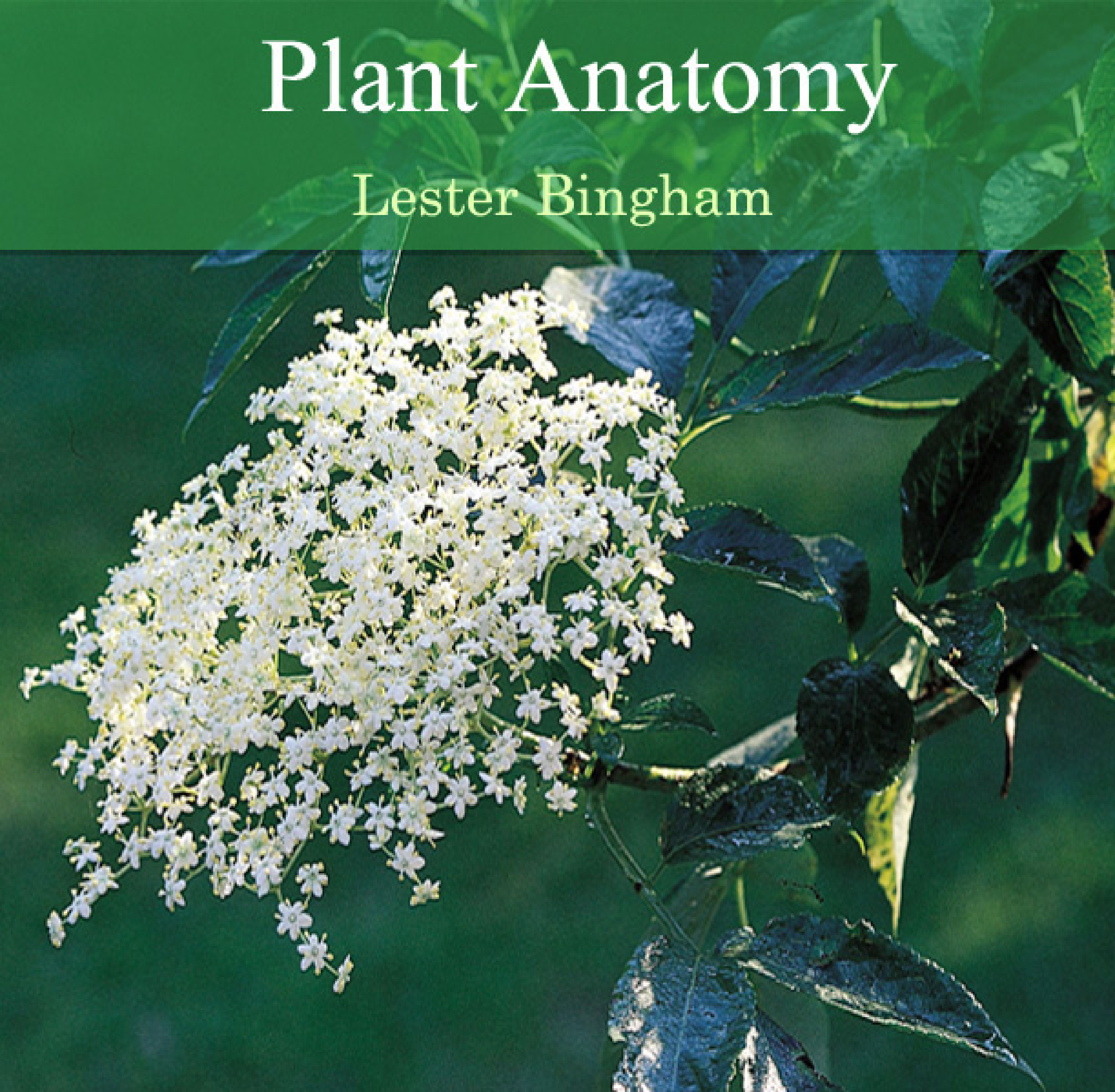
Plant Anatomy

Lester Bingham



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Chapter 1

Plant Anatomy

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

Structural divisions

Plant anatomy is sometimes divided into the following categories:

