



Subfields of Botany

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Chapter 1

Agronomy



An agronomist field sampling a trial plot of flax.

Agronomy is the science and technology of producing and using plants for food, fuel, feed, fiber, and reclamation. Agronomy encompasses work in the areas of plant genetics, plant physiology, meteorology, and soil science. Agronomy is the application of a

combination of sciences like biology, chemistry, ecology, earth science, and genetics. Agronomists today are involved with many issues including producing food, creating healthier food, managing environmental impact of agriculture, and creating energy from plants. Agronomists often specialize in areas such as crop rotation, irrigation and drainage, plant breeding, plant physiology, soil classification, soil fertility, weed control, insect and pest control.

Plant breeding

This area of agronomy involves selective breeding of plants to produce the best crops under various conditions. Plant breeding has increased crop yields and has improved the nutritional value of numerous crops, including corn, soybeans, and wheat. It also has led to the development of new types of plants. For example, a hybrid grain called triticale was produced by crossbreeding rye and wheat. Triticale contains more usable protein than does either rye or wheat. Agronomy has also been instrumental in fruit and vegetable production research. It is understood that the role of agronomist includes seeing whether produce from a field of 'x' meets the following conditions: 1. Land and water access, 2. Commercialization (market), 3. Quality and quantity of inputs, 4. Risk protection (insurance), 5. Agricultural credit.

Biotechnology



An agronomist mapping a plant genome.

Agronomists use biotechnology to extend and expedite the development of desired characteristics listed in the Plant Breeding section. Biotechnology is often a lab activity requiring field testing of the new crop varieties that are developed.

In addition to increasing crop yields agronomic biotechnology is increasingly being applied for novel uses other than food. For example, oilseed is at present used mainly for margarine and other food oils, but it can be modified to produce fatty acids for detergents, substitute fuels and petrochemicals.

Soil science



Agronomists describing a soil sample in Uganda, Africa.

Agronomists study sustainable ways to make soils more productive and profitable. They classify soils and reproduce them to determine whether they contain substances vital to plant growth such as compounds of nitrogen, phosphorus, and potassium. If a certain soil is deficient in these substances, fertilizers may provide them. Soil science also involves investigation of the movement of nutrients through the soil, the amount of nutrients absorbed by a plant's roots, and the development of roots and their relation to the soil.

Soil conservation

In addition, agronomists develop methods to preserve the soil and to decrease the effects of erosion by wind and water. For example, a technique called contour plowing may be used to prevent soil erosion and conserve rainfall. Researchers in agronomy also seek ways to use the soil more effectively in solving other problems. Such problems include the disposal of human and animal wastes; water pollution; and the build-up in the soil of pesticides. No-tilling crops is a technique now used to help prevent erosion. Planting of soil binding grasses along contours can be tried in steep slopes. For better effect, contour drains of depths up to 1 metre may help retain the soil and prevent permanent wash off.

Agroecology

Agroecology is the management of agricultural systems with an emphasis on ecological and environmental perspectives. This area is closely associated with work in the areas of sustainable agriculture, organic farming, alternative food systems and the development of alternative cropping systems.

Theoretical modeling

Agronomy schools

Agronomy programs are offered at colleges, universities, and specialized agricultural schools. Agronomy programs often involve classes across a range of departments including agriculture, biology, chemistry, and physiology. They can usually take from four to twelve years. Many companies will pay an agronomist-in-training's way through college if they agree to work for them when they graduate.

Career outlook

Due to the continued growth of the global population—and the consequent expanding need for study of food crops and agriculture in general—the outlook for agronomy and agronomists is excellent. Past agricultural research has created higher yielding crops, crops with better resistance to pests and plant pathogens, and more effective fertilizers and pesticides. Research is still necessary, however, particularly as insects and diseases continue to adapt to pesticides and as soil fertility and water quality continue to need improvement.

Emerging biotechnologies will play an ever larger role in agricultural research. Scientists will be needed to apply these technologies to the creation of new food products and other advances. Moreover, increasing demand is expected for biofuels and other agricultural products used in industrial processes. Agricultural scientists will be needed to find ways to increase the output of crops used in these products.

Agronomists will also be needed to balance increased agricultural output with protection and preservation of soil, water, and ecosystems. They increasingly encourage the practice of sustainable agriculture by developing and implementing plans to manage pests, crops, soil fertility and erosion, and animal waste in ways that reduce the use of harmful chemicals and do little damage to farms and the natural environment.

Most agronomists are consultants, researchers, or teachers. Many work for agricultural experiment stations, federal or state government agencies, industrial firms, or universities. Agronomists also serve in such international organizations as the Agency for International Development, The United States Department of Agriculture, and the Food and Agriculture Organization of the United Nations.

Agronomists career options are expanding rapidly with possible ties with golf landscaping including topsoil analysis and drainage conditions. They often work in conjunction with landscape architects and engineers to determine the best soil qualities/conditions to suit the site specifications.

Chapter 2

Economic Botany

Economic botany can be very broadly defined as a study of relationships between plants and people. Economic botany contributes significantly to anthropology, biology, conservation, botany, and other fields of science. This link between botany and anthropology explores the ways humans use plants for food, shelter, medicines, textiles, and much more.

History of economic botany

Botany itself came about through medicine and the development of herbal remedies. Thus at its advent, botany was economic as well as systematic. As plants became useful for herbals and curatives, their economic value increased. An early set of instructions drawn up by a cosmographer of Charles the fifth instructed explorers to

"determine what are the items of sustenance of the land and which onse are generally used, whether fruits or seeds, and all manner of spices, drugs, or whatever other scents, and find out the time in which one can reproduce the trees, plants, herbs, and fruits that these parts offer, and if the natives use them for medicines, as we do."

Teosinte and rice are two examples of plants modified so that their economic values would increase.

Teosinte

The teosintes are grasses of the genus *Zea*. Native Americans bred and selected teosinte for the traits we see in corn today (large ears, multiple rows of kernels). The first ears of maize were very short, with only 8 rows of kernels. Modern corn is the result of several hundred generations of selective breeding. Modern corn is incapable of reproducing without human help; the kernels will stay firmly attached to the cob and rot. This doesn't represent a useful adaptation for the species, but is excellent for harvesting and transporting corn.

Rice

Rice was first domesticated approximately 5,000 years ago, in Southeast Asia. Rice and American wild rice are believed to have been domesticated separately. Rice variants have been adapted to the tropics where they provide a grain staple, but rice can be grown almost anywhere. The introduction of dwarf rice variants made several rice-producing countries self-sufficient. Rice is suited to countries with high rainfall.

Economically important food plants

Plants that humans use for food are of high economic importance. Research into food plants generally involves increasing the size of the edible plant organ in question, or increasing the areas where the plant can be grown, and less frequently, finding new crop species. Results of such research are often published in the journal *Economic Botany*. The New Zealand-based Plant & Food Research publishes its own journal on cultivar development and sustainable production systems for high quality produce, and the design and development of new and novel functional foods.

Florida oranges

Citrus has been a major commercial product in Florida since the 19th century. Florida produces over 70% of the U.S. citrus supply. The color of oranges is not related to ripening, but is a serious component for sales. The orange color only develops in areas with cool nighttime temperatures. In tropical climates, growers often expose the fruit to ethylene, to promote the loss of chlorophyll and expose the beta-carotenes (the orange color).

North American apples

Apples are not native to North America, but today the North American continent boasts the greatest diversity of apples in the world. Part of this is due to "Johnny Appleseed," real name John Chapman. Chapman spent 48 years travelling all along the American northwest spreading apple seeds and planting trees. While apples come in literally thousands of varieties, the majority of the apple market is based on three: Red Delicious, Golden Delicious, and Granny Smith. The Red Delicious is the ideal apple, for marketing purposes, for the apple industry. It's large, intensely red, and instantly recognizable.

Economically valuable medicinal plants

Medical research in the U.S. alone has a budget of \$95 billion. A large portion of that money is spent on research into plants and plant extracts. Several key medical discoveries have been made by studying plants and the compounds they produce, to see the effect they have on humans.

Ephedrine

The Ephedra plant is the natural source of ephedrine, the plant's principle alkaloid. Ephedrine is actually a very interesting case of economic botany in medicine. While it has been taken medicinally in the past, ephedrine can be highly toxic. Because of this fact, medical researchers studied the compound and produced pseudoephedrine. This is the medicine you can buy over the counter, in Sudafed and other decongestants. Ephedrine imitates epinephrine in its effect on the human body. Originally developed by the plant as a herbivore deterrent, this compound, studied and refined by researchers, now helps fix allergy symptoms nationwide every year.

Echinacea

One of many herbal remedies out there, Echinacea represents a sizable industry. Many people take echinacea for cold and flu-like symptoms, but studies show that the plant has had mixed success fighting these viruses. However, those same studies show the plant possibly being useful for the treatment of upper respiratory infections. NCCAM is currently studying echinacea for the treatment of upper respiratory infections as well as its effect on the immune system.

Ornamental plants

Ornamental plants can be found in almost any store, and many people have at least one in their home. However, ornamental plants are not limited to houseplants. Landscaping agencies make heavy use of ornamental plants, usually with an accompanying high cost. Trees, shrubs, flowers, and grasses, all of these are planted by professional landscaping agencies regularly, with a large economic effect.

Chapter 3

Ethnobotany



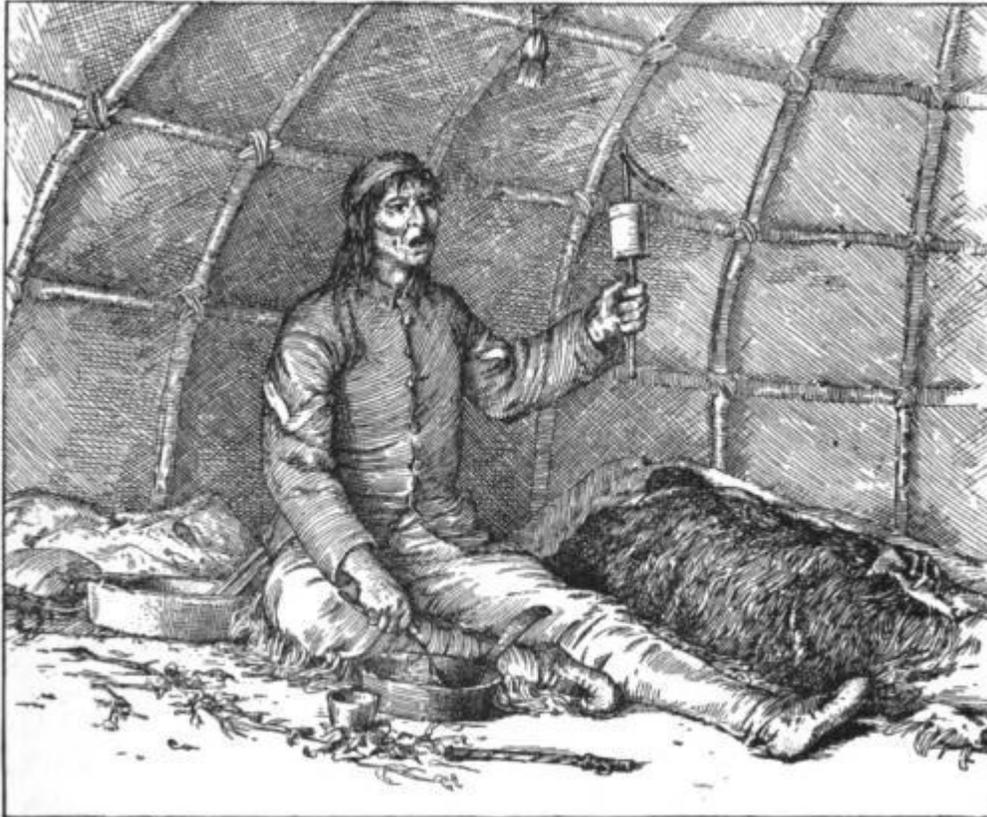
"Botanists at work" by Gerbrand van den Eeckhout, mid 17th century.

Ethnobotany is the scientific study of the relationships that exist between people and plants.

Ethnobotanists aim to document, describe and explain complex relationships between cultures and (uses of) plants: focusing, primarily, on how plants are used, managed and perceived across human societies (e.g. as foods; as medicines; in divination; in cosmetics;

in dyeing; as textiles; in construction; as tools; as currency; as clothing; in literature; in rituals; and in social life.)

History of ethnobotany



Plants have been widely used by American Indian healers, such as this Ojibwa man.

Though the term "ethnobotany" was not coined until 1895 by the US botanist John William Harshberger, the history of the field begins long before that. In A.D. 77, the Greek surgeon Dioscorides published "*De Materia Medica*", which was a catalog of about 600 plants in the Mediterranean. It also included information on how the Greeks used the plants, especially for medicinal purposes. This illustrated herbal contained information on how and when each plant was gathered, whether or not it was poisonous, its actual use, and whether or not it was edible (it even provided recipes). Dioscorides stressed the economic potential of plants. For generations, scholars learned from this herbal, but did not actually venture into the field until after the Middle Ages.

In 1542 Leonhart Fuchs, a Renaissance artist, led the way back into the field. His "*De Historia Stirpium*" cataloged 400 plants native to Germany and Austria.

John Ray (1686–1704) provided the first definition of "species" in his "*Historia Plantarum*": a species is a set of individuals who give rise through reproduction to new individuals similar to themselves.

In 1753 Carl Linnaeus wrote "*Species Plantarum*", which included information on about 5,900 plants. Linnaeus is famous for inventing the binomial method of nomenclature, in which all species get a two part name (genus, species).

The 19th century saw the peak of botanical exploration. Alexander von Humboldt collected data from the new world, and the James Cook's voyages brought back collections and information on plants from the South Pacific. At this time major botanical gardens were started, for instance the Royal Botanic Gardens, Kew.

Edward Palmer collected artifacts and botanical specimens from people in the North American West (Great Basin) and Mexico from the 1860s to the 1890s.

Once enough data existed, the field of "aboriginal botany" was founded. Aboriginal botany is the study of all forms of the vegetable world which aboriginal peoples use for food, medicine, textiles, ornaments, etc.

The first individual to study the emic perspective of the plant world was a German physician working in Sarajevo at the end of 19th Century: Leopold Glueck. His published work on traditional medical uses of plants done by rural people in Bosnia (1896) has to be considered the first modern ethnobotanical work.

The term "ethnobotany" was first used by a botanist named John W. Harshberger in 1895 while he was teaching at the University of Pennsylvania. Although the term was not used until 1895, practical interests in ethnobotany go back to the beginning of civilization when people relied on plants for survival.

Other scholars analyzed uses of plants under an indigenous/local perspective in the 20th century: e.g. Matilda Coxe Stevenson, Zuni plants (1915); Frank Cushing, Zuni foods (1920); Keewaydinoquay Peschel, Anishinaabe fungi (1998), and the team approach of Wilfred Robbins, JP Harrington, and Barbara Freire-Marreco, Tewa pueblo plants (1916).

In the beginning, ethnobotanical specimens and studies were not very reliable and sometimes not helpful. This is because the botanists and the anthropologists did not collaborate their work. The botanists focused on identifying species and how the plants were used instead of concentrating upon how plants fit into people's lives. On the other hand, anthropologists were interested in the cultural role of plants and not the scientific aspect. Therefore, early ethnobotanical data does not really include both sides. In the early twentieth century, botanists and anthropologists finally collaborated and the collection of reliable, detailed data began.

Modern ethnobotany

Beginning in the 20th century, the field of ethnobotany experienced a shift from the raw compilation of data to a greater methodological and conceptual reorientation. This is also the beginning of academic ethnobotany. The so called "father" of this discipline is Richard Evans Schultes even though he did not actually coin the term "Ethnobotany". Today the field of ethnobotany requires a variety of skills: botanical training for the identification and preservation of plant specimens; anthropological training to understand the cultural concepts around the perception of plants; linguistic training, at least enough to transcribe local terms and understand native morphology, syntax, and semantics.

A great deal of information about the traditional uses of plants is still intact with the tribals. But the native healers are often reluctant to accurately share their knowledge to outsiders. Schultes actually apprenticed himself to an Amazonian shaman, which involves a long term commitment and genuine relationship. In *Wind in the Blood: Mayan Healing & Chinese Medicine* by Garcia et al. the visiting acupuncturists were able to access levels of Mayan medicine that anthropologists could not because they had something to share in exchange. Cherokee medicine priest David Winston describes how his uncle would invent nonsense to satisfy visiting anthropologists.

Scientific journals covering ethnobotanical research

The Latin American and Caribbean Bulletin of Medicinal and Aromatic Plants (Abbreviated BLACPMA) or *Boletín latinoamericano y del caribe de plantas medicinales y aromáticas* (ISSN-0717 7917) is a bimonthly scientific publication directed to diverse professionals and technicians linked to the field of medicinal and aromatic plants. It accepts papers related with the Bulletin's areas of interest, which are agronomy, anthropology and ethnobotany, industrial applications, botany, quality and normalization, ecology and biodiversity, economy and markets, pharmacology, phytochemistry, legislation, information and diffusion of events, courses, prizes, regulations, news, market questions, reports, bibliography, or any other material type that is important to publish.

Chapter 4

Forestry



Forestry work in Austria.

Forestry is the art and science of managing forests, tree plantations, and related natural resources. The main goal of forestry is to create and implement systems that allow forests to continue a sustainable provision of environmental supplies and services. The challenge of forestry is to create systems that are socially accepted while sustaining the resource and any other resources that might be affected.

Silviculture, a related science, involves the growing and tending of trees and forests. Modern forestry generally embraces a broad range of concerns, including assisting forests to provide timber as raw material for wood products, wildlife habitat, natural water quality management, recreation, landscape and community protection, employment, aesthetically appealing landscapes, biodiversity management, watershed management, erosion control, and preserving forests as 'sinks' for atmospheric carbon dioxide. A practitioner of forestry is known as a forester. Note that the word "forestry" can also refer to a forest itself.

Forest ecosystems have come to be seen as the most important component of the biosphere, and forestry has emerged as a vital field of science, applied art, and technology.



A deciduous beech forest in Slovenia.

History

The use and management of many forest resources has a long history in China, dating from the Han Dynasty and taking place under the landowning gentry. It was also later

written of by the Ming Dynasty Chinese scholar Xu Guangqi (1562–1633). In the Western world, formal forestry practices developed during the Middle Ages, when land was largely under the control of kings. Control of the land included hunting rights, and though peasants in many places were permitted to gather firewood and building timber and to graze animals, hunting rights were retained by the members of the nobility. Systematic management of forests for a sustainable yield of timber is said to have begun in the 16th century in both the German states and Japan. Typically, a forest was divided into specific sections and mapped; the harvest of timber was planned with an eye to regeneration.



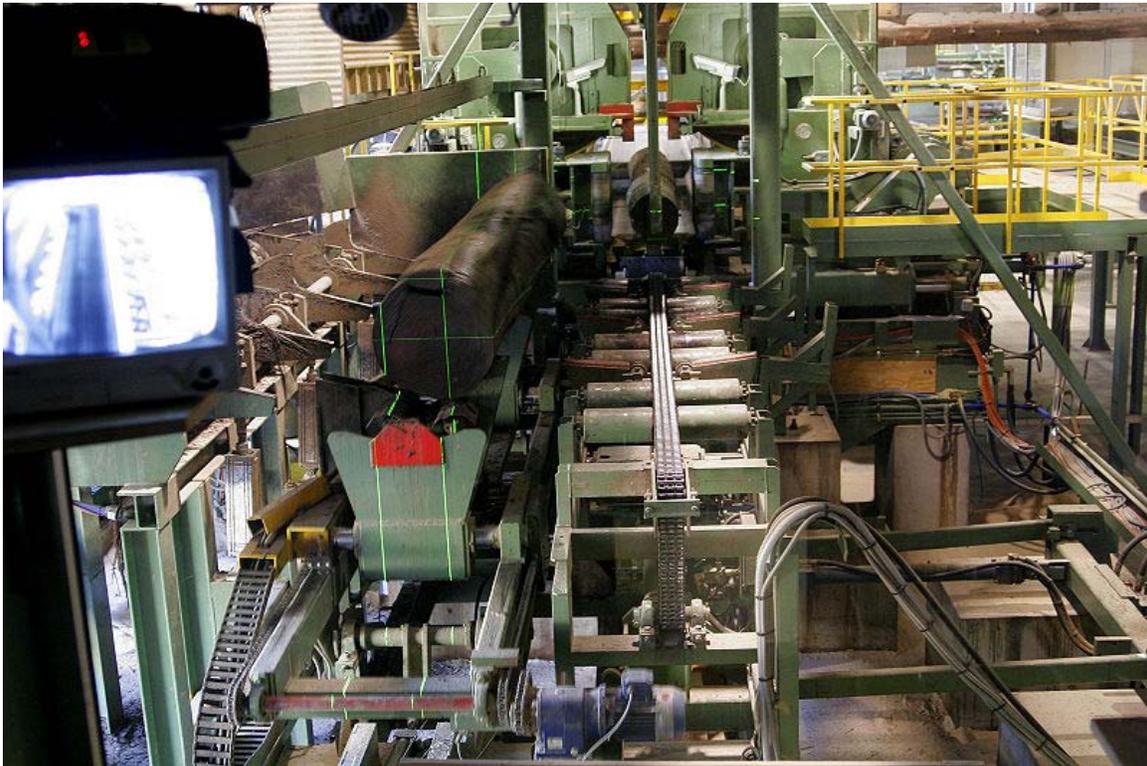
Timber harvesting is a common component of forestry

The practice of establishing tree plantations was promoted by John Evelyn; it had already acquired some popularity in the British Isles. Louis XIV's minister Jean-Baptiste Colbert's oak forest at Tronçais, planted for the future use of the French Navy, matured as expected in the mid-19th century: "Colbert had thought of everything except the steamship," Fernand Braudel observed. Schools of forestry were established after 1825; most of these schools were in Germany and France. During the nineteenth and early twentieth centuries, forest preservation programs were established in the United States, Europe, and British India. Many foresters were either from continental Europe (like Sir Dietrich Brandis), or educated there (like Gifford Pinchot).

