalis* (*Natural History*, 1938-1963), of which books 12 through 27 collect information about agriculture, horticulture, and medicinal plants, information that is widely influential throughout antiquity and the Middle Ages.

c. 78  The Greek physician Pedanius Dioscorides publishes *De materia medica* (*The Greek Herbal of Dioscorides*, 1934), in which he instructs readers on the morphology and useful properties of six hundred plant species in the Mediterranean region. The book remains a basic text for physicians and botanists well into the modern era.

c. 1248  The German philosopher Albertus Magnus writes *De vegetabilibus et plantis* (on vegetables and plants), the most significant theoretical work on plants since Theophrastus.

1267  Roger Bacon of England argues that philosophers should use experimentation to investigate natural phenomena.

c. 1450  Nicholas of Cusa suggests that plants grow by absorbing water.

1530  Otto Brunfels’s *Herbarum vivae eicones* (living pictures of herbs) offers accurate drawings of plants that encourage the scientific study of them.

1539  Hieronymus Bock (Jerome Boch) groups plants by physical similarity, the first attempt at a strictly natural classification.

1542  The German Leonhard Fuchs makes the first modern attempt to establish a botanical terminology in *Historia stirpium* (the study of vegetation).

1551-1571  Konrad Gesner publishes the widely influential *Opera botanica* (botanical works) and *Historia plantarum* (the study of Plants).

1583  Italian botanist Andrea Cesalpino, in *De plantis libri* (the book of plants), introduces the first comprehensive classification of plants since that of Theophrastus, although it is not
widely accepted and is centered on the classical master’s two major classes, woody plants and herbs.

1620 In *Prodromus theatri botanici* (an introduction to the botanical realm), the German botanist Gaspard Bauhin carefully distinguishes between species and genera of plants and proposes a binomial nomenclature on that basis.

1621 The Oxford Physic Garden opens, the first botanical garden in England.

1626 Jardin des Plantes, a botanical garden, is established in Paris. It becomes a major biological research center.

1648 In *Ortus medicinae* (*Oriatrike: Or, Physick Refined*, 1662), Jan Baptista van Helmont describes experiments which suggest to him that plants derive their substance from water.

1665 Using a microscope, Robert Hooke distinguishes “little boxes,” or *cells*, in pieces of cork, a discovery that he describes in *Micrographia*, along with other anatomical and histological features never before seen.

1670 Káibara Ekiken writes *Yamato honzô* (the flora of Japan).

1676 English scientist Nehemiah Grew proposes an accurate explanation for the nature of ovules and pollen.

1683 Antoni van Leeuwenhoek of Holland discovers bacteria.

1686-1704 John Ray of England releases his three-volume *Historia plantarum* (*A Catalogue of Mr. Ray’s English Herbal*, 1713), which contains descriptions of all plants then known and is prefaced by a theoretical introduction that recognizes plants’ different sexes and adumbrates the distinction between monocotyledons and dicotyledons.

1694 Rudolph Jakob Camerarius, or Camerer, in *De sexu plantarum epistola* (the sex of plants), explains plant sexuality.

1701 Jethro Tull invents the first agricultural machine, a seed drill.

1716 The American clergyman Cotton Mather records the first unambiguous account of plant hybridization, concerning the red and blue kernels of *Zea mays*.

1727 Vilmorin-Andrieux et Cie, a seed-breeding company, is established, which later in the century develops the sugar beet.

1727 Stephen Hales concludes that part of a plant’s nourishment comes from the atmosphere.

1730 England’s Kew Royal Botanic Gardens opens. The facility soon becomes a leading center for collection and research.

1752 James Lind argues that fresh fruit prevents scurvy.

1753 In *Species plantarum* (the species of plants) Carolus Linnaeus of Sweden proposes the first truly natural classification of plants. Its binomial nomenclature, indicating genus and species, is based upon species’ sexual characteristics and soon becomes the leading system throughout the scientific world.

1754 Charles Bonnet is the first to note plant respiration when he finds that a leaf under water, if exposed to light, emits air bubbles.

1772 Joseph Priestley of England demonstrates that plants discharge oxygen.
1789 Bernhard and Antoine-Laurent de Jussieu propose the taxonomic concept of families to supplement the Linnaean system. The latter argues that all species within a family derive from a common prototype.

1794-1796 Erasmus Darwin (grandfather of Charles) publishes *Zoönomia: Or, The Laws of Organic Life*, in which he contends that environmental influences foster changes in species.

1796 Jan Ingenhousz finds that photosynthesis and plant respiration occur simultaneously and that respiration involves carbon dioxide.

1801 French scientist Jean-Baptiste Lamarck proposes that organisms evolve as disused characteristics are lost while characteristics in continuous use are preserved.

1801 Johnny Appleseed (John Chapman) starts on his quest to plant apple trees throughout the Ohio Valley.

1802 Charles François Brisseau de Mirbel deduces that plants are composed of continuous cellular membranous tissue.

1806 Louis-Nicolas Vauquelin and Pierre-Jean Robiquet derive asparagine from asparagus. It is the first amino acid to be isolated.

1810 Scottish botanist Robert Brown draws a distinction between angiosperms and gymnosperms.

1813 Augustin Pyramus de Candolle lays out the principles of comparative morphology in *Théorie élémentaire de la botanique* (elementary botanical theory).

1818 Thomas Nuttall publishes *The Genera of North American Plants*, an important study of New World flora.

1821 Giovanni Battista Amici of Italy explains the exact nature of sexual union in plants. His microscopic studies of pollen in the stigma of portulaca show that the pollen grains grow tubes that penetrate the tissue of the stigma.

1831 Robert Brown identifies a rounded core in most cells that is denser than the surrounding medium. He dubs this core the nucleus.

1837 Henri Dutrochet finds that chlorophyll must be present for photosynthesis to occur.

1838 In Germany botanist Matthias Jakob Schleiden and zoologist Theodor Schwann advance the cell theory, which holds that for all living organisms, plant or animal, the cell is the basic structural unit and that growth is the proliferation of cells.

1839 Hugo von Mohl describes details of mitosis in plants and recognizes that the phenomenon is common in root tips and terminal buds.

1840 Justus von Liebig recognizes that plants produce organic compounds with atmospheric carbon dioxide and nitrogenous compounds with chemicals taken from the soil.

1843 John Lawes and Henry Gilbert open the Rothamsted Experimental Station in England, the first such purely agricultural research center.

1845 Karl Wilhelm von Nägeli demonstrates that cells in a plant organ grow from a progenitor “apical” cell.

1849 Wilhelm Hofmeister of Germany discovers that plant embryos develop in the embryo sac of the ovule.
1855 Alphonse de Candolle introduces the idea of competition between species to explain their geographic distribution in his monograph *Géographie botanique raisonnée*.

1859 In *On the Origin of Species by Means of Natural Selection*, Charles Darwin sets forth a theory of evolution based upon natural selection, citing examples of both plant and animal species. The book’s influence on botany is profound and lasting because it accounts for the great diversity of life.

1860 Alfred Russel Wallace, cofounder of the theory of natural selection, describes the biogeography of the Malay Archipelago, adding extensive evidence to Darwin’s in support of the theory of evolution.

1861 Anton de Bary founds mycology and modern plant pathology with his explanation of the means by which fungi parasitize plants and animals and his description of the sexual organs of fungi.

1862-1883 English taxonomists George Bentham and Joseph Dalton Hooker publish the seven-volume *Genera plantarum* (genera of plants), which proposes relationships among species that become widely accepted.

1863 French scientist Louis Pasteur invents a process to inactivate wine-souring microbes with heat. The process becomes known as pasteurization.

1866 Gregor Mendel publishes an article detailing his experiments with peas, laying out the laws governing how physical traits pass from one generation to the next. Mendel argues that traits behave as units, which he calls inheritance “factors.” His article goes largely unread until biologists rediscover it in 1900.

1866 Ernst Haeckel introduces the word “ecology” to denote the interactions of living organisms among one another and with their physical environment.

1879 During investigation of apple and pear blight, Thomas Jonathan Burrill and Joseph Charles Arthur demonstrate that some plant diseases are caused by bacteria.

1887-1899 German botanist Adolf Engler issues the multi-volume *Die natürlichen Pflanzenfamilien* (the natural plant families), an encyclopedic work of great influence for its survey of the plant kingdom based upon evolutionary principles.

1893 Liberty Hyde Bailey releases the first detailed study of plants grown under artificial lighting and later edits *Cyclopedia of American Horticulture* (1900-1902) and *Cyclopedia of American Agriculture* (1907-1909).

1898 Charles Reid Barnes coins the term “photosynthesis.”

1898 Sergey Gavrilovich Navashin notes double fertilization in plants.

1904 In a discovery with revolutionary importance to agriculture, Fritz Haber devises an efficient method for producing artificial nitrogen-bearing fertilizers by combining atmospheric with nitrogen in ammonia. In 1918 he is awarded the Nobel Prize in Chemistry for the achievement.

1905 Frederick Frost Blackman reveals that photosynthesis involves several processes. The rate of each is controlled by several possible parameters.

1905 The “factors” that Gregor Mendel believed responsible for the inheritance of physical traits from one generation to the next are found to be genes.
1905 Rowland Harry Biffen, an English researcher, demonstrates that resistance to rust fungus in one type of wheat can be heritable, beginning the scientific development of disease-resistant crop varieties.

1906 Mikhail Semenovich Tsvet introduces the technique of chromatography, which gets its name from its usefulness in separating plant pigments.

1906 Richard M. Willstätter publishes the first of a series of papers establishing that two types of chlorophyll are involved in photosynthesis and describing methods for extracting plant pigments, such as carotenoids and anthocyanins. In 1915 he receives the Nobel Prize in Chemistry for the work.

1909 Rollins Adams Emerson detects multiple allelomorphism, variations in the forms of genes, in corn and beans.

1910 P. Boysen-Jensen demonstrates that plants are phototropic (move toward light) because of the presence of auxins, hormones that transmit the growth response.

1911 Andrew Ellicott Douglass establishes a method of dating trees and analyzing ancient environmental conditions by examining tree rings. He calls the technique dendrochronology.

1914 George Harrison Shull elucidates heterosis, or hybrid vigor. Inbred strains of plants that have inferior characteristics, when crossed, can produce a new strain with far more yield and general hardiness than either parental line.

1914 George Washington Carver makes public the first fruits of his extensive research into the practical uses of peanuts and other plants.

1915 *The Mechanisms of Mendelian Heredity*, by Thomas Hunt Morgan, Calvin Bridges, and Alfred Sturtevant, confirms the chromosomal theory of Mendelian heredity. For his work in experimental evolutionary biology, Morgan receives the 1933 Nobel Prize in Physiology or Medicine.

1920 Wightman Wells Garner and Harry Ardell Allard discover the phenomenon of photoperiodism in the growth and reproduction of plants.

1922 Otto Warburg devises what becomes the standard tool for measuring metabolism in plants as he monitors the efficiency with which photosynthesis uses light energy. He wins the 1931 Nobel Prize in Physiology or Medicine but the German government does not allow him to accept it.

1923 Thorsten Ludvig Thunberg correctly analyzes photosynthesis as an oxidation-reduction reaction: Carbon dioxide is reduced as water is oxidized.

1924 Ralph Erskine Cleland solves a puzzle involving a peculiar genetic inheritance in *Oenothera lamarckiana*, which produced only heterozygous offspring, by showing that some of its chromosomes form into rings, which are lethal if paired in homozygous offspring.

1925 Roy E. Clausen and Thomas H. Goodspeed provide experimental evidence that species differentiation involves polyploidy, an excess of chromosomes.

1925 Artturi Ilmari Virtanen of Finland develops a method for preserving green fodder by controlling the pH level, for which he is awarded the 1945 Nobel Prize in Chemistry.

1926 Working with jack beans, James Batcheller Sumner becomes the first scientist to isolate enzymes in a pure state and to demonstrate that they are proteins. He receives the 1946 Nobel Prize in Chemistry for his efforts.
1926 Nikolai I. Vavilov publishes *Tsentry proiskhozhdeniia kul’turnykh rastenii* (Studies on the Origin of Cultivated Plants, 1926), in which he expounds an influential theory accounting for the genetic variation and geographical distribution of crops since ancient times.

1930 Cornelis Bernardus van Niel points out that the photosynthetic processes of bacteria and green plants are similar.

1930 While investigating mutation rates in maize, Lewis J. Stadler learns that genes mutate at greatly different rates.

1931 Paul Karrer becomes the first person to determine the chemical structure of a vitamin during his studies of carotene and vitamin A.

1931 During studies of *Zea mays*, Barbara McClintock realizes that chromosomes exchange “transposable elements” of deoxyribonucleic acid (DNA) larger than genes. Discovery of this crossover effect wins her the 1983 Nobel Prize in Physiology or Medicine.

1933 Walter Norman Haworth of England defines the chemical structure of vitamin C (extracted from oranges and cabbage), shows it to be a cure for scurvy, and later artificially synthesizes it. For this work he shares the 1937 Nobel Prize in Chemistry with Paul Karrer of Switzerland.

1934 Wendell Meredith Stanley isolates the tobacco mosaic virus, which in contradiction to earlier theories, proves to be a large, complex protein. In 1946 he shares the Nobel Prize in Chemistry for the discovery.

1935 Arthur Tansley propounds his ideas about the natural interplay among the community of organisms and their environment—that is, the ecosystem.

1937 Albert Francis Blakeslee and George S. Avery demonstrate that environmental chemicals can cause alterations in chromosome structure when they use the alkaloid poison colchicine to produce polyploidy in plant cells.

1939 Samuel Ruben, William Hassid, and Marten Kamen are the first plant science experimenters to employ radioactive isotope tracers, which they use to study photosynthesis.

1940 Paul Hermann Müller of Switzerland synthesizes dichloro-diphenyl-trichlorethane (DDT), which first proves a boon to agriculture as a pesticide and then becomes the *cause célèbre* of the popular movement to ban pesticides because of their destructive effect on animals and people. In 1948 Müller wins the Nobel Prize in Physiology or Medicine for his work.

1940 Willard Libby realizes that the radioactive decay of carbon 14 absorbed by living matter provides a means for establishing the age of long-dead organisms. His carbon 14 dating method, developed five years later, earns him the Nobel Prize in Chemistry in 1960.

1941 Samuel Ruben, Martin Kamen, Merle Randall, and James L. Hyde announce that oxygen molecules produced during photosynthesis are the byproduct of the decomposition of water.

1941 While investigating variant strains of pink bread mold (*Neurospora crassa*), George Wells Beadle and Edward L. Tatum show that specific genes are responsible for different enzymes involved in growth processes—called the “one gene, one enzyme” phenomenon.

1951 Examining the adenosine triphosphate (ATP) of plant cells, Alexander Robertus Todd deciphers the chemical structure of the nucleic acids composing deoxyribonucleic acid (DNA). He wins the 1957 Nobel Prize in Chemistry for the achievement.
1953 Englishman Francis Crick and American James Watson define the three-dimensional structure of deoxyribonucleic acid (DNA), which enables botanists to study the coding of genetic information and to analyze inheritance from a biochemical perspective.

1954 Daniel Arnon discovers that chloroplasts can photosynthesize even when removed from cells.

1957 Melvin Calvin publishes “The Path of Carbon in Photosynthesis,” in which he describes the second of the two major cycles of photosynthesis, during which atmospheric carbon dioxide is fixed and reduced into carbohydrates in plant tissue. Named the Calvin cycle in his honor, the discovery brings him the 1961 Nobel Prize in Chemistry.

1957 Tree-ring analysis shows the bristlecone pine ($\textit{Pinus aristata}$), which grow in California’s White Mountains, to be the longest-lived tree species. Some specimens are more than four thousand years old.

1959 Sterling Hendricks isolates phytochrome, a key enzyme in flowering.

1960 Robert Burns Woodward synthesizes the green plant pigment chlorophyll. For this and synthesis of other valuable compounds, including quinine, Woodward is awarded the Nobel Prize in Chemistry in 1965.

1961 Peter D. Mitchell outlines his chemiosmotic hypothesis, which describes how cells derive energy by oxidizing organic molecules in order to synthesize adenosine triphosphate (ATP). For his work, Mitchell receives the 1978 Nobel Prize in Chemistry.

1962 Rachel Carson publishes $\textit{Silent Spring}$, a scientific indictment of the environmental hazards posed by commercial pesticides. The book inspires the modern environmental movement.

1967 A. E. Porsild succeeds in germinating ten-thousand-year-old Arctic lupine seeds found in Yukon territory. The mature plants turn out to be identical with the modern species.

1970 Norman Borlaug wins the Nobel Peace Prize for his work in developing high-yield strains of rice and wheat.

1983 Scientists develop the first transgenic plant. It is a species of tobacco resistant to antibiotics.

1984 Johann Deisenhofer of Germany publishes a paper describing the complete structure of the photosynthetic reaction center of a bacterium, which he analyzed by X-ray crystallography. This work earns him the 1988 Nobel Prize in Chemistry.

1994 Flavr Savr tomato, produced by the American biotechnology firm Calgene Corporation, is the first genetically engineered food to reach the marketplace.

1996 In its first report on biodiversity, the United Nations claims that 26,100 plants face extinction and that the overall extinction rate is fifty to one hundred times higher because of human impact on the environment.

1998 Soil fungi that are symbiotic with plant roots are shown to be important to diversity and productivity in plant communities.

1999 Laboratory tests suggest that the pollen of corn bioengineered to release the pesticide $\textit{Bacillus thuringiensis}$ ($\textit{B.t.}$) endangers monarch butterfly caterpillars. Although later evidence calls the finding into question, it prompts controversy over the safety of transgenic plants.
2000 More than two-thirds of the processed foods in U.S. markets contain genetically modified ingredients, primarily soybeans or corn.

2000 The environmental organization Friends of the Earth reveals that StarLink, a genetically engineered corn variety meant only for animal fodder, has contaminated the human food supply, setting off a public backlash to genetic engineering of food plants.

Jan. 28, 2000 At a meeting in Montreal, Canada, the United Nations Convention on Biological Diversity approves the Cartegena Protocol on Biosafety, which sets the criterion internationally for patenting genetically modified organisms, including agricultural products.

Dec. 13, 2000 At a press conference, a team of more than three hundred scientists from throughout the world announce that they have sequenced the genome of a plant for the first time. The plant is the model organism Arabidopsis thaliana.

Nov. 2001 Scientists report that genetic material from transgenic corn mysteriously has turned up in the genome of native corn species near Oaxaca, Mexico. Mexico banned transgenic crops three years earlier, and the closest known crop was located beyond the range of wind-borne pollen.

Roger Smith
GLOSSARY

abscisic acid (ABA): A hormone associated with regulation of growth and rapid closure of stomata, produced in root caps and mature leaves.

abscission: Separation of leaves and fruits from stems that occurs when a layer of cells cuts off water supply to the leaf or fruit. Abscission occurs in the autumn in moist, temperate climates and during drought in deserts, causing leaves and fruits to drop.

abscission zone: Region in a leaf petiole or the stalk of a fruit where the abscission layer forms.

absorption spectrum: That portion of the sun’s wavelengths that a plant is able to use in photosynthesis.

acaulescent: Lacking an aerial stem.

accessory fruit: Fruits develop from the matured ovary of a flower. An accessory fruit includes the matured ovary and other parts of the flower as well, such as the receptacle in apples.

accessory pigment: These pigments, including carotenes and xanthophylls, absorb light energy and pass it to chlorophyll during photosynthesis.

acetyl coenzyme A: Two-carbon compound formed during the breakdown of glucose in cell respiration. It combines with an existing four-carbon compound to begin the Krebs cycle.

acme: Type of single-seeded fruit which is dry at maturity. The outer layer is formed by the fusion of the seed coat and the fruit wall, as in wheat grain or sunflower seeds.

acropetal: Pattern in which development occurs from the base upward. The development of veins into leaves as they form is acropetal.

actin filaments: Component of a cell’s cytoskeleton that gives a cell shape and allows communication between the cell membrane and the nucleus.

actinomorphic flower: Flower that is radially symmetrical when viewed from above. Examples include roses, tulips, and daffodils.

action spectrum: Measure of the ability of a type of pigment to use a particular wavelength of light in photosynthesis.

active site: That specialized region of an enzyme into which the substrate fits as tightly as a key in a lock. Alteration of the active site prevents the enzyme from being functional.

active transport: Movement of substances into or out of a cell across the cell membrane from a region of low concentration of the substance to a region of high concentration. Expenditure of cellular energy is required for this to happen.

acuminate: Leaf that ends in a long, tapered point.

adaptation: Alteration in a plant’s anatomy or physiology that improves its ability to survive in a particular environment. Adaptations are the result of permanent genetic change.

adaptive radiation: Evolution of multiple related species from one ancestral species. The different species which evolve can live in proximity to one another because they occupy different niches.

adenosine triphosphate (ATP): Chemical which is the “energy currency” of cells. This molecule can provide energy for all sorts of cellular processes and is regenerated during cellular respiration and photosynthesis. Energy is stored in an easily broken covalent bond that attaches a phosphate ion to the molecule adenosine diphosphate (ADP).

adventitious root: Root that develops from some plant organ other than another root, such as a stem or leaf. For example, adventitious roots form on stem cuttings of philodendron placed in water and from the stems of corn plants, where they are known as prop roots.

adventitious shoot: Shoot that develops from some plant organ other than another shoot, such as a root or leaf. African violet leaf stalks, when placed in water, develop both adventitious shoots and adventitious roots.

aeciospores: In the complex life cycle of rust fungi, these spores infect another host plant. In the disease black stem rust of wheat, aeciospores are produced on the alternate host, American barberry, and when released infect young wheat plants.