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

Root anatomy
Root structure

History

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

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

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

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

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

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

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

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

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

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

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

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

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

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

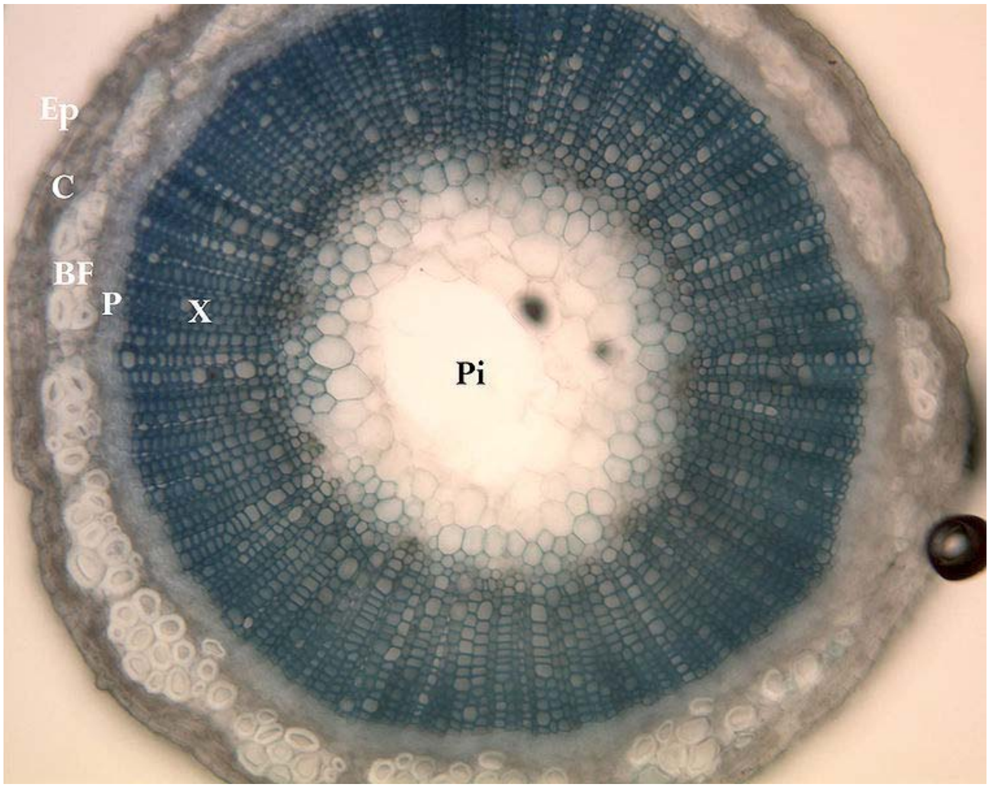
The growth of comparative plant anatomy was spearheaded by a British botanist, Agnes Arber. She published *Water Plants: A Study of Aquatic Angiosperms* in 1920, *Monocotyledons: A Morphological Study* in 1925, and *The Gramineae: A Study of Cereal, Bamboo and Grass* in 1934.

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

Chapter 2

Bast Fibre, Branch Collar and Cork Cambium

Bast fibre



Flax stem cross-section, showing locations of underlying tissues. Ep = epidermis; C = cortex; BF = bast fibres; P = phloem; X = xylem; Pi = pith

Bast fibre or **skin fibre** is plant fibre collected from the phloem (the "inner bark" or the skin) or **bast** surrounding the stem of certain, mainly dicotyledonic, plants. They support the conductive cells of the phloem and provide strength to the stem. Most of the technically important bast fibres are obtained from herbs cultivated in agriculture, as for instance flax, hemp, or ramie, but also bast fibres from wild plants, as stinging nettle, and trees such as the Tilia, have been used to some extent. Since the valuable fibres are located in the phloem, they must often be separated from the xylem material ("woody core"), and sometimes also from epidermis. The process for this is called retting, and can be performed by micro-oganisms either on land (nowadays the most important) or in water, or by chemicals (for instance high pH and chelating agents) or by pectinolytic enzymes. In the phloem bast fibres occur in bundles that are glued together by pectin and calcium ions. More intense retting separates the fibre bundles into elementary fibres, that can be several centimetres long. Often bast fibres have higher tensile strength than other kinds, and are used in high-quality textiles (sometimes in blends with cotton or synthetic fibres), ropes, yarn, paper, composite materials and burlap. A special property of bast fibres is that they contain a special structure, the *fibre node*, that represents a weak point. Seed hairs, such as cotton, do not have nodes.

