Handbook of Plant Ecology and Reproduction

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Chapter 1

Plant Ecology

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

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

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

Structure and function

Biological interactions

Herbivory

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

Distribution

Abundance

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

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

Chapter 2

Plant Life-Form

Plant life-form schemes constitute a way of classifying plants alternatively to the ordinary species-genus-family scientific classification. In colloquial speech, plants may be classified as trees, shrubs, herbs (forbs and graminoids), etc. The scientific use of life-form schemes emphasizes plant function in the ecosystem and that the same function or "adaptedness" to the environment may be achieved in a number of ways, i.e. plant species that are closely related phylogenetically may have widely different life-form, for example *Adoxa* and *Sambucus* are from the same family, but the former is a small herbaceous plant and the latter is a shrub or tree. Conversely, unrelated species may share a life-form through convergent evolution. The most widely applied life-form scheme is the Raunkiær system.

Life-form and *growth-form* are essentially synonymous concepts, despite attempts to restrict the meaning of growth-form to types differing in shoot architecture . Most life form schemes are concerned with vascular plants only. *Plant construction types* may be used in a broader sense to emcompass *planktophytes*, *benthophytes* (mainly algae) and terrestrial plants.

History

The term life-form was first coined by Eugenius Warming ("livsform") in his 1895 book Plantesamfund , but was translated to "growthform" in the 1909 English version *Oecology of Plants*. Nevertheless, earlier authors did classify species according to physiognomy , but were explicit about the entities being merely plactical classes without any relation to plant function. A marked exception was A. P. de Candolle attempt to construct a natural system of botanical classification . His system was based on the height of the lignified stem and on plant longevity. Warming, in his account, is explicit about his Candollean legacy . Warming's first attempt in life-form classification was his work *Om Skudbygning, Overvintring og Foryngelse* (translated title "On shoot architecture, perennation and rejuvenation") (1884). The classification was based on his meticulous observations while raising wild plants from seed in the Copenhagen Botanical Garden. Fourteen informal groups were recognized, based on longevity of the plant, power of vegetative propagation, duration of tillers, hypogeous or epigeous type of shoots, mode of wintering, and degree and mode of branching of rhizomes.

Warming developed his life-form scheme further in his "On the life forms in the vegetable kingdom" . He presented a hierarchic scheme, first dividing plants into heterotrophic and autotrophic, the latter group then into aquatic and terrestrial, the land plants into *muscoid*, *lichenoid*, *lianoid* and all other autonomous land plants, which again were divided into monocarpic and polycarpic. This system was incorporated into the English version of his 1895 book *Oecology of Plants* . Warming continued working on plant life-forms and intended to develop his system further. However, due to high age and illness, he was able to publish a draft of his last system only

Following Warming's line of emphasizing functional characters, Oscar Drude devised a life-form scheme in his *Die Systematische und Geographische Anordnung der Phanerogamen* (1887). This was, however, a hybrid between physiognomic and functional classification schemes as it recognized monocots and dicots as groups. Drude later modified his scheme in *Deutschlands Pflanzengeographie* (1896), and this scheme was adopted by the influential American plant ecologists Frederic Clements and Roscoe Pound

Christen C. Raunkiær's classification (1904) recognized life-forms (first called "biological types") on the basis of plant adaptation to survive the unfavorable season, be it cold or dry, that is the position of buds with respect to the soil surface . In subsequent works, he showed the correspondence between gross climate and the relative abundance of his life-forms.

G.E. Du Rietz reviewed the previous life-form schemes in 1931 and strongly criticized the attempt to include functional characters . He tabulated six parallel ways of life-form classification:

General plant physiognomy
Growth-forms / shoot architecture
Periodicity life-form - seasonal physiognomic variation
Bud height life-form (Raunkiær's scheme),
Bud structure life-form
Leaf life-form - form, size, duration, texture of leaves.

Later authors have combined these or other types of unidimensional life-form schemes into more complex schemes, in which life-forms are defined as combinations of states of several characters. Examples are the schemes proposed by Pierre Dansereau and Stephan Halloy . These schemes approach the concept of plant functional type, which has recently replaced *life-form* in a narrow sense.

Raunkiær plant life-form

The **Raunkiær system** is a system for categorizing plants using life-form categories, devised by Christen C. Raunkiær.

History

It was first proposed in a talk to the *Danish Botanical Society* in 1904 and briefly described in the society's journal Botanisk Tidsskrift .

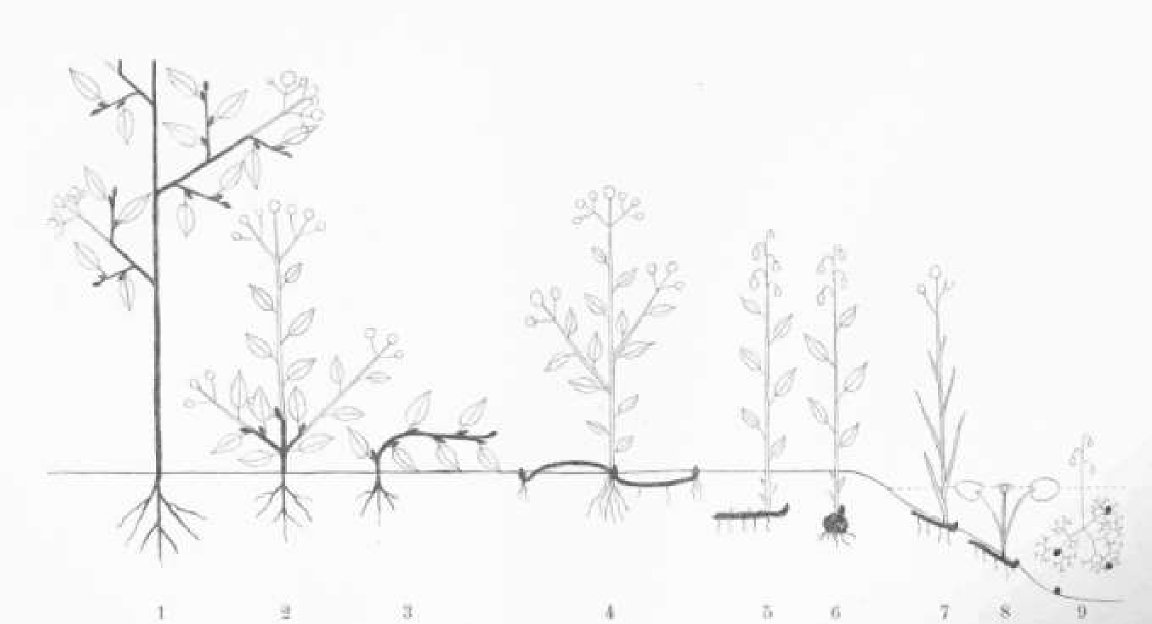
A fuller account appeared in French the following year . Raunkiær elaborated further on the system and published this in Danish in 1907.

The original note and the 1907 paper were much later translated to English and published with Raunkiær's collected works.

Modernization

Raunkiær's life-form scheme has subsequently been revised and modified by various authors , but the main structure has survived.

Subdivisions



Raunkiær's life forms:
1. Phanerophyte.
2-3. Chamaephytes.

4. Hemicryptophyte.
5-9. Cryptophytes.
* 5-6. Geophytes. * 7. Helophyte. * 8-9. Hydrophytes. Therophyte, aerophyte and epiphyte

The subdivisions of the Raunkiær system are based on the location of the plant's growth-point (bud) during seasons with adverse conditions (cold seasons, dry seasons):

Phanerophytes

Projecting into the air on stems – normally woody perennials - with resting buds more than 25 cms above soil level, e.g. trees and shrubs, but also **epiphytes**, which Raunkiær separated out as a special group in later versions of the system.

Further subgrouping

May be further subdivided according to plant height in *megaphanerophytes*, *mesophanerophytes* and *nanophanerophytes* and other characters, such as duration of leaves (evergreen or deciduous), presence of covering bracts on buds, succulence and epiphytism.

Chamaephytes

Buds on persistent shoots near the ground – woody plants with perennating buds borne close to the ground, no more than 25 cms above soil surface, (e.g. bilberry and periwinkle).

Hemicryptophytes

Buds at or near the soil surface , e.g. daisy, dandelion.

Protohemicryptophytes
only stem leaves
Partial rosette plants
both stem and basal rosette leaves
Rosette plants
only basal rosette leaves

Cryptophytes

Cryptophyte geophyte

Below ground or under water - with resting buds lying either beneath the surface of the ground as a rhizome, bulb, corm, etc., or a resting bud submerged under water. Cryptophytes are divided into 3 groups:

Geophytes
Resting in dry ground, e.g. crocus, tulip. May be further subdivided into rhizome, stem-tuber, root-tuber, bulb and root geophytes.
Helophytes

Resting in marshy ground, e.g. reedmace, marsh-marigold.
Hydrophytes
Resting by being submerged under water, e.g. water-lily, frogbit.

Therophytes

Annual plants which survive the unfavorable season in the form of seeds and complete their life-cycle during favorable seasons. Annual species are therophytes. Many desert plants are by necessity therophytes.

Aerophytes

New addition to the Raunkiaer lifeform classification. Plant that obtains moisture (though not through haustoria) and nutrients from the air and rain; usually grows on other plants but not parasitic on them. . This includes some *Tillandsia* species, as well as staghorn ferns.

Epiphytes

An **epiphyte** is a plant that grows upon another plant (such as a tree) non-parasitically or sometimes upon some other object (such as a building or a telegraph wire), derives its moisture and nutrients from the air and rain and sometimes from debris accumulating around it, and is found in the temperate zone (as many mosses, liverworts, lichens and algae) and in the tropics (as many ferns, cacti, orchids, and bromeliads) – also called *air plants*."

Near Orosí, Costa Rica

Botanic subdivision

An epiphytic bromeliad

Epiphyte is one of the subdivisions of the Raunkiær system. The term most commonly refers to higher plants, but epiphytic bacteria, fungi (epiphytic fungi), algae, lichens, mosses, and ferns exist as well. The term *epiphytic* derives from the Greek *epi-* (meaning 'upon') and *phyton* (meaning 'plant'). Epiphytic plants are sometimes called "air plants" because they do not root in soil. However, there are many aquatic species of algae, including seaweeds, that are *epiphytes* on other aquatic plants (seaweeds or aquatic angiosperms).

The best-known epiphytic plants include mosses, orchids, and bromeliads such as Spanish moss (of the genus *Tillandsia*), but epiphytic plants may be found in every major group of the plant kingdom. 89% of epiphyte species (about 24,000) are flowering plants. The second largest group are the leptosporangiate ferns, with about 2800 species (10% of epiphytes). In fact, about one third of all ferns are epiphytes. The third largest group is clubmosses, with 190 species, followed by a handful of species in each of the spikemosses, other ferns, Gnetales, and cycads.

Physiognomy

Epiphytes on a tree near Santa Elena in Costa Rica

Epiphytic organisms usually derive only physical support and not nutrition from their host, though they may sometimes damage the host. Parasitic and semiparasitic plants growing on other plants (mistletoe is well known) are not "true" epiphytes (a designation usually given to fully autotrophic epiphytes), but are still epiphytic in habit. Plants such as New Zealand species of *Griselinia*, which send long roots down towards the soil whilst fixed high in another plant and reliant upon it for physical support, are also epiphytic in habit.

Some epiphytic plants are large trees that begin their lives high in the forest canopy. Over decades they send roots down the trunk of a host tree eventually overpowering and replacing it. The strangler fig and the northern rātā (*Metrosideros robusta*.) of New Zealand are examples of this. Epiphytes that end up as free standing trees are also called hemiepiphytes.

Nutrition

Epiphytic plants use photosynthesis for energy and (where non-aquatic) obtain moisture from the air or from dampness (rain and cloud moisture) on the surface of their hosts. Roots may develop primarily for attachment, and specialized structures (for example, cups and scales) may be used to collect or hold moisture.

Ecology

An example of an epiphyte assemblage of orchids and bromeliads in a garden setting in Hawaii

The first important monograph on epiphytic plant ecology was written by A.F.W. Schimper (*Die Epiphytische Vegetation Amerikas*, 1888). Assemblages of large epiphytes occur most abundantly in moist tropical forests, but mosses and lichens occur as epiphytes in almost any environment with trees. In Europe there are no dedicated epiphytic plants using roots, but rich assemblages of mosses and lichens grow on trees in damp areas (mainly the western coastal fringe), and the common polypody fern grows epiphytically along branches. Rarely, grass, small bushes or small trees may grow in suspended soils up trees (typically in a rot-hole).

Epiphytic plants attached to their hosts high in the canopy have an advantage over herbs restricted to the ground where there is less light and herbivores may be more active. Epiphytic plants are also important to certain animals that may live in their water reservoirs, such as some types of frogs and arthropods.

Originally placed in Phanerophytes (above) but then separated because of irrelevance of soil position.

Chapter 3

Plant Defense Against Herbivory

Poison ivy produces urushiol to protect the plant from herbivores. In humans this chemical produces an allergic skin rash, known as urushiol-induced contact dermatitis.

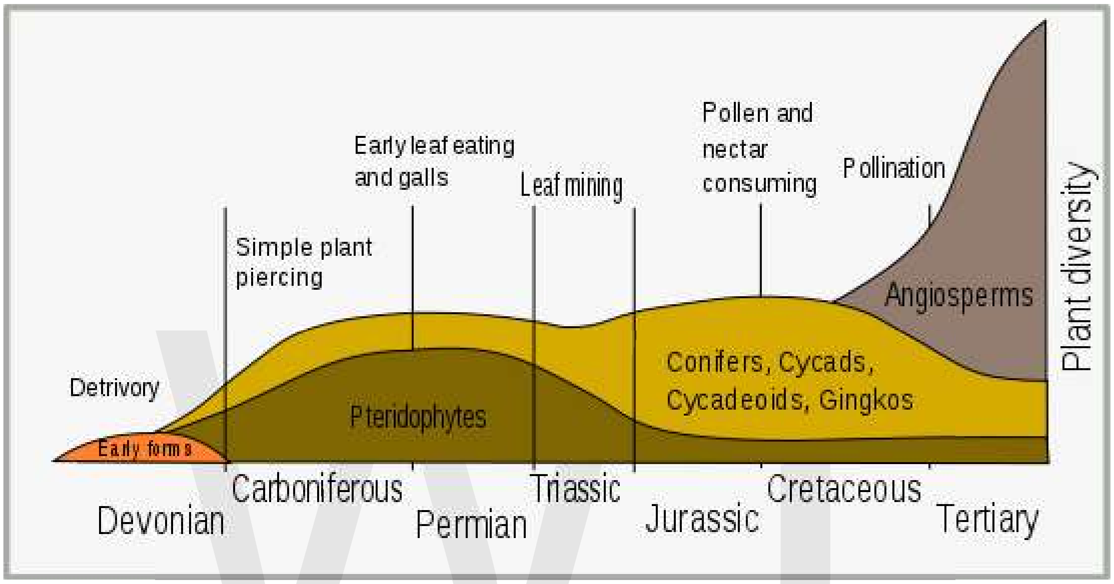
Foxgloves produce several deadly chemicals, namely cardiac and steroidal glycosides. Ingestion can cause nausea, vomiting, hallucinations, convulsions, or death.

Plant defense against herbivory or **host-plant resistance** (HPR) describes a range of adaptations evolved by plants which improve their survival and reproduction by reducing the impact of herbivores. Plants use several strategies to defend against damage caused by herbivores. Many plants produce secondary metabolites, known as allelochemicals, that influence the behavior, growth, or survival of herbivores. These chemical defenses can act as repellents or toxins to herbivores, or reduce plant digestibility.

Other defensive strategies used by plants include escaping or avoiding herbivores in time or in place, for example by growing in a location where plants are not easily found or accessed by herbivores, or by changing seasonal growth patterns. Another approach diverts herbivores toward eating non-essential parts, or enhances the ability of a plant to recover from the damage caused by herbivory. Some plants encourage the presence of natural enemies of herbivores, which in turn protect the plant. Each type of defense can be either *constitutive* (always present in the plant), or *induced* (produced in reaction to damage or stress caused by herbivores).

Historically, insects have been the most significant herbivores, and the evolution of land plants is closely associated with the evolution of insects. While most plant defenses are directed against insects, other defenses have evolved that are aimed at vertebrate herbivores, such as birds and mammals. The study of plant defenses against herbivory is important, not only from an evolutionary view point, but also in the direct impact that these defenses have on agriculture, including human and livestock food sources; as beneficial 'biological control agents' in biological pest control programs; as well as the in the search for plants of medical importance.

Evolution of defensive traits



Timeline of plant evolution and the beginnings of different modes of insect herbivory

The earliest land plants evolved from aquatic plants around 450 million years ago (Ma) in the Ordovician period. These early land plants had no vascular system and required free water for their reproduction. Vascular plants appeared later and their diversification began in the Devonian era (about 400 Ma). Their reduced dependence on water resulted from adaptations such as protective coatings to reduce evaporation from their tissues. Reproduction and dispersal of vascular plants in these dry conditions was achieved through the evolution of specialized seed structures. The diversification of flowering plants (angiosperms) during the Cretaceous period is associated with the sudden burst of speciation in insects. This diversification of insects represented a major selective force in plant evolution, and led to selection of plants that had defensive adaptations. Early insect herbivores were mandibulate and bit or chewed vegetation; but the evolution of vascular plants lead to the co-evolution of other forms of herbivory, such as sap-sucking, leaf mining, gall forming and nectar-feeding.

Records of herbivores

Viburnum lesquereuxii leaf with insect damage; Dakota Sandstone (Cretaceous) of Ellsworth County, Kansas. Scale bar is 10 mm.

Our understanding of herbivory in geological time comes from three sources: fossilised plants, which may preserve evidence of defence (such as spines), or herbivory-related damage; the observation of plant debris in fossilised animal faeces; and the construction of herbivore mouthparts.

Long thought to be a Mesozoic phenomenon, evidence for herbivory is found almost as soon as fossils which could show it. Within under 20 million years of the first fossils of sporangia and stems towards the close of the Silurian, around 420 million years ago, there is evidence that they were being consumed. Animals fed on the spores of early Devonian plants, and the Rhynie chert also provides evidence that organisms fed on plants using a "pierce and suck" technique. Many plants of this time are preserved with spine-like enations, which may have performed a defensive role before being co-opted to develop into leaves.

During the ensuing 75 million years, plants evolved a range of more complex organs - from roots to seeds. There was a gap of 50 to 100 million years between each organ evolving, and it being fed upon. Hole feeding and skeletonisation are recorded in the early Permian, with surface fluid feeding evolving by the end of that period.

A Plain Tiger *Danaus chrysippus* caterpillar making a moat to block defensive chemicals of *Calotropis* before feeding

Co-evolution

Herbivores depend on plants for food, and have evolved mechanisms to obtain this food despite the evolution of a diverse arsenal of plant defenses. Herbivore adaptations to plant defense have been likened to *offensive traits* and consist of adaptations that allow increased feeding and use of a host plant. Relationships between herbivores and their host plants often results in reciprocal evolutionary change, called co-evolution. When a herbivore eats a plant it selects for plants that can mount a defensive response. In cases where this relationship demonstrates *specificity* (the evolution of each trait is due to the other), and *reciprocity* (both traits must evolve), the species are thought to have co-evolved. The "escape and radiation" mechanism for co-evolution presents the idea that adaptations in herbivores and their host plants have been the driving force behind speciation, and have played a role in the radiation of insect species during the age of angiosperms. Some herbivores have evolved ways to hijack plant defenses to their own benefit, by sequestering these chemicals and using them to protect themselves from predators.

Types

Plant defenses can be classified generally as constitutive or induced. Constitutive defenses are always present in the plant, while induced defenses are produced or mobilized to the site where a plant is injured. There is wide variation in the composition and concentration of constitutive defenses and these range from mechanical defenses to digestibility reducers and toxins. Many external mechanical defenses and large quantitative defenses are constitutive, as they require large amounts of resources to produce and difficult to mobilize.

Induced defenses include secondary metabolic products, as well as morphological and physiological changes. An advantage of inducible, as opposed to constitutive defenses, is that they are only produced when needed, and are therefore potentially less costly, especially when herbivory is variable.

Chemical defenses

Persimmon, genus *Diospyros*, has a high tannin content which gives immature fruit, seen above, an astringent and bitter flavor.

The evolution of chemical defenses in plants is linked to the emergence of chemical substances that are not involved in the essential photosynthetic and metabolic activities. These substances, secondary metabolites, are organic compounds that are not directly involved in the normal growth, development or reproduction of organisms, and often produced as by-products during the synthesis of primary metabolic products. These secondary metabolites play a major role in defenses against herbivores.

Secondary metabolites are often characterized as either *qualitative* or *quantitative*. Qualitative metabolites are defined as toxins that interfere with an herbivore's metabolism, often by blocking specific biochemical reactions. Qualitative chemicals are present in plants in relatively low concentrations (often less than 2% dry weight), and are not dosage dependent. They are usually small, water soluble molecules, and therefore can be rapidly synthesized, transported and stored with relatively little energy cost to the plant. Qualitative allelochemicals are usually effective against non-adapted specialists and generalist herbivores.

Quantitative chemicals are those that are present in high concentration in plants (5 – 40% dry weight) and are equally effective against all specialists and generalist herbivores. Most quantitative metabolites are digestibility reducers that make plant cell walls indigestible to animals. The effects of quantitative metabolites are dosage dependent and the higher these chemicals' proportion in the herbivore's diet, the less nutrition the herbivore can gain from ingesting plant tissues. Because they are typically large molecules, these defenses are energetically expensive to produce and maintain, and often take longer to synthesise and transport.

The geranium, for example, produces a unique chemical compound in its petals to defend itself from Japanese beetles. Within 30 minutes of ingestion the chemical paralyzes the herbivore. While the chemical usually wears off within a few hours, during this time the beetle is often consumed by its own predators.

Types of chemical defenses

Plants have evolved many secondary metabolites involved in plant defense, which are collectively known as antiherbivory compounds and can be classified into three sub-groups: nitrogen compounds (including *alkaloids*, *cyanogenic glycosides* and *glucosinolates*), *terpenoids*, and *phenolics*.

Alkaloids are derived from various amino acids. Over 3000 known alkaloids exist, examples include nicotine, caffeine, morphine, colchicine, ergolines, strychnine, and quinine. Alkaloids have pharmacological effects on humans and other animals. Some alkaloids can inhibit or activate enzymes, or alter carbohydrate and fat storage by inhibiting the formation phosphodiester bonds involved in their breakdown. Certain alkaloids bind to nucleic acids and can inhibit synthesis of proteins and affect DNA repair mechanisms. Alkaloids can also affect cell membrane and cytoskeletal structure causing the cells to weaken, collapse, or leak, and can affect nerve transmission. Although alkaloids act on a diversity of metabolic systems in humans and other animals, they almost uniformly invoke an aversively bitter taste.

Cyanogenic glycosides are stored in inactive forms in plant vacuoles. They become toxic when herbivores eat the plant and break cell membranes allowing the glycosides to come into contact with enzymes in the cytoplasm releasing hydrogen cyanide which blocks cellular respiration. Glucosinolates are activated in much the same way as cyanogenic glucosides, and the products can cause gastroenteritis, salivation, diarrhea, and irritation of the mouth.

The terpenoids, sometimes referred to as isoprenoids, are organic chemicals similar to terpenes, derived from five-carbon isoprene units. There are over 10,000 known types of terpenoids. Most are multicyclic structures which differ from one another in both functional groups, and in basic carbon skeletons. Monoterpenoids, continuing 2 isoprene units, are volatile essential oils such as citronella, limonene, menthol, camphor, and pinene. Diterpenoids, 4 isoprene units, are widely distributed in latex and resins, and can be quite toxic. Diterpenes are responsible for making Rhododendron leaves poisonous. Plant steroids and sterols are also produced from terpenoid precursors, including vitamin D, glycosides (such as digitalis) and saponins (which lyse red blood cells of herbivores).

Phenolics, sometimes called *phenols*, consist of an aromatic 6-carbon ring bonded to a hydroxy group. Some phenols have antiseptic properties, while others disrupt endocrine activity. Phenolics range from simple tannins to the more complex flavonoids that give plants much of their red, blue, yellow, and white pigments. Complex phenolics called polyphenols are capable of producing many different types of effects on humans, including antioxidant properties. Some examples of phenolics used for defense in plants are: lignin, silymarin and cannabinoids. Condensed tannins, polymers composed of 2 to 50 (or more) flavonoid molecules, inhibit herbivore digestion by binding to consumed plant proteins and making them more difficult for animals to digest, and by interfering with protein absorption and digestive enzymes. Silica and lignins, which are completely indigestible to animals, grind down insect mandibles (appendages necessary for feeding).

In addition to the three larger groups of substances mentioned above, fatty acid derivates, amino acids and even peptides are used as defence. The cholinergic toxine, cicutoxin of water hemlock, is an polyyne derived from the fatty acid metabolism. β-N-Oxalyl-L-α,β-diaminopropionic acid as simple amino acid is used by the sweet pea which leads also to intoxication in humans. The synthesis of fluoroacetate in several plants is an example for the use of small molecules to disturb the metabolism of the herbivore, in this case the citric acid cycle.

Mechanical defenses

The thorns on the stem of this raspberry plant, serve as a mechanical defense against herbivory.

Plants have many external structural defenses that discourage herbivory. Depending on the herbivore's physical characteristics (i.e. size and defensive armor), plant structural defenses on stems and leaves can deter, injure, or kill the grazer. Some defensive compounds are produced internally but are released onto the plant's surface; for example, resins, lignins, silica, and wax cover the epidermis of terrestrial plants and alter the texture of the plant tissue. The leaves of holly plants, for instance, are very smooth and slippery making feeding difficult. Some plants produce gummosis or sap that traps insects.

A plant's leaves and stem may be covered with sharp prickles, spines, thorns, or trichomes- hairs on the leaf often with barbs, sometimes containing irritants or poisons. Plant structural features like spines and thorns reduce feeding by large ungulate herbivores (e.g. kudu, impala, and goats) by restricting the herbivores' feeding rate, or by wearing down the molars as in pears. The structure of a plant, its branching and leaf arrangement may also be evolved to reduce herbivore impact. The shrubs of New Zealand have evolved special wide branching adaptations believed to be a response to browsing birds such as the moas. Similarly, African Acacias have long spines low in the canopy, but very short spines high in the canopy, which is comparatively safe from herbivores such as giraffes.

Coconut palms protect their fruit by surrounding it with multiple layers of armour.

Trees such as coconut and other palms, may protect their fruit by multiple layers of armour, needing efficient tools to break through to the seed contents, and special skills to climb the tall and relatively smooth trunk.

Thigmonasty

Thigmonastic movements, those that occur in response to touch, are used as a defense in some plants. The leaves of the sensitive plant, *Mimosa pudica*, close up rapidly in response to direct touch, vibration, or even electrical and thermal stimuli. The proximate cause of this mechanical response is an abrupt change in the turgor pressure in the pulvini at the base of leaves resulting from osmotic phenomena. This is then spread via both electrical and chemical means through the plant; only a single leaflet need be disturbed.

This response lowers the surface area available to herbivores, which are presented with the underside of each leaflet, and results in a wilted appearance. It may also physically dislodge small herbivores, such as insects.

Mimicry and camouflage

Some plants mimic the presence of insect eggs on their leaves, dissuading insect species from laying their eggs there. Because female butterflies are less likely to lay their eggs on plants that already have butterfly eggs, some species of neotropical vines of the genus *Passiflora* (Passion flowers) contain physical structures resembling the yellow eggs of *Heliconius* butterflies on their leaves, which discourage oviposition by butterflies.

Indirect defenses

The large thorn-like stipules of *Acacia collinsii* are hollow and afford shelter for ants, which in return protect the plant against herbivores.

Another category of plant defenses are those features that indirectly protect the plant by enhancing the probability of attracting the natural enemies of herbivores. Such an arrangement is known as mutualism, in this case of the "enemy of my enemy" variety. One such feature are semiochemicals, given off by plants. Semiochemicals are a group of volatile organic compounds involved in interactions between organisms. One group of semiochemicals are allelochemicals; consisting of allomones, which play a defensive role in interspecies communication, and kairomones, which are used by members of higher trophic levels to locate food sources. When a plant is attacked it releases allelochemics containing an abnormal ratio of volatiles. Predators sense these volatiles as food cues, attracting them to the damaged plant, and to feeding herbivores. The subsequent reduction in the number of herbivores confers a fitness benefit to the plant and demonstrates the indirect defensive capabilities of semiochemicals. Induced volatiles also have drawbacks, however; some studies have suggested that these volatiles also attract herbivores.

Plants also provide housing and food items for natural enemies of herbivores, known as “biotic” defense mechanisms, as a means to maintain their presence. For example, trees from the genus *Macaranga* have adapted their thin stem walls to create ideal housing for an ant species (genus *Crematogaster*), which, in turn, protects the plant from herbivores. In addition to providing housing, the plant also provides the ant with its exclusive food source; from the food bodies produced by the plant. Similarly, some *Acacia* tree species have developed thorns that are swollen at the base, forming a hollowing structure that acts as housing. These *Acacia* trees also produce nectar in extrafloral nectaries on their leaves as food for the ants.

Most plants have endophytes, microbial organisms that live within them. While some cause disease, others protect plants from herbivores and pathogenic microbes. Endophytes can help the plant by producing toxins harmful to other organisms that would attack the plant, such as alkaloid producing fungi which are common in grasses such as tall fescue (*Festuca arundinacea*).

