A Comprehensive Introduction to

Botany

Joycelyn Dollar

First Edition, 2012

Table of Contents

Chapter 1

Botany

Pinguicula grandiflora commonly known as a Butterwort

Botany, **plant science**(**s**), or **plant biology** is a branch of biology that involves the scientific study of plant life. Botany covers a wide range of scientific disciplines concerned with the study of plants, algae and fungi, including structure, growth, reproduction, metabolism, development, diseases, chemical properties, and evolutionary

relationships among taxonomic groups. Botany began with early human efforts to identify edible, medicinal and poisonous plants, making it one of the oldest sciences. Today botanists study over 550,000 species of living organisms.

The term "botany" comes from Greek βοτάνη, meaning "pasture, grass, fodder", perhaps via the idea of a livestock keeper needing to know which plants are safe for livestock to eat.

Scope and importance of botany

Hibiscus

As with other life forms in biology, plant life can be studied from different perspectives, from the molecular, genetic and biochemical level through organelles, cells, tissues, organs, individuals, plant populations, and communities of plants. At each of these levels a botanist might be concerned with the classification (taxonomy), structure (anatomy and morphology), or function (physiology) of plant life.

Historically all living things were grouped as animals or plants, and botany covered all organisms not considered animals. Some organisms once included in the field of botany are no longer considered to belong to the plant kingdom – these include fungi (studied in mycology), lichens (lichenology), bacteria (bacteriology), viruses (virology) and single-celled algae, which are now grouped as part of the Protista. However, attention is still

given to these groups by botanists, and fungi, lichens, bacteria and photosynthetic protists are usually covered in introductory botany courses.

The study of plants is vital because they are a fundamental part of life on Earth, which generates the oxygen, food, fibres, fuel and medicine that allow humans and other life forms to exist. Through photosynthesis, plants absorb carbon dioxide, a greenhouse gas that in large amounts can affect global climate. Additionally, they prevent soil erosion and are influential in the water cycle. A good understanding of plants is crucial to the future of human societies as it allows us to:

- Produce food to feed an expanding population
- Understand fundamental life processes
- Produce medicine and materials to treat diseases and other ailments
- Understand environmental changes more clearly

Paleobotanists study ancient plants in the fossil record. It is believed that early in the Earth's history, the evolution of photosynthetic plants altered the global atmosphere of the earth, changing the ancient atmosphere by oxidation.

Human nutrition

Nearly all the food we eat comes (directly and indirectly) from plants like this American long grain rice

Virtually all foods eaten come from plants, either directly from staple foods and other fruit and vegetables, or indirectly through livestock or other animals, which rely on plants for their nutrition. Plants are the fundamental base of nearly all food chains because they use the energy from the sun and nutrients from the soil and atmosphere, converting them into a form that can be consumed and utilized by animals; this is what ecologists call the first trophic level. Botanists also study how plants produce food we can eat and how to increase yields and therefore their work is important in mankind's ability to feed the world and provide food security for future generations, for example, through plant breeding. Botanists also study weeds, plants which are considered to be a nuisance in a

particular location. Weeds are a considerable problem in agriculture, and botany provides some of the basic science used to understand how to minimize 'weed' impact in agriculture and native ecosystems. Ethnobotany is the study of the relationships between plants and people, and when this kind of study is turned to the investigation of plant-people relationships in past times, it is referred to as archaeobotany or paleoethnobotany.

Fundamental life processes

Plants are convenient organisms in which fundamental life processes (like cell division and protein synthesis) can be studied, without the ethical dilemmas of studying animals or humans. The genetic laws of inheritance were discovered in this way by Gregor Mendel, who was studying the way pea shape is inherited. What Mendel learned from studying plants has had far reaching benefits outside of botany. Additionally, Barbara McClintock discovered 'jumping genes' by studying maize. These are a few examples that demonstrate how botanical research has an ongoing relevance to the understanding of fundamental biological processes.

Medicine and materials

Many medicinal and recreational drugs, like tetrahydrocannabinol, caffeine, and nicotine come directly from the plant kingdom. Others are simple derivatives of botanical natural products; for example, aspirin is based on the pain killer salicylic acid which originally came from the bark of willow trees. As well, the narcotic analgesics such as morphine are derived from the opium poppy. There may be many novel cures for diseases provided by plants, waiting to be discovered. Popular stimulants like coffee, chocolate, tobacco, and tea also come from plants. Most alcoholic beverages come from fermenting plants such as barley (beer), rice (sake) and grapes (wine).

Plants also provide us with many natural materials, such as hemp, cotton, wood, paper, linen, vegetable oils, some types of rope, and rubber. The production of silk would not be possible without the cultivation of the mulberry plant. Sugarcane, rapeseed, soy and other plants with a highly fermentable sugar or oil content have recently been put to use as sources of biofuels, which are important alternatives to fossil fuels.

Environmental changes

Plants can also help us understand changes in on our environment in many ways.

- Understanding habitat destruction and species extinction is dependent on an accurate and complete catalog of plant systematics and taxonomy.
- Plant responses to ultraviolet radiation can help us monitor problems like ozone depletion.
- Analyzing pollen deposited by plants thousands or millions of years ago can help scientists to reconstruct past climates and predict future ones, an essential part of climate change research.

- Recording and analyzing the timing of plant life cycles are important parts of phenology used in climate-change research.
- Lichens, which are sensitive to atmospheric conditions, have been extensively used as pollution indicators.

In many different ways, plants can act a little like the 'miners' canary', an early warning system alerting us to important changes in our environment. In addition to these practical and scientific reasons, plants are extremely valuable as recreation for millions of people who enjoy gardening, horticultural and culinary uses of plants every day.

History

The traditional tools of a botanist

Early botany

Ancient India

Early examples of plant taxonomy occur in the Rigveda, that divides plants into *Vṛska* (tree), *Osadhi* (herbs useful to humans) and *Virudha* (creepers), which are then further subdivided. The Atharvaveda divides plants into eight classes, *Visakha* (spreading branches), *Manjari* (leaves with long clusters), *Sthambini* (bushy plants), *Prastanavati* (which expands); *Ekasṛnga* (those with monopodial growth), *Pratanavati* (creeping plants), *Amsumati* (with many stalks), and *Kandini* (plants with knotty joints). The Taittiriya Samhita classifies the plant kingdom into *vṛksa*, *vana* and *druma* (trees), *visakha* (shrubs with spreading branches), *sasa* (herbs), *amsumali* (a spreading or deliquescent plant), *vratati* (climber), *stambini* (bushy plant), *pratanavati* (creeper), and *alasala* (those spreading on the ground).

Manusmriti – Law book of Hindus – proposed a classification of plants in eight major categories. Charaka Samhitā and Sushruta Samhita and the Vaisesikas also present an elaborate taxonomy.

Parashara, the author of *Vṛksayurveda* (the science of life of trees), classifies plants into Dvimatrka (Dicotyledons) and Ekamatrka (Monocotyledons). These are further classified into *Samiganiya* (Fabaceae), *Puplikagalniya* (Rutaceae), *Svastikaganiya* (Cruciferae), *Tripuspaganiya* (Cucurbitaceae), *Mallikaganiya* (Apocynaceae), and *Kurcapuspaganiya* (Asteraceae).

Important medieval Indian works of plant physiology include the *Prthviniraparyam* of Udayana, *Nyayavindutika* of Dharmottara, *Saddarsana-samuccaya* of Gunaratna, and *Upaskara* of Sankaramisra.

Ancient Iranic people

The knowledge of medical plants and botany was considered as secret and holy by the ancient Iranic people. There is evidence of such practices in the documents that have survived from the ancient Zoroastrian writings. The practice and use of botany for medical purposes as well as various Iranic cousins and traditions is still common to this day amongst the Iranic people of the Central Asia, Near East and Europe.

Ancient China

In ancient China, the recorded listing of different plants and herb concoctions for pharmaceutical purposes spans back to at least the Warring States (481 BC-221 BC). Many Chinese writers over the centuries contributed to the written knowledge of herbal pharmaceutics. There was the Han Dynasty (202 BC-220 AD) written work of the Huangdi Neijing and the famous pharmacologist Zhang Zhongjing of the 2nd century. There was also the 11th century scientists and statesmen Su Song and Shen Kuo, who compiled treatises on herbal medicine and included the use of mineralogy.

Greco-Roman world

Among the earliest of botanical works in Europe, written around 300 B.C., are two large treatises by Theophrastus: *On the History of Plants* (*Historia Plantarum*) and *On the Causes of Plants*. Together these books constitute the most important contribution to botanical science during antiquity and on into the Middle Ages. Aristotle also wrote about plants. One theory that Greco-Romans came up with about plants was that they ate soil for nutrients.

The Greek medical writer Pedanius Dioscorides (ca.40-90) provides important evidence on Greek and Roman knowledge of medicinal plants. Dioscorides is famous for writing a five volume book in his native Greek Περί ὕλης ιατρικής (*De Materia Medica* - in the Latin translation) that is one of the most influential herbal books in history. In fact, it remained in use until about CE 1600. Approximately 1300-1400 different plant species were known under Roman reign.

Medieval botany

One of the earliest Botanical texts by Abū Ḥanīfa Dīnawarī in the year 867AD.

The earliest known work from the Muslim world dedicated to the study of agriculture was Ibn Wahshiyya's Nabatean Agriculture, which also dealt with the related field of botany and was also an early cookbook.

The Kurdish biologist Abū Ḥanīfa Dīnawarī (828-896) is considered the founder of Arabic botany for his *Book of Plants,* in which he described at least 637 plants and discussed plant development from germination to death, describing the phases of plant growth and the production of flowers and fruit.

Theophrastus's *Historia Plantarum* served as a reference point in botany for many centuries, and was further developed around 1200 A.D. by Giovanni Bodeo da Stapelio, who added a *commentarius* and drawings—*Selected pages of a 17th century edition of the 1200 A.D. version (in Italian).*

Ibn Bassal is known for his famous work named *The Classification of Soils*. Al-Asma'i was the earliest known Arab biologist, botanist and zoologist. al-Masihi was the first to recognize the science of Botany.

In the early 13th century, the Andalusian-Arabian biologist Abu al-Abbas al-Nabati developed an early scientific method for botany, introducing empirical and experimental techniques in the testing, description and identification of numerous materia medica, and separating unverified reports from those supported by actual tests and observations. His student Ibn al-Baitar (d. 1248) wrote a pharmaceutical encyclopedia describing 1,400 plants, foods, and drugs, 300 of which were his own original discoveries. A Latin translation of his work was useful to European biologists and pharmacists in the 18th and 19th centuries.

Early modern botany
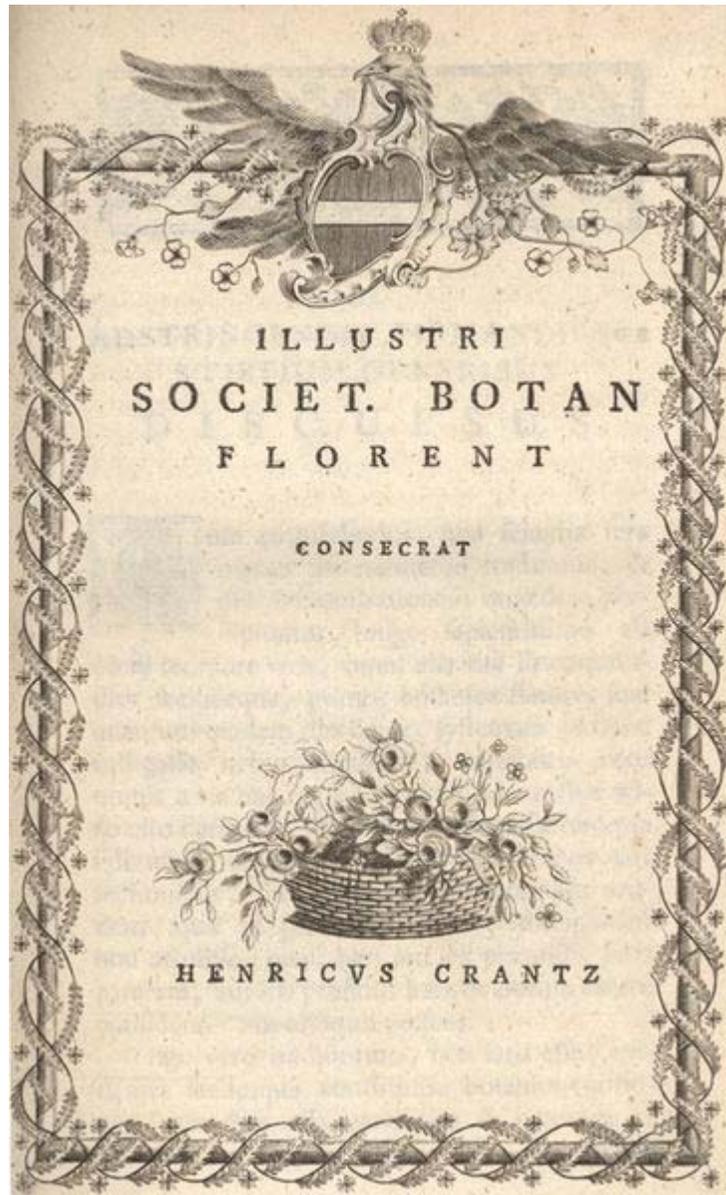
Crantz's *Classis cruciformium...*, 1769

German physician Leonhart Fuchs (1501–1566) was one of the three founding fathers of botany, along with Otto Brunfels (1489- 1534) and Hieronymus Bock (1498–1554) (also called Hieronymus Tragus).

Valerius Cordus (1515–1554) authored one of the greatest pharmacopoeias and one of the most celebrated herbals in history, *Dispensatorium* (1546). As early as the 16th century, the Italian Ulisse Aldrovandi was scientifically researching plants. In 1665, using an early microscope, Robert Hooke discovered cells in cork, and a short time later in living plant tissue. The Germans Jacob Theodor Klein and Leonhart Fuchs, the Swiss Conrad von

Gesner, and the British author Nicholas Culpeper published herbals that gave information on the medicinal uses of plants.

During the 18th century systems of classification became deliberately artificial and served only for the purpose of identification. These classifications are comparable to diagnostic keys, where taxa are artificially grouped in pairs by few, easily recognisable characters. The sequence of the taxa in keys is often totally unrelated to their natural or phyletic groupings. In the 18th century an increasing number of new plants had arrived in Europe, from newly discovered countries and the European colonies worldwide, and a larger amount of plants became available for study.

In 1754 Carl von Linné (Carl Linnaeus) divided the plant Kingdom into 25 classes. One, the *Cryptogamia*, included all the plants with concealed reproductive parts (algae, fungi, mosses and liverworts and ferns).

The increased knowledge on anatomy, morphology and life cycles, lead to the realization that there were more natural affinities between plants, than the sexual system of Linnaeus indicated. Adanson (1763), de Jussieu (1789), and Candolle (1819) all proposed various alternative natural systems that were widely followed. The ideas of natural selection as a mechanism for evolution required adaptations to the Candollean system, which started the studies on evolutionary relationships and phylogenetic classifications of plants.

Botany was greatly stimulated by the appearance of the first "modern" text book, Matthias Schleiden's *Grundzuge der Wissenschaftlichen*, published in English in 1849 as *Principles of Scientific Botany*. Carl Willdenow examined the connection between seed dispersal and distribution, the nature of plant associations and the impact of geological history. The cell nucleus was discovered by Robert Brown in 1831.

Modern botany

A considerable amount of new knowledge today is being generated from studying model plants like *Arabidopsis thaliana*. This weedy species in the mustard family was one of the first plants to have its genome sequenced. The sequencing of the rice (*Oryza sativa*) genome, its relatively small genome, and a large international research community have made rice an important cereal/grass/monocot model. Another grass species, *Brachypodium distachyon* is also emerging as an experimental model for understanding the genetic, cellular and molecular biology of temperate grasses. Other commercially important staple foods like wheat, maize, barley, rye, pearl millet and soybean are also having their genomes sequenced. Some of these are challenging to sequence because they have more than two haploid (n) sets of chromosomes, a condition known as polyploidy, common in the plant kingdom. *Chlamydomonas reinhardtii* (a single-celled, green alga) is another plant model organism that has been extensively studied and provided important insights into cell biology.

In 1998 the Angiosperm Phylogeny Group published a phylogeny of flowering plants based on an analysis of DNA sequences from most families of flowering plants. As a

result of this work, major questions such as which families represent the earliest branches in the genealogy of angiosperms are now understood. Investigating how plant species are related to each other allows botanists to better understand the process of evolution in plants.

Subdisciplines of botany

- Agronomy — Application of plant science to crop production
- Bryology — Mosses, liverworts, and hornworts
- Economic botany — Study of plants of economic use or value
- Ethnobotany — Relationship between humans and plants
- Forestry — Forest management and related studies
- Horticulture — Cultivated plants
- Lichenology — The study of lichens
- Paleobotany — Fossil plants
- Palynology — Pollen and spores
- Phycology — Algae
- Phytochemistry — Plant secondary chemistry and chemical processes
- Phytopathology — Plant diseases
- Plant anatomy — Cell and tissue structure
- Plant ecology — Role of plants in the environment
- Plant genetics — Genetic inheritance in plants
- Plant morphology — Structure and life cycles
- Plant physiology — Life functions of plants
- Plant systematics — Classification and naming of plants

Chapter 2

History of Botany

Some traditional tools of botanical science

The **history of botany** examines the human effort to understand life on Earth by tracing the historical development of the discipline of botany—that part of natural science dealing with organisms traditionally treated as plants.

Rudimentary botanical science began with empirically-based plant lore passed from generation to generation in the oral traditions of paleolithic hunter-gatherers. The first written records of plants were made in the Neolithic Revolution about 10,000 years ago as writing was developed in the settled agricultural communities where plants and animals were first domesticated. The first writings that show human curiosity about plants themselves, rather than the uses that could be made of them, appears in the teachings of Aristotle's student Theophrastus at the Lyceum in ancient Athens in about 350 BC; this is considered the starting point for modern botany. In Europe, this early botanical science was soon overshadowed by a medieval preoccupation with the medicinal properties of plants that lasted more than 1000 years. During this time, the medicinal works of classical antiquity were reproduced in manuscripts and books called herbals. In China and the Arab world, the Greco-Roman work on medicinal plants was preserved and extended.

In Europe the Renaissance of the 14th–17th centuries heralded a scientific revival during which botany gradually emerged from natural history as an independent science, distinct from medicine and agriculture. Herbals were replaced by Floras: books that described the native plants of local regions. The invention of the microscope stimulated the study of plant anatomy, and the first carefully designed experiments in plant physiology were performed. With the expansion of trade and exploration beyond Europe, the many new plants being discovered were subjected to an increasingly rigorous process of naming, description, and classification.

Progressively more sophisticated scientific technology has aided the development of contemporary botanical offshoots in the plant sciences, ranging from the applied fields of economic botany (notably agriculture, horticulture and forestry), to the detailed examination of the structure and function of plants and their interaction with the environment over many scales from the large-scale global significance of vegetation and plant communities (biogeography and ecology) through to the small scale of subjects like cell theory, molecular biology and plant biochemistry.

Introduction

Botany and zoology are, historically, the core disciplines of biology whose history is closely associated with the natural sciences chemistry, physics and geology. A distinction can be made between botanical science in a pure sense, as the study of plants themselves, and botany as applied science, which studies the human use of plants. Early natural history divided pure botany into three main streams morphology-classification, anatomy and physiology – that is, external form, internal structure, and functional operation. The most obvious topics in applied botany are horticulture, forestry and agriculture although there are many others like weed science, plant pathology, floristry, pharmacognosy, economic botany and ethnobotany which lie outside modern courses in botany. Since the

origin of botanical science there has been a progressive increase in the scope of the subject as technology has opened up new techniques and areas of study. Modern molecular systematics, for example, entails the principles and techniques of taxonomy, molecular biology, computer science and more.

Within botany there are a number of sub-disciplines that focus on particular plant groups, each with their own range of related studies (anatomy, morphology etc.). Included here are: phycology (algae), pteridology (ferns), bryology (mosses and liverworts) and palaeobotany (fossil plants) and their histories are treated elsewhere. To this list can be added mycology, the study of fungi, which were once treated as plants, but are now ranked as a unique kingdom.

Ancient and medieval knowledge

Nomadic hunter-gatherer societies passed on, by oral tradition, what they knew (their empirical observations) about the different kinds of plants that they used for food, shelter, poisons, medicines, for ceremonies and rituals etc. The uses of plants by these pre-literate societies influenced the way the plants were named and classified—their uses were embedded in folk-taxonomies, the way they were grouped according to use in everyday communication. The nomadic life-style was drastically changed when settled communities were established in about twelve centres around the world during the Neolithic Revolution which extended from about 10,000 to 2500 years ago depending on the region. With these communities came the development of the technology and skills needed for the domestication of plants and animals and the emergence of the written word provided evidence for the passing of systematic knowledge and culture from one generation to the next.

Plant lore and plant selection

A Sumerian harvester's sickle dated to 3000 BC

During the Neolithic Revolution plant knowledge increased most obviously through the use of plants for food and medicine. All of today's staple foods were domesticated in prehistoric times as a gradual process of selection of higher-yielding varieties took place, possibly unknowingly, over hundreds to thousands of years. Legumes were cultivated on all continents but cereals made up most of the regular diet: rice in East Asia, wheat and barley in the Middle east, and maize in Central and South America. By Greco-Roman times popular food plants of today, including grapes, apples, figs, and olives, were being listed as named varieties in early manuscripts. Botanical authority William Stearn has observed that "*cultivated plants are mankind's most vital and precious heritage from remote antiquity*".

It is also from the Neolithic, in about 3000 BCE, that we glimpse the first known illustrations of plants and read descriptions of impressive gardens in Egypt. However protobotany, the first pre-scientific written record of plants, did not begin with food; it was born out of the medicinal literature of Egypt, China, Mesopotamia and India. Botanical historian Alan Morton notes that agriculture was the occupation of the poor and uneducated, while medicine was the realm of socially influential shamans, priests, apothecaries, magicians and physicians, who were more likely to record their knowledge for posterity.

Early botany

Ancient India

An early example of ancient Indian plant classification is found in the Rigveda, a collection of Vedic Sanskrit hymns from about 3700–3100 BP. Plants are divided into *vṛska* (trees), *osadhi* (herbs useful to humans) and *virudha* (creepers), with further subdivisions. The sacred Hindu text Atharvaveda divides plants into eight classes: *visakha* (spreading branches), *manjari* (leaves with long clusters), *sthambini* (bushy plants), *prastanavati* (which expands); *ekasṛnga* (those with monopodial growth), *pratanavati* (creeping plants), *amsumati* (with many stalks), and *kandini* (plants with knotty joints). The Taittiriya Samhita classifies the plant kingdom into *vṛksa*, *vana* and *druma* (trees), *visakha* (shrubs with spreading branches), *sasa* (herbs), *amsumali* (spreading plant), *vratati* (climber), *stambini* (bushy plant), *pratanavati* (creeper), and *alasala* (spreading on the ground). Other examples of early Indian taxonomy include Manusmriti, the Law book of Hindus, which classifies plants into eight major categories. Elaborate taxonomies also occur in the Charaka Samhitā, Sushruta Samhita and Vaisesika.

Ancient China

In ancient China lists of different plants and herb concoctions for pharmaceutical purposes date back to at least the time of the Warring States (481 BC-221 BC). Many Chinese writers over the centuries contributed to the written knowledge of herbal pharmaceutics. The Han Dynasty (202 BC-220 AD) includes the notable work of the Huangdi Neijing and the famous pharmacologist Zhang Zhongjing. There were also the 11th century scientists and statesmen Su Song and Shen Kuo who compiled learned treatises on natural history, emphasising herbal medicine.

## Theophrastus and the origin of botanical science

"School of Athens" Fresco in Apostolic Palace, Rome, Vatican City, by Raphael 1509-1510

Ancient Athens, of the 6th century BCE, was the busy trade centre at the confluence of Egyptian, Mesopotamian and Minoan cultures at the height of Greek colonisation of the Mediterranean. The philosophical thought of this period ranged freely through many subjects. Empedocles (490–430 BCE) foreshadowed Darwinian evolutionary theory in a crude formulation of the mutability of species and natural selection. The physician Hippocrates (460–370 BCE) avoided the prevailing superstition of his day and approached healing by close observation and the test of experience. At this time a

genuine non-anthropocentric curiosity about plants emerged. The major works written about plants extended beyond the description of their medicinal uses to the topics of plant geography, morphology, physiology, nutrition, growth and reproduction.