aecium: The usually flat and colored lesion on a host plant in which aeciospores are produced.
aerial root: Root which grows exposed to the air rather than growing in soil or water. Plants with aerial roots are normally limited to moist environments, such as tropical rain forests, where many kinds of orchids, bromeliads, and ferns grow, with their roots exposed, on tree trunks and limbs.
aerobes: Organisms that require oxygen in order to produce adequate amounts of energy during cellular respiration.
aerobic: Describes organisms which need oxygen for the maximum release of energy from their food. See also anaerobes.
aethalium: Structure formed from the fusion of several sporangia, found in some slime molds.
after-ripening: Period of time following the ripening of seeds, during which physiological changes must occur before the seed is able to germinate.
aggregate fruit: Fruit formed from a flower that has more than one pistil; each pistil develops into a tiny fruit. Raspberries are examples of aggregate fruits.
agricultural revolution: Marked the transition by humans from hunting and gathering all their food to domesticating plants for food.
akinetes: Specialized, thick-walled resting spores that form in the filaments of cyanobacteria. These permit survival during periods of cold or drought.
albuminous cell: Specialized companion cells found in the phloem of gymnosperms.
alcohol fermentation: Cellular process in plants, yeasts, and bacteria whereby sugars are converted to alcohol and carbon dioxide in an environment low in oxygen.
alveolone: The outermost layer of tissue under the seed coat of a monocot seed, such as that of corn or barley.
alg: Carbohydrate produced by certain types of brown algae, used to prevent crystal formation in foods, such as ice cream and jelly beans.
alkaloids: Nitrogen-containing chemicals produced by some plants which are used as hallucinogens or medicines. Examples include nicotine, caffeine, morphine, and cocaine. Plants produce these as protection against being eaten by herbivores.
allele: Different forms of a particular gene. Any individual possesses two alleles for every gene pair in its cells. These alleles may be the same or may be different.
allelopathy: Observed phenomenon in which plants produce and release chemicals into the air or soil that inhibit the growth of other plants, either of the same or different species.
allopatric speciation: Evolution of two new species when the two evolving groups are separated from each other.
allopolyploidy: Formation of a new species resulting from the mating of two different species. Normally such a mating produces a sterile interspecific hybrid. If the total number of chromosomes is accidentally doubled, then the resulting plant is fertile but reproductively isolated from the two parent species.
allosteric enzymes: Enzymes that change shape to expose the active site. Many inactive enzymes exist in one shape; the binding of ATP alters the shape of these enzymes into their active forms.
alternate: Arrangement of leaves on a stem in which only one leaf is found at each node.
ation of generations: Plant sexual reproductive cycle in which a diploid generation that produces spores by meiotic division (sporophyte phase) follows a haploid generation (gametophyte phase) that produces gametes.
amino acids: Simple nitrogen-containing molecules which are the building blocks of proteins. Plants are able to produce all the essential amino acids from carbohydrates formed as a result of photosynthesis.
ammonification: The breakdown of protein during decomposition, producing ammonium ions which are then available for reuse.
amabolism: That part of all the metabolic reactions in a cell which results in the building of larger molecules from smaller ones. Construction of proteins from amino acids is one example of an anabolic process.
an aerobes: Organisms, including many bacteria, which live where oxygen is in short supply and do not use the oxygen-requiring pathways of cell respiration.
anerobic pathways: Series of metabolic reactions that break down complex food molecules for energy release without the involvement of oxygen gas. Typically, these pathways are not efficient ways to release energy, and organisms that depend solely on anaerobic pathways do not become very large.
analogy: Similarity in function among parts of plants.
anaphase: Stage in cell division during which time the sister chromatids separate and become two identical groups of chromosomes. In the specialized anaphase I of meiosis, homologous chromosomes separate to reduce the chromosome number for sexual reproduction.

androecium: Whorl of stamens of a flower. Literally means “house of males.”

aneuploidy: Literally, “not true sets.” Condition in which a cell or individual is missing one or more chromosomes or has one or more extra chromosomes. Does not include the condition in which all chromosomes are present in extra numbers.

angiosperm: A flowering plant. Angiosperms have flowers as their reproductive organs and produce their seeds inside fruits that develop from the ovary of the flower.

annual: Flowering plant which comes up from seeds every year after the parent plant dies in the autumn.

annual ring: In woody plants, the xylem that is added during a growing season by activity of the cambium. Annual rings are visible because the xylem added in the spring has larger diameter vessels than the xylem which grows in the summer. Addition of annual rings causes a tree to increase in circumference.

annulus: Ring of weak cells that rupture during the life cycle of a plant. The annulus in a fern sporangium breaks to allow the release of fern spores.

antenna complex: Photosynthetic light-gathering apparatus of chloroplasts. A number of pigment molecules are arranged in a complex which allows them to collect light energy and direct it to one central chlorophyll molecule.

anther: Part of the stamen of a flower. In many flowers the anther appears as a swollen area at the free end of a stalk (filament). Pollen is produced inside the anther.

antheridium (pl. antheridia): Male reproductive structure that produces sperm in algae, mosses, and lower vascular plants.

anthocyanin: Red or purple pigment produced in some flowers, fruit, and leaves. It collects in the central vacuole of plant cells and can be easily seen under a microscope in the epidermis of red onions.

anticodon: Series of three nucleotides in the structure of a transfer RNA that enable the RNA to position an amino acid in the correct location within a protein. The anticodon is complementary to a codon contained in messenger RNA.

antipodals: Three of the eight cells of an angiosperm embryo sac. These cells are furthest from the end of the sac at which the egg can be found. They usually degenerate following fertilization of the egg.

apical bud: Structure at the tip of a stem in which an apical meristem is enclosed in a protective layer of scales.

apical dominance: Production of hormones by the terminal (apical) bud on a branch that keep the lower lateral buds from growing into side shoots. Apical dominance leads to slender, unbranched stems.

apical meristem: Growing point within an apical bud where the cell division occurs that leads to the elongation of stems and formation of leaves.

apressed: Closely pressed against another object; a lateral bud that grows close to a stem is appressed.

apomixis: Reproduction that occurs without fertilization.

apoplast: In a stem or root cortex, that region which is outside the cell membranes. It includes the space occupied by the cell wall and any open spaces between cells.

apoplastic loading: Movement of substances into phloem tissue from the apoplast.

apoplastic pathway: Route taken by substances as they move through the apoplast.

apoptosis: Programmed cell death, sometimes called cell suicide, often caused by stresses within the cell. Cells dying in this manner undergo a predictable series of events that leave neighboring cells in a healthy condition. Apoptosis often occurs during development to sculpt the shape of leaves and flowers.

arbuscule: A branched organ which is tree-shaped in appearance.

archegonium (pl. archegonia): Female reproductive structure in which the egg is produced. Found in algae, mosses, lower vascular plants, and gymnosperms. Archegonia have a jacket of sterile cells surrounding the egg.

Arctic tundra: Treeless biome of very cold climates near to and north of the Arctic Circle, in which the predominant plants are low-growing, perennial woody plants and grasses. Lichens and mosses may also be common.

aril: Fleshy outer layer of the seed coat. These “yew
berries” look superficially like fruits but do not develop from a floral ovary.

**artificial selection**: Choices made by plant breeders to produce varieties of plants that have some desirable quality, such as improved yield, greater height, or an unusual flower color.

**artificial taxon**: A grouping of plants based on something other than evolutionary relationships. Grouping sunflowers, daffodils, and yellow roses because they are all yellow would be an example of an artificial taxon.

**ascogonium**: Female reproductive structure in an ascomycete fungus.

**ascospores**: Eight spores produced by meiosis during the reproduction of ascomycete fungi. The spores are enclosed in a tiny sac and are often arranged side by side in a linear fashion.

**ascus (pl. ascii)**: Small sac common to the reproduction of ascomycete fungi. The ascospores develop within the ascus.

**assimilate stream**: Movement of a substance along a pathway from where it is manufactured to a location where it is being used. For example, sucrose is manufactured in leaves and moves via an assimilate stream to a developing fruit.

**ATP**: See adenosine triphosphate.

**ATP synthase**: Enzyme, found in membranes, necessary for the formation of ATP.

**ATPases**: Enzymes that remove the terminal phosphate from a molecule of ATP and usually transfer that phosphate to some other molecule in the process of phosphorylation.

**autoecious**: Fungi that spend their entire life cycle as parasites on a single host.

**autopolyploidy**: Formation of a new species by the doubling of chromosomes of a single existing species. Many related species of plants within a genus have been found to result from repeated occurrences of autopolyploidy.

**autotroph**: Organism that can make its own food from simple substances. Green plants and algae that make carbohydrates from carbon dioxide and water are the best-known autotrophs, although autotrophic bacteria exist which build food molecules from other simple molecules.

**auxin**: Plant hormone that regulates growth by causing cell elongation.

**awn**: A slender, usually terminal, bristle. The flowers of many kinds of grasses have awns.

**axial system**: Combination of the cells, other than the cells of rays, in secondary xylem and phloem and the initials in the vascular cambium that produce those cells.

**axil**: Acute angle formed between a stem and a leaf on that stem. In woody plants, a lateral axillary bud will be located at the axil.

**axillary bud**: Bud located at the base of a leaf, where the leaf petiole joins the stem. This bud contains a meristem that may in time grow into a new branch.

**axillary bud primordium**: Very young developing axillary bud found in an apical meristem.

**bacilli (sing. bacillus)**: Rod-shaped bacteria.

**bacterial chromosome**: Single circular piece of DNA that contains the hereditary information for a bacterium. This chromosome must replicate prior to bacterial cell division.

**bacteriophage**: Virus that infects bacteria. The virus uses the bacterial cell machinery to produce and assemble more viral particles. The bacterial cell then ruptures, spilling the new particles, which can then infect neighboring bacteria.

**bark**: Layers of cork cells and phloem covering the outside of a woody plant. The cork cells are dead at maturity. They reduce evaporation from stems and roots and help protect the living tissue underneath from physical damage.

**basidiospores**: Either four or eight spores produced by meiosis in Basidiomycete fungi. The spores are borne on the outside of a basidium.

**basidium (pl. basidia)**: A club-shaped reproductive structure common to Basidiomycete fungi on which the spores are produced. Basidia form layers on the surface of the gills of mushrooms.

**basipetal**: Pattern of development in which maturation occurs from the tip downward.

**bearded**: Having long or stiff hairs. An example are the bearded petals of many irises.

**berries**: Fleshy fruit in which the seeds do not have a hard or stony seed coat. Tomatoes, cucumbers, and blueberries are examples.

**betacyanins**: Red pigments of beets and certain kinds of flowers; similar to anthocyanins, except betacyanins contain nitrogen and do not change color with changes in acidity or alkalinity.

**biennial**: Flowering plant that requires two years to flower and set seed. A typical biennial plant forms a rosette of leaves during its first growing season. It lies dormant over the winter, then makes a flower stalk during its second growing season. Carrots are biennial plants.
**binary fission**: Reproduction of one-celled organisms in which the original cell divides into two cells of approximately the same size and shape.

**binomial system of nomenclature**: Accepted method for naming new plants in which every plant receives two Latin names, a genus name (listed first) and a species name. Sugar maple trees are named *Acer saccharum* under this system. Species of the same genus are considered to be more closely related than species in different genera.

**biogeochemical cycles**: Movement of elements or water through both living and nonliving parts of an ecosystem. Carbon as carbon dioxide is made into carbohydrate during photosynthesis and released through decay to the nonliving atmosphere, from which it can later be reused in photosynthesis.

**biological clock**: Internal mechanism by which plants are given a cue to perform activities at a particular time.

**biomass**: Total amount of living plants and animals found in a particular location at a particular time.

**biome**: Large-scale type of ecosystem that is characterized by the appearance of its vegetation, which is similar throughout, and in which live similar animals. The grassland biome and the deciduous forest biome are two examples found in North America.

**biosphere**: That part of the world where living organisms are found.

**biotechnology**: Combination of techniques whereby humans are able to alter permanently the genetic makeup of organisms. Includes the industrial application of these techniques.

**bivalent**: Homologous chromosomes that have paired up during the early part of meiosis; also called a tetrad.

**blade**: Expanded, usually flat portion of a leaf.

**bolting**: Process in which a stalk bearing flowers rapidly grows from a plant that had consisted of a rosette of leaves attached to its stem.

**bottleneck effect**: In evolution, the reduction in size of a population causing a major loss of genetic variation. If the population size later expands, the new larger population will be genetically uniform and may lack the ability to survive in a changing climate.

**bract**: Modified leaf associated with a flower or an inflorescence. The red-colored structures of poinsettias and the white-colored structures of dogwood are examples of bracts.

**branch roots**: Roots which develop from the inner part of a root and which grow outward to lateral roots.

**branch trace**: Strand of xylem and phloem which diverges from the conducting tissue of the main stem and enters a branch.

**bud primordium**: See axillary bud primordium.

**bud scales**: Highly modified leaves that cover the apical meristem of terminal and axillary buds. These are especially important as protection in the winter.

**bulb**: Modified stem that grows underground. The leaves of the stem are fleshy because they contain stored food that will be used by the plant when it begins its next period of growth. Onions are an example.

**bulk flow**: Movement of a liquid, for example sap in phloem, in which all molecules move in the same direction under the influence of a driving force, such as gravity or difference in water potential.

**bulliform cells**: Special cells found near the base of leaves of grasses. These cells are large, and when water flows out of them the leaf curls, thereby reducing surface area for evaporation.

**bundle scar**: Located within a leaf scar, these scars mark the locations of veins.

**bundle sheath cell**: One of the cells that make up a bundle sheath.

**bundle sheath extension**: In some leaves a riblike portion of a bundle sheath that extends outward toward the surface of a leaf, giving added support and strength.

**bundle sheaths**: Cylinders of cells that surround the veins of leaves and vascular bundles of stems. The cells may be fiberlike and provide support or may be filled with chloroplasts and help in the process of photosynthesis as in the case of C₄ plants.

**buttress root**: Winglike thickening which develops on the trunk of a tree at the base of a root. Most common among trees that grow in wet, and thus soft, soils.

**C₃ plants**: Plants whose system of photosynthesis produces a three-carbon compound as the first identified compound after the uptake of carbon dioxide during the light-independent reactions.

**C₄ plants**: Plants whose system of photosynthesis produces a four-carbon compound as the first
identified compound after the uptake of carbon dioxide during the light-independent reactions. C₄ photosynthesis is distinguished from CAM photosynthesis (see below) because C₄ occurs during the day and CAM occurs during the night. C₄ plants are especially adapted to hot, dry climates. Corn is an example.

calloose: Type of carbohydrate that lines the pores of the sieve plates of sieve tube elements in phloem.
callus: Group of undifferentiated plant cells. In tissue culture, a callus is first grown from pith or other parenchyma, and then it is treated to induce the formation of roots and stems.

Calvin cycle (three-carbon pathway): Complex set of biochemical reactions of photosynthesis whereby the sugar glucose is synthesized from carbon dioxide and existing precursor sugars. Also known as the Calvin-Benson cycle.
calytra: Fibrous or leaflike cap cover over the top of a sporangium of a moss plant. The calytra grows up from the gametophyte and thus is haploid, unlike the sporangium, whose walls are diploid.
calyx: Outermost and lowest whorl of a flower, composed of the sepals.

CAM plants: Crassulacean acid metabolism plants of the desert, which are able to take in carbon dioxide during the night and store it as an acid, and then use the carbon dioxide in the light independent reactions during the day, when sunlight is available. Cacti are CAM plants.
cambial zone: That region of a stem or root in which is found the cambium.
cambium: One-cell-thick cylinder of cells that separates xylem and phloem in stems and roots and which divides to form new xylem and phloem, thereby leading to growth in diameter.
canopy: Uppermost portion of a forest in which are found the leafy branches of the trees.
capillary water: Water which is held in surface films and in small spaces of the soil against the pull of gravity.
capsid: Protein coat that encloses the DNA or RNA of a virus and enables it to attach to a host cell.
capsule: Sporangium of bryophytes; also a type of dry fruit that splits open upon maturity.
carbohydrates: Large class of organic molecules containing carbon, hydrogen, and oxygen and in which the ratio of hydrogen to oxygen is two to one, the same as in a molecule of water. Sugars, starch, and cellulose are examples.