Examples are:

- Jute
- Hemp
- Flax (Linen)
- Ramie
- Kenaf
- Kudzu
- Nettle
- Okra
- Paper Mulberry
- Roselle hemp
- Rattan
- Wisteria

Use of bast fibre

Bast fibres are processed for use in carpet yarn, rope, geotextile (netting or matting), traditional carpets, hessian or burlap, paper, sacks, etc. Bast fibres are also used in the non-woven, moulding, and composite technology industries for the manufacturing of non-woven mats and carpets, composite boards as furniture materials, automobile door pannels and headliners, etc. From prehistoric times through at least the early 20th century, bast shoes were woven from bast strips in the forest areas of Eastern Europe.

Branch collar

A **branch collar** is the attachment structure in woody plants that connects a branch to its parent branch or to the trunk. The branch collar consists of overlapping wood fibers.

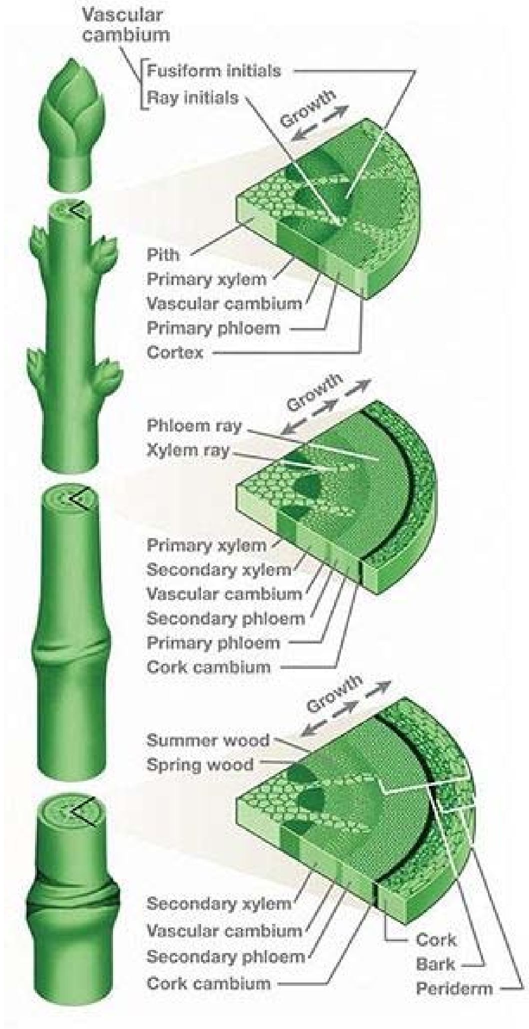
During plant growth cycles, wood on smaller branches forms first. Wood at the base of the branch extends slightly over the face of the trunk, forming the branch collar. Then, the wood of the parent branch forms over the top of the basal branch wood, usually forming a circular structure called the trunk collar. Together, the branch collar and trunk collar are simply referred to as the branch collar. Branch collars can also be flat or somewhat recessed into the trunk or parent branch, as in some conifers.

The accretion of layers of wood behind the branch collar is a conical decay-resistant structure called the branch core. The knot found in lumber is this branch core.

When woody plants naturally shed branches because they are nonproductive, usually from lack of light, these branches die back to the branch collar. Insects and fungi decompose the dead branch, and it eventually falls off, leaving the exposed branch core. The branch core resists the spread of decay organisms into the parent branch or trunk during the time it takes for the woundwood, or callus, to seal over the wound.

Events such as storms or pruning may damage the branch collar, thus defeating the naturally-occurring defense of the branch core and exposing the trunk to decay. Understanding the branch collar anatomy is important in tree pruning. Pruning practices that mimic natural branch shedding avoid unnecessary damage to the plant's defensive anatomy.

Cork cambium



Multiple cross sections of a stem showing **cork cambium**

Cork cambium (pl. **cambia** or **cambiums**) is a tissue found in many vascular plants as part of the periderm. The cork cambium is a lateral meristem and is responsible for secondary growth that replaces the epidermis in roots and stems. It is found in woody and many herbaceous dicots, gymnosperms and some monocots, which usually lack secondary growth.

Cork cambium is one of the plant's meristems - the series of tissues consisting of embryonic (incompletely differentiated) cells from which the plant grows. It is one of the many layers of bark, between the cork and primary phloem. The function of cork cambium is to produce the cork, a tough protective material.