Foremost among the scholars studying botany was Theophrastus of Eressus (Greek: Θεόφραστος; c. 371–287 BCE) who has been frequently referred to as the "Father of Botany". He was a student and close friend of Aristotle (384–322 BCE) and succeeded him as head of the Lyceum (an educational establishment like a modern university) in Athens with its tradition of peripatetic philosophy. Aristotle's special treatise on plants — θεωρία περὶ φυτῶν — is now lost, although there are many botanical observations scattered throughout his other writings (these have been assembled by Christian Wimmer in *Phytologiae Aristotelicae Fragmenta*, 1836) but they give little insight into his botanical thinking. The Lyceum prided itself in a tradition of systematic observation of causal connections, critical experiment and rational theorizing. Theophrastus challenged the superstitious medicine employed by the physicians of his day, called rhizotomi, and also the control over medicine exerted by priestly authority and tradition. Together with Aristotle he had tutored Alexander the Great whose military conquests were carried out with all the scientific resources of the day, the Lyceum garden probably containing many botanical trophies collected during his campaigns as well as other explorations in distant lands. It was in this garden where he gained much of his plant knowledge.
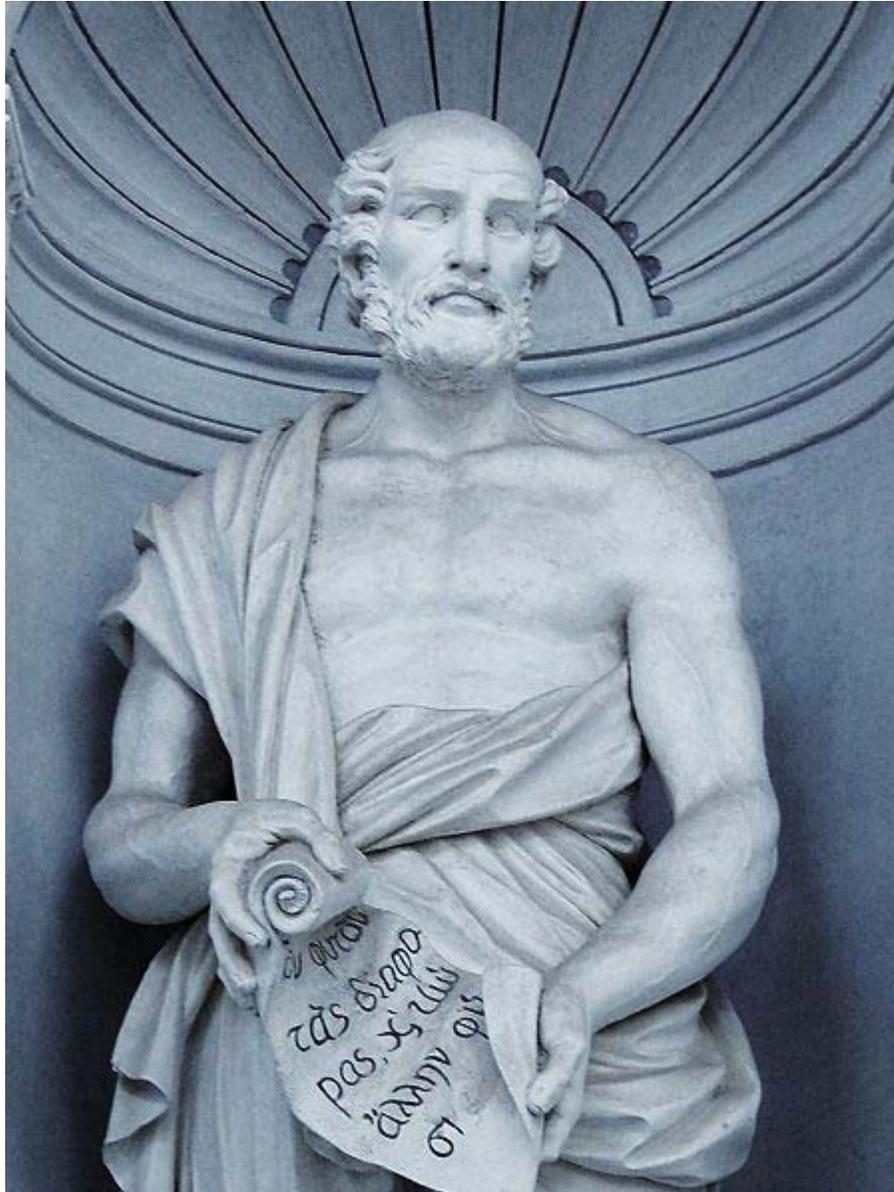
Statue of Theophrastus 371–287 BC "Father of Botany"Palermo Botanic Gardens

Theophrastus's major botanical works were the *Enquiry into Plants* (*Historia Plantarum*) and *Causes of Plants* (*Causae Plantarum*) which were his lecture notes for the Lyceum. The opening sentence of the *Enquiry* reads like a botanical manifesto: "*We must consider the distinctive characters and the general nature of plants from the point of view of their morphology, their behaviour under external conditions, their mode of generation and the whole course of their life*". The *Enquiry* is 9 books of "applied" botany dealing with the forms and classification of plants and economic botany, examining the techniques of agriculture (relationship of crops to soil, climate, water and habitat) and horticulture. He described some 500 plants in detail, often including descriptions of habitat and geographic distribution, and he recognised some plant groups that can be recognised as modern-day plant families. Some names he used, like *Crataegus*, *Daucus* and *Asparagus*

have persisted until today. His second book *Causes of Plants* covers plant growth and reproduction (akin to modern physiology). Like Aristotle he grouped plants into "trees", "undershrubs", "shrubs" and "herbs" but he also made several other important botanical distinctions and observations. He noted that plants could be annuals, perennials and biennials, they were also either monocotyledons or dicotyledons and he also noticed the difference between determinate and indeterminate growth and details of floral structure including the degree of fusion of the petals, position of the ovary and more. These lecture notes of Theophrastus comprise the first clear exposition of the rudiments of plant anatomy, physiology, morphology and ecology — presented in a way that would not be matched for another eighteen centuries.

Meanwhile the study of medicinal plants was not being neglected and a full synthesis of ancient Greek pharmacology was compiled in *Materia Medica* c. 60 CE by Pedanius Dioscorides (c. 40-90 CE) who was a Greek physician with the Roman army. This work proved to be the definitive text on medicinal herbs, both oriental and occidental, for fifteen hundred years until the dawn of the European Renaissance being slavishly copied again and again throughout this period. Though rich in medicinal information with descriptions of about 600 medicinal herbs, the botanical content of the work was extremely limited.

Ancient Rome

The Romans contributed little to the foundations of botanical science laid by the ancient Greeks, but made a sound contribution to our knowledge of applied botany as agriculture. In works titled *De Re Rustica* the principles and practice of agriculture were discussed by writers Marcus Porcius Cato (234–149 BCE), Marcus Varro (116–27 BCE) and, in particular, Columella (4–70 CE). Roman encyclopaedist Pliny the Elder (23–79 CE) deals with plants in Books 12 to 26 of his 37-volume highly influential work *Naturalis Historia* in which he frequently quotes Theophrastus but with a lack of botanical insight although he does, nevertheless, draw a distinction between true botany on the one hand, and farming and medicine on the other.

It is estimated that at the time of the Roman Empire between 1300 and 1400 plants had been recorded in the West.

Medicinal plants of the early Middle Ages

An Arabic copy of Avicenna's *Canon of Medicine* dated 1593

In Western Europe, after Theophrastus, botany passed through a bleak period of 1800 years when little progress was made and, indeed, many of the early insights were lost. As Europe entered the Middle Ages, a period of disorganised feudalism and indifference to learning, China, India and the Arab world enjoyed a golden age. Chinese philosophy had followed a similar path to that of the ancient Greeks. The Chinese dictionary-encyclopaedia Erh Ya probably dates from about 300 BCE and describes about 334 plants classed as trees or shrubs, each with a common name and illustration. Between 100 and 1700 CE many new works on pharmaceutical botany were produced including encyclopaedic accounts and treatises compiled for the Chinese imperial court. These were free of superstition and myth with carefully researched descriptions and nomenclature;

they included cultivation information and notes on economic and medicinal uses — and even elaborate monographs on ornamental plants. But there was no experimental method and no analysis of the plant sexual system, nutrition, or anatomy.

The 400-year period from the 9th to 13th centuries CE was the Islamic Renaissance, a time when Islamic culture and science thrived. Greco-Roman texts were preserved, copied and extended although new texts always emphasised the medicinal aspects of plants. Kurdish biologist Ābu Ḥanīfah Āḥmad ibn Dawūd Dīnawarī (828–896 CE) is known as the founder of Arabic botany; his *Kitâb al-nabât* ('Book of Plants') describes 637 species, discussing plant development from germination to senescence and including details of flowers and fruits. The Mutazilite philosopher and physician Ibn Sina (Avicenna) (c. 980–1037 CE) was another influential figure, his *The Canon of Medicine* being a landmark in the history of medicine treasured until the Enlightenment. In the early 13th century, the Andalusian-Arabian biologist Abu al-Abbas al-Nabati developed an early scientific method for botany, introducing empirical and experimental techniques in the testing, description and identification of numerous materia medica, and separating unverified reports from those supported by actual tests and observations. His student Ibn al-Baitar (circa, 1188–1248) was an eminent Arab scientist. His *Kitab al-Jami fi al-Adwiya al-Mufrada* was a pharmacopoeia describing 1400 species, 300 discovered by himself. Translated into Latin in 1758 this was used in Europe until the early 19th century as a critical summing up of centuries of Arab pharmacology.

In India simple artificial plant classification systems of the Rigveda, Atharvaveda and Taittiriya Samhita became more botanical with the work of Parashara (c.400–500 CE), the author of *Vṛksayurveda* (the science of life of trees). He made close observations of cells and leaves and divided plants into Dvimatrka (Dicotyledons) and Ekamatrka (Monocotyledons). The dicotyledons were further classified into groupings (ganas) akin to modern floral families: *Samiganiya* (Fabaceae), *Puplikagalniya* (Rutaceae), *Svastikaganiya* (Cruciferae), *Tripuspaganiya* (Cucurbitaceae), *Mallikaganiya* (Apocynaceae), and *Kurcapuspaganiya* (Asteraceae). Important medieval Indian works of plant physiology include the *Prthviniraparyam* of Udayana, *Nyayavindutika* of Dharmottara, *Saddarsana-samuccaya* of Gunaratna, and *Upaskara* of Sankaramisra.

The Age of Herbals
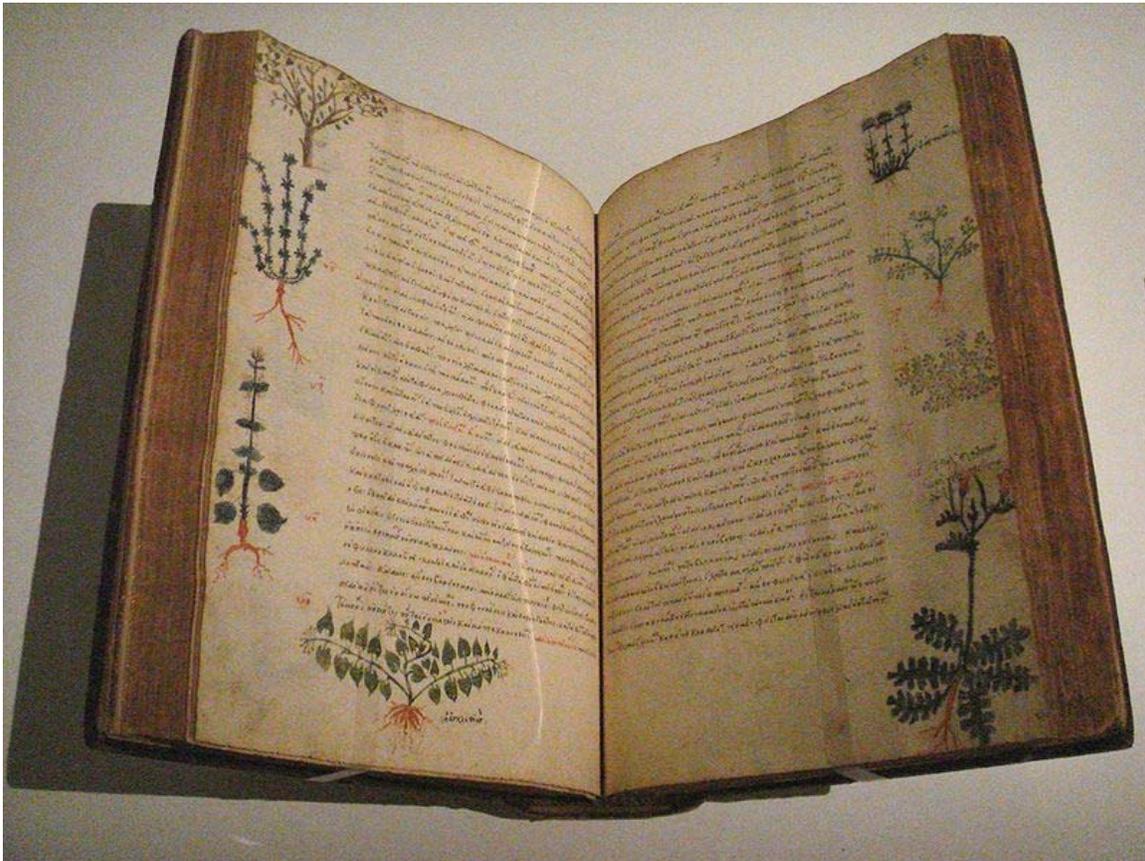
Dioscorides', *De Materia Medica*, Byzantium, 15th century.

In the European Middle Ages of the 15th and 16th centuries the lives of European citizens were based around agriculture but when printing arrived, with movable type and woodcut illustrations, it was not treatises on agriculture that were published, but lists of medicinal plants with descriptions of their properties or "virtues". These first plant books, known as herbals showed that botany was still a part of medicine, as it had been for most of ancient history. Authors of herbals were often curators of university gardens, and most herbals were derivative compilations of classic texts, especially *De Materia Medica*. However, the need for accurate and detailed plant descriptions meant that some herbals were more botanical than medicinal. German Otto Brunfels's (1464–1534) *Herbarum Vivae Icones* (1530) contained descriptions of about 47 species new to science combined with accurate illustrations. His fellow countryman Hieronymus Bock's (1498–1554) *Kreutterbuch* of 1539 described plants he found in nearby woods and fields and these were illustrated in the 1546 edition. However, it was Valerius Cordus (1515–1544) who pioneered the formal botanical description that detailed both flowers and fruits, some anatomy including the number of chambers in the ovary, and the type of ovule placentation. He also made observations on pollen and distinguished between inflorescence types. His five-volume *Historia Plantarum* was published about 18 years after his early death aged 29 in 1561-1563. In Holland Rembert Dodoens (1517–1585), in *Stirpium Historiae* (1583), included descriptions of many new species from the

Netherlands in a scientific arrangement and in England William Turner (1515–1568) in his *Libellus De Re Herbaria Novus* (1538) published names, descriptions and localities of many native British plants.

Herbals contributed to botany by setting in train the science of plant description, classification, and botanical illustration. Up to the 17th century botany and medicine were one and the same but those books emphasising medicinal aspects eventually omitted the plant lore to become modern pharmacopoeias; those that omitted the medicine became more botanical and evolved into the modern compilations of plant descriptions we call Floras. These were often backed by specimens deposited in a herbarium which was a collection of dried plants that verified the plant descriptions given in the Floras. The transition from herbal to Flora marked the final separation of botany from medicine.

1550–1800 The European Renaissance and after

The revival of learning during the European Renaissance renewed interest in plants. The church, feudal aristocracy and an increasingly influential merchant class that supported science and the arts, now jostled in a world of increasing trade. Sea voyages of exploration returned botanical treasures to the large public, private, and newly established botanic gardens, and introduced an eager population to novel crops, drugs and spices from Asia, the East Indies and the New World.

The number of scientific publications increased. In England, for example, scientific communication and causes were facilitated by learned societies like Royal Society (founded in 1660) and the Linnaean Society (founded in 1788): there was also the support and activities of botanical institutions like the Chelsea Physic Garden, Royal Botanic Gardens Kew, and the Oxford and Cambridge Botanic Gardens, as well as the influence of renowned private gardens and wealthy entrepreneurial nurserymen. Enlightenment values were reinvigorating science and in botany a new phase of plant identification, nomenclature and description began. By the early 17th century the number of plants described in Europe had risen to about 6000.

Botanical gardens and herbaria

Preparing a herbarium specimen

Public and private gardens have always been strongly associated with the historical unfolding of botanical science. Early botanical gardens were physic gardens, repositories for the medicinal plants described in the herbals. As they were generally associated with universities or other academic institutions the plants were also used for study. The directors of these gardens were eminent physicians with an educational role as "scientific gardeners" and it was staff of these institutions that produced many of the published herbals.
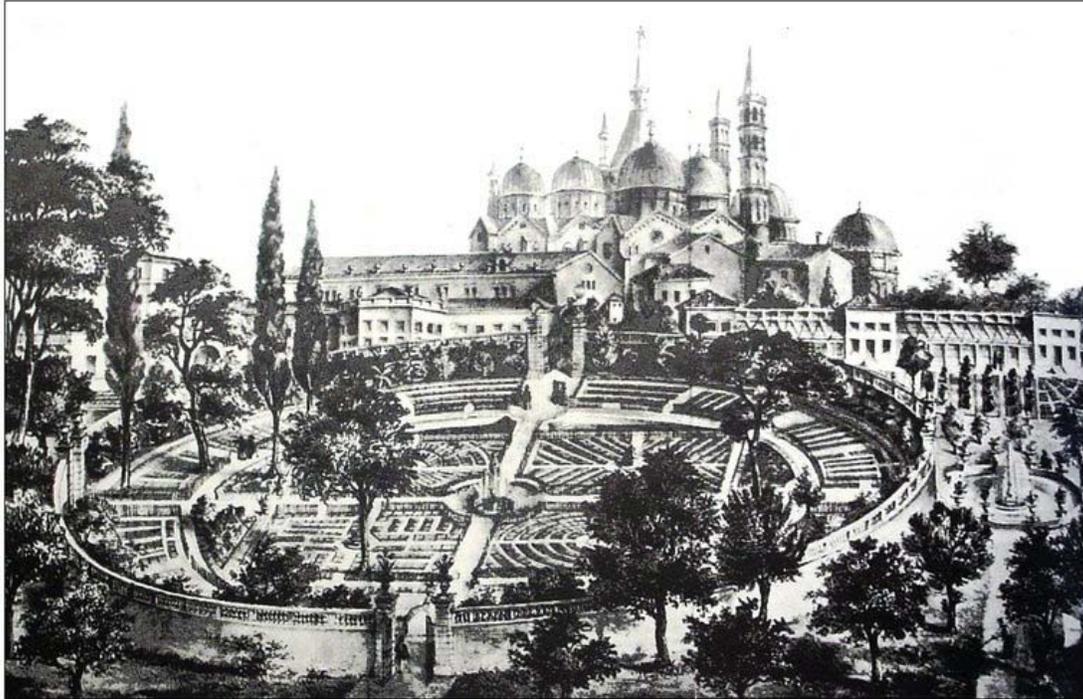
Padova: Orto dei Semplici, veduta d'insieme.

A 16th century print of the Botanical Garden of Padova (*Garden of the Simples*) — the oldest academic botanic garden that is still in its original location

The botanical gardens of the modern tradition were established in northern Italy, the first being at Pisa (1544), founded by Luca Ghini (1490–1556). Although part of a medical faculty, the first chair of *materia medica*, essentially a chair in botany, was established in Padua in 1533. Then in 1534, Ghini became Reader in *materia medica* at Bologna University. Collections of pressed and dried specimens were called a *hortus siccus* (garden of dry plants) and the first accumulation of plants in this way (including the use of a plant press) is attributed to Ghini. Buildings called herbaria housed these specimens mounted on card with descriptive labels. Stored in cupboards in systematic order they could be preserved in perpetuity and easily transferred or exchanged with other institutions, a taxonomic procedure that is still used today.

By the 18th century the physic gardens had been transformed into "order beds" that demonstrated the classification systems that were being devised by botanists of the day — but they also had to accommodate the influx of curious, beautiful and new plants pouring in from voyages of exploration that were associated with European colonial expansion.

From Herbal to Flora

Plant classification systems of the 17th and 18th centuries now related plants to one-another and not to man, marking a return to the non-anthropocentric botanical science promoted by Theophrastus over 1500 years before. This approach coupled with the new

Linnaean system of binomial nomenclature resulted in plant encyclopaedias without medicinal information called *Floras* that meticulously described and illustrated the plants growing in particular regions. The 17th century also marked the beginning of experimental botany and application of a rigorous scientific method, while improvements in the microscope launched the new discipline of plant anatomy whose foundations, laid by the careful observations of Englishman Nehemiah Grew and Italian Marcello Malpighi, would last for 150 years.

Botanical exploration

More new lands were opening up to European colonial powers, the botanical riches being returned to European botanists for description. This was a romantic era of botanical explorers, intrepid plant hunters and gardener-botanists. Significant botanical collections came from: the West Indies (Hans Sloane (1660–1753)); China (James Cunningham); the spice islands of the East Indies (Moluccas, George Rumphius (1627–1702)); China and Mozambique (João de Loureiro (1717–1791)); West Africa (Michel Adanson (1727–1806)) who devised his own classification scheme and forwarded a crude theory of the mutability of species; Canada, Hebrides, Iceland, New Zealand by Captain James Cook's chief botanist Joseph Banks (1743–1820).
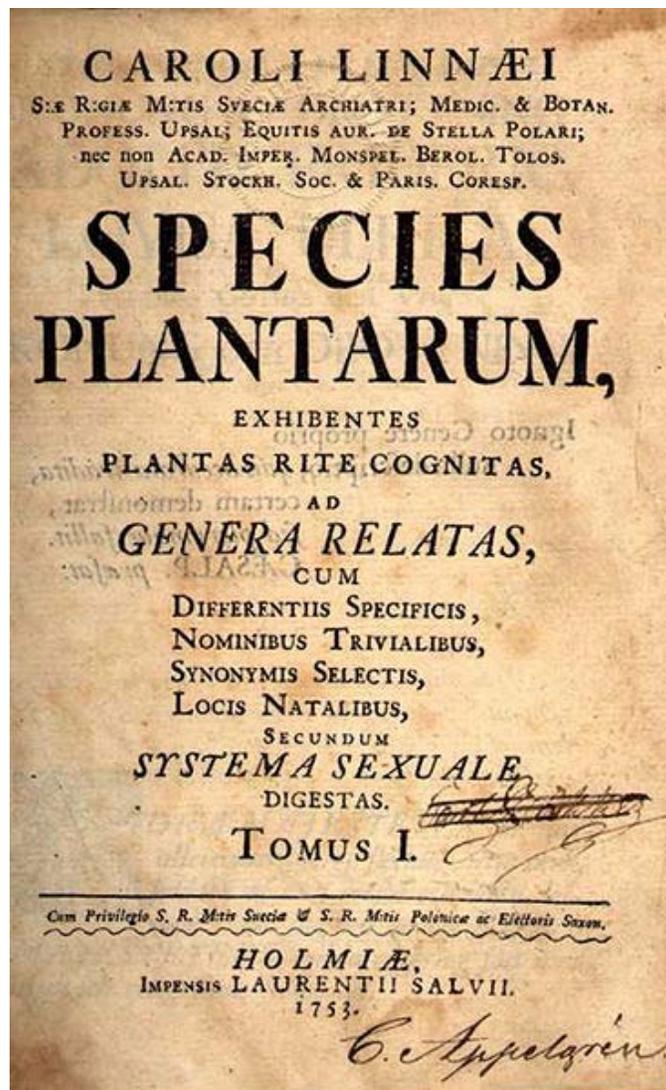
Classification and morphology
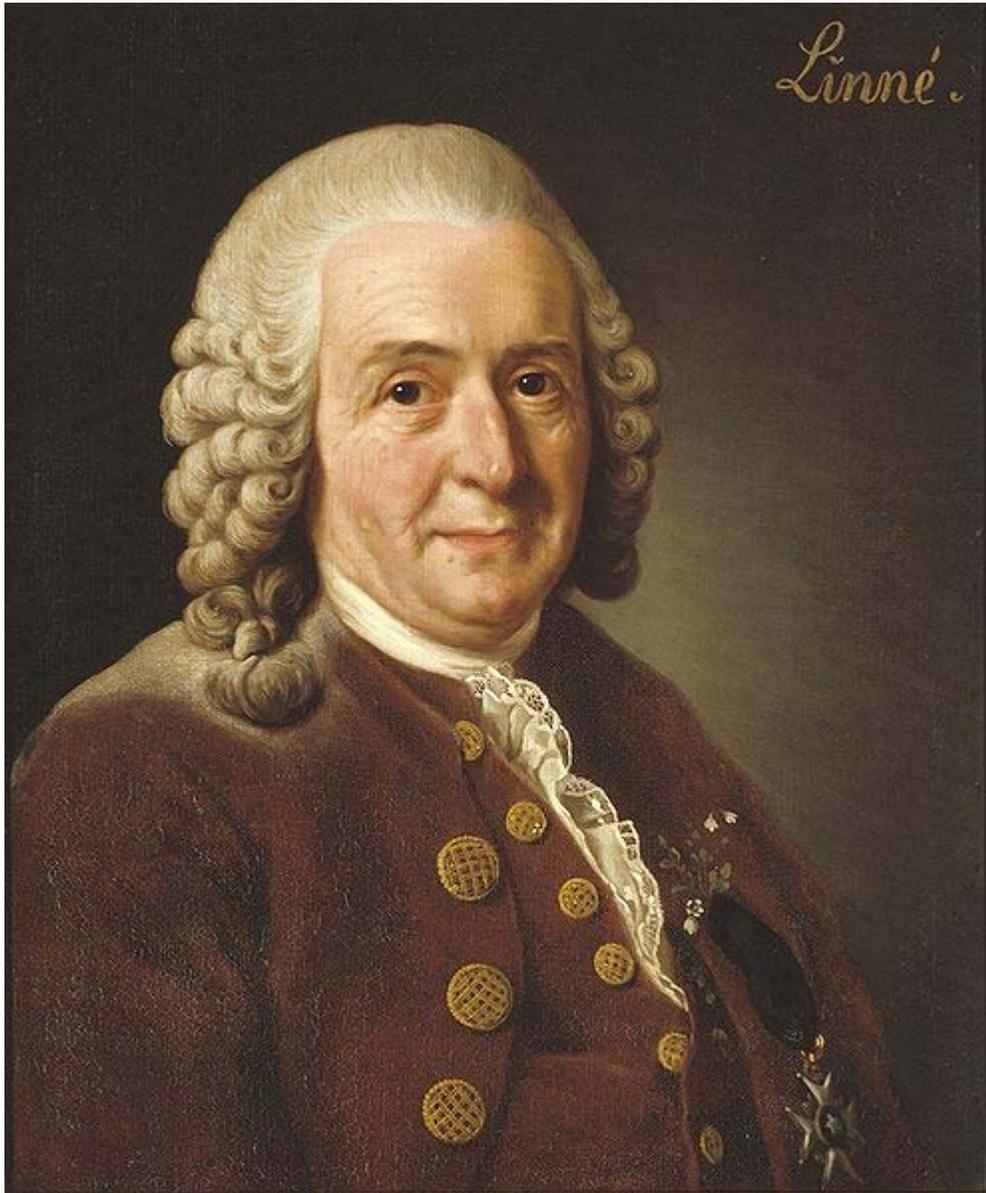
Portrait of Carl Linnaeus by Alexander Roslin, 1775

By the middle of the 18th century the botanical booty resulting from the era of exploration was accumulating in gardens and herbaria – and it needed to be systematically catalogued. This was the task of the taxonomists, the plant classifiers.

Plant classifications have changed over time from "artificial" systems based on general habit and form, to pre-evolutionary "natural" systems expressing similarity using one to many characters, leading to post-evolutionary "natural" systems that use characters to infer evolutionary relationships.

Italian physician Andrea Caesalpino (1519–1603) studied medicine and taught botany at the University of Pisa for about 40 years eventually becoming Director of the Botanic Garden of Pisa from 1554 to 1558. His sixteen-volume *De Plantis* (1583) described 1500 plants and his herbarium of 260 pages and 768 mounted specimens still remains. Caesalpino moved away from characters of form and habit to those of flower and fruit including the structure and morphology of seeds; he also applied the concept of the genus. He was the first to try and derive principles of natural classification reflecting the overall similarities between plants and he produced a classification scheme well in advance of its day. Gaspard Bauhin (1560–1624) produced two influential publications *Prodromus Theatrici Botanici* (1620) and *Pinax* (1623). These brought order to the 6000 species now described and in the latter he used binomials and synonyms that may well have influenced Linnaeus's thinking. He also insisted that taxonomy should be based on natural affinities.

Cover page of *Species Plantarum* of Carl Linnaeus published in 1753

To sharpen the precision of description and classification Joachim Jung (1587–1657) compiled a much-needed botanical terminology which has stood the test of time. English botanist John Ray (1623–1705) built on Jung's work to establish the most elaborate and insightful classification system of the day. His observations started with the local plants of Cambridge where he lived, with the *Catalogus Stirpium circa Cantabrigiam Nascentium* (1860) which later expanded to his *Synopsis Methodica Stirpium Britannicarum*, essentially the first British Flora. Although his *Historia Plantarum* (1682, 1688, 1704) provided a step towards a world Flora as he included more and more plants from his travels, first on the continent and then beyond. He extended Caesalpino's natural system with a more precise definition of the higher classification levels, deriving many modern families in the process,and asserted that all parts of plants were important in classification. He recognised that variation arises from both internal (genotypic) and external environmental (phenotypic) causes and that only the former was of taxonomic significance. He was also among the first experimental physiologists. The *Historia Plantarum* can be regarded as the first botanical synthesis and text book for modern botany. According to botanical historian Alan Morton, Ray "influenced both the theory and the practice of botany more decisively than any other single person in the latter half of the seventeenth century". Ray's family system was later extended by Pierre Magnol (1638–1715) and Joseph de Tournefort (1656–1708), a student of Magnol, achieved notoriety for his botanical expeditions, his emphasis on floral characters in classification, and for reviving the idea of the genus as the basic unit of classification.