carbon cycle: Biogeochemical cycle of the element carbon.
carbon fixation (CO₂): Process by which carbon dioxide is made into glucose during photosynthesis. This occurs during the part of photosynthesis called the Calvin cycle.
carnivorous plant: Plant that traps insects and digests them. These plants usually live in nitrogen-poor habitats and use the insect proteins to supplement their nitrogen intake.
carotene: Orange or orange-red pigments of plants. One of the groups of the carotenoids.
carotenoid: Group of pigments in green plants which can absorb light and pass the energy to chlorophyll. These yellow and orange pigments enable a plant to tap into wavelengths of light.
carpel: This structure is the basic component of the pistil in a flower. A pistil may be formed from one or more carpels, which are highly modified leaves.
carposporophyte: One of the three stages in the complex life cycle of a red alga.
carrier proteins: Proteins, often membrane-bound, that are responsible for the transport of materials across a cell membrane. Cellular energy is necessary for these proteins to function.
caryopsis: Dry, indehiscent fruit that contains only one seed and in which the seed coat is fused to the dry fruit wall. Typical of the grasses.
catabolism: Set of metabolic reactions that result in complex molecules being degraded to simpler ones. See also anabolism.
catalyst: Molecule or ion that lowers the energy required for a reaction to occur. In plant cells, most catalysts are enzymes.
cation exchange: Displacement of one type of positive ion (cation) from the surface of a soil particle because it has been replaced by a different cation, often a hydrogen ion.
catkin: Soft, furry, and flexible inflorescence in which many small flowers are attached on one stalk. Birch trees and willow trees are two examples of plants that produce flowers in catkins.
cauclusent: Possessing an aboveground stem.
cell cycle: The series of events through which a cell progresses, from the time it is formed by cell division until it has completed mitosis and formed two new cells.
cell plate: First cellular structure which forms following mitosis. The cell plate partitions the cytoplasm for the new cells. It becomes incorporated in the cell walls of the new cells.
cell sap: Cytoplasm that fills in the spaces between adjacent cell organelles.
cell wall: Rigid, nonliving structure, often made of cellulose and a matrix, that surrounds the membrane and contents of plant cells.
cells: Basic building blocks of living organisms. In multicellular plants, many different kinds of cells exist, which have different appearances and different functions.
cellular respiration: Breakdown of glucose and other small molecules within cells to release energy. Some of the energy released in this way is trapped in ATP.
cellulose: Polymer of glucose that is not easily dissolved in water. Cotton, linen, and paper have very high cellulose content.
cellulose synthase: Enzyme responsible for the construction of cellulose from smaller molecules.
central cell: In an archegonium, the precursor of the egg.
centric: Refers to the location of the centromere on a chromosome with respect to the rest of the chromosome. Usually combined with a prefix, as metacentric. Also one of the two categories of diatoms; these are circular when viewed from above.
centromere: Gene-poor region on a chromosome where the kinetochore forms to attach chromosomes to the spindle during cell division.
chalazal: The end of an embryo sac away from the micropyle.
channel proteins: Membrane-bound proteins that form pores or channels through which ions or small molecules can pass into or out of cells.
chaparral: Biome found along the coast of Southern California, characterized by short trees with leathery leaves, shrubs, and open grassy areas.
chelation: Process by which metal ions are taken out of solution by a molecule known as a chelating agent.
chemiosmotic coupling: The process in which energy released from serial oxidation-reduction reactions during photosynthesis or cell respiration is captured in the bonds of an ATP molecule.
chemosynthetic autotroph: Organisms (usually bacteria) that make complex food molecules from simpler molecules using energy of chemcal reactions rather than light energy used by photosynthetic autotrophs.
chiasma: X-shaped figures observed in chromosomes during the first meiotic division. Chromatids of homologous chromosomes lie across each other and may swap pieces. Formation of chiasma is necessary for the proper separation of homologous chromosomes.
chlorophyll: Green pigment found in plants and algae that captures light energy during the process of photosynthesis. Chlorophyll is similar in structure to animal hemoglobin, with magnesium replacing iron.
chloroplasts: Complex cell organelles found in the green parts of green plants and algae, where chlorophyll is located and where the photosynthetic reactions occur.
chlorosis: Bleaching of green plants when they have been deprived of light or adequate mineral nutrition.
chromatin: Combination of DNA and protein that composes a chromosome.
chromoplasts: Organelles of plant cells that contain pigments other than chlorophyll. Chromoplasts that develop in the skin and flesh of tomatoes make them red.
chromosome: Molecule of DNA wrapped around supporting proteins. Segments of the DNA are the genes on the chromosome.
chromosome mutations: Changes in chromosome number or structure from what is normal for the species. Plants can tolerate the addition of extra chromosomes or sets of chromosomes better than can animals.
chrysolaminarin: Polysaccharide found in the chloroplasts of yellow-green algae.
circadian rhythms: Observable cycles in a plant's physiology that take about twenty-four hours to complete.
clade: Group of organisms considered to be related because they all have one or more characteristics in common.
cladistics: System of describing evolutionary relationships in which only two groups, or clades, branch from each ancestral group. The more recently two clades diverged, the more characteristics they have in common and the closer they will appear in a cladistic diagram.
cladogram: Pictorial representation of the evolutionary relationship of different groups of organisms.
cladophyll: Leaflike segment of a stem in a cactus.
clay: Type of soil particle that is less than 0.002 micrometers in diameter and stays in suspension when mixed in water. Clay particles have negatively charged surfaces, which attract positively charged ions to them. Clay soils are fertile but do not drain well.
cleistogamy: The production of flowers that never open completely and are therefore required to be self-pollinated.
climacteric: During fruit ripening, the point at which the fruit is carrying on maximum respiration.
climax community: Group of plants that appear late in succession and are not replaced by plants of different species unless the climate changes or the area is disturbed, as by fire or cultivation.
cline: A graduated series of plants of the same species. Each plant or group of plants in the series has a slightly different physiology from the ones on each side. Clines typically develop where environmental factors change in a gradual way, such as from the bottom of a mountain to the top.
clonal propagation: Asexual reproduction, as by stem or leaf cuttings. Because no gametes are involved, the products of this reproduction are genetically identical to one another and to the plant that produced them.
close: A group of genetically identical plants derived from a single cell or individual, or one of the members of the group.
coated pits: Depressions in a cell membrane in which receptor molecules gather.
cocci (sing. coccus): Sphere-shaped bacteria.
codon: Three-nucleotide sequence in nucleic acid that specifies a particular amino acid in a protein.
coenocytic: Having multiple nuclei in a single cell.
coenzyme: Small molecule or ion that completes the structure of an enzyme. Many vitamins act as coenzymes.
coenzyme A: A sulfur-protein important in the breakdown of glucose and the release of energy.
ceoevolution: Simultaneous change through time of two species, such as a flower and its pollinating insect. Over a period of time, the two species become dependent on each other, so that one will not survive the disappearance of the other.
cofactor: A small inorganic molecule or ion necessary to complete the structure of an enzyme.
cohesion-tension (or cohesion-adhesion) theory: Explanation for the movement of water to the tops of tall trees. Interactions among water molecules cause them to stick together (cohesiveness). In the small tubes that form the xylem tissue of plants, the evaporation of water from the leaf ends of the tubes creates a pull (tension) that moves water up the xylem.
cold hardening: Physiological changes that prepare a plant to survive in winter temperatures. Loss of some water is one of the changes that occurs.
cold hardiness: Ability of a plant to withstand cold temperatures. Like other adaptations, cold hardiness is based on genetic variation.
collenchyma: Plant tissue with primary cell walls in which the corners of the cell walls are thicker than the rest of the wall. The “strings” found in celery are an example of collenchyma.
columella: Strand of sterile tissue located in the center of the sporangium of mosses and some fungi.
communities: Groups of plants and animals that live together in a particular set of environmental conditions.
companion cell: Nucleated nonconducting cell that is part of phloem tissue. The conducting cells (sieve tube elements) lack a nucleus when they are mature, and the companion cell directs their activities as well as function in loading of sugars into sieve tube elements for transport out of leaves.
competition: Condition created when two different organisms in a community vie for the same resource.
complementary DNA (cDNA): DNA produced from an RNA template by the action of RNA-dependent DNA polymerase, also known as reverse transcriptase.
complete flower: A flower that has sepals, petals, stamens, and pistil.
composite head: Inflorescence composed of many small flowers arranged to give the appearance of a single large flower. A daisy, member of the Compositae family, is an example.
compound leaf: Leaf in which the blade is composed of several small leaflets. Hickory, ash, and horse chestnut trees all have compound leaves.
concentration gradient: Gradual change through space of the concentration of a dissolved substance. The amount of the substance will be greatest at one end of the gradient and lowest at the other end.
conidia: Asexual reproductive spores produced by ascomycete fungi, such as powdery mildew.
conidiophore: Slender stalk of a hypha that produces conidia.
conifer: Woody plants with needlelike leaves. They form seeds in cones rather than in fruits, and their sperm do not have flagella.
coniferous forest: Large group of trees that are predominantly conifers. A pine forest and a spruce-fir forest are examples.
conjugation: Type of sexual reproduction that occurs in green algae such as Spirogyra and in certain kinds of fungi. Also, the transfer of genetic material from one bacterium to another through a cytoplasmic bridge.
contractile root: Root which contracts during development; that contraction causes the shoot to be shifted in position. Many bulb-forming plants have these.
contractile vacuole: Osmoregulatory structure in one-celled plants that collects excess water from the cell and squeezes it to the outside.
convergent evolution: Typified by two or more groups of organisms that appear superficially to be closely related. Closer inspection shows that they have both adapted to a particular set of environmental conditions but are only distantly related. Cacti and other succulents are an example.
coralline algae: Species of marine red algae that secrete calcium carbonate on their cell walls.
cordate: Heart-shaped leaves, such as the leaves of philodendron.
cork: Cells that are dead at maturity. They have suberin (a waterproofing substance) in their cell walls and cover the outside of a woody plant in many layers. Layers of cork form the outer bark.
cork cambium: Living cells directly below the layers of cork that undergo cell division to form new cork cells as the plant increases in diameter.
corm: Fleshy, underground stem of a perennial plant that stores food for the winter and can divide via asexual reproduction. A gladiolus corm is an example.
cormel: One of the subdivisions of a corm.
corolla: All the petals of a flower.
corona: Cup-shaped structure that sits on the petals of a daffodil flower.
cortex: Thin-walled parenchyma cells found under the epidermis of stems and roots. The cortex surrounds the vascular tissue.
corymb: Flat-topped inflorescence in which the outer flowers open first.
cotransport systems: Movement of negatively charged ions across a cell membrane, with simultaneous movement of protons in the opposite direction.
cotyledon: Component of a seed. In eudicot seeds, the cotyledons are the two fleshy halves of a seed, such as a peanut; they store food for the seed’s germination. In monocot seeds, the single cotyledon digests the food stored in the seed.
coupled reactions: Two reactions in which the occurrence of one is dependent on the occurrence of the other.
crassulacean acid metabolism: See CAM plants.
crista (pl. cistae): Fold(s) in the inner membrane of a mitochondrion resulting in increased surface area for cell respiration.
critical photoperiod: Specific day length necessary to produce flowers in long-day and short-day plants.
cross-pollination: Transfer of pollen from one flower of a species to a different flower of the same species.
crossing over: Exchange of genetic information between chromatids of homologous chromosomes. This occurs during early meiosis, when the chiasmata form.
crown: The branched, leafy part of a tree.
cultivar: Plant variety that has been bred for particular characteristics, such as variegated leaves or a particular flower color.
cuspidate: Possessing a stiff, sharp point.
cuticle: Waxy coat covering the outside of epidermal cells of leaves, stems, and fruit. The cuticle prevents excessive evaporation from these surfaces.
cutin: Waxlike substance that is the principal component of the cuticle; waxes are embedded in the cutin.
cyanobacteria: Photosynthetic prokaryotes that were once called blue-green algae.
cyclic photophosphorylation: Photosynthetic pathway in which the electrons from a chlorophyll molecule excited by light energy are raised to a higher energy level and then fall back to the same chlorophyll molecule, releasing the energy. The released energy is used to make a molecule of ATP.
cyme: Flat-topped inflorescence in which the central flowers open first.
cypsela: Type of dry, indehiscent fruit in which the seed coat is separate from the dry fruit wall. A sunflower seed is an example.
cytochromes: Electron acceptor molecules capable of repeated oxidation and reduction. Energy from electrons is released in small, controlled bursts as the electrons are passed from one cytochrome to another.
cytokinesis: Division of the cytoplasm following mitotic division of the nucleus.
cytokinin: Growth-promoting hormone that stimulates cell division.
cytology: The study of cells.
cytoplasm: General term for the contents of a cell inside of the cell membrane and outside of the nucleus.
cytoplasmic membrane: Lipid-protein membrane that surrounds the cytoplasm and selectively controls what substances enter and leave the cell.
cytoplasmic streaming: Continuous flow of cytoplasm and its organelles near the outer edges of a cell, probably under the control of microfilaments. Materials are distributed through the cell faster than would occur by diffusion alone.
cytoskeleton: Collective name for the filaments and microtubules that can be found throughout the cytoplasm. The cytoskeleton helps the cell maintain shape and is involved in signaling from the cell membrane to the nucleus.
cytosol: Liquid part of cytoplasm in which the organelles are located.
dampening-off: Fungal disease of seedlings and young plants. The stem appears to pinch in and die at a point just above the soil level.
daughter chromosome: One of the two chromosomes which form in anaphase of mitosis when two chromatids separate.
day-neutral plant: Plant whose flowering does not depend on a particular day length.
deciduous: Describes plants that lose their leaves in response to adverse environmental conditions, such as cold or drought. Maple trees and crown-of-thorns are examples.
deciduous tropical forest: Forests of tropical regions that shed their leaves during annual dry periods.
decomposers: Bacteria and fungi that break down dead organic matter. In the process, they obtain energy and facilitate the recycling of elements.
defoliant: Chemical that kills the leaves of trees.
dehiscent fruit: Fruit that splits open to release the seeds when they are ripe. A milkweed pod is an example.
dehydration synthesis: Common type of reaction resulting in the buildup of larger molecules from smaller ones. A bond is created between the two smaller molecules by the removal of a water molecule. This is also called a condensation reaction.
deletions: Loss of pieces of a chromosome. Deletions may encompass large sections of a chromosome or just a few genes.
denitrification: Process in which bacteria convert nitrogenous compounds in the soil to nitrogen gas.
dentate: Describes margin of a leaf that has coarse, sharp-pointed “teeth.”
deoxyribonucleic acid: See DNA.
desert: Biome that receives less than 10 inches of precipitation per year.
desmotubule: Tube made of membrane that runs through the center of a plasmodesma. The tube is believed to be an extension of the endoplasmic reticulum and connects the membrane systems of two adjacent cells.
determinate: Plant that exhibits determinate growth. Determinate plants are short and bushy.
determinate growth: Growth pattern in which the terminal bud does not grow indefinitely, allowing extensive growth of lateral buds.
deuteromycetes: Fungi in which sexual reproduction has never been observed.
developmental plasticity: Ability of a cell to adopt different developmental fates and therefore become one of several different types of mature cell.
diageotropic: Describes a plant organ that grows horizontally rather than vertically.
dichogamy: Mechanism by which the stamens and pistils ripen at different times, thereby ensuring cross-fertilization.
dichotomous: Branching into two.
dicot: A flowering plant whose seeds have two cotyledons.
differentiation: Process by which an embryonic cell with no distinguishing features becomes a mature cell with a specific form and function.
diffuse-porous: Type of wood in which all the conducting cells are approximately the same size in cross-section.
diffuse root system: Root system that lacks a cen-
tral taproot and is made up of numerous, finely branching lateral roots. This type of root system is an adaptation to life in habitats with low amounts of rainfall. Grass roots are an example.

diffuse secondary growth: Secondary growth that occurs throughout a structure, not limited to one region.

diffusion: Movement of atoms, molecules, or ions from an area of high concentration to an area of lower concentration. This movement is driven by the kinetic energy of the diffusing substance.

dihybrid: A plant that has different alleles (heterozygous) at two different genetic loci.

dioecious: Species of plant in which the male and female reproductive structures are borne on different individuals. Gingko trees are an example.

diploid: Having two complete sets of chromosomes. The diploid number is the number of chromosomes in each cell of the sporophyte generation.

disaccharides: Sugars that have been synthesized by a dehydration reaction between two simple sugars. These simple sugars may be the same or may be different. Maltose and sucrose are examples.

disc flower: In many composite heads, the tiny flowers that compose the center. These flowers are radially symmetrical. In a daisy, the disc flowers are yellow.

DNA: Deoxyribonucleic acid. Contains and transmits the genetic information of a plant or animal. DNA is also responsible for directing the production of a set of proteins within the cell.

DNA ligase: Enzyme that seals linear breaks between two fragments of DNA.

DNA polymerase: Enzyme that adds nucleotides to a growing strand of DNA.

DNA sequencing: Determination of the order in which nucleotides containing the bases adenine (A), guanine (G), cytosine (C), and thymine (T) occur along the length of a strand of DNA.

dolipore: Opening in the cell walls between two cells in the hyphae of a Basidiomycete fungus.

domains: Regions of a protein that perform different functions.

dominant gene: An allele that is able to mask the presence of a different allele when both are together in the same genotype.

dominant species: In a plant community, those species that are most numerous and occupy the largest amount of space.

dominant trait: The phenotypic expression of a dominant allele. Plants heterozygous at one genetic locus will often appear to have only one type of allele.

dormant, dormancy: Period of inactivity that allows a plant to survive unfavorable cold or dryness.

drip tip: Structural feature of tropical plant leaves that facilitates the removal of condensed water or rain from the leaf surface.

drip zone: The region below the outer edge of the crown of a tree in which rain water tends to accumulate.

drupes: Type of fleshy fruit that has one seed; this seed is enclosed inside of a hard, stony pit. Cherries are an example.

dry matter: Dead leaves and other plant parts forming the litter on the surface of the soil.

duplication: Change in a chromosome causing a repetition of a segment already existing on that chromosome. Duplications contribute to the raw material from which new genes develop.

eye: A female gamete, usually distinguishable by size and location from a male gamete.

elaters: In Equisetum (horsetails) and liverworts, structures that are secreted by spore walls and that expand and contract with changes in moisture to bring about spore dispersal.

electrochemical gradient: Gradient across a cell membrane that results from differences in electrical charge.
Electromagnetic spectrum: The range of wavelengths of energy from very long to very short. Visible light is one part of the spectrum.

Electron transport chain: Series of molecules capable of being serially oxidized and reduced by electrons from the Krebs cycle. Oxygen is the last molecule in the chain. Energy from food is released in short bursts as electrons travel down the chain.

Electrophoresis: Separation of molecules or fragments of molecules of different sizes in an electrical field. The smaller molecules migrate faster than the larger ones.

Electroporation: Insertion of naked DNA into cells using an electrical shock. The shock makes the cell membrane more porous.

Embryo: A young organism that does not have its adult form.

Embryo sac: Eight-celled structure inside an ovule. It is the female gametophyte of flowering plants. One of the eight cells is an egg.

Embryophytes: Plants that form embryos during their life cycle. Flowering plants and gymnosperms are examples.

Endergonic: Reaction that requires extensive input of energy to occur. Syntheses of complex molecules from smaller ones are typically endergonic.

Endocytosis: Uptake of particles or molecules by a cell when its membrane surrounds and engulfs the particle.

Endodermis: A cylinder of specialized cells that separate the cortex from the vascular tissue of a root. Endodermis functions in regulating the flow of dissolved substances into the center of the root.

Endomycorrhizae: A symbiotic relationship between a fungus and a root in which the fungus grows inside the cells of the root and aids the root in absorption of minerals and water. The fungus receives food from the root.

Endophyte: An organism living within a plant, as a fungus living in a root.

Endoplasmic reticulum: Membranes in the cytoplasm that form transport pathways and other compartments. Rough endoplasmic reticulum has ribosomes attached to its cytoplasmic face.

Endosperm: Triploid cells modified for food storage in a seed. In a monocot seed, the endosperm is the tissue where corn starch or wheat starch is stored. In a dicot seed, the endosperm is usually absorbed into the cotyledons early in seed development.

Endospore: Thick-walled, resilient resting cell formed by some bacteria.

Endosymbiotic theory: Theory that chloroplasts and mitochondria developed from bacteria that moved into and became essential to the survival of an early eukaryotic cell.

Energy: The ability to do work. Energy takes several forms, such as chemical energy in the bonds of a compound, light energy, and kinetic energy, the energy of movement.

Energy of activation: A small amount of energy necessary to start an exergonic reaction.

Entire: Describes a smooth leaf margin that has no teeth or lobes.

Entrainment: Capture of a circadian rhythm by a particular time period, commonly twenty-four hours. Without external cues, circadian rhythms may complete one cycle in more than twenty-four hours.

Entropy: The tendency of complex molecules and structures to lose energy and become degraded into simpler forms.

Enzyme: A molecule, usually a protein, that lowers the energy of activation necessary for a reaction to occur.

Ephemeral: Name given to a plant or plant part that lasts for only a short period of time.

Epidermal hair: Multicellular hair growing from the epidermis of a leaf, stem, or fruit.

Epidermis: Layer of thin-walled cells covering the surface of a plant organ.

Epigeous germination: Seed germination in which the cotyledons emerge above the soil.

Epigynous: Type of flower in which the petals are attached above the ovary.

Epiphyte: A plant that lives nonparasitically on another plant. Usually, epiphytes are not rooted in the ground and are typically found in habitats with high humidity. Spanish moss is an epiphyte.

Epistasis: Genetic phenomenon in which the expression of one pair of genes is prevented by the presence of a second pair.

Essential elements: Chemical elements that must be available from the environment for healthy plant growth. Carbon, hydrogen, oxygen, nitrogen, phosphorus, and sulfur are the major essential elements.

Ethylene: Plant growth hormone that is a gas produced by the plant.
etiolation: Process that occurs when a plant is deprived of light. The stem becomes over-elongated and weak.
eudicot: Member of one of two major classes of angiosperms, Eudicotyledones. Eudicots’ embryos have two cotyledons.
eukaryotic cell: Cell that contains a nucleus. The hereditary material is separated from the cytoplasm by an envelope of membrane.
eusporangium: Type of spore-producing organ of vascular plants, such as club mosses. The sporangium develops from a group of more than one cell and has no stalk.
eustele: The arrangement of the vascular bundles in a ring as found in the stems of dicots.
evergreen: Plant that keeps its leaves during adverse climatic conditions, such as cold temperatures. Examples are pine trees and rhododendrons.
exergonic: Chemical reaction in which large amounts of energy are released. Burning wood and the breakdown of food for cellular energy are examples.
exine: The outer layer of the coat of a pollen grain.
exocytosis: Movement of particles or molecules out of a cell.
exodermis: In monocot roots, a layer of thick-walled cells that forms under the epidermis.
exon: A length of DNA within a gene that codes for part of a protein.
eyespot: Photosensitive structure in many one-celled plants and microorganisms that orients them to light.
facilitated diffusion: Movement of molecules from an area of higher concentration to an area of lower concentration across a cell membrane. A carrier protein is involved.
facultative anaerobe: Organism that can survive in an oxygen-poor environment when necessary, using the small amount of energy available from fermentation.
FADH₂: Electron acceptor that has received electrons directly from the Krebs cycle and is thereby reduced. FADH₂ passes electrons to the lower part of the electron transport chain.
fascicle: A cluster or bundle. Pine needles occur in fascicles.
fascicular cambium: Portion of vascular cambium located within the vascular bundles of a dicot stem.
feedback inhibition: Process by which a buildup of the product of a reaction slows the rate at the reaction occurs.
fermentation: Set of reactions that change glucose into alcohol and carbon dioxide. A small amount of energy is produced, some of which is captured as ATP.
fertilization (agriculture): Addition of minerals or decayed organic matter to soil that has been depleted of nutrients by farming or other means.
fertilization (sexual reproduction): The fusion of sperm and egg to form a fertilized egg (zygote).
fiber: Thick-walled, long, slender plant cell that provides mechanical support. These cells die at maturity.
fibrous root system: Root system in which no one root is more prominent than any other.
field capacity: Water remaining in soil following rain or irrigation after excess water has been drained off by gravity.
filament: The stalk of a stamen that supports the anther.
fimbriae: Fringe of narrow teeth that surrounds the mouth of a moss capsule.
fixation: Process by which a gas has been converted to another type of molecule, usually organic.
flavonoids: Plant pigments that give flowers colors including scarlet, pink, purple, blue, and yellow.
flavonols: One of the three major groups of flavonoids.
floret: The tiny flower of a grass.
floridean starch: A special kind of storage carbohydrate made by red algae.
flower: The reproductive structure of an angiosperm.
fluid mosaic model: Current model that describes the distribution of lipid and protein molecules within a membrane.
follicle: A dry, dehiscent fruit that opens by splitting along one side. The fruits of milkweeds are follicles.
food chain: Organisms in a community, each of which serves as food for the next higher organism in the chain. A grass seed, a mouse, and an owl form a short food chain.
food web: Interwoven complex of food chains in a community. In a food web, a particular organism may be preyed on by more than one other organism. For example, a plant may be eaten by a deer, a vole, or an insect.
foot: The part of the moss sporophyte that connects it with the gametophyte. Nutrition passes through the foot from the photosynthetic gametophyte to the nonphotosynthetic sporophyte.

founder effect: Expansion of the frequency of a recessive phenotype in a community. A small initial population (founders) passed the same recessive allele to many members of subsequent generations.

four-carbon pathway: The series of reactions that occur in C4 photosynthesis.

free-energy change: Alteration in the energy level of one of the components of a substance, such as water in a salt solution.

free-running period: Time necessary for completion of one cycle by an organism whose circadian rhythm is not restricted (entrained) to a twenty-four-hour period.

frond: The leaf of a fern or a palm.

fruit: Structure that develops from a mature ovary of an angiosperm. Fruits may be fleshy or dry and are often involved in seed dispersal.

fruitlets: In an aggregate fruit, one of the subsections that developed from a single pistil. An example is the tiny spheres in a raspberry.

frustules: The overlapping cell walls of a diatom.

fucoxanthin: A brownish-colored pigment found in the cells of brown algae.

functional phloem: That portion of the phloem that is able to conduct sugars in solution.

funiculus: Stalk of an ovule. It becomes the stalk that attaches a seed to a fruit.

fusiform initials: The long, slender cells of vascular cambium that divide to form secondary xylem and phloem.

G0 phase: Cells that have exited from the cell cycle and are no longer actively dividing.

G1 phase: Part of the cell cycle following mitosis. Cells grow and satisfy the requirements of the checkpoints that guard entry into the part of the cell cycle when DNA is replicated.

G2 phase: Part of the cell cycle following replication of DNA (S-phase). Reactions within cells prepare those cells for entry into mitosis.

gamete: A haploid reproductive cell, usually a sperm or egg.

gametic meiosis: Reduction division that results in the production of cells destined to become gametes.

gametophores: Small branches on which gametes are formed in gametangia; found in some liverworts.

gametophyte: Part of a life cycle in plants with alternation of generations. The gametophyte is haploid. Some gametophytes are green and capable of independent existence; others are not.

gaps: Type of junction between adjacent cells through which cytoplasmic connections extend. Cells joined by gap junctions are electrically and chemically linked.

gas exchange: A swap of one gas for another. Often the first gas is the reactant in a chemical reaction, and the other gas is a product of the same reactions. Thus in photosynthesis, carbon dioxide (a reactant) enters the stomata of leaves by diffusion, and oxygen (a product) builds up inside the leaf tissue until it begins to diffuse out of the leaf.

gemma cups: Structures associated with asexual reproduction in liverworts. The gemmae form inside the cup-shaped structures on the liverwort surface and can be splashed out by a raindrop.

gemmae: Small, flat, green circles of cells produced asexually by liverworts inside gemma cups.

gene flow: Change in frequency of specific alleles within a population. This normally occurs where two populations with differing allele frequencies meet. Exchange of genetic material between the two adjacent populations results in gene flow.

gene (point) mutation: A change within the hereditary material of a single gene. These tiny mutations cannot be observed by inspecting pictures of chromosomes.

gene pool: All the alleles of all the genes present in a population. There is no limit to the number of alleles in a gene pool; however, an individual may not possess more than two different alleles.

generative cell: Cell in a pollen grain responsible for the production of the pollen tube.

genetic code: Form in which information relative to protein production is contained in DNA and RNA.

genetic drift: Phenomenon observed in small populations. Dramatic changes in allele frequency occur within a few generations, due to random chance.

genetic (linkage) map: Diagram of the location of specific genes on specific chromosomes.

genetic modification: Alteration of an organism’s genetic material by manipulation in the labora-
tory. The addition of new genes or the removal of genes are examples.

**genetic recombination:** Process that results in new gene combinations on a chromosome.

**genetics:** The study of genes, chromosomes, the inheritance of hereditary characteristics, and the biochemical mechanisms controlling this inheritance.

**genomic DNA library:** A collection of the hereditary material from a species. The genes are fragmented into groups, and each group is stored in a bacterium or modified virus.

**genotype:** Alleles possessed by a plant that control traits being studied; the plant’s genetic makeup.

**genus:** A group of related species having many traits in common and descended from a common ancestor.

**geotropism:** Tendency of plant parts to respond to gravity. Roots grow downward (positive geotropism); stems grow upward (negative geotropism).

**germination:** The beginning of growth of a plant embryo inside a seed. For germination to occur, the seed must be moist and given a moderately warm temperature. Once a seed is committed to germination, it cannot dry out and survive.

**germination inhibitor:** Substance that prevents germination. Many seeds make their own germination inhibitor that prevents them from beginning to grow in adverse conditions. For example, seeds of desert annuals will not germinate until sufficient rain has fallen to wash out the inhibitor. At this point, sufficient soil moisture will support the growth of the plant.