Leaf shedding and colour

There have been suggestions that leaf shedding may be a response that provides protection against diseases and certain kinds of pests such as leaf miners and gall forming insects. Other responses such as the change of leaf colours prior to fall have also been suggested as adaptations that may help undermine the camouflage of herbivores. Autumn leaf color has also been suggested to act as an honest warning signal of defensive commitment towards insect pests that migrate to the trees in autumn.

Costs and benefits

Defensive structures and chemicals are costly as they require resources that could otherwise be used by plants to maximize growth and reproduction. Many models have been proposed to explore how and why some plants make this investment in defenses against herbivores.

Optimal defense hypothesis

The optimal defense hypothesis attempts to explain how the kinds of defenses a particular plant might use reflect the threats each individual plant faces. This model considers three main factors, namely: risk of attack, value of the plant part, and the cost of defense.

The first factor determining optimal defense is risk: how likely is it that a plant or certain plant parts will be attacked? This is also related to the *plant apparency hypothesis*, which states that a plant will invest heavily in broadly effective defenses when the plant is easily found by herbivores. Examples of apparent plants that produce generalized protections include long-living trees, shrubs, and perennial grasses. Unapparent plants, such as short-lived plants of early successional stages, on the other hand, preferentially invest in small amounts of qualitative toxins that are effective against all but the most specialized herbivores.

The second factor is the value of protection: would the plant be less able to survive and reproduce after removal of part of its structure by a herbivore? Not all plant parts are of equal evolutionary value, thus valuable parts contain more defenses. A plant's stage of development at the time of feeding also affects the resulting change in fitness. Experimentally, the fitness value of a plant structure is determined by removing that part of the plant and observing the effect. In general, reproductive parts are not as easily replaced as vegetative parts, terminal leaves have greater value than basal leaves, and the loss of plant parts mid-season has a greater negative effect on fitness than removal at the beginning or end of the season. Seeds in particular tend to be very well protected. For example, the seeds of many edible fruits and nuts contain cyanogenic glycosides such as amygdalin. This results from the need to balance the effort needed to make the fruit attractive to animal dispersers while ensuring that the seeds are not destroyed by the animal.

The final consideration is cost: how much will a particular defensive strategy cost a plant in energy and materials? This is particularly important, as energy spent on defense cannot be used for other functions, such as reproduction and growth. The optimal defense hypothesis predicts that plants will allocate more energy towards defense when the benefits of protection outweigh the costs, specifically in situations where there is high herbivore pressure.

Carbon:nutrient balance hypothesis

The carbon:nutrient balance hypothesis, also known as the *environmental constraint hypothesis*, states that the various types of plant defenses are responses to variations in the levels of nutrients in the environment. This hypothesis predicts the Carbon/Nitrogen ratio in plants determines which secondary metabolites will be synthesized. For example, plants growing in nitrogen-poor soils will use carbon-based defenses (mostly digestibility reducers), while those growing in low-carbon environments (such as shady conditions) are more likely to produce nitrogen-based toxins. The hypothesis further predicts that plants can change their defences in response to changes in nutrients. For example, if plants are grown in low-nitrogen conditions, then these plants will implement a defensive strategy composed of constitutive carbon-based defenses. If nutrient levels subsequently increase, by for example the addition of fertilizers, these carbon-based defenses will decrease.

Growth rate hypothesis

The growth rate hypothesis, also known as the *resource availability hypothesis*, states that defense strategies are determined by the inherent growth rate of the plant, which is in turn determined by the resources available to the plant. A major assumption is that available resources are the limiting factor in determining the maximum growth rate of a plant species. This model predicts that the level of defense investment will increase as the potential of growth decreases. Additionally, plants in resource-poor areas, with inherently slow-growth rates, tend to have long-lived leaves and twigs, and the loss of plant appendages may result in a loss of scarce and valuable nutrients.

A recent test of this model involved a reciprocal transplants of seedlings of 20 species of trees between clay soils (nutrient rich) and white sand (nutrient poor) to determine whether trade-offs between growth rate and defenses restrict species to one habitat. Seedlings originating from the nutrient-poor sand had higher levels of constitutive carbon-based defenses, but when they were transplanted into nutrient-rich clay soils, they experienced higher mortality from herbivory. These finding suggest that defensive strategies limit the habitats of some plants.

Growth-differentiation balance hypothesis

The growth-differentiation balance hypothesis states that plant defenses are a result of a tradeoff between “growth-related processes” and “differentiation-related processes” in different environments. Differentiation-related processes are defined as “processes that enhance the structure or function of existing cells (i.e. maturation and specialization).” A plant will produce chemical defenses only when energy is available from photosynthesis, and plants with the highest concentrations of secondary metabolites are the ones with an intermediate level of available resources. The GDBH also accounts for tradeoffs between growth and defense over a resource availability gradient. In situations where resources (e.g. water and nutrients) limit photosynthesis, carbon supply is predicted to limit both growth and defense. As resource availability increases, the requirements needed to support photosynthesis are met, allowing for accumulation of carbohydrate in tissues. As resources are not sufficient to meet the large demands of growth, these carbon compounds can instead be partitioned into the synthesis of carbon based secondary metabolites (phenolics, tannins, etc.). In environments where the resource demands for growth are met, carbon is allocated to rapidly dividing meristems (high sink strength) at the expense of secondary metabolism. Thus rapidly growing plants are predicted to contain lower levels of secondary metabolites and vice versa. In addition, the tradeoff predicted by the GDBH may change over time, as evidenced by a recent study on Salix spp. Much support for this hypothesis is present in the literature, and some scientists consider the GDBH the most mature of the plant defense hypotheses.

Importance to humans

Agriculture

The variation of plant susceptibility to pests was probably known even in the early stages of agriculture in humans. In historic times, the observation of such variations in susceptibility have provided solutions for major socio-economic problems. The grape phylloxera was introduced from North America to France in 1860 and in 25 years it destroyed nearly a third (100,000 km²) of the French grape yards. Charles Valentine Riley noted that the American species *Vitis labrusca* was resistant to *Phylloxera*. Riley, with J. E. Planchon, helped save the French wine industry by suggesting the grafting of the susceptible but high quality grapes onto *Vitis labrusca* root stocks. The formal study of plant resistance to herbivory was first covered extensively in 1951 by Reginald (R.H.) Painter, who is widely regarded as the founder of this area of research, in his book *Plant Resistance to Insects*. While this work pioneered further research in the US, the work of Chesnokov was the basis of further research in the USSR.

Fresh growth of grass is sometimes high in prussic acid content and can cause poisoning of grazing livestock. The production of cyanogenic chemicals in grasses is primarily a defense against herbivores.

The human innovation of cooking may have been particularly helpful in overcoming many of the defensive chemicals of plants. Many enzyme inhibitors in cereal grains and pulses, such as trypsin inhibitors prevalent in pulse crops, are denatured by cooking, making them digestible.

It has been known since the late 17th century that plants contain noxious chemicals which are avoided by insects. These chemicals have been used by man as early insecticides; in 1690 nicotine was extracted from tobacco and used as a contact insecticide. In 1773, insect infested plants were treated with nicotine fumigation by heating tobacco and blowing the smoke over the plants. The flowers of *Chrysanthemum* species contain pyrethrin which is a potent insecticide. In later years, the applications of plant resistance became an important area of research in agriculture and plant breeding, particularly because they can serve as a safe and low-cost alternative to the use of pesticides. The important role of secondary plant substances in plant defense was described in the late 1950s by Vincent Dethier and G.S. Fraenkel. The use of botanical pesticides is widespread and notable examples include Azadirachtin from the neem (*Azadirachta indica*), d-Limonene from Citrus species, Rotenone from *Derris*, Capsaicin from Chili Pepper and Pyrethrum.

Natural materials found in the environment also induce plant resistance as well. Chitosan derived from chitin induce a plant's natural defense response against pathogens, diseases and insects including cyst nematodes, both are approved as an biopesticide by the EPA to reduce the dependence on toxic pesticides.

The selective breeding of crop plants often involves selection against the plant's intrinsic resistance strategies. This makes crop plant varieties particularly susceptible to pests unlike their wild relatives. In breeding for host-plant resistance, it is often the wild relatives that provide the source of resistance genes. These genes are incorporated using conventional approaches to plant breeding, but have also been augmented by recombinant techniques, which allow introduction of genes from completely unrelated organisms. The most famous transgenic approach is the introduction of genes from the bacterial species, *Bacillus thuringiensis*, into plants. The bacterium produces proteins that, when ingested, kill lepidopteran caterpillars. The gene encoding for these highly toxic proteins, when introduced into the host plant genome, confers resistance against caterpillars, when the same toxic proteins are produced within the plant. This approach is controversial, however, due to the possibility of ecological and toxicological side effects.

Pharmaceutical

Illustration from the 15th century manuscript *Tacuinum Sanitatis* detailing the beneficial and harmful properties of Mandrakes.

Many currently available pharmaceuticals are derived from the secondary metabolites plants use to protect themselves from herbivores, including opium, aspirin, cocaine, and atropine. These chemicals have evolved to affect the biochemistry of insects in very specific ways. However, many of these biochemical pathways are conserved in vertebrates, including humans, and the chemicals act on human biochemistry in ways similar to that of insects. It has therefore been suggested that the study of plant-insect interactions may help in bioprospecting.

There is evidence that humans began using plant alkaloids in medical preparations as early as 3000 B.C. Although the active components of most medicinal plants have been isolated only recently (beginning in the early 19th century) these substances have been used as drugs throughout the human history in potions, medicines, teas and as poisons. For example, to combat herbivory by the larvae of some Lepidoptera species, Cinchona trees produce a variety of alkaloids, the most familiar of which is quinine. Quinine is extremely bitter, making the bark of the tree quite unpalatable, it is also an anti-fever agent, known as Jesuit's bark, and is especially useful in treating malaria.

Throughout history mandrakes (*Mandragora officinarum*) have been highly sought after for their reputed aphrodisiac properties. However, the roots of the mandrake plant also contain large quantities of the alkaloid scopolamine, which, at high doses, acts as a central nervous system depressant, and makes the plant highly toxic to herbivores. Scopolamine was later found to be medicinal use in pain management before and during labor; in smaller doses it is used to prevent motion sickness. One of the most well-known medicinally valuable terpenes is an anticancer drug, taxol, isolated from the bark of the Pacific yew, *Taxus brevifolia*, in the early 1960s.

Biological pest control

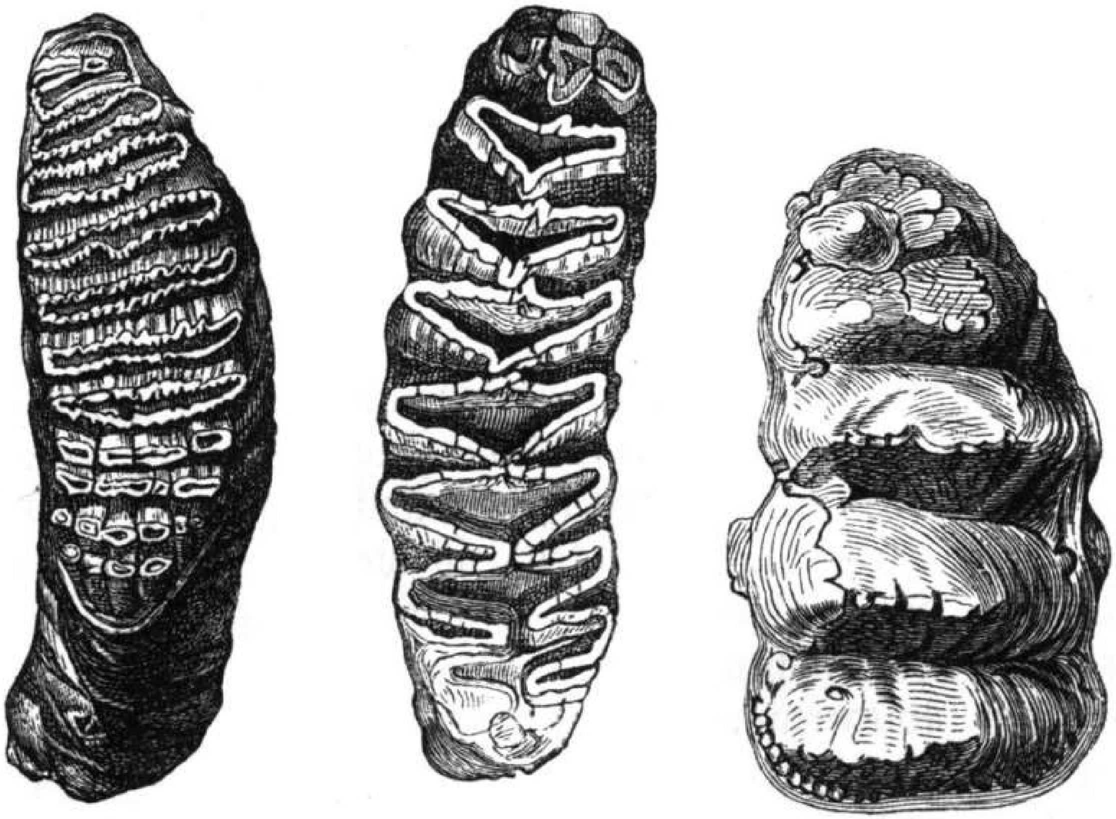
Repellent companion planting, defensive live fencing hedges, and "obstructive-repellent" interplanting, with host-plant resistance species as beneficial 'biological control agents' is a technique in biological pest control programs for: organic gardening, wildlife gardening, sustainable gardening, and sustainable landscaping; in organic farming and sustainable agriculture; and in restoration ecology methods for habitat restoration projects.

Chapter 4

Herbivore Adaptations to Plant Defense

Herbivores are dependent on plants for food, and have coevolved mechanisms to obtain this food despite the evolution of a diverse arsenal of plant defenses against herbivory. **Herbivore adaptations to plant defense** have been likened to "offensive traits" and consist of those traits that allow for increased feeding and use of a host. Plants, on the other hand, protect their resources for use in growth and reproduction, by limiting the ability of herbivores to eat them. Relationships between herbivores and their host plants often results in reciprocal evolutionary change. When an herbivore eats a plant it selects for plants that can mount a defensive response, whether the response is incorporated biochemically or physically, or induced as a counterattack. In cases where this relationship demonstrates "specificity" (the evolution of each trait is due to the other), and "reciprocity" (both traits must evolve), the species are thought to have coevolved. The escape and radiation mechanisms for coevolution, presents the idea that adaptations in herbivores and their host plants, has been the driving force behind speciation.

Mechanical adaptations



The molars of three species of elephant illustrate their different feeding preferences (l-asian elephant, c-african elephant, r-*Mastodon ginganteum*)

Herbivores have developed a diverse range of physical structures to facilitate the consumption of plant material. To break up intact plant tissues, mammals have developed teeth structures that reflect their feeding preferences. For instance, frugivores (animals that feed primarily on fruit) and herbivores that feed on soft foliage have low-crowned teeth specialized for grinding foliage and seeds. Grazing animals that tend to eat hard, silica-rich grasses, have high-crowned teeth, which are capable of grinding tough plant tissues and do not wear down as quickly as low-crowned teeth. Birds grind plant material or crush seeds using their beaks and gizzards.

Insect herbivores have evolved a wide range of tools to facilitate feeding. Often these tools reflect an individual’s feeding strategy and its preferred food type. Within the family Sphingidae (moths), it has been observed that species which eat relatively soft leaves are equipped with incisors for tearing and chewing, while the species that feed on mature leaves and grasses cut them with toothless snipping mandibles (the uppermost pair of jaws in insects, used for feeding).

An herbivore's diet often shapes its feeding adaptations. Grasshopper head size, and thus chewing power, was demonstrated to be greater for individuals raised on rye grass (a relatively hard grass) when compared to individuals raised on red clover (a soft diet). Larval lepidoptera that feed on plants with high levels of condensed tannins (as in trees) have more alkaline midguts when compared to lepidoptera that feed on herbs and forbs (pH of 8.67 vs. 8.29 respectively). This morphological difference can be explained by the fact that insoluble tannin-protein complexes can be broken down and absorbed as nutrients at alkaline pH levels.

Biochemical adaptations

Herbivores generate enzymes that counter and reduce the effectiveness of numerous toxic secondary metabolic products produced by plants. One such enzyme group, mixed function oxidases (MFOs), detoxify harmful plant compounds by catalyzing oxidative reactions. Cytochrome P450 oxidases (or P-450), a specific class of MFO, have been specifically connected to detoxification of plant secondary metabolic products. One group linked herbivore feeding on plant material protected by chemical defenses with P-450 detoxification in larval tobacco hornworms. The induction of P-450 after initial nicotine ingestion allowed the larval tobacco hornworms to increase feeding on the toxic plant tissues.

Herbivores may also produce salivary enzymes that reduce the degree of defense generated by a host plant. The enzyme glucose oxidase, a component of saliva for the caterpillar *Helicoverpa zea*, counteracts the production of induced defenses in tobacco. Similarly, aphid saliva reduces its host's induced response by forming a barrier between the aphid's stylet and the plant cells.

Behavioral adaptations

Herbivores can avoid plant defenses by eating plants selectively in space and time. For the winter moth, feeding on oak leaves early in the season maximized the amount of protein and nutrients available to the moth, while minimizing the amount of tannins produced by the tree. Herbivores can also spatially avoid plant defenses. The piercing mouthparts of species in *Hemiptera* allow them to feed around areas of high toxin concentration. Several species of caterpillar feed on maple leaves by "window feeding" on pieces of leaf and avoiding the tough areas, or those with a high lignin concentration. Similarly, the cotton leaf perforator selectively avoids eating the epidermis and pigment glands of their hosts, which contain defensive terpenoid aldehydes. Some plants only produce toxins in small amounts, and rapidly deploy them to the area under attack. Some beetles counter this adaptation by attacking target plants in groups, thereby allowing each individual beetle to avoid ingesting too much toxin. Some animals ingest large amounts of poisons in their food, but then eat clay or other minerals, which neutralize the poisons. This behavior is known as geophagy.

Plant defense may explain, in part, why herbivores employ different life history strategies. Monophagous species (animals that eat plants from a single genus) must produce specialized enzymes to detoxify their food, or develop specialized structures to deal with sequestered chemicals. Polyphagous species (animals that eat plants from many different families), on the other hand, produce more detoxyfying enzymes (specifically MFO) to deal with a range of plant chemical defenses. Polyphagy often develops when an herbivore's host plants are rare as a necessity to gain enough food. Monophagy is favored when there is interspecific competition for food, where specialization often increases an animals' competitive ability to use a resource.

Microbial symbionts

Galls (upper left and right) A knopper gall formed on an acorn on the branch of an English Oak tree by the parthenogenetic gall wasp *Andricus quercuscalicis*.

Herbivores are unable to digest complex cellulose and rely on mutualistic, internal symbiotic bacteria, fungi, or protozoa to break down cellulose so it can be used by the herbivore. Microbial symbionts also allow herbivores to eat plants that would otherwise be inedible by detoxifying plant secondary metabolites. For example, fungal symbionts of cigarette beetles (*Lasioderma serricorne*) use certain plant allelochemicals as their source of carbon, in addition to producing detoxification enzymes (esterases) to get rid of other toxins. Microbial symbionts also assist in the acquisition of plant material by weakening a host plant's defenses. Some herbivores are more successful at feeding on damaged hosts. As an example, several species of bark beetle introduce blue stain fungi of the genera *Ceratocystis* and *Ophiostoma* into trees before feeding. The blue stain fungi cause lesions that reduce the trees' defensive mechanisms and allow the bark beetles to feed.

Host manipulation

Herbivores often manipulate their host plants to use them better as resources. Herbivorous insects favorably alter the microhabitat in which the herbivore feeds to counter existing plant defenses. For example, caterpillars from the families Pyralidae and Ctenuchidae roll mature leaves of the neotropical shrub *Psychotria horizontalis* around an expanding bud that they consume. By rolling the leaves, the insects reduce the amount of light reaching the bud by 95%, and this shading prevents leaf toughness and leaf tannin concentrations in the expanding bud, while maintaining the amount of nutritional gain of nitrogen. Lepidoptera larvae also tie leaves together and feed on the inside of the leaves to decrease the effectiveness of the phototoxin hypericin in St. John's-wort.

Herbivores also manipulate their microhabitat by forming galls, plant structures made of plant tissue but controlled by the herbivore. Galls act as both domatia (housing), and food sources for the gall maker. The interior of a gall is composed of edible nutritious tissue. Aphid galls in narrow leaf cottonwood (*Populus angustifolia*) act as "physiologic sinks," concentrating resources in the gall from the surrounding plant parts. Galls may also provide the herbivore protection from predators.

Some herbivores use feeding behaviors that are capable of disarming the defenses of their host plants. One such plant defensive strategy is the use of latex and resin canals that contain sticky toxins and digestibility reducers. These canal systems store fluids under pressure, and when ruptured (i.e. from herbivory) secondary metabolic products flow to the release point. Herbivores can evade this defense, however, by damaging the leaf veins. This technique minimizes the outflow of latex or resin beyond the cut and allows herbivores to freely feed above the damaged section. Several strategies are employed by herbivores to relieve canal pressure, including vein cutting and trenching. The technique used by the herbivore corresponds to the architecture of the canal system. Dussourd and Denno examined the behavior of 33 species of insect herbivores on 10 families of plants with canals and found that herbivores on plants with branching canal systems used vein cutting, while herbivores found on plants with net-like canal systems employed trenching to evade plant defenses.

Herbivore use of plant chemicals

Monarch butterflies obtain poison from the plants they feed on as larvae, their distinctive appearance serving to warn predators.

Plant chemical defenses can be used by herbivores, by storing eaten plant chemicals, and using them in defense against predators. To be effective defensive agents, the sequestered chemicals cannot be metabolized into inactive products. Using plant chemicals can be costly to herbivores because it often requires specialized handling, storage, and modification. This cost can be seen when plants that use chemical defenses are compared to those plants that do not, in situations when herbivores are excluded. Caterpillar and adult monarch butterflies store cardiac glycosides from milkweed, making these organisms distasteful. After eating a monarch caterpillar or butterfly, the bird predator will usually vomit, leading the bird to avoid eating similar looking butterflies in the future. Two different species of milkweed bug in the family Hemiptera, *Lygaeus kalmii* and Large Milkweed Bug *(Oncopeltus fasciatus)*, are colored with bright orange and black, and are said to be aposematically colored, in that they "advertise" their distastefulness by being brightly colored.

Secondary metabolic products can also be useful to herbivores due to the antibiotic properties of the toxins, which can protect herbivores against pathogens. Additionally, secondary metabolic products can act as cues to identify a plant for feeding or oviposition (egg laying) by herbivores.

Chapter 5

Plant Reproduction

Plant reproduction is the production of new individuals or offspring in plants, which can be accomplished by sexual or asexual means. Sexual reproduction produces offspring by the fusion of gametes, resulting in offspring genetically different from the parent or parents. Asexual reproduction produces new individuals without the fusion of gametes, genetically identical to the parent plants and each other, except when mutations occur. In seed plants, the offspring can be packaged in a protective seed, which is used as an agent of dispersal.

Asexual reproduction

Plants have two main types of asexual reproduction in which new plants are produced that are genetically identical clones of the parent individual. "Vegetative" reproduction involves a vegetative piece of the original plant (budding, tillering, etc.) and is distinguished from "apomixis", which is a "replacement" for sexual reproduction, and in some cases involves seeds. Apomixis occurs in many plant species and also in some non-plant organisms.

Natural vegetative reproduction is mostly a process found in herbaceous and woody perennial plants, and typically involves structural modifications of the stem or roots and in a few species leaves. Most plant species that employ vegetative reproduction, do so as a means to perennialize the plants, allowing them to survive from one season to the next and often facilitating their expansion in size. A plant that persists in a location through vegetative reproduction of individuals constitutes a clonal colony, a single ramet, or apparent individual, of a clonal colony is genetically identical to all others in the same colony. The distance that a plant can move during vegetative reproduction is limited, though some plants can produce ramets from branching rhizomes or stolons that cover a wide area, often in only a few growing seasons. In a sense, this process is not one of "reproduction" but one of survival and expansion of biomass of the individual. When an individual organism increases in size via cell multiplication and remains intact, the process is called "vegetative growth". However, in vegetative reproduction, the new plants that result are new individuals in almost every respect except genetic. A major disadvantage to vegetative reproduction, is the transmission of pathogens from parent to daughter plants; it is uncommon for pathogens to be transmitted from the plant to its seeds, though there are occasions when it occurs.

Seeds generated by apomixis are a means of asexual reproduction, involving the formation and dispersal of seeds that do not originate from the fertilization of the embryos. Hawkweed (*Hieracium*), dandelion (*Taraxacum*), some Citrus (*Citrus*) and Kentucky blue grass (*Poa pratensis*) all use this form of asexual reproduction. Pseudogamy occurs in some plants that have apomictic seeds, where pollination is often needed to initiate embryo growth, though the pollen contributes no genetic material to the developing offspring. Other forms of apomixis occur in plants also, including the generation of a plantlet in replacement of a seed or the generation of bulbils instead of flowers, where new cloned individuals are produced.

Natural vegetative structures

The **rhizome** is a modified underground stem serving as an organ of vegetative reproduction, e. g. Polypody, Iris, Couch Grass and Nettles.

Prostrate aerial stems, called **runners** or **stolons** are important vegetative reproduction organs in some species, such as the strawberry, numerous grasses, and some ferns.

Adventitious buds form on roots near the ground surface, on damaged stems (as on the stumps of cut trees), or on old roots. These develop into above-ground stems and leaves.

A form of budding called **suckering** is the reproduction or regeneration of a plant by shoots that arise from an existing root system. Species that characteristically produce suckers include Elm (*Ulmus*), Dandelion (*Taraxacum*), and members of the Rose Family (*Rosa*).

Another type of a vegetative reproduction is the production of bulbs. Plants like onion (*Allium cepa*), hyacinth (*Hyacinth*), narcissus (*Narcissus*) and tulips (*Tulipa*) reproduce by forming bulbs.

Other plants like potatoes (*Solanum tuberosum*) and dahlia (*Dahlia*) reproduce by a method similar to bulbs: they produce tubers.

Gladioli and crocuses (*Crocus*) reproduce by forming a bulb-like structure called a corm.

Human uses of asexual reproduction

The most common form of plant reproduction utilized by people is seeds, but a number of asexual methods are utilized which are usually enhancements of natural processes, including: cutting, grafting, budding, layering, division, sectioning of rhizomes or roots, stolons, tillers (suckers) and artificial propagation by laboratory tissue cloning. Asexual methods are most often used to propagate cultivars with individual desirable characteristics that do not come true from seed. Fruit tree propagation is frequently performed by budding or grafting desirable cultivars (clones), onto rootstocks that are also clones, propagated by layering.

In horticulture, a "cutting" is a branch that has been cut off from a mother plant below an internode and then rooted, often with the help of a rooting liquid or powder containing hormones. When a full root has formed and leaves begin to sprout anew, the clone is a self-sufficient plant, genetically identical to the mother plant. Examples include cuttings from the stems of blackberries (*Rubus occidentalis*), African violets (*Saintpaulia*), verbenas (*Verbena*) to produce new plants. A related use of cuttings is grafting, where a stem or bud is joined onto a different stem. Nurseries offer for sale trees with grafted stems that can produce four or more varieties of related fruits, including apples. The most common usage of grafting is the propagation of cultivars onto already rooted plants, sometimes the rootstock is used to dwarf the plants or protect them from root damaging pathogens.

Since vegetatively propagated plants are clones, they are important tools in plant research. When a clone is grown in various conditions, differences in growth can be ascribes to environmental effects instead of genetic differences.

Sexual reproduction

Sexual reproduction involves two fundamental processes, meiosis which rearranges the genes and reduces the number of chromosomes, and fusion of gametes which restores the chromosome to a complete diploid number. In between these two processes, different types of plants vary. In plants and algae that undergo alternation of generations, a gametophyte is the multicellular structure, or phase, that is haploid, containing a single set of chromosomes:

The gametophyte produces male or female gametes (or both), by a process of cell division called mitosis. The fusion of male and female gametes produces a diploid zygote, which develops by repeated mitotic cell divisions into a multicellular sporophyte. Because the sporophyte is the product of the fusion of two haploid gametes, its cells are diploid, containing two sets of chromosomes. The mature sporophyte produces spores by a process called meiosis, sometimes referred to as "reduction division" because the chromosome pairs are separated once again to form single sets. The spores are therefore once again haploid and develop into a haploid gametophyte. In land plants such as ferns, mosses and liverworts the gametophyte is very small, as in ferns and their relatives. In flowering plants (angiosperms) It is reduced to only a few cells, where the female gametophyte (embryo sac) is known as a megagametophyte and the male gametophyte (pollen) is called a microgametophyte.