The enactment and evolution of forestry laws and binding regulations occurred in most Western nations in the 20th century in response to growing conservation concerns and the increasing technological capacity of logging companies.

Tropical forestry is a separate branch of forestry which deals mainly with equatorial forests that yield woods such as teak and mahogany. Sir Dietrich Brandis is considered the father of tropical forestry.

Today



A modern sawmill

Today a strong body of research exists regarding the management of forest ecosystems and genetic improvement of tree species and varieties. Forestry also includes the development of better methods for the planting, protecting, thinning, controlled burning, felling, extracting, and processing of timber. One of the applications of modern forestry is reforestation, in which trees are planted and tended in a given area.

In many regions the forest industry is of major ecological, economic, and social importance. Third-party certification systems that provide independent verification of sound forest stewardship and sustainable forestry have become commonplace in many areas since the 1990s. These certification systems were developed as a response to criticism of some forestry practices, particularly deforestation in less developed regions along with concerns over resource management in the developed world. Some

certification systems are criticised for primarily acting as marketing tools and lacking in their claimed independence.

In topographically severe forested terrain, proper forestry is important for the prevention or minimization of serious soil erosion or even landslides. In areas with a high potential for landslides, forests can stabilize soils and prevent property damage or loss, human injury, or loss of life.

Public perception of forest management has become controversial, with growing public concern over perceived mismanagement of the forest and increasing demands that forest land be managed for uses other than pure timber production, for example, indigenous rights, recreation, watershed management, and preservation of wilderness, waterways and wildlife habitat. Sharp disagreements over the role of forest fires, logging, motorized recreation and others drives debate while the public demand for wood products continues to increase.

Foresters



Foresters of UACH in the Valdivian forests of San Pablo de Tregua, Panguipulli, Chile

Foresters work for the timber industry, government agencies, conservation groups, local authorities, urban parks boards, citizens' associations, and private landowners. The forestry profession includes a wide diversity of jobs, with educational requirements ranging from college bachelor's degrees to PhDs for highly specialized work. Industrial foresters plan forest regeneration starting with careful harvesting. Urban foresters manage trees in urban green spaces. Foresters work in tree nurseries growing seedlings for woodland creation or regeneration projects. Foresters improve tree genetics. Forest engineers develop new building systems. Professional foresters measure and model the growth of forests with tools like geographic information systems. Foresters may combat insect infestation, disease, forest and grassland wildfire, but increasingly allow these natural aspects of forest ecosystems to run their course when the likelihood of epidemics or risk of life or property are low. Increasingly, foresters participate in wildlife conservation planning and watershed protection. Foresters have been mainly concerned with timber management, especially reforestation, maintaining forests at prime conditions, and fire control.

Forestry plans

Foresters develop and implement forest management plans relying on tree inventories showing an area's topographical features as well as its distribution of trees (by species) and other plant cover. Plans also include roads, culverts, proximity to human habitation, hydrological conditions, and soil reports. Forest management plans include the projected use of the land and a timetable for that use. Traditional forest management plans focus on providing logs used for timber, veneer, plywood, paper, wood fuel or other industries. Hence, considerations of product quality and quantity, employment, and profit have been of central, though not always exclusive, importance. Foresters frequently develop post-harvest site plans for reforestation, weed control, fertilization, or thinning. The objectives of landowners and leaseholder influence plans for harvest and subsequent site treatment. In Britain, plans featuring "good forestry practice" must always consider the needs of other stakeholders such as nearby communities or rural residents living within or adjacent to woodland areas. Foresters consider tree felling and environmental legislation when developing plans. Plans instruct the sustainable harvesting and replacement of trees. They indicate whether road building or other forest engineering operations are required.

Agriculture and forest leaders are also trying to understand how the climate change legislation will affect what they do. The information gathered will provide the data that will determine the role of agriculture and forestry in a new climate change regulatory system.

Education



Prescribed burning is used by foresters to reduce fuel loads

The first dedicated forestry school was established by Georg Hartig at Dillenburg in Germany in 1787, though forestry had been taught much earlier in central Europe.

In 1877, the first issue of *Šumarski list* (Forestry Review) was published in Croatia by Croatian Forestry Society.

In 1886, the first issue of *Revista Pădurilor* (Forestry Review) was published in Romania.

The first in North America, the Biltmore Forest School was established near Asheville, North Carolina, by Carl A. Schenck on September 1, 1898, on the grounds of George W. Vanderbilt's Biltmore Estate. Another early school was the New York State College of Forestry, established at Cornell University just a few weeks later, in September 1898. Early 19th century North American foresters went to Germany to study forestry. Some early German foresters also emigrated to North America.

In South America the first forestry school was established in Brazil, specifically in Viçosa, Minas Gerais, and later moved to Curitiba, Paraná.

Today, an acceptably trained forester must be educated in general biology, botany, genetics, soil science, climatology, hydrology, economics and forest management. Education in the basics of sociology and political science is often considered an advantage.

In India, forestry education is imparted in the agricultural universities and in Forest Research Institutes (deemed universities). Four year degree programmes are conducted in

these universities at the undergraduate level. Masters and Doctorate degrees are also available in these universities.

In the United States, postsecondary forestry education leading to a Bachelor's degree or Master's degree is accredited by the Society of American Foresters.

In Canada the Canadian Institute of Forestry awards silver rings to graduates from accredited university BSc programs, as well as college and technical programs.

The International Union of Forest Research Organizations is the only international organization that coordinates forest science efforts world-wide. Organizations such as the Forest Policy Education Network are dedicated to facilitating international forest politics and exchanging information on the subject.

Chapter 5

Horticulture



Hybrid tomatoes growth by hydroponic methods on straw bales

Horticulture is the industry and science of plant cultivation including the process of preparing soil for the planting of seeds, tubers, or cuttings. Horticulturists work and conduct research in the disciplines of plant propagation and cultivation, crop production, plant breeding and genetic engineering, plant biochemistry, and plant physiology. The work involves fruits, berries, nuts, vegetables, flowers, trees, shrubs, and turf.

Horticulturists work to improve crop yield, quality, nutritional value, and resistance to insects, diseases, and environmental stresses. Horticulture usually refers to gardening on a smaller scale, while agriculture refers to the large-scale cultivation of crops.

Etymology

The word *horticulture* is modeled after *agriculture*, and comes from the Latin *hortus* "garden" and *cultūra* "cultivation", from *cultus*, the perfect passive participle of the verb *colō* "I cultivate".

Areas of study

Horticulture involves eight areas of study, which can be grouped into two broad sections - ornamentals and edibles:

- Arboriculture is the study of, and the selection, planting, care, and removal of, individual trees, shrubs, vines, and other perennial woody plants.
- Floriculture includes the production and marketing of floral crops.
- Landscape horticulture includes the production, marketing and maintenance of landscape plants.
- Olericulture includes the production and marketing of vegetables.
- Pomology includes the production and marketing of fruits.
- Viticulture includes the production and marketing of grapes.
- Oenology includes all aspects of wine and winemaking.
- Postharvest physiology involves maintaining the quality of and preventing the spoilage of horticultural crops.

Horticulturists can work in industry, government or educational institutions or private collections. They can be cropping systems engineers, wholesale or retail business managers, propagators and tissue culture specialists (fruits, vegetables, ornamentals, and turf), crop inspectors, crop production advisers, extension specialists, plant breeders, research scientists, and of course, teachers.

Disciplines which complement horticulture include biology, botany, entomology, chemistry, mathematics, genetics, physiology, statistics, computer science, and communications, garden design, planting design. Plant science and horticulture courses include: plant materials, plant propagation, tissue culture, crop production, post-harvest handling, plant breeding, pollination management, crop nutrition, entomology, plant pathology, economics, and business. Some careers in horticultural science require a masters (MS) or doctoral (PhD) degree.

Horticulture is practiced in many gardens, "plant growth centres" and nurseries. Activities in nurseries range from preparing seeds and cuttings to growing fully mature plants. These are often sold or transferred to ornamental gardens or market gardens.

Anthropology

Horticulture has a very long history. The study and science of horticulture dates all the way back to the times of Alexander the Great, and has been going on ever since, with present day horticulturists such as Freeman S. Howlett, the revolutionary horticulturist. The origins of horticulture lie in the transition of human communities from nomadic hunter-gatherers to sedentary or semi-sedentary horticultural communities, cultivating a variety of crops on a small scale around their dwellings or in specialized plots visited occasionally during migrations from one area to the next (such as the "milpa" or maize field of Mesoamerican cultures). In the Pre-Columbian Amazon Rainforest, natives are believed to have used biochar to enhance soil productivity by smoldering plant waste. European settlers called it *Terra Preta de Indio*. In forest areas such horticulture is often carried out in swiddens ("slash and burn" areas). A characteristic of horticultural communities is that useful trees are often to be found planted around communities or specially retained from the natural ecosystem.

Horticulture primarily differs from agriculture in two ways, firstly it generally encompasses a smaller scale of cultivation, using small plots of mixed crops rather than large fields of single crops. Secondly horticultural cultivations generally include a wide variety of crops, even including fruit trees with ground crops. Agricultural cultivations however as a rule focus on one primary crop. In pre-contact North America the semi-sedentary horticultural communities of the Eastern Woodlands (growing maize, squash and sunflower) contrasted markedly with the mobile hunter-gatherer communities of the Plains people. In Central America, Maya horticulture involved augmentation of the forest with useful trees such as papaya, avocado, cacao, ceiba and sapodilla. In the cornfields, multiple crops were grown such as beans (using cornstalks as supports), squash, pumpkins and chilli peppers, in some cultures tended mainly or exclusively by women.



The Butchart Gardens, British Columbia, Canada



Cool climate greenhouse extend the growing season



Community gardens often have several horticultural practices in use

Chapter 6

Paleobotany

Paleobotany, also spelled as **palaeobotany** (from the Greek words *paleon* = old and "botany", study of plants), is the branch of paleontology or paleobiology dealing with the recovery and identification of plant remains from geological contexts, and their use for the biological reconstruction of past environments (paleogeography), and both the evolutionary history of plants, with a bearing upon the evolution of life in general. A synonym is **paleophytology**. Paleobotany includes the study of terrestrial plant fossils, as well as the study of prehistoric marine photoautotrophs, such as photosynthetic algae, seaweeds or kelp. A closely-related field is palynology, which is the study of fossilized and extant spores and pollen.

Paleobotany is important in the reconstruction of ancient ecological systems and climate, known as paleoecology and paleoclimatology respectively; and is fundamental to the study of green plant development and evolution. Paleobotany has also become important to the field of archaeology, primarily for the use of phytoliths in relative dating and in paleoethnobotany,

Overview of the paleobotanical record

Macroscopic remains of true vascular plants are first found in the fossil record during the Silurian Period of the Paleozoic era. Some dispersed, fragmentary fossils of disputed affinity, primarily spores and cuticles, have been found in rocks from the Ordovician Period in Oman, and are thought to derive from liverwort- or moss-grade fossil plants (Wellman et al., 2003).



An unpolished hand sample of the Lower Devonian Rhynie Chert from Scotland.

An important early land plant fossil locality is the Rhynie Chert, found outside the village of Rhynie in Scotland. The Rhynie chert is an Early Devonian sinter (hot spring) deposit composed primarily of silica. It is exceptional due to its preservation of several different clades of plants, from mosses and lycopods to more unusual, problematic forms. Many fossil animals, including arthropods and arachnids, are also found in the Rhynie Chert, and it offers a unique window on the history of early terrestrial life.

Plant-derived macrofossils become abundant in the Late Devonian and include tree trunks, fronds, and roots. The earliest tree is *Archaeopteris*, which bears simple, fern-like leaves spirally arranged on branches atop a conifer-like trunk (Meyer-Berthaud et al., 1999).

Widespread coal swamp deposits across North America and Europe during the Carboniferous Period contain a wealth of fossils containing arborescent lycopods up to 30 meters tall, abundant seed plants, such as conifers and seed ferns, and countless smaller, herbaceous plants.

Angiosperms (flowering plants) evolved during the Mesozoic, and flowering plant pollen and leaves first appear during the Early Cretaceous, approximately 130 million years ago.

Plant fossils

A plant fossil is any preserved part of a plant that has long since died. Such fossils may be prehistoric impressions that are many millions of years old, or bits of charcoal that are only a few hundred years old. Prehistoric plants are various groups of plants that lived before recorded history (before about 3500 BC).

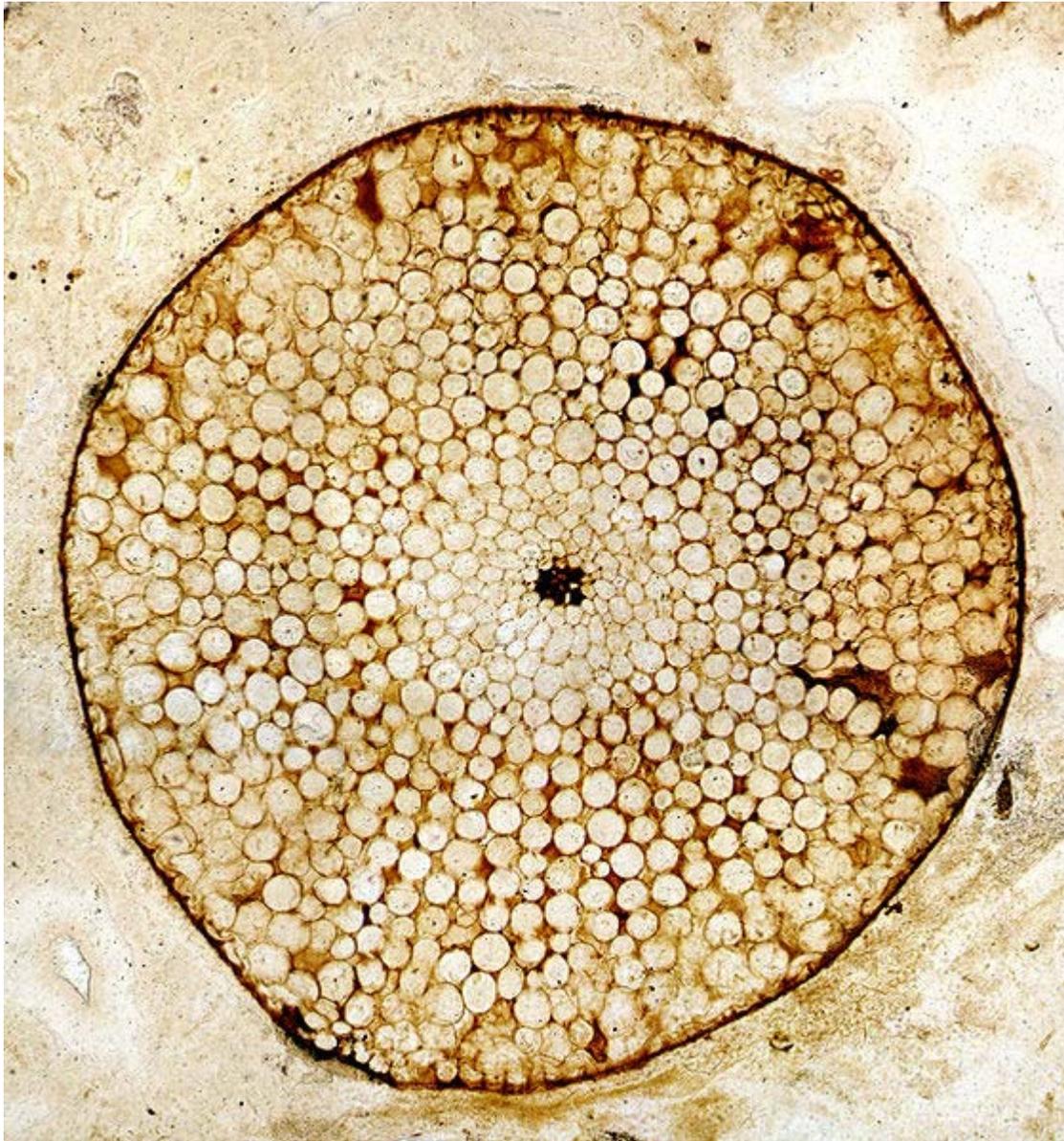
Preservation of plant fossils



Ginkgoites huttonii, Middle Jurassic, Yorkshire, UK. Leaves preserved as compressions. Specimen in Munich Palaeontological Museum, Germany. Photo by Ghedoghedo

Plant fossils can be preserved in a variety of ways, each of which can give different types of information about the original parent plant. These modes of preservation are discussed in the general pages on fossils but may be summarised in a palaeobotanical context as follows.

1. **Adpressions (compressions - impressions).** These are the most commonly found type of plant fossil. They provide good morphological detail, especially of dorsiventral (flattened) plant parts such as leaves. If the cuticle is preserved, they can also yield fine anatomical detail of the epidermis. Little other detail of cellular anatomy is normally preserved.



Rhynia, Lower Devonian Rhynie Chert, Scotland, UK. Transverse section through a stem preserved as a silica petrifaction. Photo by Plantsurfer

2. **Petrifactions (permineralisations or anatomically preserved fossils).** These provide fine detail of the cell anatomy of the plant tissue. Morphological detail can also be determined by serial sectioning, but this is both time consuming and difficult.

3. **Moulds and casts.** These only tend to preserve the more robust plant parts such as seeds or woody stems . They can provide information about the three-dimensional form of the plant, and in the case of casts of tree stumps can provide evidence of the density of the original vegetation. However, they rarely preserve any fine morphological detail or cell anatomy. A subset of such fossils are **pith casts**, where the centre of a stem is either hollow or has delicate pith. After death, sediment enters and forms a cast of the central cavity of the stem. The best known examples of pith casts are in the Carboniferous Sphenophyta (*Calamites*) and cordaites (*Artisia*).



Crossotheca hughesiana Kidston, Middle Pennsylvanian, Coseley, near Dudley, UK. A lyginopteridalean pollen organ preserved as an authigenic mineralisation. Specimen in Sedgwick Museum, Cambridge, UK. Photo by Verisimilus.

4. **Authigenic mineralisations.** These can provide very fine, three-dimensional morphological detail, and have proved especially important in the study of reproductive structures that can be severely distorted in adpressions. However, as they are formed in mineral nodules, such fossils can rarely be of large size.

5. **Fusain.** Fire normally destroys plant tissue but sometimes charcoalfied remains can preserve fine morphological detail that is lost in other modes of preservation; some of the best evidence of early flowers has been preserved in fusain. Fusian fossils are delicate

and often small, but because of their buoyancy can often drift for long distances and can thus provide evidence of vegetation away from areas of sedimentation.

Fossil-taxa

Plant fossils almost always represent disarticulated parts of plants; even small herbaceous plants are rarely preserved whole. Those few examples of plant fossils that appear to be the remains of whole plants in fact are incomplete as the internal cellular tissue and fine micromorphological detail is normally lost during fossilisation. An added complication is that, as explained above, plant remains can be preserved in a variety of ways, each revealing different features of the original parent plant.

Because of these difficulties, palaeobotanists usually assign different taxonomic names to different parts of the plant in different modes of preservation. For instance, in the subarborescent Palaeozoic sphenophytes, an impression of a leaf might be assigned to the genus *Annularia*, a compression of a cone assigned to *Palaeostachya*, and the stem assigned to either *Calamites* or *Arthroxyton* depending on whether it is preserved as a cast or a petrification. All of these fossils may have originated from the same parent plant but they are each given their own taxonomic name. This approach to naming plant fossils originated with the work of Brongniart (1822) and has stood the test of time; although non-palaeobotanist may find it a confusing system, it is generally regarded as the most practical way to overcome the special taphonomic difficulties encountered with plant fossils.

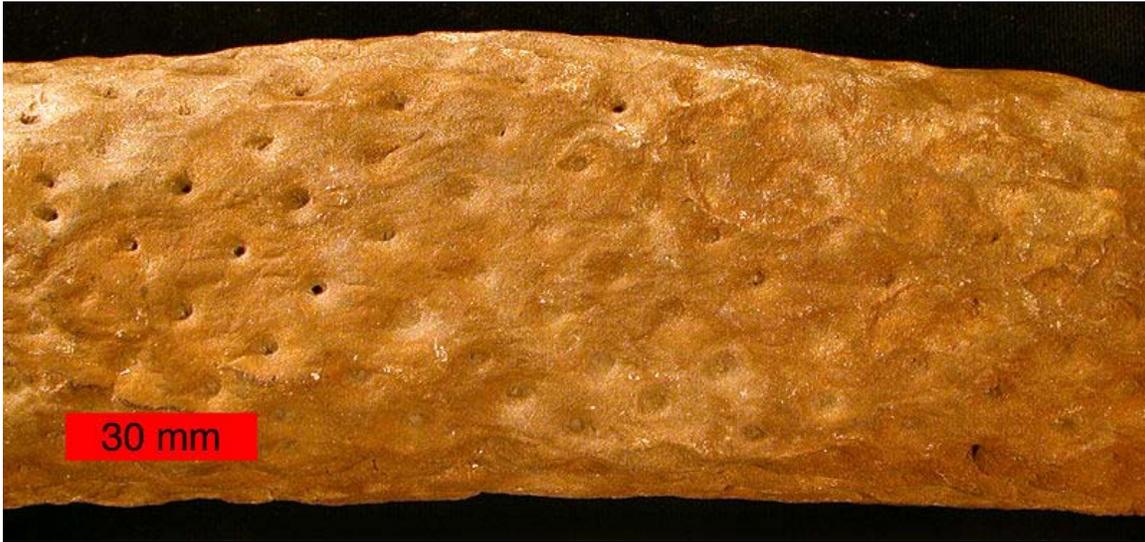
For many years this approach to naming plant fossils was tacitly accepted by palaeobotanists but not formalised within the *International Rules of Botanical Nomenclature* (e.g. Briquet, 1906). Eventually, Thomas (1935) and Jongmans et al. (1935) proposed a set of formal provisions, the essence of which was introduced into the first *International Code of Botanical Nomenclature* (Lanjou et al., 1952). These early provisions allowed fossils representing particular parts of plants in a particular state of preservation to be referred to organ-genera. In addition, a small subset of organ-genera, to be known as form-genera, were recognised based on the artificial taxa introduced by Brongniart (1822) mainly for foliage fossils. Over the years, the concepts and regulations surrounding organ- and form-genera became modified within successive *International Codes of Botanical Nomenclature*, reflecting a failure of the palaeobotanical community to agree on how this aspect of plant taxonomic nomenclature should work (a history reviewed by Cleal & Thomas, 2010). Eventually, the use of organ- and fossil-genera was abandoned with the *St Louis Code* (Greuter et al., 2000).