Synonyms for cork cambium are **bark cambium**, **pericambium** or **phellogen**. Phellogen is defined as the meristematic cell layer responsible for the development of the periderm. Cells that grow inwards from the phellogen are termed *phelloderm*, and cells that develops outwards are termed *phellem* or cork (note similarity with vascular cambium). The periderm thus consists of three different layers:

- phelloderm,
- phellogen (cork cambium) and
- phellem.

Growth and development of cork cambium is very variable between different species, and also highly dependent on age, growth conditions etc. as can be observed from the different surfaces of bark; smooth, fissured, tesselated, scaly, flaking off, etc.

Economic importance

- Commercial cork is derived from the bark of the cork oak *(Quercus suber).* Cork has many uses including wine bottle stoppers, bulletin boards, coasters, hot pads to protect tables from hot pans, insulation, sealing for lids, flooring, gaskets for engines, fishing bobbers, handles for fishing rods and tennis rackets, etc. It is also a high strength-to-weight/cost ablative material for aerodynamic prototypes in wind tunnels, as well as satellite launch vehicle payload fairings, reentry surfaces, and compression joints in thrust-vectored solid rocket motor nozzles.
- Many types of bark are used as mulch.

Chapter 3

Cotyledon

Cotyledon in formation before the accumulation of the reserve seen at Judas-tree (*Cercis siliquastrum*)

Comparison of a monocot and dicot sprouting. Note that the visible part of the monocot plant (left) is actually the first true leaf produced from the meristem; the cotyledon itself remains within the seed

Two-weeks-old cotyledons of Douglas-fir.

A **cotyledon** is a significant part of the embryo within the seed of a plant. Upon germination, the cotyledon may become the embryonic first leaves of a seedling. The number of cotyledons present is one characteristic used by botanists to classify the flowering plants (angiosperms). Species with one cotyledon are called monocotyledonous (or, "monocots") and placed in the class Liliopsida. Plants with two embryonic leaves are termed dicotyledonous ("dicots") and placed in the class Magnoliopsida.

In the case of dicot seedlings whose cotyledons are photosynthetic, the cotyledons are functionally similar to leaves. However, true leaves and cotyledons are developmentally distinct. Cotyledons are formed during embryogenesis, along with the root and shoot meristems, and are therefore present in the seed prior to germination. True leaves, however, are formed post-embryonically (i.e. after germination) from the shoot apical meristem, which is responsible for generating subsequent aerial portions of the plant.

The cotyledon of grasses and many other monocotyledons is a highly modified leaf composed of a *scutellum* and a *coleoptile*. The scutellum is a tissue within the seed that is specialized to absorb stored food from the adjacent endosperm. The coleoptile is a protective cap that covers the *plumule* (precursor to the stem and leaves of the plant).

Features	Monocotyledon	Dicotyledon
Leaf structure	Parallel veins	Network veins
Roots	Fibrous roots	Tap roots
Stem	Soft	Hard
No. of cotyledons	1	2
Number of petals	Divisible by 3	Divisible by 4 or 5

Gymnosperm seedlings also have cotyledons, and these are often variable in number (multicotyledonous), with from 2 to 24 cotyledons forming a whorl at the top of the hypocotyl (the embryonic stem) surrounding the plumule. Within each species, there is often still some variation in cotyledon numbers, e.g. Monterey Pine (*Pinus radiata*) seedlings have 5–9, and Jeffrey Pine (*Pinus jeffreyi*) 7–13 (Mirov 1967), but other species are more fixed, with e.g. Mediterranean Cypress always having just two cotyledons. The highest number reported is for Big-cone Pinyon (*Pinus maximartinezii*), with 24 (Farjon & Styles 1997).

A seedling of Pinus halepensis with eight cotyledons

The cotyledons may be ephemeral, lasting only days after emergence, or persistent, enduring a year or more on the plant. The cotyledons contain (or in the case of gymnosperms and monocotyledons, have access to) the stored food reserves of the seed. As these reserves are used up, the cotyledons may turn green and begin photosynthesis, or may wither as the first true leaves take over food production for the seedling.

Epigeal versus hypogeal development

Cotyledons may be either epigeal, expanding on the germination of the seed, throwing off the seed shell, rising above the ground, and perhaps becoming photosynthetic; or hypogeal, not expanding, remaining below ground and not becoming photosynthetic. The latter is typically the case where the cotyledons act as a storage organ, as in many nuts and acorns.