**gibberellins:** Class of plant growth hormones that cause stem elongation, flowering, and digestion of starch in germinating seeds.

**glossary:** Without hairs.

**gland:** Structure that secretes substances such as nectar or salt.

**glaucescent:** Taxonomic characteristic of lacking hairs and with a whitish coloration.

**glycolysis:** Series of chemical reactions beginning with glucose and ending with pyruvic acid. A small amount of ATP is produced during glycolysis.

**glycoprotein:** Proteins with sugar chains attached.

**Golgi complex:** Stacks of membranes located near the nucleus where cell products are modified and prepared for secretion from the cell.

**Gondwanaland:** Mega-continent that broke up during continental drift into Pangaea and Laurasia.

**gradualism model of evolution:** Accumulation of small genetic changes over an extended period of time.

**grafting:** Process by which a piece of one plant, usually a small branch, is attached to the stem of another plant.

**gram-negative:** Bacteria that do not stain darkly when exposed to a stain made of crystal violet and iodine. The lighter colors of these bacteria are the result of picking up color from the counterstain.

**gram-positive:** Bacteria that become dark-colored when exposed to a stain made of crystal violet and iodine. The thickness or other aspect of the bacterial cell wall determines whether a bacterium is gram-positive.

**grana (pl. grana):** A stack of membrane-bound compartments in a chloroplast. Grana are covered in chlorophyll and are the locations of the light-dependent, energy-capturing reactions of photosynthesis.

**grassland:** Biome in which the dominant plants are grasses.

**gravitropism:** Plant growth response to gravity. See also geotropism.

**Green Revolution:** Several decades of dramatic advances in yield and quality of crop species. This was the outcome of attempts to increase food production begun in the 1940’s.

**greenhouse effect:** Increase in carbon dioxide and other gases in the earth’s atmosphere. These gases serve to trap heat radiating from the earth into space. The result of the greenhouse effect is global warming.

**ground meristem:** A meristematic region behind the apical meristem of a stem or root in which cells divide and differentiate to become cortex and pith.

**ground tissue system:** The cortex and pith of stems and roots.

**growth:** Increase in size and complexity. This process turns a fertilized egg into a mature adult.

**growth retardant:** A chemical that slows the growth of a plant.

**growth ring:** Xylem tissue added to a tree during the growing season in a temperate climate. The age of a tree may be approximated by counting growth rings.
guard cell: One of a pair of cells surrounding a stoma on the surface of a leaf. Guard cells shrink and swell to open or close the stoma, thereby regulating the rate of evaporation from the inside of the leaf.
gum: Resinous carbohydrates produced by a variety of angiosperm trees and other plants. Gums are soft when moist and hard when dry. Chicle, which forms the base of chewing gum, is an example.
guttation: Production of water at the tips of grass blades as a result of the presence of special secretory structures called hydathodes. This process is most visible when the soil is well-watered and humidity is high.
gymnosperm: Large group of plants whose seeds are not covered by a fruit but are borne naked on modified leaves.
gynoecium: The group of carpels that make up the female part of a flower.

hadrom: The conducting cells of xylem.
halophile: Plant that is adapted to an above-average amount of salt in its environment.
haploid: Having one set of chromosomes and one of each kind of gene. This condition is common in eggs, sperm, and the somatic cells of gametophytes.
hardwood: Species of trees in which there are fibers in the xylem. All angiosperms are hardwoods.
Hardy-Weinberg theorem: Statement of genetic change within populations. Given a stable population, the frequency (commonality) of alleles and genotypes will not change from one generation to the next.
haustorium: Branch of a hypha of a parasitic fungus that enters host cells and extracts nutrients.
heartwood: The dark-colored wood in the center of a tree trunk. The color results from tannins that accumulate in the cells of this part of the wood.
heliotropism: Growth response in which a flower turns toward the sun. Sunflowers display heliotropism as their flower heads move in the course of a day.
hemicelluloses: A group of polysaccharides that, along with pectins, make up the matrix of a primary cell wall. Cellulose fibers are embedded in the matrix.
hemiparasite: Plant with some chlorophyll which lives as a parasite. Mistletoe is an example.
herb: Type of plant that does not make woody tis-
a forest, the horizon closest to the top will contain more organic matter than will the deeper layers.

**hormogonia**: Elongated portions of filaments of cyanobacteria.

**hormone**: Chemical compound produced in small amounts in one part of an organism that has an effect in a different part of the same organism. Auxins, gibberellins, cytokinins, and ethylene are examples in plants.

**host**: In a parasitic relationship, the host is the organism that is giving up energy-containing molecules to the parasite.

**humus**: Decayed organic matter of plant or animal origin that has broken down sufficiently to lose most recognizable structure.

**hybrid**: An organism that is heterozygous at one or more genetic loci. Many crop plants, such as wheat or corn, are hybrids.

**hybrid maize**: Variety of corn developed as a hybrid.

**hybrid vigor**: Improved growth and hardiness of hybrid organisms. This vigor is one of the benefits of producing and growing hybrids.

**hydathode**: Specialized structures at the tips of blades of grass that exude water when water is in plentiful supply in the soil.

**hydroids**: Water-conducting cells of some mosses.

**hydrolisis**: Breaking a covalent bond by adding the two fragments of a water molecule to either end of the bond.

**hydophilic**: Compound or part of a compound that is attracted to and mixes well with water. The hydrophilic end of a molecule shows slight charge differences, as do the different parts of a water molecule.

**hydophobic**: Compound or part of a compound that does not mix with water.

**hydrophyte**: Plant that is adapted to living in a very wet environment. Water lilies are hydrophytes.

**hydrotropism**: Plant growth response in which the root grows toward moisture.

**hymenium**: Layer of basidia that forms on the surface of the gills of a mushroom.

**hypertonic**: Solution that has a lower concentration of water and greater concentration of solutes than a second solution. The first solution is said to be hypertonic to the second solution.

**hypocotyl**: The part of an embryo between the embryonic root and the point where the cotyledons attach to the embryonic stem. In eudicot germination, it is usually the first structure to appear above the ground.

**hypogeous germination**: Seed germination in which the cotyledons remain in the soil.

**hypogynous**: Flower in which the petals attach below the ovary.

**hypotonic**: Solution that contains a greater concentration of water and less dissolved solute than another solution. The first solution is said to be hypotonic to the second solution.

**imbibition**: Uptake of water by dry seeds.

**imbricate**: Overlapping, like the shingles on a roof; usually refers to bud scales.

**incomplete dominance**: Intermediate phenotype produced by a heterozygous genotype. The single allele which is capable of producing a product cannot produce enough to equal the appearance of an individual with two such active alleles.

**incomplete flower**: Flower that lacks one of the whorls of parts found in a complete flower.

**indehiscent fruit**: Dry fruit that does not split open when mature.

**indeterminate growth**: Growth in which the terminal meristem remains active for the life of the plant.

**indusium**: In many ferns, a flap of tissue that covers or surrounds a group of sporangia.

**inferior**: Describes the ovary of an epigynous flower.

**inflorescence**: The group of flowers that forms at the top of a flower stalk. Inflorescences may be compact, like that of a daisy, or loose, like that of a mustard.

**initials**: The generalized name for any cell in a meristem.

**insectivorous plant**: Plant that traps insects and digests them for the nitrogen-containing compounds they possess. Plants of this type grow in boggy soil that is typically low in nitrogen.

**integral proteins**: Proteins that are part of a cellular membrane. These are also known as intrinsic proteins.

**integuments**: Layers of tissue that form the outer wall of an ovule. They become the seed coat in a mature seed.

**intercalary meristem**: Group of dividing cells that forms in the center of a group of mature cells. Grass blades have these meristems within the leaf blade near the base. As a consequence, they
can keep growing upward even after having been cut.

**interfascicular cambium:** That portion of the vascular cambium that forms out of the cortex between the vascular bundles of a dicot stem. See also fascicular cambium.

**interfascicular parenchyma:** Parenchyma that fills the spaces between vascular bundles in stems.

**internode:** A length of stem from the base of one leaf to the base of the next leaf.

**interphase:** The major part of the cell cycle that includes all phases except mitosis. Replication of the chromosomes occurs during S of interphase.

**intine:** Inner layer of the wall of a pollen grain.

**intron:** Segment within a gene that is transcribed into RNA but eliminated prior to translation of the RNA.

**inversion:** Chromosome mutation in which a piece of the chromosome breaks, turns 180 degrees, and reattaches. Inversions place genes into new regions of the chromosome, where they may be more or less active than normal.

**involucrue:** Ring of bracts surrounding the base of an inflorescence. The thick, edible bracts on an artichoke are its involucre.

**iron-sulfur proteins:** Proteins found associated with reaction centers in photosystems of photosynthesis.

**irregular or bilaterally symmetrical:** Refers to a flower that can only be divided one way to give two mirror halves. Snapdragons and orchids have irregular flowers.

**isotonic:** Two solutions containing the same concentration of water and dissolved solutes.

**isozymes:** Slightly different forms of the same enzyme that can be separated by biochemical means.

**jojoba:** Desert shrub whose seeds produce a liquid wax that is used in cosmetics, as a lubricant, and as a cooking oil.

**kinetochores:** Structures that form at the centromere of chromosomes in prophase. The microtubules of the spindle attach to the kinetochores prior to separation of the chromosomes.

**Kranz anatomy:** Pattern of cellular arrangement found in C4 plants, in which the veins of the leaves are surrounded by a ring of large cells filled with many chloroplasts.

**Krebs cycle:** Part of the process of cell respiration in which two-carbon molecules derived from glucose are broken down into carbon dioxide. Electrons are removed from the fragment; these are picked up by the electron acceptor at the top of the electron transport chain.

**lanceolate:** Long, slender, and tapering to a point.

**late summer species:** Plants that flower late in the growing season.

**late wood:** Secondary xylem for forms at the end of the summer.

**lateral bud (also called axillary bud):** Bud found in the axil between a leaf and a stem. Lateral buds become branches from the main stem.

**lateral meristem:** Group of actively dividing cells located around the circumference of a woody stem or root. Vascular cambium and cork cambium are the two lateral meristems.

**lateral roots:** Roots that branch from the original or from a large main root.

**latex:** Often milky fluid containing rubber or similar compounds; produced in stems and leaves of plants, such as rubber and milkweeds.

**laticifer:** Parenchyma-lined canal that produces latex in stems and leaves.

**layering:** Formation of adventitious roots from a stem that comes in contact with the soil. In horticulture, adventitious root production is stimulated by scarring the stem, wrapping it in wet peat moss, and covering the area with plastic.

**leaf:** The usually broad, flattened photosynthetic organs attached to stems.

**leaf gap:** Space in the vascular tissue of a stem formed as the result of a strand of vascular tissue leaving the stem and entering a leaf.

**leaf primordium:** An undifferentiated group of cells in the apical region of a stem that will grow into a leaf.

**leaf rosette:** A ring of leaves that grows near the ground; often the first year's growth of a biennial plant. The flower stalk grows out of the center in the second year.

**leaf scar:** Corky area on a woody stem that marks the location where a leaf fell off. Leaf scars indicate the arrangement of leaves on a woody twig and are useful in plant identification.

**leaf tendril:** Long, flexible strand of leaf tissue that is a highly modified leaf. Used by climbing plants, such as peas, to attach to a support.

**leaf trace:** The strand of vascular tissue that leaves a stem and enters a leaf.
leaflet: One section of the blade of a compound leaf.

leghemoglobin: Proteins in legumes that are capable of binding oxygen.

legumes: Plants capable of extracting gaseous nitrogen from the air and turning it into nitrogen-containing organic compounds. Legumes can do this because of bacteria that live in swellings in the legume roots. Legume seeds are particularly rich in protein as a result. Peas, beans, and soybeans are examples of legumes.

lenticel: Pore in the bark of some trees that facilitates gas exchange with the living cells under the bark.

leptoids: Conducting cells found in gametophytes of some mosses, which resemble phloem.

leptom: The conducting cells of phloem.

leptosporangium: Type of sporangium produced by most ferns. It is characterized by a long slender stalk and an annulus.

leucoplasts: Plastids that do not contain chlorophyll but are the repository for starch manufactured by the plant. Thin sections of potato tuber show large numbers of leucoplasts.

liana: Tropical vine.

lichen: A symbiotic relationship between a fungus and an alga. The alga is protected from drying by the fungus, while the fungus receives food molecules from the alga.

light absorption: Acquisition of light energy by a pigment molecule, such as chlorophyll, during photosynthesis. Light must be absorbed before it can be fixed in the bonds of glucose.

light reactions: Series of reactions that occur in a chloroplast during photosynthesis. Light energy is captured as ATP and NADPH.

light reactions: Series of reactions that occur in a chloroplast during photosynthesis. Light energy is captured as ATP and NADPH.

lignin: Phenolic compound that is the matrix of secondary cell walls and makes them strong and hard.

linked genes: Genes that are located near each other on the same chromosome and tend to segregate into the same gamete during meiosis. The result is that they are frequently inherited together.

lipids: Organic molecules composed of carbon, hydrogen, and oxygen; the amount of oxygen is very small compared with the amount in carbohydrates. Lipids form a large part of cell membranes.

living stone: A succulent plant native to dry regions that has the general shape and appearance of a small stone.

loam soils: Soils having a mineral particle size larger than clay particles but smaller than sand grains.

locule: Space inside a carpel where seeds develop.

locus: A point on a chromosome where a particular gene is found. Homologous chromosomes will normally have the same genes at the same loci.

long-day plant: Plant that flowers under the influence of a long light period and a short dark period in successive twenty-four-hour days. Poinsettias and chrysanthemums are long-day plants.

M phase: That part of the cell cycle where the chromosomes separate into two groups. M phase includes prophase, metaphase, anaphase, and telophase.

macroleaves: Evolution that results in new taxa above the species level.

macromolecule: Large organic molecule important in living organisms. Starch, cellulose, protein, and nucleic acids are examples.

macronutrients: Chemical elements required for plant growth in relatively large amounts.

magnoliids: Members of the class of flowering plants called the Magnoliopsida.

maize: Individuals of the species Zea mays, commonly called corn in the United States. In other countries, “corn” can refer to other grains.

major vein: Largest bundle of conducting tissue found in a leaf.

mannitol: Sugar alcohol that is the form in which carbohydrates are transported in many members of the rose family.

mediterranean scrub: Type of vegetation found in places, such as Southern California, which experience wet winters and long, dry summers.

megaphyll: Leaf type which has branching veins and is associated with a leaf gap.

megaspore: Cells produced by meiosis that grow into female gametophytes.

megasporangium: Reproductive structure in which megaspores are produced.

megaspora: Cells produced by meiosis that grow into female gametophytes.

megasporocyte (megaspore mother cell): The single cell that divides by meiosis to produce four megaspores.

meiosis: Process of cell division that results in the formation of cells with only half as many chromosomes as the original cell. In plants with alternation of generations, meiosis occurs prior to the formation of the gametophyte.
membrane: Lipid bilayer with embedded proteins. Membranes form the basis of many subcellular structures as well as surrounding the cytoplasm and the nucleus.

membrane potential: Gradient in voltage across a cell membrane that results in the movement of ions.

meristem: Region of active cell division. Meristems occur primarily at the tips of stems, at the tips of roots, and around the circumference of woody plants under the bark.

mesophyll: Tissue composed of mesophyll cells.

mesophyll cells: Chloroplast-filled parenchyma cells of a leaf.

mesophyte: Plant species whose requirements for moisture place it midway on the scale between wet and dry.

messenger RNA (mRNA): RNA that carries information for the construction of a protein from the DNA in the nucleus to a ribosome.

metabolic pathway: A series of reactions leading to the production of a particular product.

metabolism: The sum of all the synthetic (anabolic) and degrading (catabolic) reactions an organism can carry out.

metabolites: Compounds formed as the result of biochemical pathways in an organism.

metaphase: Phase of mitosis in which chromosomes line up on the equator of the spindle.

metaxylem: That part of the primary xylem of a stem or root that matures last.

methanogen: Type of bacterium that produces methane during its autotrophic activities. Methanogens live in oxygen-poor environments.

microevolution: Change within a group of plants that results in large-scale differences. Macroevolution produces new genera, families, and orders.

microfibril: Strands of cellulose molecules connected to one another by hydrogen bonds.

micronutrients: Chemical elements necessary for plant growth, required in very small quantities.

microphyll: Leaf that possesses a single unbranched vein and is not associated with a leaf gap.

micropyle: Opening in an ovule through which the pollen tube grows.

microsponga: Reproductive organ in which meiosis produces spores that upon germination form male gametophytes.

microspores: The products of a microsporangium.

microsporocyte (microspore mother cell): A cell that undergoes meiosis to produce four microspores.

microtubules: Hollow cylinders of tubulin protein molecules that form networks in the cytoplasm and the mitotic spindle.

middle lamella: Material that cements two adjacent plant cells to each other. May be pectin or lignin.

mimicry: The phenomenon in which one plant species has evolved to look superficially like a second species. Often the mimic benefits because the second species is bad-tasting or poisonous, and thus herbivores avoid both species.

minerals: Chemical elements in ionic form absorbed from the soil and used by plants in a variety of metabolic pathways.

minor vein: One of the small, branching veins that form a network in a leaf.

mitochondria: Cellular organelles responsible for the breakdown of food and the release of energy from that food.

mitochondrial matrix: The portion of a mitochondrion that is enclosed by the inner membrane.

mitosis: Separation of replicated chromosomes into two equal groups. The result of mitosis is two nuclei that are identical to each other and to the original nucleus.

mitotic spindle: Football-shaped structure of microtubules that forms in the early stages of mitosis. Chromosomes attach to tubules of the mitotic spindle by kinetochores that form at the centromeres.

molecular biology: Study of the molecules of living organisms, their pathways, and their interactions.

molecular clock: Accumulation of genetic changes that develops when two species diverge. The longer two species have been separate, the more changes will be evident. The clock does not tick at the same rate in every species or every molecule.

molecular systematics: Study of the classification of organisms based upon differences at the molecular level, particularly in DNA.

molecule: Chemical unit composed of two or more atoms. The atoms may be of the same element or different elements.

monocot: One of the two major groups of flowering plants, Monocotyledones. The seeds of monocots
have only one cotyledon. Corn and grass are examples.

**monoecious**: Describes plants in which both the male and female sex organs are produced in the same flower.

**monohybrid**: Organism that is heterozygous for one pair of genes.

**monomer**: Small molecules that are the building blocks for more complex molecules. Glucose is the monomer that is built up into starch and cellulose.

**monophyletic**: Evolutionary concept in which a group of related organisms can be shown to be descended from a single ancestor.

**monosaccharide**: Simple sugar, such as glucose or fructose. These can combine to make larger carbohydrates.

**monospore**: In the algae, a diploid spore that germinates to form another diploid plant.

**monounsaturated fats**: Lipid that has only one carbon-carbon double bond in each of its three fatty acid chains. Olive oil is composed mostly of a monounsaturated lipid.

**monsoon forest**: Forest type found in tropical regions of the world where there are annual periods of high rainfall.

**morphogenesis**: Development of patterns of form or structure.

**motor proteins**: Specialized proteins capable of moving chromosomes, organelles, or molecules from one part of a cell to another.

**mucigel**: The combination of mucilage secreted by a root, bacteria that are attracted to the mucilage, and fine soil particles that accumulate around the root.

**mucorhiza (pl. mycorrhizae)**: A symbiotic relationship between a root and a fungus in which the fungus lives either in or on the root and gains food from it. The fungus increases absorption of water and minerals for the root.

**mycotoxins**: Poisonous substances produced by fungi. Aflatoxin that sometimes contaminates stored food is an example.

**myxamoebas**: Uninucleate stage in the life cycle of slime molds.

**NADH**: Reduced form of the electron-accepting molecule nicotinamide adenine dinucleotide. NAD+, the oxidized form, receives electrons from the breakdown of carbohydrates in the Krebs cycle and passes those electrons down the electron transport chain.

**nastic movements**: Movements that occur in a plant during the daytime. The plant stem or tendril rotates around the vertical axis.

**natural selection**: The evolutionary process in which organisms of a species are produced in quantity larger than the environment can support. These organisms differ slightly from another in their genetic makeup. Those with genetic changes that best suit them to live in a particular environment will survive better and produce more offspring than organisms that are not as fit.

**neck canal cells**: Found in archegonia in plants, such as ferns and mosses, these cells fill the canal protecting the egg until it is ready for fertilization. Then the neck canal cells break down and permit the passage of sperm to the egg.

**necrosis**: Death of tissue from disease, damage, or nutrient deficiency.

**nectar**: Sugary solution produced by flowers that attracts pollinators.

**nectar guide**: Ultraviolet light reflecting lines found on some flower petals that direct pollinating insects to the nectar.

**nectary**: Gland in a flower that produces and secretes nectar.

**netted venation**: Type of vein pattern found in dicot leaves, in which veins branch to form a network of large and small veins throughout the leaf.

**niche**: The combination of the habitat and ecological role of a species within an ecosystem. It includes the resources the species needs, the way it finds them, and the way it harvests them.
nitrification: Process by which bacteria convert ammonium ions or ammonia to nitrate.

nitrogen cycle: The biogeochemical cycle of the element nitrogen.

nitrogen fixation: Process by which bacteria convert atmospheric nitrogen to nitrogen-containing compounds, such as amino acids.

nitrogenase: Enzymes that convert atmospheric nitrogen into ammonia.

node: The location on a stem at which leaves and lateral buds are attached.

nodules: Swellings on roots of legumes and other plants in which symbiotic nitrogen-fixing bacteria live.

noncyclic photophosphorylation: Production of ATP following the absorption of light energy by electrons of a chlorophyll molecule. The electrons release their energy in a stepwise fashion but are then picked up by a different molecule of chlorophyll. The original chlorophyll molecule receives replacement electrons from the breakdown of water molecules.

nonvascular plants: Plants that lack the special conducting tissues xylem and phloem. The nonvascular plants are the bryophytes—liverworts, hornworts, and mosses—and were the earliest colonizers of land.