Above all it was Swedish Carl Linnaeus (1707–1778) who eased the task of plant cataloguing. He adopted a sexual system of classification using stamens and pistils as important characters. Among his most important publications were Systema Naturae (1735), Genera Plantarum (1737), and Philosophia Botanica (1751) but it was in his Species Plantarum (1753) that he gave every species a binomial thus setting the path for the future accepted method of designating the names of all organisms. Linnaean thought and books dominated the world of taxonomy for nearly a century. His sexual system was later elaborated by Bernard de Jussieu (1699–1777) whose nephew Antoine-Laurent de Jussieu (1748–1836) extended it yet again to include about 100 orders (present-day families). Frenchman Michel Adanson (1727–1806) in his *Familles des Plantes* (1763, 1764), apart from extending the current system of family names, emphasized that a natural classification must be based on a consideration of all characters, even though these may later be given different emphasis according to their diagnostic value for the particular plant group. Adanson's method has, in essence, been followed to this day.

18th century plant taxonomy bequeathed to the 19th century a precise binomial nomenclature and botanical terminology, a system of classification based on natural affinities, and a clear idea of the ranks of family, genus and species — although the taxa to be placed within these ranks remains, as always, the subject of taxonomic research.

Anatomy

Robert Hooke's microscope which he described in the 1665 *Micrographia*: he coined the biological use of the term *cell*

In the first half of the 18th century botany was beginning to move beyond descriptive science into experimental science. Although the microscope was invented in 1590 it was only in the late 17th century that lens grinding by Antony van Leeuwenhoek provided the resolution needed to make major discoveries. Important general biological observations were made by Robert Hooke (1635–1703) but the foundations of plant anatomy were laid by Italian Marcello Malpighi (1628–1694) of the University of Bologna in his *Anatome Plantarum* (1675) and Royal Society Englishman Nehemiah Grew (1628–1711) in his *The Anatomy of Plants Begun* (1671) and *Anatomy of Plants* (1682). These botanists explored what is now called developmental anatomy and morphology, by carefully

observing, describing and drawing the developmental transition from seed to mature plant recording stem and wood formation. This work included the discovery and naming of parenchyma and stomata.

Physiology

In plant physiology research interest was focused on the movement of sap and the absorption of substances through the roots. Jan Helmont (1577–1644) by experimental observation and calculation, noted that the increase in weight of a growing plant cannot be derived purely from the soil, and concluded it must relate to water uptake. Englishman Stephen Hales (1677–1761) established by quantitative experiment that there is uptake of water by plants and a loss of water by transpiration and that this is influenced by environmental conditions: he distinguished "root pressure", "leaf suction" and "imbibition" and also noted that the major direction of sap flow in woody tissue is upward. His results were published in *Vegetable Staticks* (1727) He also noted that "air makes a very considerable part of the substance of vegetables". English chemist Joseph Priestly (1733–1804) is noted for his discovery of oxygen (as now called) and its production by plants. Later Jan Ingenhousz (1730–1799) observed that only in sunlight do the green parts of plants absorb air and release oxygen, this being more rapid in bright sunlight while, at night, the air (CO_2) is released from all parts. His results were published in *Experiments upon vegetables* (1779) and with this the foundations for 20th century studies of carbon fixation were laid. From his observations he sketched the cycle of carbon in nature even though the composition of carbon dioxide was yet to be resolved. Studies in plant nutrition had also progressed. In 1804 Nicolas-Théodore de Saussure's (1767–1845) *Recherches Chimiques sur la Végétation* was an exemplary study of scientific exactitude that demonstrated the similarity of respiration in both plants and animals, that the fixation of carbon dioxide includes water, and that just minute amounts of salts and nutrients (which he analysed in chemical detail from plant ash) have a powerful influence on plant growth.
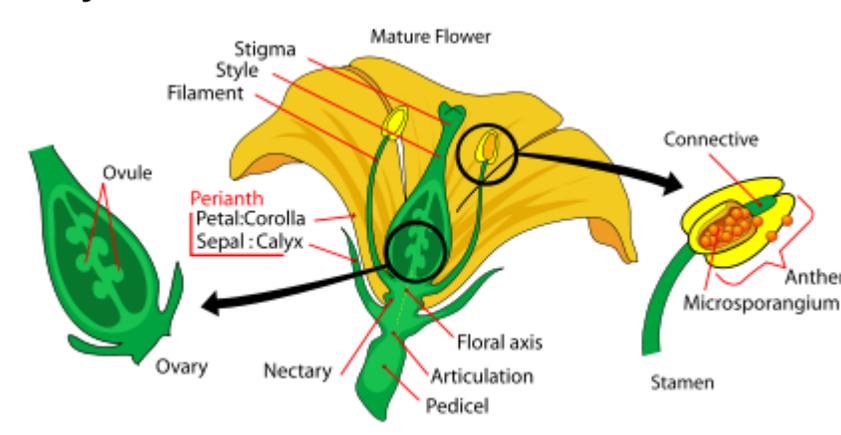
Plant sexuality

Diagram showing the sexual parts of a mature flower

It was Rudolf Camerarius (1665–1721) who was the first to establish plant sexuality conclusively by experiment. He declared in a letter to a colleague dated 1694 and titled *De Sexu Plantarum Epistola* that "no ovules of plants could ever develop into seeds from the female style and ovary without first being prepared by the pollen from the stamens, the male sexual organs of the plant".

Much was learned about plant sexuality by unravelling the reproductive mechanisms of mosses, liverworts and algae. In his *Vergleichende Untersuchungen* of 1851 Wilhelm Hofmeister (1824–1877) starting with the ferns and bryophytes demonstrated that the process of sexual reproduction in plants entails an "alternation of generations" between sporophytes and gametophytes. This initiated the new field of comparative morphology which, largely through the combined work of William Farlow (1844–1919), Nathanael Pringsheim (1823–1894), Frederick Bower, Eduard Strasburger and others, established that an "alternation of generations" occurs throughout the plant kingdom.

Some time later the German academic and natural historian Joseph Kölreuter (1733–1806) extended this work by noting the function of nectar in attracting pollinators and the role of wind and insects in pollination. He also produced deliberate hybrids, observed the microscopic structure of pollen grains and how the transfer of matter from the pollen to the ovary inducing the formation of the embryo.
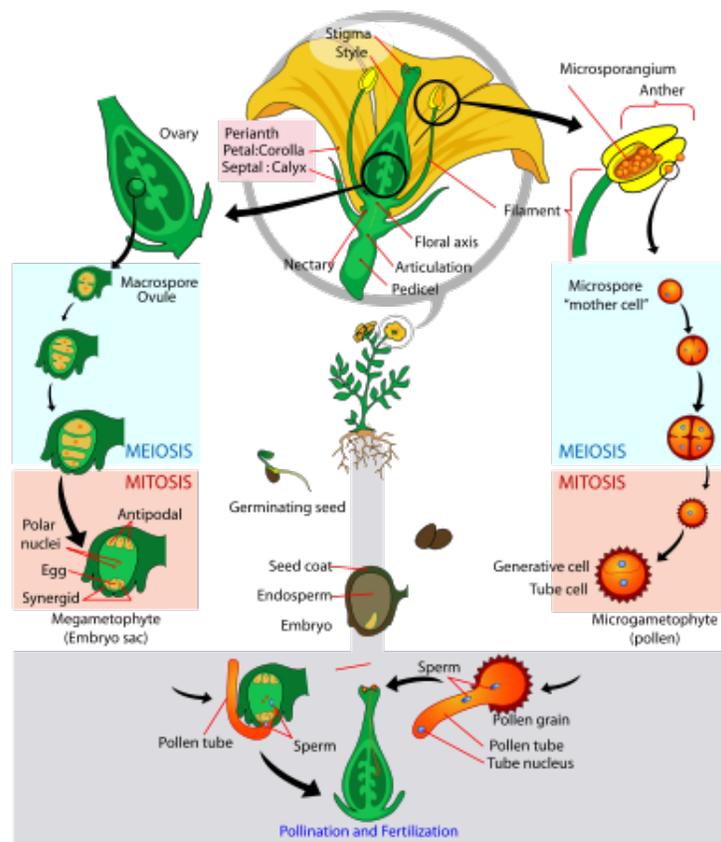

Angiosperm (flowering plant) life cycle showing alternation of generations

One hundred years after Camerarius, in 1793, Christian Sprengel (1750–1816) broadened the understanding of flowers by describing the role of nectar guides in pollination, the adaptive floral mechanisms used for pollination, and the prevalence of cross-pollination, even though male and female parts are usually together on the same flower.

Nineteenth century foundations of modern botany

In about the mid-19th century scientific communication changed. Until this time ideas were largely exchanged by reading the works of authoritative individuals who dominated in their field: these were often wealthy and influential "gentlemen scientists". Now research was reported by the publication of "papers" that emanated from research "schools" that promoted the questioning of conventional wisdom. This process had started in the late 18th century when specialist journals began to appear. Even so, botany was greatly stimulated by the appearance of the first "modern" text book, Matthias Schleiden's (1804–1881) *Grundzuge der Wissenschaftlichen*, published in English in 1849 as *Principles of Scientific Botany*. By 1850 an invigorated organic chemistry had revealed the structure of many plant constituents. Although the great era of plant classification had now passed the work of description continued. Augustin de Candolle (1778–1841) succeeded Antoine-Laurent de Jussieu in managing the botanical project *Prodromus Systematis Naturalis Regni Vegetabilis* (1824–1841) which involved 35 authors: it contained all the dicotyledons known in his day, some 58000 species in 161 families, and he doubled the number of recognized plant families, the work being completed by his son Alphonse (1806–1893) in the years from 1841 to 1873.

Plant geography and ecology
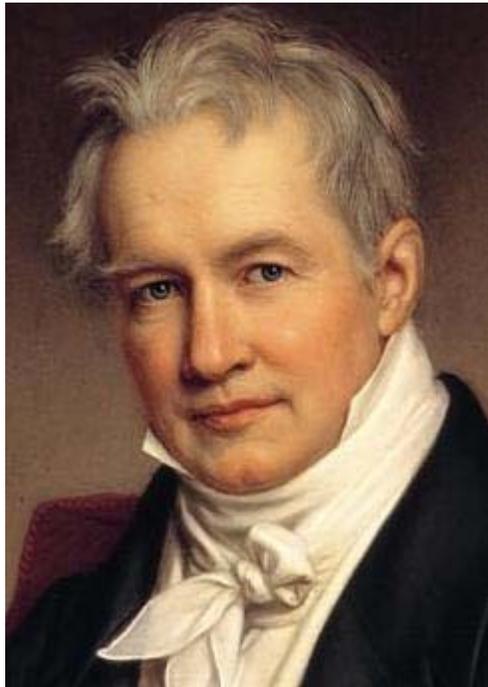
Alexander von Humboldt 1769–1859 painted by Joseph Stieler in 1843

The opening of the 19th century was marked by an increase in interest in the connection between climate and plant distribution. Carl Willdenow (1765–1812) examined the connection between seed dispersal and distribution, the nature of plant associations and the impact of geological history. He noticed the similarities between the floras of N America and N Asia, the Cape and Australia, and he explored the ideas of "centre of diversity" and "centre of origin". German Alexander von Humbolt (1769–1859) and Frenchman Aime Bonpland (1773–1858) published a massive and highly influential 30 volume work on their travels; Robert Brown (1773–1852) noted the similarities between the floras of S Africa, Australia and India, while Joakim Schouw (1789–1852) explored more deeply than anyone else the influence on plant distribution of temperature, soil factors, especially soil water, and light, work that was continued by Alphonse de Candolle (1806–1893). Joseph Hooker (1817–1911) pushed the boundaries of floristic studies with his work on Antarctica, India and the Middle East with special attention to endemism. August Grisebach (1814–1879) in *Die Vegetation der Erde* (1872) examined physiognomy in relation to climate and in America geographic studies were pioneered by Asa Gray (1810–1888).

Physiological plant geography, perhaps more familiarly termed ecology, emerged out of floristic biogeography in the late 19th century as environmental influences on plants received greater recognition. Early work in this area was synthesised by Danish professor Eugenius Warming (1841–1924) in his book *Plantesamfund* (Ecology of Plants, generally taken to mark the beginning of modern ecology) including new ideas on plant communities, their adaptations and environmental influences. This was followed by another grand synthesis, the *Pflanzengeographie auf Physiologischer Grundlage* of Andreas Schimper (1856–1901) in 1898 (published in English in 1903 as Plant-geography upon a physiological basis translated by W. R. Fischer, Oxford: Clarendon press, 839 pp.)

Anatomy
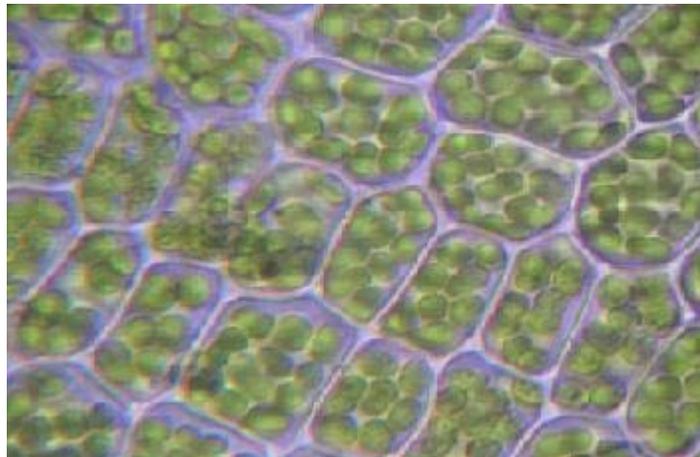
Plant cells with visible chloroplasts

During the 19th century German scientists led the way towards a unitary theory of the structure and life-cycle of plants. Following improvements in the microscope at the end

of the 18th century, Charles Mirbel (1776–1854) in 1802 published his *Traité d'Anatomie et de Physiologie Végétale* and Johann Moldenhawer (1766–1827) published *Beyträge zur Anatomie der Pflanzen* (1812) in which he describes techniques for separating cells from the middle lamella. He identified vascular and parenchymatous tissues, described vascular bundles, observed the cells in the cambium, and interpreted tree rings. He found that stomata were composed of pairs of cells, rather than a single cell with a hole.

Anatomical studies on the stele were consolidated by Carl Sanio (1832–1891) who described the secondary tissues and meristem including cambium and its action. Hugo von Mohl (1805–1872) summarized work in anatomy leading up to 1850 in *Die Vegetabilische Zelle* (1851) but this work was later eclipsed by the encyclopaedic comparative anatomy of Heinrich Anton de Bary in 1877. An overview of knowledge of the stele in root and stem was completed by Van Tieghem (1839–1914) and of the meristem by Karl Nägeli (1817–1891). Studies had also begun on the origins of the carpel and flower that continue to the present day.

Water relations

The riddle of water and nutrient transport through the plant remained. Physiologist Von Mohl explored solute transport and the theory of water uptake by the roots using the concepts of cohesion, transpirational pull, capillarity and root pressure. German dominance in the field of physiology was underlined by the publication of the definitive textbook on plant physiology synthesising the work of this period, Sach's *Vorlesungen über Pflanzenphysiologie* of 1882. There were, however, some advances elsewhere such as the early exploration of geotropism (the effect of gravity on growth) by Englishman Thomas Knight, and the discovery and naming of osmosis by Frenchman Henri Dutrochet (1776–1847).

Cytology

The cell nucleus was discovered by Robert Brown in 1831. Demonstration of the cellular composition of all organisms, with each cell possessing all the characteristics of life, is attributed to the combined efforts of botanist Matthias Schleiden and zoologist Theodor Schwann (1810–1882) in the early 19th century although Moldenhawer had already shown that plants were wholly cellular with each cell having its own wall and Julius von Sachs had shown the continuity protoplasm between cell walls.

From 1870 to 1880 it became clear that cell nuclei are never formed anew but always derived from the substance of another nucleus. In 1882 Flemming observed the longitudinal splitting of chromosomes in the dividing nucleus and concluded that each daughter nucleus received half of each of the chromosomes of the mother nucleus: then by the early 20th century it was found that the number of chromosomes in a given species is constant. With genetic continuity confirmed and the finding by Eduard Strasburger that the nuclei of reproductive cells (in pollen and embryo) have a reducing division (halving of chromosomes, now known as meiosis) the field of heredity was opened up. By 1926 Thomas Morgan was able to outline a theory of the gene and its structure and function.

The form and function of plastids received similar attention, the association with starch being noted at an early date. With observation of the cellular structure of all organisms and the process of cell division and continuity of genetic material, the analysis of the structure of protoplasm and the cell wall as well as that of plastids and vacuoles – what is now known as cytology, or cell theory became firmly established.

Later, the cytological basis of the gene-chromosome theory of heredity extended from about 1900–1944 and was initiated by the rediscovery of Gregor Mendel's (1822–1884) laws of plant heredity first published in 1866 in *Experiments on Plant Hybridization* and based on cultivated pea, *Pisum sativum*: this heralded the opening up of plant genetics. The cytological basis for gene-chromosome theory was explored through the role of polyploidy and hybridization in speciation and it was becoming better understood that interbreeding populations were the unit of adaptive change in biology.

Developmental morphology and evolution

Until the 1860s it was believed that species had remained unchanged through time: each biological form was the result of an independent act of creation and therefore absolutely distinct and immutable. But the hard reality of geological formations and strange fossils needed scientific explanation. Charles Darwin's *Origin of Species* (1859) replaced the assumption of constancy with the theory of descent with modification. Phylogeny became a new principle as "natural" classifications became classifications reflecting, not just similarities, but evolutionary relationships. Wilhelm Hofmeister established that there was a similar pattern of organization in all plants expressed through the alternation of generations and extensive homology of structures.

Polymath German intellect Johann Goethe (1749–1832) had interests and influence that extended into botany. In *Die Metamorphose der Pflanzen* (1790) he provided a theory of plant morphology (he coined the word "morphology") and he included within his concept of "metamorphosis" modification during evolution, thus linking comparative morphology with phylogeny. Though the botanical basis of his work has been challenged there is no doubt that he prompted discussion and research on the origin and function of floral parts. His theory probably stimulated the opposing views of German botanists Alexander Braun (1805–1877) and Matthias Schleiden who applied the experimental method to the principles of growth and form that were later extended by Augustin de Candolle (1778–1841).

Carbon fixation (photosynthesis)
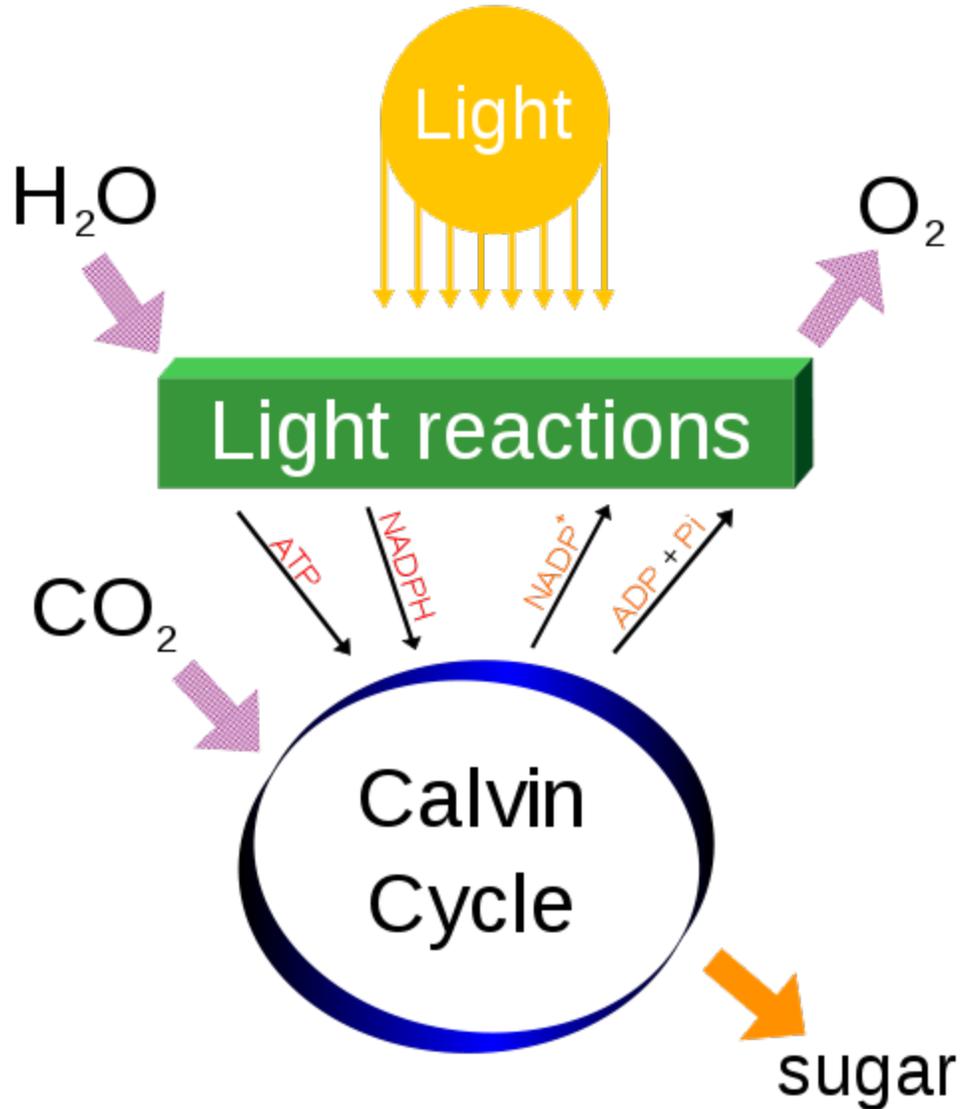
Photosynthesis splits water to liberate O_2 and fixes CO_2 into sugar

At the start of the 19th century the idea that plants could synthesise almost all their tissues from atmospheric gases had not yet emerged. The energy component of photosynthesis, the capture and storage of the Sun's radiant energy in carbon bonds (a process on which all life depends) was first elucidated in 1847 by Mayer, but the details of how this was done would take many more years. Chlorophyll was named in 1818 and its chemistry gradually determined, to be finally resolved in the early 20th century. The mechanism of photosynthesis remained a mystery until the mid-19th century when Sachs, in 1862, noted that starch was formed in green cells only in the presence of light and in 1882 he confirmed carbohydrates as the starting point for all other organic compounds in plants. The connection between the pigment chlorophyll and starch production was

finally made in 1864 but tracing the precise biochemical pathway of starch formation did not begin until about 1915.

Nitrogen fixation

Significant discoveries relating to nitrogen assimilation and metabolism, including ammonification, nitrification and nitrogen fixation (the uptake of atmospheric nitrogen by symbiotic soil microorganisms) had to wait for advances in chemistry and bacteriology in the late 19th century and this was followed in the early 20th century by the elucidation of protein and amino-acid synthesis and their role in plant metabolism. With this knowledge it was then possible to outline the global nitrogen cycle.

Twentieth century

Thin layer chromatography is used to separate components of chlorophyll

20th century science grew out of the solid foundations laid by the breadth of vision and detailed experimental observations of the 19th century. A vastly increased research force was now rapidly extending the horizons of botanical knowledge at all levels of plant organization from molecules to global plant ecology. There was now an awareness of the unity of biological structure and function at the cellular and biochemical levels of organisation. Botanical advance was closely associated with advances in physics and chemistry with the greatest advances in the 20th century mainly relating to the penetration of molecular organization. However, at the level of plant communities it would take until mid century to consolidate work on ecology and population genetics. By 1910 experiments using labelled isotopes were being used to elucidate plant biochemical pathways, to open the line of research leading to gene technology. On a more practical level research funding was now becoming available from agriculture and industry.

Molecules

In 1903 Chlorophylls a and b were separated by thin layer chromatography then, through the 1920s and 1930s, biochemists, notably Hans Krebs (1900–1981) and Carl (1896–1984) and Gerty Cori (1896–1957) began tracing out the central metabolic pathways of life. Between the 1930s and 1950s it was determined that ATP, located in mitochondria, was the source of cellular chemical energy and the constituent reactions of photosynthesis were progressively revealed. Then, in 1944 DNA was extracted for the first time. Along with these revelations there was the discovery of plant hormones or "growth substances", notably auxins, (1934) gibberellins (1934) and cytokinins (1964) and the effects of photoperiodism, the control of plant processes, especially flowering, by the relative lengths of day and night.

Following the establishment of Mendel's laws, the gene-chromosome theory of heredity was confirmed by the work of August Weismann who identified chromosomes as the hereditary material. Also, in observing the halving of the chromosome number in germ cells he anticipated work to follow on the details of meiosis, the complex process of redistribution of hereditary material that occurs in the germ cells. In the 1920s and 1930s population genetics combined the theory of evolution with Mendelian genetics to produce the modern synthesis. By the mid-1960s the molecular basis of metabolism and reproduction was firmly established through the new discipline of molecular biology. Genetic engineering, the insertion of genes into a host cell for cloning, began in the 1970s with the invention of recombinant DNA techniques and its commercial applications applied to agricultural crops followed in the 1990s. There was now the potential to identify organisms by molecular "fingerprinting" and to estimate the times in the past when critical evolutionary changes had occurred through the use of "molecular clocks".

## Computers, electron microscopes and evolution

Electron microscope constructed by Ernst Ruska in 1933

Increased experimental precision combined with vastly improved scientific instrumentation was opening up exciting new fields. In 1936 Alexander Oparin (1894–1980) demonstrated a possible mechanism for the synthesis of organic matter from inorganic molecules. In the 1960s it was determined that the Earth's earliest life-forms treated as plants, the cyanobacteria known as stromatolites, dated back some 3.5 billion years.

Mid-century transmission and scanning electron microscopy presented another level of resolution to the structure of matter, taking anatomy into the new world of "ultrastructure".

New and revised "phylogenetic" classification systems of the plant kingdom were produced, perhaps the most notable being that of August Eichler (1839–1887), and the massive 23 volume *Die natürlichen Pflanzenfamilien* of Adolf Engler (1844–1930) & Karl Prantl (1849–1893) published over the period 1887 and 1915. Taxonomy based on gross morphology was now being supplemented by using characters revealed by pollen morphology, embryology, anatomy, cytology, serology, macromolecules and more. The introduction of computers facilitated the rapid analysis of large data sets used for numerical taxonomy (also called taximetrics or phenetics). The emphasis on truly natural phylogenies spawned the disciplines of cladistics and phylogenetic systematics. The grand taxonomic synthesis *An Integrated System of Classification of Flowering Plants* (1981) of American Arthur Cronquist (1919–1992) was superseded when, in 1998, the Angiosperm Phylogeny Group published a phylogeny of flowering plants based on the analysis of DNA sequences using the techniques of the new molecular systematics which was resolving questions concerning the earliest evolutionary branches of the angiosperms (flowering plants). The exact relationship of fungi to plants had for some time been uncertain. Several lines of evidence pointed to fungi being different from plants, animals and bacteria – indeed, more closely related to animals than plants. In the 1980s-90s molecular analysis revealed an evolutionary divergence of fungi from other organisms about 1 billion years ago – sufficient reason to erect a unique kingdom separate from plants.