The situation in the current *Code* (McNeill et al., 2006) is that any plant taxon whose type is a fossil is referred to as a fossil-taxon. Such taxa can refer to a particular part of a plant preserved in a particular way, as defined in the diagnosis of that taxon. Otherwise, the names of fossil-taxa are subject to essentially the same regulations as control the nomenclature of living plants, notably that the names are fixed to a type specimen, and that competing names are chosen mainly on the basis of chronological priority of first publication. Although the name is always fixed to the type specimen, the circumscription

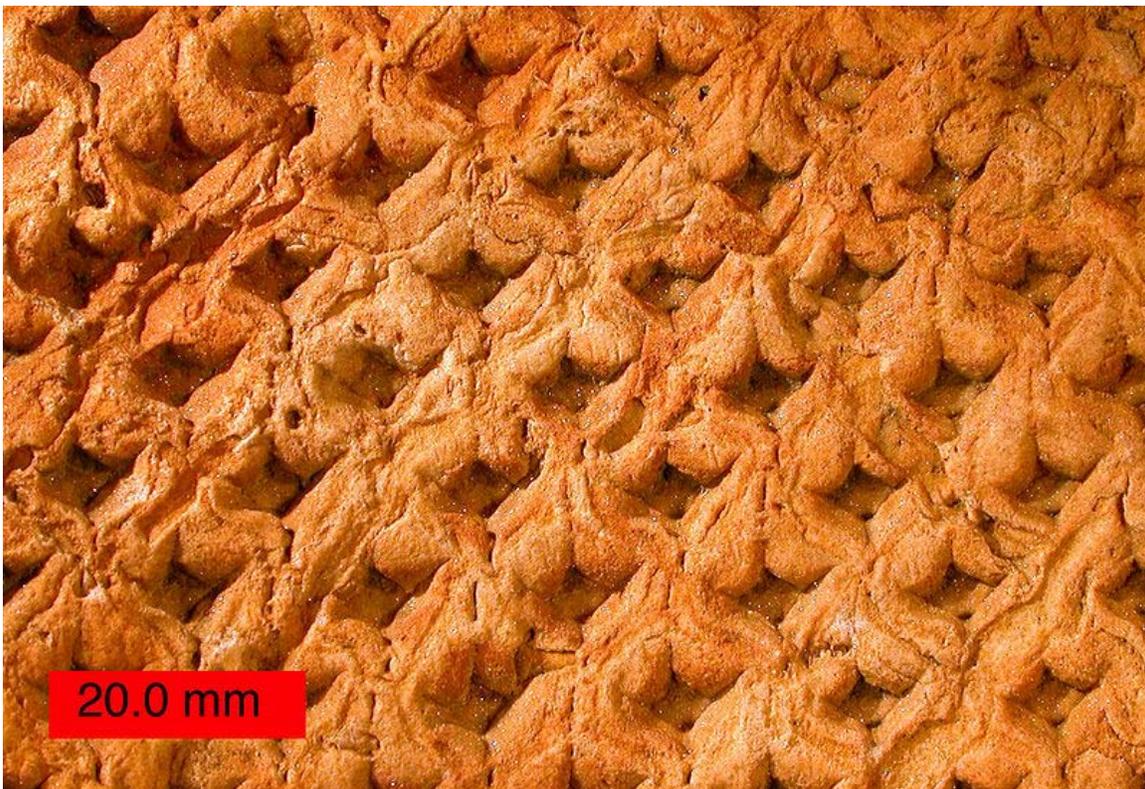
(i.e. range of specimens that may be included within the taxon) is defined by the diagnosis and can be changed by formal emendation. Such emendation could result in an expansion of the range of plant parts and/or preservation states that can be incorporated within the taxon. For instance, a fossil-genus originally based on compressions of ovules could be emended so that it also included the multi-ovulate cupules within which the ovules were originally borne. A complication can arise if, in this case, there was an already named fossil-genus for these cupules. If palaeobotanists were confident that the type of the ovule fossil-genus and of the cupule fossil-genus could be included within the newly emended genus, then the two names would compete as to being the correct one for the newly emended genus. However, this only happens if the actual type specimens (and not just specimens that are similar to the types) can be included within the newly revised taxon.

The current *Code* also refers to a specific subset of fossil-taxa that are known as morphotaxa. These differ from normal fossil-taxa in that they can only be used for fossils that represent the same part of the parent plant and that are preserved in the same way as the type specimen. Morphotaxa were introduced to try to overcome the issue of competing names that represented different plant parts and/or preservation states. What would you do if the species-name of a pollen-organ was pre-dated by the species name of the type of pollen produced by that pollen organ. It was argued that palaeobotanists would be unhappy if the pollen organs were named using the taxonomic name whose type specimen is a pollen grain. As pointed out by Cleal & Thomas (2010), however, the risk of the name of a pollen grain supplanting the name of a pollen organ is most unlikely. Palaeobotanists would have to be totally confident that the type specimen of the pollen species, which would normally be a dispersed grain, definitely came from the same plant that produced the pollen organ. We know from modern plants that closely related but distinct species can produce virtually indistinguishable pollen. It would seem that morphotaxa offer no real advantage to palaeobotanists over normal fossil-taxa and the concept is best abandoned.

Fossil groups of plants



Stigmaria, a common fossil tree root. Upper Carboniferous of northeastern Ohio.



External mold of *Lepidodendron* from the Upper Carboniferous of Ohio.

Some plants have remained remarkably unchanged throughout earth's geological time scale. Early ferns had developed by the Mississippian, conifers by the Pennsylvanian.

Some plants of prehistory are the same ones around today and are thus living fossils, such as *Ginkgo biloba* and *Sciadopitys verticillata*. Other plants have changed radically, or have gone extinct entirely.

Examples of prehistoric plants are:

- *Araucaria mirabilis*
- *Archaeopteris*
- *Calamites*
- *Glossopteris*
- *Hymenaea protera*
- *Nelumbo aureavallis*
- *Protosalvinia*
- *Palaeoraphe*
- *Trochodendron nastae*
- *Dillhoffia*
- *Peltandra primaeva*

Notable Paleobotanists

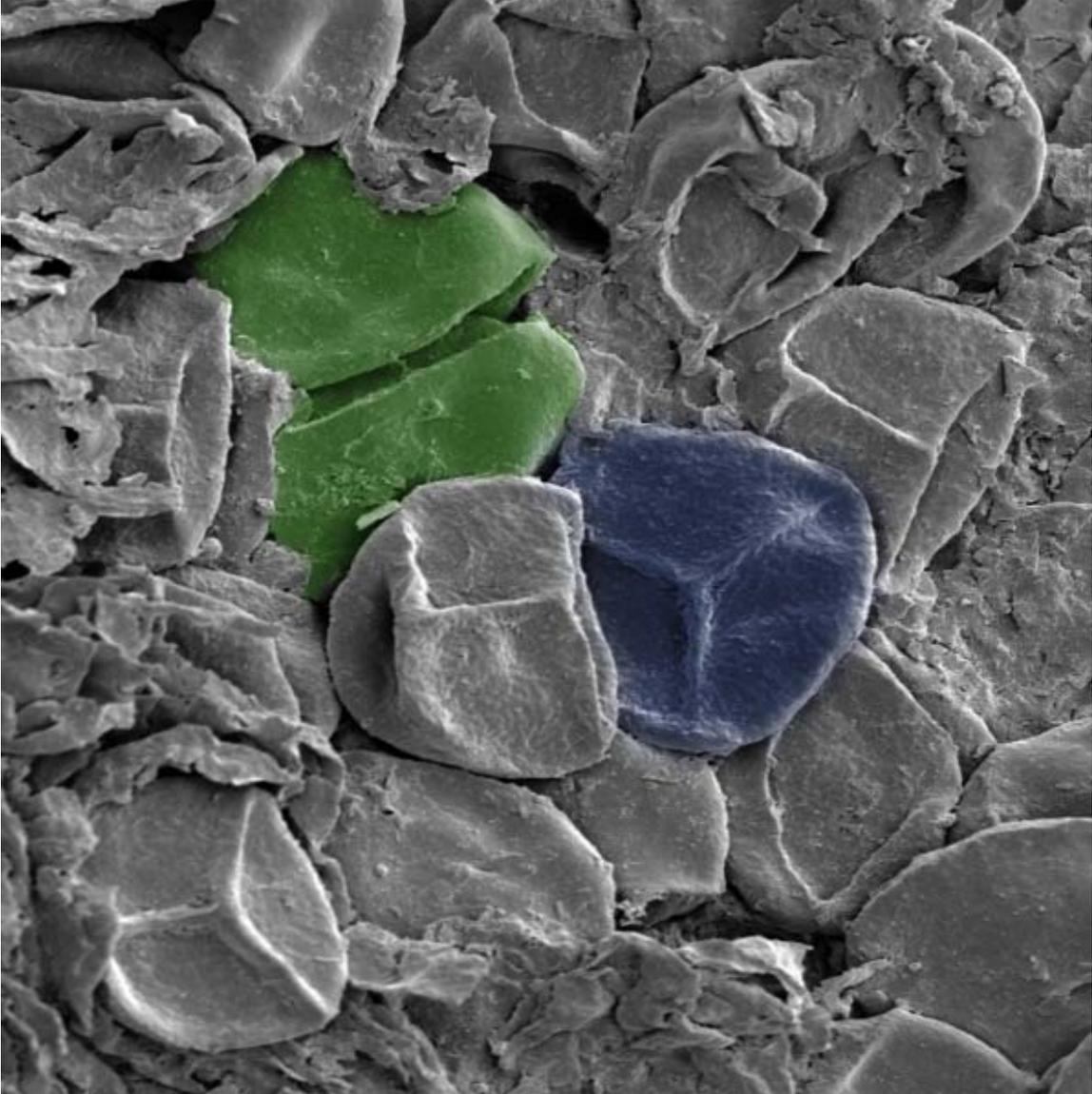
- Edward W. Berry (1875–1945), paleoecology and phytogeography
- Constantin von Ettingshausen (1826–1897), Tertiary floras
- Dunkinfield Henry Scott (1854–1934), analysis of the structures of fossil plants
- Kaspar Maria von Sternberg (1761–1838), the "father of paleobotany"
- Franz Unger (1800–1870), pioneer in plant physiology, phytotomy and soil science
- Jack A. Wolfe (1936–2005) Tertiary paleoclimate of western North America.

Chapter 7

Palynology



Pine Pollen under the microscope



A late Silurian sporangium bearing trilete spores. Such spores are the earliest evidence of life on land. **Green:** A spore tetrad. **Blue:** A spore bearing a trilete mark – the Y-shaped scar. The spores are about 30–35 μm across.

Palynology is the science that studies contemporary and fossil palynomorphs, including pollen, spores, orbicules, dinoflagellate cysts, acritarchs, chitinozoans and scolecodonts, together with particulate organic matter (POM) and kerogen found in sedimentary rocks and sediments. Palynology does not include diatoms, foraminiferans or other organisms with siliceous or calcareous exoskeletons.

Palynology is an interdisciplinary science and is a branch of earth science (geology or geological science) and biological science (biology), particularly plant science (botany). Stratigraphical palynology is a branch of micropalaeontology and paleobotany which studies fossil palynomorphs from the Precambrian to the Holocene.

A history of palynology

Early history

The earliest reported observations of pollen under a microscope are likely to have been in the 1640s by the English botanist Nehemiah Grew who described pollen, the stamen and successfully predicted that pollen was required for successful reproduction in plants. As microscopes began to improve further studies included work by Robert Kidston and P. Reinsch examined the presence of spores in coal and compared them to modern spores. The early pioneers also included Christian Gottfried Ehrenberg (radiolarians and diatoms), Gideon Mantell (desmids) and Henry Hopley White (dinoflagellates).

Modern palynology

The earliest quantitative analysis of pollen was published by Lennart von Post who laid out the foundations of modern pollen analysis in his Kristiania lecture of 1916. Pollen analysis was initially confined to Nordic countries because many early publications were in Nordic languages. This isolation ended with the publication of Gunnar Erdtman's thesis of 1921 when pollen analysis became widespread throughout Europe and North America for use in studies of Quaternary vegetation and climate change.

The term *palynology* was introduced by Hyde and Williams in 1944, following correspondence with the Swedish geologist Antevs, in the pages of the Pollen Analysis Circular (one of the first journals devoted to pollen analysis, produced by Paul Sears in North America). Hyde and Williams chose *palynology* on the basis of the Greek words *paluno* meaning 'to sprinkle' and *pale* meaning 'dust' (and thus similar to the Latin word *pollen*).

Methods of study

Palynomorphs are broadly defined as organic-walled microfossils between 5 and 500 micrometres in size. They are extracted from rocks and sediment cores both physically, by wet sieving, often after ultrasonic treatment, and chemically, by using chemical digestion to remove the non-organic fraction.

Chemical preparation

Chemical digestion follows a number of steps. Initially the only chemical treatment used by researchers was treatment with KOH to remove humic substances; defloculation was accomplished through surface treatment or ultra-sonic treatment, although sonification may cause the pollen exine to rupture. The use of hydrofluoric acid (HF) to digest silicate minerals was introduced by Assarson and Granlund in 1924, greatly reducing the amount of time required to scan slides for palynomorphs. Palynological studies using peats presented a particular challenge because of the presence of well preserved organic material including fine rootlets, moss leaflets and organic litter. This was the last major

challenge in the chemical preparation of materials for palynological study. Acetolysis was developed by Gunnar Erdtman and his brother to remove these fine cellulose materials by dissolving them. In acetolysis the material is treated with acetic anhydride and sulfuric acid, dissolving cellulosic materials and providing better visibility for palynomorphs.

Some steps of the chemical treatments require special care for safety reasons, in particular the use of HF which diffuses very fast through the skin and could cause severe chemical burns.

Other treatments include kerosene flotation for chitinous materials.

Analysis

Once samples have been prepared chemically, they are mounted on microscope slides using silicon oil, glycerol or glycerol-jelly and examined using light microscopy or scanning electron microscopy.

Researchers will often study either modern samples from a number of unique sites within a given area, or samples from a single site with a record through time, such as samples obtained from peat or lake sediments. More recent studies have used the modern analog technique in which paleo-samples are compared to modern samples for which the parent vegetation is known.

When the slides are observed under a microscope, the researcher counts the number of grains of each pollen taxon. This record is next used to produce a pollen diagram. These data can be used to detect anthropogenic effects, such as logging, traditional patterns of land use or long term changes in regional climate.

Palynology can be applied to problems in many fields including geology, botany, paleontology, archaeology, pedology (soil study), and geography.

Applications

Palynology is used for a diverse range of applications, related to many scientific disciplines:

- Biostratigraphy and geochronology. Geologists use palynological studies in biostratigraphy to correlate strata and determine the relative age of a given bed, horizon, formation or stratigraphical sequence.
- Palaeoecology and climate change. Palynology can be used to reconstruct past vegetation (land plants) and marine and freshwater phytoplankton communities, and so infer past environmental (palaeoenvironmental) and palaeoclimatic conditions.
- Organic palynofacies studies, which examine the preservation of the particulate organic matter and palynomorphs provides information on the depositional

- environment of sediments and depositional palaeoenvironments of sedimentary rocks.
- Geothermal alteration studies examine the colour of palynomorphs extracted from rocks to give the thermal alteration and maturation of sedimentary sequences, which provides estimates of maximum palaeotemperatures.
 - Limnology studies. Freshwater palynomorphs and animal and plant fragments, including the prasinophytes and desmids (green algae) can be used to study past lake levels and long term climate change.
 - Taxonomy and evolutionary studies.
 - Forensic palynology — the study of pollen and other palynomorphs for evidence at a crime scene.
 - Allergy studies. Studies of the geographic distribution and seasonal production of pollen, can help sufferers of allergies such as hay fever.
 - Melissopalynology — the study of pollen and spores found in honey.
 - Archaeological palynology examines human uses of plants in the past. This can help determine seasonality of site occupation, presence or absence of agricultural practices or products and plant-related activity areas within an archaeological context. Bonfire Shelter is one such example of this application.

Because the distribution of acritarchs, chitinozoans, dinoflagellate cysts, pollen and spores provides evidence of stratigraphical correlation through biostratigraphy and palaeoenvironmental reconstruction, one common and lucrative application of palynology is in oil and gas exploration.

Palynology also allows scientists to infer the climatic conditions from the vegetation present in an area thousands or millions of years ago. This is a fundamental part of research into climate change.

Chapter 8

Phytochemistry and Plant Anatomy

Phytochemistry

Phytochemistry is in the strict sense of the word the study of phytochemicals. These are chemicals derived from plants. In a narrower sense the terms are often used to describe the large number of secondary metabolic compounds found in plants. Many of these are known to provide protection against insect attacks and plant diseases. They also exhibit a number of protective functions for human consumers.

Techniques commonly used in the field of phytochemistry are extraction, isolation and structural elucidation (MS, 1D and 2D NMR) of natural products, as well as various chromatography techniques (MPLC, HPLC, LC-MS).

Constituent elements

The list of simple elements of which plants are primarily constructed—carbon, oxygen, hydrogen, calcium, phosphorus, etc.—is not different from similar lists for animals, fungi, or even bacteria. The fundamental atomic components of plants are the same as for all life; only the details of the way in which they are assembled differs.

The following tables list element nutrients essential to plants. Uses within plants are generalized.

Macronutrients. (Necessary in large quantities)		
Element	Form of uptake	Notes
Nitrogen	NO_3^- NH_4^+	Nucleic acids, proteins, hormones, etc.
Oxygen	O_2 H_2O	Various organic compounds
Carbon	CO_2	Various organic compounds
Hydrogen	H_2O	Various organic compounds
Potassium	K^+	Cofactor in protein synthesis, water balance, etc.
Calcium	Ca^{2+}	Membrane synthesis and stabilization
Magnesium	Mg^{2+}	Element essential for chlorophyll

Phosphorus	H_2PO_4^-	Nucleic acids, phospholipids, ATP
Sulfur	SO_4^{2-}	Constituent of proteins and coenzymes
Micronutrients. (Necessary in small quantities)		
Element	Form of uptake	Notes
Chlorine	Cl^-	Aids in root growth
Boron	H BO_3	Affects reproduction
Manganese	Mn^{2+}	Activity of some enzymes
Zinc	Zn^{2+}	Involved in the synthesis of enzymes and chlorophyll
Copper	Cu^+	Enzymes for lignin synthesis
Molybdenum	MoO_4^{2-}	Nitrogen fixation, reduction of nitrates
Nickel	Ni^{2+}	Enzymatic cofactor in the metabolism of nitrogen compounds

Photosynthesis

Eastern medicine

Phytochemistry is widely used in the field of Chinese medicine especially in the field of herbal medicine.

Phytochemical technique mainly applies to the quality control of Chinese medicine or herbal medicine of various chemical components, such as saponins, alkaloids, volatile oils, flavonoids and anthraquinones. In the development of rapid and reproducible analytical techniques, the combination of HPLC with different detectors, such as diode array detector (DAD), refractive index detector (RID), evaporative light scattering detector (ELSD) and mass spectrometric detector (MSD), has been widely developed.

In most cases, biologically active compounds in Chinese medicine or herbal medicine have not been determined. Therefore, it is important to use the phytochemical methods to screen and analyze bioactive components, not only for the quality control of crude drugs, but also for the elucidation of their therapeutic mechanisms. Modern pharmacological studies indicate that binding to receptors or ion channels on cell membranes is the first step of some drug actions. A new method in phytochemistry called biochromatography has been developed. This method combines human red cell membrane extraction and high performance liquid chromatography to screen potential active components in Chinese medicine.

Types of substances studied

- Polyphenols
- Phytosterols
- Alkaloids
- Saponins

Plant anatomy

Plant anatomy or **phytotomy** is the general term for the study of the internal structure of plants. While originally it included plant morphology, which is the description of the physical form and external structure of plants, since the mid-20th century the investigations of plant anatomy are considered a separate, distinct field, and plant anatomy refers to *just* the internal plant structures. Plant anatomy is now frequently investigated at the cellular level, and often involves the sectioning of tissues and microscopy.

Structural divisions

Plant anatomy is sometimes divided into the following categories:

- Flower anatomy
 - Calyx
 - Corolla
 - Androecium
 - Gynoecium
- Leaf anatomy
- Leaf anatomy
- Stem anatomy
- Stem structure
- Fruit/Seed anatomy
 - Ovule
 - Seed structure
 - Pericarp
 - Accessory fruit
- Wood anatomy
 - Bark
 - Cork
 - Phloem
 - Vascular cambium
 - Heartwood and sapwood
 - branch collar

Root anatomy
Root structure

History

About 300 BCE Theophrastus wrote a number of plant treatises, only two of which survive. He developed concepts of plant morphology and classification, which did not withstand the scientific scrutiny of the Renaissance.