History of sexual reproduction

Unlike animals, plants are immobile, and cannot seek out sexual partners for reproduction. In the evolution of early plants, abiotic means, including water and wind, transported sperm for reproduction. The first plants were aquatic and released sperm freely into the water to be carried with the currents. Primitive land plants like liverworts and mosses had motile sperm that swam in a thin film of water or were splashed in water droplets from the male reproduction organs onto the female organs. As taller and more complex plants evolved, modifications in the alternation of generations evolved; in the Paleozoic era progymnosperms reproduced by using spores dispersed on the wind. The seed plants including seed ferns, conifers and cordaites, which were all gymnosperms, evolved 350 million years ago; they had pollen grains that contained the male gametes for protection of the sperm during the process of transfer from the male to female parts. It is believed that insects fed on the pollen, and plants thus evolved to use insects to actively carry pollen from one plant to the next. Seed producing plants, which include the angiosperms and the gymnosperms, have heteromorphic alternation of generations with large sporophytes containing much reduced gametophytes. Angiosperms have distinctive reproductive organs called flowers, with carpels, and the female gametophyte is greatly reduced to a female embryo sac, with as few as eight cells. The male gametophyte consists of the pollen grains. The sperm of seed plants are non-motile, except for two older groups of plants, the Cycadophyta and the Ginkgophyta, which have flagellated sperm.

Flowering plants

Flowering plants are the dominant plant form on land and they reproduce by sexual and asexual means. Often their most distinguishing feature is their reproductive organs, commonly called flowers. Sexual reproduction in flowering plants involves the production of male and female gametes, the transfer of the male gametes to the female ovules in a process called pollination. After pollination occurs, fertilization happens and the ovules grow into seeds with in a fruit. After the seeds are ready for dispersal, the fruit ripens and by various means the seeds are freed from the fruit and after varying amounts of time and under specific conditions the seeds germinate and grow into the next generation.

The anther produces male gametophytes, the sperm is produced in pollen grains, which attach to the stigma on top of a carpel, in which the female gametophytes (inside ovules) are located. After the pollen tube grows through the carpel's style, the sex cell nuclei from the pollen grain migrate into the ovule to fertilize the egg cell and endosperm nuclei within the female gametophyte in a process termed double fertilization. The resulting zygote develops into an embryo, while the triploid endosperm (one sperm cell plus two female cells) and female tissues of the ovule give rise to the surrounding tissues in the developing seed. The ovary, which produced the female gametophyte(s), then grows into a fruit, which surrounds the seed(s). Plants may either self-pollinate or cross-pollinate. Nonflowering plants like ferns, moss and liverworts use other means of sexual reproduction.

Adaptations

An Orchid flower.

Flowers of wind pollinated plants tend to lack petals and or sepals. Typically large amounts of pollen are produced and pollination often occurs early in the growing season before leaves can interfere with the dispersal of the pollen. Many trees and all grasses and sedges are wind pollinated, as such they have no need for large fancy flowers. In plants that use insects or other animals to move pollen from one flower to the next, plants have developed greatly modified flower parts to attract pollinators and to facilitate the movement of pollen from one flower to the insect and from the insect back to the next flower. Plants have a number of different means to attract pollinators including color, scent, heat, nectar glands, eatable pollen and flower shape. Along with modifications involving the above structures two other conditions play a very important role in the sexual reproduction of flowering plants, the first is timing of flowering and the other is the size or number of flowers produced. Often plant species have a few large, very showy flower while others produce many small flowers, often flowers are collected together into large inflorescences to maximize their visual effect, becoming more noticeable to passing pollinators. Flowers are attraction strategies and sexual expressions are functional strategies used to produce the next generation of plants, with pollinators and plants having co-evolved, often to some extraordinary degrees, very often rendering mutual benefit.

Flower heads showing disk and ray florets.

The largest family of flowering plants is the orchids (Orchidaceae), estimated by some specialists to include up to 35,000 species, which often have highly specialized flowers used to attract insects and facilitate pollination. The stamens are modified to produce pollen in clusters called pollinium, which are attached to insects when crawling into the flower. The flower shapes are modified to force insects to pass by the pollen, which is "glued" to the insect. Some orchids are even more highly specialized, with flower shapes that mimic the shape of insects to attract them to 'mate' with the flowers, a few even have scents that mimic insect pheromones.

Another large group of flowering plants is the Asteraceae or sunflower family with close to 22,000 species, which also have highly modified inflorescences that are flowers collected together in heads composed of a composite of individual flowers called florets. Heads with florets of one sex, when the flowers are pistillate or functionally staminate, or made up of all bisexual florets, are called homogamous and can include discoid and liguliflorous type heads. Some radiate heads may be homogamous too. Plants with heads that have florets of two or more sexual forms are called heterogamous and include radiate and disciform head forms, though some radiate heads may be heterogamous too.

Ferns

Ferns typically produce large diploid sporophytes with rhizomes, roots and leaves; and on fertile leaves called sporangium, spores are produced. The spores are released and germinate to produce short, thin gametophytes that are typically heart shaped, small and green in color. The gametophytes or thallus, produce both motile sperm in the antheridia and egg cells in separate archegonia. After rains or when dew deposits a film of water, the motile sperm are splashed away from the antheridia, which are normally produce on the top side of the thallus, and swim in the film of water to the antheridia where they fertilize the egg. To promote out crossing or cross fertilization the sperm are released before the eggs are receptive of the sperm, making it more likely that the sperm will fertilize the eggs of different thallus. A zygote is formed after fertilization, which grows into a new sporophytic plant. The condition of having separate sporephyte and gametophyte plants is call alternation of generations. Other plants with similar reproductive means include the *Psilotum*, *Lycopodium*, *Selaginella* and *Equisetum*.

Bryophytes

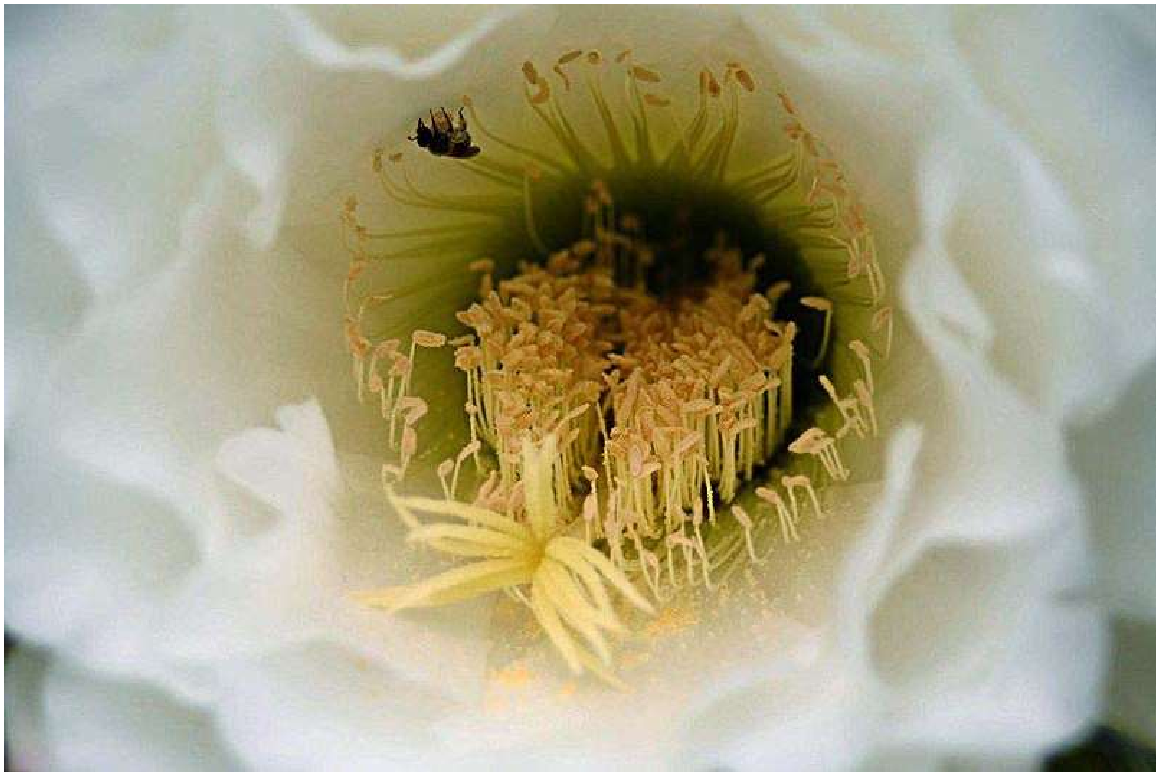
The bryophytes, which include liverworts, hornworts and mosses, reproduce both sexually and vegetatively. The gametophyte is the most commonly known phase of the plant. An early developmental stage in the gametophyte of mosses (immediately following germination of the meiospore) is called the protonema. All are small plants found growing in moist locations and like ferns, have motile sperm with flagella and need water to facilitate sexual reproduction. These plants start as a haploid spore that grows into the dominate form, which is a multicellular haploid body with leaf-like structures that photosynthesize. Haploid gametes are produced in antherida and archegonia by mitosis. The sperm released from the antherida respond to chemicals released by ripe archegonia and swim to them in a film of water and fertilize the egg cells thus producing a zygote. The zygote divides by mitotic division and grows into a sporophyte that is diploid. The multicellular diploid sporophyte produces structures called spore capsules, which are connected by seta to the archegonia. The spore capsules produce spores by meiosis, when ripe the capsules burst open and the spores are released. Bryophytes show considerable variation in their breeding structures and the above is a basic outline. Also in some species each plant is one sex while other species produce both sexes on the same plant.

Sexual expression

Many plants have evolved a complex sexuality, which is expressed in different combinations of their reproductive organs. Some species have separate male and female individuals, some have separate male and female flowers on the same plant, abut the majority of plants have both male and female parts in the same flower. Some plants change their gender expression depending on a number of factors like age, time of day, or because of environmental conditions. Plant sexuality also varies within different populations of some species.

Chapter 6

Plant Sexuality



Close-up of an *Echinopsis spachiana* flower, showing both carpels (only the styles and stigmas are visible) and stamens, making it a perfect flower.

Plant sexuality covers the wide variety of sexual reproduction systems found across the plant kingdom.

Among all living organisms, flowers, which are the reproductive structures of angiosperms, are the most varied physically and show the greatest diversity in methods of reproduction of all biological systems. Carolus Linnaeus (1735 and 1753) proposed a system of classification of flowering plants based on plant structures, since plants employ many different morphological adaptations involving sexual reproduction, flowers played an important role in that classification system. Later on Christian Konrad Sprengel (1793) studied plant sexuality and called it the "revealed secret of nature" and for the first time it was understood that the pollination process involved both biotic and abiotic interactions (Charles Darwin's theories of natural selection utilized this work to promote his idea of evolution). Plants that are not flowering plants (green alga, mosses, liverworts, hornworts, ferns and gymnosperms such as conifers) also have complex interplays between morphological adaptation and environmental factors in their sexual reproduction. The breeding system, or how the sperm from one plant fertilizes the ovum of another, is the single most important determinant of the mating structure of nonclonal plant populations. The mating structure or morphology of the flower parts and their arrangement on the plant in turn controls the amount and distribution of genetic variation, a central element in the evolutionary process.

Terminology

The flowers of angiosperms are determinate shoots that have sporophylls. The parts of flowers are named by scientists and show great variation in shape, these flower parts include sepals, petals, stamens and carpels. As a group the sepals form the calyx and as a group the petals form the corolla, together the corolla and the calyx is called the perianth. In flowers which possess indistinguishable calyx and corolla, the individual units are then called "tepals". The stamens collectively are called the androecium and the carpels collectively are called the gynoecium.

The complexity of the systems and devices used by plants to achieve sexual reproduction has resulted in botanists and evolutionary biologists using numerous terms to describe physical structures and functional strategies. Dellaporta and Calderon-Urrea (1993) list and define a variety of terms used to describe the modes of sexuality at different levels in flowering plants. This list is reproduced here, generalized to fit more than just plants that have flowers, and expanded to include other terms and more complete definitions.

The Alder is **monoecious**. Shown here: maturing male flower catkins on right, last year's female catkins on left

Individual reproductive unit (a flower in angiosperms)

- **Bisexual** or **perfect** flowers have both male (androecium) and female (gynoecium) reproductive structures, including stamens, carpels, and an ovary. Flowers that contain both androecium and gynoecium are called androgynous or hermaphroditic. Examples of plants with perfect or bisexual flowers include the lily, rose, and most plants with large showy flowers, though a perfect flower does not have to have petals or sepals. Other terms widely used are **hermaphrodite**, **monoclinous**, and **synoecious**. A **complete** flower is a perfect flower with petals and sepals.
- **Unisexual**: Reproductive structure that is either functionally male or functionally female. In angiosperms this condition is also called **diclinous**, **imperfect**, or **incomplete**.

Individual plant sexuality

Many plants have complete flowers that have both male and female parts, others only have male or female parts and still other plants have flowers on the same plant that are a mix of male and female flowers. Some plants even have mixes that include all three types of flowers, where some flowers are only male, some are only female and some are both male and female. A distinction needs to be made between arrangements of sexual parts and the expression of sexuality in single plants versus the larger plant population. Some plants also undergo what is called **Sex-switching**, like *Arisaema triphyllum* which express sexual differences at different stages of growth. In some arums smaller plants produce all or mostly male flowers and as plants grow larger over the years the male flowers are replaced by more female flowers on the same plant. *Arisaema triphyllum* thus covers a multitude of sexual conditions in its life time; from nonsexual juvenile plants to young plants that are all male, as plants grow larger they have a mix of both male and female flowers, to large plants that have mostly female flowers. Other plant populations have plants that produce more male flowers early in the year and as plants bloom later in the growing season they produce more female flowers. In plants like *Thalictrum dioicum* all the plants in the species are either male or female.

Specific terms are used to describe the sexual expression of individual plants within a population.

- **Hermaphrodite**, a plant that has only bisexual reproductive units (flowers, conifer cones, or functionally equivalent structures). In angiosperm terminology a synonym is **monoclinous** from the Greek "one bed".
- **Monoecious**, an individual that has both male and female reproductive units (flowers, conifer cones, or functionally equivalent structures) on the same plant; from Greek for "one household". Individuals bearing separate flowers of both sexes at the same time are called simultaneously or synchronously monoecious. Individuals that bear flowers of one sex at one time are called consecutively monoecious; plants may first have single sexed flowers and then later have flowers of the other sex. **Protoandrous** describes individuals that function first as males and then change to females; **protogynous** describes individuals that function first as females and then change to males.
- **Dioecious** refers to a plant population having separate male and female plants. That is, no individual plant of the population produces both microgametophytes (pollen) and megagametophytes (ovules); individual plants are either male or female. From Greek for "two households". [Individual plants are not called dioecious; they are either gynoecious (female plants) or androecious (male plants).]
    - **Androecious**, plants producing male flowers only, produce pollen but no seeds, the male plants of a dioecious population.
    - **Gynoecious**, plants producing female flowers only, produces seeds but no pollen, the female of a dioecious population. In some plant populations, all individuals are gynoecious with non sexual reproduction used to produce the next generation.
- **Subdioecious**, a tendency in some dioecious populations to produce monoecious plants. The population produces normally male or female plants but some are hermaphroditic, with female plants producing some male or hermaphroditic flowers or vice versa. The condition is thought to represent a transition between hermaphroditism and dioecy.
    - **Gynomonoecious** has both hermaphrodite and female structures.

  - **Andromonoecious** has both hermaphrodite and male structures.
  - **Subandroecious** has mostly male flowers, with a few female or hermaphrodite flowers.
  - **Subgynoecious** has mostly female flowers, with a few male or hermaphrodite flowers.
- **Polygamy**, plants with male, female, and perfect (hermaphrodite) flowers on the same plant, called **trimonoecious** or **polygamomonoecious** plants. A polygamous inflorescence has both unisexual and bisexual flowers.
  - **Trimonoecious** (polygamous) - male, female, and hermaphrodite floral morphs all appear on the same plant.
- **Diclinous** ("two beds"), an angiosperm term, includes all species with unisexual flowers, although particularly those with *only* unisexual flowers, i.e. the monoecious and dioecious species.

Holly (*Ilex aquifolium*) is dioecious: (above) shoot with flowers from male plant; (top right) male flower enlarged, showing stamens with pollen and reduced, sterile stigma; (below) shoot with flowers from female plant; (lower right) female flower enlarged, showing stigma and reduced, sterile stamens with no pollen

Plant population

Most often plants show uniform sexual expression in populations or species wide and specific terms are used to describe the sexual expression of the population or species.

- **Hermaphrodite**, plants whose flowers have both male and female parts.

- **Monoecious** plants have separate male and female flowers on the same plant. A plant population where the male and female organs are found in different flowers on the same plant. These plants are often wind pollinated. Examples of monoecious plants include corn, birch and pine trees, and most fig species.
- **Dioecious**, all plants are either female or male. The American Holly (*Ilex opaca*) is a famous example.
- **Androdioecious**, both male and hermaphrodite plants present.
- **Gynodioecious**, both female and hermaphrodite plants present. In some plants, strictly female plants are produced by the degeneration of the tapetum, a shell-like structure in the anther of a flower where the pollen cells form,
- **Gynoecy** plants are all females in a population, often regulated by environmental factors like temperature, photo period or water availability.
- **Polygamous**, when there is a mix of hermaphrodite and unisexual plants in the natural population.
    - **Subdioecious**, population of unisexual (dioecious) plants, with monoecious individuals too.
    - **Trioecious**, sometimes used in place of subdioecious when male, female, and hermaphrodite plants are more equally mixed within the same population.
- **Polygamodioecious**, having bisexual and male flowers on some plants, and bisexual and female flowers on others.

About 11% of all angiosperms are strictly dioecious or monoecious. Intermediate forms of sexual dimorphism, including gynodioecy and androdioecy, represent 7% of the species examined of a survey of 120,000 plant species. In the same survey, 10% of the species contain both unisexual and bisexual flowers.

The majority of plant species use **allogamy**, also called cross-pollination, as a means of breeding. Many plants are self-fertile and the male parts can pollinate the female parts of the same flower and/or same plant. Some plants use a method known as self-incompatibility to promote outcrossing. In these plants, the male organs cannot fertilize the female parts of the same plant; other plants produce male and female flowers at different times to promote outcrossing.

Dichogamy is common in flowering plants, and occurs when bisexual (perfect) flowers (or sometimes entire plants) produce pollen when the stigmas of the same flower is not receptive of the pollen. This promotes outcrossing by limiting what is called autopollination or self pollination or selfing. These plants are called dichogamous. Some plants have bisexual flowers but the pollen is produced before the stigma of the same flower is receptive of pollen, these are described as **protandrous** flowers; in a similar way, **protogyny** describes flowers that have stigmas that can accept pollen before the same flower or plant sheds its pollen.

Dichogamy, also known as sequential hermaphrodism, is the separation in time of gender expression in a hermaphroditic organism, a characteristic of some fishes, gastropods, crustaceans and most flowering plants. This is the opposite of simultaneous hermaphrodites, or homogamy.

In flowering plants

In the context of the plant sexuality of flowering plants (angiosperms), there are two forms of dichogamy: ***protogyny***—female function precedes male function—and ***protandry***—male function precedes female function.

Historically, dichogamy has been regarded as a mechanism for reducing inbreeding (e.g., Darwin, 1862). However, a survey of the angiosperms found that self-incompatible (SI) plants, which are incapable of inbreeding, were as likely to be dichogamous as were self-compatible (SC) plants (Bertin, 1993). This finding led to a reinterpretation of dichogamy as a more general mechanism for reducing the impact of pollen-pistil interference on pollen import and export (reviewed in Lloyd & Webb, 1986; Barrett, 2002). Unlike the inbreeding-avoidance hypothesis, which focused on female function, this interference-avoidance hypothesis considers both gender functions.

In many hermaphroditic species, the close physical proximity of anthers and stigma makes interference unavoidable, either within a flower or between flowers on an inflorescence. Within-flower interference, which occurs when either the pistil interrupts pollen removal or the anthers prevent pollen deposition, can result in autonomous or facilitated self-pollination (Lloyd & Webb, 1986; Lloyd & Schoen, 1992). Between-flower interference results from similar mechanisms, except that the interfering structures occur on different flowers within the same inflorescence and it requires pollinator activity. This results in geitonogamous pollination, the transfer of pollen between flowers of the same individual (Lloyd & Schoen, 1992; de Jong et al., 1993). In contrast to within-flower interference, geitonogamy necessarily involves the same processes as outcrossing: pollinator attraction, reward provisioning, and pollen removal. Therefore, between-flower interference not only carries the cost of self-fertilization (inbreeding depression; Charlesworth & Charlesworth, 1987; Husband & Schemske, 1996), but also reduces the amount of pollen available for export (so-called "pollen discounting"; Harder & Wilson, 1998). Because pollen discounting diminishes outcross siring success, interference avoidance may be an important evolutionary force in floral biology (Harder & Barrett, 1995, 1996; Harder & Wilson, 1998; Barrett, 2002).

Dichogamy may reduce between-flower interference by minimizing the temporal overlap between stigma and anthers within an inflorescence. Large inflorescences attract more pollinators, potentially enhancing reproductive success by increasing pollen import and export (Schemske, 1980; Queller, 1983; Bell, 1985; Geber, 1985; Schmid-Hempel & Speiser, 1988; Klinkhamer & de Jong, 1990). However, large inflorescences also increase the opportunities for both geitonogamy and pollen discounting, so that the opportunity for between-flower interference increases with inflorescence size (Harder & Barrett, 1996). Consequently, the evolution of floral display size may represent a compromise between maximizing pollinator visitation and minimizing geitonogamy and pollen discounting (Klinkhamer & de Jong, 1993; Barrett et al., 1994; Holsinger, 1996; Snow et al., 1996).

Protandry may be particularly relevant to this compromise, because it often results in an inflorescence structure with female phase flowers positioned below male phase flowers (Bertin & Newman, 1993). Given the tendency of many insect pollinators to forage upwards through inflorescences (Galen & Plowright, 1988), protandry may enhance pollen export by reducing between-flower interference (Darwin, 1862; Harder et al., 2000). Furthermore, this enhanced pollen export should increase as floral display size increases, because between-flower interference should increase with floral display size. These effects of protandry on between-flower interference may decouple the benefits of large inflorescences from the consequences of geitonogamy and pollen discounting. Such a decoupling would provide a significant reproductive advantage through increased pollinator visitation and siring success.

Harder et al. (2000) demonstrated experimentally that dichogamy both reduced rates of self-fertilization and enhanced outcross siring success through reductions in geitonogamy and pollen discounting, respectively. Routley & Husband (2003)examined the influence of inflorescence size on this siring advantage and found a bimodal distribution with increased siring success with both small and large display sizes.

Flower morphology

A species such as the ash tree (*Fraxinus excelsior* L.), demonstrates the possible range of variation in morphology and functionality exhibited by flowers with respect to gender. Flowers of the ash are wind-pollinated and lack petals and sepals. Structurally, the flowers may be either male or female, or even hermaphroditic, consisting of two anthers and an ovary. A male flower can be morphologically male or hermaphroditic, with anthers and a rudimentary gynoecium. Ash flowers can also be morphologically female, or hermaphroditic and functionally female.

The Asteraceae or sunflower family with close to 22,000 species, have highly modified inflorescences that are flowers collected together in heads composed of a composite of individual flowers called florets. Heads with florets of one sex, when the flowers are pistillate or functionally staminate, or made up of all bisexual florets, are called homogamous and can include discoid and liguliflorous type heads. Some radiate heads may be homogamous too. Plants with heads that have florets of two or more sexual forms are called heterogamous and include radiate and disciform head forms, though some radiate heads may be heterogamous too.

Evolution

Angiosperms

It is thought that flowering plants evolved from a common hermaphrodite ancestor, and that dioecy evolved from hermaphroditism. Hermaphroditism is very common in flowering plants; over 85% are hermaphroditic, whereas only about 6-7% are dioecious and 5-6% are monoecious.

A fair degree of correlation (though far from complete) exists between dioecy/sub-dioecy and plants that have seeds dispersed by birds (both nuts and berries). It is hypothesized that the concentration of fruit in half of the plants increases dispersal efficiency; female plants can produce a higher density of fruit as they do not expend resources on pollen production, and the dispersal agents (birds) need not waste time looking for fruit on male plants. Other correlations with dioecy include: tropical distribution, woody growth form, perenniality, fleshy fruits, and small, green flowers.

Plant growth regulators can be used to alter flower and plant sexuality, in cucumbers ethephon is used to delay staminate flowering and transforms monoecious lines into all-pistillate or female lines. Gibberellins also increase maleness in cucumbers. Cytokinins have been used in grapes that have undeveloped pistils to produce functional female organs and seed formation. Grapes are good examples of bisexual plant.

Chapter 7

Alternation of Generations

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

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

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

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

Definition

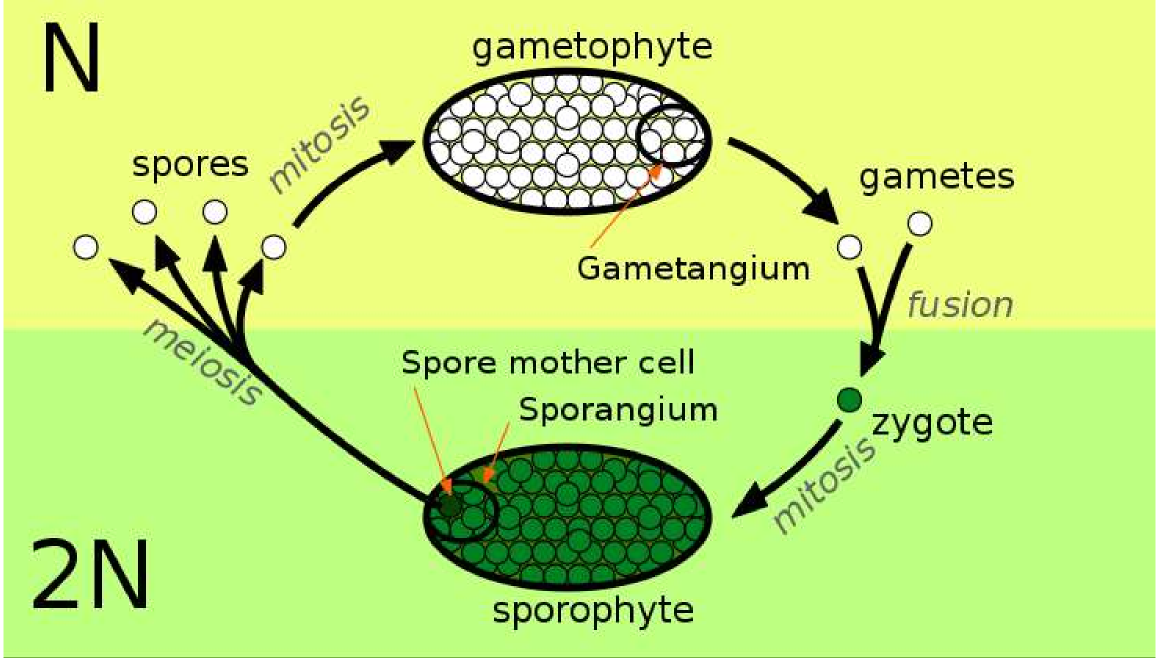
The discussion of 'alternation of generations' above treats the alternation of a multicellular diploid form with a multicellular haploid form as the defining characteristic, regardless of whether these forms are free-living or not. In some species, such as the alga *Ulva lactuca*, the diploid and haploid forms are indeed both free-living independent organisms, essentially identical in appearance. The free-swimming gametes form a zygote which germinates into a diploid sporophyte; the free-swimming spores germinate into a haploid gametophyte. Alternation of *generations* is an appropriate term.

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

Alternation of generations in plants

Fundamental elements

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



- Two single-celled haploid gametes, each containing N unpaired chromosomes, fuse to form a single-celled diploid zygote, which now contains N paired chromosomes, i.e. 2N chromosomes in total.
- The single-celled diploid zygote germinates, dividing by the normal process (mitosis), which maintains the number of chromosomes at 2N. The result is a multi-cellular diploid organism, called the *sporophyte* (because at maturity it produces spores).
- When it reaches maturity, the sporophyte produces one or more **sporangia** (singular sporangium) which are the organs which produce diploid spore mother cells (sporocytes). These divide by a special process (meiosis) which reduces the number of chromosomes by a half. This results in four single-celled haploid spores, each containing N unpaired chromosomes.
- The single-celled haploid spore germinates, dividing by the normal process (mitosis), which maintains the number of chromosomes at N. The result is a multi-cellular haploid organism, called the *gametophyte* (because at maturity it produces gametes).
- When it reaches maturity, the gametophyte produces one or more **gametangia** (singular gametangium) which are the organs which produce haploid gametes. At least one kind of gamete possesses some mechanism for reaching another gamete in order to fuse with it.

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

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

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

Variations

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

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

Possible variations are:

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

Gametophyte of *Mnium hornum*, a moss.

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

Sporophyte of *Blechnum discolor*, a fern.