NPK ratio: In commercial fertilizer, the relative amounts of nitrogen (N), phosphorus (P), and potassium (K). For example, a fertilizer labeled 12-12-12 has equal amounts of these three mineral nutrients.

nucellus: Thin-walled cells found in sporangia that provide nutrition to developing spores.

nucleic acid hybridization: Hydrogen bonding of two nucleic acid strands that are somewhat complementary in their base sequence. The two strands were not originally part of the same molecule but, as single-stranded molecules in solution, are attracted to each other. Hybrids may form from the same type of nucleic acid (such as DNA-DNA hybrids) or two different types (such as DNA-RNA hybrids).

nucleic acids: Large molecules made up of nucleotides. These molecules are involved with the transmission of inherited characteristics from one generation to the next and with the production of products encoded in the genes.

nucleoid: The part of a bacterium that includes its chromosome.

nucleolus (pl. nucleoli): Collection of protein and RNA molecules that form at specific sites on chromosomes (nucleolar organizing centers). The function of the nucleolus is the production of ribosomes.

nucleosome: A length of DNA wrapped twice around a collection of histone proteins. Six nucleosomes form one turn of a coil that is the interphase chromosomes.

nucleotides: Building blocks of nucleic acid. Each nucleotide consists of a five-carbon sugar, an organic base, and three phosphate groups.

nucleus: Cell structure of eukaryotic cells in which the hereditary material is separated from the cytoplasm by a double lipid-protein membrane (the nuclear envelope).

nut: Type of fruit in which the outer wall of the fruit is fleshy or leathery and the inner wall of the fruit is woody or stony. The seed coat is fused with the woody inner wall.

nutrient cycles, nutrient cycling: Large-scale movements of elements and water through the living and nonliving portions of an ecosystem.

nutrient uptake: Process of absorption of minerals as ions from soil.

nyctinastic movements: The opening and closing of flowers corresponding with day and night.

obovate: Oval-shaped but broader toward the tip than toward the base.

Okazaki fragments: During the replication of DNA, one of the two strands is replicated continuously from beginning to end; the other strand is replicated in successive short pieces (Okazaki fragments). The difference comes about because of different orientation of the two DNA strands.

oogonium: The female reproductive structure of algae, in which a single egg is formed from one precursor cell. These have no sterile jacket.

oospore: In the life cycle of water molds (Oomycota), name applied to fertilized eggs.

operculum: Flaplike structure that closes the opening to the moss capsule, composed of sporophyte tissue. See also calyptra.

operon: In bacteria, a group of genes regulated by the same promoter. The genes usually make products involved in the same biochemical pathway.

opposite: Leaf pattern in which two leaves come off the stem at the same node.

organ: A complex anatomical structure composed of different types of tissues, all functioning to-
gathered for a particular purpose. A leaf, a stem, and a root are all plant organs.

**organelle:** Structures within a cell, surrounded by membranes. Mitochondria, chloroplasts, and Golgi bodies are examples.

**organic:** Chemical compounds containing both carbon and hydrogen and having some of the hydrogen attached directly to the carbon atoms.

**organism:** Any individual living creature.

**osmosis:** Movement of water through a selectively permeable (also called differentially permeable) membrane from an area of higher concentration to an area of lower concentration.

**osmotic potential:** Difference in concentration of water in two adjoining solutions separated by a selectively permeable membrane.

**osmotic pressure:** The amount of free energy of water in a solution.

**outgroup:** A group of organisms only distantly related to the groups being examined in a cladistic study.

**ovary:** Female reproductive structure that houses the ovules and matures into a fruit. Among plants, ovaries are found only in angiosperms.

**ovate:** Oval-shaped but broader toward the base than toward the tip.

**ovulary:** The swollen base of a pistil; also called an ovary.

**ovule:** Female reproductive structure that matures into a seed containing an embryo.

**ovuliferous scales:** Flat plates of a gymnosperm cone to which ovules are attached.

**oxidation-reduction (redox) reaction:** Coupled reactions in which the loss of electrons from one molecule (oxidation) results in the gain of electrons by a second molecule (reduction).

**oxidative phosphorylation:** Production of ATP driven by the movement of electrons from the Krebs cycle of cell respiration to oxygen.

**P-protein:** In sieve tube elements, a special protein that clumps together to seal the ends of the elements when they are injured or when the plant goes dormant.

**paleobotany:** Study of fossil plants or plant parts, such as pollen.

**palisade cell:** In a leaf, the sausage-shaped parenchyma cells found just below the upper epidermis. Palisade cells are well supplied with chloroplasts and packed beside one another with minimal space between them.

**palisade parenchyma:** All the palisade cells of a leaf. The tissue gets its name from its resemblance to a stockade fence (palisade). Much of the photosynthesis in a typical plant occurs in this tissue.

**palmate venation:** Pattern of major veins in a leaf. The veins spread out from a central point where the petiole meets the blade of the leaf. There is a superficial resemblance to spread fingers “branching” from the palm of the hand.

**palmately compound leaf:** Leaf with palmate venation but with the blade divided into leaflets. Each leaflet receives one major vein. These leaves look like groups of long fingers. Horse chestnut leaves are an example.

**panicle:** Type of inflorescence with branches from a main stalk. Those branches are branched in turn. An example is the inflorescence that results in a cluster of grapes.

**pappus:** Fine hairs, bristles, or flattened awns attached to a seed of a composite that aid in wind dispersal. Dandelion seeds are examples.

**parallel venation:** Pattern of veins in a monocot leaf. The large veins do not intersect as they traverse the length of the leaf.

**paraphyletic:** Taxonomic grouping that includes some, but not all, of a group of related species.

**parasexualite:** Special type of reproduction found in some deuteromycetes involving nuclear fusion in a hypha without normal processes of meiosis and zygote formation.

**parasite:** Organism that uses a living plant or animal as a source of nutrition. Parasites often have adaptations for this lifestyle.

**parenchyma:** Thin-walled plant cells that may contain chloroplasts. Parenchyma cells fill spaces in leaves, stems, roots, and fruit.

**parthenocarpic fruits:** Fruits that develop without pollination and fertilization. Hothouse tomatoes are produced this way by spraying them with an auxin.

**passage cells:** Found in the endodermis of some roots, these specialized cells are not suberized and allow unimpeded movement of water and dissolved minerals into the xylem.

**passive transport:** Movement from one side of a cell membrane to the other without the expenditure of metabolic energy.

**pectin:** Carbohydrate that is a major part of the matrix of primary cell walls and the middle lamella. Extracted pectin is sold for jelly-making.
pedicel: The stalk of a single flower, whether the flower is borne singly or in an inflorescence.

peduncle: The stalk that supports an inflorescence of flowers.

pelllicle: Tough outer layer of the cell membrane of some one-celled organisms.

pennate: Describes a diatom which is long and slender when viewed from above, as opposed to centric, which is circular.

PEP carboxylase: An enzyme necessary for C₄ photosynthesis. It combines CO₂ with PEP (phosphoenolpyruvate) to form malic or aspartic acid.

pepo: Type of berry that has a hard or leathery rind when ripe; squash is an example.

peptide bond: A covalent bond that connects two amino acids in a protein.

peptidoglycans: Compound molecule composed of sugar chains and a polypeptide.

perennial: Plant that comes up in successive years from the same root.

perfect: Describes a flower that contains both male and female sex organs.

perforation plate: Region in the cell wall of a sieve tube element that is characterized by small pores through the wall. These plates are found in end walls and sometimes in lateral walls.

perianth: The combination of sepals and petals in a flower.

pericarp: Outer layer of a fruit. Examples are the fleshy part of a berry, the stony part of a nut, and the pod of a pea.

pericycle: Layer of potentially meristematic cells separating the endodermis from the phloem and xylem of a root.

periderm: In the bark, the combination of cork, cork cambium, and cork parenchyma.

perigynous: Describes a flower in which a rim of the receptacle grows up around the base of the ovary. The petals, sepals, and stamens are attached to this rim of tissue.

peripheral protein: Proteins that are loosely bound to the surface of a membrane, not embedded in the membrane.

perisperm: Nutritive tissue found in a seed outside of the embryo sac and distinct from the endosperm.

peristome: Ring of small, toothlike projections that surround the opening of a moss capsule.

permafrost: Permanently frozen layer of soil underlying tundra vegetation.

permanent wilting percentage: Amount of water remaining in soil when plants rooted in that soil reach the point of permanent wilting. If the soil is not watered, the plants will die.

peroxisomes: Organelles that contain enzymes which produce hydrogen peroxide.

petal: One of the parts of a flower that is flat and often brightly colored, found in a whorl between the whorl of sepals and the whorl of stamens.

petiolate leaf: Leaf that has a stalk attaching it to a stem.

petiole: Stalk that connects the flat blade of a leaf to the stem. The vascular tissue to the leaf runs through the petiole.

pH: Measure of acidity of a solution. The lower the pH, the higher the concentration of hydrogen ions, and the more acidic the solution.

phagocytosis: Process of ingestion by a cell in which the cell engulfs large particles; a form of endocytosis.

phelloderm: Technical name for cork parenchyma that is produced by the cork cambium.

phenolics: Aromatic chemical compounds produced by plants. Included are tannins, lignin, and flavonoid pigments.

phenotype: Any gene-based anatomical or physiological trait that can be observed is part of a plant’s phenotype.

phloem: Conducting tissue responsible for moving food manufactured in the leaves to other parts of the plant, including the roots.

phloem loading, phloem unloading: Process by which sugars and other substances are transferred into or out of sieve tube elements in phloem.

phloem ray: A flat, vertically oriented sheet of parenchyma cells that extends from the vascular cambium outward through the phloem. These rays permit lateral movement of substances within the phloem and into the xylem.

phosphoglycolate: Chemical important in photosynthesis.

phosphorylation: The attachment of a phosphate group to another molecule, often a protein or molecule of ADP. Phosphorylation increases the potential energy of the molecule to which the phosphate is added.

photomorphogenesis: Growth response to light by plants.
photons: Packets of light energy.

photoperiodism: Regulation of a plant process, such as flowering, by the relative length of light and dark periods in a twenty-four hour day.

photophosphorylation: Use of light to attach a phosphate group to another molecule, usually to ADP.

photorespiration: Physiological process that occurs during photosynthesis when the ratio of carbon dioxide to oxygen becomes too low. It results in the production of less sugar than during regular photosynthesis, and some carbon dioxide is formed.

photosynthesis: Production of food molecules, six-carbon sugars, from simple chemical compounds in the presence of light energy.

photosynthetic autotrophs: Organisms capable of using light energy to manufacture food.

Photosystem I, Photosystem II: Stages in the energy-capturing light reactions of photosynthesis. Photosystem II yields ATP, whereas Photosystem I yields reduced NADPH.

phototropism: Growth response in which the plant stem, leaf, or flower grows either toward or away from light.

phragmoplast: Set of microtubules that organizes the formation of a new cell wall separating two daughter cells as part of cytokinesis.

phragmosome: Area within a dividing cell in which the phragmoplast forms.

phycobilins: Found in red algae and cyanobacteria, a special class of pigments that absorb green light and reflect blue and red light.

phycoplast: Similar to phragmoplast but found only in a few green algae.

phyllotaxy: Study of the arrangement of leaves on a stem.

phylogenetic tree: Branching diagram, also called an evolutionary tree, that illustrates the evolutionary relationship among groups of organisms.

phylogeny: Study of evolutionary origins of related groups.

phytoalexins: Chemicals produced by plants that help to limit the spread of bacterial and fungal infections.

phytochrome: Class of pigments found in leaves that regulate photoperiodic responses in plants.

phytoplankton: Small plants, often single-celled, that float in water. Phytoplankton in the ocean are responsible for much of the earth’s oxygen production.

phytotoxin: Chemical produced by a plant that is harmful to another plant. See also allelopathy.

pigment: An organic molecule capable of absorbing and reflecting specific wavelengths of light.

pili: Bridges of cytoplasm that form between conjugating bacteria. Genetic material is transferred from one cell to another through a pilus.

pilose: Having long, soft hairs.

pinnate venation: Pattern of leaf veins that resemble a feather, with a main vein up the middle of the leaf and smaller veins branching in parallel from the main vein.

pinnately compound leaf: Leaf with pinnate venation but with the blade divided into sections (leafletlets). A large vein branching from the main midrib enters each leaflet.

pinocytosis: Intake of liquids as tiny vesicles formed when the cell membrane invaginates.

pistil: The female part of a flower composed of stigma, style, and ovary.

pit: Often circular or oval gap in the secondary cell wall. Plasmodesmata pass from cell to cell through the pits and associated pit fields in the primary cell wall.

pith: Region of parenchyma tissue found in the center of a dicot stem.

pith meristem: The part of the ground meristem in which the cells of the pith divide and differentiate.

pith ray: In the young stem of a dicot, the parenchyma tissue that separates the vascular bundles from one another.

pits: Plural of pit (see above). Also refers to the stony inner part of a drupe. Prune pits are an example.

placenta: Point at which an ovule attaches to the carpel wall. Nutrients stored in the developing seed pass from the plant through the placenta.

placentation: Pattern of ovule attachment to the carpel wall. In central placentation, all the ovules are attached to the innermost axis of the carpel.

plagiotropic: Pattern of growth that results in branches growing more or less parallel to the ground. Lateral tree limbs are plagiotropic.

plankton: Small plants and animals that float freely in water; their small size prevents them from having to swim to keep from sinking.

plant anatomy: Study of plant structure, especially the arrangement of different types of cells to make tissues and organs.
plant biotechnology: Alteration of plant hereditary material, particularly by the insertion of foreign genes. Biotechnology has applications in agriculture, industry, and medicine.

plant growth regulator: Chemicals produced in one location in a plant that have a growth-modifying effect elsewhere in the plant. Auxins, gibberellins, cytokinins, and ethylene are classes of growth regulators.

plant morphology: Study of the plant kingdom, especially with regard to evolution, reproduction, and structure.

plant physiology: Study of the functioning of plants.

plant taxonomy: Science of the naming and classification of plants.

plasma membrane: Lipid-protein bilayer that surrounds the cytoplasm and regulates movement of compounds in and out of the cell.

plasmid: Circle of DNA found in the cytoplasm of bacteria that contains genes not found in the nucleus.

plasmodesma (pl. plasmodesmata): Small strands of cytoplasm that extend through the cell membranes and cell walls connecting two adjacent cells.

plasmodiocarp: Fruiting body of a slime mold.

plasmodium: Amoebalike thallus of a plasmodial slime mold.

plasmolysis: Loss of water from the central vacuole of a plant cell that causes the cytoplasm and cell membrane to pull away from the cell wall. Continued plasmolysis leads to the death of the cell.

pleiotropy: When one gene is able to affect several different structures in a single organism.

plurilocular gametangia: In brown algae, a group of several cells, all of which produce either eggs or sperm.

plurilocular sporangia: In brown algae, a group of several cells, all of which produce spores.

pneumatophores: Projections of roots upward from saturated soils or water, such as the knees of bald cypress.

pod: Type of dry, dehiscent fruit; known also as a legume.

polar nuclei: Two nuclei located in the center of an embryo sac. These nuclei fuse with a sperm to produce the endoderm tissue in a seed.

polar transport: Movement of a substance from the tip of a stem downward.

pollen: Male gametophytes of gymnosperms and angiosperms. Pollen is adapted to transfer from one plant to another by wind or insects.

pollen grain: A single male gametophyte. Most pollen grains have distinctive sculpturing of their outer surfaces.

pollen sac: Chamber inside an anther where pollen is produced.

pollen tube: Tube which grows from an angiosperm pollen grain after it has landed on a compatible stigma. The tube grows down the style and into an ovule in the ovary. The sperm move down the tube to effect fertilization.

pollination: Transfer of pollen to a stigma in angiosperms or an ovule in gymnosperms.

pollinium: Pollen sac produced by orchids. Insects entering orchid flowers must pass the pollinia and inadvertently pick them up. They stick to the insect’s body and are transferred to another orchid flower.

polymorphony: The development of more than one embryo in a seed.

polygenic inheritance: Several genes cooperating to produce a single trait. Each gene adds only a small increment to the final end product, making polygenic traits, also known as quantitative traits.

polymerase chain reaction: Laboratory process for copying strands of DNA. A single piece of DNA is separated into two strands by heating. Primers are added to the strands, and DNA polymerase uses each strand to make a complete piece of DNA. The process is repeated over and over.

polymerization: Chemical process by which many similar small molecules (monomers) are joined to make one large complex molecule.

polymers: Complex molecules composed of repeating units. A protein made of amino acids is an example.

polypeptides: Strands composed of several amino acid molecules. A single polypeptide may become a functional protein, or it may join with other polypeptides to form a protein.

polyphtletic: Describes a group of organisms that have similar characteristics but which originated from more than one ancestor.

polyploid: Organism having more than two complete sets of chromosomes.

polyploidy: Genetic condition in which the hereditary material is present in three or more complete sets. Plants may be triploid (three sets of chromosomes), tetraploid, or have even greater numbers.
**polysaccharides:** Polymers built up from monosaccharide molecules. Starch and cellulose are examples of plant polysaccharides.

**polysome (polyribosome):** Piece of messenger RNA attached to several ribosomes, each of which is producing a nascent protein at a different stage of completion.

**pome:** A type of fleshy fruit in which the seeds are found in chambers that are lined with a tough, papery material. Most of the flesh develops from the receptacle of the flower, rather than exclusively from the ovary. Apples and pears are examples.

**population genetics:** Branch of genetics that examines the movement of genes through populations. A population geneticist might study genetic drift, founder effect, or Hardy-Weinberg theorem.

**predaceous fungi:** Soil fungi that form loops to lasso nematode worms. The trapped worm is then digested by the fungus.

**preprophase band:** Ringlike group of microtubules that encircles a cell where a future equatorial plane will form during mitosis.

**pressure-flow hypothesis:** Model to explain the movement of dissolved substances in the phloem. The solutes are swept along with moving water. The water is moving because of differences in water pressure between the top of the column and the bottom.

**prickle:** A slender thorn or spine, often found in groups.

**primary cell wall:** The first wall, and often the only wall, to form around a plant cell. Primary walls are thin. Apple flesh, for example, is composed of cells with primary walls.

**primary consumers:** Animals that eat plants as their primary source of food. Deer, cows, mice, and seed-eating birds are examples.

**primary endosperm nucleus:** Nucleus formed by the fusion of the two polar nuclei and a sperm nucleus in an embryo sac. This nucleus divides to form the endosperm of a seed.

**primary growth:** Stem and root elongation and expansion of leaves resulting from cell division and elongation.

**primary metabolites:** Sugar phosphates, amino acids, lipids, proteins, and nucleic acids, all of which comprise the basic molecules necessary for a cell to function.

**primary phloem:** Phloem produced in stems, roots, and leaves during the process of primary growth.

**primary pit-fields:** Regions of primary cell walls adjacent to pits in the secondary cell wall. Plasmodesmata are concentrated in these pit-fields.

**primary plant body:** The stems, roots, and leaves produced by primary growth of an embryo.

**primary producers:** In an ecosystem, those organisms that form foods from energy and simple chemical molecules.

**primary root:** The first root produced by an embryo.

**primary structure:** Part of the primary plant body.

**primary tissue:** Tissue produced during primary growth. Cortex, pith, and epidermis are examples.

**primary xylem:** That xylem that is formed during primary growth.

**principle of competitive exclusion:** If two or more species compete for the same niche, one of them will be successful, and the other will be eliminated over time.

**principle of parsimony:** When two different explanations are offered, the most likely one is the simplest one.

**prochlorophyte:** Ancestral green plant.

**prokaryotic cell:** Cell in which the hereditary material is not separated from the cytoplasm by a nuclear envelope. Bacteria are prokaryotes.

**prop roots:** Adventitious roots that grow from stems and help support the stem. Corn plants produce prop roots just above the soil.

**prophase:** First phase of mitosis, during which the chromosomes condense and the spindle forms.

**proplastids:** The precursors of plastids, such as chloroplasts.

**proteins:** Complex polymers composed of amino acid monomers. Although many proteins function as enzymes, there are proteins that have other functions in a cell.

**prothallial cells:** Sterile cells produced in pollen grains of gymnosperms.

**prothallus:** Name given to the haploid, free-living gametophyte of ferns.

**protonema (pl. protonemata):** A filament of cells produced by a germinating spore of a moss.

**protoplasm:** General term for living matter.

**protoplast:** The living contents of a cell.

**protoplast fusion:** The merging of the protoplasts of two different cells.
protostele: Arrangement of xylem and phloem in which the xylem is a solid strand in the center of a root or stem, and the phloem is arranged in a concentric ring around it. Typical of primitive vascular plant stems.

protoxylem: During the differentiation of cells to become primary xylem, the first cells to differentiate into vessel elements or tracheids. In dicot roots these are at the ends of the arms of primary xylem, and in dicot stems they are in the part of the vascular bundle nearest the pith.

protracheophyte: The ancestor of plants that have vascular tissue.

pseudoplasmodium: In cellular slime molds, the name given to the multinucleate, amoeba-like structure that forms from the merger of thousands of uninucleate single cells.

pubescent: Possessing hairs.

pulvinus: Zone of cells at the base of a leaf or leaflet that can rapidly lose water and cause the leaflet or leaf to fold up.

pumps: Cellular mechanisms to move substances against a concentration gradient into or out of cells.

punctuated equilibrium model of evolution: Theory that evolution occurs in bursts of large changes followed by extended periods of time when little change occurs.

pyrenoid: Regions of a chloroplast in some algae where starch accumulates.

pyruvate: End product of glycolysis. During cell respiration, glucose is converted to two molecules of pyruvate with a small number of ATPs formed in the process.

quiescent center: A dome-shaped mass of cells at the very tip of a root. In this region cell division is far less frequent than in the apical meristem immediately above it or the root cap below it.

raceme: Inflorescence type in which there is a single stalk with individual flowers attached directly to the stalk.

rachis: The stiff midvein of a pinnately compound leaf, to which the leaflets are attached. This term is used especially with fern leaves.

radial system: All of the rays together in the secondary xylem and phloem of a plant.

radicle: The embryonic root.

rain forest: Biome found in regions of the world where rainfall is high and there are no dry periods. Rain forests occur in the tropics and along the northwest coast of the United States.

raphide: A needle-shaped type of crystal of calcium oxalate found in leaves, stems, bark, and roots. These are irritating to the skin.

ray flower: In a composite inflorescence, those asymmetrical flowers that have a long, straplike petal.

ray initials: Cells of the vascular cambium that divide to form new parenchyma cells of rays.

ray parenchyma cell: One of the cells of a ray, such as are found in xylem and phloem.

reaction center: Located in the membranes of thylakoids, these are groups of chlorophyll and carotenoid pigments along with associated proteins, where the light-dependent reactions of photosynthesis begin. Reaction centers absorb light energy and transfer it to pathways where it is incorporated in molecules of ATP and NADPH.

reaction wood: When a tree bends horizontally, secondary xylem grows on the lower side, in response to gravity, and causes the tree’s trunk to grow back into an upright position.

receptacle: Usually expanded tip of the stalk to which the whorls of a flower are attached.

receptors: Proteins or protein-carbohydrate combinations located on the outer surface of cell membranes, which are the sites to which various chemicals attach, causing reactions to occur within the cell.

recessive allele: Form of a gene whose expression is masked by a dominant allele in the same genotype.

recessive trait: Phenotypic characteristic that normally is observable only when two recessive alleles are present in the genotype.

recombinant DNA: DNA that is formed by the splicing of DNA fragments from two different species.

region of cell division: That part of the meristem where mitosis occurs.

region of elongation: That part or zone of a primary root or primary stem in which cells grow to their maximum length.

region of maturation: That part of a primary root or primary stem in which cells differentiate to form the primary tissues.

regular or radially symmetrical: Describes a flower that has its parts organized along radii, much like the spokes of a wheel. When cut along any
diameter, the flower will produce two mirror images.