Hypogeal plants have (on average) significantly larger seeds than epigeal ones. They also are capable of surviving if the seedling is clipped off, as meristem buds remain underground (with epigeal plants, the meristem is clipped off if the seedling is grazed). The tradeoff is whether the plant should produce a large number of small seeds, or a smaller number of seeds which are more likely to survive.

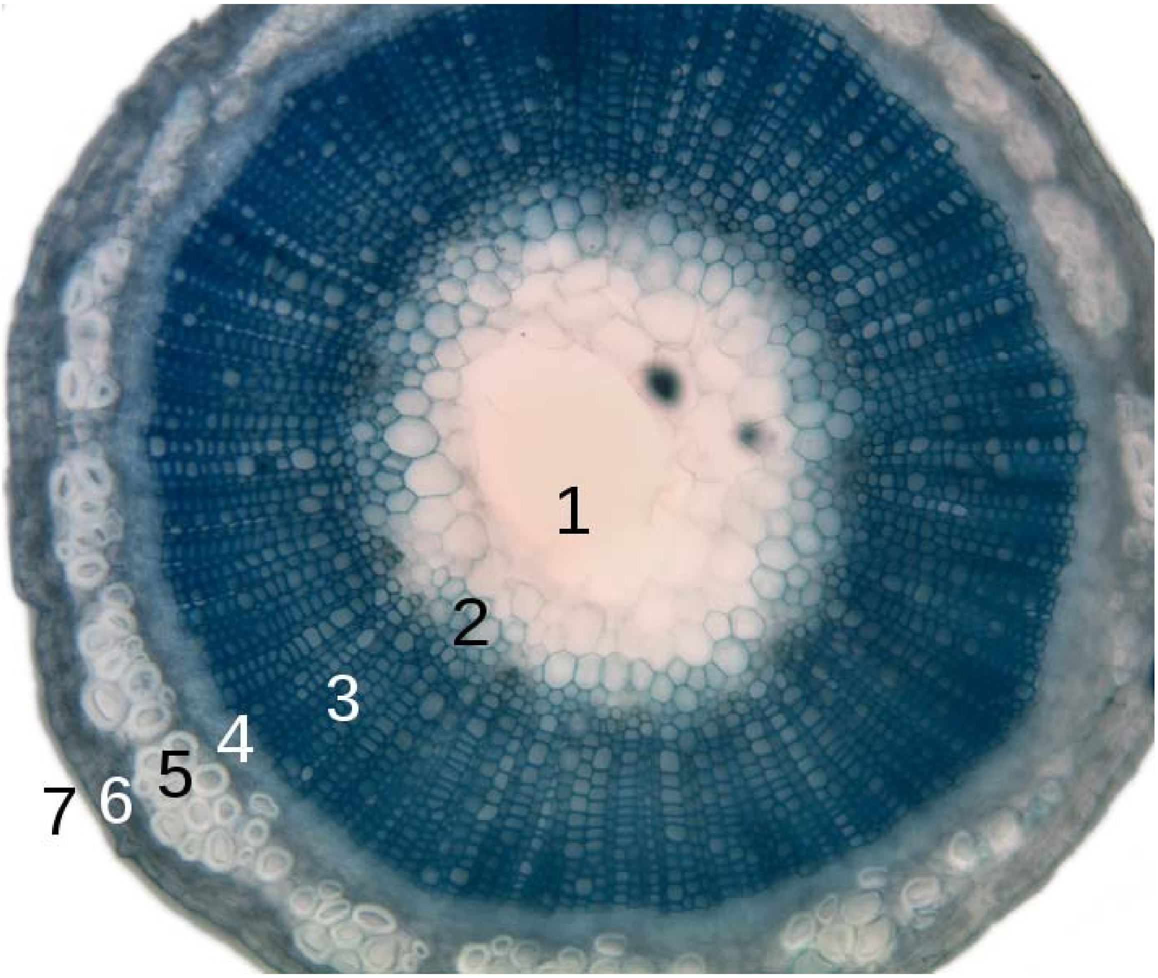
Related plants show a mixture of hypogeal and epigeal development, even within the same plant family. Groups which contain both hypogeal and epigeal species include, for example, the Araucariaceae family of Southern Hemisphere conifers, the Fabaceae (pea family), and the genus *Lilium*.