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

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

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

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

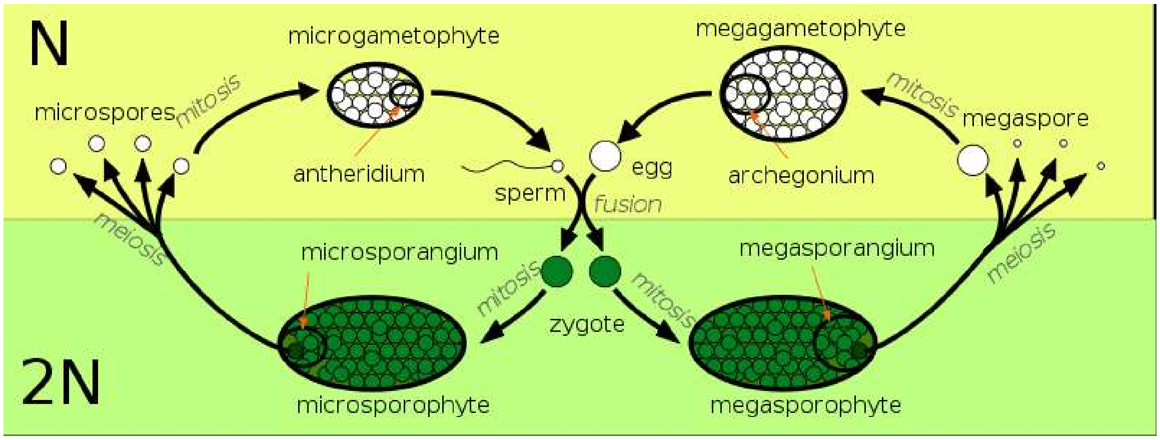
        - *Antheridia and archegonia occur on different gametophytes,* which are then called **dioicous**.
          The moss *Mnium hornum* has the gametophyte as the dominant generation. It is dioicous: male plants produce only antheridia in terminal rosettes, female plants produce only archegonia in the form of stalked capsules. Seed plants are also dioicous; however, the extreme reduction of the gametophyte, particularly the microgametophyte, means that the antheridia and archegonia are microscopic.
- *Differentiation of the spores.*
    - *All spores the same size* (**homospory** or isospory).
      Horsetails (species of *Equisetum*) have spores which are all of the same size.
    - *Spores of two distinct sizes* (**heterospory** or anisospory): larger **megaspores** and smaller **microspores**. When the two kinds of spore are produced in different kinds of sporangia, these are called **megasporangia** and **microsporangia**. A megaspore often (but not always) develops at the expense of the other three cells resulting from meiosis, which abort.
        - *Megasporangia and microsporangia occur on the same sporophyte,* which is then called **monoecious**.
          Most flowering plants fall into this category. Thus the flower of a lily contains six stamens (the microsporangia) which produce microspores which develop into pollen grains (the microgametophytes), and three fused carpels (the megasporangia) which produce megaspores which develop into ovules (the megagametophytes). In other plants, such as hazel, some flowers have only stamens, others only carpels, but the same plant (i.e. sporophyte) has both kinds of flower and so is monoecious.

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

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

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

A complex life cycle



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

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

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

Life cycles of different plant groups

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

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

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

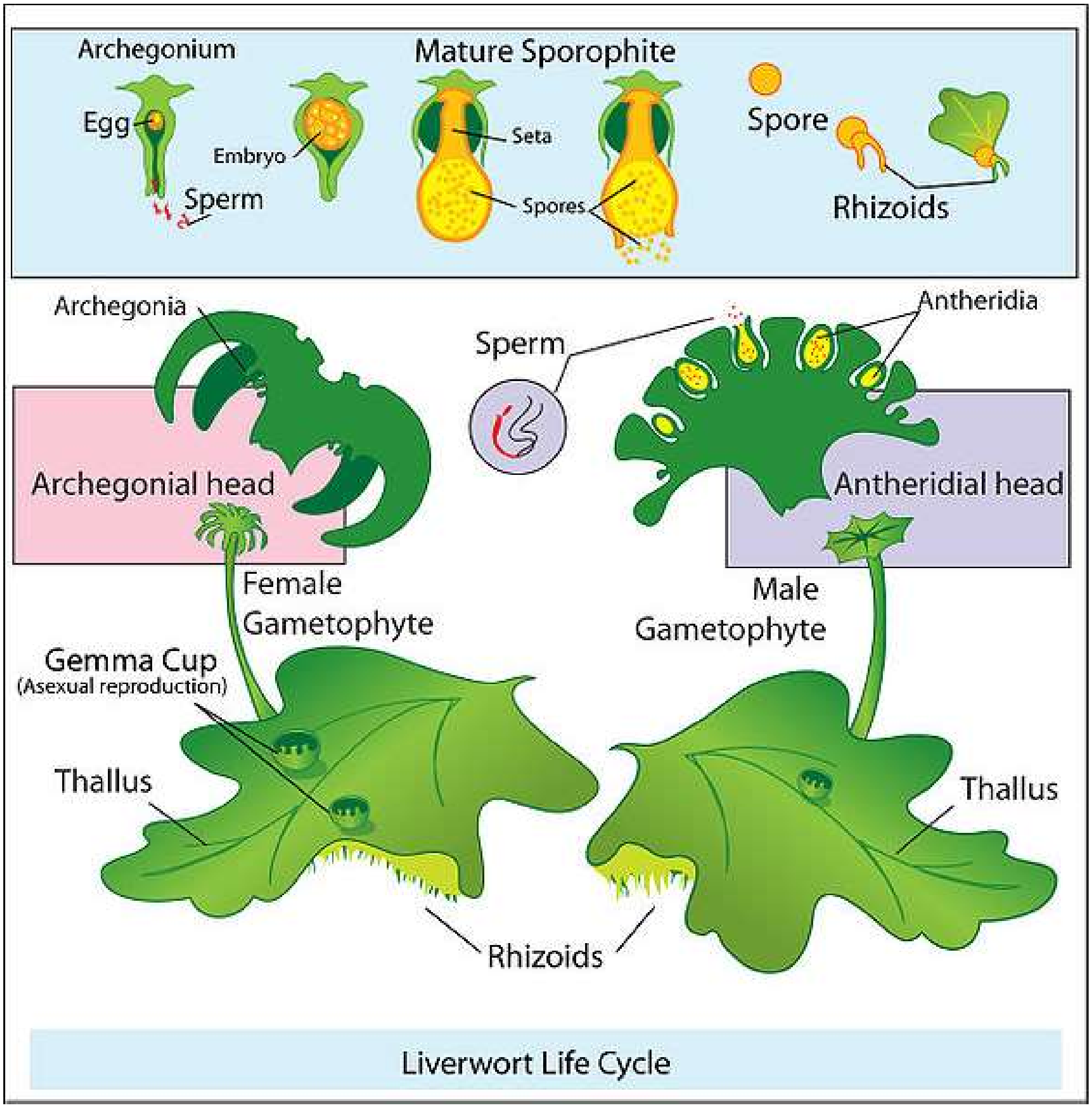
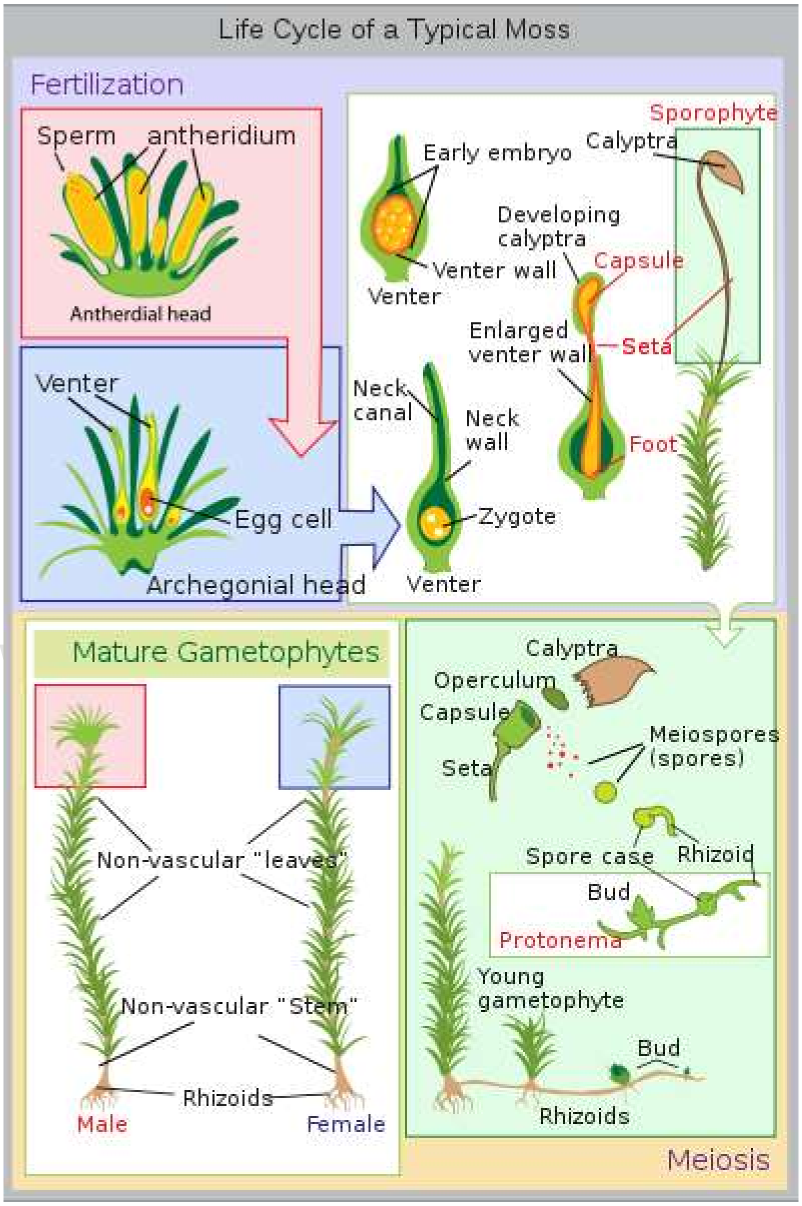
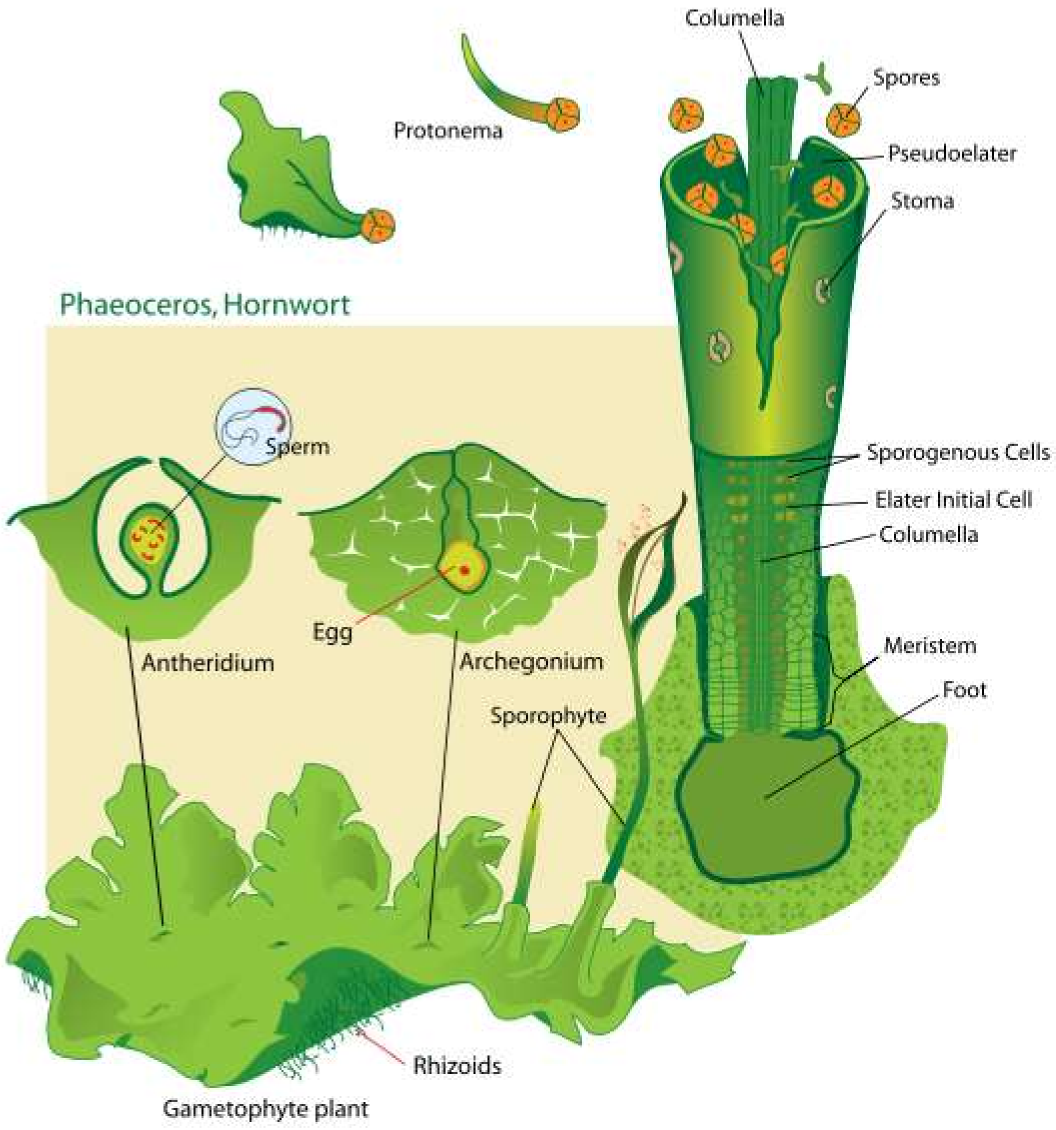


Diagram of alternation of generations in liverworts.



Moss life cycle diagram



Hornwort life cycle diagram

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

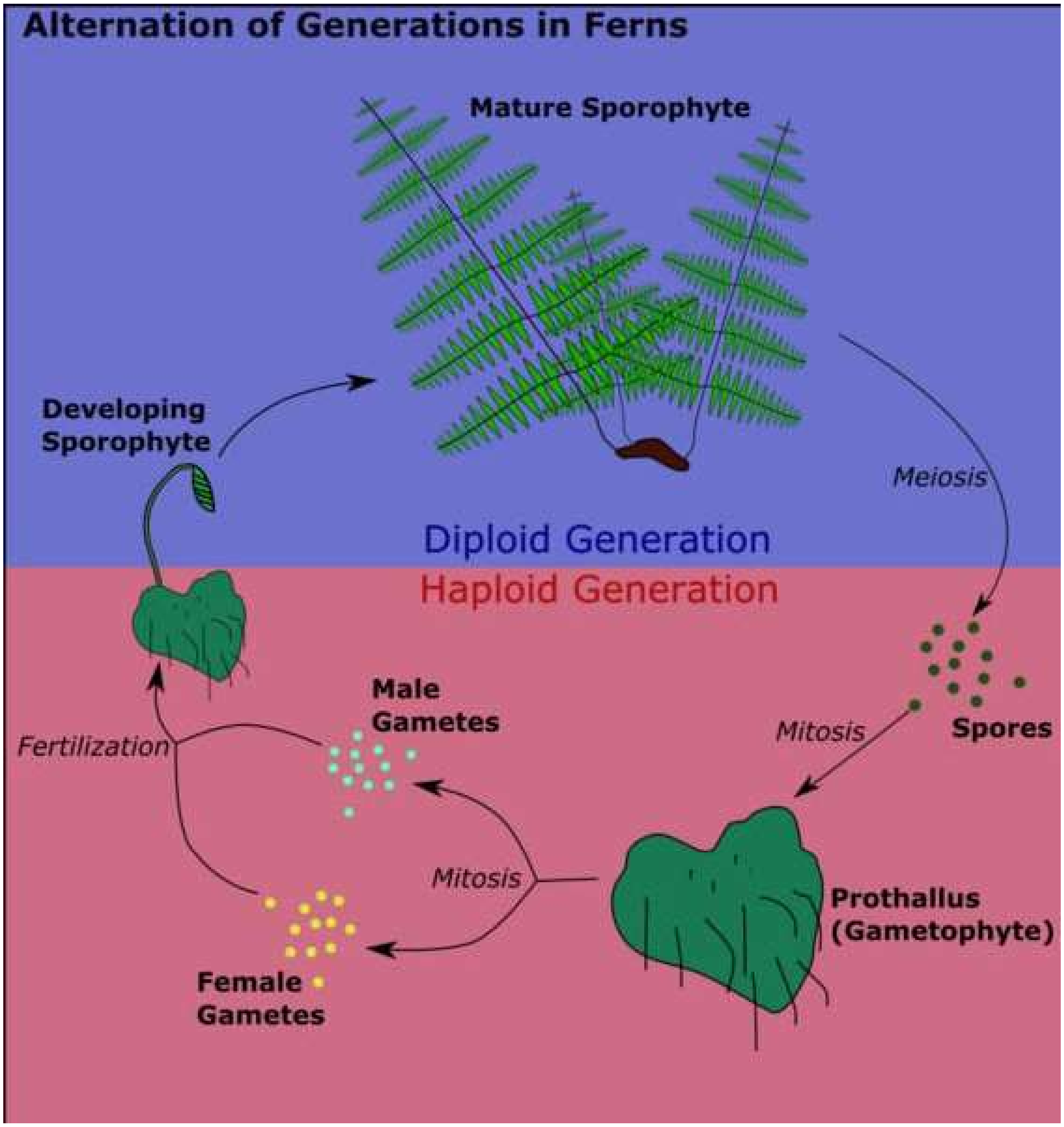


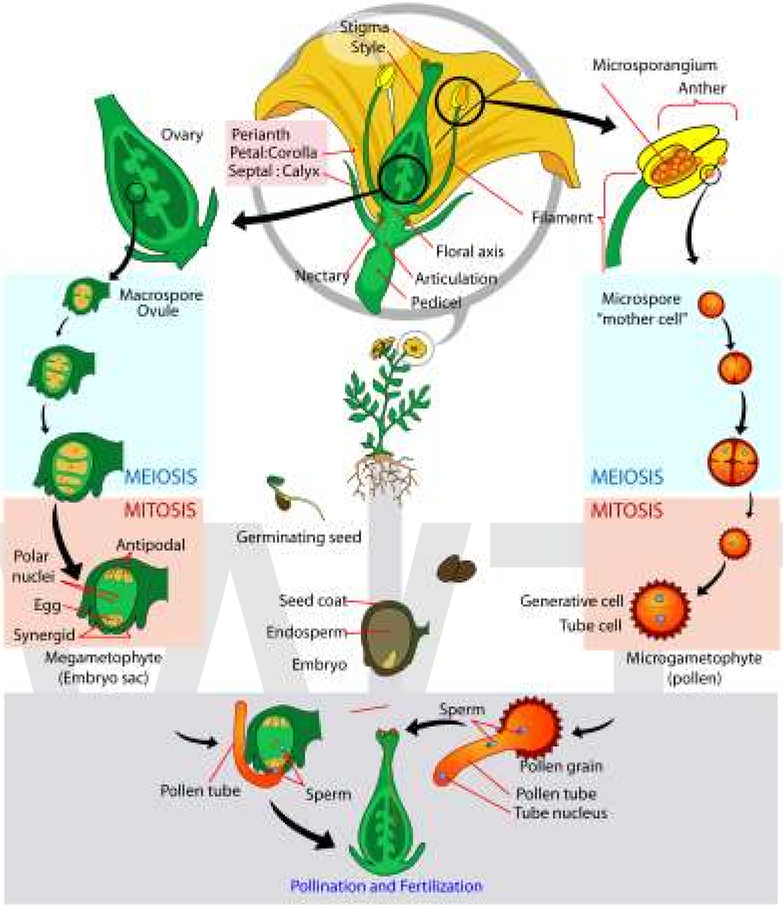
Diagram of alternation of generations in ferns.

A gametophyte (prothallus) of *Dicksonia sp.*

A sporophyte of *Dicksonia antarctica*.

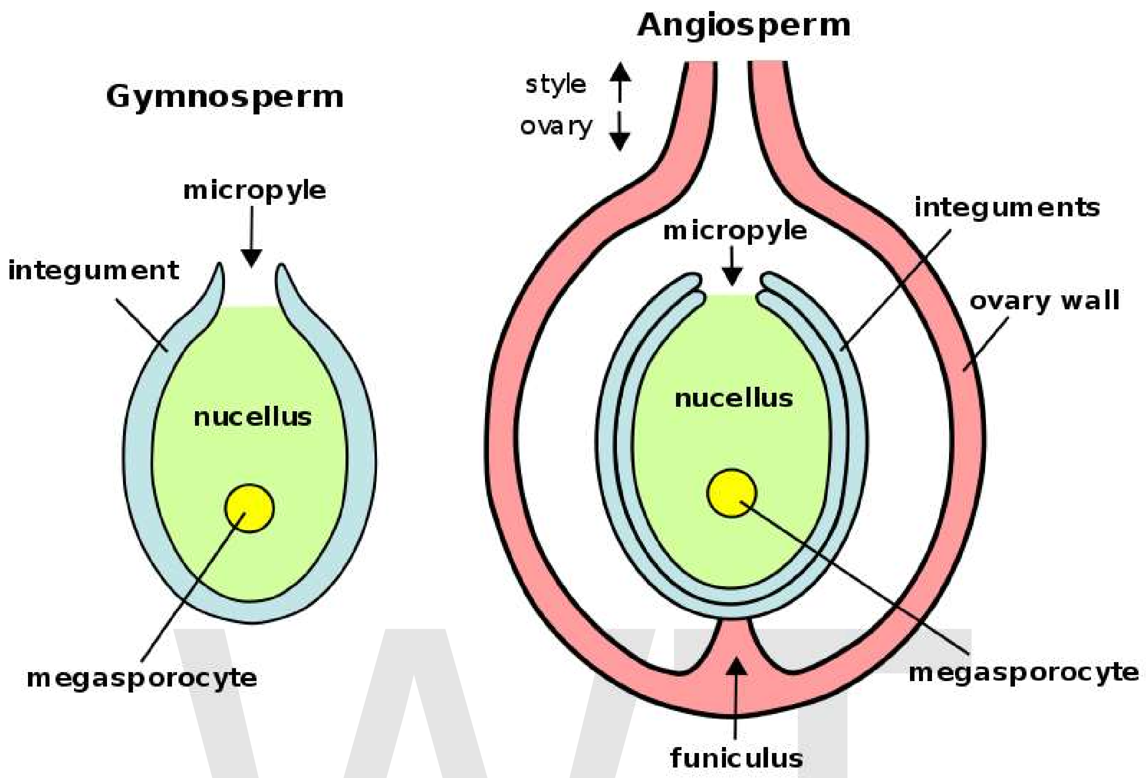
The underside of a *Dicksonia antarctica* frond showing the sori, or spore-producing structures.

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

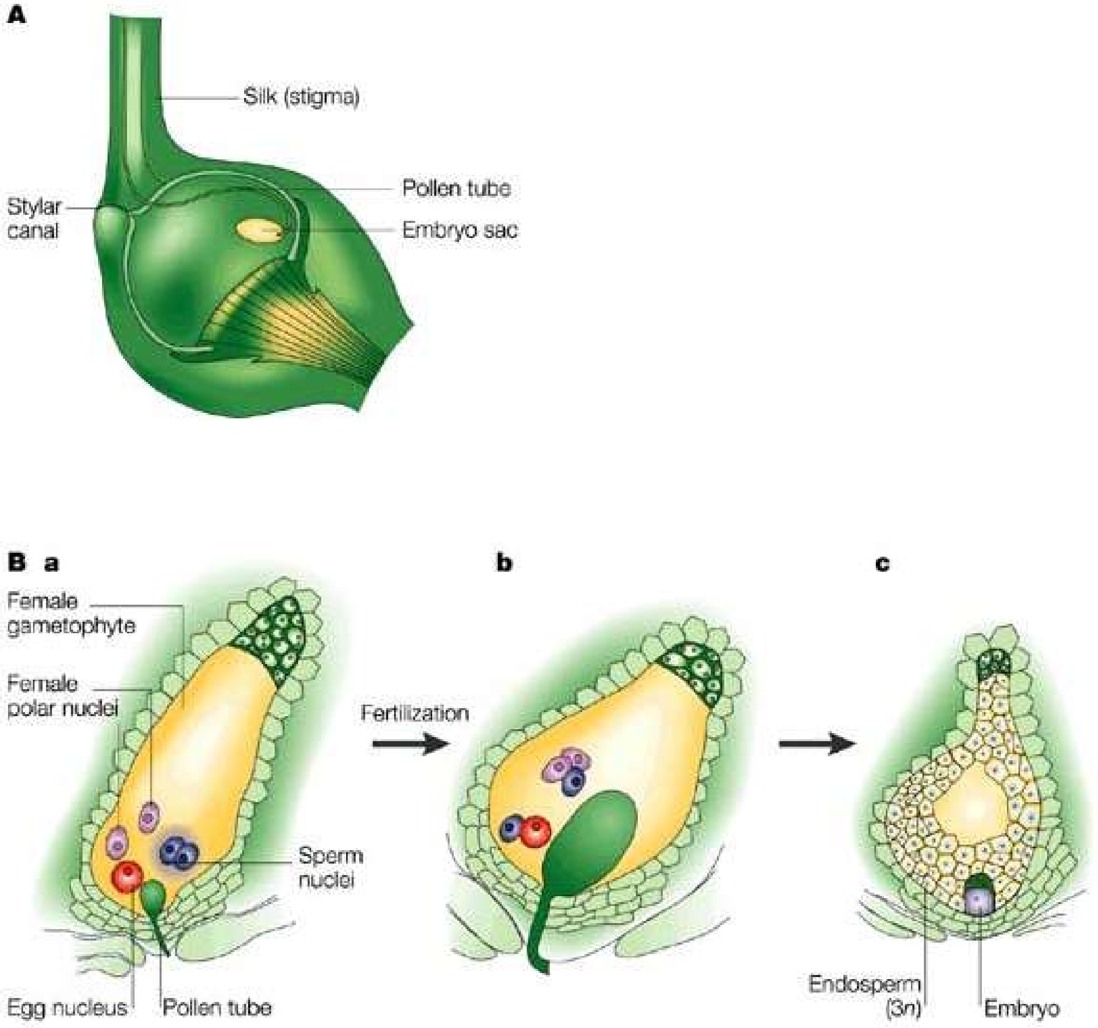


Angiosperm life cycle

Tip of tulip stamen showing pollen (microgametophytes)



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



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Double fertilization

Other groups of organism

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

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

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

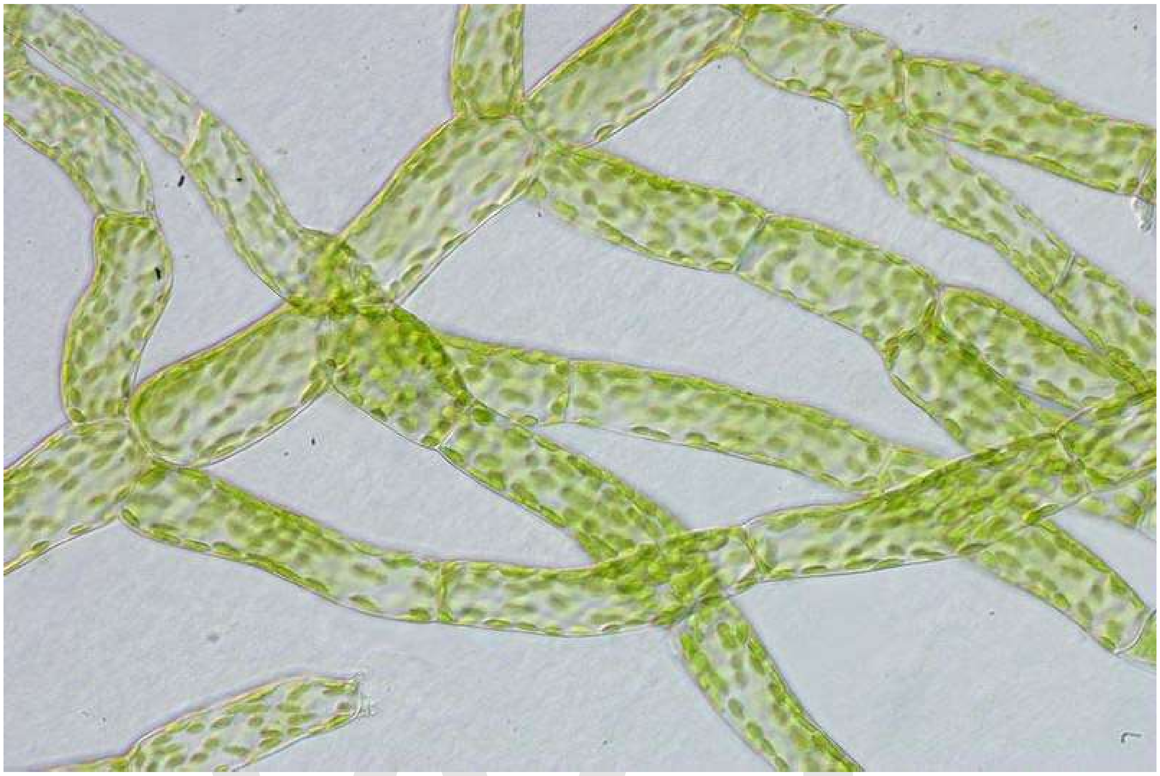
In some animals, there is an alternation between parthenogenic and sexually reproductive phases (**heterogamy**). Although in some ways similar to alternation of generations, the genetics of heterogamy is significantly different.

Chapter 8

Gametophyte and Sporophyte

Gametophyte

Several gametophytes growing in a terrarium.



Protonema of the moss *Physcomitrella patens*

A **gametophyte** is the haploid, multicellular phase of plants and algae that undergo alternation of generations, with each of its cells containing only a single set of chromosomes.