**repetitive DNA**: DNA sequences found repeated many times in a single cell. The repeated sequences may exist in the same region of a chromosome, in which case they are known as tandem repeats.

**replication**: Copying of a DNA molecule, so that the two molecules formed are identical to each other and to the original molecule. The two molecules formed are each composed of one strand from the original DNA molecule and one newly synthesized strand.

**reporter genes**: Genes that make a detectable product, such as one that is colored. Reporter genes are used in genetic research to show the tissues or stages of development in which a particular gene is active.

**reproductive (genetic) isolation**: Describes any of many mechanisms that prevent one organism from sexually reproducing with a second.

**resin**: Sticky, aromatic substance produced in the wood, bark, and needles of conifers. When injured, the resin oozes out and reduces the risk of insects, fungi, or bacteria getting into the plant.

**resin canal**: A tube that forms through the wood, bark, or needles of a conifer. The tube is lined with parenchyma cells that produce and secrete resin. Also called a resin duct.

**respiration**: The stepwise breakdown of glucose or fragments of lipids and proteins with the release of energy to molecules of ATP.

**restoration ecology**: A subdivision of the field of ecology that works to reclaim damaged ecosystems and return them to their original condition.

**restriction enzyme**: Bacterial enzyme that cuts DNA at a location marked by a specific base sequence.

**reticulate venation**: A pattern of veins in leaves in which the branch veins form a complete network with a regular pattern throughout the leaves.

**rhizobia**: Any bacteria of the genus *Rhizobium*. These bacteria live in nodules on the roots of legumes, where they fix atmospheric nitrogen.

**rhizoids**: Small filamentlike growths out of the bases of bryophytes, some algae, and some fungi, which help attach the plant to the substrate and channel water into the plant.

**rhizome**: A stem that grows horizontally either in the soil or right on the top of the soil. Irises and many grasses have rhizomes; those of irises are fleshy.

**rhizosphere**: Region of soil in the immediate vicinity of the root system of a plant. It is in this rhizosphere that the plant absorbs its needed water and minerals.

**ribonucleic acid**. See RNA.

**ribosomal RNA (rRNA)**: RNA that makes up part of the structure of the ribosome and is necessary to its functioning.

**ribosome**: Subcellular structure composed of RNA and protein. The ribosome is the cellular machinery for the production of proteins from amino acids.

**ribulose 1,5-bisphosphate (RuBP)**: First and last compound in the Calvin cycle of photosynthesis. RuBP combines with carbon dioxide to start the cycle and is regenerated at the end of the cycle.

**ring-porous**: Describes wood in which the early wood (produced in spring and early summer) has significantly larger vessel elements than does the late wood (produced in late summer and fall). The wood of oaks is ring-porous.

**ripeness-to-flower**: Physiological condition that must be met before a plant will be able to respond to external stimuli, such as temperature or photoperiod, that are the cues to flowering.

**RNA**: Ribonucleic acid, a nucleic acid formed on chromosomal DNA; involved in protein synthesis.

**RNA polymerase**: Enzyme that connects nucleotides to form RNA. The sequence of nucleotides in the RNA is copied in complementary fashion from the sequence of nucleotides in a DNA template.

**root**: Portion of a plant axis that typically grows underground, possesses a root cap, branches internally from its pericycle, and does not have the ability to produce leaves or buds.

**root cap**: Mass of thin-walled cells that covers the tip of a root. These cells lubricate the pathway of the root through the abrasive soil and protect the delicate root tip from damage.

**root hairs**: Single-celled outgrowth of root epidermal cells. Root hairs vastly increase the absorbing surface of a root.

**root nodules**: Small, tumorlike growths that form on roots of legumes and other kinds of plants. Roots produce nodules in response to bacteria, such as the genus *Rhizobium*, which grow in them and fix atmospheric nitrogen.
root pressure: Force created by differences in concentration of water between the soil and a root that causes water to ooze out of a stem if it is cut just above the junction with its root.

root primordium: A very young, still-developing branch root.

root system: All the roots, large and small, that are part of an individual plant.

root tuber: Swollen portion of a root in which are stored large amounts of food. Sweet potatoes and yams are root tubers.

rugose: Having a wrinkled surface.

runner: Stem that grows horizontally along the ground, periodically sending up new upright branches. Strawberries produce numerous runners.

RuBP carboxylase/oxygenase (Rubisco): Enzyme that causes the combining of ribulose-bisphosphate with carbon dioxide during the light-independent reactions of photosynthesis. During photorespiration (see above), Rubisco causes the combining of ribulose-bisphosphate with oxygen. Rubisco is the most abundant enzyme on earth.

rusts: Type of parasitic pathogenic Basidiomycete fungi that have more than two types of spores in their life cycle. One of the stages in the life cycle causes lesions on the host plant in which are formed reddish-brown spores. Black stem rust of wheat is a notorious plant disease caused by a rust fungus.

S phase: That portion of the cell cycle when DNA is synthesized and the chromosomes replicate.

sagittate: Shaped like an arrowhead.

samara: Type of dry fruit that grows a flat wing. The seed in enclosed in a swollen region at one end. Maples and ashes produce samaras.

sand: Class of mineral particles of soil in which the particles are between 0.05 and 2.0 millimeters in diameter.

saprophyte: Type of fungus or plant that gets its nutrition by digesting dead plants. Many mushrooms grow as saprophytes.

sapwood: Lighter-colored wood toward the outside of a stem. See also heartwood.

saturated fats: Lipids in which many or all of the carbons in the fatty acid chains have hydrogen atoms bonded to them.

savanna: Biome type characterized by widely spaced trees separated by open, grassy regions.

scabrous: Having a rough surface.

scarification: Physical abrasion of the seed coat of a seed. Many seeds, especially of desert plants, have hard seed coats that must be scarified before water can get in to start germination. Occurs naturally when seeds are tumbled over rocks in running water, when seeds are blown over rock, or when seeds are chewed by insects.

schizocarp: Type of dry, indehiscent fruit made of several individual chambers that separate from one another when mature. The members of the celery and parsley family form schizocarps.

scion: Branch or twig that is grafted onto another plant, the stock.

 scleroid: Type of cell that has extremely thick and hard secondary cell walls and that is more or less spherical in shape. Also called stone cells. The “grit” in a pear is a mass of sclereids.

sclerenchyma: Simple tissue of plants in which the cells have extremely thick and hard secondary cell walls. Elongated sclerenchyma cells are fibers, and more or less spherical ones are sclereids.

sclerotium: Dried, dense mat of hyphae of a fungus.

scrub community: Plant community characterized by stunted trees and shrubs that may be widely spaced. Typical of poor soils.

second messengers: Part of the signaling pathways in a cell. The arrival of one signal at the cell surface begins a chain of events that can result in the production of multiple small molecules (second messengers). These, in turn, trigger other reactions, but due to their larger numbers, the original signal is now amplified.

secondary consumers: Carnivorous animals that eat herbivorous animals (primary consumers).

secondary growth: Growth in diameter of a stem or root resulting from divisions of the vascular cambium and the cork cambium. Secondary growth occurs after the section of stem or root has reached its maximum length (primary growth).

secondary metabolites (secondary products): Chemicals synthesized by a plant that are not part of the basic molecular structure of a cell. Chlorophyll is an example.

secondary phloem: Phloem produced by activity of the vascular cambium.

secondary wall: Plant cell wall formed inside of the primary cell wall after a cell has reached its mature size.
**secondary xylem**: Xylem produced by activity of the vascular cambium.

**seed banks**: Storage facilities where numerous strains of cultivated plants are kept as seeds. These seeds are preserved to maintain a large pool of genetic variation that may have been eliminated from modern highly inbred stocks.

**seed coat**: Outer layer of a seed.

**seed dispersal**: Process by which the seeds of a plant are distributed over a wide area, away from the parent plant. Many seeds are adapted for dispersal by wind or animals.

**seed germination**: Initiation of growth by the embryo of a seed. The emergence of the primary root is usually the first indication that germination has occurred.

**seed leaf**: A cotyledon in a dicot seed. These are the first leaflike structures to appear when the seed germinates.

**seed-scale complex**: The combination of bract, scale, and seed in a cone of a conifer.

**seedling**: A young plant, usually with at least one set of true leaves.

**seeds**: Mature ovules that contain an embryo and a source of nutrition for the growth of the embryo enclosed in a seed coat.

**selectively permeable membranes**: Membranes that permit water to pass easily but solutes in the water to pass very slowly, if at all.

**self-pollination**: When pollen from the anther of a flower lands on the stigma of the same flower.

**senescence**: Normal part of the aging process that results in the death of a plant organ or a whole plant.

**sensitivity**: In bacteria, the lack of ability to tolerate an antibiotic. Bacteria that are killed by ampicillin are said to be ampicillin-sensitive; those that are not killed are called ampicillin-resistant.

**sepal**: Member of the outermost whorl of flower parts.

**septate**: Divided into sections by partitions.

**septum**: A wall between two compartments.

**serial endosymbiotic theory**: Endocytosis (see above) that occurred by the progressive incorporation of one type of bacteria in an evolving eukaryotic cell, later followed by the incorporation of another type of bacteria.

**serrate**: Having a leaf margin with many small teeth.

**sessile leaf**: Leaf without a petiole that is attached directly to the stem.

**seta**: Stalk of a moss sporophyte.

**shade-tolerant**: Describes a species that is able to grow in low light intensity, such as on the floor of a forest.

**sheath**: Thin, leaflike structure that surrounds or encloses a plant part.

**shoot**: That part of the plant that includes the stem and leaves.

**short-day plant**: Plant that flowers under the influence of long, unbroken nights and short days. Chrysanthemums are an example of short-day plants.

**shrub**: Woody plant with multiple stems.

**sieve area**: Region on the wall of a sieve cell or sieve tube element in which are located numerous small pores.

**sieve cell**: Type of cell found in phloem of gymnosperms and lower vascular plants, characterized by end walls that lack sieve plates.

**sieve plate**: Location on the wall of a sieve tube element that has one or more sieve areas.

**sieve tube**: In phloem, a column of sieve tube elements arranged end to end and connected by sieve plates.

**sieve tube element**: Conducting cells of phloem typical of angiosperms, in which the end walls possess sieve plates.

**signal transduction**: Movement of a chemical signal from one part of a cell, such as the cell membrane, to a different part of a cell, such as the nucleus.

**silicle**: Type of dry fruit typical of the mustard family. It is short and broad, and divided lengthwise into two compartments.

**siliquae**: Type of dry fruit typical of the mustard family. It is elongated and divided lengthwise into two compartments.

**silt**: Class of mineral particles of soil that has particles with diameters between 0.002 and 0.05 millimeter.

**simple diffusion**: Movement of a substance from a region of higher concentration of the substance to a region of lower concentration of the same substance. Only the kinetic energy of the molecules is involved.

**simple fruit**: Fruit that develops from a single pistil.

**simple leaf**: Leaf that has an undivided blade. Orange leaves are an example.

**simple tissue**: Plant tissue composed of one type of cell.
single-copy DNA: Nonrepetitive DNA. Most genes are examples of single-copy DNA.
sink: Site to which a substance or energy travels.
siphonostele: Arrangement of xylem and phloem characterized by a column of pith running through the center of the stem or root.
sister chromatids: Result of replication of a chromosome. The two chromatids are held together at the centromere prior to separation during cell division.
smuts: Fungal diseases of plants in which sticky, dark-colored masses of asexual spores form from eruptions in the tissue of the infected plant.
softwood: Species of trees that lack fibers in their xylem. All conifers are softwoods.
solar tracking: Describes a plant whose flowers or leaves follow the sun from east to west during the day.
somatic hybrids: Plants that result from the fusion of two somatic (nonreproductive) cells.
soredia: Reproductive structures of a lichen that consist of tufts of hyphae combined with algal cells.
sorus (pl. sori): Cluster of sporangia found on the leaves of ferns.
species: Group of morphologically and physiologically similar organisms that are potentially capable of breeding with one another and are incapable of breeding with members of other groups.
specific epithet: The second name in the two-part Latin name of a plant species. In Quercus alba, the name alba is the specific epithet.
sperm: Haploid cells produced by the male gametophyte. A sperm fuses with an egg during the process of fertilization.
spermagonia: Structure in which nonmotile sperm are produced in some fungi and algae.
spermatogenous cells: Cells capable of dividing to form sperm.
spices: Aromatic flavorings derived from the dried seeds, fruits, or barks of a variety of plants.
spike: Inflorescence that has a long axis to which are attached sessile flowers.
spine: Highly modified leaf or part of a leaf that forms a sharp projection.
spirillum: One of the three basic morphological forms of bacteria. These bacteria are elongated, S-shaped, and possess flagella.
spongy parenchyma: Loosely packed, thin-walled photosynthetic cells located next to the lower epidermis in the interior of a leaf; also called spongy mesophyll.
sporangiophore: Small branch on which are formed sporangia.
sporangium (pl. sporangia): Plant organ in which are formed reproductive cells that grow directly into new plants without sexual fusion.
spore: Reproductive cell that grows directly into a new plant without sexual fusion. May be either haploid or diploid.
sporocarp: A hard case enclosing the sporangia of water ferns.
sporophyll: Leaf on which sporangia form.
sporophyte: The diploid generation in a plant having alternation of generations.
spring ephemerals: Herbaceous plants that flower in the spring for a brief period of time. In a forest, these appear before the trees leaf out. In a desert, they appear following winter rains.
springwood: Secondary xylem that forms during the first part of the growing season; often contains more and larger vessels and fewer fibers than summerwood.
spur: Elongated projection formed as part of a petal or petals.
stamen: Male reproductive structure in a flower.
staminate: Flower or cone that bears only pollen.
starch: Carbohydrate composed of long chains of glucose molecules. Starch is typically found as the storage product in seeds, roots, and underground stems.
stem: The usually aerial part of a plant on which are formed leaves and axillary buds.
stereile cell: Nonreproductive cell that forms the wall of sporangia and gametangia.
stereoids: Class of lipidlike organic compounds characterized by four rings of carbon atoms. Like hormones, they have effects on growth in very small quantities.
sticky ends: Refers to the ends of a piece of DNA that has been cut with a restriction enzyme.
stigma: Receptive top of a pistil where the pollen grains land.

stigmatic tissue: Tissue of a stigma.

stilt root: Adventitious root that grows downward from a branch into the soil and supports the branch. Red mangrove trees form stilt roots.

stinging hair: An epidermal hair that contains an irritating chemical.

stipule: Bladelike projections that usually grow in pairs from the base of the petiole of some kinds of leaves.

stock: Woody plant that receives a graft.

stolon: Rhizome that grows along the surface of the soil and forms roots at its nodes.

stomata (sing. stomate): Openings in the epidermis of leaves and green stems that allow gas exchange to occur.

stone cell: Isodiametric cells with extremely thick and hard secondary cell walls. Forms of sclerenchyma are found scattered in the flesh of pears and forming the hard shells of nuts.

stratification: Division of a plant community into layers, such as canopy, shrub, and herb layers of a forest. Also physiological conditioning of seeds or bulbs necessary before germination or flower production can occur. Stratification occurs during a period of a few to several weeks of cool, damp conditions.

stromatolite: Fossilized masses of cyanobacteria that represent some of the first evidence of photosynthetic life on earth.

structural gene: Gene that codes for a protein product.

style: Usually elongated portion of a pistil between the ovary and the stigma.

suberin: Waxlike substance that waterproofs the thick cell walls of cork cells and forms the Casparian strips of endodermis cells.

substrate: The substance, such as soil or bark, on which a plant grows. Also, in biochemical reactions, the chemical compound upon which an enzyme acts.

succession: Orderly progression of plant communities that replace one another over time at a given site.

sucker: Rapidly growing branch from an otherwise unbranched stem.

summerwood: Xylem tissue that forms in the later part of the growing season. It often has fewer and smaller vessel elements and more fibers than does springwood.

sustainable agriculture: Farming methods that do not destroy the ability of the land to produce future crops.

symbiont: Member of a symbiotic relationship.

symbiosis: Relationship involving two unrelated organisms that live together and impact each other. The relationship may benefit both or only one.

sympatric speciation: Evolution of two groups into separate species while living in overlapping geographic locations.

symplast: Interconnected cytoplasm of a plant composed of the cytoplasm of its cells and the plasmodesmata that connect those cells.

symplastic loading: Movement of substances from one cell to another via the symplast.

symplastic pathway: Route taken by substances as they are moved through the cytoplasm and plasmodesmata into other cells.

sympot: Movement of two solutes in the same direction at the same time. An example is the transport of sucrose and protons across a membrane.

synergids: Haploid cells at one end of an embryo sac that bracket the egg. The synergids have been found to signal the egg's location to the sperm.

systematics: The study of the naming and classification of plants on the basis of evolutionary relationships.

T-region (T-DNA): Portion of the Ti plasmid that is transferred into a plant cell by Agrobacterium. The T-region integrates into the plant genome.

taiga: Biome located across Canada, northern Europe, and northern Asia that consists of forests of spruces, firs, and birches.

tannin: Soluble phenolic substances, brown or black in color, that are produced by plants and used to tan hides or make ink.

tapetum: Nutritive cells found in sporangia.

taproot: A long, tapering root that is an elongation of the primary root of an embryo.

taproot system: Type of root system with one main root and many lateral branches that are much smaller in diameter than the main root.

taxon: Related group of organisms. A taxon may be small (species) or large (order, division).

taxonomy: Study of the relationships of plant groups to one another.

teliospores: Thick-walled resting spores of the pathogenic rust and smut fungi.
telium: Lesion on a plant in which the teliospores of a pathogenic fungus are formed.
telomeres: Areas of repetitive DNA occurring at the ends of chromosomes. The telomeres protect the coding parts of the chromosomes from erosion during cell division.
telophase: The final stage of M-phase of cell division when nuclear envelopes reform around the two groups of chromosomes.
temperate deciduous forest: Biome located in eastern North America south of the taiga, central Europe, and eastern China, characterized by forests of tree species, most of which lose their leaves every autumn.
temperate mixed forest: A subdivision of the temperate deciduous forest in which pines share importance with deciduous trees. These forests are usually found on sandy soils in the southeastern United States.
tendril: Modified leaf or stem that is long, slender, and highly flexible. They coil around objects with which they come in contact to support the tendril-bearing plant.
tepal: One of the units of the perianth that is not differentiated into petals and sepals in flowers such as tulips.
terminal bud: Structure at the tip of a stem or branch consisting of the stem apical meristem, usually covered by bud scales.
terminal bud scale scar: Scar left on a twig when the scales covering the terminal bud are shed at the beginning of the growing season.
terpenoids: Very large and diverse group of organic molecules produced by plants. The group includes carotenoid pigments, latex, and essential oils that give distinctive odors and flavors.
testcross: In genetics, a mating between an organism showing one or more dominant traits with a homozygous recessive organism of the same species.
tetrad: Chromosome configuration formed by synapsis of two replicated homologous chromosomes during Prophase I of meiosis.
tetrasporophyte: Stage in the life cycle of red algae during which meiosis occurs.
thalli (sing. thallus): The bodies of algae, fungi, and bryophytes that are not differentiated into stems, roots, or leaves.
theca: Stiff covering of some of the dinoflagellates and other unicellular organisms.
thermophile: Bacterium that lives in very hot water, such as in the hot springs at Yellowstone National Park.
thigmomorphogenesis: Growth pattern found in vines caused by tendrils touching and curling around supporting objects.
thigmomonastic movements: Movement of tendrils that occurs until they come in contact with and twine around supporting objects.
thigmotropism: Growth response in a plant resulting from the plant touching other objects.
thorn: Sharp woody projection from a stem.
thylakoids: Chlorophyll-containing membrane sacs in a chloroplast. A granum is a stack of thylakoids.
Ti plasmid: Circle of DNA found in the bacterium that causes crown gall tumor. Genes on the plasmid enable Agrobacterium to stimulate cell division and cause the formation of a tumor.
tissue: Group of similar cells that cooperate to carry out a particular function. Epidermis is an example.
tissue culture: Growth of cells in a laboratory container. The cells are supplied with nutrient media and growth factors.
tissue system: A tissue or group of tissues that function together as a unit. The dermal system, vascular system, and the ground tissue system are usually recognized.
tomentose: Covered with dense, woolly hairs.
tonoplast: Membrane that surrounds the vacuole in a plant cell; also known as a vacuolar membrane.
torus: In the pits of tracheids of some conifers, a thickening in the primary cell wall. It may function in the movement of water in and out of a tracheid.
totipotency: Ability of a cell to differentiate into any kind of mature cell in a plant. Cells of the apical meristem are totipotent.
trace element: Chemical element required in very small quantities for plant growth. Examples are molybdenum, boron, copper, manganese, and zinc.
tracheary elements: Any of the conducting cells found in xylem.
tracheid: Conducting cell of xylem whose end walls have pits but not pores. These are found in all vascular plants and are the only kind of tracheary elements in conifers.
tracheophytes: Classification category that includes all plants containing xylem and phloem.
**transcription:** Transfer of information from DNA to RNA.  
**transduction:** Use of a virus to carry new genetic information into a cell.  
**transfer cell:** Special cells of the phloem that facilitate loading of sugars into sieve tube elements.  
**transfer RNA (tRNA):** RNA that associates with specific amino acids and positions them at the ribosome in the order specified by messenger RNA.  
**transformation:** Uptake of DNA by a bacterium. Transformation usually results in the bacterium acquiring new genetic information, such as that which causes antibiotic resistance.  
**transgenic plants:** Plants that have had their original genetic information altered by the addition of new genes.  
**transition region:** Region in the axis of a plant where the stem changes into the root.  
**translation:** Process by which the information coded in messenger RNA is converted into a protein or other polypeptide product.  
**translocation:** Movement of dissolved substances from place to place in the phloem.  
**transmembrane proteins:** Proteins that are embedded in a membrane and have one terminus outside of the cell and the other terminus inside the cytoplasm. Some signal receptors are transmembrane proteins.  
**transmitting tissue:** Tissue in the style of a pistil through which a pollen tube grows on its way to the ovule in the ovary.  
**transpiration:** Evaporation of water from the leaves and stems of plants. Most transpiration occurs through open stomata.  
**transpiration stream:** Moving column of water through the xylem of stems and leaves. The movement is powered by transpiration.  
**transpirational pull:** Force created by evaporation from the top of a column of water in a plant. This force causes the movement of water up a tree from the roots to the leaves.  
**transport proteins:** Proteins that move specific solutes across cell membranes. Often the expenditure of cellular energy is needed for this transport.  
**transposon:** Mobile segment of DNA that is able to move among the chromosomes in a nucleus.  
**tree:** Woody plant of substantial size, usually consisting of a single trunk and multiple branches.  
**trichome:** Multicellular hairlike structure that grows out from the epidermis of leaves and herbaceous stems.  
**triglycerides:** Lipid composed of glycerol attached to three long-chain fatty acids.  
**triticale:** Allotetraploid grain bred from wheat and rye. It combines the hardiness of rye with the productivity of wheat.  
**trophic levels:** Positions at which specific organisms obtain their nutrition within a food chain. Plants usually occupy the first trophic level.  
**tropical rain forest:** Biome found in tropical regions throughout the world that experience rainfall year-round. These are the most biodiverse ecosystems, often containing thousands of species of plants in a single acre.  
**tropism:** Plant growth response to an external stimulus. The plant may grow toward or away from the stimulus.  
**tube cell:** One of the two cells of a pollen grain. The tube cell elongates to form the pollen tube.  
**tuber:** Large, fleshy underground stem where food is stored. A white potato is an example.  
**tuberous root:** Root that possesses swollen regions containing stored food. Sweet potatoes are an example.  
**tunica-corpus:** Arrangement of the cells of an apical meristem in which the outer two layers of cells, the tunica, are distinct from a mound of cells beneath them, the corpus.  
**turgid:** Describes a cell whose central vacuole is full, causing the cytoplasm and cell membrane to be pressed against the cell wall. The crispness of carrots and celery results from their cells being turgid.  
**turgor pressure:** Pressure of the cell wall against the cell contents that is generated when a plant cell is turgid.  
**twig:** Youngest portion of a branching stem.  
**tyloses:** Projections of parenchyma cells into tracheids and vessel elements that appear as inclusions.  
**type specimen:** Herbarium specimen designated by the author of a new species as being typical of that species.  
**umbel:** Flat-topped inflorescence in which each of the tiny flowers is at the end of its own stalk. Found in the parsley family.  
**unilocular sporangia:** In brown algae, the sporangium in which haploid spores are formed by meiosis.
unsaturated lipids: Lipid molecules in which many of the carbons of the fatty acid chains are connected by double bonds. These contain less hydrogen than do saturated lipids.