Biogeography and ecology
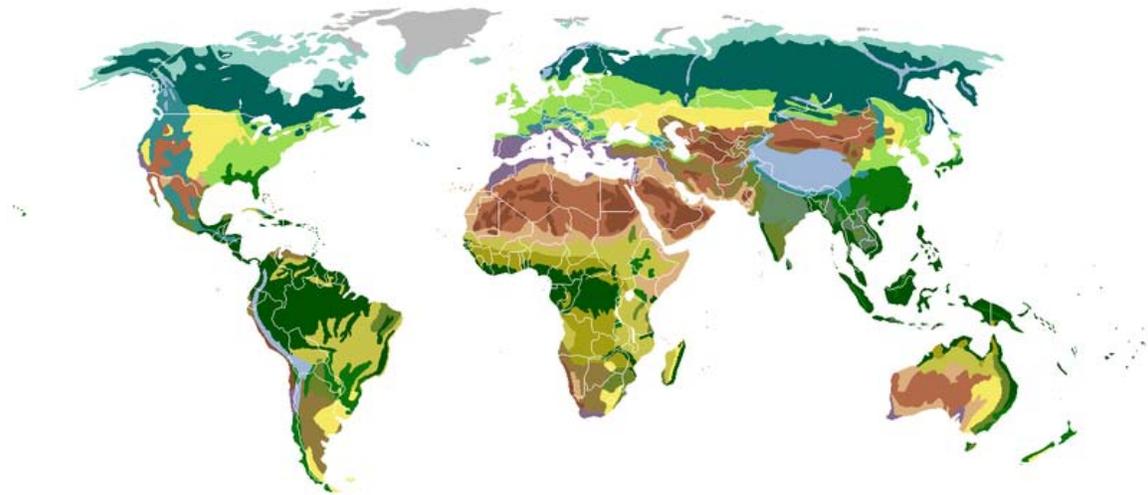
Map of terrestrial biomes classified by vegetation type

The publication of Alfred Wegener's (1880–1930) theory of continental drift 1912 gave additional impetus to comparative physiology and the study of biogeography while ecology in the 1930s contributed the important ideas of plant community, succession, community change, and energy flows. From 1940 to 1950 ecology matured to become an independent discipline as Eugene Odum (1913–2002) formulated many of the concepts

of ecosystem ecology, emphasising relationships between groups of organisms (especially material and energy relationships) as key factors in the field. Building on the extensive earlier work of Alphonse de Candolle, Nikolai Vavilov (1887–1943) from 1914 to 1940 produced accounts of the geography, centres of origin, and evolutionary history of economic plants.

Twenty-first century

In reviewing the sweep of botanical history it is evident that, through the power of the scientific method, most of the basic questions concerning the structure and function of plants have, in principle, been resolved. Now the distinction between pure and applied botany becomes blurred as our historically accumulated botanical wisdom at all levels of plant organisation is needed (but especially at the molecular and global levels) to improve human custodianship of planet earth. The most urgent unanswered botanical questions now relate to the role of plants as primary producers in the global cycling of life's basic ingredients: energy, carbon, hydrogen, oxygen, and nitrogen, and ways that our plant stewardship can help address the global environmental issues of resource management, conservation, human food security, biologically invasive organisms, carbon sequestration, climate change, and sustainability.

Chapter 3

Paleobotany

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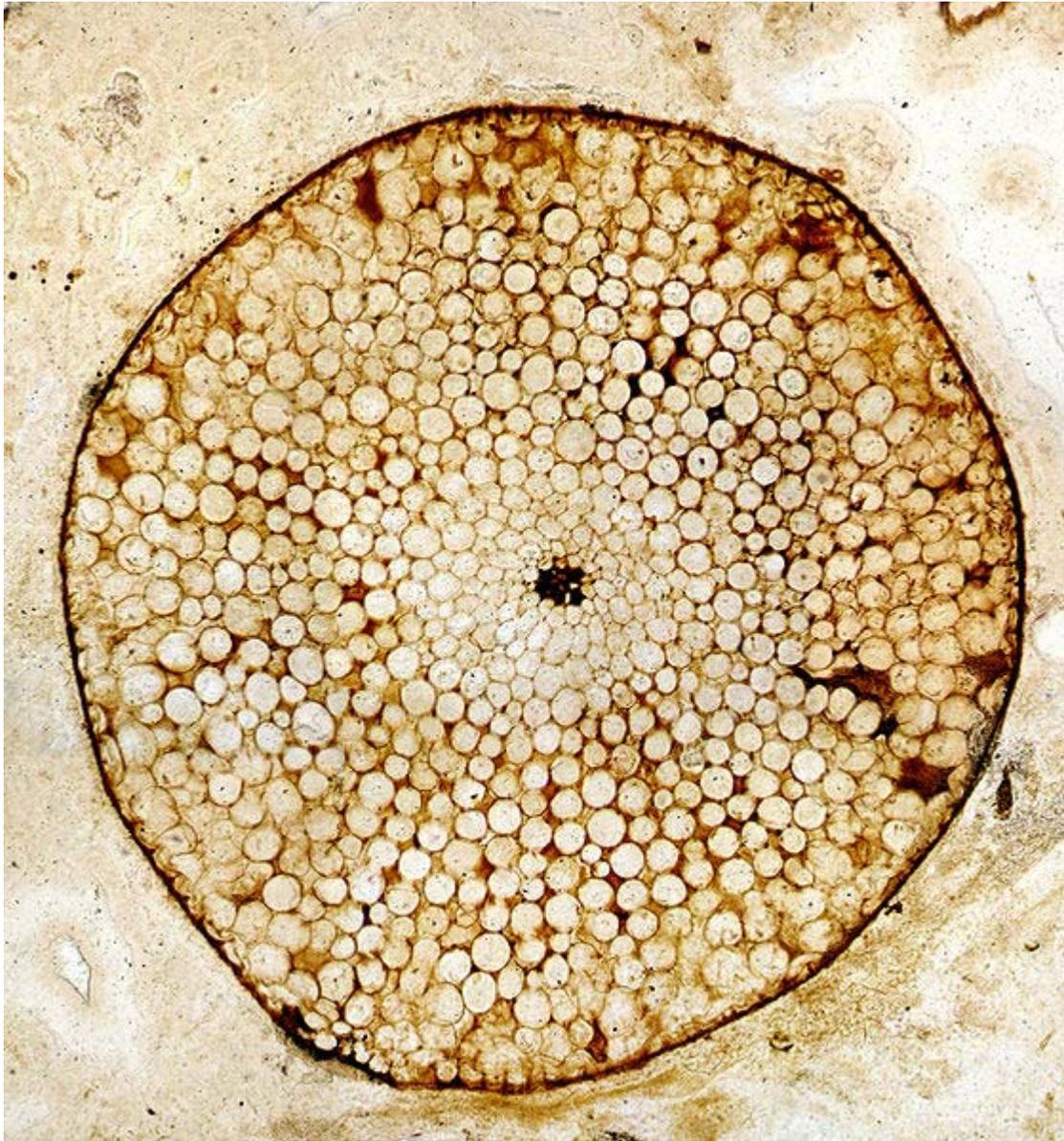
Rhynia, Lower Devonian Rhynie Chert, Scotland, UK. Transverse section through a stem preserved as a silica petrifaction. Photo by Plantsurfer

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 charcoalified 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 bouyancy 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 *Arthroxylon* depending on whether it is preserved as a cast or a petrifaction. 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
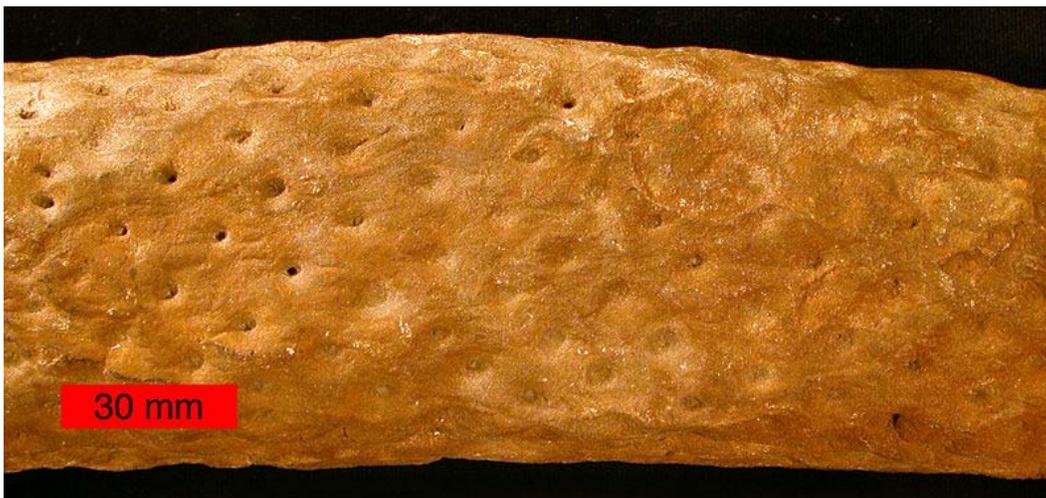
Stigmaria, a common fossil tree root. Upper Carboniferous of northeastern Ohio.
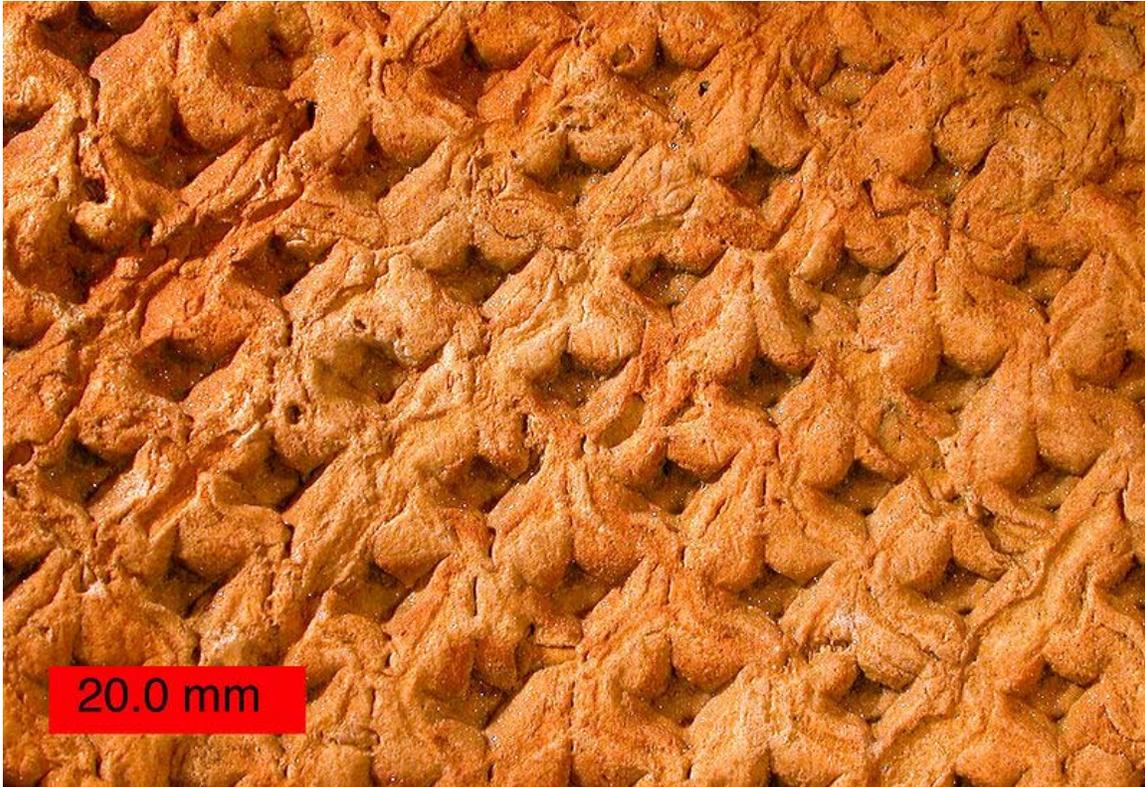
External mold of *Lepidodendron* from the Upper Carboniferous of Ohio.

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 4

Flora

Plant species diversity
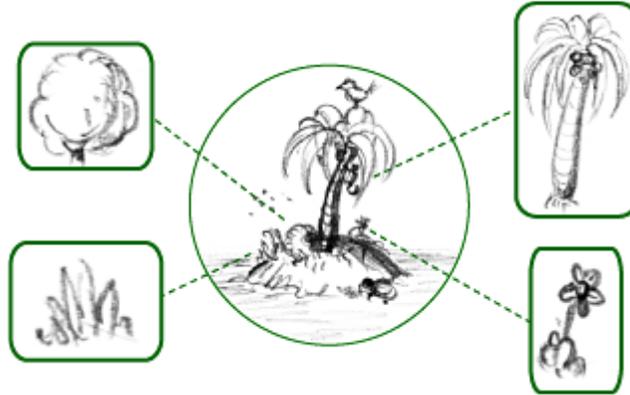
Simplified schematic of an island's flora - all its plant species, highlighted in boxes.

In botany, *flora* (plural: floras or florae) has two meanings:

- A **flora** (with a lower case 'f') refers to the plant life occurring in a particular region, generally the naturally occurring or indigenous plant life. Botanists and paleobotanists use the term to refer to a typical collection of animals found in a specific time or place, e.g. the "Sonoran Desert flora" or the "Caenozoic flora". It also can refer to a given subset of the flora of a given region, as in: "... Southern Africa has a rich Ericaceous flora ...".

- A **Flora** (with a capital 'F') refers to a book or other work describing a flora and including aids for the identification of the plants it contains such as botanical keys and line drawings that illustrate the characters that distinguish the different plants. Floristics is the study of floras, including the preparation of Floras.

The term "flora" comes from Latin language Flora, the goddess of flowers in Roman mythology. The corresponding term for animal life is fauna. *Flora*, *fauna* and other forms of life such as fungi are collectively referred to as biota. Some classic and modern floras are listed below.

Flora classifications

Plants are grouped into floras based on region, period, special environment, or climate. Regions can be geographically distinct habitats like mountain vs. flatland. Floras can mean plant life of an historic era as in *fossil flora*. Lastly, floras may be subdivided by special environments:

- *Native flora*. The native and indigenous flora of an area.
- *Agricultural and garden flora*. The plants that are deliberately grown by humans.
- *Weed flora*. Traditionally this classification was applied to plants regarded as undesirable, and studied in efforts to control or eradicate them. Today the designation is less often used as a classification of plant life, since it includes three different types of plants: weedy species, invasive species (that may or may

not be weedy), and native and introduced non-weedy species that are agriculturally undesirable. Many native plants previously considered weeds have been shown to be beneficial or even necessary to various ecosystems.

Bacterial organisms are sometimes included in a flora, and sometimes the terms *bacterial flora* and *plant flora* are used separately.

Flora treatises
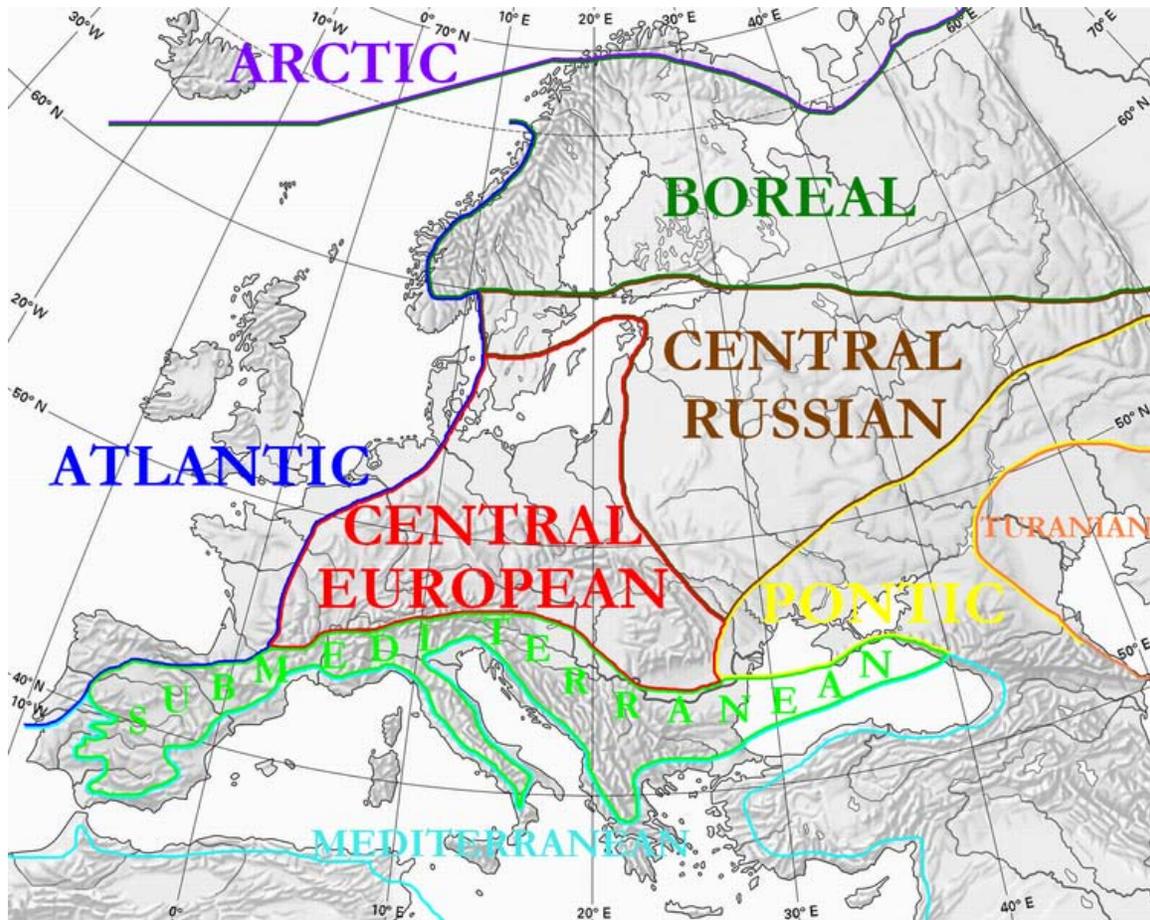
Floristic regions in Europe according to Wolfgang Frey and Rainer Lösch

Plants

A fossil leaf from the extinct Comptonia columbiana, 48.5 million years old. Klondike Mountain Formation, Republic, Ferry County, Washington, USA. Stonerose Interpretive Center.

Traditionally floras are books, but some are now published on CD-ROM or websites. The area that a flora covers can be either geographically or politically defined. Floras usually require some specialist botanical knowledge to use with any effectiveness.

It is said that the *Flora Sinensis* by the Polish Jesuit Michał Boym was the first book that used the name "Flora" in this meaning, a book covering the plant world of a region. However, despite its title it covered not only plants, but also some animals of the region.

A flora often contains diagnostic keys. Often these are *dichotomous* keys, which require the user to repeatedly examine a plant, and decide which one of two alternatives given in the flora best applies to the plant.

A compendium of world floras has been compiled by David Frodin.

Classic floras

Europe

- *Flora Londinensis*, William Curtis. England 1777- 1798
- *Flora Graeca*, John Sibthorp. (England) 1806 - 1840
- *Flora Danica*, Simon Paulli. Denmark, 1847.
- *Flora Jenensis*, Heinrich Bernhard Rupp Germany, 1718.
- *Flora Suecica*, Carolus Linnaeus. 1745.

India

- *Hortus indicus malabaricus*, Hendrik van Rheede 1683–1703

Indonesia

- *Flora Javae*, Carl Ludwig Blume and Joanne Baptista Fischer. 1828.

China

- *Flora Sinensis*, Michał Boym, 1656

America

- *Flora Brasiliensis*, Martius, Endlicher, et al. 1840 to 1906

Modern floras

America

Caribbean

- Britton, N. L., and Percy Wilson. *Scientific Survey of Porto Rico and the Virgin Islands — Volume V, Part 1: Botany of Porto Rico and the Virgin Islands: Pandanales to Thymeleales*. New York: New York Academy of Sciences, 1924.

Central & South America

- *Flora of São Paulo* in Brazil
- *Flora de Chile*
- *Manual de Plantas de Costa Rica*
- *Flora of Ecuador*

- *Flora of Guatemala*
- *Flora de Nicaragua*
- *Flora of Peru*
- *Flora of the Guianas*
- *Flora of Panama*
- *Flora del Paraguay*
- *Flora of Suriname*
- *Flora Mesoamericana* (1994-ongoing) Introduction
- *Flora of the Venezuelan Guayana*
- *Flora Neotropica* (1968-ongoing) Organising committee website.

North America

- *Flora of North America*
- Kearney, Thomas H. *Arizona Flora*. University of California Press, 1940.
- Hickman, James C., editor. *The Jepson Manual: Higher Plants of California*. University of California Press, 1993.
- Hultén, Eric. *Flora of Alaska and Neighboring Territories: A Manual of the Vascular Plants*. Stanford University Press, 1968.
- Radford, Albert E. *Manual of the Vascular Flora of the Carolinas*. University of North Carolina Press, 1968.
- Hitchcock, C. Leo, and Arthur Cronquist. *Flora of the Pacific Northwest*. University of Washington Press, 1973.
- Chadde, Steve W., and Steve Chadde. *A Great Lakes Wetland Flora*. 2nd ed. Pocketflora Press, 2002. ISBN 0-9651385-5-0
- P. D. Strausbaugh and Earl L. Core. *Flora of West Virginia*. 2nd ed. Seneca Books Inc., 1964. ISBN 0-89092-010-9
- Ann Fouler Rhoads and Timothy A. Block. *The Plants of Pennsylvania*. University of Pennsylvania Press, 2000. ISBN 0-8122-3535-5
- Nathaniel Lord Britton and Hon. Addison Brown. *An Illustrated Flora of the Northern United States and Canada*. In three volumes. Dover Publications, 1913, 1970. ISBN 0-486-22642-5

Asia

Taxus chinensis, Chinese Yew tree. Morton Arboretum

East Asia

- *Flora of the People's Republic of China*
- *Flora of China in eFloras*
- *Flora of Japan*
- *Flora of Taiwan*

Southeast Asia

- *Flora of Thailand*

- *Florae Siamensis Enumeratio*
- *Flora Malesiana* (1951-ongoing)
- *Flora of the Malay Peninsula*
- *Flore du Cambodge, du Laos et du Viêt-Nam*

Indian region and Sri Lanka

- *Flora of Bhutan*
- Flora of the Presidency of Madras by J.S. Gamble (1915–36)
- *Flora of Nepal*
- Bengal Plants by D. Prain (1903)
- Flora of the upper Gangetic plains by J. F. Duthie (1903–29)
- Botany of Bihar and Orissa by H.H. Haines (1921–25)
- Flora of British India (1872–1897) by Sir J.D. Hooker

Middle East and western Asia

- Flora of Turkey
- Flora Iranica
- Flora Palaestina:
    - M. Zohary (1966). Flora Palaestina part 1.
    - M. Zohary (1972). Flora Palaestina part 2.
    - N. Feinbrun (1978). Flora Palaestina part 3.
    - N. Feinbrun (1986). Flora Palaestina part 4.
    - A. Danin, (2004). Distribution Atlas of Plants in the Flora Palaestina Area (Flora Palaestina part 5).

Australia

A closing venus fly trap.

- *Flora of Australia*
- *Flora of New Zealand* series:
    - Allan, H.H. 1961, reprinted 1982. *Flora of New Zealand. Volume I: Indigenous Tracheophyta - Psilopsida, Lycopsida, Filicopsida, Gymnospermae, Dicotyledons.* ISBN 0-477-01056-3.
    - Moore, L.B.; Edgar, E. 1970, reprinted 1976. *Flora of New Zealand. Volume II: Indigenous Tracheophyta - Monocotyledons except Graminae.* ISBN 0-477-01889-0.
    - Healy, A.J.; Edgar, E. 1980. Flora of New Zealand Volume III. Adventive Cyperaceous, Petalous & Spathaceous Monocotyledons. *ISBN 0-477-01041-5.*
    - Webb, C.J.; Sykes, W.R.;Garnock-Jones, P.J. 1988. *Flora of New Zealand Volume IV: Naturalised Pteridophytes, Gymnosperms, Dicotyledons.* ISBN 0-477-02529-3.
    - Edgar, E.; Connor, H.E. 2000. *Flora of New Zealand Volume V: Grasses.* ISBN 0-478-09331-4.
    - Volumes I-V: First electronic edition, Landcare Research, June 2004. Transcribed by A.D. Wilton and I.M.L. Andres.
- Galloway, D.J. 1985. *Flora of New Zealand: Lichens.* ISBN 0-477-01266-3.
- Croasdale, H.; Flint, E.A. 1986. *Flora of New Zealand: Desmids. Volume I.* ISBN 0-477-02530-7.

- Croasdale, H.; Flint, E.A. 1988. *Flora of New Zealand: Desmids. Volume II.* ISBN 0-477-01353-8.
- Croasdale, H.; Flint, E.A.;Racine, M.M. 1994. *Flora of New Zealand: Desmids. Volume III.* ISBN 0-477-01642-1.
- Sykes, W.R.; West, C.J.; Beever, J.E.; Fife, A.J. 2000. *Kermadec Islands Flora - Special Edition.* ISBN 0-478-09339-X.

Pacific Islands

- *Flora Vitiensis Nova, a New Flora of Fiji*
- *Manual of the Flowering Plants of Hawai'i*, Warren L. Wagner and Derral R. Herbst (1991) + suppl.
- *Flore de la Nouvelle-Calédonie*
- *Flore de la Polynésie Française* (J. Florence, vol. 1 & 2, 1997 & 2004)

Europe
British Isles

- Morton, O.1994. *Marine Algae of Northern Ireland.* Ulster Museum, Belfast. ISBN 0-900761-28-8
- Stace, Clive Anthony, and Hilli Thompson (illustrator). *A New Flora of the British Isles.* 2nd ed. Cambridge University Press, 1997. ISBN 0-521-58935-5.
- Beesley, S. and J. Wilde. *Urban Flora of Belfast.* Belfast: Institute of Irish Studies, Queen's University of Belfast, 1997.
- Killick, John, Roy Perry and Stan Woodell. *Flora of Oxfordshire.* Pisces Publications, 1998. ISBN 1-874357-07-2.
- Bowen, Humphry. *The Flora of Dorset.* Pisces Publications, 2000. ISBN 1-874357-16-1.
- Flora Celtica Plants and people in Celtic Europe
- Flora Europaea at the site of The Royal Botanical Gardens of Edinburgh Flora Europaea
- Flora of Europe
- Flora iberica
- Flora of Acores
- Flora Danica
- Flora of Romania

Africa and Madagascar

- Flore du Gabon
- Flore du Cameroun
- Flora of Tropical Africa
- Flora of Tropical East Africa
- Flora Capensis
- *Flora Zambesiaca*
- Flora of South Africa

- Flore du Rwanda
- Flore de Madagascar et des Comores

Chapter 5

Adventitiousness and Ampelography

Adventitiousness

Adventitious, in botany, refers to structures that develop in an unusual place, and in medicine, it refers to conditions acquired after birth. Here we discuss adventitious roots, buds and shoots, which are very common in vascular plants.