A Swiss physician and botanist, Gaspard Bauhin, introduced binomial nomenclature into plant taxonomy. He published *Pinax theatri botanici* in 1596, which was the first to use this convention for naming of species. His criteria for classification included natural relationships, or 'affinities', which in many cases were structural.

Italian doctor and microscopist, Marcello Malpighi, was one of the two founders of plant anatomy. In 1671 he published his *Anatomia Plantarum*, the first major advance in plant physiogamy since Aristotle.

The British doctor, Nehemiah Grew was one of the two founders of plant anatomy. He published *An Idea of a Philosophical History of Plants* in 1672 and *The Anatomy of Plants* in 1682. Grew is credited with the recognition of plant cells, although he called them 'vesicles' and 'bladders'. He correctly identified and described the sexual organs of plants (flowers) and their parts.

In the Eighteenth Century, Carolus Linnaeus established taxonomy based on structure, and his early work was with plant anatomy. While the exact structural level which is to be considered to be scientifically valid for comparison and differentiation has changed with the growth of knowledge, the basic principles were established by Linnaeus. He published his master work, *Species Plantarum* in 1753.

In 1802, French botanist, Charles-François Brisseau de Mirbel, published *Traité d'anatomie et de physiologie végétale (Treatise on Plant Anatomy and Physiology)* establishing the beginnings of the science of plant cytology.

In 1812, Johann Jacob Paul Moldenhawer published *Beyträge zur Anatomie der Pflanzen*, describing microscopic studies of plant tissues.

In 1813 a Swiss botanist, Augustin Pyrame de Candolle, published *Théorie élémentaire de la botanique*, in which he argued that plant anatomy, not physiology, ought to be the sole basis for plant classification. Using a scientific basis, he established structural criteria for defining and separating plant genera.

In 1830, Franz Meyen published *Phytotomie*, the first comprehensive review of plant anatomy.

In 1838 German botanist, Matthias Jakob Schleiden, published *Contributions to Phytogenesis*, stating, "the lower plants all consist of one cell, while the higher plants are composed of (many) individual cells" thus confirming and continuing Mirabel's work.

A German-Polish botanist, Eduard Strasburger, described the mitotic process in plant cells and further demonstrated that new cell nuclei can only arise from the division of other pre-existing nuclei. His *Studien über Protoplasma* was published in 1876.

Gottlieb Haberlandt, a German botanist, studied plant physiology and classified plant tissue based upon function. On this basis, in 1884 he published *Physiologische Pflanzenanatomie (Physiological Plant Anatomy)* in which he described twelve types of tissue systems (absorptive, mechanical, photosynthetic, etc.).

British paleobotanists Dunkinfield Henry Scott and William Crawford Williamson described the structures of fossilized plants at the end of the Nineteenth Century. Scott's *Studies in Fossil Botany* was published in 1900.

Following Charles Darwin's *Origin of Species* a Canadian botanist, Edward Charles Jeffrey, who was studying the comparative anatomy and phylogeny of different vascular plant groups, applied the theory to plants using the form and structure of plants to establish a number of evolutionary lines. He published his *The Anatomy of Woody Plants* in 1917.

The growth of comparative plant anatomy was spearheaded by a British botanist, Agnes Arber. She published *Water Plants: A Study of Aquatic Angiosperms* in 1920, *Monocotyledons: A Morphological Study* in 1925, and *The Gramineae: A Study of Cereal, Bamboo and Grass* in 1934.

Following World War II, Katherine Esau published, *Plant Anatomy* (1953), which became the definitive textbook on plant structure in North American universities and elsewhere, it was still in print as of 2006. She followed up with her *Anatomy of seed plants* in 1960.

Chapter 9

Plant Pathology

Plant pathology (also **phytopathology**) is the scientific study of plant diseases caused by pathogens (infectious diseases) and environmental conditions (physiological factors). Organisms that cause infectious disease include fungi, oomycetes, bacteria, viruses, viroids, virus-like organisms, phytoplasmas, protozoa, nematodes and parasitic plants. Not included are ectoparasites like insects, mites, vertebrate or other pests that affect plant health by consumption of plant tissues. Plant pathology also involves the study of pathogen identification, disease etiology, disease cycles, economic impact, plant disease epidemiology, plant disease resistance, how plant diseases affect humans and animals, pathosystem genetics, and management of plant diseases.

Plant pathogens

Fungi

The majority of phytopathogenic fungi belong to the Ascomycetes and the Basidiomycetes.

The fungi reproduce both sexually and asexually via the production of spores. These spores may be spread long distances by air or water, or they may be soil borne. Many soil borne spores, normally zoospores, are capable of living saprotrophically, carrying out the first part of their lifecycle in the soil.

Fungal diseases can be controlled through the use of fungicides in agriculture, however new races of fungi often evolve that are resistant to various fungicides.



Powdery mildew, a Biotrophic Fungus



Rice blast, a necrotrophic fungus

Biotrophic fungal pathogens colonize living plant tissue and obtain nutrients from living

host cells. Necrotrophic fungal pathogens infect and kill host tissue and extract nutrients from the dead host cells.

Significant fungal plant pathogens include:

Ascomycetes

- *Fusarium* spp. (causal agents of Fusarium wilt disease)
- *Thielaviopsis* spp. (causal agents of: canker rot, black root rot, *Thielaviopsis* root rot)
- *Verticillium* spp.
- *Magnaporthe grisea* (causal agent of blast of rice and gray leaf spot in turfgrasses)

Basidiomycetes

- *Rhizoctonia* spp.
- *Phakospora pachyrhizi* (causal agent of soybean rust)
- *Puccinia* spp. (causal agents of severe rusts of virtually all cereal grains and cultivated grasses)

Oomycetes

The oomycetes are not true fungi but are fungus-like organisms. They include some of the most destructive plant pathogens including the genus *Phytophthora* which includes the causal agents of potato late blight and sudden oak death.

Despite not being closely related to the fungi, the oomycetes have developed very similar infection strategies and so many plant pathologists group them with fungal pathogens.

Significant oomycete plant pathogens

- *Pythium* spp.
- *Phytophthora* spp.; including the causal agent of the Great Irish Famine (1845–1849)

Bacteria



Crown gall disease caused by *Agrobacterium*

Most bacteria that are associated with plants are actually saprotrophic, and do no harm to the plant itself. However, a small number, around 100 species, are able to cause disease. Bacterial diseases are much more prevalent in sub-tropical and tropical regions of the world.

Most plant pathogenic bacteria are rod shaped (bacilli). In order to be able to colonize the plant they have specific pathogenicity factors. Five main types of bacterial pathogenicity factors are known:

1. **Cell wall degrading enzymes** – used to break down the plant cell wall in order to release the nutrients inside. Used by pathogens such as *Erwinia* to cause soft rot.
2. **Toxins** These can be non-host specific, and damage all plants, or host specific and only cause damage on a host plant.
3. **Effector proteins** These can be secreted into the extracellular environment or directly into the host cell, often via the Type three secretion system. Some effectors are known to suppress host defense processes.
4. **Phytohormones** – for example *Agrobacterium* changes the level of auxins to cause tumours.

5. **Exopolysaccharides** – these are produced by bacteria and block xylem vessels, often leading to the death of the plant.

Bacteria control the production of pathogenicity factors via quorum sensing.

Significant bacterial plant pathogens

- Burkholderia
- Proteobacteria
 - *Xanthomonas* spp.
 - *Pseudomonas* spp.

Phytoplasmas ('Mycoplasma-like organisms') and spiroplasmas



Vitis vinifera with "Ca. *Phytoplasma vitis*" infection

Phytoplasma and *Spiroplasma* are a genre of bacteria that lack cell walls, and are related to the mycoplasmas which are human pathogens. Together they are referred to as the mollicutes. They also tend to have smaller genomes than true bacteria. They are normally transmitted by sap-sucking insects, being transferred into the plants phloem where it reproduces.

Viruses, viroids and virus-like organisms



Tobacco mosaic virus

There are many types of plant virus, and some are even asymptomatic. Normally plant viruses only cause a loss of crop yield. Therefore it is not economically viable to try to control them, the exception being when they infect perennial species, such as fruit trees.

Most plant viruses have small, single stranded RNA genomes. These genomes may only encode three or four proteins: a replicase, a coat protein, a movement protein to allow cell to cell movement through plasmodesmata and sometimes a protein that allows transmission by a vector.

Plant viruses must be transmitted from plant to plant by a vector. This is often by an insect (for example, aphids), but some fungi, nematodes and protozoa have been shown to be viral vectors.

Nematodes



Root-knot nematode galls

Nematodes are small, multicellular wormlike creatures. Many live freely in the soil, but there are some species which parasitize plant roots. They are a problem in tropical and subtropical regions of the world, where they may infect crops. Potato cyst nematodes (*Globodera pallida* and *G. rostochiensis*) are widely distributed in Europe and North and South America and cause \$300 million worth of damage in Europe every year. Root knot nematodes have quite a large host range, whereas cyst nematodes tend to only be able to infect a few species. Nematodes are able to cause radical changes in root cells in order to facilitate their lifestyle.

Protozoa

There are a few examples of plant diseases caused by protozoa. They are transmitted as zoospores which are very durable, and may be able to survive in a resting state in the soil for many years. They have also been shown to transmit plant viruses.

When the motile zoospores come into contact with a root hair they produce a plasmodium and invade the roots.

Parasitic plants

Parasitic plants such as mistletoe and dodder are included in the study of phytopathology. Dodder, for example, is used as a conduit for the transmission of viruses or virus-like agents from a host plant to either a plant that is not typically a host or for an agent that is not graft-transmissible.

Physiological plant disorders

Significant abiotic disorders can be caused by:

Natural

Drought

Frost damage, and breakage by snow and hail

Flooding and poor drainage

Nutrient deficiency

Salt deposition and other soluble mineral excesses (e.g. gypsum)

Wind (windburn, and breakage by hurricanes and tornadoes)

Lightning and wildfire (also often man-made)

Man-made (arguably not abiotic, but usually regarded as such)

Soil compaction

Pollution of air, soil, or both

Salt from winter road salt application or irrigation

Herbicide over-application

Poor education and training of people working with plants (e.g. lawnmower damage to trees)

Vandalism

Management

Quarantine

Wherein a diseased patch of vegetation or individual plants are isolated from other, healthy growth. Specimens may be destroyed or relocated into a greenhouse for treatment/study. Another option is to avoid introduction of harmful non-native organisms by controlling all human traffic and activity (for e.g., AQIS) although legislation and enforcement are key in order to ensure lasting effectiveness.

Cultural

Farming in some societies is kept on a small scale, tended by peoples whose culture includes farming traditions going back to ancient times. (An example of such traditions would be lifelong training in techniques of plot terracing, weather anticipation and response, fertilization, grafting, seed care, and dedicated gardening.) Plants that are intently monitored often benefit not only from active external protection, but a greater overall vigor as well. While primitive in the sense of being the most labor-intensive solution by far, where practical or necessary it is more than adequate.

Plant resistance

Sophisticated agricultural developments now allow growers to choose from among systematically cross-bred species to ensure the greatest hardiness in their crops, as suited for a particular region's pathological profile. Breeding practices have been perfected over centuries, but with the advent of genetic manipulation even finer control of a crop's immunity traits is possible. The engineering of

foodplants may be less rewarding however, as higher output is frequently offset by popular suspicion and negative opinion about this "tampering" with nature.

Chemical

Many natural and synthetic compounds exist that could be employed to combat the above threats. This method works by directly eliminating disease-causing organisms or curbing their spread; however it has been shown to have too broad an effect, typically, to be good for the local ecosystem. From an economic standpoint all but the simplest natural additives may disqualify a product from "organic" status, potentially reducing the value of the yield.

Biological

Crop rotation may be an effective means to prevent a parasitic population from becoming well established, as an organism affecting leaves would be starved when the leafy crop is replaced by a tuberous type, etc. Other means to undermine parasites without attacking them directly may exist.

Integrated

The use of two or more of these methods in combination offers a higher chance of effectiveness.

Chapter 10

Plant Ecology

Plant ecology is a subdiscipline of ecology which studies the distribution and abundance of plants, the interactions among and between members of plant species, and their interactions with their environment. Plant ecology has its roots both in plant geography and in studies of the interactions between individual plants and their environment.

Broadly speaking, the scope of plant ecology encompasses plant ecophysiology, plant population ecology, community ecology, ecosystem ecology and landscape ecology.

Most plants are rooted in the soil, and often they reproduce vegetatively in a way that makes it difficult to distinguish individual plants of the same species. These characteristic features of plants necessitate a somewhat different scientific methodology than used in e.g. animal ecology, but the different subdisciplines of ecology is integrated in ecosystem ecology.

Biological interactions

Competition

When plants grow close to other plants they may compete for resources, such as light, water and nutrients, that are needed for plant growth. Plants may compete for a single growth-limiting resource e.g. light in agricultural systems with sufficient water and nutrients, but in most natural ecosystems plants probably are adapted to respond to the environment in such a way that they are colimited by several resources, e.g. light, phosphorus and nitrogen at the same time.

In principle, it is possible to examine competition at the level of the limiting resources if a detailed knowledge of the physiological processes of the competing plants is available. However, in most terrestrial ecological studies, there is only little information on the uptake and dynamics of the resources that limit the growth of different plant species, and, instead, competition is inferred from observed negative effects of neighbouring plants without knowing precisely which resources the plants were competing for.

Facilitation

Facilitation among neighboring plants may act by reducing the negative impacts of a stressful environment, and in general, facilitation is more likely to occur in physically stressful environments than in favorable environments, where competition may be the most important interaction among species

Herbivory

An important ecological function of plants is that they produce organic compounds for herbivores in the bottom of the food web. Oppositely, herbivory is an important source of disturbance for many plant species, and they have evolved many different forms of defensive physical structures and chemical compounds to prevent herbivory.

Distribution

Plant communities are broadly distributed into biomes based on the structure of dominant plant species. Biomes are determined by regional climates, namely temperature and precipitation, and follow general latitudinal trends. Within biomes, there may be many ecological communities, which are impacted not only by climate and a variety of smaller-scale features, including soils, hydrology, and disturbance regime.

In the same way that plant communities vary at differing latitudes, plant communities vary with elevation. Communities at high elevations often resemble those found at higher latitudes.

Abundance

The ecological success of a plant species in a specific environment may be quantified by its abundance, and depending on the life form of the plant different measures of abundance may be relevant, e.g. density, biomass, or plant cover.

The change in the abundance of a plant species may be due to both abiotic factors, e.g. climate change, or biotic factors, e.g herbivory or interspecific competition.

Colonisation and local extinction

Whether a plant species is present at a local area depends on the processes of colonisation and local extinction. The probability of colonisation decreases with distance to neighboring habitats where the species is present and increases with plant abundance and fecundity in neighboring habitats and the dispersal distance of the species. The probability of local extinction decreases with abundance (both living plants and seeds in the soil seed bank).

Chapter 11

Plant Genetics



An image of multiple chromosomes, making up a genome

Plant genetics is a very broad term. There are many facets of genetics in general, and of course there are many facets to plants. The definition of genetics is the branch of biology

that deals with heredity, especially the mechanisms of hereditary transmission and the variation of inherited characteristics among similar or related organisms. And the definition of a plant is any of various photosynthetic, eukaryotic, multicellular organisms of the kingdom Plantae characteristically producing embryos, containing chloroplasts, having cell walls which contain cellulose, and lacking the power of locomotion. Although there has been a revolution in the biological sciences in the past twenty years, there is still a great deal that remains to be discovered. The completion of the sequencing of the human genome, as well as the genomes of some agriculturally and scientifically important plants (for example rice), has increased the possibilities of genetic research immeasurably.

Features of plant biology

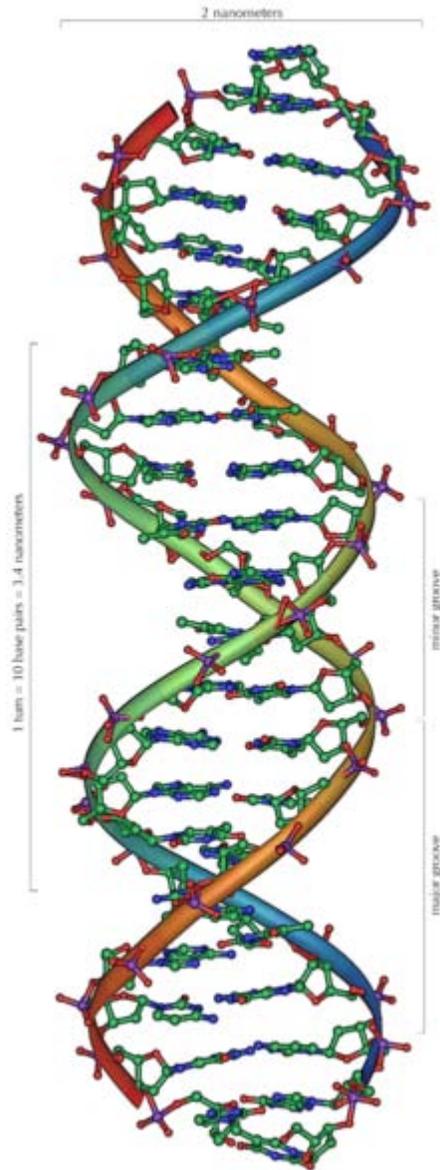
Plants differ from animals in a few ways that make the study of plant genetics interesting. Like mitochondria, chloroplasts have their own DNA, complicating pedigrees somewhat. Like animals, plants have somatic mutations regularly, but these mutations can contribute to the germ line with ease, since flowers develop at the ends of branches composed of somatic cells. People have known of this for centuries, and mutant branches are called "sports". If the fruit on the sport is economically desirable, a new cultivar may be obtained.

Some plant species are capable of self-fertilization, and some are nearly exclusively self-fertilizers. This means that a plant can be both mother and father to its offspring, a rare occurrence in the animals. Scientists and hobbyists attempting to make crosses between different plants must take special measures to prevent the plants from self-fertilizing.

Plants are generally more capable of surviving, and indeed flourishing, as polyploids. Polyploidy, the presence of extra sets of chromosomes, is not usually compatible with life in animals. In plants, polyploid individuals are created frequently by a variety of processes, and once created usually cannot cross back to the parental type. Polyploid individuals, if capable of self-fertilizing, can give rise to a new genetically distinct lineage, which can be the start of a new species. This is often called "instant speciation". Polyploids generally have larger fruit, an economically desirable trait, and many human food crops, including wheat, maize, potatoes, peanuts, strawberries and tobacco, are either accidentally or deliberately created polyploids.

Hybrids between plant species are easy to create by hand-pollination, and may be more successful on average than hybrids between animal species. Often tens of thousands of offspring from a single cross are raised and tested to obtain a single individual with desired characteristics. People create hybrids for economic and aesthetic reasons, especially with orchids.

DNA



The structure of part of a DNA double helix

Deoxyribonucleic acid (DNA) is a nucleic acid that contains the genetic instructions used in the development and functioning of all known living organisms and some viruses. The main role of DNA molecules is the long-term storage of information. DNA is often compared to a set of blueprints or a recipe, or a code, since it contains the instructions needed to construct other components of cells, such as proteins and RNA molecules. The DNA segments that carry this genetic information are called genes, but other DNA sequences have structural purposes, or are involved in regulating the use of this genetic information. Geneticists, including plant geneticists, use this sequencing of DNA to their

advantage as they splice and delete certain genes and regions of the DNA molecule to produce a different or desired genotype and thus, also producing a different phenotype.

Gregor Mendel

Gregor Mendel was an Augustinian priest and scientist, and is often called the father of genetics for his study of the inheritance of certain traits in pea plants. Mendel showed that the inheritance of these traits follows particular laws, which were later named after him. The significance of Mendel's work was not recognized until the turn of the 20th century. Its rediscovery prompted the foundation of the discipline of genetics allows geneticists today to accurately predict the outcome of such crosses and in determining the phenotypical effects of the crosses. He was born on 20 July 1822 and died on 6 January 1884 from chronic nephritis. His nationality was Austria-Hungary. His field was Genetics and went to the Abbey of St. Thomas in Brno. He was well-known for discovering genetics.

Modern ways to genetically modify plants

There are two predominant procedures of transforming genes in organisms: the "Gene gun" method and the *Agrobacterium* method.

"Gene gun" method

The "Gene Gun" method is also referred to as "biolistics" (ballistics using biological components). This technique is used for in vivo, within a living organism, transformation and has been especially useful in transforming monocot species like corn, otherwise known as maize, and rice. This approach literally shoots genes into plant cells and plant cell chloroplasts. DNA is coated onto small particles of gold or tungsten approximately two micrometres in diameter. The particles are placed in a vacuum chamber and the plant tissue to be engineered is placed below the chamber. The particles are propelled at high velocity using a short pulse of high pressure helium gas, and hit a fine mesh baffle placed above the tissue while the DNA coating continues into any target cell or tissue.