History

The term *cotyledon* was coined by Marcello Malpighi. John Ray was the first botanist to recognise that some plants have two and others only one, and eventually the first to recognise the immense importance of this fact to systematics.

Chapter 4

Epidermis (Botany)



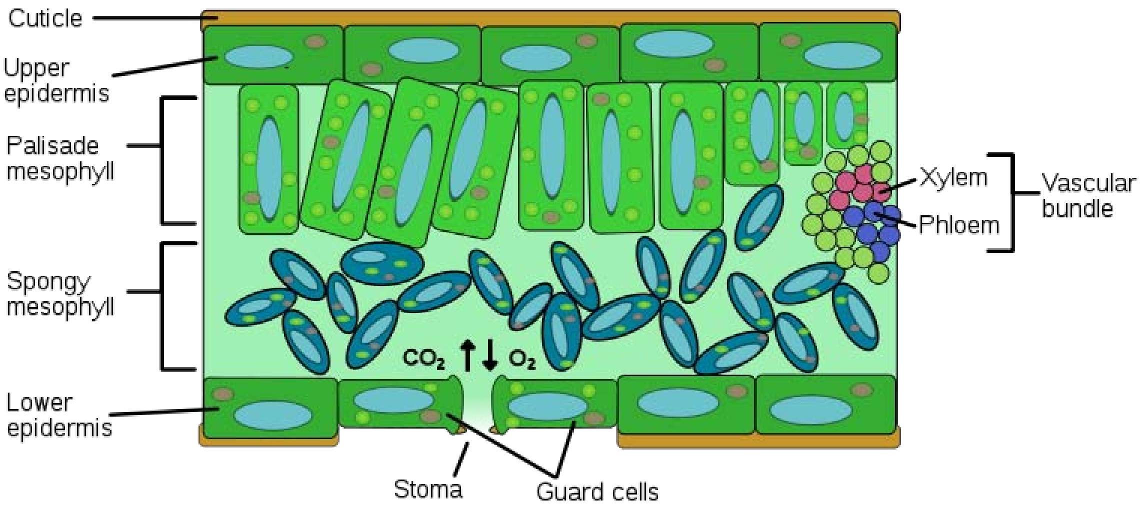
Cross-section of a flax plant stem:
1. Pith,
2. Protoxylem,

3. Xylem I,
4. Phloem I,
5. Sclerenchyma (bast fibre),
6. Cortex,
7. **Epidermis**

The **epidermis** is a single-layered group of cells that covers plants' leaves, flowers, roots and stems. It forms a boundary between the plant and the external world. The epidermis serves several functions, it protects against water loss, regulates gas exchange, secretes metabolic compounds, and (especially in roots) absorbs water and mineral nutrients. The epidermis of most leaves shows dorsoventral anatomy: the upper (adaxial) and lower (abaxial) surfaces have somewhat different construction and may serve different functions. Woody stems and some other stem structures produce a secondary covering called the periderm that replaces the epidermis as the protective covering.

Description

The epidermis is the outermost cell layer of the primary plant body, it is the dermal tissue system of leaves (diagrammed below), stems, roots, flowers, fruits, and seeds; it is usually transparent (epidermal cells lack chloroplasts, except for the guard cells.) The cells of the epidermis are structurally and functionally variable. Most plants have an epidermis that is a single cell layer thick. Some plants like *Ficus elastica* and *Peperomia*, which have periclinal cellular division within the protoderm of the leaves, have an epidermis with multiple cell layers. Epidermal cells are tightly linked to each other and provide mechanical strength and protection to the plant. The walls of the epidermal cells of the above ground parts of plants contain cutin, and are covered with a cuticle. The cuticle reduces water loss to the atmosphere, it is sometimes covered with wax in smooth sheets or long filaments. Thick wax layers give some plants a whitish or bluish surface color. Surface wax acts as a moisture barrier and protects the plant from intense sunlight and wind. The underside of many leaves have a thinner cuticle than the top side, and leaves of plants from dry climates often have thickened cuticles to conserve water by reducing transpiration.