Adventitious buds and shoots

Adventitious buds develop from places other than a shoot apical meristem, which occurs at the tip of a stem. They may develop on stems, roots or leaves. Shoot apical meristems produce one or more axillary or lateral buds at each node. When stems produce considerable secondary growth, the axillary buds may be destroyed. Adventitious buds may then develop on stems with secondary growth.

Adventitious buds are often formed after the stem is wounded or pruned. The adventitious buds help to replace lost branches. Adventitious buds and shoots also may develop on mature tree trunks when a shaded trunk is exposed to bright sunlight because surrounding trees are cut down. Redwood (*Sequoia sempervirens*) trees often develop many adventitious buds on their lower trunks. If the main trunk dies, a new one often sprouts from one of the adventitious buds. Small pieces of redwood trunk are sold as souvenirs termed redwood burls. They are placed in a pan of water, and the adventitious buds sprout to form shoots.

Some plants normally develop adventitious buds on their roots, which can extend quite a distance from the plant. Shoots that develop from adventitious buds on roots are termed suckers. They are a type of natural vegetative reproduction in many species, e.g. many grasses, quaking aspen and Canada thistle. The Pando quaking aspen grew from one trunk to 47,000 trunks via adventitious bud formation on a single root system.

Some leaves develop adventitious buds, which then form adventitious roots, as part of vegetative reproduction; e.g. piggyback plant (*Tolmiea menziesii*) and mother-of-thousands (*Kalanchoe daigremontiana*). The adventitious plantlets then drop off the parent plant and develop as separate clones of the parent.

Coppicing is the practice of cutting tree stems to the ground to promote rapid growth of adventitious shoots. It is traditionally used to produce poles, fence material or firewood. It is also practiced for biomass crops grown for fuel, such as poplar or willow.

Adventitious Roots

Adventitious rooting may be a stress-avoidance acclimation for some species, driven by such inputs as hypoxia/anoxia (Drew et al. 1979 Ethylene-promoted adventitious rooting and development of cortical air spaces (aerenchyma) in roots may be adaptive responses to flooding in Zea mays L. Planta 147 1; 83-88), (Visser et al. 1996) or nutrient deficiency. Another ecologically important function of adventitious rooting is the vegetative propagation of tree species such as *Salix* and *Sequoia* in riparian settings (Naiman and & Decamps 1997 The Ecology of Interfaces: Riparian Zones. Annual Reviews in Ecological Systems)

The ability of plant stems to form adventitious roots is utilised in commercial propagation by cuttings. Understanding of the physiological mechanisms behind adventitious rooting has allowed some progress to be made in improving the rooting of cuttings by the application of synthetic auxins as rooting powders and by the use of selective basal wounding (Klerk et al. 1999 Review the formation of adventitious roots: new concepts, new possibilities. In Vitro Cell & Developmental Biology - Plant 35 3;189-199). Further progress will be made in future years by applying research into other regulatory mechanisms to commercial propagation and by the comparative analysis of molecular and ecophysiological control of adventitious rooting in 'hard to root' Vs. 'easy to root' species.

Location of origin

Adventitious roots and buds usually develop near the existing vascular tissues so they can connect to the xylem and phloem. However, the exact location varies greatly. In young stems, adventitious roots often form from parenchyma between the vascular bundles. In stems with secondary growth, adventitious roots often originate in phloem parenchyma near the vascular cambium. In stem cuttings, adventitious roots sometimes also originate in the callus cells that form at the cut surface. Leaf cuttings of the *Crassula* form adventitious roots in the epidermis.

Modification of adventitious root

Tuberous roots are without any definite shape; example: sweet Potato.

Fasciculated root (tuberous root) occur in clusters at the base of the stem; example: asparagus, dahlia.

**Nodulose roots** become swollen near the tips; example: turmeric.

Stilt roots arise from the first few nodes of the stem. These penetrate obliquely down in to the soil and give support to the plant; example: maize, sugarcane.

Prop roots give mechanical support to the aerial branches. The lateral branches grow vertically downward into the soil and acts as pillars; example: banyan.

Vegetative propagation

Adventitious roots and buds are very important when people propagate plants via cuttings, layering, tissue culture. Plant hormones, termed auxins, are often applied to stem, shoot or leaf cuttings to promote adventitious root formation, e.g. African violet and sedum leaves and shoots of poinsettia and coleus. Propagation via root cuttings requires adventitious bud formation, e.g. in horseradish and apple. In layering, adventitious roots are formed on aerial stems before the stem section is removed to make a new plant. Large houseplants are often propagated by air layering. Adventitious roots and buds must develop in tissue culture propagation of plants.

Ampelography
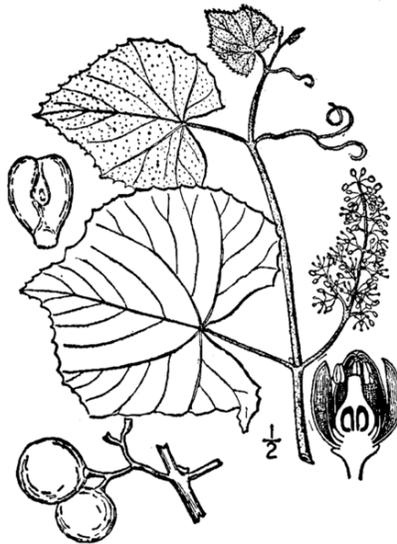
Vitis labrusca

Ampelography is the field of botany concerned with the identification and classification of grapevines, *Vitis spp.* Traditionally this has been done by comparing the shape and colour of the vine leaves and grape berries; more recently the study of vines has been revolutionised by DNA fingerprinting.

Early history

The grape vine is an extremely variable species, and some varieties, such as Pinot, mutate particularly frequently. At the same time, the wine and table grape industries have been important since ancient times, so large sums of money can depend on the correct identification of different varieties and clones of grapevines.

The science of ampelography began seriously in the 19th century, when it suddenly became important to understand more about the different species of vine, as they had very different resistance to disease and pests such as phylloxera.

Many vine identification books were published at this time, of which one of the greatest is Victor Rendu's *Ampélographie française* of 1857, featuring beautiful hand-coloured lithographs by Eugene Grobon.

Pierre Galet

Up until the Second World War, ampelography had been an art. Then Pierre Galet of the Ecole Nationale Supérieure Agronomique de Montpellier made a systematic assembly of criteria for the identification of vines. The Galet system was based on the shape and contours of the leaves, the characteristics of growing shoots, shoot tips, petioles, the sex of the flowers, the shape of the grape clusters, and the colour, size and pips of the grapes themselves. The grapes are less affected by environmental factors than the leaves and the shoots, but are obviously not around for as long. He even included grape flavour as a criterion, but this is rather subjective.

Galet then published the definitive book, *Ampélographie Pratique*, in 1952, featuring 9600 types of vine. *Ampélographie Pratique* was translated into English by Lucie Morton and published in 1979; it was updated in 2000.

DNA

Carole Meredith at the University of California, Davis pioneered the use of genetic fingerprinting for vine identification. Famous successes with the technique include proving the identity of Zinfandel, Primitivo, and Crljenak Kaštelanski, and identifying the parents of Sangiovese as Ciliegiolo and Calabrese Montenuovo. Such exercises are giving valuable insight into historical patterns of trade and migration.

DNA fingerprinting uses segments of DNA that do not affect the look or taste of the grapes. More recent work has identified the genes responsible for the differences between grape varieties, such as the VvMYBA1 and VvMYBA2 genes that control grape colour, or the VvGAI1 gene that is mutated in some cells of Pinot meunier compared to Pinot noir.

Chapter 6

Chimera (Plant) and Evergreen

Chimera (plant)

Ficus benjamina L. Variegated chlorophyll-deficient chimera.

Chimeras (or **chimaeras**) in botany are usually single organisms composed of two genetically different types of tissue. They occur in plants, on the same general basis as with animal chimeras. However, unlike animal chimeras, both types of tissues may have originated from the same zygote, and the difference is often due to mutation during ordinary cell division.

Types of plant chimera

A sectorial chimera of *Aesculus hippocastanum*

Variegated plants

The best-known plant chimeras are those cultivated for their variegation. Generally the genetic difference is due to mutation in meristematic tissue of a normal plant. For most variegation, the mutation involved is the loss of the chloroplasts in the mutated tissue, so that part of the plant tissue has no green pigment and no photosynthetic ability. This mutated tissue is unable to survive on its own but is kept alive by its partnership with normal photosynthetic tissue.

Thornless plants

Other types of chimera are valued by gardeners and other horticulturists because the skin tissue lacks the spine-producing characteristic of the underlying tissue.

Graft-chimeras

A distinct type of plant chimera is the graft-chimera (or, incorrectly, graft-hybrid), involving tissues from two genetically different parents, different cultivars or different species (which may belong to different genera). The tissues may be partially fused together following grafting to form a single growing organism that preserves both types of tissue in a single shoot. The first such known chimera was probably the Bizzaria which

is a confusion of the Florentine citron and the sour orange. Perhaps the best-known example of a graft-chimera is +*Laburnocytisus* 'Adamii', caused by a fusion of a *Laburnum* and a broom.

Propagation

Because chimeras have more than one type of genetic material, while they may produce viable offspring from seed, these will not be true to type. All propagation that preserves the variation has to be by cuttings or division. Some types of cuttings, such as root cuttings, will produce entirely new growing points, usually from the inner one of the two types of tissue, so that these cannot be used either.

Derivation

The word chimera in these senses is a reference to the monstrous chimera of ancient Greek mythology, a legendary beast made up of parts of several different animals.

Evergreen
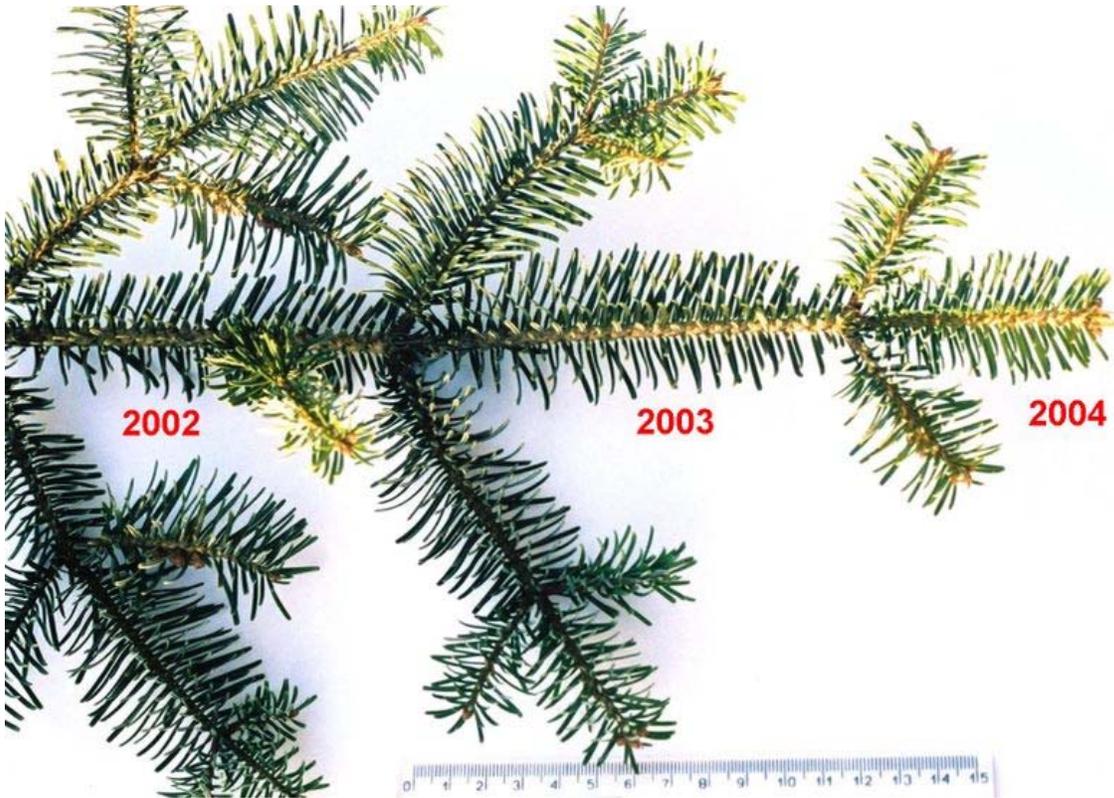
A Silver Fir shoot showing three successive years of retained leaves.

In botany, an **evergreen** plant is a plant that has leaves in all seasons. This contrasts with deciduous plants, which completely lose their foliage during the winter or dry season.

There are many different kinds of evergreen plants, both trees and shrubs. Evergreens include:

- most species of conifers (e.g., hemlock, blue spruce, red cedar, and white/scots/jack pine)

- live oak, holly, and "ancient" gymnosperms such as cycads

- most angiosperms from frost-free climates, such as eucalypts and rainforest trees

An additional special case exists in *Welwitschia,* an African gymnosperm plant that produces only two leaves, which grow continuously throughout the plant's life but gradually wear away at the apex, giving 20–40 years' persistence of leaf tissue.

Leaf persistence in evergreen plants varies from a few months (with new leaves constantly being grown as old ones are shed) to several decades (over thirty years in the Great Basin Bristlecone Pine).

Reasons for being evergreen or deciduous

Deciduous trees shed their leaves usually as an adaptation to a cold or dry season. Most tropical rainforest plants are evergreens, replacing their leaves gradually throughout the year as the leaves age and fall, whereas species growing in seasonally arid climates may be either evergreen or deciduous. Most warm temperate climate plants are also evergreen. In cool temperate climates, fewer plants are evergreen, with a predominance of conifers, as few evergreen broadleaf plants can tolerate severe cold below about -30 °C.

In areas where there is a reason for being deciduous (e.g. a cold season or dry season), being evergreen is usually an adaptation to low nutrient levels. Deciduous trees lose nutrients whenever they lose their leaves. In warmer areas, species such as some pines and cypresses grow on poor soils and disturbed ground. In *Rhododendron*, a genus with many broadleaf evergreens, several species grow in mature forests but are usually found on highly acidic soil where the nutrients are less available to plants. In taiga or boreal forests, it is too cold for the organic matter in the soil to decay rapidly, so the nutrients in the soil are less easily available to plants, thus favouring evergreens.

In temperate climates, evergreens can reinforce their own survival; evergreen leaf and needle litter has a higher carbon-nitrogen ratio than deciduous leaf litter, contributing to a higher soil acidity and lower soil nitrogen content. These conditions favour the growth of more evergreens and make it more difficult for deciduous plants to persist. In addition, the shelter provided by existing evergreen plants can make it easier for younger evergreen plants to survive cold and/or drought.

Evergreen plants and deciduous plants have almost all the same **diseases and pests**, but long-term air pollution, ash and toxic substances in the air are more injurious for evergreen plants than deciduous plants (for example spruce Picea abies in European cities).

A Southern Live Oak in winter.

Metaphorical use

Owing to the botanical meaning, the term "evergreen" can refer metaphorically to something that is continuously renewed or is self-renewing.

Chapter 7

Plant Intelligence

Vine tendril. Note how the plant reaches for and purposely wraps around the galvanised wire provided for the purpose. This is a very tough twig and appears to have no other purpose than support for the plant. Nothing else grows from it. It must reach out softly, then wrap around and then dry and toughen.

In botany, **plant intelligence** is the ability of plants to sense the environment and adjust their morphology, physiology and phenotype accordingly. Research draws on the fields of plant physiology, ecology and molecular biology.

Intelligence is an umbrella term describing abilities such as the capacities for abstract thought, understanding, communication, reasoning, learning, learning from past experiences, planning, and problem solving. Studies indicate plants are capable of problem solving and communication.

Problem solving

Plants adapt their behaviour in a variety of ways:

- Active foraging for light and nutrients. They do this by changing their architecture, physiology and phenotype.
- Leaves and branches are positioned and oriented in response to light source.
- Ability to detect soil volume and adapt growth accordingly independently of nutrient availability.
- Adaptively defend against herbivores.

Communication

Plants respond to volatile signals produced by other plants.

Mechanisms

In plants, the mechanism responsible for adaptation is signal transduction. Plants do not have a brain or neuronal network, but reactions within signalling pathways may provide a biochemical basis for learning and memory. Controversially, the brain is used as a metaphor in plant intelligence to provide an integrated view of signalling.

Plant cells can be electrically excitable and can display rapid electrical responses (action potentials) to environmental stimuli. These action potentials can influence processes such as actin-based cytoplasmic streaming, plant organ movements, wound responses, respiration, photosynthesis and flowering.

Senses in plants

Plants have many strategies to fight off pests. For example, they can produce different toxins (phytoalexins) against invaders or they can induce rapid cell death in invading cells to hinder the pests from spreading out. These strategies depend on quick and reliable recognition-systems.

Smell

Wounded tomatoes are known to produce the volatile odour methyl-jasmonate as an alarm-signal. Plants in the neighbourhood can then smell the danger and prepare for the attack by producing chemicals that defend insects or attract predators.

Light and electromagnetic waves

Many plant-organs contain photo-sensitive compounds (phototropins, cryptochromes and phytochromes) each reacting very specifically to certain wavelengths of light. These light-sensors tell the plant if it's day or night, how long the day is (photoperiodism), how much light is available and from where the light comes. Plants also can detect harmful ultraviolet B-rays and then start producing pigments which filter out these rays.

Touch

The mimosa plant (*Mimosa pudica*) makes its thin leaves point down at the slightest touch and carnivorous plants such as the Venus flytrap snap shut by the touch of insects. But a sense of touch is something every plant has, as Coughlin describes: "Ordinary plants need a sense of touch to respond to the buffeting of the wind, which can cause damage to foliage. They try to resist wind by strengthening tissues that are being swayed. The extra energy expended stiffening tissue can cost farmers dear, however. One experiment showed that when maize plants are shaken for 30 seconds each day, yields drop by 30 to 40% compared with unshaken plants" (New Scientist).

Hearing

Mechanical perturbation can also be detected by plants. Jasmonate levels also increase rapidly in response to mechanical perturbations such as tendril coiling.

Mordecai Jaffe (Wake Forest University) used an instrument that made a loud "warble" and got a doubling in the growth of dwarf pea plants. Jaffe suspects that the plant hormone gibberellic acid, which is instrumental in shoot elongation and seed germination, is involved in the "hearing" response. When Jaffe added chemicals to the pea plants inhibiting the biosynthesis of this hormone, he was unable to reproduce the original effects.

Poplar stems can detect reorientation and inclination (equilibrioception).

Criticism

It has been argued that although plants are capable of adaptation, it should not be called intelligence. *"A bacterium can monitor its environment and instigate developmental processes appropriate to the prevailing circumstances, but is that intelligence? Such simple adaptation behaviour might be bacterial intelligence but is clearly not animal intelligence."* However, plant intelligence fits with the definition of intelligence proposed by David Stenhouse in a book he wrote about evolution where he described it as "adaptively variable behaviour during the lifetime of the individual".

It is also argued that a plant cannot have goals because operational control of the plant's organs is devolved.

History

Charles Darwin studied the movement of plants and in 1880 published a book The Power of Movement in Plants. In the book he concludes:

It is hardly an exaggeration to say that the tip of the radicle thus endowed [..] acts like the brain of one of the lower animals; the brain being situated within the anterior end of the body, receiving impressions from the sense-organs, and directing the several movements.

Indian scientist Sir Jagdish Chandra Bose began to conduct experiments on plants in the year 1900. He found that every plant and every part of a plant appeared to have a sensitive nervous system and responded to shock by a spasm just as an animal muscle does.

Bose's experiments stopped at this conclusion, but American polygraph expert Cleve Backster conducted research that led him to believe that plants can communicate with other lifeforms. Backster's interest in the subject began in February 1966, when Backster wondered if he could measure the rate at which water rises from a philodendron's root area into its leaves. Because a polygraph or "lie detector" can measure electrical resistance, and water would alter the resistance of the leaf, he decided that this was the correct instrument to use. After attaching a polygraph to one of the plant's leaves, Backster claimed that, to his immense surprise, "the tracing began to show a pattern typical of the response you get when you subject a human to emotional stimulation of short duration".

Chapter 8

Myco-heterotrophy and Nutation in Plants

Myco-heterotrophy

Monotropa uniflora, an obligate myco-heterotroph known to parasitize fungi belonging to the Russulaceae.

Myco-heterotrophy is a symbiotic relationship between certain kinds of plants and fungi, in which the plant gets all or part of its food from parasitism upon fungi rather than from photosynthesis. A **myco-heterotroph** is the parasitic plant partner in this

relationship. Myco-heterotrophy is considered a kind of cheating relationship and myco-heterotrophs are sometimes informally referred to as **"mycorrhizal cheaters"**. This relationship is sometimes referred to as **mycotrophy**, though this term is also used for plants that engage in mutualistic mycorrhizal relationships.

Relationship between myco-heterotrophs and host fungi

Myco-heterotrophic roots of *Monotropa uniflora* with *Russula brevipes* mycelium

Full (or obligate) myco-heterotrophy exists when a non-photosynthetic plant (a plant largely lacking in chlorophyll or otherwise lacking a functional photosystem) gets all of its food from the fungi that it parasitizes. Partial (or facultative) myco-heterotrophy exists when a plant is capable of photosynthesis, but parasitizes fungi as a supplementary food supply. There are also plants, such as some orchid species, that are non-photosynthetic and obligately myco-heterotrophic for part of their life cycle, and photosynthetic and facultatively myco-heterotrophic or non-myco-heterotrophic for the rest of their life cycle. Not all non-photosynthetic or "achlorophyllous" plants are myco-heterotrophic – some non-photosynthetic plants like dodder directly parasitize the vascular tissue of other plants.

In the past, non-photosynthetic plants were mistakenly thought to get food by breaking down organic matter in a manner similar to saprotrophic fungi. Such plants were therefore called "saprophytes". It is now known that no plant is physiologically capable of direct breakdown of organic matter and that in order to get food, non-photosynthetic plants must engage in parasitism, either through myco-heterotrophy or direct parasitism of other plants.

The interface between the plant and fungal partners in this association is between the roots of the plant and the mycelium of the fungus. Myco-heterotrophy therefore closely resembles mycorrhiza (and indeed is thought to have evolved from mycorrhiza), except that in myco-heterotrophy, the flow of carbon is from the fungus to the plant, rather than vice versa.

Most myco-heterotrophs can therefore be seen as ultimately being epiparasites, since they take energy from fungi that in turn get their energy from vascular plants. Indeed, much myco-heterotrophy takes place in the context of a common mycorrhizal network, in which plants use mycorrhizal fungi to exchange carbon and nutrients with other plants. In these systems, myco-heterotrophs play the role of "mycorrhizal cheaters", taking carbon from the common network, with no known reward.

In congruence with older reports, it has been recently shown that some myco-heterotrophic orchids can be supported by saprotrophic fungi, exploiting litter- or wood-decaying fungi. In addition, several green plants (evolutionarily close to myco-heterotrophic species) have been shown to engage in partial myco-heterotrophy, that is, they are able to take carbon from mycorrhizal fungi, in addition to their photosynthetic intake.

Species diversity of myco-heterotrophs and host fungi

Myco-heterotrophs are found among a number of plant groups. All monotropes and non-photosynthetic orchids are full myco-heterotrophs, as is the non-photosynthetic liverwort *Cryptothallus*. Partial myco-heterotrophy is common in the Gentian family, with a few genera such as *Voyria* being fully myco-heterotrophic, in photosynthetic orchids, and a number of other plant groups. Some ferns and clubmosses have myco-heterotrophic gametophyte stages. The fungi that are parasitized by myco-heterotrophs are typically fungi with large energy reserves to draw on, usually mycorrhizal fungi, though there is some evidence that they may also parasitize parasitic fungi that form extensive mycelial networks, such as *Armillaria*.

Nutation in plants

Nutation, in plants, is the bending movements executed by some plant organs, such as stems, leaves, roots, etc., by which the part is inclined successively in various directions. Nutations are due to the unequal rate of growth of different sides of the organ, an inequality which, so far as is known at present (c. 1915), is dependent upon internal (unknown) causes and is not called forth by the action of external stimuli. The word is often used in a broad sense in the phrase *nutational movement*, to include all the movements in plants caused by growth in contrast to *variation movements* or movements produced by reversible turgor changes.

Simple nutation occurs in dorsiventral organs, such as flat leaves, both foliage and floral. The movements are only in one plane, depending upon the unequal growth of the opposite sides. When young the growth of the foliage leaves is most rapid upon their outer (dorsal) face, in consequence of which the lear applies itself to the axis, arches over the apex, and with its neighbirs forms a compact bud. Later growth becomes more rapid on the inner (ventral) face, the bud opens, and the leaves straighten out. Similar inequality of growth, but more sharply localized, leads to the folding and rolling of the leaf in the bud. Like movements of radial organs, such as stems, cylindrical leaves, and roots, have been termed circumnutation, or revolving nutation, to distinguish them from the simple nutation of dorsiventral organs. When any plant is in vigorous growth the axis rarely grows in length uniformly on all sides. The side on which growth is most rapid will push the apex over towards the side on which growth is less rapid. If the region of more rapid growth changes, shifting around the axis, the tip will be inclined successively to all points of the compass and with its simultaneous upward growth will describe a spiral, but, since the rate of growth is not uniform at successive intervals, the path described will be a very irregular spiral.

Movements quite similar to those above described are called forth in plant organs by external stimuli. Thus twining plants exhibit both true nutation and nutation due to geotropic sensitiveness. Changes in temperature cause flowers to open or close by movements which resemble the simple nutation of dorsiventral organs. Thus, the tulip, crocus, and other vernal flowers are very sensitive to changes in temperature. The crocus can perceive a change of 0.5°C (0.9°F), and will respond to a change of 20°C (36°F) in two minutes.

Chapter 9

Myrmecophyte

Acacia ants

Myrmecophyte is a plant that lives in a mutualistic association with a colony of ants. There are over 100 different genera of myrmecophytes. These plants possess structural adaptations that provide ants with food and/or shelter. These specialized structures include domatia, food bodies, and extrafloral nectaries . In exchange for food and shelter, ants aid the myrmecophyte in pollination, seed dispersal, gathering of essential nutrients, and/or defense. Specifically, domatia adapted to ants may be called myrmecodomatia.

Mutualism

Myrmecophytes share a mutualistic relationship with ants, benefiting both the plants and ants. This association may be either facultative or obligate.