***Agrobacterium* method**

Transformation via *Agrobacterium* has been successfully practiced in dicots, i.e. broadleaf plants, such as soybeans and tomatoes, for many years. Recently it has been adapted and is now effective in monocots like grasses, including corn and rice. In general, the *Agrobacterium* method is considered preferable to the gene gun, because of a greater frequency of single-site insertions of the foreign DNA, which allows for easier monitoring. In this method, the tumor inducing (Ti) region is removed from the T-DNA (transfer DNA) and replaced with the desired gene and a marker, which is then inserted into the organism. This may involve direct inoculation of the tissue with a culture of transformed *Agrobacterium*, or inoculation following treatment with micro-projectile bombardment, which wounds the tissue. Wounding of the target tissue causes the release

of phenolic compounds by the plant, which induces invasion of the tissue by *Agrobacterium*. Because of this, microprojectile bombardment often increases the efficiency of infection with *Agrobacterium*. The marker is used to find the organism which has successfully taken up the desired gene. Tissues of the organism are then transferred to a medium containing an antibiotic or herbicide, depending on which marker was used. The *Agrobacterium* present is also killed by the antibiotic. Only tissues expressing the marker will survive and possess the gene of interest. Thus, subsequent steps in the process will only use these surviving plants. In order to obtain whole plants from these tissues, they are grown under controlled environmental conditions in tissue culture. This is a process of a series of media, each containing nutrients and hormones. Once the plants are grown and produce seed, the process of evaluating the progeny begins. This process entails selection of the seeds with the desired traits and then retesting and growing to make sure that the entire process has been completed successfully with the desired results.

Genetically engineered crops

Benefits of genetically engineered crops

The use of genetically engineered crops has helped many farmers deal with pest problems that reduce their crop production. The impact of pest-resistant crops has led to a much higher yield for farmers in today's world. They can use less pesticides which reduces the chemicals that they put into the ground. Certain engineered crops such as Roundup Ready Corn, a patented transgenic maize variety, has led to farmers all over the world and in the United States to increase crop yield exponentially in recent years. Farmers can use a Roundup herbicide to kill weeds, yet the genetically engineered corn is resistant to the herbicide and is left unaffected. Thus, fields are produced that are virtually weed free. Genetically engineered crops can also benefit farmers when dealing with potentially harmful viruses and bacteria. In the case of the 1990s a mutant strain of virus was decimating the commercial corn fields of the United States. Scientists found a virus resistant strain of maize in the highlands of Mexico and extracted the part of the maize's genome that coded for resistance against the virus and incorporated it into their existing strain of commercial corn. This allowed the commercial strain to produce progeny that were resistant to the virus. Thus, the crops were saved from decimation.

Potential detrimental effects of genetically engineered plants

According to Vaughan A. Hilder and Donald Boulter at the Department of Biological Sciences, University of Durham, there have been serious failures in resistance to targeted pests in Bt cotton; most plant-derived resistance factors produce chronic rather than acute effects; and many serious pests are simply not susceptible to known resistance factors. According to John E. Berringer the outcome of releasing genetically modified organisms into the environment is still not known.

Chapter 12

Plant Morphology

Plant morphology (or **phytomorphology**) is the general term for the study of the morphology (physical form and external structure) of plants. This is usually considered distinct from plant anatomy, which is the study of the internal structure of plants, especially at the microscopic level. Plant morphology is useful in the identification of plants.



Inflorescences emerging from protective coverings

Scope

Plant morphology "represents a study of the development, form, and structure of plants, and, by implication, an attempt to interpret these on the basis of similarity of plan and origin." There are four major areas of investigation in plant morphology, and each overlaps with another field of the biological sciences.

First of all, morphology is **comparative**, meaning that the morphologist examines structures in many different plants of the same or different species, then draws comparisons and formulates ideas about similarities. When structures in different species are believed to exist and develop as a result of common, inherited genetic pathways, those structures are termed homologous. For example, the leaves of pine, oak, and cabbage all look very different, but share certain basic structures and arrangement of parts. The homology of leaves is an easy conclusion to make. The plant morphologist goes further, and discovers that the spines of cactus also share the same basic structure and development as leaves in other plants, and therefore cactus spines are homologous to leaves as well. This aspect of plant morphology overlaps with the study of plant evolution and paleobotany.



Asclepias syriaca showing complex morphology of the flowers.

Secondly, plant morphology observes both the **vegetative (somatic)** structures of plants, as well as the **reproductive** structures. The vegetative structures of vascular plants includes the study of the shoot system, composed of stems and leaves, as well as the root system. The reproductive structures are more varied, and are usually specific to a particular group of plants, such as flowers and seeds, fern sori, and moss capsules. The detailed study of reproductive structures in plants led to the discovery of the alternation of generations found in all plants and most algae. This area of plant morphology overlaps with the study of biodiversity and plant systematics.

Thirdly, plant morphology studies plant structure at a range of scales. At the smallest scales are **ultrastructure**, the general structural features of cells visible only with the aid of an electron microscope, and **cytology**, the study of cells using optical microscopy. At this scale, plant morphology overlaps with plant anatomy as a field of study. At the largest scale is the study of plant **growth habit**, the overall architecture of a plant. The pattern of branching in a tree will vary from species to species, as will the appearance of a plant as a tree, herb, or grass.

Fourthly, plant morphology examines the pattern of **development**, the process by which structures originate and mature as a plant grows. While animals produce all the body parts they will ever have from early in their life, plants constantly produce new tissues and structures throughout their life. A living plant always has embryonic tissues. The way in which new structures mature as they are produced may be affected by the point in the plants life when they begin to develop, as well as by the environment to which the structures are exposed. A morphologist studies this process, the causes, and its result. This area of plant morphology overlaps with plant physiology and ecology.

A comparative science

A plant morphologist makes comparisons between structures in many different plants of the same or different species. Making such comparisons between similar structures in different plants tackles the question of *why* the structures are similar. It is quite likely that similar underlying causes of genetics, physiology, or response to the environment have led to this similarity in appearance. The result of scientific investigation into these causes can lead to one of two insights into the underlying biology:

1. **Homology** - the structure is similar between the two species because of shared ancestry and common genetics.
2. **Convergence** - the structure is similar between the two species because of independent adaptation to common environmental pressures.

Understanding which characteristics and structures belong to each type is an important part of understanding plant evolution. The evolutionary biologist relies on the plant morphologist to interpret structures, and in turn provides phylogenies of plant relationships that may lead to new morphological insights.

Homology

When structures in different species are believed to exist and develop as a result of common, inherited genetic pathways, those structures are termed *homologous*. For example, the leaves of pine, oak, and cabbage all look very different, but share certain basic structures and arrangement of parts. The homology of leaves is an easy conclusion to make. The plant morphologist goes further, and discovers that the spines of cactus also share the same basic structure and development as leaves in other plants, and therefore cactus spines are homologous to leaves as well.

Convergence

When structures in different species are believed to exist and develop as a result of common adaptive responses to environmental pressure, those structures are termed *convergent*. For example, the fronds of *Bryopsis plumosa* and stems of *Asparagus setaceus* both have the same feathery branching appearance, even though one is an alga and one is a flowering plant. The similarity in overall structure occurs independently as a result of convergence. The growth form of many cacti and species of *Euphorbia* is very similar, even though they belong to widely distant families. The similarity results from common solutions to the problem of surviving in a hot, dry environment.



Euphorbia obesa, a spurge



Astrophytum asterias, a cactus.

Vegetative and reproductive characters

Plant morphology treats both the vegetative structures of plants, as well as the reproductive structures.

The **vegetative (somatic)** structures of vascular plants include two major organ systems: (1) a **shoot system**, composed of stems and leaves, and (2) a **root system**. These two systems are common to nearly all vascular plants, and provide a unifying theme for the study of plant morphology.

By contrast, the **reproductive** structures are varied, and are usually specific to a particular group of plants. Structures such as flowers and fruits are only found in the angiosperms; sori are only found in ferns; and seed cones are only found in conifers and other gymnosperms. Reproductive characters are therefore regarded as more useful for the classification of plants than vegetative characters.

Use in identification

Plant biologists use morphological characters of plants which can be compared, measured counted and described to assess the differences or similarities in plant taxa and use these characters for plant identification, classification and descriptions.

When characters are used in descriptions or for identification they are called **diagnostic** or **key characters** which can be either qualitative and quantitative.

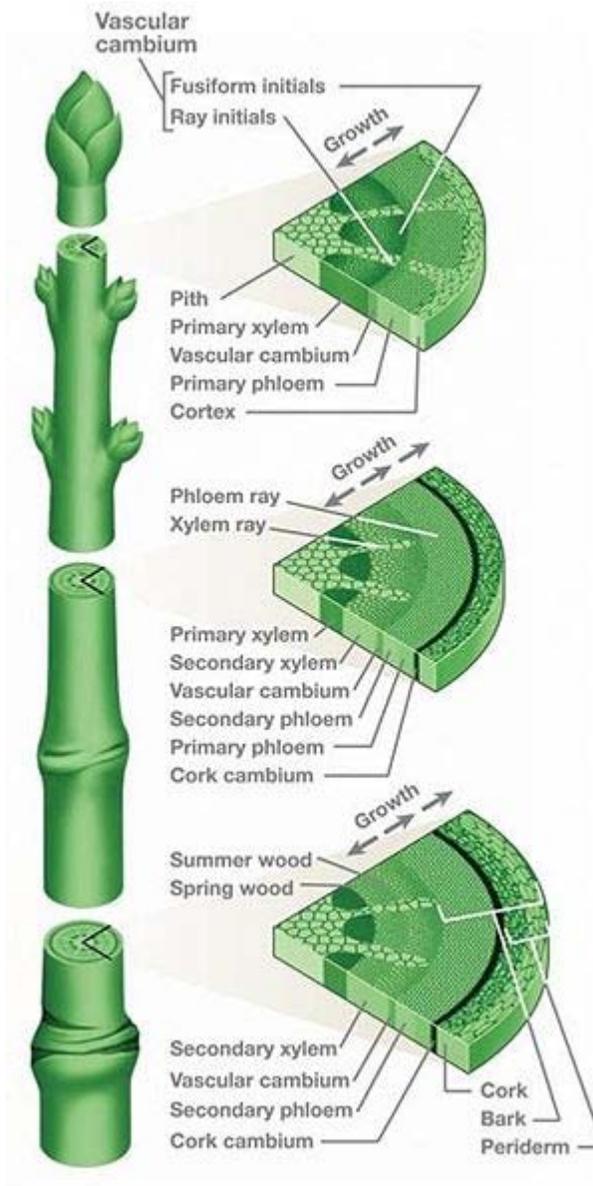
1. Quantitative characters are morphological features that can be counted or measured for example a plant species has flower petals 10–12 mm wide.
2. Qualitative characters are morphological features such as leaf shape, flower color or pubescence.

Both kinds of characters can be very useful for the identification of plants.

Alternation of generations

The detailed study of reproductive structures in plants led to the discovery of the alternation of generations, found in all plants and most algae, by the German botanist Wilhelm Hofmeister. This discovery is one of the most important made in all of plant morphology, since it provides a common basis for understanding the life cycle of all plants.

Plant development



Progressive sections of a stem, showing internal development and growth.

Plant **development** is the process by which structures originate and mature as a plant grows. It is a subject studies in plant anatomy and plant physiology as well as plant morphology.

The process of development in plants is fundamentally different from that seen in vertebrate animals. When an animal embryo begins to develop, it will very early produce all of the body parts that it will ever have in its life. When the animal is born (or hatches from its egg), it has all its body parts and from that point will only grow larger and more

mature. By contrast, plants constantly produce new tissues and structures throughout their life from **meristems** located at the tips of organs, or between mature tissues. Thus, a living plant always has embryonic tissues.

The properties of organization seen in a plant are **emergent properties** which are more than the sum of the individual parts. "The assembly of these tissues and functions into an integrated multicellular organism yields not only the characteristics of the separate parts and processes but also quite a new set of characteristics which would not have been predictable on the basis of examination of the separate parts." In other words, knowing everything about the molecules in a plant are not enough to predict characteristics of the cells; and knowing all the properties of the cells will not predict all the properties of a plant's structure.

Plant growth

A vascular plant begins from a single celled zygote, formed by fertilisation of an egg cell by a sperm cell. From that point, it begins to divide to form a plant embryo through the process of **embryogenesis**. As this happens, the resulting cells will organize so that one end becomes the first root, while the other end forms the tip of the shoot. In seed plants, the embryo will develop one or more "seed leaves" (cotyledons). By the end of embryogenesis, the young plant will have all the parts necessary to begin in its life.

Once the embryo germinates from its seed or parent plant, it begins to produce additional organs (leaves, stems, and roots) through the process of **organogenesis**. New roots grow from root meristems located at the tip of the root, and new stems and leaves grow from shoot meristems located at the tip of the shoot. Branching occurs when small clumps of cells left behind by the meristem, and which have not yet undergone cellular differentiation to form a specialized tissue, begin to grow as the tip of a new root or shoot. Growth from any such meristem at the tip of a root or shoot is termed primary growth and results in the lengthening of that root or shoot. Secondary growth results in widening of a root or shoot from divisions of cells in a cambium.

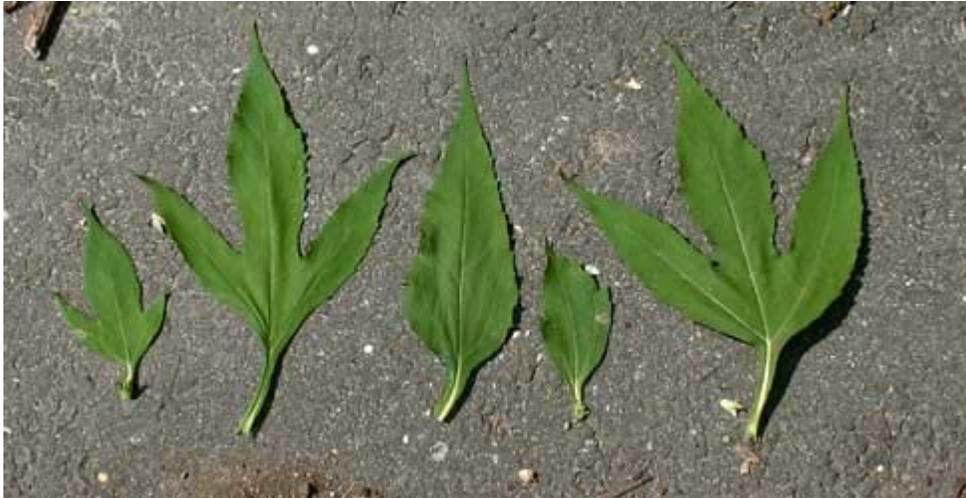
In addition to growth by cell division, a plant may grow through **cell elongation**. This occurs when individual cells or groups of cells grow longer. Not all plant cells will grow to the same length. When cells on one side of a stem grow longer and faster than cells on the other side, the stem will bend to the side of the slower growing cells as a result. This directional growth can occur via a plant's response to a particular stimulus, such as light (phototropism), gravity (gravitropism), water, (hydrotropism), and physical contact (thigmotropism).

Morphological variation

Plants exhibit natural variation in their form and structure. While all organisms vary from individual to individual, plants exhibit an additional type of variation. Within a single individual, parts are repeated which may differ in form and structure from other similar parts. This variation is most easily seen in the leaves of a plant, though other organs such

as stems and flowers may show similar variation. There are three primary causes of this variation: positional effects, environmental effects, and juvenility.

Positional effects



Variation in leaves from the giant ragweed illustrating positional effects. The lobed leaves come from the base of the plant, while the unlobed leaves come from the top of the plant.

Although plants produce numerous copies of the same organ during their lives, not all copies of a particular organ will be identical. There is variation among the parts of a mature plant resulting from the relative position where the organ is produced. For example, along a new branch the leaves may vary in a consistent pattern along the branch. The form of leaves produced near the base of the branch will differ from leaves produced at the tip of the plant, and this difference is consistent from branch to branch on a given plant and in a given species. This difference persists after the leaves at both ends of the branch have matured, and is not the result of some leaves being younger than others.

Environmental effects

The way in which new structures mature as they are produced may be affected by the point in the plants life when they begin to develop, as well as by the environment to which the structures are exposed. This can be seen in aquatic plants and emergent plants.

Juvenility



Juvenility in a seedling of European beech. Notice the difference in shape between the first dark green "seed leaves" and the lighter second pair of leaves.

The organs and tissues produced by a young plant, such as a seedling, are often different from those that are produced by the same plant when it is older. This phenomenon is known as **juvenility**. For example, young trees will produce longer, leaner branches that grow upwards more than the branches they will produce as a fully grown tree. In addition, leaves produced during early growth tend to be larger, thinner, and more irregular than leaves on the adult plant. Species of juvenile plants may look so completely different from the adult leaves that egg-laying insects do not recognize the plant as food for their young.

Some recent developments

Rolf Sattler has revised fundamental concepts of comparative morphology such as the concept of homology. He emphasized that homology should also include partial homology and quantitative homology. This leads to a continuum morphology that demonstrates a continuum between the morphological categories of root, shoot, stem (caulome), leaf (phyllome), and hair (trichome). How intermediates between the categories are best described has been discussed by Bruce K. Kirchoff et al.

Honoring Agnes Arber, author of the partial-shoot theory of the leaf, Rutishauser and Isler called the continuum approach Fuzzy Arberian Morphology (FAM). “Fuzzy” refers to fuzzy logic, “Arberian” to Agnes Arber. Rutishauser and Isler emphasized that this approach is not only supported by many morphological data but also by evidence from molecular genetics.

Process morphology (dynamic morphology) describes and analyzes the dynamic continuum of plant form. According to this approach, structures do not *have* process(es), they *are* process(es). Thus, the structure/process dichotomy is overcome by "an enlargement of our concept of 'structure' so as to include and recognize that in the living organism it is not merely a question of spatial structure with an 'activity' as something over or against it, but that the concrete organism is a spatio-temporal structure and that this spatio-temporal structure is the activity itself."

For Jeune, Barabé and Lacroix, classical morphology (that is, mainstream morphology, based on a qualitative homology concept implying mutually exclusive categories) and continuum morphology are sub-classes of the more encompassing process morphology (dynamic morphology).

Chapter 13

Plant Physiology



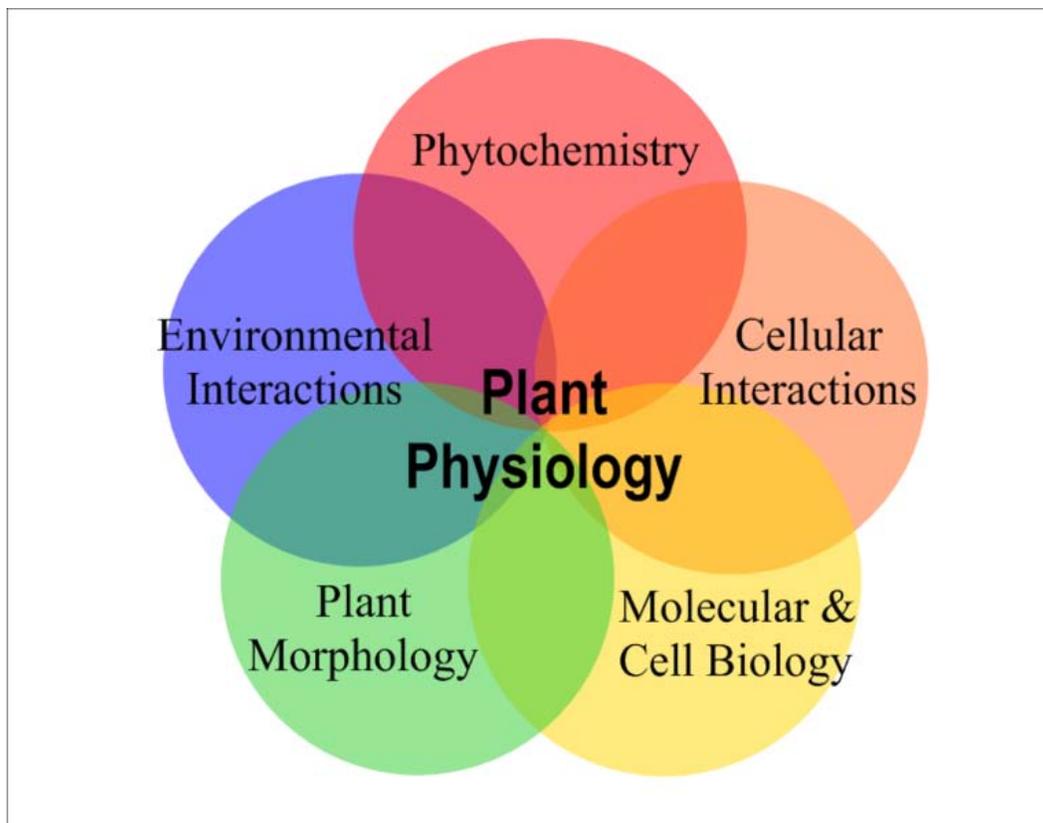
A germination rate experiment

Plant physiology is a subdiscipline of botany concerned with the functioning, or physiology, of plants. Closely related fields include plant morphology (structure of plants), plant ecology (interactions with the environment), phytochemistry (biochemistry of plants), cell biology, and molecular biology.

Fundamental processes such as photosynthesis, respiration, plant nutrition, plant hormone functions, tropisms, nastic movements, photoperiodism, photomorphogenesis, circadian rhythms, environmental stress physiology, seed germination, dormancy and stomata function and transpiration, both part of plant water relations, are studied by plant physiologists.

Scope

The field of plant physiology includes the study of all the internal activities of plants—those chemical and physical processes associated with life as they occur in plants. This includes study at many levels of scale of size and time. At the smallest scale are molecular interactions of photosynthesis and internal diffusion of water, minerals, and nutrients. At the largest scale are the processes of plant development, seasonality, dormancy, and reproductive control. Major subdisciplines of plant physiology include phytochemistry (the study of the biochemistry of plants) and phytopathology (the study of disease in plants). The scope of plant physiology as a discipline may be divided into several major areas of research.



Five key areas of study within plant physiology.