The gametophyte produces male or female gametes (or both), by a process of cell division called mitosis. The fusion of male and female gametes produces a diploid zygote, which develops by repeated mitotic cell divisions into a multicellular sporophyte. Because the sporophyte is the product of the fusion of two haploid gametes, its cells are diploid, containing two sets of chromosomes. The mature sporophyte produces spores by a process called meiosis, sometimes referred to as "reduction division" because the chromosome pairs are separated once again to form single sets. The spores are therefore once again haploid and develop into a haploid gametophyte.

In mosses, liverworts and hornworts (bryophytes), the gametophyte is the commonly known phase of the plant. An early developmental stage in the gametophyte of mosses (immediately following germination of the meiospore) is called the protonema. The adult gametophyte of mosses is called the gametophore as it carries the gamete-producing sex organs.

In most other land plants, the gametophyte is very small. In ferns the gametophyte is a free living organism called the prothallus, in contrast to angiosperms.

In gymnosperms and angiosperms, the gametophyte are reduced to only a few cells; in angiosperms the female gametophyte (embryo sac) is known as a **megagametophyte** and the male gametophyte (pollen) is called a **microgametophyte**.

In some multicellular green algae, red algae, or brown algae (*Ulva* is one example), the sporophytes and gametophytes are often isomorphic, but in some species the gametophyte may be reduced.

Sporophyte

Young sporophytes of the common moss *Tortula muralis*. In mosses, the gametophyte is the dominant generation, while the sporophytes consist of sporangium-bearing stalks growing from the tips of the gametophytes

All land plants, and some algae, have life cycles in which a haploid gametophyte generation alternates with a **diploid sporophyte**, the generation of a plant or algae that has a double set of chromosomes. A multicellular sporophyte generation or phase is present in the life cycle of all land plants and in some green algae. For common flowering plants (*Angiosperms*), the sporophyte generation makes up almost their whole life cycle (i.e. whole green plant, roots etc.), except phases of small reproductive structures (pollen and ovule).

The **sporophyte** produces spores (hence the name), by meiosis. These meiospores develop into a gametophyte. Both the spores and the resulting gametophyte are haploid, meaning they only have one set of homologous chromosomes. The mature gametophyte produces male or female gametes (or both) by mitosis. The fusion of male and female gametes produces a diploid zygote which develops into a new sporophyte. This cycle is known as alternation of generations or alternation of phases.

In flowering plants, the sporophyte comprises the whole multicellular body except the pollen and embryo sac

In the normal course of events, the zygote and sporophyte will have a full double set of chromosomes again. An exception is when a diploid and haploid gamete fuse, resulting in a triploid sporophyte, which will usually be sterile, as dividing three sets of chromosomes into two halves causes complications.

Bryophytes (mosses, liverworts and hornworts) have a dominant gametophyte stage on which the adult sporophyte is dependent on the gametophyte for nutrition. The embryo of the sporophyte develops from the zygote within the female sex organ or archegonium, and in its early development is therefore nurtured by the gametophyte. Because this embryo-nurturing feature of the life cycle is common to all land plants they are known collectively as the Embryophytes.

Cleistocarpous sporophyte of the moss *Physcomitrella patens*

Most algae have dominant gametophyte generations, but in some species the gametophytes and sporophytes are morphologically similar (isomorphic). An independent sporophyte is the dominant form in all clubmosses, horsetails, ferns, gymnosperms, and angiosperms (flowering plants) that have survived to the present day. Early land plants had sporophytes that produced identical spores (isosporous or homosporous) but the ancestors of the gymnosperms evolved complex heterosporous life cycles in which the spores producing male and female gametophytes were of different sizes, the female megaspores tending to be larger, and fewer in number, than the male microspores.

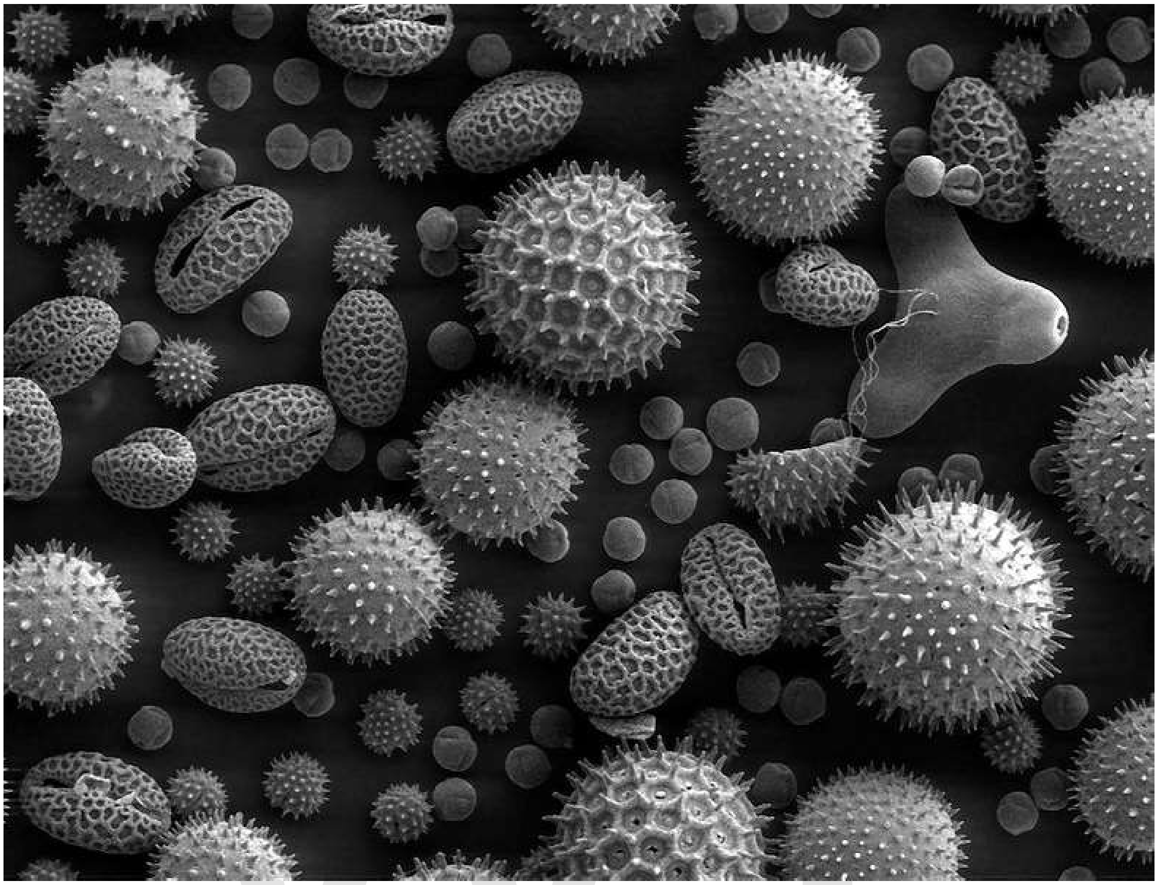
During the Devonian period several plant groups independently evolved heterospory and subsequently the habit of endospory, in which single megaspores were retained within the sporangia of the parent sporophyte, instead of being freely liberated into the environment as in ancestral exosporous plants. These endosporic megaspores contained within them a miniature multicellular female gametophyte complete with female sex organs or archegonia containing oocytes which were fertilised by free-swimming sperm produced by windborne miniatuarised male gametophytes in the form of pre-pollen. The resulting zygote developed into the next sporophyte generation while still retained within the pre-ovule, the single large female meiospore or megaspore contained in the modified sporangium or nucellus of the parent sporophyte. The evolution of heterospory and endospory were among the earliest steps in the evolution of seeds of the kind produced by gymnosperms and angiosperms today.

Chapter 9

Pollen

Tip of a tulip stamen with many grains of pollen

Closeup image of a cactus flower and its stamens



Scanning electron microscope image of pollen grains from a variety of common plants: sunflower (*Helianthus annuus*), morning glory (*Ipomoea purpurea*), prairie hollyhock (*Sidalcea malviflora*), oriental lily (*Lilium auratum*), evening primrose (*Oenothera fruticosa*), and castor bean (*Ricinus communis*).

European honey bee carrying pollen in a pollen basket back to the hive

Pollen sticking to a bee. Insects involuntarily transporting pollen from flower to flower play an important role in many plants' reproductive cycles.

Marmalade fly sitting on a grey-haired rockrose, its face and legs covered in pollen.

Pollen is a fine to coarse powder containing the ***microgametophytes*** of seed plants, which produce the male gametes (**sperm cells**). Pollen grains have a hard coat that protects the sperm cells during the process of their movement between the stamens to the pistil of flowering plants or from the male cone to the female cone of coniferous plants. When pollen lands on a compatible pistil of flowering plants, it germinates and produces a pollen tube that transfers the sperm to the ovule of a receptive ovary.

The structure and formation of pollen

Pollen itself is not the male gamete. Each pollen grain contains **vegetative** (non-reproductive) **cells** (only a single cell in most flowering plants but several in other seed plants) and a **generative** (reproductive) **cell** containing two nuclei: a tube nucleus (that produces the pollen tube) and a generative nucleus (that divides to form the two sperm cells). The group of cells is surrounded by a cellulose-rich cell wall called the intine, and a resistant outer wall composed largely of sporopollenin called the exine.

Pollen is produced in the 'microsporangium' (contained in the anther of an angiosperm flower, male cone of a coniferous plant, or male cone of other seed plants). Pollen grains come in a wide variety of shapes (most often spherical), sizes, and surface markings characteristic of the species. Pollen grains of pines, firs, and spruces are winged. The smallest pollen grain, that of the Forget-me-not (*Myosotis* spp.), is around 6 µm (0.006 mm) in diameter. Wind-borne pollen grains can be as large as about 90-100 µm. The study of pollen is called palynology and is highly useful in paleoecology, paleontology, archeology, and forensics.

In angiosperms, during flower development the anther is composed of a mass of cells that appear undifferentiated, except for a partially differentiated dermis. As the flower develops, four groups of sporogenous cells form with in the anther, the fertile sporogenous cells are surrounded by layers of sterile cells that grow into the wall of the pollen sac, some of the cells grow into nutritive cells that supply nutrition for the microspores that form by meiotic division from the sporogenous cells. In a process called **microsporogenesis**, four haploid microspores are produced from each diploid sporogenous cell (microsporocyte), after meiotic division. After the formation of the four microspores, which are contained by callose walls, the development of the pollen grain walls begins. The callose wall is broken down by an enzyme called callase and the freed pollen grains grow in size and develop their characteristic shape and form a resistant outer wall called the exine and an inner wall called the intine. The exine is what is preserved in the fossil record.

The pollen wall protects the sperm nucleus while the pollen grain is moving from the anther to the stigma, it protects the vital genetic material from drying out and solar radiation. The pollen grain surface is covered with waxes and proteins, which are held in place by structures called sculpture elements on the surface of the grain. The outer pollen wall prevents the pollen grain from shrinking and crushing the genetic material during desiccation and it is composed of two layers. These two layers are the tectum and the foot layer, which is just above the intine. The tectum and foot layer are separated by a region called the columella, which is composed of strengthening rods. The outer wall is constructed with a resistant biopolymer called sporopollenin. The pollen tube passes through the wall by way of structures called apertures.

Pollen apertures are any modification of the wall of the pollen grain. These modifications include thinning, ridges and pores, they serve as an exit for the pollen contents and allow shrinking and swelling of the grain caused by changes in moisture content. The elongated apertues/ furrows in the pollen grain are called colpi (*s. colpus*) which along with pores, are a chief criteria for the identifying pollen classes.

Pollen grains may have furrows, the orientation of which (relative to the original tetrad of microspores) classify the pollen as **colpate** or **sulcate**. The number of furrows or pores helps classify the flowering plants, with eudicots having three colpi (**tricolpate**), and other groups having one sulcus.

Except in the case of some submerged aquatic plants, the mature pollen-grain has a double wall, a thin delicate wall of unaltered cellulose (the endospore or **intine**) and a tough outer cuticularized exospore or **exine**. The exine often bears spines or warts, or is variously sculptured, and the character of the markings is often of value for identifying genus, species, or even cultivar or individual. In some flowering plants, germination of the pollen grain often begins before it leaves the microsporangium, with the generative cell forming the two sperm cells.

Pollination

The transfer of pollen grains to the female reproductive structure (***pistil*** in angiosperms) is called **pollination**. This transfer can be mediated by the wind, in which case the plant is described as **anemophilous** (literally wind-loving). Anemophilous plants typically produce great quantities of very lightweight pollen grains, sometimes with air-sacs. Non-flowering seed plants (e.g. pine trees) are characteristically anemophilous. Anemophilous flowering plants generally have inconspicuous flowers. **Entomophilous** (literally insect-loving) plants produce pollen that is relatively heavy, sticky and protein-rich, for dispersal by insect pollinators attracted to their flowers. Many insects and some mites are specialized to feed on pollen, and are called palynivores.

In non-flowering seed plants, pollen germinates in the pollen chamber, located beneath and inside the micropyle. A pollen tube is produced, which grows into the nucellus to provide nutrients for the developing sperm cells. Sperm cells of Pinophyta and Gnetophyta are without flagella, and are carried by the pollen tube, while those of Cycadophyta and Ginkgophyta have many flagella.

When placed on the stigma of a flowering plant, under favorable circumstances, a pollen grain puts forth a pollen tube which grows down the tissue of the style to the ovary, and makes its way along the placenta, guided by projections or hairs, to the micropyle of an ovule. The nucleus of the tube cell has meanwhile passed into the tube, as does also the generative nucleus which divides (if it hasn't already) to form two sperm cells. The sperm cells are carried to their destination in the tip of the pollen-tube.

Pollen as a carrier of ecological information in plants

A Russian theoretical biologist has suggested that the quantity of pollen reaching a pistillate flower can transmit ecological information and also regulate evolutionary plasticity in cross-pollinating plants. Plentiful pollen indicates optimum environmental conditions (for example a plant that is situated at the center of its natural range, in ideal growing conditions, with a large number of male plants nearby, and favorable weather conditions), whereas a small amount of pollen indicates extreme conditions (at the borders of its range, with a deficiency of male plants, and adverse weather conditions). Geodakian believes that the quantity of pollen reaching a pistillate flower defines the sex ratio, dispersion and sexual dimorphism of a plant population. High pollen quantity leads to a reduction of these characteristics and stabilization of a population. Small quantity leads to their increase and destabilization of a population.

Dependence of the secondary sex ratio on the amount of fertilizing pollen was confirmed on four dioecious plant species from three families — Rumex acetosa (Polygonaceae), Melandrium album (Cariophyllaceae), Cannabis sativa and Humulus japonicus (Cannabinaceae).

Dependence of offspring phenotype variety on amount of pollen was observed by Ter-Avanesyan in 1949. All three studied species of plants (cotton plant, black-eyed pea, and wheat) showed dependence in the direction forecast by the theory — fertilization with a small amount of pollen resulted in an increase in the diversity of the offspring. Ter-Avanesian writes that as a result of a limited pollination “instead of homogenous sorts we get populations”.

Pollen in the fossil record

Pollen's sporopollenin outer sheath affords it some resistance to the rigours of the fossilisation process that destroy weaker objects; it is also produced in huge quantities. As such, there is an extensive fossil record of pollen grains, often disassociated from their parent plant. The discipline of palynology is devoted to the study of pollen, which can be used both for biostratigraphy and to gain information about the abundance and variety of plants alive — which can itself yield important information about paleoclimates. Pollen is first found in the fossil record in the late Devonian period and increases in abundance until the present day.

Hay fever

Allergy to pollen is called hay fever. Generally pollens that cause allergies are those of anemophilous plants (pollen is dispersed by air currents.) Such plants produce large quantities of lightweight pollen (because wind dispersal is random and the likelihood of one pollen grain landing on another flower is small) which can be carried for great distances and are easily inhaled, bringing it into contact with the sensitive nasal passages.

In the US, people often mistakenly blame the conspicuous goldenrod flower for allergies. Since this plant is entomophilous (its pollen is dispersed by animals), its heavy, sticky pollen does not become independently airborne. Most late summer and fall pollen allergies are probably caused by ragweed, a widespread anemophilous plant.

Arizona was once regarded as a haven for people with pollen allergies, although several ragweed species grow in the desert. However, as suburbs grew and people began establishing irrigated lawns and gardens, more irritating species of ragweed gained a foothold and Arizona lost its claim of freedom from hay fever.

Anemophilous spring blooming plants such as oak, birch, hickory, pecan, and early summer grasses may also induce pollen allergies. Most cultivated plants with showy flowers are entomophilous and do not cause pollen allergies. In the US, oak pollen starts to cause problems for sufferers in February and is gone by the end of April.

The percentage of people in the United States affected by hay fever varies between 10% and 20%, and such allergy has proven to be the most frequent allergic response in the nation. There are certain evidential suggestions pointing out hay fever and similar allergies to be of hereditary origin. Individuals who suffer from eczema or are asthmatic tend to be more susceptible to developing long-term hay fever.

The most efficient way to handle a pollen allergy is by preventing contact with the material. Individuals carrying the ailment may at first believe that they have a simple summer cold, but hay fever becomes more evident when the apparent cold does not disappear. The confirmation of hay fever can be obtained after examination by a general physician.

Treatment

Antihistamines are effective at treating mild cases of hay fever, this type of non-prescribed drugs includes loratadine, cetirizine and chlorphenamine. They do not prevent the discharge of histamine, but it has been proven that they do prevent a part of the chain reaction activated by this biogenic amine, which considerably lowers hay fever symptoms. A side effect of antihistamines is somnolence, and it is therefore recommended not to take these drugs while driving an automobile or during the consumption of alcoholic beverages. However, the side effects of these medications can vary from person to person.

Decongestants can be administered in different ways such as tablets and nasal sprays. Decongestants such as pseudoephedrine, xylometazoline and drixoral can be acquired as over-the-counter medications. Since oral decongestant drugs raise blood pressure levels, individuals with hypertension are advised to avoid them. The oral decongestant type can aggravate the symptoms of an enlarged prostate, making the process of urinating more complicated.

Nutrition

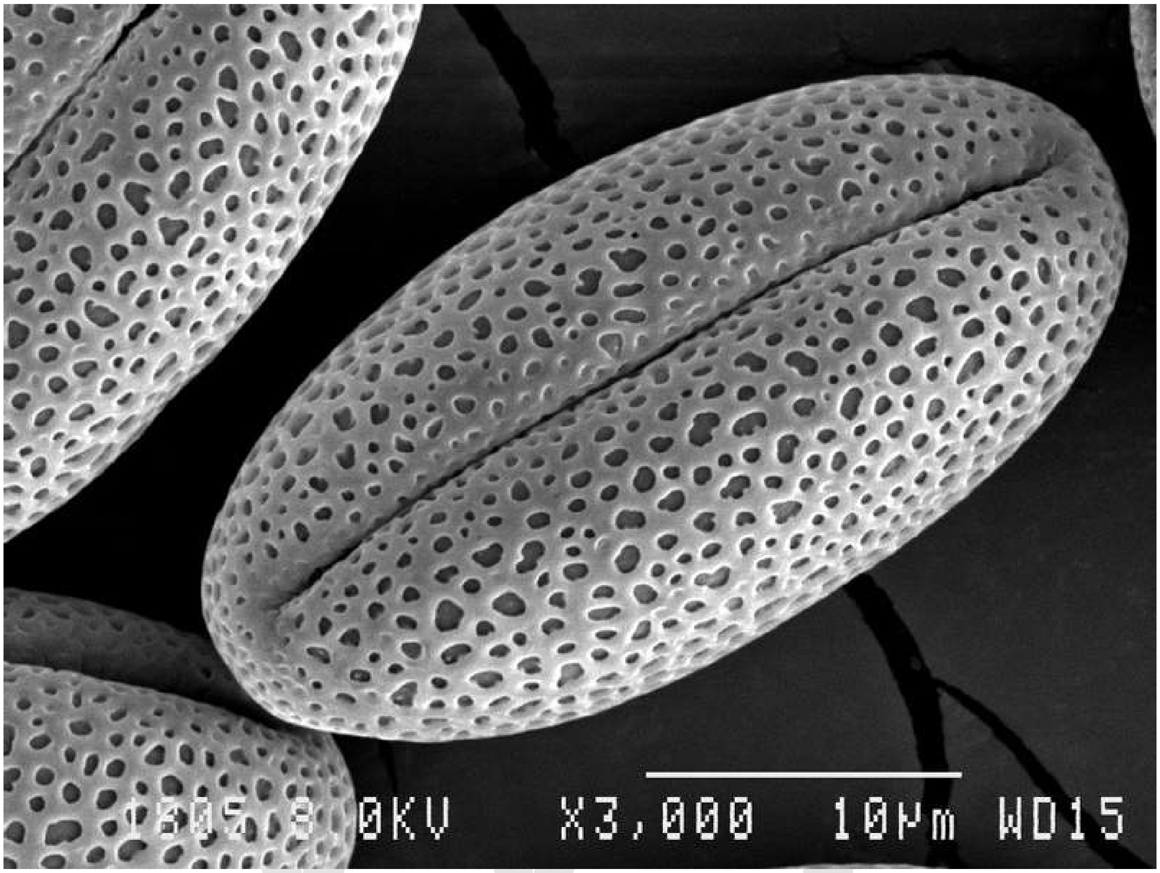
Most major classes of predatory and parasitic arthropods contain species that eat pollen, despite the common perception that bees are the primary pollen-consuming arthropod group. Many other Hymenoptera other than bees consume pollen as adults, though only a small number feed on pollen as larvae (including some ant larvae). Spiders are normally considered carnivores but pollen is an important source of food for several species, particularly for spiderlings which catch pollen on their webs. It is not clear how spiderlings manage to eat pollen however, since their mouths are not large enough to consume pollen grains. Some predatory mites also feed on pollen, with some species being able to subsist solely on pollen, such as *Euseius tularensis*, which feeds on the pollen of dozens of plant species. Members of some beetle families such as Mordellidae and Melyridae feed almost exclusively on pollen as adults, while various lineages within larger families such as Curculionidae, Chrysomelidae, Cerambycidae, and Scarabaeidae are pollen specialists even though most members of their families are not (e.g., only 36 of 40000 species of ground beetles, which are typically predatory, have been shown to eat pollen -- but this is thought to be a severe underestimate as the feeding habits are only known for 1000 species). Similarly, Ladybird beetles mainly eat insects, but many species also eat pollen, as either part or all of their diet. Hemiptera are mostly herbivores or omnivores but pollen feeding is known (and has only been well studied in the Anthocoridae). Many adult flies, especially Syrphidae, feed on pollen, and three UK syrphid species feed strictly on pollen (syrphids, like all flies, cannot eat pollen directly due to the structure of their mouthparts, but can consume pollen contents that are dissolved in a fluid).). Some species of fungus, including *Fomes fomentarius*, are able to break down grains of pollen as a secondary nutrition source which is particularly high in nitrogen.

In humans

A variety of producers have started selling pollen for human consumption, often marketed as a food (rather than a dietary supplement). The largest constituent is carbohydrates, with protein content ranging from 7 to 35 percent depending on the plant species collected by bees.

The U.S. Food and Drug Administration (FDA) has not found any harmful effects of pollen consumption, except from the usual allergies. However, FDA does not allow pollen marketers in the United States to make health claims about their produce, as no scientific basis for these has ever been proven. Furthermore, there are possible dangers not only from allergic reactions but also from contaminants such as pesticides and from fungi and bacteria growth related to poor storage procedures. A manufacturers's claim that pollen collecting helps the bee colonies is also controversial.

Forensic palynology



An SEM micrograph of Redbud pollen. Scanning Electron Microscopes are major instruments in palynology.

In forensic biology, pollen can tell a lot about where a person or object has been, because regions of the world, or even more particular locations such a certain set of bushes, will have a distinctive collection of pollen species. Pollen evidence can also reveal the season in which a particular object picked up the pollen. Pollen has been used to trace activity at mass graves in Bosnia, catch a burglar who brushed against a *Hypericum* bush during a crime, and has even been proposed as an additive for bullets to enable tracking them.

Chapter 10

Pollination

Carpenter bee with pollen collected from Night-blooming cereus

Tip of a tulip stamen. Note the grains of pollen

Pollination is the process by which pollen is transferred in plants, thereby enabling fertilization and sexual reproduction. Pollen grains, which contain the male gametes (sperm) to where the female gamete(s) are contained within the carpel; in gymnosperms the pollen is directly applied to the ovule itself. The receptive part of the carpel is called a *stigma* in the flowers of angiosperms. The receptive part of the gymnosperm ovule is called the *micropyle*. Pollination is a necessary step in the reproduction of flowering plants, resulting in the production of offspring that are genetically diverse.

The study of pollination brings together many disciplines, such as botany, horticulture, entomology, and ecology. The pollination process as an interaction between flower and vector was first addressed in the 18th century by Christian Konrad Sprengel. It is important in horticulture and agriculture, because fruiting is dependent on fertilisation, which is the end result of pollination.

Types

Abiotic pollination

Caroli Linnæi
Medic: et Botan: Cult.
ſtipend: Reg:
Praeludia
Sponsaliarum
Plantarum
in quibus
Phyſiologia earum explica
tur, Sexus demonſtratur,
modus generationis dete
gitur, nec non ſumma plan
tarum cum animalibus analo
gia concluditur
Upſal: 1729.

Abiotic pollination by wind, depicted in *Praeludia Sponsaliorum Plantarum* by Carl Linnaeus, 1729.

Abiotic pollination refers to situations where pollination is mediated without the involvement of other organisms. Only 10% of flowering plants are pollinated without animal assistance. The most common form of abiotic pollination, anemophily, is pollination by wind. This form of pollination is predominant in grasses, most conifers, and many deciduous trees. Hydrophily is pollination by water and occurs in aquatic plants which release their pollen directly into the surrounding water. About 80% of all plant pollination is biotic. In gymnosperms,biotic pollination never takes place. These plants always exhibit anemophily that is wind pollination. Of the 20% of abiotically pollinated species, 98% is by wind and 2% by water.

Biotic pollination

A hummingbird feeding

More commonly, the process of pollination requires pollinators: organisms that carry or move the pollen grains from the anther to the receptive part of the carpel or pistil. This is **biotic pollination**. The various flower traits (and combinations thereof) that differentially attract one type of pollinator or another are known as pollination syndromes.

There are roughly 200,000 varieties of animal pollinators in the wild, most of which are insects. Entomophily, pollination by insects, often occurs on plants that have developed colored petals and a strong scent to attract insects such as, bees, wasps and occasionally ants (Hymenoptera), beetles (Coleoptera), moths and butterflies (Lepidoptera), and flies (Diptera). In zoophily, pollination is performed by vertebrates such as birds and bats, particularly, hummingbirds, sunbirds, spiderhunters, honeyeaters, and fruit bats. Plants adapted to using bats or moths as pollinators typically have white petals and a strong scent, while plants that use birds as pollinators tend to develop red petals and rarely develop a scent (few birds have a sense of smell).

Insect pollinators such as honeybees (*Apis millifera*) , bumblebees (*Bombus terrestris*) , and butterflies (*Thymelicus flavus*) have been observed to engage in flower constancy, which means they are more likely to transfer pollen to other conspecific plants . This can be beneficial for the pollenisers, as flower constancy prevents the loss of pollen during interspecific flights and pollinators from clogging stigmas with pollen of other flower species .

Mechanics

Pollination can be accomplished by **cross-pollination** or by **self-pollination** :

- Cross-pollination, also called *allogamy* occurs when pollen is delivered to a flower from a different plant. Plants adapted to outcross or cross-pollinate often have taller stamens than carpels or use other mechanisms to better ensure the spread of pollen to other plants' flowers.

A European honey bee collects nectar, while pollen collects on its body.

- Self-pollination occurs when pollen from one flower pollinates the same flower or other flowers of the same individual. It is thought to have evolved under conditions when pollinators were not reliable vectors for pollen transport, and is most often seen in short-lived annual species and plants that colonize new locations. Self pollination may include *autogamy*, where pollen moves to the female part of the same flower; or *geitonogamy*, when pollen is transferred to another flower on the same plant. Plants adapted to self-fertilize often have similar stamen and carpel lengths. Plants that can pollinate themselves and produce viable offspring are called self-fertile. Plants that cannot fertilize themselves are called self-sterile, a condition which mandates cross pollination for the production of offspring.

- *Cleistogamy*: is self-pollination that occurs before the flower opens. The pollen is released from the anther within the flower or the pollen on the anther grows a tube down the style to the ovules. It is a type of sexual breeding, in contrast to asexual systems such as apomixis. Some *cleistogamous* flowers never open, in contrast to *chasmogamous* flowers that open and are then pollinated. Cleistogamous flowers by necessity are self-compatible or self-fertile plants. Many plants are self-incompatible, and these two conditions are end points on a continuum.

Pollination also requires consideration of pollenizers. The terms "pollinator" and "pollenizer" are often confused: a *pollinator* is the agent that moves the pollen, whether it be bees, flies, bats, moths, or birds; a *pollenizer* is the plant that serves as the pollen source for other plants. Some plants are *self-fertile* or *self-compatible* and can pollinate themselves (e.g., they act as their own pollenizer). Other plants have chemical or physical barriers to self-pollination.

In agriculture and horticulture pollination management, a good pollenizer is a plant that provides compatible, viable and plentiful pollen and blooms at the same time as the plant that is to be pollinated or has pollen that can be stored and used when needed to pollinate the desired flowers. Hybridization is effective pollination between flowers of different species, or between different breeding lines or populations.