Obligate Mutualism

In obligate mutualisms, both of the organisms involved are interdependent; they cannot survive on their own. An example of this type of mutualism can be found in the *Macaranga* genus of plants. All species of this genus provide food for ants in various forms, but only the obligate species produce domatia. Some of the most common species of myrmecophytic *Macaranga* interact with ants in the *Crematogaster* genus. C. *borneensis* have been found to be completely dependent on its partner plant, not being able to survive without the provided nesting spaces and food bodies. In laboratory tests, the worker ants did not survive away from the plants, and in their natural habitat they were never found anywhere else.

Facultative Mutualism

Facultative mutualism is a type of relationship where the survival of both parties (plant and ants, in this instance), is not dependent upon the interaction. Both organisms can survive without the other species. Facultative mutualisms most often occur in plants that have extrafloral nectaries but no other specialized structures for the ants. These non-exclusive nectaries allow a variety of animal species to interact with the plant. Facultative relationships can also develop between non-native plant and ant species, where co-evolution has not occurred. For example, Old World legumes that were introduced to North America can be protected by ants that originated from a different region.

Structural Adaptations of Myrmecophytes

Tuber on *Myrmecodia tuberosa*.

Domatia

Domatia are internal plant structures that appear to be specifically adapted for habitation by ants. These cavities are found primarily in the stems, leaves, and spines of plants. Many different genera of plants offer domatia. Plants of the *Acacia* genus have some of the most widely recognized forms of domatia and offer some of the best examples of ant-plant obligate mutualism. Different species of *Acacia* provide a variety of resources needed for their codependent counterparts. One of these resources is the need for shelter. *Acacia* have enlarged thorns on their stems that are excavated by ants for use as housing structures. Since the tree contains their nest, these aggressive ants react strongly to any

disturbance of the tree, providing the myrmecophyte with defense from grazing herbivores and encroaching vines.

Domatia can also be found within the tubers of certain plants. Tubers form when the hypocotyls of a seedling swells to form a hollow, chambered structure that can become inhabited by ants. The Rubiaceae family of plants contains the most commonly known tuberous myrmecophyte, *Myrmecodia*, literally meaning "ant-house".

Enlarged thorns and beltian bodies on *Acacia*.

Food Bodies

Some plants produce food bodies for use by other organisms. These small epidermal structures contain a variety of nutrients that are removed and consumed by foragers. Food bodies are identified by the main nutrient they contain and by the genus of plant producing them. Beltian bodies are found on the leaflet tips of *Acacia* plants and contain primarily protein. Beccarian bodies are found on young leaves of the *Macaranga* genus and are especially rich in lipids. Lipids are also the main nutrient found in Pearl bodies, found on the leaves and stems of *Ochroma* plants. Most ant inhabitantsof *Cecropia* plants harvest the last type of food body, as their primary food source. Remarkably these Müllerian bodies, found on the stalk of the leaf, are primarily glycogen. Glycogen is the principal storage carbohydrate found in animals and is extremely rare in plants.

Nutrient Content of Various Food Bodies

Food Bodies	Main Nutrient Contained	Plant Genus	Location on Plants
Beltian bodies	Protein	*Acacia*	Leaflet tips
Beccarian bodies	Lipids	*Macaranga*	Young leaves
Pearl bodies	Lipids	*Ochroma*	Leaves and stems
Müllerian bodies	Glycogen	*Cecropia*	Petiole of the leaf

Extrafloral nectaries on the petiole of a *Prunus avium* leaf.

Extrafloral Nectaries

Extrafloral nectaries are sugar-producing glands found outside the flower structures of plants. They occur in many different plant species around the world and are most commonly associated with vegetative structures that normally do not have nectaries, such as leaves, stems, and twigs. These secreting structures are non-exclusive in that nectar can be taken by a variety of animals. Ants offer these myrmecophytes with protection against harmful visiting fauna that may come to feed on the nectar. A species of deciduous tree that displays extrafloral nectaries, *Catalpa speciosa*, shows a decreased loss of leaf tissue on branches protected by ants, and an increase in number of seeds produced.

Types of Ant-Plant Interactions

Ants as Pollinators

Unlike their bee relatives, ants rarely pollinate plants. Various assumptions have been made as to why ants are poor pollinators, although none have been verified: a) ants do not fly limiting their transport of pollen far enough to effect cross-pollination, b) ants do not systematically forage like bees do, and c) ants are not hairy, and clean themselves too frequently to allow pollen to be carried to other plants. In most cases of ant pollination, the ants are one of multiple pollinators; meaning that the plants are not completely dependent on ants for pollination. However the orchid, *Leporella fimbriata* can only be pollinated by its winged male ant partner.

Afzelia africana seeds bearing elaiosomes.

Ants and Seed Dispersal

Myrmecochory, literally translated as "ant-dispersal," is the collection and dispersal of seeds by ants. Ants disperse more than 30% of the spring-flowering herbaceous plants in eastern North America. Both the plant and the ant benefit in this scenario. The ants are provided with an elaiosome, a detachable food body found on the surface of the seed. Elaiosomes have diverse compositions, usually high in lipids and fatty acids, but also containing amino acids, sugars, and protein. The ants remove the elaiosome once the seed has been transported to the colony. As a result, the seeds are safely placed in nutrient-rich

substrate protected from predators, benefiting the plant with optimum establishment conditions for its seed.

Ants Feeding Plants

Myrmecotrophy, meaning "ant-fed," is the ability of plants to absorb nutrients from debris piles left by ant nests. The tropical tree *Cecropia peltata* obtains 98% of its nitrogen from the waste deposited by its ant counterparts.


Ants collaborating to dismember an intruding ant.

Ants as Defense

Since plants provide essential resources for ants, the need to protect the plant and those resources is extremely important. Many myrmecophytes are defended from both herbivores and other competing plants by their ant counterparts. *Acacia cornigera*, for example, is thoroughly guarded by its obligate ant partner, *Pseudomyrmex ferruginea*. A single colony of *P. ferruginea* may contain more than 30,000 ants, and can tend multiple *Acacia* trees. The soldier ants are extremely aggressive, patrolling the trees twenty-four hours a day. Any disturbance to the tree alerts ants, who then recruit more workers from inside the horn domatia. These ants defend the *Acacia* by biting, violently stinging, and pruning any trespassers. The ants keep the plant free from other insects and vertebrate herbivores, but also from invading fungi and other plants.

Chapter 10

Photosynthesis
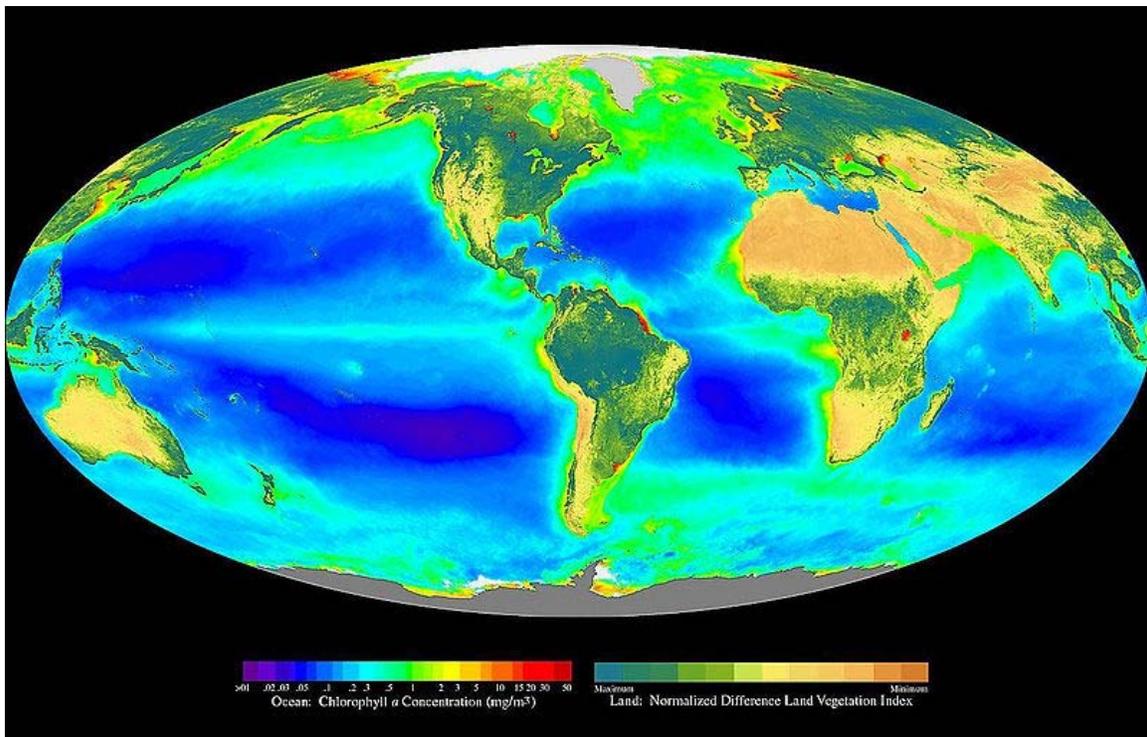
Composite image showing the global distribution of photosynthesis, including both oceanic phytoplankton and vegetation
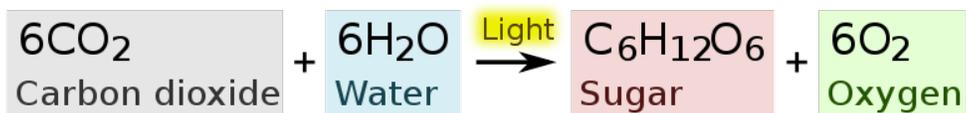

Overall equation for the type of photosynthesis that occurs in plants

Photosynthesis is a process that converts carbon dioxide into organic compounds, especially sugars, using the energy from sunlight. Photosynthesis occurs in plants, algae,

and many species of bacteria, but not in archaea. Photosynthetic organisms are called *photoautotrophs*, since they can create their own food. In plants, algae, and cyanobacteria, photosynthesis uses carbon dioxide and water, releasing oxygen as a waste product. Photosynthesis is vital for all aerobic life on Earth. As well as maintaining the normal level of oxygen in the atmosphere, nearly all life either depends on it directly as a source of energy, or indirectly as the ultimate source of the energy in their food (the exceptions are chemoautotrophs that live in rocks or around deep sea hydrothermal vents). The rate of energy capture by photosynthesis is immense, approximately 100 terawatts, which is about six times larger than the power consumption of human civilization. As well as energy, photosynthesis is also the source of the carbon in all the organic compounds within organisms' bodies. In all, photosynthetic organisms convert around 100–115 teragrams of carbon into biomass per year.

Although photosynthesis can happen in different ways in different species, some features are always the same. For example, the process always begins when energy from light is absorbed by proteins called photosynthetic reaction centers that contain chlorophylls. In plants, these proteins are held inside organelles called chloroplasts, while in bacteria they are embedded in the plasma membrane. Some of the light energy gathered by chlorophylls is stored in the form of adenosine triphosphate (ATP). The rest of the energy is used to remove electrons from a substance such as water. These electrons are then used in the reactions that turn carbon dioxide into organic compounds. In plants, algae and cyanobacteria, this is done by a sequence of reactions called the Calvin cycle, but different sets of reactions are found in some bacteria, such as the reverse Krebs cycle in *Chlorobium*. Many photosynthetic organisms have adaptations that concentrate or store carbon dioxide. This helps reduce a wasteful process called photorespiration that can consume part of the sugar produced during photosynthesis.
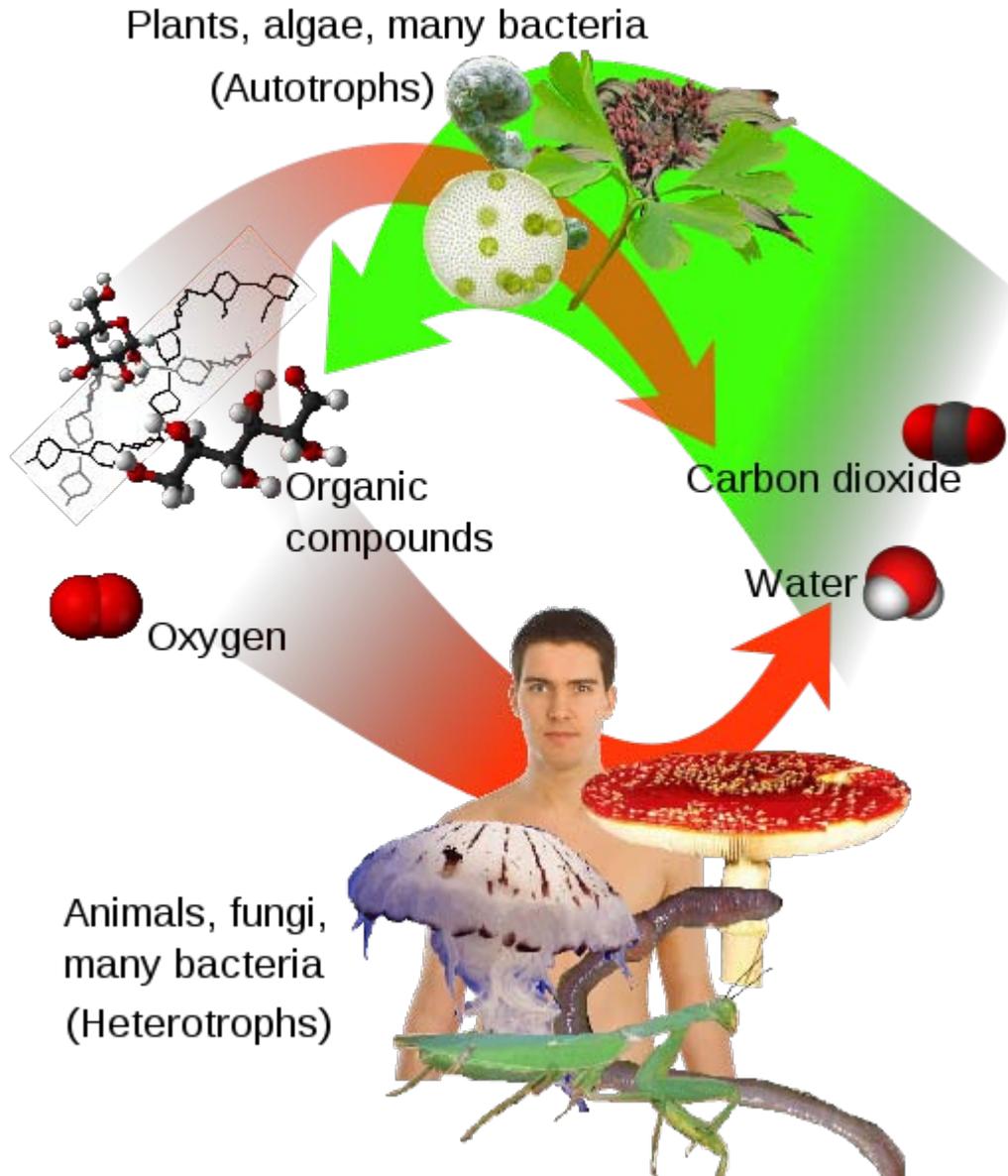
Overview of cycle between autotrophs and heterotrophs. Photosynthesis is the main means by which plants, algae and many bacteria produce organic compounds and oxygen from carbon dioxide and water (green arrow).

The first photosynthetic organisms probably evolved about 3,500 million years ago, early in the evolutionary history of life, when all forms of life on Earth were microorganisms and the atmosphere had much more carbon dioxide. They most likely used hydrogen or hydrogen sulfide as sources of electrons, rather than water. Cyanobacteria appeared later, around 3,000 million years ago, and drastically changed the Earth when they began to oxygenate the atmosphere, beginning about 2,400 million years ago. This new atmosphere allowed the evolution of complex life such as protists. Eventually, no later than a billion years ago, one of these protists formed a symbiotic relationship with a

cyanobacterium, producing the ancestor of many plants and algae. The chloroplasts in modern plants are the descendants of these ancient symbiotic cyanobacteria.

Overview
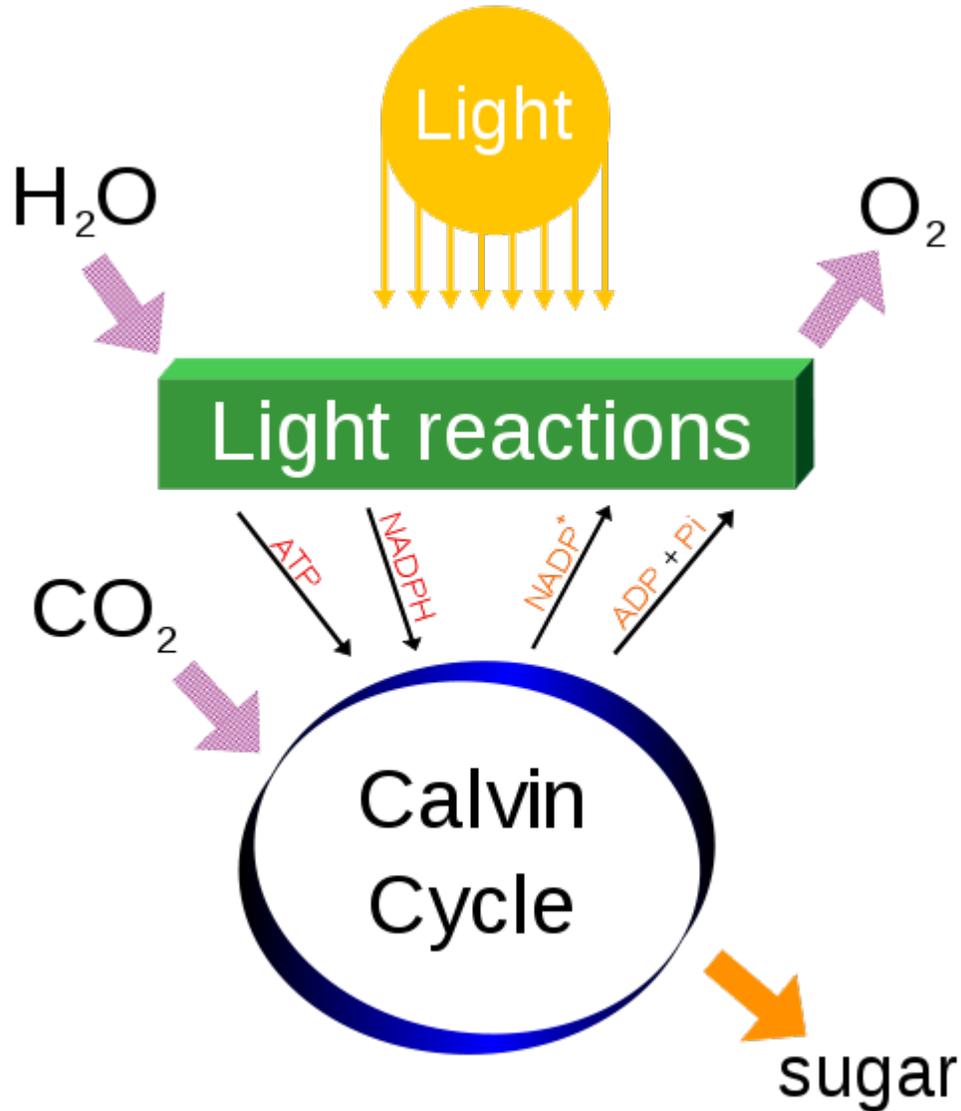
Photosynthesis changes the energy from the sun into chemical energy, splits water to liberate O_2, and fixes CO_2 into sugar.

Photosynthetic organisms are photoautotrophs, which means that they are able to synthesize food directly from carbon dioxide using energy from light. However, not all organisms that use light as a source of energy carry out photosynthesis, since *photoheterotrophs* use organic compounds, rather than carbon dioxide, as a source of carbon. In plants, algae and cyanobacteria, photosynthesis releases oxygen. This is called *oxygenic photosynthesis*. Although there are some differences between oxygenic

photosynthesis in plants, algae and cyanobacteria, the overall process is quite similar in these organisms. However, there are some types of bacteria that carry out anoxygenic photosynthesis, which consumes carbon dioxide but does not release oxygen.

Carbon dioxide is converted into sugars in a process called carbon fixation. Carbon fixation is a redox reaction, so photosynthesis needs to supply both a source of energy to drive this process, and the electrons needed to convert carbon dioxide into carbohydrate, which is a reduction reaction. In general outline, photosynthesis is the opposite of cellular respiration, where glucose and other compounds are oxidized to produce carbon dioxide, water, and release chemical energy. However, the two processes take place through a different sequence of chemical reactions and in different cellular compartments.
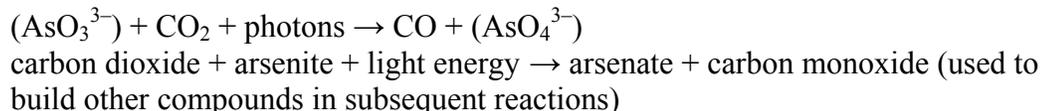
The general equation for photosynthesis is therefore:

$$2n\ CO_2 + 2n\ H_2O + \text{photons} \rightarrow 2(CH_2O)_n + n\ O_2 + 2n\ A$$
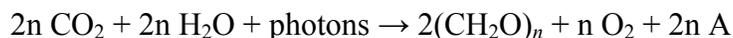
Carbon dioxide + electron donor + light energy → carbohydrate + oxygen + oxidized electron donor

Since water is used as the electron donor in oxygenic photosynthesis, the equation for this process is:

$$2n\ CO_2 + 2n\ H_2O + \text{photons} \rightarrow 2(CH_2O)_n + 2n\ O_2$$
carbon dioxide + water + light energy → carbohydrate + oxygen
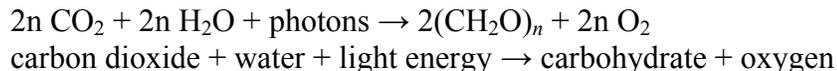
Other processes substitute other compounds (such as arsenite) for water in the electron-supply role; the microbes use sunlight to oxidize arsenite to arsenate: The equation for this reaction is:

$$(AsO_3^{3-}) + CO_2 + \text{photons} \rightarrow CO + (AsO_4^{3-})$$
carbon dioxide + arsenite + light energy → arsenate + carbon monoxide (used to build other compounds in subsequent reactions)

Photosynthesis occurs in two stages. In the first stage, *light-dependent reactions* or *light reactions* capture the energy of light and use it to make the energy-storage molecules ATP and NADPH. During the second stage, the *light-independent reactions* use these products to capture and reduce carbon dioxide.

Most organisms that utilize photosynthesis to produce oxygen use visible light to do so, although at least three use infrared radiation.

Photosynthetic membranes and organelles
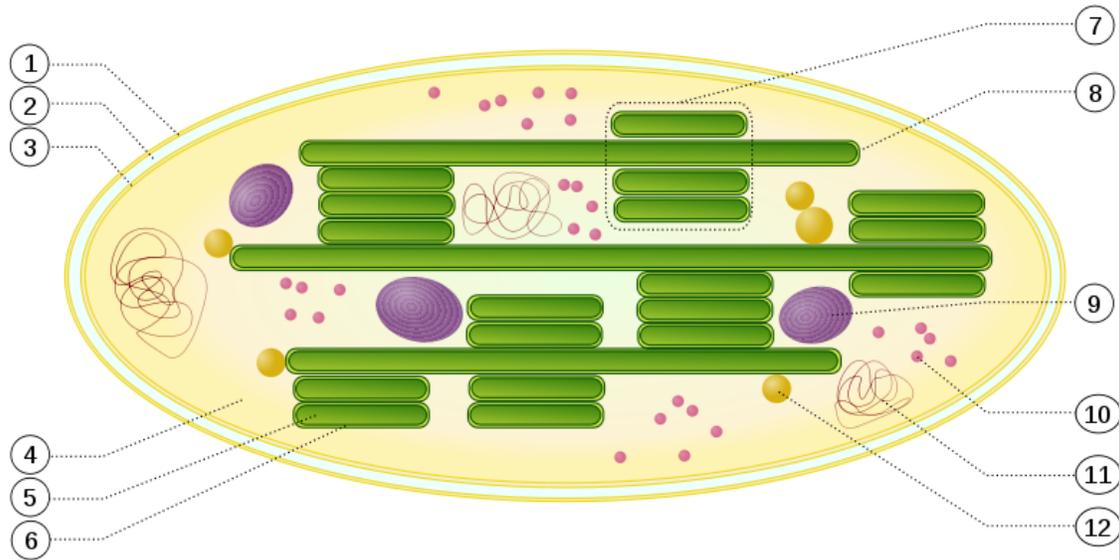
Chloroplast ultrastructure:
1. outer membrane
2. intermembrane space
3. inner membrane (1+2+3: envelope)
4. stroma (aqueous fluid)
5. thylakoid lumen (inside of thylakoid)
6. thylakoid membrane
7. granum (stack of thylakoids)
8. thylakoid (lamella)
9. starch
10. ribosome
11. plastidial DNA
12. plastoglobule (drop of lipids)

The proteins that gather light for photosynthesis are embedded within cell membranes. The simplest way these are arranged is in photosynthetic bacteria, where these proteins are held within the plasma membrane. However, this membrane may be tightly folded into cylindrical sheets called thylakoids, or bunched up into round vesicles called *intracytoplasmic membranes*. These structures can fill most of the interior of a cell, giving the membrane a very large surface area and therefore increasing the amount of light that the bacteria can absorb.

In plants and algae, photosynthesis takes place in organelles called chloroplasts. A typical plant cell contains about 10 to 100 chloroplasts. The chloroplast is enclosed by a membrane. This membrane is composed of a phospholipid inner membrane, a phospholipid outer membrane, and an intermembrane space between them. Within the membrane is an aqueous fluid called the stroma. The stroma contains stacks (grana) of thylakoids, which are the site of photosynthesis. The thylakoids are flattened disks,

bounded by a membrane with a lumen or thylakoid space within it. The site of photosynthesis is the thylakoid membrane, which contains integral and peripheral membrane protein complexes, including the pigments that absorb light energy, which form the photosystems.

Plants absorb light primarily using the pigment chlorophyll, which is the reason that most plants have a green color. Besides chlorophyll, plants also use pigments such as carotenes and xanthophylls. Algae also use chlorophyll, but various other pigments are present as phycocyanin, carotenes, and xanthophylls in green algae, phycoerythrin in red algae (rhodophytes) and fucoxanthin in brown algae and diatoms resulting in a wide variety of colors.

These pigments are embedded in plants and algae in special antenna-proteins. In such proteins all the pigments are ordered to work well together. Such a protein is also called a light-harvesting complex.