First, the study of phytochemistry (plant chemistry) is included within the domain of plant physiology. In order to function and survive, plants produce a wide array of

chemical compounds not found in other organisms. Photosynthesis requires a large array of pigments, enzymes, and other compounds to function. Because they cannot move, plants must also defend themselves chemically from herbivores, pathogens and competition from other plants. They do this by producing toxins and foul-tasting or smelling chemicals. Other compounds defend plants against disease, permit survival during drought, and prepare plants for dormancy. While other compounds are used to attract pollinators or herbivores to spread ripe seeds.

Secondly, plant physiology includes the study of biological and chemical processes of individual plant cells. Plant cells have a number of features that distinguish them from cells of animals, and which lead to major differences in the way that plant life behaves and responds differently from animal life. For example, plant cells have a cell wall which restricts the shape of plant cells and thereby limits the flexibility and mobility of plants. Plant cells also contain chlorophyll, a chemical compound that interacts with light in a way that enables plants to manufacture their own nutrients rather than consuming other living things as animals do.

Thirdly, plant physiology deals with interactions between cells, tissues, and organs within a plant. Different cells and tissues are physically and chemically specialized to perform different functions. Roots and rhizoids function to anchor the plant and acquire minerals in the soil. Leaves function to catch light in order to manufacture nutrients. For both of these organs to remain living, the minerals acquired by the roots must be transported to the leaves and the nutrients manufactured in the leaves must be transported to the roots. Plants have developed a number of means by which this transport may occur, such as vascular tissue, and the functioning of the various modes of transport is studied by plant physiologists.

Fourthly, plant physiologists study the ways that plants control or regulate internal functions. Like animals, plants produce chemicals called hormones which are produced in one part of the plant to signal cells in another part of the plant to respond. Many flowering plants bloom at the appropriate time because of light-sensitive compounds that respond to the length of the night, a phenomenon known as photoperiodism. The ripening of fruit and loss of leaves in the winter are controlled in part by the production of the gas ethylene by the plant.

Finally, plant physiology includes the study of how plants respond to conditions and variation in the environment, a field known as environmental physiology. Stress from water loss, changes in air chemistry, or crowding by other plants can lead to changes in the way a plant functions. These changes may be affected by genetic, chemical, and physical factors.

Biochemistry of plants



Latex being collected from a tapped rubber tree.

The list of simple elements of which plants are primarily constructed—carbon, oxygen, hydrogen, calcium, phosphorus, etc.—is not different from similar lists for animals, fungi, or even bacteria. The fundamental atomic components of plants are the same as for all life; only the details of the way in which they are assembled differs.

Despite this underlying similarity, plants produce a vast array of chemical compounds with unusual properties which they use to cope with their environment. Pigments are used by plants to absorb or detect light, and are extracted by humans for use in dyes. Other

plant products may be used for the manufacture of commercially important rubber or biofuel. Perhaps the most celebrated compounds from plants are those with pharmacological activity, such as salicylic acid (aspirin), morphine, and digitalis. Drug companies spend billions of dollars each year researching plant compounds for potential medicinal benefits.

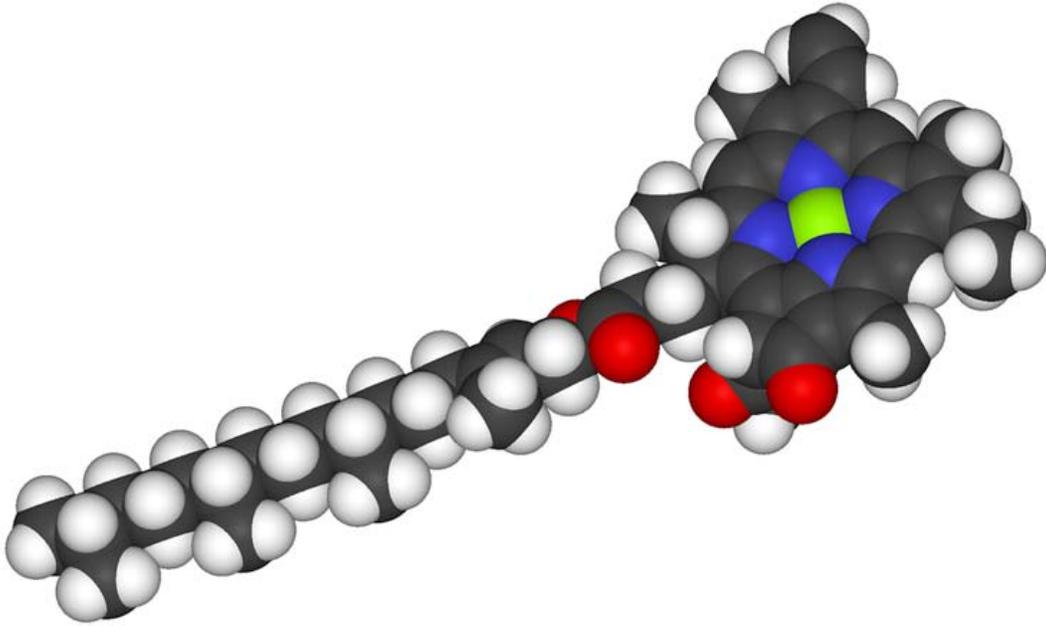
Constituent elements

Plants require some nutrients, such as carbon and nitrogen, in large quantities to survive. Such nutrients are termed macronutrients, where the prefix *macro-* (large) refers to the quantity needed, not the size of the nutrient particles themselves. Other nutrients, called micronutrients, are required only in trace amounts for plants to remain healthy. Such micronutrients are usually absorbed as ions dissolved in water taken from the soil, though carnivorous plants acquire some of their micronutrients from captured prey.

The following tables list element nutrients essential to plants. Uses within plants are generalized.

Macronutrients. (Necessary in large quantities)		
Element	Form of uptake	Notes
Nitrogen	NO_3^- , NH_4^+	Nucleic acids, proteins, hormones, etc.
Oxygen	O_2 H_2O	Cellulose, starch, other organic compounds
Carbon	CO_2	Cellulose, starch, other organic compounds
Hydrogen	H_2O	Cellulose, starch, other organic compounds
Potassium	K^+	Cofactor in protein synthesis, water balance, etc.
Calcium	Ca^{2+}	Membrane synthesis and stabilization
Magnesium	Mg^{2+}	Element essential for chlorophyll
Phosphorus	H_2PO_4^-	Nucleic acids, phospholipids, ATP
Sulfur	SO_4^{2-}	Constituent of proteins and coenzymes
Micronutrients. (Necessary in small quantities)		
Element	Form of uptake	Notes
Chlorine	Cl^-	Photosystem II and stomata function
Iron	Fe^{2+} , Fe^{3+}	Chlorophyll formation
Boron	HBO_3	Crosslinking pectin
Manganese	Mn^{2+}	Activity of some enzymes
Zinc	Zn^{2+}	Involved in the synthesis of enzymes and chlorophyll
Copper	Cu^+	Enzymes for lignin synthesis
Molybdenum	MoO_4^{2-}	Nitrogen fixation, reduction of nitrates
Nickel	Ni^{2+}	Enzymatic cofactor in the metabolism of nitrogen compounds

Pigments



Space-filling model of the chlorophyll molecule.



Anthocyanin gives these pansies their dark purple pigmentation.

Among the most important molecules for plant function are the pigments. Plant pigments include a variety of different kinds of molecules, including porphyrins, carotenoids, and anthocyanins. All biological pigments selectively absorb certain wavelengths of light while reflecting others. The light that is absorbed may be used by the plant to power chemical reactions, while the reflected wavelengths of light determine the color the pigment will appear to the eye.

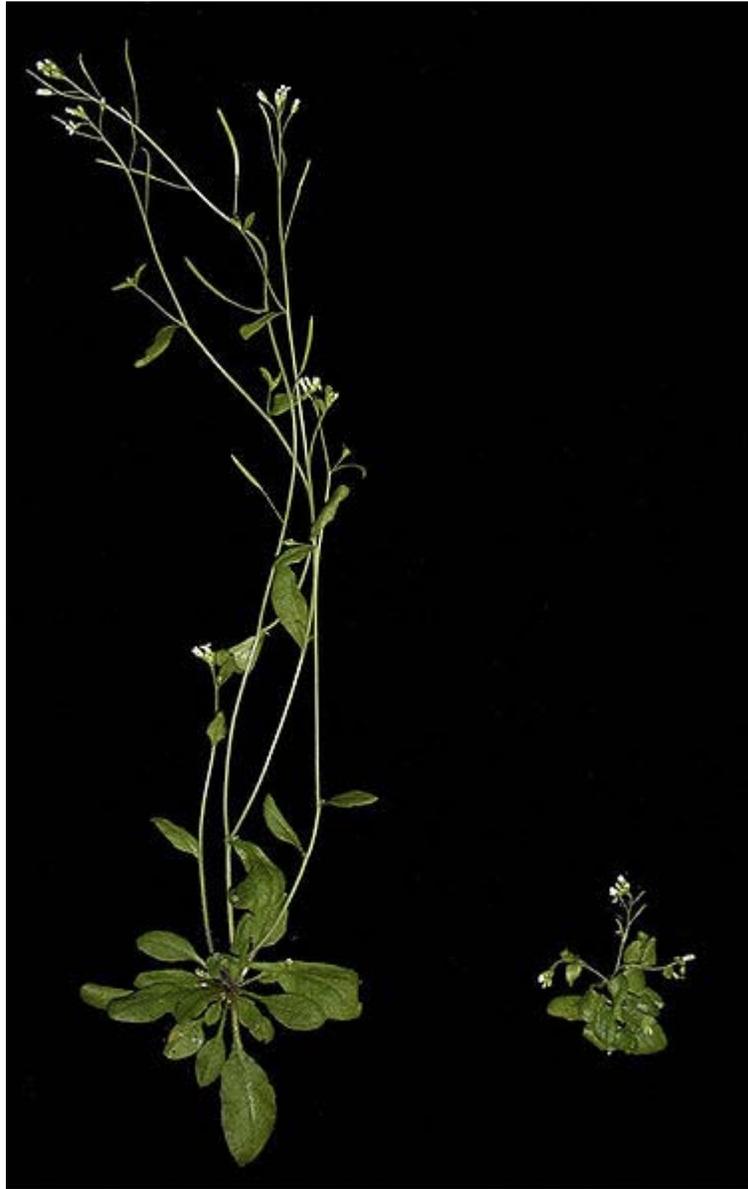
Chlorophyll is the primary pigment in plants; it is a porphyrin that absorbs red and blue wavelengths of light while reflecting green. It is the presence and relative abundance of chlorophyll that gives plants their green color. All land plants and green algae possess two forms of this pigment: chlorophyll *a* and chlorophyll *b*. Kelps, diatoms, and other photosynthetic heterokonts contain chlorophyll *c* instead of *b*, while red algae possess only chlorophyll *a*. All chlorophylls serve as the primary means plants use to intercept light in order to fuel photosynthesis.

Carotenoids are red, orange, or yellow tetraterpenoids. They function as accessory pigments in plants, helping to fuel photosynthesis by gathering wavelengths of light not readily absorbed by chlorophyll. The most familiar carotenoids are carotene (an orange pigment found in carrots), lutein (a yellow pigment found in fruits and vegetables), and lycopene (the red pigment responsible for the color of tomatoes). Carotenoids have been shown to act as antioxidants and to promote healthy eyesight in humans.

Anthocyanins (literally "flower blue") are water-soluble flavonoid pigments that appear red to blue, according to pH. They occur in all tissues of higher plants, providing color in leaves, stems, roots, flowers, and fruits, though not always in sufficient quantities to be noticeable. Anthocyanins are most visible in the petals of flowers, where they may make up as much as 30% of the dry weight of the tissue. They are also responsible for the purple color seen on the underside of tropical shade plants such as *Tradescantia zebrina*; in these plants, the anthocyanin catches light that has passed through the leaf and reflects it back towards regions bearing chlorophyll, in order to maximize the use of available light.

Betalains are red or yellow pigments. Like anthocyanins they are water-soluble, but unlike anthocyanins they are indole-derived compounds synthesized from tyrosine. This class of pigments is found only in the Caryophyllales (including cactus and amaranth), and never co-occur in plants with anthocyanins. Betalains are responsible for the deep red color of beets, and are used commercially as food-coloring agents. Plant physiologists are uncertain of the function that betalains have in plants which possess them, but there is some preliminary evidence that they may have fungicidal properties.

Signals and regulators



A mutation that stops *Arabidopsis thaliana* responding to auxin causes abnormal growth (right)

Plants produce hormones and other growth regulators which act to signal a physiological response in their tissues. They also produce compounds such as phytochrome that are sensitive to light and which serve to trigger growth or development in response to environmental signals.

Plant hormones

Plant hormones, known as plant growth regulators (PGRs) or phytohormones, are chemicals that regulate a plant's growth. According to a standard animal definition, hormones are signal molecules produced at specific locations, that occur in very low concentrations, and cause altered processes in target cells at other locations. Unlike animals, plants lack specific hormone-producing tissues or organs. Plant hormones are often not transported to other parts of the plant and production is not limited to specific locations.

Plant hormones are chemicals that in small amounts promote and influence the growth, development and differentiation of cells and tissues. Hormones are vital to plant growth; affecting processes in plants from flowering to seed development, dormancy, and germination. They regulate which tissues grow upwards and which grow downwards, leaf formation and stem growth, fruit development and ripening, as well as leaf abscission and even plant death.

The most important plant hormones are abscissic acid (ABA), auxins, ethylene, gibberellins, and cytokinins, though there are many other substances that serve to regulate plant physiology.

Photomorphogenesis

While most people know that light is important for photosynthesis in plants, few realize that plant sensitivity to light plays a role in the control of plant structural development (morphogenesis). The use of light to control structural development is called photomorphogenesis, and is dependent upon the presence of specialized photoreceptors, which are chemical pigments capable of absorbing specific wavelengths of light.

Plants use four kinds of photoreceptors: phytochrome, cryptochrome, a UV-B photoreceptor, and protochlorophyllide *a*. The first two of these, phytochrome and cryptochrome, are photoreceptor proteins, complex molecular structures formed by joining a protein with a light-sensitive pigment. Cryptochrome is also known as the UV-A photoreceptor, because it absorbs ultraviolet light in the long wave "A" region. The UV-B receptor is one or more compounds that have yet to be identified with certainty, though some evidence suggests carotene or riboflavin as candidates. Protochlorophyllide *a*, as its name suggests, is a chemical precursor of chlorophyll.

The most studied of the photoreceptors in plants is phytochrome. It is sensitive to light in the red and far-red region of the visible spectrum. Many flowering plants use it to regulate the time of flowering based on the length of day and night (photoperiodism) and to set circadian rhythms. It also regulates other responses including the germination of seeds, elongation of seedlings, the size, shape and number of leaves, the synthesis of chlorophyll, and the straightening of the epicotyl or hypocotyl hook of dicot seedlings.

Photoperiodism



The poinsettia is a short-day plant, requiring two months of long nights prior to blooming.

Many flowering plants use the pigment phytochrome to sense seasonal changes in day length, which they take as signals to flower. This sensitivity to day length is termed photoperiodism. Broadly speaking, flowering plants can be classified as long day plants, short day plants, or day neutral plants, depending on their particular response to changes in day length. Long day plants require a certain minimum length of daylight to initiate flowering, so these plants flower in the spring or summer. Conversely, short day plants will flower when the length of daylight falls below a certain critical level. Day neutral plants do not initiate flowering based on photoperiodism, though some may use temperature sensitivity (vernalization) instead.

Although a short day plant cannot flower during the long days of summer, it is not actually the period of light exposure that limits flowering. Rather, a short day plant requires a minimal length of uninterrupted darkness in each 24 hour period (a short daylength) before floral development can begin. It has been determined experimentally that a short day plant (long night) will not flower if a flash of phytochrome activating light is used on the plant during the night.

Plants make use of the phytochrome system to sense day length or photoperiod. This fact is utilized by florists and greenhouse gardeners to control and even induce flowering out of season, such as the *Poinsettia*.

Environmental physiology



Phototropism in *Arabidopsis thaliana* is regulated by blue to UV light.

Paradoxically, the subdiscipline of environmental physiology is on the one hand a recent field of study in plant ecology and on the other hand one of the oldest. Environmental physiology is the preferred name of the subdiscipline among plant physiologists, but it goes by a number of other names in the applied sciences. It is roughly synonymous with ecophysiology, crop ecology, horticulture and agronomy. The particular name applied to the subdiscipline is specific to the viewpoint and goals of research. Whatever name is applied, it deals with the ways in which plants respond to their environment and so overlaps with the field of ecology.

Environmental physiologists examine plant response to physical factors such as radiation (including light and ultraviolet radiation), temperature, fire, and wind. Of particular importance are water relations (which can be measured with the Pressure bomb) and the stress of drought or inundation, exchange of gases with the atmosphere, as well as the cycling of nutrients such as nitrogen and carbon.

Environmental physiologists also examine plant response to biological factors. This includes not only negative interactions, such as competition, herbivory, disease and parasitism, but also positive interactions, such as mutualism and pollination.

Tropisms and nastic movements

Plants may respond both to directional and nondirectional stimuli. A response to a directional stimulus, such as gravity or sunlight, is called a tropism. A response to a nondirectional stimulus, such as temperature or humidity, is a nastic movement.

Tropisms in plants are the result of differential cell growth, in which the cells on one side of the plant elongate more than those on the other side, causing the part to bend toward the side with less growth. Among the common tropisms seen in plants is phototropism, the bending of the plant toward a source of light. Phototropism allows the plant to maximize light exposure in plants which require additional light for photosynthesis, or to minimize it in plants subjected to intense light and heat. Geotropism allows the roots of a plant to determine the direction of gravity and grow downwards. Tropisms generally result from an interaction between the environment and production of one or more plant hormones.

In contrast to tropisms, nastic movements result from changes in turgor pressure within plant tissues, and may occur rapidly. A familiar example is thigmonasty (response to touch) in the Venus fly trap, a carnivorous plant. The traps consist of modified leaf blades which bear sensitive trigger hairs. When the hairs are touched by an insect or other animal, the leaf folds shut. This mechanism allows the plant to trap and digest small insects for additional nutrients. Although the trap is rapidly shut by changes in internal cell pressures, the leaf must grow slowly in order to reset for a second opportunity to trap insects.

Plant disease



Powdery mildew on crop leaves

Economically, one of the most important areas of research in environmental physiology is that of phytopathology, the study of diseases in plants and the manner in which plants resist or cope with infection. Plants are susceptible to the same kinds of disease organisms as animals, including viruses, bacteria, and fungi, as well as physical invasion by insects and roundworms.

Because the biology of plants differs from animals, their symptoms and responses are quite different. In some cases, a plant can simply shed infected leaves or flowers to prevent the spread of disease, in a process called abscission. Most animals do not have this option as a means of controlling disease. Plant disease organisms themselves also differ from those causing disease in animals because plants cannot usually spread infection through casual physical contact. Plant pathogens tend to spread via spores or are carried by animal vectors.

One of the most important advances in the control of plant disease was the discovery of Bordeaux mixture in the nineteenth century. The mixture is the first known fungicide and is a combination of copper sulfate and lime. Application of the mixture served to inhibit the growth of downy mildew that threatened to seriously damage the French wine industry.

History

Early history



Jan Baptist van Helmont.

Sir Francis Bacon published one of the first plant physiology experiments in 1627 in the book, *Sylva Sylvarum*. Bacon grew several terrestrial plants, including a rose, in water and concluded that soil was only needed to keep the plant upright. Jan Baptist van Helmont published what is considered the first quantitative experiment in plant physiology in 1648. He grew a willow tree for five years in a pot containing 200 pounds of oven-dry soil. The soil lost just two ounces of dry weight and van Helmont concluded that plants get all their weight from water, not soil. In 1699, John Woodward published experiments on growth of spearmint in different sources of water. He found that plants grew much better in water with soil added than in distilled water.

Stephen Hales is considered the Father of Plant Physiology for the many experiments in the 1727 book; though Julius von Sachs unified the pieces of plant physiology and put them together as a discipline. His *Lehrbuch der Botanik* was the plant physiology bible of its time.

Researchers discovered in the 1800s that plants absorb essential mineral nutrients as inorganic ions in water. In natural conditions, soil acts as a mineral nutrient reservoir but the soil itself is not essential to plant growth. When the mineral nutrients in the soil are

dissolved in water, plant roots absorb nutrients readily, soil is no longer required for the plant to thrive. This observation is the basis for hydroponics, the growing of plants in a water solution rather than soil, which has become a standard technique in biological research, teaching lab exercises, crop production and as a hobby.

Current research

One of the leading journals in the field is *Plant Physiology*, started in 1926. All its back issues are available online for free. Many other journals often carry plant physiology articles, including *Physiologia Plantarum*, *Journal of Experimental Botany*, *American Journal of Botany*, *Annals of Botany*, *Journal of Plant Nutrition* and *Proceedings of the National Academy of Sciences*.

Economic applications

Food production

In horticulture and agriculture along with food science, plant physiology is an important topic relating to fruits, vegetables, and other consumable parts of plants. Topics studied include: *climatic* requirements, fruit drop, nutrition, ripening, fruit set. The production of food crops also hinges on the study of plant physiology covering such topics as Optimal planting and harvesting times and post harvest storage of plant products for human consumption and the production of secondary products like drugs and cosmetics.

Chapter 14

Phycology and Plant Taxonomy

Phycology



Phycology is the scientific study of algae. Phycology is a branch of life science and often is regarded as a subdiscipline of botany.

Algae are important plants as primary producers in aquatic ecosystems. Most algae are eukaryotic, photosynthetic organisms that live in a wet environment. They are distinguished from the higher plants by a lack of true roots, stems or leaves. Many species are single-celled and microscopic (including phytoplankton and other

microalgae); many others are multicellular to one degree or another, some of these growing to large size (for example, seaweeds such as kelp and *Sargassum*).