Peaches are considered self-fertile because a commercial crop can be produced without cross-pollination, though cross-pollination usually gives a better crop. Apples are considered self-incompatible, because a commercial crop must be cross-pollinated. Many commercial fruit tree varieties are grafted clones, genetically identical. An orchard block of apples of one variety is genetically a single plant. Many growers now consider this a mistake. One means of correcting this mistake is to graft a limb of an appropriate pollenizer (generally a variety of crabapple) every six trees or so.

Evolution of plant/pollinator interactions

Pollination syndromes are flower traits that attract pollinators, and can be highly specialized. Plants and their pollinators are often in coevolutionary mutualisms.

The first fossil record for abiotic pollination is from fern-like plants in the late Carboniferous period. Gymnosperms show evidence for biotic pollination as early as the Triassic period. Many fossilized pollen grains show characteristics similar to the biotically dispersed pollen today. Furthermore, the gut contents, wing structures, and mouthpart morphologies of fossilized beetles and flies suggest that they acted as early pollinators. The association between beetles and angiosperms during the early Cretaceous period led to parallel radiations of angiosperms and insects into the late Cretaceous. The evolution of nectaries in late Cretaceous flowers signals the beginning of the mutualism between hymenopterans and angiosperms.

In agriculture

An *Andrena* bee collects pollen among the stamens of a rose. The female carpel structure appears rough and globular to the left. The bee's stash of pollen is on its hind leg.

Pollination management is a branch of agriculture that seeks to protect and enhance present pollinators and often involves the culture and addition of pollinators in monoculture situations, such as commercial fruit orchards. The largest managed pollination event in the world is in Californian almond orchards, where nearly half (about one million hives) of the US honey bees are trucked to the almond orchards each spring. New York's apple crop requires about 30,000 hives; Maine's blueberry crop uses about 50,000 hives each year.

Bees are also brought to commercial plantings of cucumbers, squash, melons, strawberries, and many other crops. Honey bees are not the only managed pollinators: a few other species of bees are also raised as pollinators. The alfalfa leafcutter bee is an important pollinator for alfalfa seed in western United States and Canada. Bumblebees are increasingly raised and used extensively for greenhouse tomatoes and other crops.

Well-pollinated blackberry blossom begins to develop fruit. Each incipient drupelet has its own stigma and good pollination requires the delivery of many grains of pollen to the flower so that all drupelets develop.

Blueberries being pollinated by bumblebees. Bumblebee hives need to be bought each year as the queens must hibernate (unlike honey bees). They are used nonetheless as they offer advantages with certain fruits as blueberries (such as the fact that they are active even at colder outdoor ambient temperature).

The ecological and financial importance of natural pollination by insects to agricultural crops, improving their quality and quantity, becomes more and more appreciated and has given rise to new financial opportunities. The vicinity of a forest or wild grasslands with native pollinators near agricultural crops, such as apples, almonds or coffee can improve their yield by about 20%. The benefits of native pollinators may result in forest owners demanding payment for their contribution in the improved crop results - a simple example of the economic value of ecological services.

The American Institute of Biological Sciences reports that native insect pollination saves the United States agricultural economy nearly an estimated $3.1 billion annually through natural crop production; pollination produces some $40 billion worth of products annually in the United States alone.

Pollination of food crops has become an environmental issue, due to two trends. The trend to monoculture means that greater concentrations of pollinators are needed at bloom time than ever before, yet the area is forage poor or even deadly to bees for the rest of the season. The other trend is the decline of pollinator populations, due to pesticide misuse and overuse, new diseases and parasites of bees, clearcut logging, decline of beekeeping, suburban development, removal of hedges and other habitat from farms, and public paranoia about bees. Widespread aerial spraying for mosquitoes due to West Nile fears is causing an acceleration of the loss of pollinators.

The US solution to the pollinator shortage, so far, has been for commercial beekeepers to become pollination contractors and to migrate. Just as the combine harvesters follow the wheat harvest from Texas to Manitoba, beekeepers follow the bloom from south to north, to provide pollination for many different crops.

Environmental impacts

Loss of pollinators, also known as Pollinator decline (of which colony collapse disorder is perhaps the most well known) has been noticed in recent years. Observed losses would have significant economic impacts. Possible explanations for pollinator decline include habitat destruction, pesticide, parasitism/diseases, and others.

Chapter 11

Seed

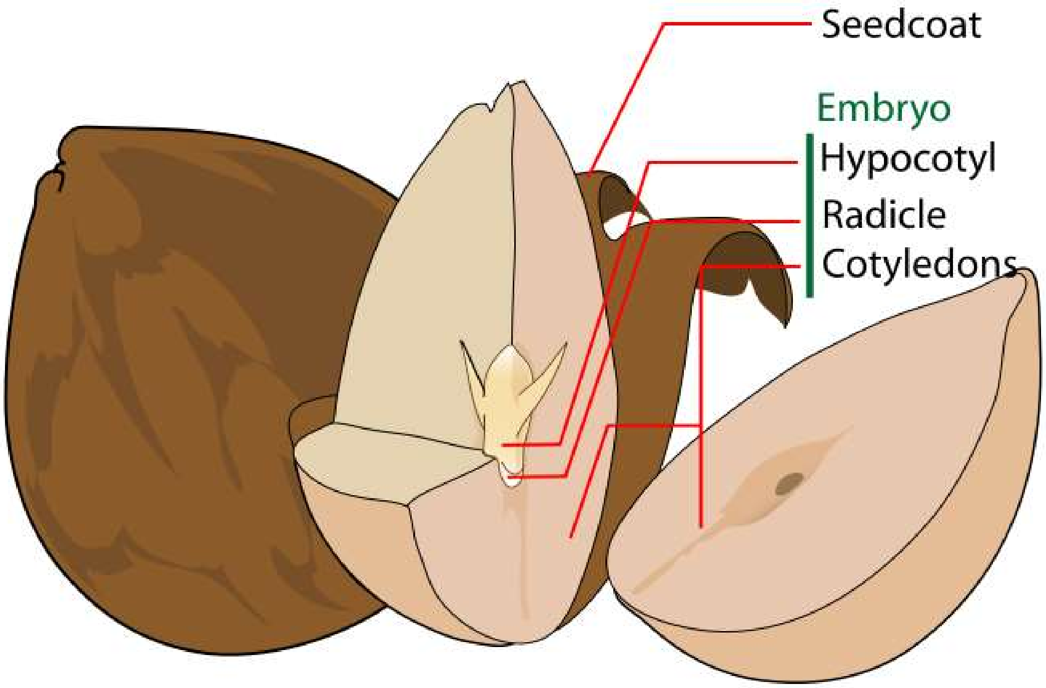
Brown flax seeds

A **seed** is a small embryonic plant enclosed in a covering called the seed coat, usually with some stored food. It is the product of the ripened ovule of gymnosperm and angiosperm plants which occurs after fertilization and some growth within the mother plant. The formation of the seed completes the process of reproduction in seed plants (started with the development of flowers and pollination), with the embryo developed from the zygote and the seed coat from the integuments of the ovule.

Seeds have been an important development in the reproduction and spread of flowering plants, relative to more primitive plants like mosses, ferns and liverworts, which do not have seeds and use other means to propagate themselves. This can be seen by the success of seed plants (both gymnosperms and angiosperms) in dominating biological niches on land, from forests to grasslands both in hot and cold climates.

The term *seed* also has a general meaning that predates the above — anything that can be sown, e.g. "seed" potatoes, "seeds" of corn or sunflower "seeds". In the case of sunflower and corn "seeds", what is sown is the seed enclosed in a shell or hull, and the potato is a tuber.

Seed structure



The parts of an avocado seed (a dicot), showing the seed coat, endosperm, and embryo.

A typical seed includes three basic parts: (1) an embryo, (2) a supply of nutrients for the embryo, and (3) a seed coat.

The embryo is an immature plant from which a new plant will grow under proper conditions. The embryo has one cotyledon or seed leaf in monocotyledons, two cotyledons in almost all dicotyledons and two or more in gymnosperms. The radicle is the embryonic root. The plumule is the embryonic shoot. The embryonic stem above the point of attachment of the cotyledon(s) is the epicotyl. The embryonic stem below the point of attachment is the hypocotyl.

Within the seed, there usually is a store of nutrients for the seedling that will grow from the embryo. The form of the stored nutrition varies depending on the kind of plant. In angiosperms, the stored food begins as a tissue called the endosperm, which is derived from the parent plant via double fertilization. The usually triploid endosperm is rich in oil or starch and protein. In gymnosperms, such as conifers, the food storage tissue is part of the female gametophyte, a haploid tissue. In some species, the embryo is embedded in the endosperm or female gametophyte, which the seedling will use upon germination. In others, the endosperm is absorbed by the embryo as the latter grows within the developing seed, and the cotyledons of the embryo become filled with this stored food. At maturity, seeds of these species have no endosperm and are termed exalbuminous seeds. Some exalbuminous seeds are bean, pea, oak, walnut, squash, sunflower, and radish. Seeds with an endosperm at maturity are termed albuminous seeds. Most monocots (e.g. grasses and palms) and many dicots (e.g. brazil nut and castor bean) have albuminous seeds. All gymnosperm seeds are albuminous.

The seed coat (or *testa*) develops from the tissue, the integument, originally surrounding the ovule. The seed coat in the mature seed can be a paper-thin layer (e.g. peanut) or something more substantial (e.g. thick and hard in honey locust and coconut). The seed coat helps protect the embryo from mechanical injury and from drying out.

In addition to the three basic seed parts, some seeds have an appendage on the seed coat such an aril (as in yew and nutmeg) or an elaiosome (as in Corydalis) or hairs (as in cotton). There may also be a scar on the seed coat, called the hilum; it is where the seed was attached to the ovary wall by the funiculus.

Seed production

Immature Elm seeds.

Seeds are produced in several related groups of plants, and their manner of production distinguishes the angiosperms ("enclosed seeds") from the gymnosperms ("naked seeds"). Angiosperm seeds are produced in a hard or fleshy structure called a fruit that encloses the seeds, hence the name. (Some fruits have layers of both hard and fleshy material). In gymnosperms, no special structure develops to enclose the seeds, which begin their development "naked" on the bracts of cones. However, the seeds do become covered by the cone scales as they develop in some species of conifer.

Seed production in natural plant populations vary widely from year-to-year in response to weather variables, insects and diseases, and internal cycles within the plants themselves. Over a 20-year period, for example, forests composed of loblolly pine and shortleaf pine produced from 0 to nearly 5 million sound pine seeds per hectare. Over this period, there were six bumper seeds, five poor seeds crops, and nine good seed crops, when evaluated in regard to producing adequate seedlings for natural forest reproduction.

Kinds of seeds

Many structures commonly referred to as "seeds" are actually dry fruits. Sunflower seeds are sold commercially while still enclosed within the hard wall of the fruit, which must be split open to reach the seed. Different groups of plants have other modifications, the so-called *stone* fruits (such as the peach) have a hardened fruit layer (the **endocarp**) fused to and surrounding the actual seed. Nuts are the one-seeded, hard shelled fruit, of some plants, with an indehiscent seed, such as an acorn or hazelnut.

Seed development

The inside of a *Ginkgo* seed, showing a well-developed embryo, nutritive tissue (megagametophyte), and a bit of the surrounding seed coat.

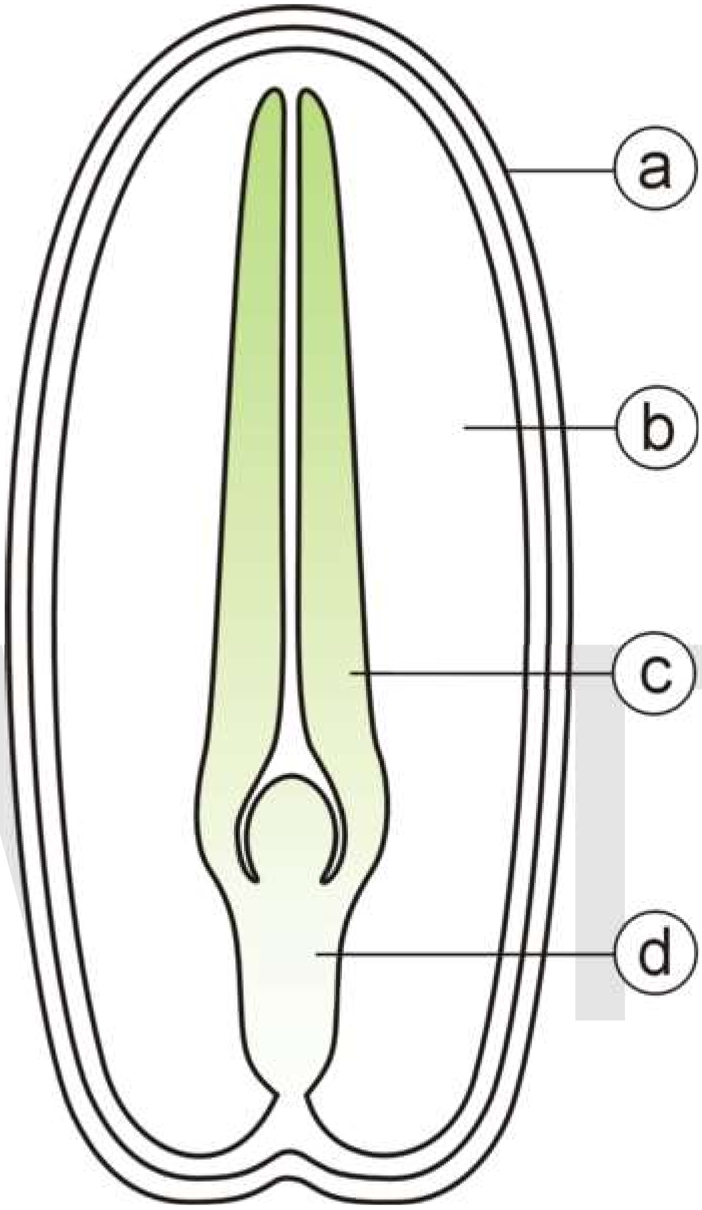


Diagram of the internal structure of a dicot seed and embryo. (a) seed coat, (b) endosperm, (c) cotyledon, (d) hypocotyl.

The seed, which is an embryo with two points of growth (one of which forms the stems the other the roots) is enclosed in a seed coat with some food reserves. Angiosperm seeds consist of three genetically distinct constituents: (1) the embryo formed from the zygote, (2) the endosperm, which is normally triploid, (3) the seed coat from tissue derived from the maternal tissue of the ovule. In angiosperms, the process of seed development begins with double fertilization and involves the fusion of the egg and sperm nuclei into a zygote. The second part of this process is the fusion of the polar nuclei with a second sperm cell nucleus, thus forming a primary endosperm. Right after fertilization, the zygote is mostly inactive but the primary endosperm divides rapidly to form the endosperm tissue. This tissue becomes the food that the young plant will consume until the roots have developed after germination or it develops into a hard seed coat. The seed coat forms from the two integuments or outer layers of cells of the ovule, which derive from tissue from the mother plant, the inner integument forms the tegmen and the outer forms the testa. When the seed coat forms from only one layer it is also called the testa, though not all such testa are homologous from one species to the next.

In gymnosperms, the two sperm cells transferred from the pollen do not develop seed by double fertilization but one sperm nucleus unites with the egg nucleus and the other sperm is not used. Sometimes each sperm fertilizes an egg cell and one zygote is then aborted or absorbed during early development. The seed is composed of the embryo (the result of fertilization) and tissue from the mother plant, which also form a cone around the seed in coniferous plants like Pine and Spruce.

The ovules after fertilization develop into the seeds; the main parts of the ovule are the funicle; which attaches the ovule to the placenta, the nucellus; the main region of the ovule were the embryo sac develops, the micropyle; A small pore or opening in the ovule where the pollen tube usually enters during the process of fertilization, and the chalaza; the base of the ovule opposite the micropyle, where integument and nucellus are joined together.

The shape of the ovules as they develop often affects the finale shape of the seeds. Plants generally produce ovules of four shapes: the most common shape is called anatropous, with a curved shape. Orthotropous ovules are straight with all the parts of the ovule lined up in a long row producing an uncurved seed. Campylotropous ovules have a curved embryo sac often giving the seed a tight “c” shape. The last ovule shape is called amphitropous, where the ovule is partly inverted and turned back 90 degrees on its stalk or funicle.

In the majority of flowering plants, the zygote's first division is transversely oriented in regards to the long axis, and this establishes the polarity of the embryo. The upper or chalazal pole becomes the main area of growth of the embryo, while the lower or micropylar pole produces the stalk-like suspensor that attaches to the micropyle. The suspensor absorbs and manufacturers nutrients from the endosperm that are utilized during the embryos growth.

The embryo is composed of different parts; the **epicotyle** will grow into the shoot, the **radicle** grows into the primary root, the **hypocotyl** connects the epicotyle and the radicle, the **cotyledons** form the seed leaves, the **testa** or seed coat forms the outer covering of the seed. Monocotyledonous plants like corn, have other structures; instead of the hypocotyle-epicotyle, it has a **coleoptile** that forms the first leaf and connects to the **coleorhiza** that connects to the primary root and adventitious roots form from the sides. The seeds of corn are constructed with these structures; pericarp, scutellum (single large cotyledon) that absorbs nutrients from the endosperm, endosperm, plumule, radicle, coleoptile and coleorhiza - these last two structures are sheath-like and enclose the plumule and radicle, acting as a protective covering. The testa or seed coats of both monocots and dicots are often marked with patterns and textured markings, or have wings or tufts of hair.

Seed size and seed set

Seeds are very diverse in size. The dust-like orchid seeds are the smallest with about one million seeds per gram; they are often embryonic seeds with immature embryos and no significant energy reserves. Orchids and a few other groups of plants are myco-heterotrophs which depend on mycorrhizal fungi for nutrition during germination and the early growth of the seedling. Some terrestrial Orchid seedlings, in fact, spend the first few years of their life deriving energy from the fungus and do not produce green leaves. At over 20 kg, the largest seed is the coco de mer. Plants that produce smaller seeds can generate many more seeds per flower, while plants with larger seeds invest more resources into those seeds and normally produce fewer seeds. Small seeds are quicker to ripen and can be dispersed sooner, so fall blooming plants often have small seeds. Many annual plants produce great quantities of smaller seeds; this helps to ensure that at least a few will end in a favorable place for growth. Herbaceous perennials and woody plants often have larger seeds, they can produce seeds over many years, and larger seeds have more energy reserves for germination and seedling growth and produce larger, more established seedlings after germination.

Seed functions

Seeds serve several functions for the plants that produce them. Key among these functions are nourishment of the embryo, dispersal to a new location, and dormancy during unfavorable conditions. Seeds fundamentally are a means of reproduction and most seeds are the product of sexual reproduction which produces a remixing of genetic material and phenotype variability that natural selection acts on.

Embryo nourishment

Seeds protect and nourish the embryo or young plant. Seeds usually give a seedling a faster start than a sporeling from a spore, because of the larger food reserves in the seed and the multicellularity of the enclosed embryo.

Seed dispersal

Unlike animals, plants are limited in their ability to seek out favorable conditions for life and growth. As a result, plants have evolved many ways to disperse their offspring by dispersing their seeds. A seed must somehow "arrive" at a location and be there at a time favorable for germination and growth. When the fruits open and release their seeds in a regular way, it is called dehiscent, which is often distinctive for related groups of plants, these fruits include; Capsules, follicles, legumes, silicles and siliques. When fruits do not open and release their seeds in a regular fashion they are called indehiscent, which include the fruits achenes, caryopsis, nuts, samaras, and utricles.

Seed dispersal is seen most obviously in fruits; however many seeds aid in their own dispersal. Some kinds of seeds are dispersed while still inside a fruit or cone, which later opens or disintegrates to release the seeds. Other seeds are expelled or released from the fruit prior to dispersal. For example, milkweeds produce a fruit type, known as a *follicle*, that splits open along one side to release the seeds. Iris capsules split into three "valves" to release their seeds.

By wind (anemochory)

Dandelion seeds (achenes) can be carried long distances by the wind.

The seed pod of milkweed (Asclepias syriaca)

- Many seeds (e.g. maple, pine) have a wing that aids in wind dispersal.
- The dustlike seeds of orchids are carried efficiently by the wind.
- Some seeds, (e.g. dandelion, milkweed, poplar) have hairs that aid in wind dispersal.

Some winged seeds have two, and some have only one wing.

By water (hydrochory)

- Some plants, such as *Mucuna* and *Dioclea*, produce buoyant seeds termed sea-beans or drift seeds because they float in rivers to the oceans and wash up on beaches.

By animals (zoochory)

- Seeds (burrs) with barbs or hooks (e.g. acaena, burdock, dock) which attach to animal fur or feathers, and then drop off later.
- Seeds with a fleshy covering (e.g. apple, cherry, juniper) are eaten by animals (birds, mammals, reptiles, fish) which then disperse these seeds in their droppings.
- Seeds (nuts) which are an attractive long-term storable food resource for animals (e.g. acorns, hazelnut, walnut); the seeds are stored some distance from the parent plant, and some escape being eaten if the animal forgets them.

Myrmecochory is the dispersal of seeds by ants. Foraging ants disperse seeds which have appendages called elaiosomes (e.g. bloodroot, trilliums, Acacias, and many species of Proteaceae). Elaiosomes are soft, fleshy structures that contain nutrients for animals that eat them. The ants carry such seeds back to their nest, where the elaiosomes are eaten. The remainder of the seed, which is hard and inedible to the ants, then germinates either within the nest or at a removal site where the seed has been discarded by the ants. This dispersal relationship is an example of mutualism, since the plants depend upon the ants to disperse seeds, while the ants depend upon the plants seeds for food. As a result, a drop in numbers of one partner can reduce success of the other. In South Africa, the Argentine ant (*Linepithema humile*) has invaded and displaced native species of ants. Unlike the native ant species, Argentine ants do not collect the seeds of *Mimetes cucullatus* or eat the elaiosomes. In areas where these ants have invaded, the numbers of *Mimetes* seedlings have dropped.

Seed dormancy

Seed dormancy has two main functions: the first is synchronizing germination with the optimal conditions for survival of the resulting seedling; the second is spreading germination of a batch of seeds over time so that a catastrophe after germination (e.g. late frosts, drought, herbivory) does not result in the death of all offspring of a plant (bet-hedging). Seed dormancy is defined as a seed failing to germinate under environmental conditions optimal for germination, normally when the environment is at a suitable temperature with proper soil moisture. This true dormancy or innate dormancy is therefore caused by conditions within the seed that prevent germination. Thus dormancy is a state of the seed, not of the environment. Induced dormancy, enforced dormancy or seed quiescence occurs when a seed fails to germinate because the external environmental conditions are inappropriate for germination, mostly in response to conditions being too dark or light, too cold or hot, or too dry.

Seed dormancy is not the same as seed persistence in the soil or on the plant, though even in scientific publications dormancy and persistence are often confused or used as synonyms.

Often seed dormancy is divided into four major categories: exogenous; endogenous; combinational; and secondary. A more recent system distinguishes five classes of dormancy:morphological, physiological, morphophysiological, physical and combinational dormancy.

Exogenous dormancy is caused by conditions outside the embryo including:

- **Physical dormancy** or **hard seed coats** occurs when seeds are impermeable to water. At dormancy break a specialized structure, the ‘water gap’, is disrupted in response to environmental cues, especially temperature, so that water can enter the seed and germination can occur. Plant families where physical dormancy occurs include Anacardiaceae, Cannaceae, Convulvulaceae, Fabaceae and Malvaceae.
- **Chemical dormancy** considers species that lack physiological dormancy, but where a chemical prevents germination. This chemical can be leached out of the seed by rainwater or snow melt or be deactivated somehow. Leaching of chemical inhibitors from the seed by rain water is often cited as an important cause of dormancy release in seeds of desert plants, however little evidence exists to support this claim.

Endogenous dormancy is caused by conditions within the embryo itself, including:

- **Morphological dormancy** where germination is prevented due to morphological characteristics of the embryo. In some species the embryo is just a mass of cells when seeds are dispersed, it is not differentiated. Before germination can take place both differentiation and growth of the embryo have to occur. In other species the embryo is differentiated but not fully grown (underdeveloped) at dispersal and embryo growth up to a species specific length is required before germination can occur. Examples of plant families where morphological dormancy occurs are Apiaceae, Cycadaceae, Liliaceae, Magnoliaceae and Ranunculaceae.
- **Morphophysiological dormancy** seeds with underdeveloped embryos, and which in addition have physiological components to dormancy. These seeds therefore require a dormancy-breaking treatments as well as a period of time to develop fully grown embryos. Plant families where morphophysiological dormancy occurs include Apiaceae, Aquifoliaceae, Liliaceae, Magnoliaceae, Papaveraceae and Ranunculaceae. Some plants with morphophysiological dormancy like Asarum or Trillium species have multiple types of dormancy, one affects radicle (root) growth while the other affects plumule (shoot) growth. The terms "double dormancy" and "2-year seeds" are used for species whose seeds need two years to complete germination or at least two winters and one summer.

Dormancy of the radicle (seedling root)is broken during the first winter after dispersal while dormancy of the shoot bud is broken during the second winter.

- **Physiological dormancy** means that the embryo can, due to physiological causes, not generate enough power to break through the seed coat, endosperm or other covering structures. Dormancy is typically broken at cool wet, warm wet or warm dry conditions. Abscisic acid is usually the growth inhibitor in seeds and its production can be affected by light.
    - **Drying**; some plants including a number of grasses and those from seasonally arid regions need a period of drying before they will germinate, the seeds are released but need to have a lower moisture content before germination can begin. If the seeds remain moist after dispersal, germination can be delayed for many months or even years. Many herbaceous plants from temperate climate zones have physiological dormancy that disappears with drying of the seeds. Other species will germinate after dispersal only under very narrow temperature ranges, but as the seeds dry they are able to germinate over a wider temperature range.

- **Combinational dormancy** In seeds with combinational dormancy the seed or fruit coat is impermeable to water and the embryo has physiological dormancy. Depending on the species physical dormancy can be broken before or after physiological dormancy is broken.

- **Secondary dormancy*** is caused by conditions after the seed has been dispersed and occurs in some seeds when non-dormant seed is exposed to conditions that are not favorable to germination, very often high temperatures. The mechanisms of secondary dormancy are not yet fully understood but might involve the loss of sensitivity in receptors in the plasma membrane.

The following types of seed dormancy do not involve seed dormancy strictly spoken as lack of germination is prevented by the environment not by characteristics of the seed itself :

- **Photodormancy** or light sensitivity affects germination of some seeds. These photoblastic seeds need a period of darkness or light to germinate. In species with thin seed coats, light may be able to penetrate into the dormant embryo. The presence of light or the absence of light may trigger the germination process, inhibiting germination in some seeds buried too deeply or in others not buried in the soil.
- **Thermodormancy** is seed sensitivity to heat or cold. Some seeds including cocklebur and amaranth germinate only at high temperatures (30C or 86F) many plants that have seed that germinate in early to mid summer have thermodormancy and germinate only when the soil temperature is warm. Other seeds need cool soils to germinate, while others like celery are inhibited when soil temperatures are too warm. Often thermodormancy requirements disappear as the seed ages or dries.

Not all seeds undergo a period of dormancy. Seeds of some mangroves are viviparous, they begin to germinate while still attached to the parent. The large, heavy root allows the seed to penetrate into the ground when it falls. Many garden plants have seeds that will germinate readily as soon as they have water and are warm enough, though their wild ancestors may have had dormancy, these cultivated plants lack seed dormancy. After many generations of selective pressure by plant breeders and gardeners dormancy has been selected out.

For annuals, seeds are a way for the species to survive dry or cold seasons. Ephemeral plants are usually annuals that can go from seed to seed in as few as six weeks.

Seed persistence and seed banks

Seed germination

Germinating sunflower seedlings.

Seed germination is a process by which a seed embryo develops into a seedling. It involves the reactivation of the metabolic pathways that lead to growth and the emergence of the radicle or seed root and plumule or shoot. The emergence of the seedling above the soil surface is the next phase of the plants growth and is called seedling establishment.

Three fundamental conditions must exist before germination can occur. (1) The embryo must be alive, called seed viability. (2) Any dormancy requirements that prevent germination must be overcome. (3) The proper environmental conditions must exist for germination.

Seed viability is the ability of the embryo to germinate and is affected by a number of different conditions. Some plants do not produce seeds that have functional complete embryos or the seed may have no embryo at all, often called empty seeds. Predators and pathogens can damage or kill the seed while it is still in the fruit or after it is dispersed. Environmental conditions like flooding or heat can kill the seed before or during germination. The age of the seed affects its health and germination ability: since the seed has a living embryo, over time cells die and cannot be replaced. Some seeds can live for a long time before germination, while others can only survive for a short period after dispersal before they die.

Seed vigor is a measure of the quality of seed, and involves the viability of the seed, the germination percentage, germination rate and the strength of the seedlings produced.

The **germination percentage** is simply the proportion of seeds that germinate from all seeds subject to the right conditions for growth. The **germination rate** is the length of time it takes for the seeds to germinate. Germination percentages and rates are affected by seed viability, dormancy and environmental effects that impact on the seed and seedling. In agriculture and horticulture quality seeds have high viability, measured by germination percentage plus the rate of germination. This is given as a percent of germination over a certain amount of time, 90% germination in 20 days, for example. 'Dormancy' is covered above; many plants produce seeds with varying degrees of dormancy, and different seeds from the same fruit can have different degrees of dormancy. It's possible to have seeds with no dormancy if they are dispersed right away and do not dry (if the seeds dry they go into physiological dormancy). There is great variation amongst plants and a dormant seed is still a viable seed even though the germination rate might be very low.