urediniospores: Spores produced in the life cycle of a rust fungus that are capable of reinfecting the host plant.

uredinium: In the life cycle of a rust, the orange-colored lesion where urediniospores are formed.

vacuole: Fluid-filled space surrounded by a membrane. In many plant cells, there is a large central vacuole.

variegation, variegated: Refers to leaves that have both green and non-green areas. Only the green areas are photosynthetic.

vascular bundle: One of the strands of xylem and phloem that run lengthwise in a herbaceous stem.

vascular cambium: Meristematic tissue that forms a cylinder separating xylem and phloem in stems and roots. The vascular cambium divides to form secondary xylem and secondary phloem.

vascular cylinder: All of the xylem and phloem in the center of a root or stem.

vascular plant: Any plant that has xylem and phloem as conducting tissues. Excludes the algae, bryophytes, and fungi.

vascular ray: Flat group of cells, several to many cells high and one to several cells thick, found in woody stems. Rays are oriented in lines running from the center of a stem outward through the xylem and phloem and appear as radial lines in a cross-section.

vascular system: The interconnected network of xylem and phloem throughout a plant.

vascular tissue: Tissue capable of conduction and support, including both xylem and phloem.

vein: Bundle of xylem and phloem that is part of the vascular tissue network of a leaf.

velamen: Outer layer of cells covering the aerial root of an epiphytic orchid.

venter: Swollen base of an archegonium that contains the egg.

vernalization: Physiological process in which a seedling plant is exposed to several weeks of cool temperatures. This exposure is necessary to induce the formation of flowers in that plant.

vesicle: Small, fluid-filled bubble surrounded by membrane and located in the cytoplasm.

vesicle-mediated transport: Movement of substances in vesicles, often from the Golgi body to the cell membrane, where the vesicle releases its contents.

vessel: Hollow tube formed from vessel elements stacked one on top of another. Vessels carry water and dissolved minerals.

vessel elements (also called vessel members): Cells of xylem that are hollow and dead at maturity. They have secondary cell walls with large open pores in the end walls.

viability: The capacity to live and develop; an organism is said to be viable if it can live and thrive.

virion: A virus particle consisting of genetic material surrounded by a protein coat.

viroid: Small, viruslike infectious molecules of RNA without protein coats.

water conduction: Movement of water, usually in xylem, from place to place in a plant.

water-holding capacity: Ability of a soil to hold water against the pull of gravity.

water loss: Evaporation of water from plant surfaces.

water potential: Free energy of water in a substance, such as a sugar solution. The more water relative to dissolved substances, the higher the water potential of the solution. Pure water has the highest possible water potential.

water storage: Retention of water in the vacuoles of parenchyma cells. Succulent plants, such as cacti, retain large amounts of water following rain for later use.

water uptake: Movement of water from soil into a plant.

whorled: Arrangement of plant parts, such as leaves on a stem. A whorl consists of three or more parts in a ring.

wood: Secondary xylem composed of vessels, fibers, and tracheids.

xanthophyll: Type of carotenoid pigment, yellow in color.

xerophyte: Plant adapted to dry habitats.

xylem: Vascular tissue composed of vessels, fibers, and tracheids that is responsible for upward conduction of water and dissolved substances (usually minerals). Xylem is also the supporting tissue of stems.

xylem ray: Vascular ray found in secondary xylem.

yeasts: Single-celled fungi that reproduce by budding. They are able to ferment sugar into carbon
dioxygen and alcohol and therefore are the foundation of both the baking and brewing industries.

zooplankton: Small animals, often single-celled, that float or swim weakly.

zoanthellae: Algae that live symbiotically in coral and some other animals.

zygomorphic flower: Flower that is bilaterally symmetrical. Snapdragon flowers are an example.

zygosporangium: In bread molds and their relatives, a structure in which zygospores are formed from the fusion of gametes.

zygospore: Thick-walled spore with multiple nuclei that develops after the fusion of gametes in the life cycle of bread molds and their relatives.

zygote: A fertilized egg formed by the union of a haploid egg and sperm.

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BIBLIOGRAPHY

This annotated, selected bibliography is intended to provide a representative sample of books for supplemental reference, reading, and study on plant life. All of the selected works were readily available at libraries or bookstores at the time of compilation. Most are suitable for general audiences; however, some cover complex topics and require background in the sciences for maximal understanding. Many are illustrated. The books are grouped into broad subject areas and are listed alphabetically by author or by editor.

Jeannie P. Miller

General Reference Works


Cole, Trevor, Christopher Brickell, and Elvin McDonald, eds. *American Horticultural Society Encyclopedia of Gardening: The Definitive Practical Guide to Gardening Techniques, Planning, and Maintenance*. New York: Dorling Kindersley, 2000. This definitive guide is organized into four sections, including creating a garden, which discusses garden style, scale, proportion, and use of color and texture; a plant catalog, profiling four thousand plants by plant type, growing season, and color of flowers or foliage; a plant dictionary of more than eight thousand terms; and an index of about twenty-five hundred common names.

Coombes, Allen J. *Dictionary of Plant Names*. Port Jervis, N.Y.: Lubrecht & Cramer, 1985. Main entries for common plants are alphabetically arranged by genus name, with species listed under each genus. Includes references, from common names and synonyms to scientific names. Gives pronunciation, meaning, derivation of scientific name, family, common name, country of origin, and hardiness.

Gledhill, David. *The Names of Plants*. 2d ed. New York: Cambridge University Press, 1989. The first part chronicles how the naming of plants has changed over time and why the changes were necessary. The second part is a glossary of genus and species names with brief definitions.

standard horticultural reference originally published in 1992. Comprehensive in scope, its authority is assured by the credentials of the 250 internationally recognized contributors. Presents botanical accounts of some fifty thousand plants grown worldwide in domestic gardens, commercial operations, or in special collections.


Stearn, William T. *Stearn's Dictionary of Plant Names for Gardeners.* Poole, Dorset, England: Cassell PLC, 1996. This technical dictionary includes concise definitions, six thousand botanical terms, and three thousand common names with cross references. Covers plant names, Greek and Latin botanical terms and derivations, and individuals associated with plant nomenclature. Added features are introductory essays on botanical and vernacular names.


**Biotechnology**


Breeding and Genetics
Agrawal, Rattan Lal. *Fundamentals of Plant Breeding and Hybrid Seed Production*. Enfield, N.H.: Science, 1998. Presents the art and science of plant breeding, including conventional breeding techniques, tissue culture, genetic engineering, breeding for specific traits, release and maintenance of varieties, plant variety protection, and production of hybrid seed.


Cassells, Alan C., and Peter W. Jones. *The Methodology of Plant Genetic Manipulation: Criteria for Decision Making*. Hingham, Mass.: Kluwer Academic, 1995. Presents classical breeding methods as well as new techniques based on the integration of plant cell biology and molecular biology. The fifty-five papers also explain how the choice of breeding technique is limited by the breeding system of the crop, the breeding objective, and applicable tissue culture systems.


Endangered Species and Conservation


Beacham, Walton, Frank Castronova, and Suzanne Sessine, eds. *Beacham’s Guide to Endangered Species of North America*. Farmington Hills, Mich.: Gale Group, 2000. Provides basic information on all (about twelve hundred) plants and animals on the U.S. Fish and Wildlife Service list of federally endangered or threatened species as of April, 2000. Entries are arranged by taxonomic group and include both common and scientific names, descriptions, behavior, habitats, distribution, threats, conservation and recovery, contacts, and references. Most entries include color photographs.


Evolution and Ecology


and environmental condition necessary for germination of more than thirty-five hundred species of trees, shrubs, vines, and herbs.


Beck, Charles B., ed. Origin and Evolution of Gymnosperms. New York: Columbia University Press. Emphasizes the evolutionary patterns and phylogenetic relationships of gymnosperms and presents recent data on many groups or subgroups.

Bell, Peter R. Green Plants: Their Origin and Diversity. 2d ed. New York: Cambridge University Press, 2000. This comprehensive reference to the plant kingdom provides concise accounts of all algae and land plants and covers topics from cellular structures to life cycles and reproduction. Includes new information on plants previously known only as fossils and reflects current thinking on the origin of major plant groups.


Gifford, Ernest M. Morphology and Evolution of Vascular Plants. 3d ed. Gordonsville, Va.: W. H. Freeman, 1989. This is a thoroughly updated edition of a widely used and popular text used in comparative study of extinct and extant vascular plants.


Morley, Robert J. Origin and Evolution of Tropical Rain Forests. New York: Jossey-Bass, 2000. This is the first book to examine the evolution of tropical rain forests on a continent-by-continent basis. It uses a long-term geological timescale, beginning some 100 million years ago with the origin of angiosperms and concluding with the destruction of rain forests in the twentieth century.

Pearson, Lorentz C. The Diversity and Evolution of Plants. Boca Raton, Fla.: CRC Press, 1995. This textbook presents a complete and through classification of the plant kingdom. Emphasizes evolution as the basis of diversity and focuses on ecology and conservation. Each plant class is introduced, followed by descriptions of its members, including origin, ecological requirements and contributions, economic uses, and potential in scientific research.


Surrey, W., L. Jacobs, and Joy Everett. Grasses: Systematics and Evolution. Silver Spring, Md.: CSIRO, 2000. This compilation of proceedings papers highlights the progress and new findings relative to grass evolutionary biology. The forty-one papers are arranged thematically and include taxonomy, physiology and ecology, breeding systems, and biogeography.

**Plant Products**

Press, 1995. The contributed papers survey the literature on medicinal uses of tropical plants. Coverage includes ethnobotany, biodiversity, ethnomedicine, and pharmacognosy. Regional work covers Africa, Asia, the Caribbean, and Central and South America. This readable work should appeal to the general public.


Crackower, Sydney, Barry A. Bohn, and Rodney Langlinais. *Two M.D.’s and a Pharmacist Ask, “Are You Getting it Five Times a Day?”: Fruits and Vegetables, Enzymes, Antioxidants, and Fiber*. Rev. ed. Prescott, Ariz.: One World Press, 1999. This is an easy to read presentation on the benefits of fruits and vegetables in the human diet. Sample chapters in the table of contents include free radicals, aging and cancer; beta-carotene, promoter of healthy bodies; vitamin C for support and shape; vitamin E, the most versatile antioxidant; fiber and the digestive system; aging and the retina; the power of garlic; and indoles and breast cancer.


**Plant Types**

Anderson, Miles. *The Ultimate Book of Cacti and Succulents*. London: Lorenz Books, 1998. The botany and classification of cacti and succulents, as well as their diversity, is detailed in this comprehensive volume. Features a photographic plant directory and a section on cultivation, including buying and techniques for planting propagation, grafting, and maintenance.
Armitage, Allan M. *Herbaceous Perennial Plants: A Treatise on their Identification, Culture, and Garden Attributes*. 2d ed. Champaign, Ill.: Stipes, 1997. Describes ordinary and rare perennials, with a limited number of photographs and other illustrations.


*Bota\'nica\'s Annuals and Perennials*. San Diego: Laurel Glen, 1999. A comprehensive alphabetic guide to more than two thousand flowering plants, including annuals, biennials, and perennials. Features some twenty-five hundred color illustrations as well as a handy reference table and an index of common names and synonyms.

*Bota\'nica\'s Trees and Shrubs*. San Diego: Laurel Glen, 1999. Identifies more than two thousand plants and provides information on cultivation in different climates and soil conditions. Format and added features are similar to the work on annuals and perennials.


Dirr, Michael A. *Dirr's Hardy Trees and Shrubs: An Illustrated Encyclopedia*. Portland, Oreg.: Timber Press, 1997. This illustrated guide describes the best trees and shrubs for cooler climates, that is, U.S. Department of Agriculture Hardiness Zones 3 to 6. Includes more than five hundred species, some seven hundred additional cultivars, and more than sixteen hundred color photographs.


Hickey, Michael, and Clive King. *Common Families of Flowering Plants*. New York: Cambridge University Press, 1996. Introduces students of botany or other plant sciences to twenty-five commonly occurring families of flowering plants, with selection based on economic,
ornamental, or ecological importance. Entries for each family include distribution, classification, general features, and economic importance as well as detailed descriptions of a representative species.

Jones, David L. *Encyclopedia of Ferns*. Vol. 1. Portland, Oreg.: Timber Press, 1992. The botanical information and descriptions of more than seven hundred ferns are intended for a general audience. Worldwide in scope, the volume covers both tropical and temperate ferns. Includes color plates, line drawings, glossary, and an international list of fern societies and study groups.


**Processes and Structures**


American Horticultural Society. *Plant Propagation*. Edited by Alan Toogood. New York: Dorling Kindersley, 1999. This practical, beautifully illustrated guide details reproduction of plants by seeds, cuttings, grafting, division, and other methods of propagation. The extensive introduction explains the botany and physiology involved in propagation, while the encyclopedic, alphabetical entries describe appropriate techniques for propagation of more than one thousand plants.


Fenner, Michael, ed. *Seeds: The Ecology of Regeneration in Plant Communities*. 2d ed. New York: Oxford University Press, 2001. The sixteen chapters written by international experts cover various pertinent topics, such as seed size, seedling establishment, fire and fire gaps in regeneration, maternal effects in seed development, the role of temperature in dormancy and germination, and the influence of seedling regeneration on plant communities and ecosystems.


Press, 1999. This is an advanced treatise, providing a clear and concise introduction to a complex process. Includes line illustrations and color plates.


**Special Adaptations**


Chapman, A. R. *Functional Diversity of Plants in the Sea and on Land*. Sudbury, Mass.: Jones & Bartlett, 1986. Introduces the plant taxa and examines the history of plant life from an aquatic environment to various land types. Topics include phytoplankton in the sea, seaweeds, terrestrial conditions and plant life, mechanical properties of land plants, water absorption and loss, carbon dioxide exchange and vascular transport, drought avoidance in desert plants, reproduction in vascular plants, systematic survey, and evolutionary history of vascular plants, bryophytes, and fungi.


dred species of low-maintenance and drought-resistant plants. Includes 430 color photographs as well as useful charts to assist in selection of appropriate plants.

Eleuterius, Lionel N. *Tidal Marsh Plants*. Dunlap, Ill.: Firebird Press Books, 1990. Describes four hundred vascular plants that grow in the salt marshes along the Gulf and Atlantic coasts of the United States. Entries include drawings of plants, their location, scientific and common names, and identifying traits.

Redington, Charles B. *Plants in Wetlands*. Dubuque, Iowa: Kendall/Hunt, 2000. Considers the biological interactions among plants and the full range of animal groups in wetlands. Describes more than one hundred plant species and includes a simple wetlands delineation method and a key to wetland communities as well as appendices on spiders, community interactions, and human and economic uses.


Miscellaneous Texts

Musgrave, Toby, Christina Gardner, and William Musgrave. *The Plant Hunters: Two Hundred Years of Adventure & Discovery Around the World*. London: Ward Lock, 1999. Details the adventures of daring explorers as they gathered plants from all over the world and introduced some seven thousand plant species into habitats that they would never have reached naturally. Features Sir Joseph Banks, who established a “systematic, worldwide plant hunting program” during the eighteenth century at Kew Gardens, London, as well his protégé Francis Mason and seven others who carried this work into the nineteenth century.


WEB SITES

The sites listed below were visited by the editors of Salem Press in March of 2002. Because URLs frequently change or are moved, their accuracy cannot be guaranteed; however, long-standing sites—such as those of university departments, national organizations, and government agencies—generally offer links when sites move or otherwise may upgrade their offerings and hence remain useful. Moreover, sites often provide lists of links to other useful resources on the Internet. Sites with an affiliation of N/A are, to our knowledge, unallied, mounted by an individual person, or “uncredited.”

Roger Smith

GENERAL

AgNIC Plant Science Home Page
http://www.unl.edu/agnicpls/agnic.html
Affiliated with: University of Nebraska, Lincoln
• An information resource that fields questions from users and posts information about genetics, taxonomy, plant protection, and crop products, with links and directions to e-journals and e-newsletters.

The Biota of North American Program
http://www.bonap.org/
Affiliated with: North Carolina Botanical Garden, University of North Carolina, Chapel Hill
• Maintains a database of taxonomic, nomenclatural, and biogeographical data on North American vascular plants (and vertebrates) in order to develop a unified digital system for assessing the continent’s species (north of Mexico).

Botanical Ecological Unit
http://www.fs.fed.us/biology/plants/beu.html
Affiliated with: U.S. Forest Service
• A virtual office with information on rare and threatened U.S. plants and environmental initiatives and with links to similar sites, experts, and publications.

Botanical Electronic News
http://www.ou.edu/cas/botany-micro/ben/
Affiliated with: N/A
• A professional e-journal covering a different topic in botany each month.

Botanical Glossaries
Affiliated with: Centre for Plant Biodiversity Research
• A list of links to online glossaries of botanical terms contained on Web sites in Australia and the United States.

Botany
http://www.nmnh.si.edu/departments/botany.html
Affiliated with: Department of Systematic Biology, Smithsonian Institution
• An extensive directory of online and print resources devoted to all aspects of botany, maintained by America’s premier natural history institution. Contains a catalog of more than three thousand botanical illustrations.

Botany.com
http://www.botany.com/
Affiliated with: N/A
• An online encyclopedia for gardeners maintained by an e-commerce company. The site offers information about common and botanical names, pests and diseases, leaf shapes, and a botanical dictionary.

Botany Online: The Internet Hypertextbook
http://www.biologie.uni-hamburg.de/b-online/
Affiliated with: University of Hamburg, Germany
• A comprehensive online information source featuring the Internet Library, which teaches users about topics in botany and related subjects, directions about how to use the World Wide Web productively, and links. Designed for university students.
Centre for Plant Architecture Informatics
http://www.cpai.uq.edu.au/
Affiliated with: University of Queensland, Australia
- A sophisticated site containing images, virtual plants, and animations created by a collaboration of biologists, mathematicians, and computer scientists in order to aid research in the three-dimensional dynamics of plants.

Delta
http://biodiversity.uno.edu/delta/
Affiliated with: CSIRO, Australia
- A site for scientists involved with the DEscription Language for TAxonomy, or Delta, which records taxonomic descriptions of plants for computer analysis. Offers information on plants, lichen, soil, and some insects, primarily species in Australia and North America.

Electronic Sites of Leading Botany, Plant Biology, and Science Journals
http://www.e-journals.org/botany/
Affiliated with: e-journals.org
- Lists links to 750 journals from throughout the world devoted to plant sciences or related topics.

Food and Agriculture Organization
http://www.fao.org/
Affiliated with: United Nations
- Extensive informational resources, including texts, photos, and statistics, concerning agriculture and forestry, among other topics, for all users, in English, French, Arabic, and Chinese.

GardenNet
http://gardenet.com/
Affiliated with: N/A
- An information and shopping resource for gardeners listing plants by species and equipment, garden types, and events.

Index Nominum Genericorum
http://rathbun.si.edu/botany/ing/
Affiliated with: The Smithsonian Institution and the International Association for Plant Taxonomy
- Provides a search engine for a database of the generic names of all recorded plants. The database offers information about their classification and nomenclature and bibliographical citations.

Integrated Taxonomic Information System
http://www.itis.usda.gov/
Affiliated with: U.S. Department of Agriculture
- Guides users to taxonomic information, focusing especially on North American species but also with links to resources worldwide. Its search engine supports searches by common or scientific name.

International Organization for Plant Information
http://iopi.csu.edu.au/iopi/
Affiliated with: International Union of Biological Sciences
- Affords general botanical information through databases and links to similar sites and hosts three projects: the Global Plant Checklist, Species Plantarum Project (concerning publications about plants of the world), and Database of Plant Databases. Designed with scientists in mind.