Phycology includes the study of prokaryotic forms known as blue-green algae or cyanobacteria. A number of microscopic algae also occur as symbionts in lichens.

A *phycologist* is a person who studies algae as described above.

Notable phycologists

- Elsie M. Burrows (Dr.) (1913–1986)
 - Blackler, Margaret Constance Helen (1902–1981)
 - Elsie Conway (née) Phillips) (1902–1992) Visited University of British Columbia in 1969–1970 and researched there in 1972–1974. She was president of the British Phycological Society 1965–1967. Retired in 1969.
 - de Váléra, Máirin (1912–1984).
 - Kathleen Mary Drew-Baker (Dr) (1901 - 1957)
 - Dixon, Peter Stanley (1929–1993).
 - Eifion Jones, Willian (1925–2004)
 - Irvine, David Edward Guthrie (1924–1995)
 - Manton, Irene. (1904–1988)
 - Newton, Lilly (née Batten) (1893–1981)
 - Papenfuss, George Frederik (1903–1981)
 - Parke, Mary (1908– 1989)
 - Taylor, William Randolph. (1895–1990)
-
- prof Dr V krishnamurty (born 1921), Director Krishnamurthy institute of algology

Plant taxonomy

Plant taxonomy is the science that finds, describes, classifies, identifies, and names plants. It thus is one of the main branches of taxonomy.

Plant taxonomy is closely allied to plant systematics, and there is no sharp boundary between the two. In practice, "plant systematics" is involved with relationships between plants and their evolution, especially at the higher levels, whereas "plant taxonomy" deals with the actual handling of plant specimens. The precise relationship between taxonomy and systematics, however, has changed along with the goals and methods employed.

Plant taxonomy is well known for being turbulent, and traditionally there is no really close agreement on circumscription and placement of taxa.

Identification and classification

Two goals of plant taxonomy are the identification and classification of plants. The distinction between these two goals is important and often overlooked.

Plant identification is the determination of the identity of an unknown plant by comparison with previously collected specimens or with the aid of books or identification manuals. The process of identification connects the specimen with a published name. Once a plant specimen has been identified, its name and properties are known.

Plant classification is the placing of known plants into groups or categories to show some relationship. Scientific classification follows a system of rules that standardizes the results, and groups successive categories into a hierarchy. For example, the family to which the lilies belong is classified as follows:

- Kingdom: Plantae
- Division: Magnoliophyta
- Class: Liliopsida
- Order: Liliales
- **Family: Liliaceae**
- Genera

The classification of plants results in an organized system for the naming and cataloging of future specimens, and ideally reflects scientific ideas about plant inter-relationships.

Classification systems

- APG system
- APG II system
- APG III system
- Bessey system
- Cronquist system
- Melchior system

Chapter 15

Alternation of Generations

Alternation of generations (also known as **alternation of phases** or **metagenesis**) is a term primarily used in describing the life cycle of plants (taken here to mean the Archaeplastida). A multicellular diploid sporophyte, with N paired chromosomes (i.e. $2N$ in total), alternates with a multicellular haploid gametophyte, with N unpaired chromosomes. A mature sporophyte produces spores by meiosis, a process which results in a reduction of the number of chromosomes by a half. Spores germinate and grow into a gametophyte. At maturity, the gametophyte produces gametes by mitosis. Two gametes (originating from different organisms of the same species or from the same organism) fuse to produce a zygote, which develops into a diploid sporophyte. This cycle, from sporophyte to sporophyte (or equally from gametophyte to gametophyte), is the way in which all land plants and many algae undergo sexual reproduction.

All animals develop differently. A mature animal is diploid and so is, in one sense, equivalent to a sporophyte. However, an animal *directly* produces haploid gametes by meiosis. No haploid spores capable of dividing are produced, so neither is a haploid gametophyte. There is no alternation between diploid and haploid forms.

Other organisms, such as fungi, can have life cycles in which different kinds of organism alternate. The term 'alternation of generations' has also been applied to these cases.

Life cycles, such as those of plants, with alternating haploid and diploid phases can be referred to as **diplohaplontic** (the equivalent terms **haplodiplontic**, **diplobiontic** or **dibiontic** are also in use). Life cycles, such as those of animals, in which there is only a diploid phase are referred to as **diplontic**. (Life cycles in which there is only a haploid phase are referred to as **haplontic**.)

Definition

The discussion of 'alternation of generations' above treats the alternation of a multicellular diploid form with a multicellular haploid form as the defining characteristic, regardless of whether these forms are free-living or not. In some species, such as the alga *Ulva lactuca*, the diploid and haploid forms are indeed both free-living independent organisms, essentially identical in appearance. The free-swimming gametes form a

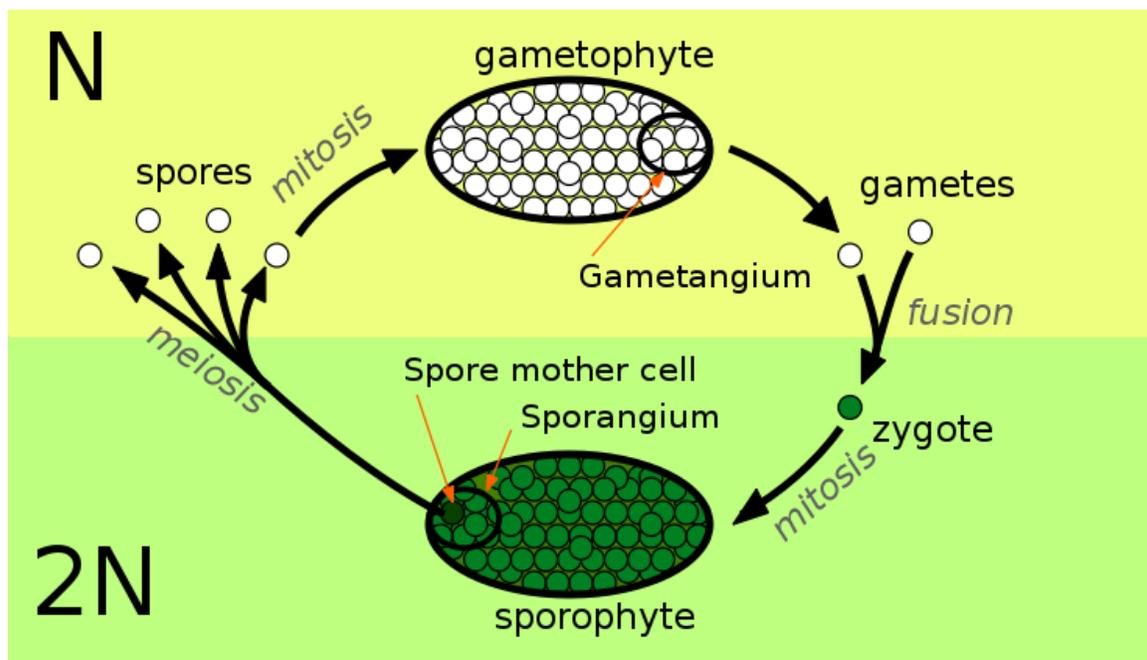
zygote which germinates into a diploid sporophyte; the free-swimming spores germinate into a haploid gametophyte. Alternation of *generations* is an appropriate term.

However, in other species, either the sporophyte or the gametophyte is very much reduced and is incapable of free-living. For example, in seed plants, the gametophyte 'generation' develops totally within the sporophyte which protects and nurtures it, with the sole exception of pollen grains, which are the 'male' gametophytes, but which have been reduced to only three cells. Here the notion of two generations is less obvious; as Bateman & Dimichele say "[s]porophyte and gametophyte effectively function as a single organism". The alternative term 'alternation of phases' may then be more appropriate.

Alternation of generations in plants

Fundamental elements

The diagram below shows the fundamental elements of the alternation of generations in plants. It is vital to have a good understanding of these fundamentals before considering the many variations found in different groups of plants. Starting from the right of the diagram, the processes involved are as follows:



- Two single-celled haploid gametes, each containing N unpaired chromosomes, fuse to form a single-celled diploid zygote, which now contains N paired chromosomes, i.e. $2N$ chromosomes in total.
- The single-celled diploid zygote germinates, dividing by the normal process (mitosis), which maintains the number of chromosomes at $2N$. The result is a multi-celled diploid organism, called the *sporophyte* (because at maturity it produces spores).

- When it reaches maturity, the sporophyte produces one or more **sporangia** (singular sporangium) which are the organs which produce diploid spore mother cells (sporocytes). These divide by a special process (meiosis) which reduces the number of chromosomes by a half. This results in four single-celled haploid spores, each containing N unpaired chromosomes.
- The single-celled haploid spore germinates, dividing by the normal process (mitosis), which maintains the number of chromosomes at N. The result is a multi-cellular haploid organism, called the *gametophyte* (because at maturity it produces gametes).
- When it reaches maturity, the gametophyte produces one or more **gametangia** (singular gametangium) which are the organs which produce haploid gametes. At least one kind of gamete possesses some mechanism for reaching another gamete in order to fuse with it.

The 'alternation of generations' in the life cycle is thus between a diploid (2N) generation of sporophytes and a haploid (N) generation of gametophytes.



Gametophyte of the fern *Onoclea sensibilis* (the flat thallus at the bottom of the picture) with a descendant sporophyte beginning to grow from it (the small frond at the top of the picture).

The situation is quite different in all animals, where the fundamental process is that a diploid ($2N$) individual *directly* produces haploid (N) gametes by meiosis. Spores (i.e. haploid cells which are able to undergo mitosis) are not produced, so neither is a haploid multi-cellular organism. The single-celled gametes are the only entities which are haploid.

Variations

The diagram shown above is a good representation of the life cycle of some multi-cellular algae (e.g. the genus *Cladophora*) which have sporophytes and gametophytes of very similar, if not identical, appearance, and which do not have different kinds of spores or gametes.

However, there are many possible variations on the fundamental elements of a life cycle which has alternation of generations. Each variation may occur separately or in combination, resulting in a bewildering variety of life cycles. The terms used by botanists in describing these life cycles can be equally bewildering. As Bateman and Dimichele say "[...] the alternation of generations has become a terminological morass; often, one term represents several concepts or one concept is represented by several terms."

Possible variations are:

- *Relative importance of the sporophyte and the gametophyte.*
 - *Equal (homomorphy or isomorphy).*
Filamentous algae of the genus *Cladophora*, which are predominantly found in fresh water, have diploid sporophytes and haploid gametophytes which are externally indistinguishable. No living land plant has equally dominant sporophytes and gametophytes, although some theories of the evolution of alternation of generations suggest that ancestral land plants did.
 - *Unequal (heteromorphy or anisomorphy).*



Gametophyte of *Mnium hornum*, a moss.

- *Dominant gametophyte (gametophytic).*
In liverworts, mosses and hornworts, the dominant form is the haploid gametophyte. The diploid sporophyte is not capable of an independent existence, gaining most of its nutrition from the parent gametophyte, and having no chlorophyll when mature.



Sporophyte of *Blechnum discolor*, a fern.

- *Dominant sporophyte (sporophytic).*
In ferns, both the sporophyte and the gametophyte are capable of living independently, but the dominant form is the diploid sporophyte. The haploid gametophyte is much smaller and simpler in structure. In seed plants, the gametophyte is even more reduced (at the minimum to only three cells), gaining all its nutrition from the sporophyte. The extreme reduction in the size of the gametophyte and its retention within the sporophyte means that when applied to seed plants the term 'alternation of generations' is somewhat misleading: "[s]porophyte and gametophyte effectively function as a single organism". Some authors have preferred the term 'alternation of phases'.
- *Differentiation of the gametes.*
 - *Both gametes the same (isogamy).*
Like other species of *Cladophora*, *C. callicoma* has flagellated gametes which are identical in appearance and ability to move.
 - *Gametes of two distinct sizes (anisogamy).*
 - *Both of similar motility.*
Species of *Ulva*, the sea lettuce, have gametes which all have two flagella and so are motile. However they are of two sizes: larger 'female' gametes and smaller 'male' gametes.

- *One large and sessile, one small and motile (oogamy).* The larger sessile megagametes are eggs (ova), and smaller motile microgametes are sperm (spermatazoa, spermatozoids). The degree of motility of the sperm may be very limited (as in the case of flowering plants) but all are able to move towards the sessile eggs. When (as is almost always the case) the sperm and eggs are produced in different kinds of gametangia, these are called **antheridia** (singular antheridium) and **archegonia** (singular archegonium) respectively.



Gametophyte of *Pellia epiphylla* with sporophytes growing from the remains of archegonia.

- *Antheridia and archegonia occur on the same gametophyte,* which is then called **monoicous**. (Many sources, including those concerned with bryophytes, use the term 'monoecious' for this situation and 'dioecious' for the opposite. Here 'monoecious' and 'dioecious' are used only for sporophytes.)
The liverwort *Pellia epiphylla* has the gametophyte as the dominant generation. It is monoicous: the small reddish antheridia are scattered along the midrib while the archegonia grow nearer the tip of divisions of the plant.

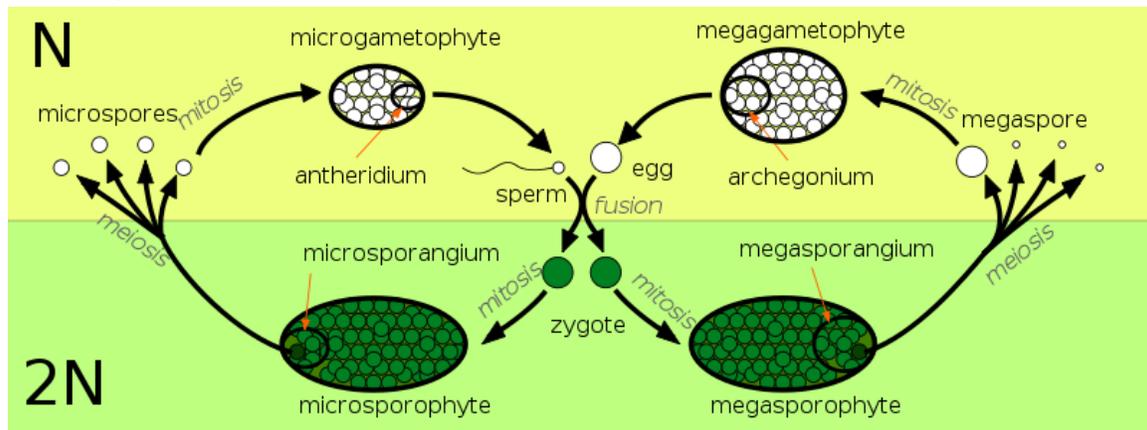


Flowers of European Holly, a dioecious species: male above, female below (leaves cut to show flowers more clearly)

- *Megasporangia and microsporangia occur on different sporophytes, which are then called **dioecious**.*
An individual tree of the European holly (*Ilex aquifolium*) produces either 'male' flowers which have only functional stamens (microsporangia) producing microspores which develop into pollen grains (microgametophytes) or 'female' flowers which have only functional carpels (megasporangia) producing megaspores which develop into ovules (megagametophytes).

There are some correlations between these variations, but they are just that, correlations, and not absolute. For example, in flowering plants, microspores ultimately produce microgametes (sperm) and megaspores ultimately produce megagametes (eggs). However, in pteridophytes there are groups with undifferentiated spores but differentiated gametophytes. For example, the fern *Ceratopteris thalictroides* has spores of only one kind, which vary continuously in size. Smaller spores tend to produce gametophytes which have only sperm-producing antheridia.

A complex life cycle



The diagram shows the alternation of generations in a species which is heteromorphic, sporophytic, oogametic, dioicous, heterosporic and dioecious. A seed plant example is a willow tree (genus *Salix*). Starting in the centre of the diagram, the processes involved are:

- An immobile egg, typically remaining in the archegonium, fuses with a mobile sperm, released from an antheridium. The resulting zygote is either 'male' or 'female'.
- A 'male' zygote develops by mitosis into a microsporophyte, which at maturity produces one or more microsporangia. Microspores develop within the microsporangium by meiosis.
In a willow (like all seed plants) the zygote first develops into a seed within the ovule (megasporangium). Later the seed is shed and grows into a mature tree. A 'male' willow tree (a microsporophyte) produces flowers with only stamens, the anthers of which are the microsporangia.
- Microspores germinate producing microgametophytes; at maturity one or more antheridia are produced. Sperm develop within the antheridia.
In a willow, microspores are not liberated from the anther (the microsporangium), but develop into pollen grains (microgametophytes) within it. The whole pollen grain is moved (typically by an insect) to an ovule (megagametophyte), where a sperm is produced which moves down a pollen tube to reach the egg.
- A 'female' zygote develops by mitosis into a megasporophyte, which at maturity produces one or more megasporangia. Megaspores develop within the megasporangium; typically one of the four spores produced by meiosis gains bulk at the expense of the remaining three, which disappear.
'Female' willow trees (megasporophytes) produce flowers with only carpels (the megasporangia).
- Megaspores germinate producing megagametophytes; at maturity one or more archegonia are produced. Eggs develop within the archegonia.
In a willow, megaspores develop into ovules (megagametophytes) within the carpels (megasporangia). An archegonium develops within the ovule and produces an egg. All of this happens within the carpel (the megasporangium). The

whole of the gametophytic 'generation' remains within the protection of the sporophyte except for pollen grains (which have been reduced to just three cells).

Life cycles of different plant groups

The term 'plants' is taken here to mean the Archaeplastida, i.e. the glaucophytes, red and green algae and land plants.

Alternation of generations occurs in almost all multicellular red and green algae, both freshwater forms (such as *Cladophora*) and seaweeds (such as *Ulva*). In most, the generations are homomorphic (isomorphic) and free-living. Some species of red algae have a complex triphasic alternation of generations, in which there is a gametophyte phase and two distinct sporophyte phases.

Land plants all have heteromorphic (anisomorphic) alternation of generations, in which the sporophyte and gametophyte are distinctly different. All bryophytes, i.e. liverworts, mosses and hornworts, have the gametophyte generation as the most conspicuous. As an illustration, consider a monoicous moss. Antheridia and archegonia develop on the mature plant (the gametophyte). In the presence of water, the biflagellate sperm from the antheridia swim to the archegonia and fertilisation occurs, leading to the production of a diploid sporophyte. The sporophyte grows up from the archegonium. Its body comprises a long stalk topped by a capsule within which spore-producing cells undergo meiosis to form haploid spores. Most mosses rely on the wind to disperse these spores.