Environmental conditions effecting seed germination include; water, oxygen, temperature and light.

Three distinct phases of seed germination occur: water imbibition; lag phase; and radicle emergence.

In order for the seed coat to split, the embryo must imbibe (soak up water), which causes it to swell, splitting the seed coat. However, the nature of the seed coat determines how rapidly water can penetrate and subsequently initiate germination. The rate of imbibition is dependent on the permeability of the seed coat, amount of water in the environment and the area of contact the seed has to the source of water. For some seeds, imbibing too much water too quickly can kill the seed. For some seeds, once water is imbibed the germination process cannot be stopped, and drying then becomes fatal. Other seeds can imbibe and lose water a few times without causing ill effects, but drying can cause secondary dormancy.

Inducing germination

A number of different strategies are used by gardeners and horticulturists to break seed dormancy.

Scarification which allows water and gases to penetrate into the seed, include methods that physically break the hard seed coats or soften them by chemicals. Means of scarification include soaking in hot water or poking holes in the seed with a pin or rubbing them on sandpaper or cracking with a press or hammer. Soaking the seeds in solvents or acids is also effective for many seeds. Sometimes fruits are harvested while the seeds are still immature and the seed coat is not fully developed and sown right away before the seed coat become impermeable. Under natural conditions seed coats are worn down by rodents chewing on the seed, the seeds rubbing against rocks (seeds are moved by the wind or water currents), by undergoing freezing and thawing of surface water, or passing through an animal's digestive tract. In the latter case, the seed coat protects the seed from digestion, while often weakening the seed coat such that the embryo is ready to sprout when it gets deposited (along with a bit of fertilizer) far from the parent plant. Microorganisms are often effective in breaking down hard seed coats and are sometimes used by people as a treatment, the seeds are stored in a moist warm sandy medium for several months under non-sterile conditions.

Stratification also called moist-chilling is a method to break down physiological dormancy and involves the addition of moisture to the seeds so they imbibe water and then the seeds are subject to a period of moist chilling to after-ripen the embryo. Sowing outside in late summer and fall and allowing to overwinter outside under cool conditions is an effective way to stratify seeds, some seeds respond more favorably to periods of oscillating temperatures which are part of the natural environment.

Leaching or the soaking in water removes chemical inhibitors in some seeds that prevent germination. Rain and melting snow naturally accomplish this task. For seeds planted in gardens, running water is best - if soaked in a container, 12 to 24 hours of soaking is sufficient. Soaking longer, especially in stagnant water that is not changed, can result in oxygen starvation and seed death. Seeds with hard seed coats can be soaked in hot water to break open the impermeable cell layers that prevent water intake.

Other methods used to assist in the germination of seeds that have dormancy include prechilling, predrying, daily alternation of temperature, light exposure, potassium nitrate, the use of plant growth regulators like gibberellins, cytokinins, ethylene, thiourea, sodium hypochlorite plus others. Some seeds germinate best after a fire, for some seeds fire cracks hard seed coats while in other seeds chemical dormancy is broken in reaction to the presence of smoke, liquid smoke is often used by gardeners to assist in the germination of these species.

Origin and evolution

The origin of seed plants is a problem that still remains unsolved. However, more and more data tends to place this origin in the middle Devonian. The description in 2004 of the proto-seed *Runcaria heinzelinii* in the Givetian of Belgium is an indication of that ancient origin of seed-plants. As with modern ferns, most land plants before this time reproduced by sending spores into the air, that would land and become whole new plants.

The first "true" seeds are described from the upper Devonian, which is probably the theater of their true first evolutionary radiation. The seed plants progressively became one of the major elements of nearly all ecosystems.

Economic importance

A variety of bean seeds.

Edible seeds

Many seeds are edible and the majority of human calories comes from seeds, especially from cereals, legumes and nuts. Seeds also provide most cooking oils, many beverages and spices and some important food additives. In different seeds the seed embryo or the endosperm dominates and provides most of the nutrients. The storage proteins of the embryo and endosperm differ in their amino acid content and physical properties. For example the gluten of wheat, important in providing the elastic property to bread dough is strictly an endosperm protein.

Seeds are used to propagate many crops such as cereals, legumes, forest trees, turfgrasses and pasture grasses. Particularly in developing countries, a major constraint faced is the inadequacy of the marketing channels to get the seed to poor farmers. Thus the use of farmer-retained seed remains quite common.

Seeds are also eaten by animals, and are fed to livestock. Many seeds are used as birdseed.

Poison and food safety

While some seeds are edible, others are harmful, poisonous or deadly. Plants and seeds often contain chemical compounds to discourage herbivores and seed predators. In some cases, these compounds simply taste bad (such as in mustard), but other compounds are toxic or break down into toxic compounds within the digestive system. Children, being smaller than adults, are more susceptible to poisoning by plants and seeds.

A deadly poison, ricin, comes from seeds of the castor bean. Reported lethal doses are anywhere from two to eight seeds, though only a few deaths have been reported when castor beans have been ingested by animals.

In addition, seeds containing amygdalin—apple, apricot, bitter almond, peach, plum, cherry, quince, and others—when consumed in sufficient amounts, may cause Cyanide poisoning. Other seeds that contain poisons include annona, cotton, custard apple, datura, uncooked durian, golden chain, horse-chestnut, larkspur, locoweed, lychee, nectarine, rambutan, rosary pea, sour sop, sugar apple, wisteria, and yew. The seeds of the strychnine tree are also poisonous, containing the poison strychnine.

The seeds of many legumes, including the common bean (*Phaseolus vulgaris*), contain proteins called lectins which can cause gastric distress if the beans are eaten without cooking. The common bean and many others, including the soybean, also contain trypsin inhibitors which interfere with the action of the digestive enzyme trypsin. Normal cooking processes degrade lectins and trypsin inhibitors to harmless forms.

Other uses

Flax seed oil (in bottles) and coconut oil (in jars in the middle).

Cotton fiber grows attached to cotton plant seeds. Other seed fibers are from kapok and milkweed.

Many important nonfood oils are extracted from seeds. Linseed oil is used in paints. Oil from jojoba and crambe are similar to whale oil.

Seeds are the source of some medicines including castor oil, tea tree oil and the discredited cancer drug, Laetrile.

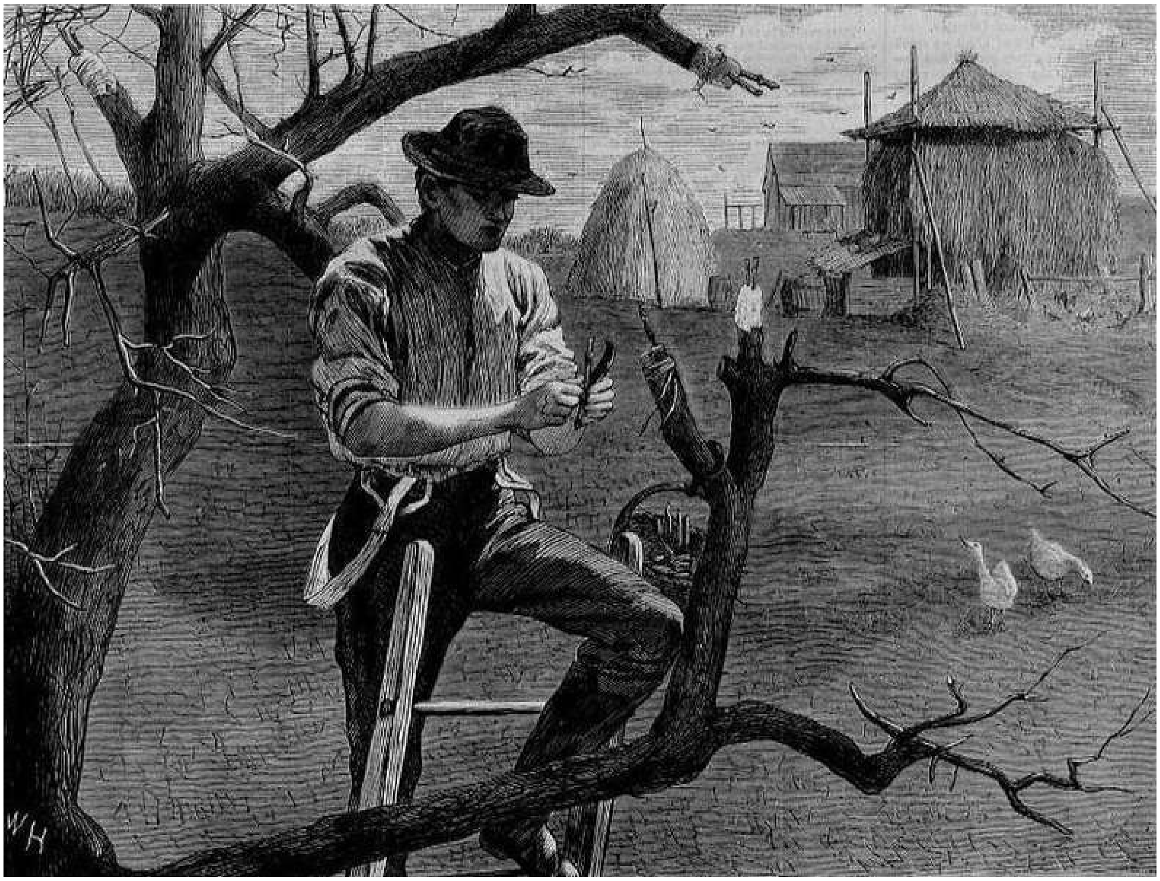
Many seeds have been used as beads in necklaces and rosaries including Job's tears, Chinaberry, rosary pea, and castor bean. However, the latter three are also poisonous.

Other seed uses include:

- Seeds once used as weights for balances.
- Seeds used as toys by children, such as for the game Conkers.
- Resin from *Clusia rosea* seeds used to caulk boats.
- Nematicide from milkweed seeds.

Chapter 12

Fruit Tree Propagation



Grafting, 1870, by Winslow Homer

Fruit tree propagation is usually carried out through asexual reproduction by grafting or budding the desired variety onto a suitable rootstock.

Perennial plants can be propagated either by sexual or vegetative means. Sexual reproduction begins when a male germ cell (pollen) from one flower fertilises a female germ cell (ovule, incipient seed) of the same species, initiating the development of a fruit containing seeds. Each seed, when germinated, can grow to become a new specimen tree. However, the new tree inherits characteristics of both its parents, and it will not grow 'true' to the variety of either parent from which it came. That is, it will be a fresh individual with an unpredictable combination of characteristics of its own. Although this is desirable in terms of producing novel combinations from the richness of the gene pool of the two parent plants (such sexual recombination is the source of new cultivars), only rarely will the resulting new fruit tree be directly useful or attractive to the tastes of humankind. Most new plants will have characteristics that lie somewhere between those of the two parents.

Therefore, from the orchard grower or gardener's point of view, it is preferable to propagate fruit cultivars vegetatively in order to ensure reliability. This involves taking a cutting (or scion) of wood from a desirable parent tree which is then grown on to produce a new plant or 'clone' of the original. In effect this means that the original Bramley apple tree, for example, was a successful variety grown from a pip, but that every Bramley since then has been propagated by taking cuttings of living matter from that tree, or one of its descendants.

Methods

The essentials of our present methods of propagating of fruit trees date from pre-Classical times. Grafting as a technique was first developed in China from where it was imported to Greece and Rome. Classical authors wrote extensively about the technical skills of fruit cultivation, including grafting techniques and rootstock selection. The oldest surviving named varieties of fruits date from classical times.

The simplest method of propagating a tree asexually is **rooting**. A **cutting** (a piece of the parent plant) is cut and stuck into soil. Artificial rooting hormones are sometimes used to assure success. If the cutting does not die of desiccation first, roots grow from the buried portion of the cutting to become a complete plant. Though this works well for some plants (such as figs and olives), most fruit trees are unsuited to this method.

Root cuttings (pieces of root induced to grow a new trunk) are used with some kinds of plants. This method also is suitable only for some plants.

A refinement on rooting is **layering**. This is rooting a piece of a wood that is still attached to its parent and continues to receive nourishment from it. The new plant is severed only after it has successfully grown roots. Layering is the technique most used for propagation of clonal apple rootstocks.

The most common method of propagating fruit trees, suitable for nearly all species, is **grafting** onto rootstocks. These are varieties selected for characteristics such as their vigour of growth, hardiness, soil tolerance, and compatibility with the desired variety that will form the aerial part of the plant (called the **scion**). For example, grape rootstocks descended from North American grapes allow European grapes to be grown in areas infested with *Phylloxera*, a soil-dwelling insect that attacks and kills European grapes when grown on their own roots. Grafting is the process of joining these two varieties, ensuring maximum contact between the cambium tissue (that is, the layer of growing plant material just below the bark) of each so that they grow together successfully. Two of the most common grafting techniques are 'whip and tongue', carried out in spring as the sap rises, and 'budding', which is performed around the end of summer.

Bud grafting

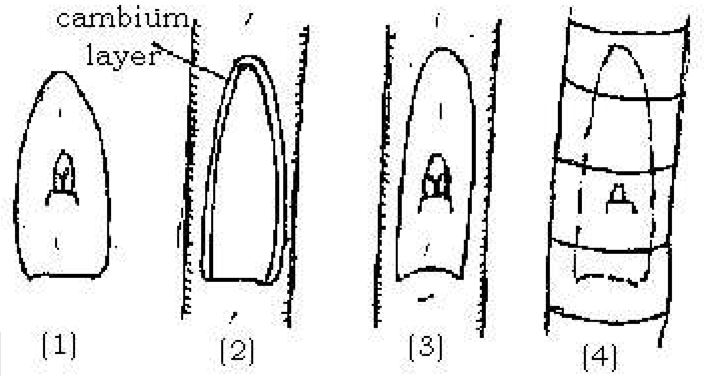
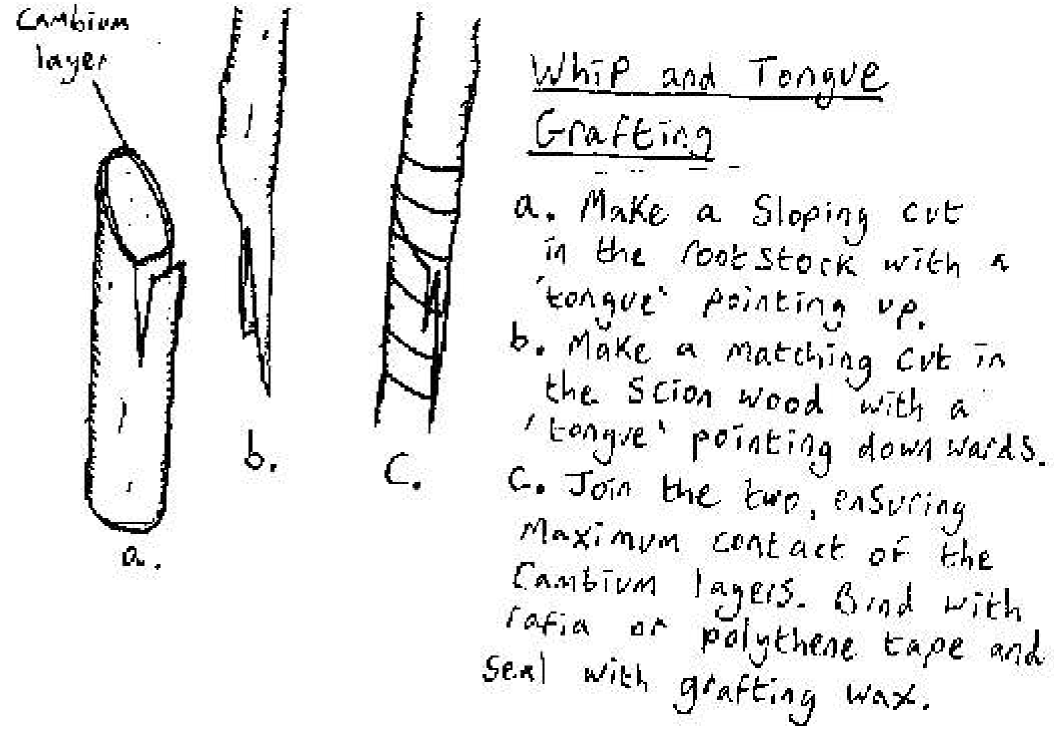


Diagram illustrating the bud grafting technique

1. Cut a slice of bud and bark from the parent tree.
2. Cut a similar sliver off the rootstock, making a little lip at the base to slot the scion into.
3. Join the two together and bind.
4. In time, the scion bud will grow into a shoot, which will develop into the desired tree.

Whip and Tongue grafting



Whip and Tongue Grafting

a. Make a Sloping cut in the rootstock with a 'tongue' pointing up.
b. Make a matching cut in the Scion wood with a 'tongue' pointing downwards.
c. Join the two, ensuring Maximum contact of the Cambium layers. Bind with rafia or polythene tape and seal with grafting wax.

Diagram illustrating the whip and tongue grafting technique

1. Make a sloping cut in the rootstock with a 'tongue
2. Make a matching cut in the scion wood with a 'tongue' pointing downwards.
3. Join the two, ensuring maximum contact of the cambium layers. Bind with raffia or polythene tape or wound around with a 5mm wide strip of elastic band (this is particularly successful because it keeps pressure on the cambium layers to be joined and eventually falls away with out cutting into the bark as the tree grows) (and seal with grafting wax.

Apple Rootstocks

Another reason for grafting onto rootstocks is that this enables the grower to determine the tree's eventual size. Apple tree size classes number one to ten in increasing height and breadth. A "1" is a dwarf which can be productive and as short as three(3) feet with proper pruning. A "10" is the standard sized tree with no dwarfing and will grow to twenty(20) or more feet tall and wide, dependent upon the variety chosen. In general the class range is (1) 10-20% of full size, (2) 20-30%, (3) 30-40% and so forth to size 10 which is 100% of full size.

Apple tree rootstocks are referred to by numbers prefixed by letters indicating the developer of the rootstock.

"M" designates Malling series developed stocks. East Malling Research is a pioneer in the development of dwarfing rootstocks. East Malling Research Station in Kent, England collected clones of the Paradise stocks from France in 1912 from which 24 "M" were designated with no particular order to the rootstock characteristics other than where they were located in the garden at the time the numbers were assigned. In other words, M.2 is larger tree than M.9 while M.27 is smaller than M.26.

"MM" designates Malling-Merton stocks developed from joint breeding program by John Innes Institute, in Merton, England, & East Malling Research Station in the early 1950s. The "MM" series was developed primarily to provide resistance to Woolly Apple Aphid(Eriosomatinae) infestation.

"EMLA" designates East Malling / Long Ashton research stations who took the "M" stocks and developed virus free versions. E.g., EMLA 7 is M 7 with a guaranteed virus free stock. EMLA characteristics are often different from the parent "M" rootstock. Note that nearly all the apple rootstocks in the industry are now virus free.

"CG" or **"G"** designates Cornell-Geneva stocks which are those developed via the Cornell & USDA collaboration at the New York Agricultural Experiment Station in Geneva, NY. The "G" is the old designation. All newer stocks are "CG" followed by numbers that actually provide some information about the stock. As one might surmise, this is a huge improvement in the classical naming scheme which has no identification method at all.

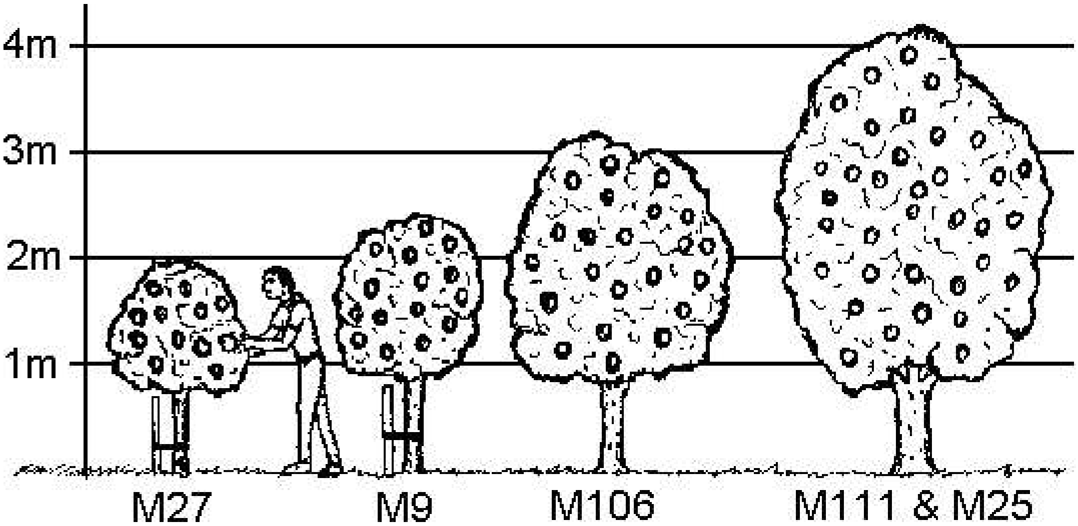


Diagram illustrating comparative sizes of apple trees depending on rootstock grafting

- **M.27** Malling 27: A very dwarfing rootstock. Unless the central leader is supported, the tree will be very small. Often only used as an intermediate stem piece on MM.106 or MM.111. If handled and spaced properly, it can be a very productive stock for a vertical axe system. Trees can be grown three to four feet tall and produce about 45 fruit, roughly 2 pecks, depending on fruit cultivar.

- **M.9**: Very dwarfing - Reaches a height of 8 to 10 ft (2.4 to 3.0 m), coming into fruit after 3–4 years, reaching full capacity of 50 to 65 pounds (23 to 29 kg) after 5 to 6 years. It will grow under average soil conditions, but needs a good rich soil to thrive. A good choice where space is limited and fertility is high. Permanent staking is required, as is routine feeding and watering. Trees on this rootstock always require leader support. The rootstock is very susceptible to fire blight and can develop burr knots.

- **G.41** Geneva 41, released in 2005, produces trees the size of M.9. The rootstock was developed from a cross between M.27 and Robusta 5 made in 1975. Resistant to Crown|Collar|Root rot(Phytopthora) and fire blight.

- **M.26**: Dwarfing - Similar to M9 in effect, although somewhat more vigorous and generally stronger, with a higher expected eventual yield of 65–75 pounds (29–34 kg) and height of 8 to 10 ft (2.4 to 3.0 m). A good choice where soil quality is average and compact growth is required. Comes into fruit after 3–4 years, reaching full cropping capacity after 5 to 6 years. Staking needed for first five years of its life. It is susceptible to collar rot and fire blight and should not be planted in a wet site. Certain varieties when grafted onto this rootstock may exhibit signs of graft union incompatibility(i.e., the union breaks).

- **G.11** Geneva 11 is the second release of the Cornell breeding program similar in size to M.26(Class 4) but more productive. Has the advantage of being resistant to fire blight and crown rot as well as only rarely producing suckers or burr knots.

- **G.202** Geneva 202(CG 5202) is a semidwarfing rootstock that produces a tree in class 5 slightly larger than M.26(Size Class 4) and is more productive than M.26. It was developed from a cross of M.27(Size Class 1) and Robusta 5 to be fire blight and Phytopthora resistant as well as having resistance to woolly apple aphids. In a 9-year study with the scion cultivar of the "Liberty" apple, G.202 was about 50 percent smaller than M.7 but had much greater production efficiency.

- **M.7** Malling 7 rootstock produces a semidwarf tree of Class 6 that is freestanding in deep well drained soils but in rocky, steep, or shallow soils, it tends to lean. The rootstock may sucker profusely and is susceptible to collar rot(Phytopthora).

- **MM.106**: Semi-dwarfing - Sometimes referred to as semi-vigorous, this is the most widely used of rootstocks. It is probably the best choice for the average garden under average conditions, being tolerant of a wide range of soils, and producing a tree with an eventual size of 14 to 18 ft (4.3 to 5.5 m). Trees on this stock begin producing fruit within three to four years, and yield 90 to 110 pounds (41 to 50 kg) after some seven or eight years. MM106 is very suitable for use with weaker varieties that would produce under sized bushes with more dwarfing rootstocks. Can be trained as a half standard tree, but is rather too vigorous for cordons unless the soil is poor. Requires staking for the first five years or so of its life. Trees on MM.106 are highly susceptible to collar rot especially when planted in soils that remain wet(poor percolation).

- **M.111** : Vigorous - Not generally suitable for garden scale growing, being both too large and spreading (18-25'), and too slow to come into cropping. They are however suitable for growing as specimen standards in the large garden, or for producing medium sized bushes on poorer soils. Begins to fruit after six or seven years, reaching full capacity of 160 to 360 lb (73 to 160 kg) after eight to nine years. It is the most cold-hardy rootstock readily available. Planting depth of this rootstock is critical. The union should be no higher than 1 to 2 inches above the final soil line.

- **M.25**: Very vigorous - Suitable for a grassed orchard, and to grow on as a full standard. Plant 20 ft (6.1 m) apart, makes a tree of 15 to 20 ft (4.6 to 6.1 m) or more height and spread, eventually yielding 200 to 400 lb (91 to 180 kg) per tree. This rootstock is primarily used in UK and is rarely seen in USA where M.111(size Class 8) is used for this size tree.

- **Seedling**: Very vigorous trees produced on a rootstock grown from seed. There is greater variability than with the vegetatively propagated rootstocks. Apples used for production of seedling rootstocks include 'Dolgo' and 'Antonovka', which are both extremely hardy and vigorous.

That is only a sample of some of the more important current apple rootstocks that are available. There are at least a hundred more that have been developed to either provide enhancement or prevent potential damage from one kind of pest or another.

The problem with growing fruit trees, especially apple trees, is that they are subject to many different types of damage from bacteria, fungi and insects. The general approach of the commercial industry has been to use as many chemicals as necessary to insure attractive and marketable fruit. The attitude, still prevalent, has been "Who cares? Nobody eats a tree!" but as environmental problems increase and the general public pushes for low or no-spray fruit, there has become a commercial need for fruit that does not require such intensive spray programs. This is being achieved, albeit slowly, by rootstocks and trees that are bred to have natural disease and pest resistance.

The Malling series and clones have been standard rootstocks for apples for many years and remain the standard "workhorses" for the commercial industry in the USA and the UK. However, since most of them are susceptible to disease some Malling rootstocks are being replaced by new breeds, including the Cornell-Geneva series. One of the newest rootstocks, only released commercially in 2004, is CG5202(G.202) which adds resistance to the woolly apple aphid(WAA) for the "CG" series of stocks which already has resistance to the major problems preventing quality production of apples utilizing organic control systems. Combined with highly resistant trees such as "Liberty" it is showing great potential.

That leads to another characteristic of rootstocks that is or can be bred into them: environmental adaptability. This may be tolerance to wet|dry soil conditions, acidity|alkalinity of soil or even hot|cold air temperature.

Rootstocks based on Siberian Crab apple are being used in colder areas for more cold tolerance.

The ability of rootstocks to modify or augment characteristics of fruit trees is limited and often disappointing in the final results. It takes ten years to get a full picture of the effects of any one rootstock so a rootstock that appears promising in the first five years of a trial may fail in the last five years. The Mark (apple) rootstock was such a stock and has now fallen mostly into disfavor. Another, the G.30, has proved to be an excellent stock for production but it was only after a number of years of trials that it was found to be somewhat incompatible with **"Gala"** apple(and possibly others) so that it is now recommended to be staked and wired.

To get a clear picture and push the industry forward, a consortium was founded and the so-called **"NC-140"** trials of rootstocks began. These test many pome rootstocks in many different sites across the USA and thereby provide growers, be they backyard or commercial, a clearer picture of what to expect when growing fruit trees on specific stock, in specific planting methods in their specific area of the USA. As one can imagine, this has the potential for a large economic benefit to both growers and consumers as well as going a long way to eliminating the need to spray pesticides as frequently as is currently required.

Pear Rootstocks

Pears are usually grafted onto quince rootstocks, which produce small to medium sized trees. Some varieties however are not compatible with quince, and these require double working. This means that a piece of pear graft-work compatible with both the quince rootstock and the pear variety is used as an intermediate between the two. If this is not done the pear and the rootstock could eventually separate at the graft. Varieties that require double working include 'Bristol Cross', 'Dr Jules Guyot', 'Doyenné d' été' and 'Williams Bon Chrétien'.

- **Quince C**: Moderately vigorous- Makes a bush pear tree about 8 to 18 ft (2.4 to 5.5 m) tall, bearing fruit within four to eight years. Suitable for highly fertile soils and vigorous varieties, but not where conditions are poor. Used for bush, cordon and espalier growing. Old stocks of Quince C may be infected with a virus, so care should be taken to obtain certified virus free stock. If in doubt, use Quince A as there is not a great amount of difference in vigour between the two.

- **Quince A**: Medium vigour- Slightly more vigorous than Quince C, this is the most common variety upon which pears are grafted. Bears fruit between four to eight years, making a tree of some 10 to 20 ft (3.0 to 6.1 m) in height and spread. Suitable for all forms of pear trees except standards.

Pear stock: Very vigorous- Pears grafted onto pear rootstocks make very large standard trees, not suitable for most gardens.