The International Plant Names Index
http://www.ipni.org/
Affiliated with: The Royal Botanic Gardens, Kew; Harvard University Herbaria; Australian National Herbaria
- Contains a database of the names and bibliographical references for all recorded seed plants, continually updated, for general use.

Internet Directory for Botany
http://www.botany.net/IDB
Affiliated with: SHL Systemhouse, Edmonton, Canada
- Offers alphabetical and subject category searches for botanical information in Web sites of arboreta, botanical gardens, herbaria, botanical societies, and botanical research institutes. Created and maintained by scientists in the United States, Finland, and Canada primarily for colleagues worldwide.

MedBioWorld
http://www.medbioworld.com/bio/journals/plants.html
Affiliated with: N/A
- Provides links to more than one hundred journals about the plant sciences from throughout the world and has search engines for abstracts, articles, and images.
Natural Perspective
http://www.perspective.com/nature/index.html
Affiliated with: N/A
- For general users, a site describing the characteristics of organisms in four taxonomic kingdoms, including one for plants and one for fungi.

Plant Facts
http://plantfacts.ohio-state.edu/
Affiliated with: Ohio State University
- Hosts two search engines: one that guides users to university and government sites in the United States and Canada for answers to plant-related questions; a second helps prospective students obtain admissions and degree information from forty university departments in the United States.

Plant Information Systems
http://www.wes.army.mil/el/squa/cdroms.html
Affiliated with: Army Corps of Engineers
- Access page to two repositories of information: one covering identification and management of more than sixty aquatic and wetlands plant species; another concerning more than sixty noxious and nuisance species.

The Plants Database
http://plants.usda.gov/topics.html
Affiliated with: Natural Resources Conservation Service, U.S. Department of Agriculture
- Performs searches of the PLANTS database for taxonomy, life form and nativity, legal status, images, and conservation plant characteristics, all for the general public. Also informs farmers and homeowners about alternative crops; provides the taxonomic hierarchy for any vascular plant, North American nonvascular plant, or lichen; discusses the usage, management, and importance of culturally significant plants; and lists hundreds of links.

Species 2000
http://www.sp2000.org
Affiliated with: Global Biodiversity Information Facility
- Part of the attempt to catalog all species of life on earth, this site offers a species locator, catalog of life, checklist, and name location service and explains the initiative’s technical plan. Also, lists links to mirror sites.

The Virtual Library of Botany
http://www.ou.edu/cas/botany-micro/www-vl/ 
Affiliated with: University of Oklahoma
- Lists hundreds of Web links and newsgroups worldwide that treat topics in botany, agriculture, and other biosciences.

W3 Tropicos
http://mobot.mobot.org/W3T/search/image/imagefr.html
Affiliated with: Missouri Botanical Gardens
- Hosts a search engine for information on plant species and a large resource list, arranged by plant taxa, of drawings, photos of living plants, and photos of specimens in the holdings of museums and libraries.

AGRICULTURE, FORESTRY, AND HORTICULTURE

AGRICOLA
http://www.nal.usda.gov/ag98/
Affiliated with: National Agricultural Library, U.S. Department of Agriculture
- The online catalog for the National Agricultural Library’s holdings—including books, serials, and audiovisual materials—about plants. The holdings themselves are not available online but can be delivered by mail.

Center for Subtropical Agroforestry
http://cstaf.ifas.ufl.edu/
Affiliated with: University of Florida
- A research resource for scientists and landowners developing the technology of raising trees as crops, with links and a newsletter.

CPM Magazine
http://www.crop-net.com/cpmmagazine/
Rooms/Home Page
Affiliated with: N/A
- Collects and posts information for the agricultural industry about weeds, diseases, and insects affecting crops.

4Plants.com
http://4plants.4anything.com/
Affiliated with: 4Anything Network
- Maintains information about gardening and medicinal and poisonous plants for the general public.
Hortiplex
http://plants.gardenweb.com/plants/
Affiliated with: Garden Web
• A search engine dedicated to browsing the entire Web for information about plants that filters out nonplant-related hits. Designed for nonspecialists, with a glossary of botanical terms.

Internet Guidepost for Plant Production
http://www.fb.u-tokai.ac.jp/plant/production
Affiliated with: Tokai University, Japan
• A search engine for resources about agriculture, horticulture, botany, and gardening worldwide, with an emphasis upon Japan, for plant sciences researchers.

National Agroforestry Center
http://www.unl.edu/nac/
Affiliated with: U.S. Department of Agriculture
• Instructs public on agroforestry, which combines agriculture and forestry technologies for sustainable land use.

National Plant Germplasm System
http://www.ars-grin.gov/npgs/
Affiliated with: U.S. Department of Agriculture
• Supports a cooperative effort of federal, state, and private organizations helping scientists preserve the genetic diversity of crop plants. Offers search engines concerning crop science, plant variety, and taxonomy and accepts requests for germplasm (genetic material) for research.

Plant Search
http://www.ag.auburn.edu/landscape/database/search.php3
Affiliated with: Auburn University
• Provides a database allowing users to type in common names and call up color photos, descriptors, and information about the horticultural use of plants.

Plants for a Future
http://www.scs.leeds.ac.uk/pfaf/index.html
Affiliated with: N/A
• Contains articles, fact sheets, links, and a database of about seven thousand plants, all to promote research and provide information on ecologically sustainable horticulture. Maintained by a British charitable organization.

BOTANICAL GARDENS AND COLLECTIONS

Botanical Garden and Botanical Museum Berlin-Dahlem
http://www.bgblm.fu-berlin.de/
Affiliated with: Free University, Berlin, Germany
• An extensive collection, begun more than three hundred years ago, and among the world’s largest today. This home page tells users about its plants, events, the affiliated museum, and research at the site.

Botanique
http://www.botanique.com/
Affiliated with: N/A
• A guide to gardens, arboreta, and nature sites for the public. It lists more than 2,300 in North America, with a search program by type of facility or by state, and has a list of events and links.

Desert Botanical Garden
http://www.dbg.org/
Affiliated with: N/A
• A Phoenix, Arizona, facility that opened in 2002. The site covers the garden’s collection and events and has information about desert gardening in general, research, and conservation.

Lady Bird Johnson Wildflower Center
http://www.wildflower.org/index.html
Affiliated with: N/A
• Although concerned primarily with wildflowers in Texas, the Web site for the former first lady’s botanical center is well designed and offers information on species and a special page for children.

Missouri Botanical Garden
http://www.mobot.org/
Affiliated with: N/A
• A leading American botanical garden, located in St. Louis. The Web site presents information about the collection as well as help to gardeners and pages devoted to its history, horticulture, the Shaw Nature Reserve, images, and a schedule of plants in bloom.
Montreal Botanical Garden
http://www2.ville.montreal.qc.ca/jardin/en/menu.htm
Affiliated with: N/A

- A well organized Web site, listing information about the collection, activities, and scientific programs and with images of particularly lovely specimens, although some of the related text is available only in French.

The National Garden
http://www.nationalgarden.org/
Affiliated with: United States Botanical Garden

- Located in Washington, D.C., the oldest continuously operated botanical garden in the United States. The Web site is devoted to the collection and its associated facilities.

National Tropical Botanical Garden
http://www.nthg.org/
Affiliated with: N/A

- An association of three preserves and four gardens in south Florida and Hawaii. The site contains information about the location, collections, and events schedule for each facility, a generous summary of each issue of Plant Talk, the organization’s magazine, and pages featuring news stories and research.

The New York Botanical Garden
http://www.nybg.org/
Affiliated with: N/A

- Describes the extensive gardens, located in the Bronx, New York City, and activities there but also maintains pages about gardening and data on plants.

Royal Botanical Gardens
http://www.rbg.ca/
Affiliated with: N/A

- Located in Ontario, Canada’s premier botanical garden. The home page concerns the collection, activities, and educational resources.

Royal Botanic Gardens, Kew
http://www.rbgkew.org.uk/index.html
Affiliated with: RBG, Kew

- Home page of one of the most prestigious and scientifically successful botanical gardens in the world, offering database resources consonant with its mission to develop worldwide collections, foster research, support conservation, and inform the general public. Major categories of information include science and horticulture, botanical collections, conservation and wildlife, education, and data and publications.

University of California Botanical Garden
http://www.mip.berkeley.edu/garden/
Affiliated with: University of California, Berkeley

- Introduces users to the extensive botanical collection and its history.

What Are Herbaria?
http://www.rom.on.ca/biodiversity/herbaria/herbwhat/html
Affiliated with: Centre for Biodiversity and Conservation Biology

- Explains the history and nature of collections of labeled, preserved plant specimens and offers extensive information about those in the Centre’s collection.

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**FLORA**

**Bryophytes**
http://bryophytes.plant.siu.edu/index.html
Affiliated with: Southern Illinois University at Carbondale

- Teaches about mosses, liverworts, and hornworts and gives information to those interested in studying them at Southern Illinois University in Carbondale’s Department of Plant Biology.

**Checklist of World Ferns**
http://homepages.coverock.net.nz/~bj/fern/
Affiliated with: N/A

- Maintains well-ordered lists of information about the classification and description of ferns and their distribution worldwide.

**Dendro Home**
http://www.snr.vt.edu/dendro/dendrology/main.htm
Affiliated with: Virginia Polytechnic and State University

- Displays basic facts and photos of trees and tree structures for North American species and encourages users to ask questions of Dr. Dendro, the resident tree expert.
Find Wild Flowers
http://www.reticule.co.uk/flora/
Affiliated with: N/A
- A Web site for British flora. It enables users to identify wildflowers they have found by filling out a questionnaire that a computer program analyzes. It also offers a checklist of plants to be found in specific habitats.

Grassland Index
Affiliated with: Food and Agriculture Organization, United Nations
- Searches database by genus, Latin name, or common name for information on grasses and legumes. Includes a bibliography and photos of selected species.

Lichen Information System
http://lis.freeweb.supereva.it/index.htm?p
Affiliated with: N/A
- A collection of links to sites with information on lichen biology, collections, professional meetings, and organizations.

Manual of Grasses for North America North of Mexico
http://herbarium.usu.edu/GrassManual/default.htm
Affiliated with: Utah State University
- Supplies range maps, illustrations, and text descriptions of grasses.

Silvics of North America
Affiliated with: U.S. Department of Agriculture
- An online manual reprinting edited research papers describing the characteristics of 127 trees, both hardwoods and conifers.

Vascular Family Plant Access Page
http://www.botany.hawaii.edu/faculty/carr/pfamilies.html
Affiliated with: University of Hawaii
- Intended to aid instructors, this site offers basic information, images, and diagrams concerning plant families and their phylogenetic relationships.

Wildland Shrubs of the United States and Its Territories
http://www.fs.fed.us/global/iiwf/wildland_shrubs.htm
Affiliated with: U.S. Forest Service
- Contains downloadable files describing shrub species.

World Gymnosperm Database
http://www.botanik.uni-bonn.de/conifers/topics/big_index.htm
Affiliated with: University of Bonn, Germany
- A database containing extensive information, images, and range maps about conifers worldwide.

IMAGES

Cal’s Plant of the Week
http://www.plantoftheweek.org/
Affiliated with: N/A
- Displays an image of a new species of plant each week, followed by information about its habitat, cultivation, propagation, and care.

Grass Images
http://www.csdl.tamu.edu/FLORA/image/poacr2ba.htm
Affiliated with: Texas A&M University and Hunt Institute for Botanical Documentation
- Preserves approximately 6,500 images of grass species, scanned from drawings.

Natural Resources Conservation Service Photo Gallery
http://photogallery.nrcs.usda.gov/PhotoGallery.asp
Affiliated with: U.S. Department of Agriculture
- Shows color photographs of plant species in the United States, searchable by category or state.

The Plant Kaleidoscope
http://www.biologie.uni-ulm.de/systax/dendrologie/index.html
Affiliated with: N/A
- Offers 665 color photos and 331 descriptions of rare and unusual plants cultivated in Europe.
U.S. Department of Agriculture Forest Service Collections
http://huntbot.andrew.cmu.edu/USDA/USDA.html
Affiliated with: Hunt Institute for Botanical Documentation
● Offers 2308 scanned ink drawings from the archives of the U.S. Forest Service, covering species in the continental United States, Puerto Rico, and the Virgin Islands.

FOR K-12 STUDENTS AND TEACHERS

Dragonfly
http://miavx1.muohio.edu/dragonfly/
Affiliated with: Miami University of Ohio
● An award-winning science Web site for children that includes articles on plants, the web of life, and trees. Also offers workshops for teachers.

The Mining Company’s Botany Site
http://botany.miningco.com/cs/botany
Affiliated with: About.com
● Offers explanations of botanical concepts for students, teaching aids for teachers, images, an index of plants and herbs, and links.

Photosynthesis, Energy, and Life
http://www.ftexploring.com/photosyn/photosynth.html
Affiliated with: Flying Turtle
● Displays articles explaining how photosynthesis works and its importance to the environment, as well as links. A science site for grammar school children.

Tree World
http://www.domtar.com/arbre/english/start.htm
Affiliated with: Domtar and the Minister of Education of Québec
● Articles about the uses and conservation of trees, designed both for schoolchildren and their teachers.

The Tulip Project
http://www.uwlax.edu/faculty/gerber/
Affiliated with: University of Wisconsin, La Crosse
● Contains guidance for the improvement of K-12 education about plants by providing information and suggesting activities for teachers, with links to similarly dedicated sites.

USDA for Kids
Affiliated with: U.S. Department of Agriculture
● Among other topics, offers children information about agriculture, food, gardening, and conservation.

ORGANIZATIONS

American Bryological and Lichenological Society
http://www.unomaha.edu/~abls
Affiliated with: N/A
● Mainly offers information and activities for members of the society, which is made up of scientists interested in mosses and lichens, but has a large listing of links to other resources about bryology and botany in general.

The American Fern Society
http://www.amerfernssoc.org/
Affiliated with: N/A
● Provides information to its international membership and arranges exchange of specimens. Also has links and a forum where members post remarks on topics of current interest.

American Forests
http://www.americanforests.org/
Affiliated with: N/A
● The home page for an environmental organization encouraging the planting and preservation of trees. Includes history, information about purchasing and planting trees, images, and resources for children.

The American Society for Horticultural Science
http://www.ashs.org/
Affiliated with: N/A
● Provides information, links, and publications for members of the society, which include scientists, educators, growers, and field agents.

The American Society of Plant Biologists
http://www.aspb.org/
Affiliated with: N/A
● Offers information about the society and its publications and activities to the university students and scientists that make up its membership. Also
has a large list of links to related academic and government sites.

**American Society of Plant Taxonomists**
http://www.sysbot.org/
*Affiliated with: N/A*
- Provides information on the society’s activities for scientists, including its journal, newsletter, and monograph series, all addressing topics in taxonomy.

**APSnet**
http://www.apsnet.org/
*Affiliated with: The American Phytopathological Society*
- Displays society information about activities, research, educational and job opportunities, and links for its international membership of scientists who study plant diseases.

**ASC Web**
http://www.nscalliance.org/
*Affiliated with: Natural Science Collections Alliance*
- Site of a nonprofit organization, formerly called the Association of Systematics Collections, for the international community of museums, botanical gardens, herbariums, and institutions with natural science collections. Offers society news, links, information about collections, and databases.

**Botanical Society of America**
http://www.botany.org/
*Affiliated with: N/A*
- Maintains pages that support the purpose of the society: to foster formal and informal education about plants and research, to supply expertise for issues connected to ecosystems, and to expand communications among scientists and between scientists and the public. Directs visitors to print publications, conferences, career opportunities, and links. Offers eight hundred botanical images for instructional use.

**The Botanical Society of the British Isles**
*Affiliated with: N/A*
- In addition to society news, provides information and atlases about British and Irish flowering plants and ferns, along with links.

**California Native Plant Society**
http://www.cnps.org/
*Affiliated with: N/A*
- Provides information about the society’s programs, including plant inventory and conservation campaign, but also has a photo gallery and a site for kids that explains botanical concepts.

**The Ecological Society of America**
http://www.esa.org/
*Affiliated with: N/A*
- Offers information, links, and notice of the nonprofit society’s activities, which are to help ecologists share information and raise public awareness about biotechnology, ecosystem management, species extinction and habitat destruction, and sustainable systems.

**The Herb Society of America**
http://www.herbsociety.org/
*Affiliated with: N/A*
- Information resources, links, and descriptions of projects and meetings for a nonprofit organization dedicated to the cultivation of herbs and study of their history and uses.

**International Association for Plant Taxonomy**
http://www.botanik.univie.ac.at/iapt/
*Affiliated with: N/A*
- Fosters projects by systematic botanists, especially those related to classification and nomenclature, and acts as a repository of information to be shared by scientists worldwide.

**International Oak Society**
http://www.saintmarys.edu/~rjensen/ios.html
*Affiliated with: N/A*
- Informs members about the status of the society’s efforts to advance scientific knowledge about oaks and their preservation.

**International Palm Society**
http://www.palms.org/
*Affiliated with: N/A*
- In addition to society business, contains images, links, a bulletin board, and online articles about palm trees.

**The Mycological Society of America**
http://www.erin.utoronto.ca/~w3msa/
*Affiliated with: N/A*
• Updates members on society news and publications and offers a bulletin board and links.

National Arbor Day Foundation  
http://www.arborday.org/  
Affiliated with: N/A  
• An rich home page with information about the name, habitat, and care of trees in the United States; Arbor Day activities; resources for children; and images.

National Gardening Association  
http://www.garden.org/  
Affiliated with: N/A  
• A nonprofit organization. The site guides gardeners to information resources, maintains a bulletin board for members, and offers an online newsletter.

The Phycological Society of America  
http://www.psaalgae.org/  
Affiliated with: N/A  
• A professional organization devoted to the study of algae. The site primarily concerns society affairs but has links to related resources.

Plant Conservation Alliance  
http://www.nps.gov/plants/index.htm  
Affiliated with: N/A  
• A Web site supported by ten federal agencies and more than 145 nongovernmental contributors, including organizations of biologists, botanists, habitat preservationists, horticulturists, and soil scientists working to prevent native plant extinction and habitat restoration. Lists ongoing projects, publications, meetings, and links.

Society for Economic Botany  
http://www.econbot.org/home.html  
Affiliated with: N/A  
• A professional organization dedicated to scientific research and education regarding the uses of plants and the relationship between people and plants. The site concerns society business, but its online journal is downloadable.

• A professional organization’s site that fosters exchange of information about forestry science, posts the latest news about forestry and ecology, and offers aids to education.

SPECIALTY SITES

The Arabidopsis Information Resource  
http://www.arabidopsis.org/home.html  
Affiliated with: A consortium of university departments and government agencies  
• Supplies the means for plant scientists to search a database containing the completely decoded genome of the weed *Arabidopsis thaliana*, a widely used model plant and the first plant species to be genetically sequenced.

Atlas of the Flora of New England  
http://www.herbaria.harvard.edu/~rangelo/Neatlas0/WebIntro.html  
Affiliated with: Harvard University Herbaria  
• A repository of basic ecological information and range maps of ferns, mosses, flowering plants, gymnosperms, and grasses in New England.

Carnivorous Plant Database  
http://www2.labs.agilent.com/bot/cp_home  
Affiliated with: Agilent Labs  
• Presents slide shows, photographs, and a database with taxonomic, descriptive, and habitat information about more than three thousand plants that eat insects.

Center for Aquatic and Invasive Plants  
http://aquat1.ifas.ufl.edu/  
Affiliated with: University of Florida  
• Contains images, drawings, basic information, and a bibliographic database, with links to full-text articles, concerning freshwater and wetland plants (about 55,000 citations in all). Also has links and articles about plant management.

ESA Panel of Vegetation Classification  
http://esa.sdsc.edu/vegwebpg.htm  
Affiliated with: Ecological Society of America  
• Affords access to information about the program for experts and organizations that are part of an effort to develop a science-based national classification system, which is intended to aid research and conservation.
Exotic and Invasive Weeds Research Unit  
http://wric.ucdavis.edu/exotic/exotic.htm  
**Affiliated with:** U.S. Department of Agriculture  
- Provides technical information and cites professional articles about plants introduced into the United States from other environments, along with photographs and links to other resources. Geared to botanists and agricultural scientists.

Herbal Information Resource  
http://www.stevenfoster.com/education/index.html  
**Affiliated with:** Steven Foster Group  
- Collects monographs and links regarding plants that can be used as food, medicine, flavoring, or fragrance in order to promote their use among the public.

Invasivespecies.gov  
http://invasivespecies.gov/  
**Affiliated with:** National Biological Information Infrastructure  
- The federal government’s gateway to agencies and nongovernmental organizations worldwide that work with invasive species identification and control. Contains articles about the impact of, means of spreading, response to, and laws concerning invasive species, as well as databases.

Manual of Leaf Architecture  
http://www.peabody.yale.edu/collections/pb/MLA/  
**Affiliated with:** Peabody Museum, Yale University  
- A downloadable PDF manual of the morphological descriptions and categorization of leaves of angiosperms.

Native American Ethnobotany Database  
http://www.umd.umich.edu/cgi-bin/herb  
**Affiliated with:** University of Michigan, Dearborn  
- Provides information on foods, drugs, dyes, and fibers that is derived from the practical knowledge of plants accumulated by native North American peoples. Compiled by an anthropology professor for general use and provides citations of the source of information about each plant cited.

Native Plants Network  
http://www.nativeplantnetwork.org/  
**Affiliated with:** N/A  
- Shares information on how to propagate native American plants, with a database devoted to species, links to government and university members, and the *The Native Plants Journal*.

The Parasitic Plant Connection  
http://www.science.siu.edu/parasitic-plants/  
**Affiliated with:** Southern Illinois University at Carbondale  
- A repository of information about the taxonomy, phylogenetic relationships, and molecular data of parasitic plants for researchers and educators, with links and a glossary of terms about parasites.

Poisonous Plant Database  
http://vm.cfsan.fda.gov/~djw/readme.html  
**Affiliated with:** U.S. Food and Drug Administration  
- Contains a list of plants worldwide that are harmful to animals and humans and citations of scientific articles that can be e-mailed upon request.

Ultimate Tree-Ring Web Page  
http://web.utk.edu/~grissino/  
**Affiliated with:** University of Tennessee  
- Supplies explanations of tree-ring dating methods (dendrochronology) and links to other sources, designed for public school students and the general public. With a gallery of images and software related to dendrochronology for downloading.

The Weed Hall of Shame  
**Affiliated with:** Bureau of Land Management  
- A cleverly designed site about scourges of public lands—exotic plants, such as purple loosestrife and spotted knapweed—that are crowding out native species. With images and informative narratives.
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