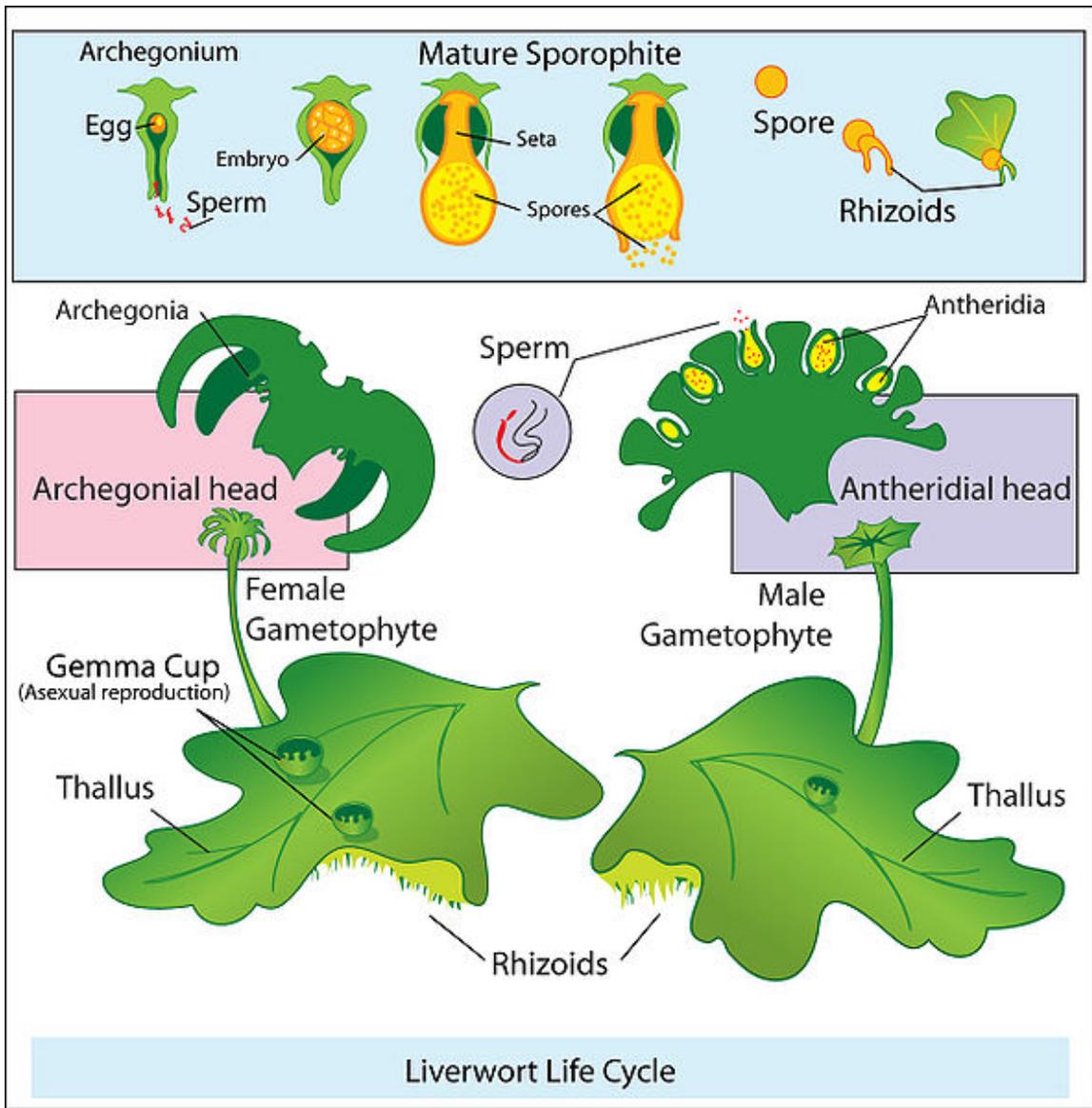
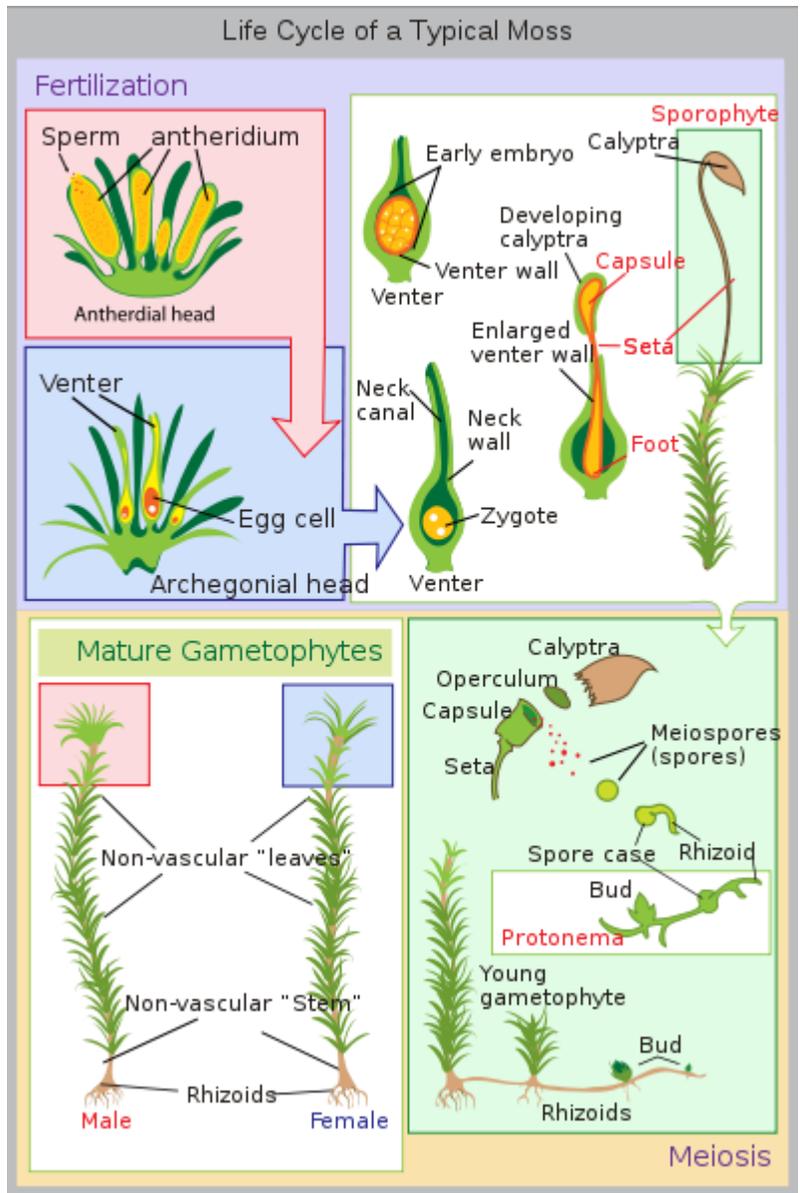
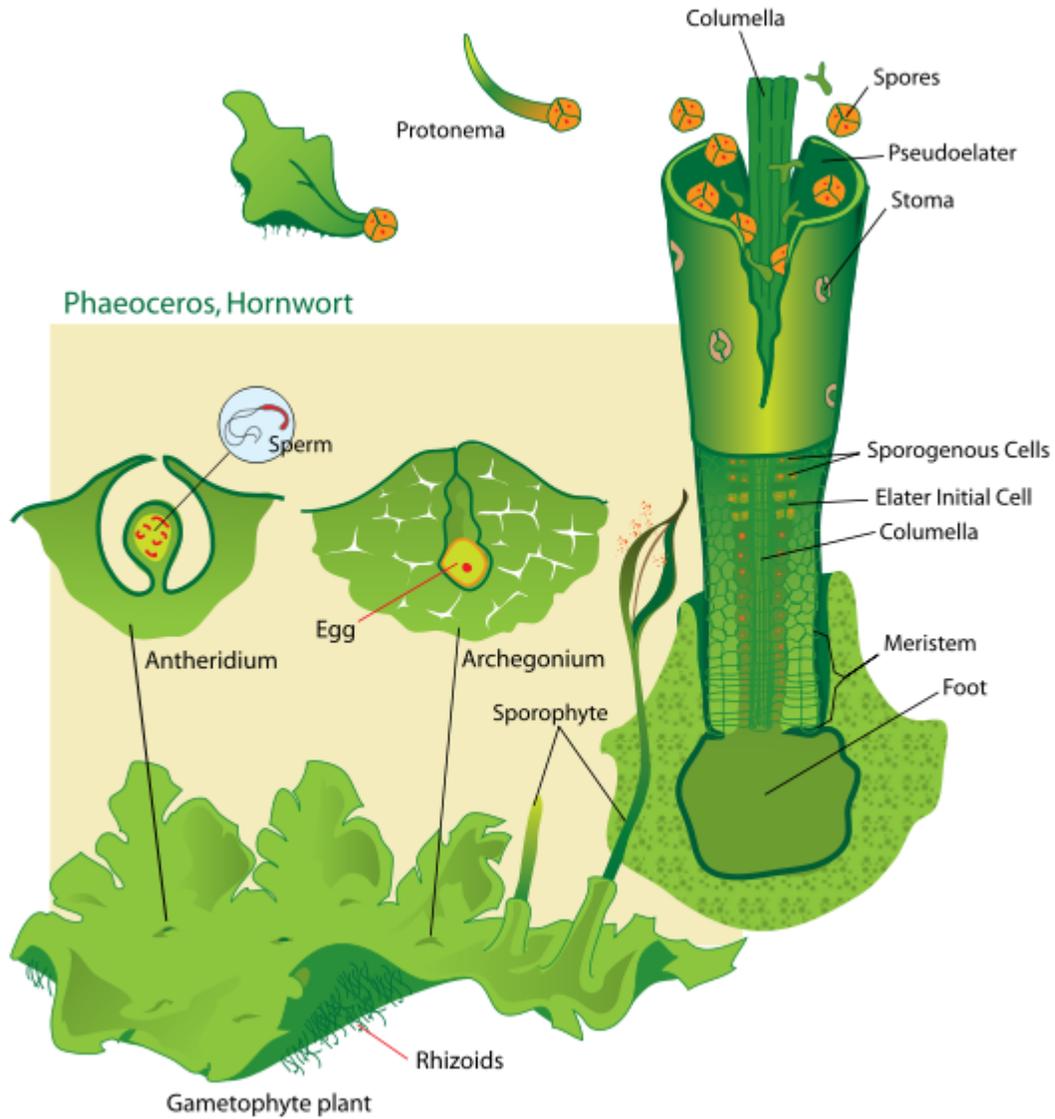


Diagram of alternation of generations in liverworts.



Moss life cycle diagram



Hornwort life cycle diagram

In ferns and their allies, including clubmosses and horsetails, the conspicuous plant observed in the field is the diploid sporophyte. The haploid spores develop in sori on the underside of the fronds and are dispersed by the wind (or in some cases, by floating on water). If conditions are right, a spore will germinate and grow into a rather inconspicuous plant body called a prothallus. The haploid prothallus does not resemble the sporophyte, and as such ferns and their allies have a heteromorphic alternation of generations. The prothallus is short-lived, but carries out sexual reproduction, producing the diploid zygote that then grows out of the prothallus as the sporophyte.

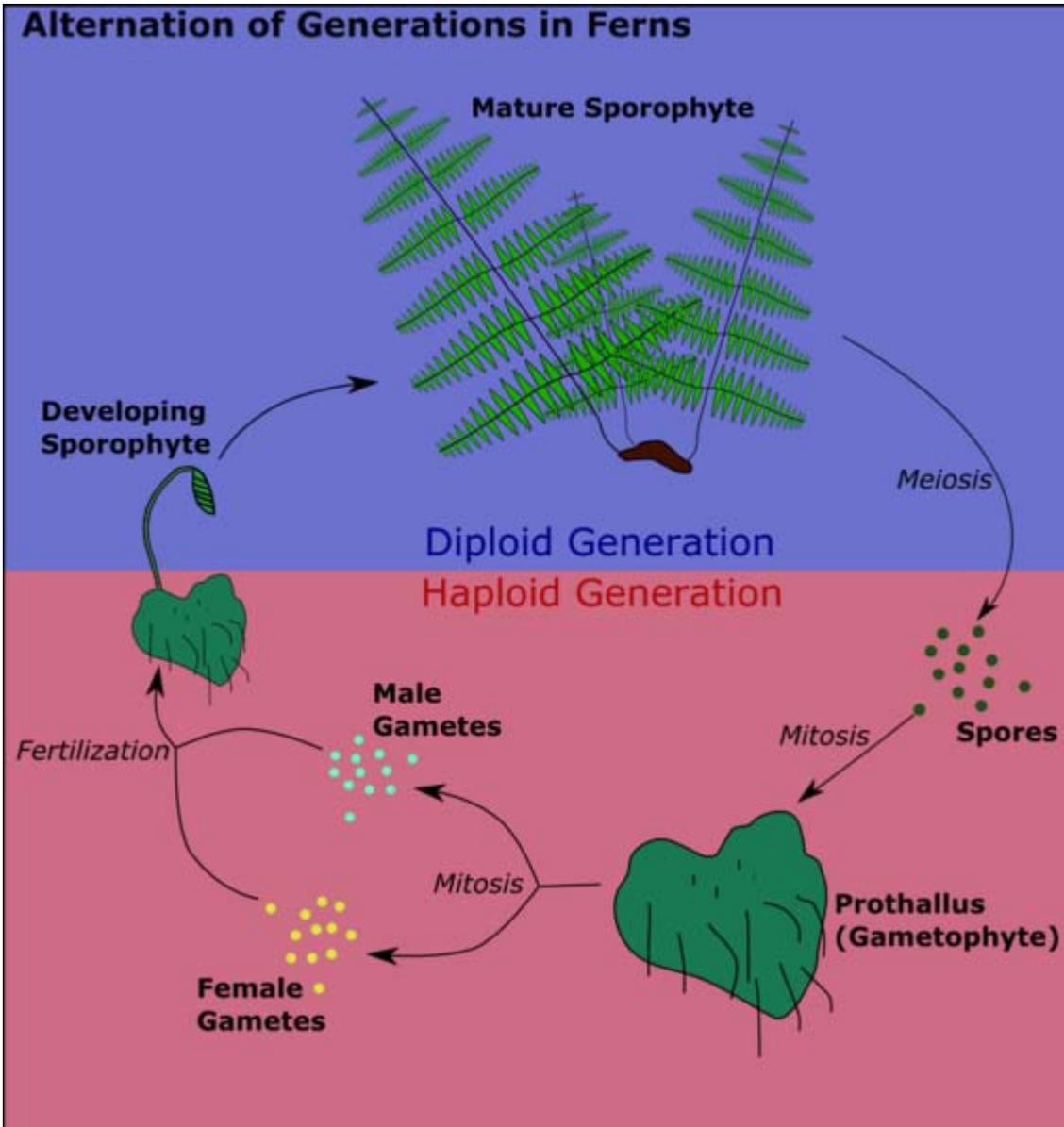


Diagram of alternation of generations in ferns.



A gametophyte (prothallus) of *Dicksonia* sp.



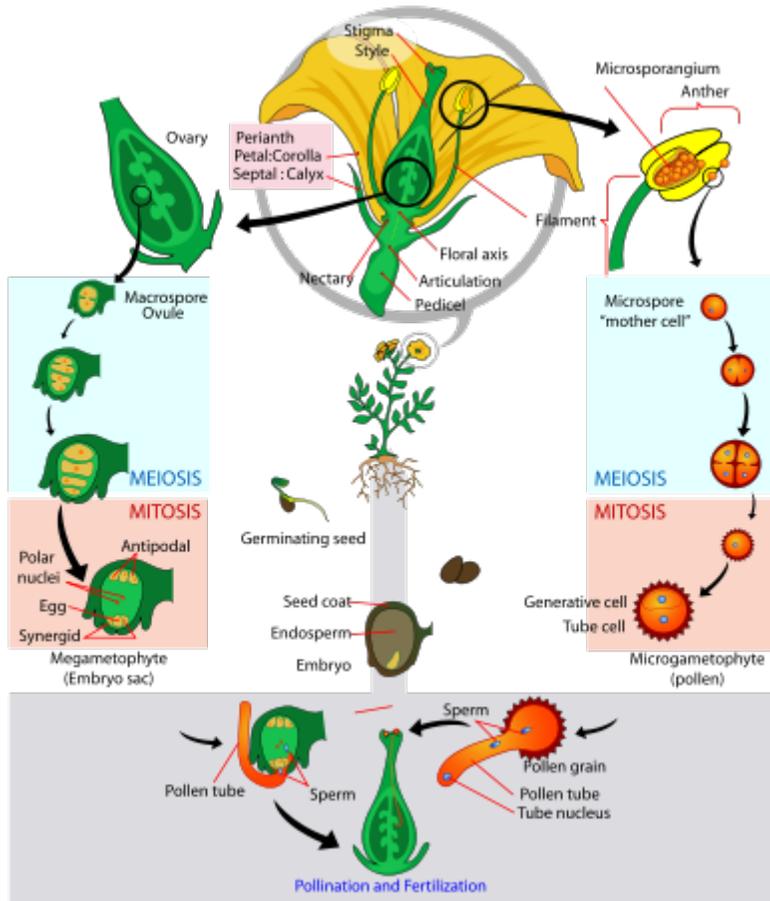
A sporophyte of *Dicksonia antarctica*.



The underside of a *Dicksonia antarctica* frond showing the sori, or spore-producing structures.

In the spermatophytes, the seed plants, the sporophyte is the dominant multicellular phase; the gametophytes are strongly reduced in size and very different in morphology. The entire gametophyte generation, with the sole exception of pollen grains (microgametophytes), is contained within the sporophyte. The life cycle of a dioecious flowering plant (angiosperm), the willow, has been outlined in some detail in an earlier section (A complex life cycle). The life cycle of a gymnosperm is similar. However, flowering plants have in addition a phenomenon called 'double fertilization'. Two sperm nuclei from a pollen grain (the microgametophyte), rather than a single sperm, enter the archegonium of the megagametophyte; one fuses with the egg nucleus to form the zygote,

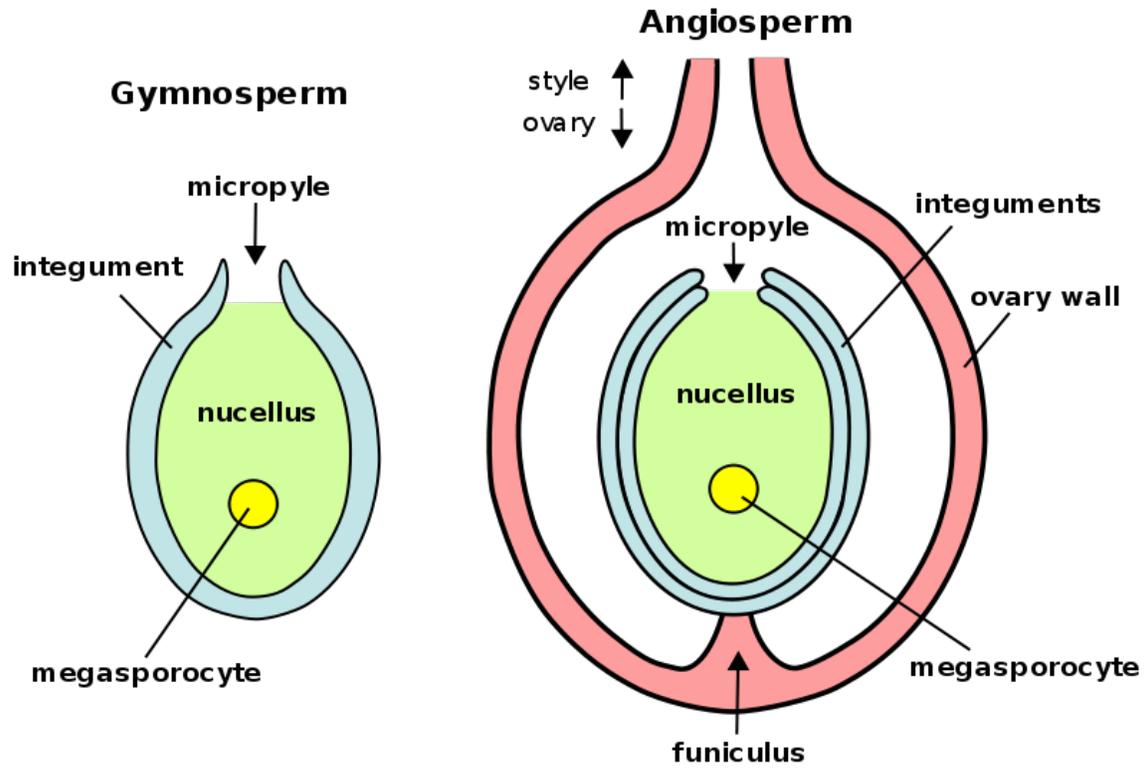
the other fuses with two other nuclei of the gametophyte to form 'endosperm', which nourishes the developing embryo.



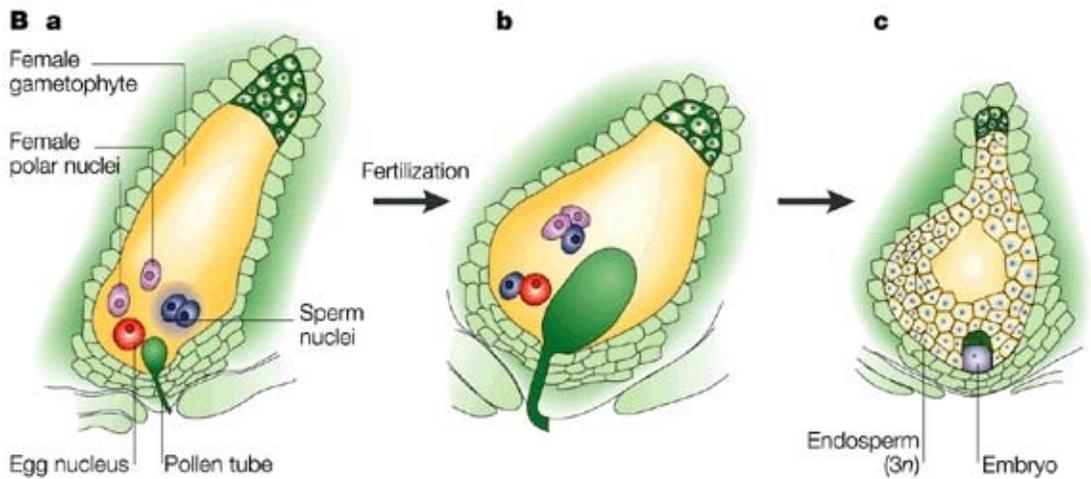
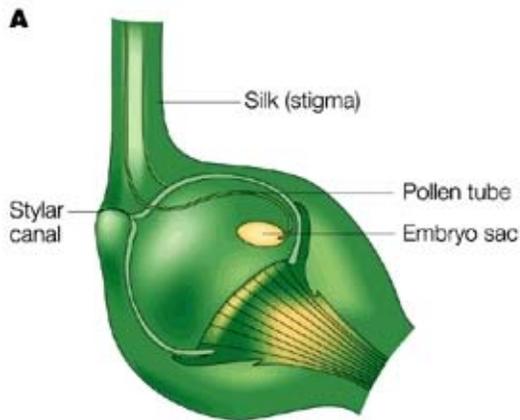
Angiosperm life cycle



Tip of tulip stamen showing pollen (microgametophytes)



Plant ovules (megagametophytes): Gymnosperm ovule on left, angiosperm ovule (inside ovary) on right



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Double fertilization

Other groups of organism

Some organisms currently classified in the Chromalveolata, and thus not plants in the sense used here, exhibit alternation of generations. Kelp are an example of a brown alga with a heteromorphic alternation of generations. Species from the genus *Laminaria* have a large sporophytic thallus that produces haploid spores which germinate to produce free-living microscopic male and female gametophytes. Foraminifera undergo a heteromorphic alternation of generations between haploid *gamont* and diploid *agamont* forms. The single-celled haploid organism is typically much larger than the diploid organism.

Fungal mycelia are typically haploid. When mycelia of different mating types meet, they produce two multinucleate ball-shaped cells, which join via a "mating bridge". Nuclei move from one mycelium into the other, forming a *heterokaryon* (meaning "different nuclei"). This process is called *plasmogamy*. Actual fusion to form diploid nuclei is called *karyogamy*, and may not occur until sporangia are formed. Karogamy produces a diploid zygote, which is a short-lived sporophyte that soon undergoes meiosis to form haploid spores. When the spores germinate, they develop into new mycelia.

The life cycle of slime moulds is very similar to that of fungi. Haploid spores germinate to form swarm cells or *myxamoebae*. These fuse in a process referred to as *plasmogamy* and *karyogamy* to form a diploid zygote. The zygote develops into a plasmodium, and the mature plasmodium produces, depending on the species, one to many fruiting bodies containing haploid spores.

In some animals, there is an alternation between parthenogenic and sexually reproductive phases (**heterogamy**). Although in some ways similar to alternation of generations, the genetics of heterogamy is significantly different.