Although all cells in the green parts of a plant have chloroplasts, most of the energy is captured in the leaves. The cells in the interior tissues of a leaf, called the mesophyll, can contain between 450,000 and 800,000 chloroplasts for every square millimeter of leaf. The surface of the leaf is uniformly coated with a water-resistant waxy cuticle that protects the leaf from excessive evaporation of water and decreases the absorption of ultraviolet or blue light to reduce heating. The transparent epidermis layer allows light to pass through to the palisade mesophyll cells where most of the photosynthesis takes place.
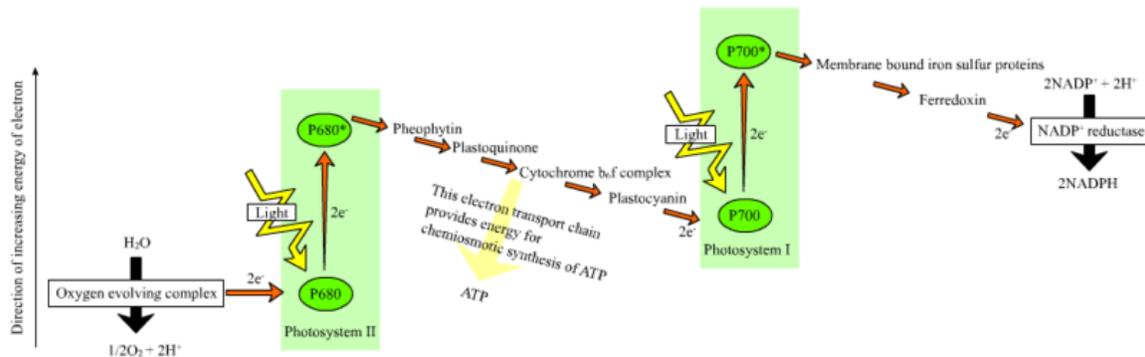
Light reactions
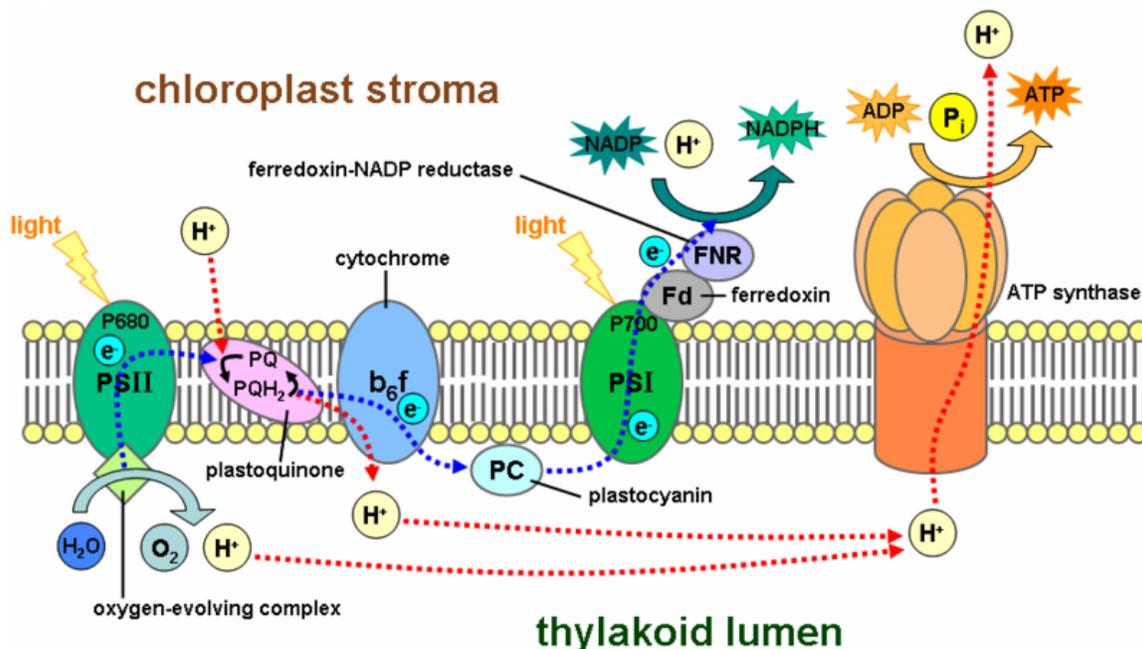
Light-dependent reactions of photosynthesis at the thylakoid membrane

In the light reactions, one molecule of the pigment chlorophyll absorbs one photon and loses one electron. This electron is passed to a modified form of chlorophyll called pheophytin, which passes the electron to a quinone molecule, allowing the start of a flow of electrons down an electron transport chain that leads to the ultimate reduction of NADP to NADPH. In addition, this creates a proton gradient across the chloroplast membrane; its dissipation is used by ATP synthase for the concomitant synthesis of ATP. The chlorophyll molecule regains the lost electron from a water molecule through a process called photolysis, which releases a dioxygen (O_2) molecule. The overall equation for the light-dependent reactions under the conditions of non-cyclic electron flow in green plants is:

$$2\ H_2O + 2\ NADP^+ + 3\ ADP + 3\ P_i + light \rightarrow 2\ NADPH + 2\ H^+ + 3\ ATP + O_2$$

Not all wavelengths of light can support photosynthesis. The photosynthetic action spectrum depends on the type of accessory pigments present. For example, in green plants, the action spectrum resembles the absorption spectrum for chlorophylls and carotenoids with peaks for violet-blue and red light. In red algae, the action spectrum overlaps with the absorption spectrum of phycobilins for blue-green light, which allows these algae to grow in deeper waters that filter out the longer wavelengths used by green plants. The non-absorbed part of the light spectrum is what gives photosynthetic organisms their color (e.g., green plants, red algae, purple bacteria) and is the least effective for photosynthesis in the respective organisms.

Z scheme

The "Z scheme"

In plants, light-dependent reactions occur in the thylakoid membranes of the chloroplasts and use light energy to synthesize ATP and NADPH. The light-dependent reaction has two forms: cyclic and non-cyclic. In the non-cyclic reaction, the photons are captured in the light-harvesting antenna complexes of photosystem II by chlorophyll and other accessory pigments. When a chlorophyll molecule at the core of the photosystem II reaction center obtains sufficient excitation energy from the adjacent antenna pigments, an electron is transferred to the primary electron-acceptor molecule, pheophytin, through a process called photoinduced charge separation. These electrons are shuttled through an electron transport chain, the so called *Z-scheme* shown in the diagram, that initially

functions to generate a chemiosmotic potential across the membrane. An ATP synthase enzyme uses the chemiosmotic potential to make ATP during photophosphorylation, whereas NADPH is a product of the terminal redox reaction in the *Z-scheme*. The electron enters a chlorophyll molecule in Photosystem I. The electron is excited due to the light absorbed by the photosystem. A second electron carrier accepts the electron, which again is passed down lowering energies of electron acceptors. The energy created by the electron acceptors is used to move hydrogen ions across the thylakoid membrane into the lumen. The electron is used to reduce the co-enzyme NADP, which has functions in the light-independent reaction. The cyclic reaction is similar to that of the non-cyclic, but differs in the form that it generates only ATP, and no reduced NADP (NADPH) is created. The cyclic reaction takes place only at photosystem I. Once the electron is displaced from the photosystem, the electron is passed down the electron acceptor molecules and returns back to photosystem I, from where it was emitted, hence the name *cyclic reaction*.

Water photolysis

The NADPH is the main reducing agent in chloroplasts, providing a source of energetic electrons to other reactions. Its production leaves chlorophyll with a deficit of electrons (oxidized), which must be obtained from some other reducing agent. The excited electrons lost from chlorophyll in photosystem I are replaced from the electron transport chain by plastocyanin. However, since photosystem II includes the first steps of the *Z-scheme*, an external source of electrons is required to reduce its oxidized **chlorophyll *a*** molecules. The source of electrons in green-plant and cyanobacterial photosynthesis is water. Two water molecules are oxidized by four successive charge-separation reactions by photosystem II to yield a molecule of diatomic oxygen and four hydrogen ions; the electron yielded in each step is transferred to a redox-active tyrosine residue that then reduces the photoxidized paired-chlorophyll *a* species called P680 that serves as the primary (light-driven) electron donor in the photosystem II reaction center. The oxidation of water is catalyzed in photosystem II by a redox-active structure that contains four manganese ions and a calcium ion; this oxygen-evolving complex binds two water molecules and stores the four oxidizing equivalents that are required to drive the water-oxidizing reaction. Photosystem II is the only known biological enzyme that carries out this oxidation of water. The hydrogen ions contribute to the transmembrane chemiosmotic potential that leads to ATP synthesis. Oxygen is a waste product of light-dependent reactions, but the majority of organisms on Earth use oxygen for cellular respiration, including photosynthetic organisms.

Light-independent reactions

The Calvin Cycle

In the Light-independent or dark reactions the enzyme RuBisCO captures CO_2 from the atmosphere and in a process that requires the newly formed NADPH, called the Calvin-Benson Cycle, releases three-carbon sugars, which are later combined to form sucrose and starch. The overall equation for the light-independent reactions in green plants is:

$$3\ CO_2 + 9\ ATP + 6\ NADPH + 6\ H^+ \rightarrow C_3H_6O_3\text{-phosphate} + 9\ ADP + 8\ P_i + 6\ NADP^+ + 3\ H_2O$$
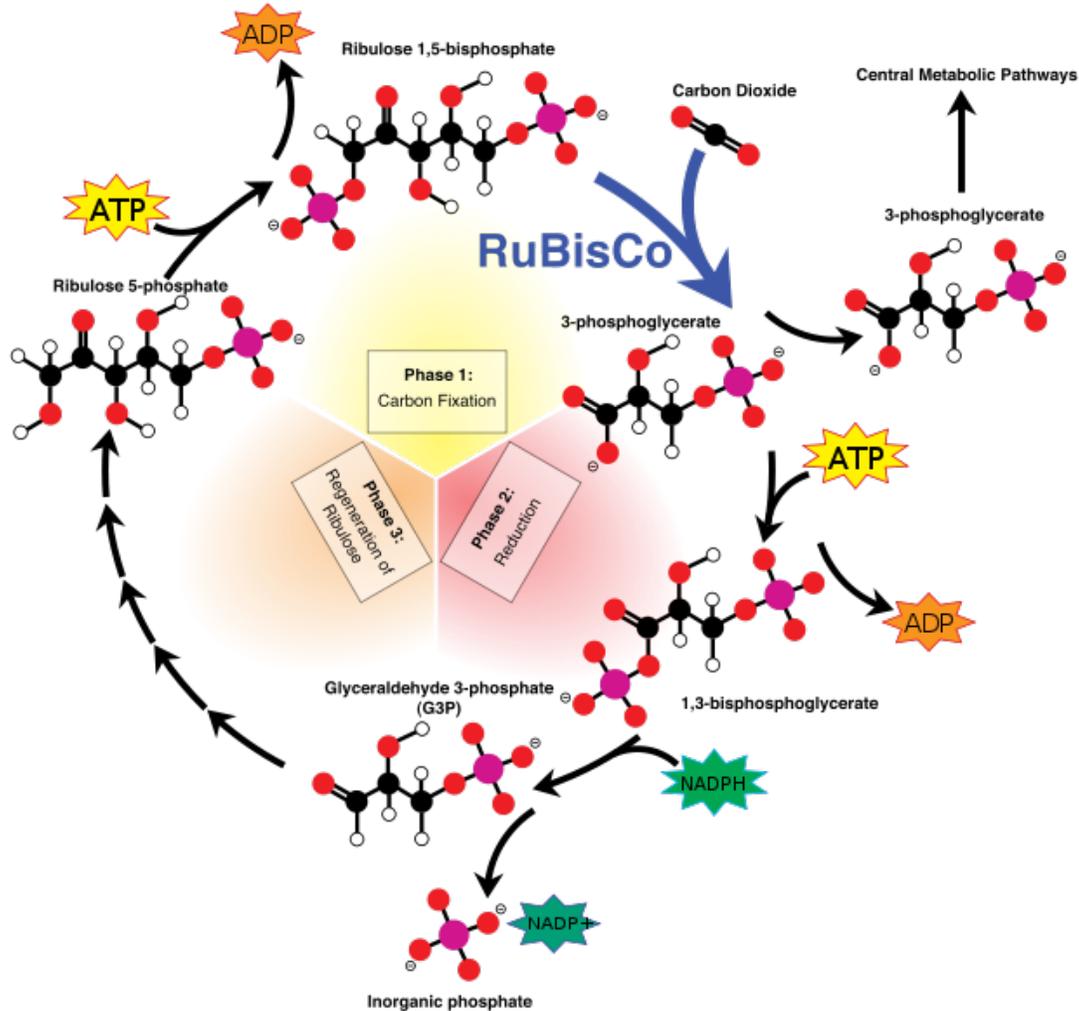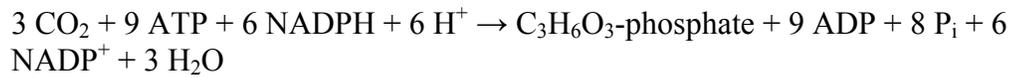
Overview of the Calvin cycle and carbon fixation

To be more specific, carbon fixation produces an intermediate product, which is then converted to the final carbohydrate products. The carbon skeletons produced by photosynthesis are then variously used to form other organic compounds, such as the building material cellulose, as precursors for lipid and amino acid biosynthesis, or as a fuel in cellular respiration. The latter occurs not only in plants but also in animals when the energy from plants gets passed through a food chain.

The fixation or reduction of carbon dioxide is a process in which carbon dioxide combines with a five-carbon sugar, ribulose 1,5-bisphosphate (RuBP), to yield two molecules of a three-carbon compound, glycerate 3-phosphate (GP), also known as 3-phosphoglycerate (PGA). GP, in the presence of ATP and NADPH from the light-dependent stages, is reduced to glyceraldehyde 3-phosphate (G3P). This product is also referred to as 3-phosphoglyceraldehyde (PGAL) or even as triose phosphate. Triose is a

3-carbon sugar. Most (5 out of 6 molecules) of the G3P produced is used to regenerate RuBP so the process can continue. The 1 out of 6 molecules of the triose phosphates not "recycled" often condense to form hexose phosphates, which ultimately yield sucrose, starch and cellulose. The sugars produced during carbon metabolism yield carbon skeletons that can be used for other metabolic reactions like the production of amino acids and lipids.

Carbon concentrating mechanisms

On land
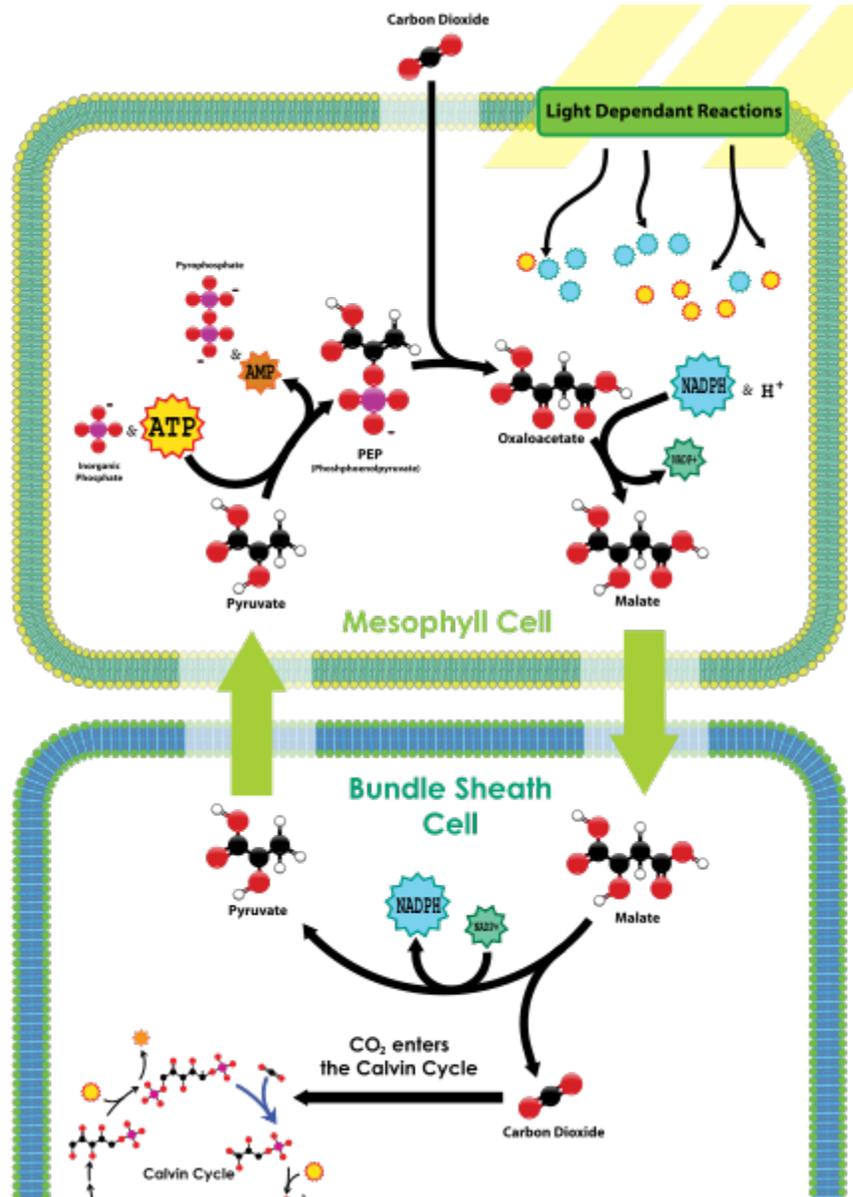
Overview of C4 carbon fixation

In hot and dry conditions, plants close their stomata to prevent the loss of water. Under these conditions, CO_2 will decrease, and oxygen gas, produced by the light reactions of photosynthesis, will decrease in the stem, not leaves, causing an increase of photorespiration by the oxygenase activity of ribulose-1,5-bisphosphate carboxylase/oxygenase and decrease in carbon fixation. Some plants have evolved mechanisms to increase the CO_2 concentration in the leaves under these conditions.

C_4 plants chemically fix carbon dioxide in the cells of the mesophyll by adding it to the three-carbon molecule phosphoenolpyruvate (PEP), a reaction catalyzed by an enzyme called PEP carboxylase, creating the four-carbon organic acid oxaloacetic acid. Oxaloacetic acid or malate synthesized by this process is then translocated to specialized bundle sheath cells where the enzyme RuBisCO and other Calvin cycle enzymes are located, and where CO_2 released by decarboxylation of the four-carbon acids is then fixed by RuBisCO activity to the three-carbon sugar 3-phosphoglyceric acids. The physical separation of RuBisCO from the oxygen-generating light reactions reduces photorespiration and increases CO_2 fixation and, thus, photosynthetic capacity of the leaf. C_4 plants can produce more sugar than C_3 plants in conditions of high light and temperature. Many important crop plants are C_4 plants, including maize, sorghum, sugarcane, and millet. Plants that do not use PEP-carboxylase in carbon fixation are called C_3 plants because the primary carboxylation reaction, catalyzed by RuBisCO, produces the three-carbon sugar 3-phosphoglyceric acids directly in the Calvin-Benson cycle. Over 90% of plants use C_3 carbon fixation, compared to 3% that use C_4 carbon fixation.

Xerophytes, such as cacti and most succulents, also use PEP carboxylase to capture carbon dioxide in a process called Crassulacean acid metabolism (CAM). In contrast to C_4 metabolism, which *physically* separates the CO_2 fixation to PEP from the Calvin cycle, CAM *temporally* separates these two processes. CAM plants have a different leaf anatomy from C_3 plants, and fix the CO_2 at night, when their stomata are open. CAM plants store the CO_2 mostly in the form of malic acid via carboxylation of phosphoenolpyruvate to oxaloacetate, which is then reduced to malate. Decarboxylation of malate during the day releases CO_2 inside the leaves, thus allowing carbon fixation to 3-phosphoglycerate by RuBisCO. Sixteen thousand species of plants use CAM.

In water

Cyanobacteria possess carboxysomes, which increase the concentration of CO_2 around RuBisCO to increase the rate of photosynthesis. This operates by carbonic anhydrase, producing hydrocarbonate ions (HCO_3^-), which are then pumped into the carboxysome, before being processed by a different carbonic anhydrase to produce CO_2. Pyrenoids in algae and hornworts also act to concentrate CO_2 around rubisco.

Order and kinetics

The overall process of photosynthesis takes place in four stages. The first, energy transfer in antenna chlorophyll takes place in the femtosecond (1 femtosecond (fs) = 10^{-15} s) to

picosecond (1 picosecond (ps) = 10^{-12} s) time scale. The next phase, the transfer of electrons in photochemical reactions, takes place in the picosecond to nanosecond time scale (1 nanosecond (ns) = 10^{-9} s). The third phase, the electron transport chain and ATP synthesis, takes place on the microsecond (1 microsecond (μs) = 10^{-6} s) to millisecond (1 millisecond (ms) = 10^{-3} s) time scale. The final phase is carbon fixation and export of stable products, which takes place in the millisecond-to-second time scale. The first three stages occur in the thylakoid membranes.

Efficiency

Plants usually convert light into chemical energy with a photosynthetic efficiency of 3–6%. Actual plants' photosynthetic efficiency varies with the frequency of the light being converted, light intensity, temperature and proportion of carbon dioxide in the atmosphere, and can vary from 0.1% to 8%. By comparison, solar panels convert light into electric energy at an efficiency of approximately 6–20% for mass-produced panels, and up to 41% in a research laboratory.

Evolution
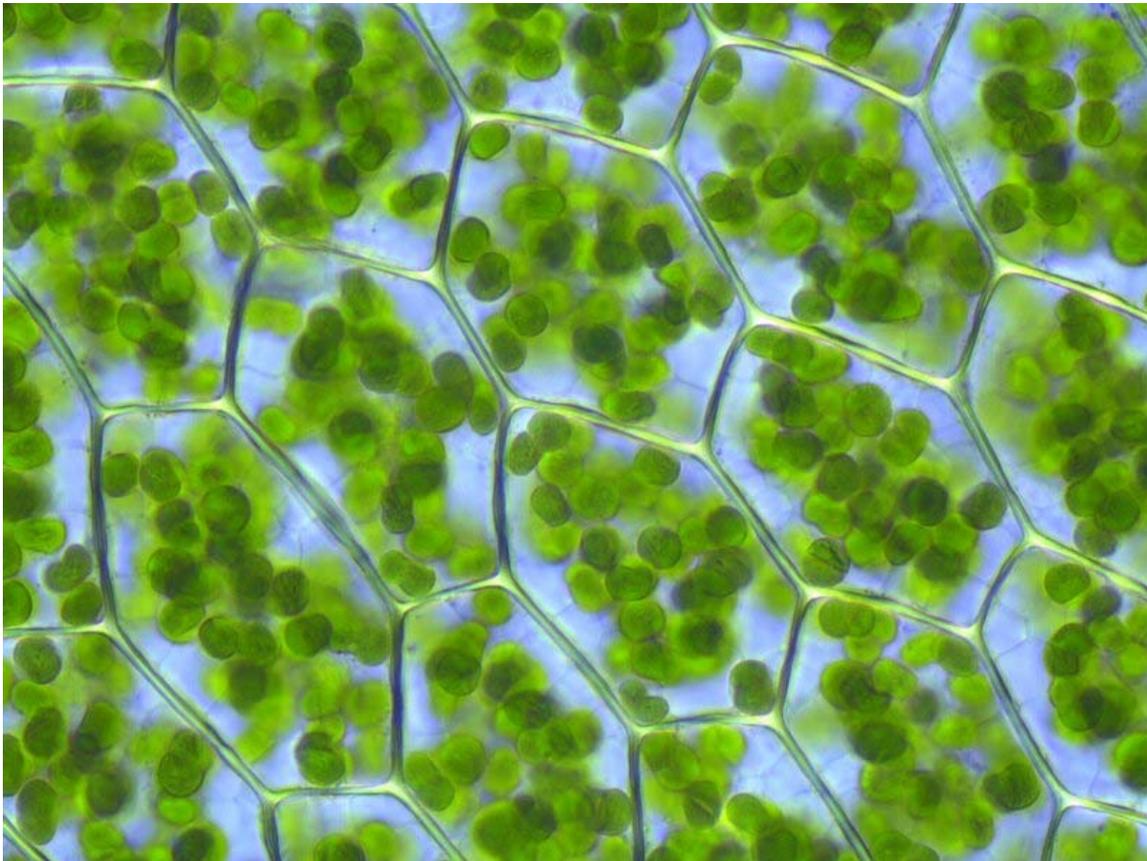
Plant cells with visible chloroplasts (from a moss, *Plagiomnium affine*)

Early photosynthetic systems, such as those from green and purple sulfur and green and purple nonsulfur bacteria, are thought to have been anoxygenic, using various molecules as electron donors. Green and purple sulfur bacteria are thought to have used hydrogen and sulfur as an electron donor. Green nonsulfur bacteria used various amino and other organic acids. Purple nonsulfur bacteria used a variety of nonspecific organic molecules. The use of these molecules is consistent with the geological evidence that the atmosphere was highly reduced at that time.

Fossils of what are thought to be filamentous photosynthetic organisms have been dated at 3.4 billion years old.

The main source of oxygen in the atmosphere is oxygenic photosynthesis, and its first appearance is sometimes referred to as the oxygen catastrophe. Geological evidence suggests that oxygenic photosynthesis, such as that in cyanobacteria, became important during the Paleoproterozoic era around 2 billion years ago. Modern photosynthesis in plants and most photosynthetic prokaryotes is oxygenic. Oxygenic photosynthesis uses water as an electron donor, which is oxidized to molecular oxygen (O_2) in the photosynthetic reaction center.

Symbiosis and the origin of chloroplasts

Several groups of animals have formed symbiotic relationships with photosynthetic algae. These are most common in corals, sponges and sea anemones. It is presumed that this is due to the particularly simple body plans and large surface areas of these animals compared to their volumes. In addition, a few marine mollusks *Elysia viridis* and *Elysia chlorotica* also maintain a symbiotic relationship with chloroplasts they capture from the algae in their diet and then store in their bodies. This allows the molluscs to survive solely by photosynthesis for several months at a time. Some of the genes from the plant cell nucleus have even been transferred to the slugs, so that the chloroplasts can be supplied with proteins that they need to survive.

An even closer form of symbiosis may explain the origin of chloroplasts. Chloroplasts have many similarities with photosynthetic bacteria, including a circular chromosome, prokaryotic-type ribosomes, and similar proteins in the photosynthetic reaction center. The endosymbiotic theory suggests that photosynthetic bacteria were acquired (by endocytosis) by early eukaryotic cells to form the first plant cells. Therefore, chloroplasts may be photosynthetic bacteria that adapted to life inside plant cells. Like mitochondria, chloroplasts still possess their own DNA, separate from the nuclear DNA of their plant host cells and the genes in this chloroplast DNA resemble those in cyanobacteria. DNA in chloroplasts codes for redox proteins such as photosynthetic reaction centers. The CoRR Hypothesis proposes that this **Co**-location is required for **R**edox **R**egulation.

Cyanobacteria and the evolution of photosynthesis

The biochemical capacity to use water as the source for electrons in photosynthesis evolved once, in a common ancestor of extant cyanobacteria. The geological record

indicates that this transforming event took place early in Earth's history, at least 2450–2320 million years ago (Ma), and, it is speculated, much earlier. Available evidence from geobiological studies of Archean (>2500 Ma) sedimentary rocks indicates that life existed 3500 Ma, but the question of when oxygenic photosynthesis evolved is still unanswered. A clear paleontological window on cyanobacterial evolution opened about 2000 Ma, revealing an already-diverse biota of blue-greens. Cyanobacteria remained principal primary producers throughout the Proterozoic Eon (2500–543 Ma), in part because the redox structure of the oceans favored photoautotrophs capable of nitrogen fixation. Green algae joined blue-greens as major primary producers on continental shelves near the end of the Proterozoic, but only with the Mesozoic (251–65 Ma) radiations of dinoflagellates, coccolithophorids, and diatoms did primary production in marine shelf waters take modern form. Cyanobacteria remain critical to marine ecosystems as primary producers in oceanic gyres, as agents of biological nitrogen fixation, and, in modified form, as the plastids of marine algae.