Cherries

Until the 1970s, cherries were grown of the vigorous Malling F12/1, Mazzard (*Prunus avium*), or Maheleb (*P. maheleb*) rootstocks, which required much space and time before cropping began, thus the growing of cherries was not a realistic option on a garden scale. The introduction of the rootstock 'Colt' enables trees reaching a maximum height of 12 to 15 ft (3.7 to 4.6 m) to be grown, and if trained as a pyramid it is possible to restrict growth to about 10 ft (3.0 m). The popular sweet variety 'Stella' could even be grafted onto a 'Colt' rootstock and successfully grown in a pot on the patio.

Plums

Plum rootstocks include;

- **Pixy** - A dwarfing rootstock, suitable for bush trees planted 8-10 (3 m) apart.
- **St. Julien A** - A semi vigorous rootstock suitable for bush and half standards planted 12 to 15 ft (3.7 to 4.6 m) apart. Also suitable for peaches, nectarines and apricots.
- Brompton or Myrobalan B- Suitable for half standards planted 18 to 22 ft (5.5 to 6.7 m) apart. Also suitable for peaches, nectarines and apricots.
- **Myro-29C** - Semi-dwarf rootstock. Shallow, vigorous, good choice for hard soils. Somewhat drought tolerant.
- **Citation** - Semi-dwarf rootstock. Shallow, vigorous, good choice for hard soils. Prefers a wetter soil.

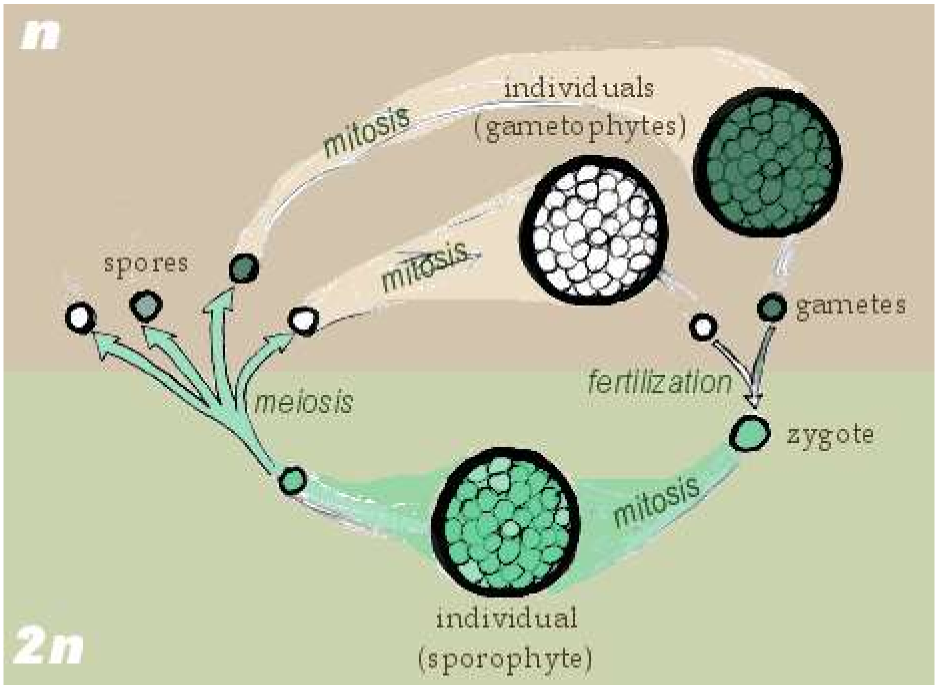
Own-Root Fruit Trees

Many species of fruit are commonly grown on their own roots: fig, filbert, olive, pomegranate, gooseberry, bramble as there may be no great advantages to using a special rootstock and/or rootstocks are not available.
However, there can be many advantages to growing fruit trees which are commonly grafted on their own rootstock instead. These advantages include better tree health; fruit that is more distinctive to the variety and of better quality (shape, size and flavor) and

that lasts longer in storage; trees with better fruit set; trees with better self pollination. Trees grown on their own roots can be more easily transplanted. And importantly, they can be used in the traditional coppicing systems advocated in both Sustainable agriculture and Permaculture. Disadvantages of using own root trees include excessive size, excessive production of wood (thus very long times until the start of fruit production), and a lack of research on the use of this technique in large scale systems. There are several techniques available to cause trees to start fruiting earlier including: withholding nitrogen and/or water (except in case of drought); training branches on the horizontal to induce budding, and limiting pruning to summer only.

Chapter 13

Spore



Spores produced in a sporic life cycle.

In biology, a **spore** is a reproductive structure that is adapted for dispersal and surviving for extended periods of time in unfavorable conditions. Spores form part of the life cycles of many bacteria, plants, algae, fungi and some protozoans. A chief difference between spores and seeds as dispersal units is that spores have very little stored food resources compared with seeds.

Spores are usually haploid and unicellular and are produced by meiosis in the sporangium by the sporophyte. Once conditions are favorable, the spore can develop into a new organism using mitotic division, producing a multicellular gametophyte, which eventually goes on to produce gametes. Two gametes fuse to create a new sporophyte. This cycle is known as alternation of generations, but a better term is "biological life cycle", as there may be more than one phase and so it cannot be a direct alternation. Haploid spores produced by mitosis (known as mitospores) are used by many fungi for asexual reproduction.

Many species of fern, especially those adapted to dry conditions, produce diploid spores. This form of asexual reproduction is called apogamy. It is a form of apomixis.

Spores are the units of asexual reproduction, because a single spore develops into a new organism. By contrast, gametes are the units of sexual reproduction, as two gametes need to fuse to create a new organism.

Definition

The term *spore* derives from the ancient Greek word σπορά *spora*, meaning "seed, sowing," related to σπόρος *sporos*, "sowing," and σπείρειν *speirein*, "to sow."

In common parlance, the difference between a "spore" and a "gamete" (both together called gonites) is that a spore will germinate and develop into a sporeling, while a gamete needs to combine with another gamete before developing further. However, the terms are somewhat interchangeable when referring to gametes.

A chief difference between spores and seeds as dispersal units is that spores have little food storage compared with seeds, and thus require more favorable conditions in order to successfully germinate. (This is not without its exceptions, however: many orchid seeds, although multicellular, are microscopic and lack endosperm, and spores of some fungi in the Glomeromycota commonly exceed 300 µm in diameter.) Seeds, therefore, are more resistant to harsh conditions and require less energy to start mitosis. Spores are produced in large numbers to increase the chance of a spore surviving in a number of notable examples.

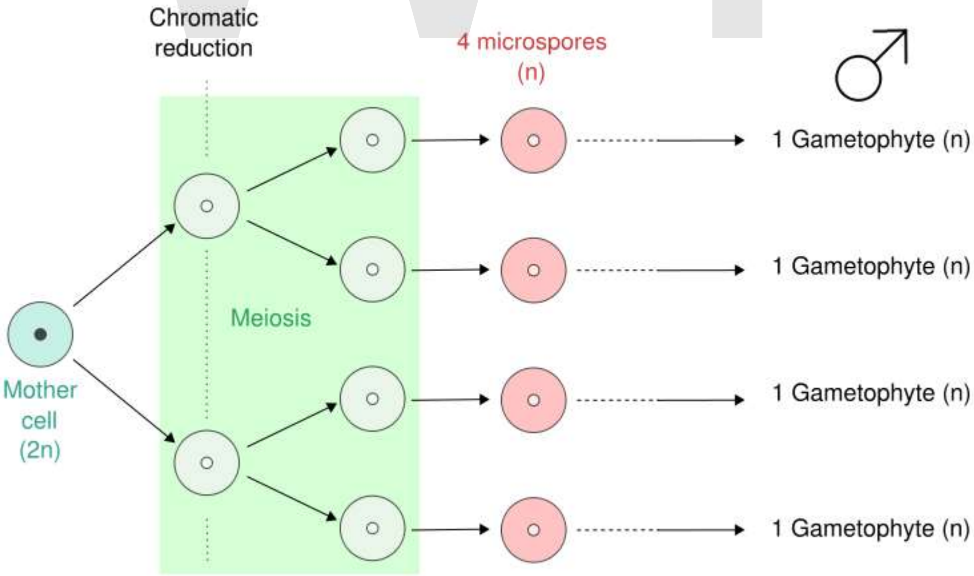
Classification

Spores can be classified in several ways:

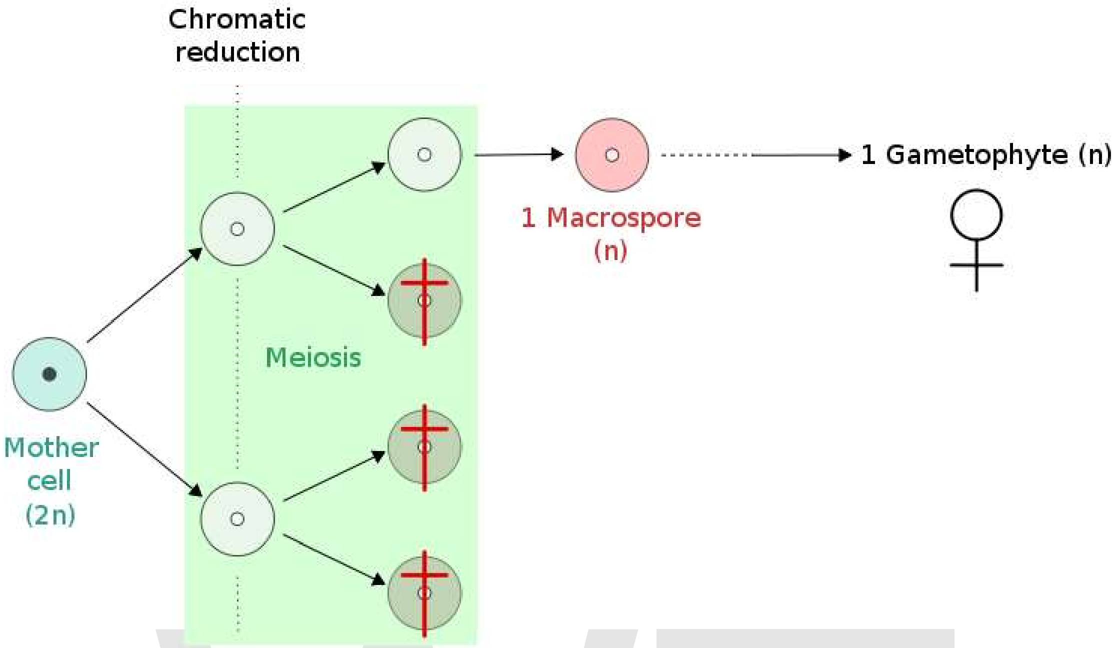
By spore-producing structure

Fresh snow partially covers Rough-stalked Feather-moss *(Brachythecium rutabulum)*, growing on a thinned hybrid black poplar *(Populus x canadensis)*. The last stage of the moss lifecycle is shown, where the sporophytes are visible before dispersion of their spores: the calyptra (**1**) is still attached to the capsule (**2**). The tops of the gametophytes (**3**) can be discerned as well. Inset shows the surrounding, black poplars growing on sandy loam on the bank of a kolk, with the detail area marked.

Asci of *Morchella elata*, containing ascospores



In plants, microspores, and in some cases megaspores, are formed from all four products of meiosis.



In contrast, in many seed plants and heterosporous ferns, only a single product of meiosis will become a megaspore (macrospore), with the rest degenerating.

In fungi and fungus-like organisms, spores are often classified by the structure in which meiosis and spore production occurs. Since fungi are often classified according to their spore-producing structures, these spores are often characteristic of a particular taxon of the fungi.

- **Sporangiospores**: spores produced by a sporangium in many fungi such as zygomycetes.
- **Zygospores**: spores produced by a zygosporangium, characteristic of zygomycetes.
- **Ascospores**: spores produced by an ascus, characteristic of ascomycetes.
- **Basidiospores**: spores produced by a basidium, characteristic of basidiomycetes.
- **Aeciospores**: spores produced by a aecium in some fungi such as rusts or smuts.
- **Urediospores**: spores produced by a uredinium in some fungi such as rusts or smuts.
- **Teliospores**: spores produced by a telium in some fungi such as rusts or smuts.
- **Oospores**: spores produced by a oogonium, characteristic of oomycetes.
- **Carpospores**: spores produced by a carposporophyte, characteristic of red algae.
- **Tetraspores**: spores produced by a tetrasporophyte, characteristic of red algae.

By function

- **Chlamydospores**: thick-walled resting spores of fungi produced to survive unfavorable conditions.

- **Parasitic fungal spores** may be classified into internal spores, which germinate within the host, and external spores, also called environmental spores, released by the host to infest other hosts.

By origin during life cycle

- **Meiospores**: spores produced by meiosis; they are thus haploid, and give rise to a haploid daughter cell(s) or a haploid individual. Examples are the precursor cells of gametophytes of seed plants found in flowers (angiosperms) or cones (gymnosperms).
    - **Microspores**: meiospores that give rise to a male gametophyte, (pollen in seed plants).
    - **Megaspores** (or **macrospores**): meiospores that give rise to a female gametophyte, (an ovule in seed plants).
- **Mitospores** (or **conidia**, **conidiospores**): spores produced by mitosis; they are characteristic of Ascomycetes. Fungi in which only mitospores are found are called “mitosporic fungi” or “anamorphic fungi”, and are previously classified under the taxon Deuteromycota.

By motility

Spores can be differentiated by whether they can move or not.

- **Zoospores**: mobile spores that move by means of one or more flagella, and can be found in some algae and fungi.
- **Aplanospores**: immobile spores that may nevertheless potentially grow flagella.
- **Autospores**: immobile spores that cannot develop flagella.
- **Ballistospores**: spores that are actively discharged from the body of the fungal fruiting body. Most basidiospores are also ballistospores, and another notable example is spores of *Pilobolus*.
- **Statismospores**: spores that are not actively discharged from the fungal fruiting body. Examples are puffballs.

Anatomy

Under high magnification, spores can be categorized as either **monolete spores** or **trilete spores**. In monolete spores, there is a single line on the spore indicating the axis on which the mother spore was split into four along a vertical axis. In trilete spores, all four spores share a common origin and are in contact with each other, so when they separate, each spore shows three lines radiating from a center pole.

Vascular plant spores are always haploid. Vascular plants are either ***homosporous (or isosporous)*** or ***heterosporous***. Plants that are *homosporous* produce spores of the same size and type. *Heterosporous* plants, such as spikemosses, quillworts, and some aquatic ferns produce spores of two different sizes: the larger spore in effect functioning as a "female" spore and the smaller functioning as a "male".

Trilete spores

Trilete spores, formed by the dissociation of a spore tetrad, are taken as the earliest evidence of life on land, dating to the mid-Ordovician (early Llanvirn, ~470 million years ago).

Dispersal

Spores being ejected by fungi.

In fungi, both asexual and sexual spores or sporangiospores of many fungal species are actively dispersed by forcible ejection from their reproductive structures. This ejection ensures exit of the spores from the reproductive structures as well as travelling through the air over long distances. Many fungi thereby possess specialized mechanical and physiological mechanisms as well as spore-surface structures, such as hydrophobins, for spore ejection. These mechanisms include, for example, forcible discharge of ascospores enabled by the structure of the ascus and accumulation of osmolytes in the fluids of the ascus that lead to explosive discharge of the ascospores into the air. The forcible discharge of single spores termed *ballistospores* involves formation of a small drop of water (Buller's drop), which upon contact with the spore leads to its projectile release with an initial acceleration of more than 10,000 g. Other fungi rely on alternative mechanisms for spore release, such as external mechanical forces, exemplified by puffballs. Attracting insects, such as flies, to fruiting structures, by virtue of their having lively colours and a putrid odour, for dispersal of fungal spores is yet another strategy, most prominently used by the stinkhorns.

In the case of spore-shedding vascular plants such as ferns, wind distribution of very light spores provides great capacity for dispersal. Also, spores are less subject to animal predation than seeds because they contain almost no food reserve; however they are more subject to fungal and bacterial predation. Their chief advantage is that, of all forms of progeny, spores require the least energy and materials to produce.

Chapter 14

Grafting

Grafted apple tree *Malus* sp., consolidated 'V' graft

Newly grafted cherry tree, tape has been used to bind the rootstock and scion at the graft and tar paint to protect the cut end of the scion from desiccation. The buds will burst within the next few weeks to produce leaves and shoots

A grafted tree showing two different color blossoms

Grafting is a method of asexual plant propagation widely used in agriculture and horticulture where the tissues of one plant are encouraged to fuse with those of another. It is most commonly used for the propagation of trees and shrubs grown commercially.

In most cases, one plant is selected for its roots, and this is called the **stock** or rootstock. The other plant is selected for its stems, leaves, flowers, or fruits and is called the **scion**. The scion contains the desired genes to be duplicated in future production by the stock/scion plant.

In stem grafting, a common grafting method, a shoot of a selected, desired plant cultivar is grafted onto the stock of another type. In another common form called budding, a dormant side bud is grafted on the stem of another stock plant, and when it has fused successfully, it is encouraged to grow by cutting out the stem above the new bud.

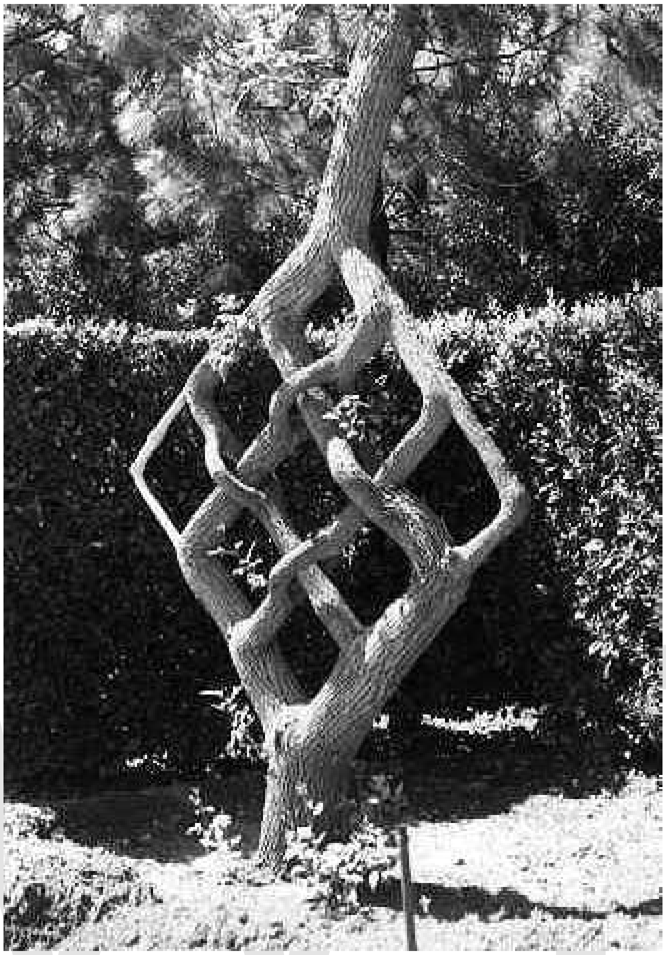
For successful grafting to take place, the vascular cambium tissues of the stock and scion plants must be placed in contact with each other. Both tissues must be kept alive until the graft has taken, usually a period of a few weeks. Successful grafting only requires that a vascular connection take place between the two tissues. A physical weak point often still occurs at the graft, because the structural tissue of the two distinct plants, such as wood, may not fuse.

Advantages

Graft particular to plum Cherry. The scion is the largest in the plant, due to the imperfect union of the two. It can be seen on the trunk is enlarged: this accumulation of starch is an indication of imperfection.

- **Precocity**: The ability to induce fruitfulness without the need for completing the juvenile phase. Juvenility is the natural state through which a seedling plant must pass before it can become reproductive. In most fruiting trees, juvenility may last between 5 and 9 years, but in some tropical fruits e.g. Mangosteen, juvenility may be prolonged for up to 15 years. Grafting of mature scions onto rootstocks can result in fruiting in as little as two years.

- **Dwarfing**: To induce dwarfing or cold tolerance or other characteristics to the scion. Most apple trees in modern orchards are grafted on to dwarf or semi-dwarf trees planted at high density. They provide more fruit per unit of land, higher quality fruit, and reduce the danger of accidents by harvest crews working on ladders.
- **Ease of propagation**: Because the scion is difficult to propagate vegetatively by other means, such as by cuttings. In this case, cuttings of an easily rooted plant are used to provide a rootstock. In some cases, the scion may be easily propagated, but grafting may still be used because it is commercially the most cost-effective way of raising a particular type of plant.
- **Hybrid breeding**: To speed maturity of hybrids in fruit tree breeding programs. Hybrid seedlings may take ten or more years to flower and fruit on their own roots. Grafting can reduce the time to flowering and shorten the breeding program.
- **Hardiness**: Because the scion has weak roots or the roots of the stock plants have roots tolerant of difficult conditions. e.g. many showy Western Australian plants are sensitive to dieback on heavy soils, common in urban gardens, and are grafted onto hardier eastern Australian relatives. Grevilleas and eucalypts are examples.
- **Sturdiness**: To provide a strong, tall trunk for certain ornamental shrubs and trees. In these cases, a graft is made at a desired height on a stock plant with a strong stem. This is used to raise 'standard' roses, which are rose bushes on a high stem, and it is also used for some ornamental trees, such as certain weeping cherries.
- **Pollen source**: To provide pollenizers. For example, in tightly planted or badly planned apple orchards of a single variety, limbs of crab apple may be grafted at regularly spaced intervals onto trees down rows, say every fourth tree. This takes care of pollen needs at blossom time, yet does not confuse pickers who might otherwise mix varieties while harvesting, as the mature crab apples are so distinct from other apple varieties.
- **Repair**: To repair damage to the trunk of a tree that would prohibit nutrient flow, such as stripping of the bark by rodents that completely girdles the trunk. In this case a bridge graft may be used to connect tissues receiving flow from the roots to tissues above the damage that have been severed from the flow. Where a watershoot, basal shoot or sapling of the same species is growing nearby, any of these can be grafted to the area above the damage by a method called inarch grafting. These alternatives to scions must be of the correct length to span the gap of the wound.
- **Changing cultivars**: To change the cultivar in a fruit orchard to a more profitable cultivar, called *topworking*. It may be faster to graft a new cultivar onto existing limbs of established trees than to replant an entire orchard.
- **Maintain consistency**: Apples are notorious for their genetic variability, even differing in multiple characteristics, such as, size, color, and flavor, of fruits located on the same tree. In the commercial farming industry, consistency is maintained by grafting a scion with desired fruit traits onto a hardy stock.



An example of approach grafting by Axel Erlandson.

- **Curiosities**
    - A practice sometimes carried out by gardeners is to graft related potatoes and tomatoes so that both are produced on the same plant, one above ground and one underground.
    - Cacti of widely different forms are sometimes grafted on to each other.
    - Multiple cultivars of fruits such as apples are sometimes grafted on a single tree. This so-called "family tree" provides more fruit variety for small spaces such as a suburban backyard, and also takes care of the need for pollenizers. The drawback is that the gardener must be sufficiently trained to prune them correctly, or one strong variety will usually "take over".
    - Ornamental and functional, tree shaping uses grafting techniques to join separate trees or parts of the same tree to itself. Furniture, hearts, entry archways are examples. Axel Erlandson was a prolific tree shaper who grew over 75 mature specimens.

Techniques

Approach

Approach grafting or inarching is used to join together plants that are otherwise difficult to join. The plants are grown close together, and then joined so that each plant has roots below and growth above the point of union. Both scion and stock retain their respective parents that may or may not be removed after joining. Also used in pleaching. The graft can be successfully accomplished any time of year.

Budding

T budding

Grafting with a single eye or bud. Normally performed at the height of the growing season by inserting a dormant bud into a shallow slice under the rind of the tree. The bud is sealed from drying and bound in place. There are many styles of budding depending on the cutting and fitting methods, the most popular being shield budding.

Other budding styles include the inverted T, patch budding, double shield, flute budding and chip budding.

Cleft

The most common form of grafting is cleft grafting. This is best done in the spring and is useful for joining a thin scion about 1 cm (0.39 in) diameter to a thicker branch or stock. It is best if the latter is 2–7 cm (0.79–2.8 in) in diameter and has 3-5 buds. The branch or stock should be split carefully down the middle to form a cleft about 3 cm (1.2 in) deep. If it is a branch that is not vertical then the cleft should be cut horizontally. The end of the scion should be cut cleanly to a long shallow wedge, preferably with a single cut for each wedge surface, and not whittled. A third cut may be made across the end of the wedge to make it straight across.

Slide the wedge into the cleft so that it is at the edge of the stock and the centre of the wedge faces are against the cambium layer between the bark and the wood. It is preferable if a second scion is inserted in a similar way into the other side of the cleft. This helps to seal off the cleft. Tape around the top of the stock to hold the scion/s in place and cover with grafting wax or sealing compound. This stops the cambium layers from drying out and also prevents the ingress of water into the cleft.

Successful cleft graft after 2 years' growth

Whip

Also known as the whip and tongue graft, this is considered the most difficult to master but has the highest rate of success as it offers the most cambium contact between the 2 species. It is the most common graft used in top-dressing commercial fruit trees. It is generally used with stock less than $\frac{1}{2}$ in (1.3 cm) diameter, with the ideal diameter closer to $\frac{3}{8}$ in (0.95 cm) and the scion should be of roughly the same diameter as the stock.

The stock is cut through on one side only at a shallow angle with a sharp knife. (If the stock is a branch and not the main trunk of the rootstock then the cut surface should face outward from the centre of the tree.) The scion is similarly sliced through at an equal angle starting just below a bud, so that the bud is at the top of the cut and on the other side than the cut face.

A notch is cut downwards into the sliced face of the stock and a similar cut upwards into the face of the scion cut. These act as the tongues and it requires some skill to make the cuts so that the scion and the stock marry up neatly. The join is then taped around and treated with tree sealing compound or grafting wax.

The elongated "Z" shape adds strength, removing the need for a companion rod in the first season.

Successful whip graft

Successful whip graft needing additional pruning the following season

Stub

Stub grafting is a technique that requires less stock than cleft grafting, and retains the shape of a tree. Also scions are generally of 6-8 buds in this process.

An incision is made into the branch 1 cm (0.39 in) long, then the scion is wedged and forced into the branch. The scion should be at an angle of at most 35° to the parent tree so that the crotch remains strong. The graft is covered with grafting compound.

After the graft has taken, the branch is removed and treated a few cm above the graft, to be fully removed when the graft is strong.

Successful stub graft, healed

Awl

Awl grafting takes the least resources and the least time. It is best done by an experienced grafter, as it is possible to accidentally drive the tool too far into the stock, reducing the scion's chance of survival. Awl grafting can be done by using a screwdriver to make a slit in the bark, not penetrating the cambium layer completely. Then inset the wedged scion into the incision.

Veneer

Veneer grafting, or inlay grafting, is a method used for stocks larger than three centimeters in diameter. The scion is recommended to be about as thick as a pencil. Clefts are made of the same size as the scion on the side of the branch, not on top. The scion end is shaped as a wedge, inserted, and wrapped with tape to the scaffolding branches to give it more strength.

Natural grafting

Possible deliberate grafts on a Sessile Oak in Ayrshire, Scotland

A Husband and Wife tree - Natural grafting in blackthorn Prunus spinosa

Tree branches and more often roots of the same species will sometimes naturally graft, this is called inosculation. When roots make physical contact with each other they often grow together. A group of trees can share water and mineral nutrients via root grafts, which may be advantageous to weaker trees, and may also form a larger rootmass as an adaptation to promote fire resistance and regeneration as exemplified by the California Black Oak (*Quercus kelloggii*).

A problem with root grafts is that they allow transmission of certain pathogens, such as Dutch elm disease. Inosculation also sometimes occurs where two stems on the same tree, shrub or vine make contact with each other. This is common in plants such as strawberries and potatoes.

Graft hybrids

Occasionally, a so-called "graft hybrid" can occur where the tissues of the stock continue to grow within the scion. Such a plant can produce flowers and foliage typical of both plants as well as shoots intermediate between the two. The best-known example this is probably +*Laburnocytisus* 'Adamii', a graft hybrid between laburnum and broom, which originated in a nursery near Paris, France in 1825. This small tree bears yellow flowers typical of *Laburnum anagyroides*, purple flowers typical of *Chamaecytisus purpureus* and curious coppery-pink flowers that show characteristics of both "parents".

Scientific uses

Grafting has been important in flowering research. Leaves or shoots from plants induced to flower can be grafted onto uninduced plants and transmit a floral stimulus that induces them to flower.

The transmission of plant viruses has been studied using grafting. Virus indexing involves grafting a symptom-less plant that is suspected of carrying a virus onto an indicator plant that is very susceptible to the virus.

Herbaceous grafting

Grafting is often done for non-woody and vegetable plants (tomato, cucumber, eggplant and watermelon). Tomato grafting is very popular in Asia and Europe, and is gaining popularity in the United States. The main advantage of grafting is for disease-resistant rootstocks. Researchers in Japan developed automated processes using grafting robots as early as 1987.

History

Grafting with detached scions has been practiced for thousands of years. It was in use by the Chinese before 2000 B.C and spread to the rest of Eurasia. The practice was almost commonplace in ancient Greece. Without the development of grafting, heterosexual fruit trees such as apples and cherries would never have been domesticated, as their natural sexual reproductive method prevents useful genes from being passed on consistently.