A 2010 study by researchers at Tel Aviv University discovered that the Oriental hornet (*Vespa orientalis*) converts sunlight into electric power using a pigment called xanthopterin. This is the first scientific evidence of a member of the animal kingdom engaging in photosynthesis.

Discovery

Although some of the steps in photosynthesis are still not completely understood, the overall photosynthetic equation has been known since the 19th century.

Jan van Helmont began the research of the process in the mid-17th century when he carefully measured the mass of the soil used by a plant and the mass of the plant as it grew. After noticing that the soil mass changed very little, he hypothesized that the mass of the growing plant must come from the water, the only substance he added to the potted plant. His hypothesis was partially accurate — much of the gained mass also comes from carbon dioxide as well as water. However, this was a signaling point to the idea that the bulk of a plant's biomass comes from the inputs of photosynthesis, not the soil itself.

Joseph Priestley, a chemist and minister, discovered that, when he isolated a volume of air under an inverted jar, and burned a candle in it, the candle would burn out very quickly, much before it ran out of wax. He further discovered that a mouse could similarly "injure" air. He then showed that the air that had been "injured" by the candle and the mouse could be restored by a plant.

In 1778, Jan Ingenhousz, court physician to the Austrian Empress, repeated Priestley's experiments. He discovered that it was the influence of sunlight on the plant that could cause it to revive a mouse in a matter of hours.

In 1796, Jean Senebier, a Swiss pastor, botanist, and naturalist, demonstrated that green plants consume carbon dioxide and release oxygen under the influence of light. Soon afterward, Nicolas-Théodore de Saussure showed that the increase in mass of the plant as

it grows could not be due only to uptake of CO_2 but also to the incorporation of water. Thus, the basic reaction by which photosynthesis is used to produce food (such as glucose) was outlined.

Cornelis Van Niel made key discoveries explaining the chemistry of photosynthesis. By studying purple sulfur bacteria and green bacteria he was the first scientist to demonstrate that photosynthesis is a light-dependent redox reaction, in which hydrogen reduces carbon dioxide.

Robert Emerson discovered two light reactions by testing plant productivity using different wavelengths of light. With the red alone, the light reactions were suppressed. When blue and red were combined, the output was much more substantial. Thus, there were two photosystems, one aborbing up to 600 nm wavelengths, the other up to 700. The former is known as PSII, the latter is PSI. PSI contains only chlorophyll a, PSII contains primarily chlorophyll a with most of the available chlorophyll b, among other pigments.

Further experiments to prove that the oxygen developed during the photosynthesis of green plants came from water, were performed by Robert Hill in 1937 and 1939. He showed that isolated chloroplasts give off oxygen in the presence of unnatural reducing agents like iron oxalate, ferricyanide or benzoquinone after exposure to light. The Hill reaction is as follows:

$$2\ H_2O + 2\ A + (\text{light, chloroplasts}) \rightarrow 2\ AH_2 + O_2$$

where A is the electron acceptor. Therefore, in light, the electron acceptor is reduced and oxygen is evolved. Cyt b_6, now known as a plastoquinone, is one electron acceptor.

Samuel Ruben and Martin Kamen used radioactive isotopes to determine that the oxygen liberated in photosynthesis came from the water.

Melvin Calvin and Andrew Benson, along with James Bassham, elucidated the path of carbon assimilation (the photosynthetic carbon reduction cycle) in plants. The carbon reduction cycle is known as the Calvin cycle, which ignores the contribution of Bassham and Benson. Many scientists refer to the cycle as the Calvin-Benson Cycle, Benson-Calvin, and some even call it the Calvin-Benson-Bassham (or CBB) Cycle.

Nobel Prize-winning scientist Rudolph A. Marcus was able to discover the function and significance of the electron transport chain.

Otto Heinrich Warburg and Dean Burk discovered the I-quantum photosynthesis reaction that splits the CO2, activated by the respiration.

Factors

The leaf is the primary site of photosynthesis in plants.

There are three main factors affecting photosynthesis and several corollary factors. The three main are:

- Light irradiance and wavelength
- Carbon dioxide concentration
- Temperature.

Light intensity (irradiance), wavelength and temperature

In the early 20th century, Frederick Frost Blackman along with Albert Einstein investigated the effects of light intensity (irradiance) and temperature on the rate of carbon assimilation.

- At constant temperature, the rate of carbon assimilation varies with irradiance, initially increasing as the irradiance increases. However, at higher irradiance, this relationship no longer holds and the rate of carbon assimilation reaches a plateau.
- At constant irradiance, the rate of carbon assimilation increases as the temperature is increased over a limited range. This effect is seen only at high irradiance levels.

At low irradiance, increasing the temperature has little influence on the rate of carbon assimilation.
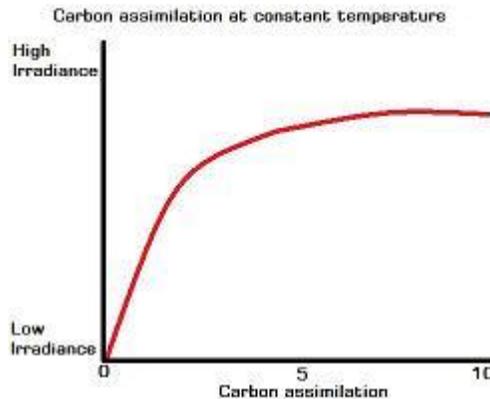
Carbon assimilation at a constant temperature.

These two experiments illustrate vital points: First, from research it is known that, in general, photochemical reactions are not affected by temperature. However, these experiments clearly show that temperature affects the rate of carbon assimilation, so there must be two sets of reactions in the full process of carbon assimilation. These are, of course, the light-dependent 'photochemical' stage and the light-independent, temperature-dependent stage. Second, Blackman's experiments illustrate the concept of limiting factors. Another limiting factor is the wavelength of light. Cyanobacteria, which reside several meters underwater, cannot receive the correct wavelengths required to cause photoinduced charge separation in conventional photosynthetic pigments. To combat this problem, a series of proteins with different pigments surround the reaction center.This unit is called a phycobilisome.

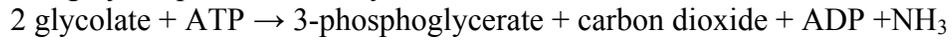## Carbon dioxide levels and photorespiration

As carbon dioxide concentrations rise, the rate at which sugars are made by the light-independent reactions increases until limited by other factors. RuBisCO, the enzyme that captures carbon dioxide in the light-independent reactions, has a binding affinity for both carbon dioxide and oxygen. When the concentration of carbon dioxide is high, RuBisCO will fix carbon dioxide. However, if the carbon dioxide concentration is low, RuBisCO will bind oxygen instead of carbon dioxide. This process, called photorespiration, uses energy, but does not produce sugars.

RuBisCO oxygenase activity is disadvantageous to plants for several reasons:

1. One product of oxygenase activity is phosphoglycolate (2 carbon) instead of 3-phosphoglycerate (3 carbon). Phosphoglycolate cannot be metabolized by the Calvin-Benson cycle and represents carbon lost from the cycle. A high oxygenase activity, therefore, drains the sugars that are required to recycle ribulose 5-bisphosphate and for the continuation of the Calvin-Benson cycle.

2. Phosphoglycolate is quickly metabolized to glycolate that is toxic to a plant at a high concentration; it inhibits photosynthesis.
3. Salvaging glycolate is an energetically expensive process that uses the glycolate pathway, and only 75% of the carbon is returned to the Calvin-Benson cycle as 3-phosphoglycerate. The reactions also produce ammonia (NH_3), which is able to diffuse out of the plant, leading to a loss of nitrogen.

   A highly simplified summary is:
   2 glycolate + ATP → 3-phosphoglycerate + carbon dioxide + ADP +NH_3

The salvaging pathway for the products of RuBisCO oxygenase activity is more commonly known as photorespiration, since it is characterized by light-dependent oxygen consumption and the release of carbon dioxide.

Chapter 11

Plant Nutrition

Plant nutrition is the study of the chemical elements that are necessary for growth. In 1972, E. Epstein defined 2 criteria for an element to be essential for plant growth: (1) in its absence the plant is unable to complete a normal life cycle or (2) that the element is part of some essential plant constituent or metabolite, this is all in accordance with Liebig's law of the minimum. There are 17 essential plant nutrients. Carbon and oxygen are absorbed from the air, while other nutrients including water are obtained from the soil. Plants must obtain the following mineral nutrients from the growing media:

- the three primary macronutrients: nitrogen (N), phosphorus (P), and potassium (K).
- the three secondary macronutrients such as calcium (Ca), sulphur (S), magnesium (Mg).
- the macronutrient Silicon (Si)
- and micronutrients or trace minerals: boron (B), chlorine (Cl), manganese (Mn), iron (Fe), zinc (Zn), copper (Cu), molybdenum (Mo), nickel (Ni), selenium (Se), and sodium (Na).

The macronutrients are consumed in larger quantities and are present in plant tissue in quantities from 0.2% to 4.0% (on a dry matter weight basis). Micronutrients are present in plant tissue in quantities measured in parts per million, ranging from 5 to 200 ppm, or less than 0.02% dry weight.

Most soil conditions across the world can provide plants with adequate nutrition and do not require fertilizer for a complete life cycle. However, man can artificially modify soil through the addition of fertilizer to promote vigorous growth and increase yield. The plants are able to obtain their required nutrients from the fertilizer added to the soil. A colloidal carbonaceous residue, known as humus, can serve as a nutrient reservoir. Besides lack of water and sunshine, nutrient deficiency is a major growth limiting factor.

Nutrient uptake in the soil is achieved by cation exchange, where in root hairs pump hydrogen ions (H^+) into the soil through proton pumps. These hydrogen ions displace

cations attached to negatively charged soil particles so that the cations are available for uptake by the root.

Plant nutrition is a difficult subject to understand completely, partially because of the variation between different plants and even between different species or individuals of a given clone. An element present at a low level may cause deficiency symptoms, while the same element at a higher level may cause toxicity. Further, deficiency of one element may present as symptoms of toxicity from another element. An abundance of one nutrient may cause a deficiency of another nutrient. Also a lowered availability of a given nutrient, such as SO_2^{-4} can affect the uptake of another nutrient, such as NO_3^-. Also, K^+ uptake can be influenced by the amount NH_4^+ available.

The root, especially the root hair, is the most essential organ for the uptake of nutrients. The structure and architecture of the root can alter the rate of nutrient uptake. Nutrient ions are transported to the center of the root, the stele in order for the nutrients to reach the conducting tissues, xylem and phloem. The Casparian strip, a cell wall outside of the stele but within the root, prevents passive flow of water and nutrients to help regulate the uptake of nutrients and water. Xylem moves water and inorganic molecules within the plant and phloem counts organic molecule transportation. Water potential plays a key role in a plants nutrient uptake. If the water potential is more negative within the plant than the surrounding soils, the nutrients will move from the more higher solute (soil) concentration to lower solute concentration (plant).

There are 3 fundamental ways plants uptake nutrients through the root: 1.) simple diffusion, occurs when a nonpolar molecule, such as O_2, CO_2, and NH_3 that follow a concentration gradient, can passively move through the lipid bilayer membrane without the use of transport proteins. 2.) facilitated diffusion, is the rapid movement of solutes or ions following a concentration gradient, facilitated by transport proteins. 3.) Active transport, is the active transport of ions or molecules against a concentration gradient that requires an energy source, usually ATP, to pump the ions or molecules through the membrane.

Nutrients are moved inside a plant to where they are most needed. For example, a plant will try to supply more nutrients to its younger leaves than its older ones. So when nutrients are mobile, the lack of nutrients is first visible on older leaves. However, not all nutrients are equally mobile. When a less mobile nutrient is lacking, the younger leaves suffer because the nutrient does not move up to them but stays lower in the older leaves. Nitrogen, phosphorus, and potassium are mobile nutrients, while the others have varying degrees of mobility. This phenomenon is helpful in determining what nutrients a plant may be lacking.

A symbiotic relationship may exist with 1.) Nitrogen-fixing bacteria, like rhizobia which are involved with nitrogen fixation, and 2.) mycorrhiza, which help to create a larger root surface area. Both of these mutualistic relationships enhance nutrient uptake.

Though nitrogen is plentiful in the Earth's atmosphere, relatively few plants engage in nitrogen fixation (conversion of atmospheric nitrogen to a biologically useful form). Most plants therefore require nitrogen compounds to be present in the soil in which they grow. These can either be supplied by decaying matter, nitrogen fixing bacteria, animal waste, or through the agricultural application of purpose made fertilizers.

Hydroponics, is growing plants in a water-nutrient solution without the use of nutrient-rich soil. It allows researchers and home gardeners to grow their plants in a controlled environment. The most common solution, is the Hoaglund Solution, developed by D. R. Hoaglund in 1933, the solution consists of all the essential nutrients in the correct proportions necessary for most plant growth. An aerator is used to prevent an anoxic event or hypoxia. Hypoxia can affect nutrient uptake of a plant because without oxygen present, respiration becomes inhibited within the root cells. The Nutrient film technique is a variation of hydroponic technique. The roots are not fully submerged which allows for adequate aeration of the roots, while a "film" thin layer of nutrient rich water is pumped through the system to provide nutrients and water to the plant.

Processes important to plant nutrition

Plants uptake essential elements from the soil through their roots and from the air (mainly consisting of carbon and oxygen) through their leaves.

In the leaves, transpiration occurs, where stomata open to take in carbon dioxide and expel oxygen that drives the movement of water and nutrients to the plant Green plants obtain their carbohydrate supply from the carbon dioxide in the air by the process of photosynthesis.

Functions of nutrients

Each of these nutrients is used in a different place for a different essential function.

Macro nutrients

Carbon

Carbon forms the backbone of many plants biomolecules, including starches and cellulose. Carbon is fixed through photosynthesis from the carbon dioxide in the air and is a part of the carbohydrates that store energy in the plant.

Hydrogen

Hydrogen also is necessary for building sugars and building the plant. It is obtained almost entirely from water. Hydrogen ions are imperative for a proton gradient to help drive the electron transport chain in photosynthesis and for respiration.

Oxygen

Oxygen is necessary for cellular respiration. Cellular respiration is the process of generating energy-rich adenosine triphosphate (ATP) via the consumption of sugars made in photosynthesis. Plants produce oxygen gas during photosynthesis to produce glucose but then require oxygen to undergo aerobic cellular respiration and break down this glucose and produce ATP.

Phosphorus

Phosphorus is important in plant bioenergetics. As a component of ATP, phosphorus is needed for the conversion of light energy to chemical energy (ATP) during photosynthesis. Phosphorus can also be used to modify the activity of various enzymes by phosphorylation, and can be used for cell signalling. Since ATP can be used for the biosynthesis of many plant biomolecules, phosphorus is important for plant growth and flower/seed formation. Phosphate esters make up DNA, RNA, and phospholipids. Most common in the form of polyprotic phosphoric acid (H_3PO_4) in soil, but it is taken up most readily in the form of H_2PO_4. Phosphorus is limited in most soils because it is released very slowly from insoluble phosphates. Under most environmental conditions it is the limiting element because of its small concentration in soil and high demand by plants and microorganisms. Plants can increase phosphorus uptake by a mutualism with mycorrhiza.

A Phosphorus deficiency in plants is characterized by an intense green coloration in leaves. If the plant is experiencing high phosphorus deficiencies the leaves may become denatured and show signs of necrosis. Occasionally the leaves may appear purple from an accumulation of anthocyanin. Because phosphorus is a mobile nutrient, older leaves will show the first signs of deficiency.

High phosphorus content fertilizers, such as bone meal, is useful to apply to perennials to help with successful root formation.

Potassium

Potassium regulates the opening and closing of the stomata by a potassium ion pump. Since stomata are important in water regulation, potassium reduces water loss from the leaves and increases drought tolerance. Potassium deficiency may cause necrosis or interveinal chlorosis. K^+ is highly mobile and can aid in balancing the anion charges within the plant. It also has high solubility in water and leaches out of soils that rocky or sandy that can result in potassium deficiency. It serves as an activator of enzymes used in photosynthesis and respiration Potassium is used to build cellulose and aids in photosynthesis by the formation of a chlorophyll precursor.

Potassium deficiency may result in higher risk of pathogens, wilting, chlorosis, brown spotting, and higher chances of damage from frost and heat.

Nitrogen

Nitrogen is an essential component of all proteins. Nitrogen deficiency most often results in stunted growth, slow growth, and chlorsis. Nitrogen deficient plants will also exhibit a purple appearance on the stems, petioles and underside of leaves from an accumulation of anthocyanin pigements

Most of the nitrogen taken up by plants is from the soil in the forms of NO_3^-. Amino acids and proteins can only be built from NH_4^+ so NO_3^- must be reduced. Under many agricultural settings, nitrogen is the limiting nutrient of high growth. Some plants require more nitrogen than others, such as corn (*Zea mays*). Because nitrogen is mobile, the older leaves exhibit chlorosis and necrosis earlier than the younger leaves. Soluble forms of nitrogen are transported as amines and amides

Sulphur

Sulphur is a structural component of some amino acids and vitamins, and is essential in the manufacturing of chloroplasts.

Calcium

Calcium regulates transport of other nutrients into the plant and is also involved in the activation of certain plant enzymes. Calcium deficiency results in stunting.

Magnesium

Magnesium is an important part of chlorophyll, a critical plant pigment important in photosynthesis. It is important in the production of ATP through its role as an enzyme cofactor.

Silicon

Silicon is deposited in cell walls and contributes to its mechanical properties including rigidity and elasticity

Micronutrients

Iron

Iron is necessary for photosynthesis and is present as an enzyme cofactor in plants. Iron deficiency can result in interveinal chlorosis and necrosis.

Molybdenum

Molybdenum is a cofactor to enzymes important in building amino acids.

Boron

Boron is important for binding of pectins in the RGII region of the primary cell wall, secondary roles may be in sugar transport, cell division, and synthesizing certain enzymes. Boron deficiency causes necrosis in young leaves and stunting.

Copper

Copper is important for photosynthesis. Symptoms for copper deficiency include chlorosis. Involved in many enzyme processes. Necessary for proper photosythesis. Involved in the manufacture of lignin (cell walls). Involved in grain production.

Manganese

Manganese is necessary for building the chloroplasts. Manganese deficiency may result in coloration abnormalities, such as discolored spots on the foliage.

Sodium

Sodium is involved in the regeneration of phosphoenolpyruvate in CAM and C4 plants. It can also substitute for potassium in some circumstances.

Zinc

Zinc is required in a large number of enzymes and plays an essential role in DNA transcription. A typical symptom of zinc deficiency is the stunted growth of leaves, commonly known as "little leaf" and is caused by the oxidative degradation of the growth hormone auxin.

Nickel

In higher plants, Nickel is essential for activation of urease, an enzyme involved with nitrogen metabolism that is required to process urea. Without Nickel, toxic levels of urea accumulate, leading to the formation of necrotic lesions. In lower plants, Nickel activates several enzymes involved in a variety of processes, and can substitute for Zinc and Iron as a cofactor in some enzymes.

Chlorine

Chlorine is necessary for osmosis and ionic balance; it also plays a role in photosynthesis.

Cobalt has proven to be beneficial to at least some plants, but is essential in others, such as legumes where it is required for nitrogen fixation for the symbiotic relationship it has with nitrogen-fixing bacteria. Vanadium may be required by some plants, but at very low

concentrations. It may also be substituting for molybdenum. Selenium and sodium may also be beneficial. Sodium can replace potassium's regulation of stomatal opening and closing

Other

Some elements are directly involved in plant metabolism (Arnon and Stout, 1939). However, this principle does not account for the so-called beneficial elements, whose presence, while not required, has clear positive effects on plant growth.

Chapter 12

Vegetation

Vegetation is a general term for the plant life of a region; it refers to the ground cover provided by plants. It is a general term, without specific reference to particular taxa, life forms, structure, spatial extent, or any other specific botanical or geographic characteristics. It is broader than the term *flora* which refers exclusively to species composition. Perhaps the closest synonym is plant community, but *vegetation* can, and often does, refer to a wider range of spatial scales than that term does, including scales as large as the global. Primeval redwood forests, coastal mangrove stands, sphagnum bogs, desert soil crusts, roadside weed patches, wheat fields, cultivated gardens and lawns; all are encompassed by the term *vegetation*.

Classification
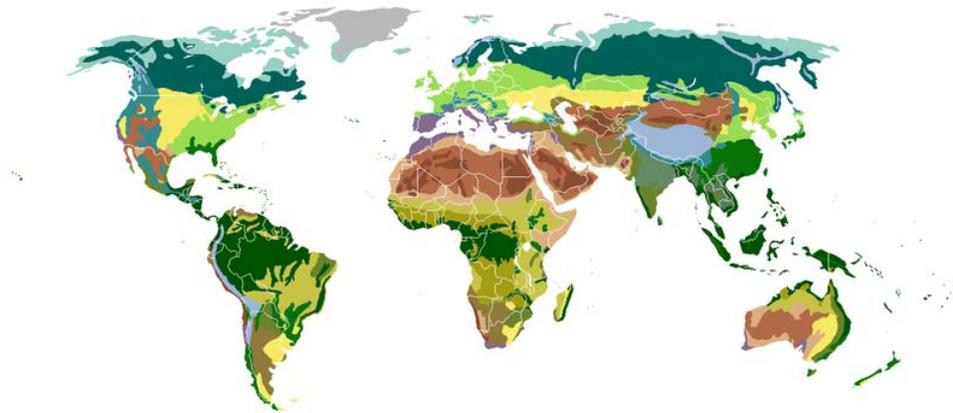
Biomes classified by vegetation

Ice desert	Mediterranean	Grass savanna
Tundra	Monsoon forest	Tree savanna
Taiga	Desert	Subtropical dry forest
Temperate broadleaf	Xeric shrubland	Tropical rainforest
Temperate steppe	Dry steppe	Alpine tundra
Subtropical rainforest	Semidesert	Montane forests

Much of the work on vegetation classification comes from European and North American ecologists, and they have fundamentally different approaches. In North America, vegetation types are based on a combination of the following criteria: climate pattern, plant habit, phenology and/or growth form, and dominant species. In the current US standard (adopted by the Federal Geographic Data Committee (FGDC), and originally developed by UNESCO and The Nature Conservancy), the classification is hierarchical and incorporates the non-floristic criteria into the upper (most general) five levels and limited floristic criteria only into the lower (most specific) two levels. In Europe, classification often relies much more heavily, sometimes entirely, on floristic (species) composition alone, without explicit reference to climate, phenology or growth forms. It often emphasizes indicator or diagnostic species which separate one type from another.

In the FGDC standard, the hierarchy levels, from most general to most specific, are: *system, class, subclass, group, formation, alliance,* and *association*. The lowest level, or association, is thus the most precisely defined, and incorporates the names of the dominant one to three (usually two) species of the type. An example of a vegetation type defined at the level of class might be "*Forest, canopy cover > 60%*"; at the level of a formation as "*Winter-rain, broad-leaved, evergreen, sclerophyllous, closed-canopy forest*"; at the level of alliance as "*Arbutus menziesii* forest"; and at the level of association as "*Arbutus menziesii-Lithocarpus densiflora* forest", referring to Pacific madrone-tanoak forests which occur in California and Oregon, USA. In practice, the levels of the alliance and/or association are the most often used, particularly in vegetation mapping, just as the Latin binomial is most often used in discussing particular species in taxonomy and in general communication.

Victoria in Australia classifies its vegetation by Ecological Vegetation Class.

Dynamics

Like all biological systems, plant communities are temporally and spatially dynamic; they change at all possible scales. Dynamism in vegetation is defined primarily as changes in species composition and/or vegetation structure.

Temporal dynamics

Temporally, a large number of processes or events can cause change, but for sake of simplicity they can be categorized roughly as either abrupt or gradual. Abrupt changes are generally referred to as disturbances; these include things like wildfires, high winds, landslides, floods, avalanches and the like. Their causes are usually external (exogenous) to the community—they are natural processes occurring (mostly) independently of the natural processes of the community (such as germination, growth, death, etc.). Such events can change vegetation structure and species composition very quickly and for long time periods, and they can do so over large areas. Very few ecosystems are without some type of disturbance as a regular and recurring part of the long term system dynamic. Fire and wind disturbances are particularly common throughout many vegetation types worldwide. Fire is particularly potent because of its ability to destroy not only living

plants, but also the seeds, spores, and living meristems representing the potential next generation, and because of fire's impact on fauna populations, soil characteristics and other ecosystem elements and processes.

Temporal change at a slower pace is ubiquitous; it comprises the field of ecological succession. Succession is the relatively gradual change in structure and taxonomic composition that arises as the vegetation itself modifies various environmental variables over time, including light, water and nutrient levels. These modifications change the suite of species most adapted to grow, survive and reproduce in an area, causing floristic changes. These floristic changes contribute to structural changes that are inherent in plant growth even in the absence of species changes (especially where plants have a large maximum size, i.e. trees), causing slow and broadly predictable changes in the vegetation. Succession can be interrupted at any time by disturbance, setting the system either back to a previous state, or off on another trajectory altogether. Because of this, successional processes may or may not lead to some static, final state. Moreover, accurately predicting the characteristics of such a state, even if it does arise, is not always possible. In short, vegetative communities are subject to many variables that together set limits on the predictability of future conditions.

Spatial dynamics

A coastal dune grassland on the Pacific Coast, USA

As a general rule, the larger an area under consideration, the more likely the vegetation will be heterogeneous across it. Two main factors are at work. First, the temporal

dynamics of disturbance and succession are increasingly unlikely to be in synchrony across any area as the size of that area increases. That is, different areas will be at different developmental stages due to different local histories, particularly their times since last major disturbance. This fact interacts with inherent environmental variability (e.g. in soils, climate, topography, etc.), which is also a function of area. Environmental variability constrains the suite of species that can occupy a given area, and the two factors together interact to create a mosaic of vegetation conditions across the landscape. Only in agricultural or horticultural systems does vegetation ever approach perfect uniformity. In natural systems, there is always heterogeneity, although its scale and intensity will vary widely. A natural grassland may be homogeneous when compared to the same area of partially burned forest, but highly diverse and heterogeneous when compared to the wheat field next to it.

Global vegetation patterns and determinants

At regional and global scales there is predictability of certain vegetation characteristics, especially physiognomic ones, which are related to the predictability in certain environmental characteristics. Much of the variation in these global patterns is directly explainable by corresponding patterns of temperature and precipitation (sometimes referred to as the energy and moisture balances). These two factors are highly interactive in their effect on plant growth, and their relationship to each other throughout the year is critical.