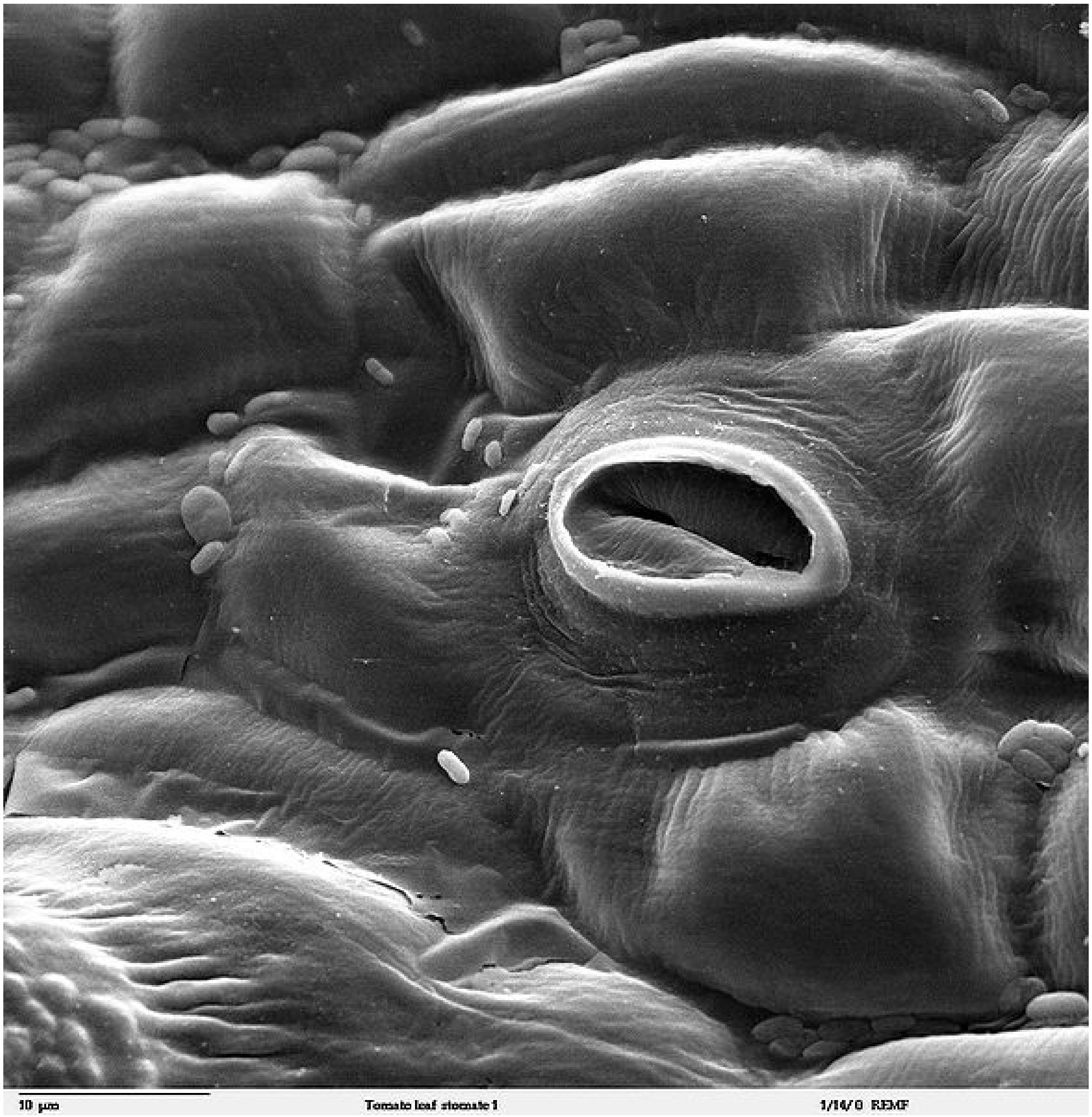


The epidermal tissue includes several differentiated cell types: epidermal cells, guard cells, subsidiary cells, and epidermal hairs (trichomes). The epidermal cells are the most numerous, largest, and least specialized. These are typically more elongated in the leaves of monocots than in those of dicots.

Trichomes or hairs grow out from the epidermis in many species. In root epidermis, epidermal hairs, termed root hairs are common and are specialized for absorption of water and mineral nutrients.

In plants with secondary growth, the epidermis of roots and stems is usually replaced by a periderm through the action of a cork cambium.

Guard cells



Stoma in a tomato leaf (microscope image)

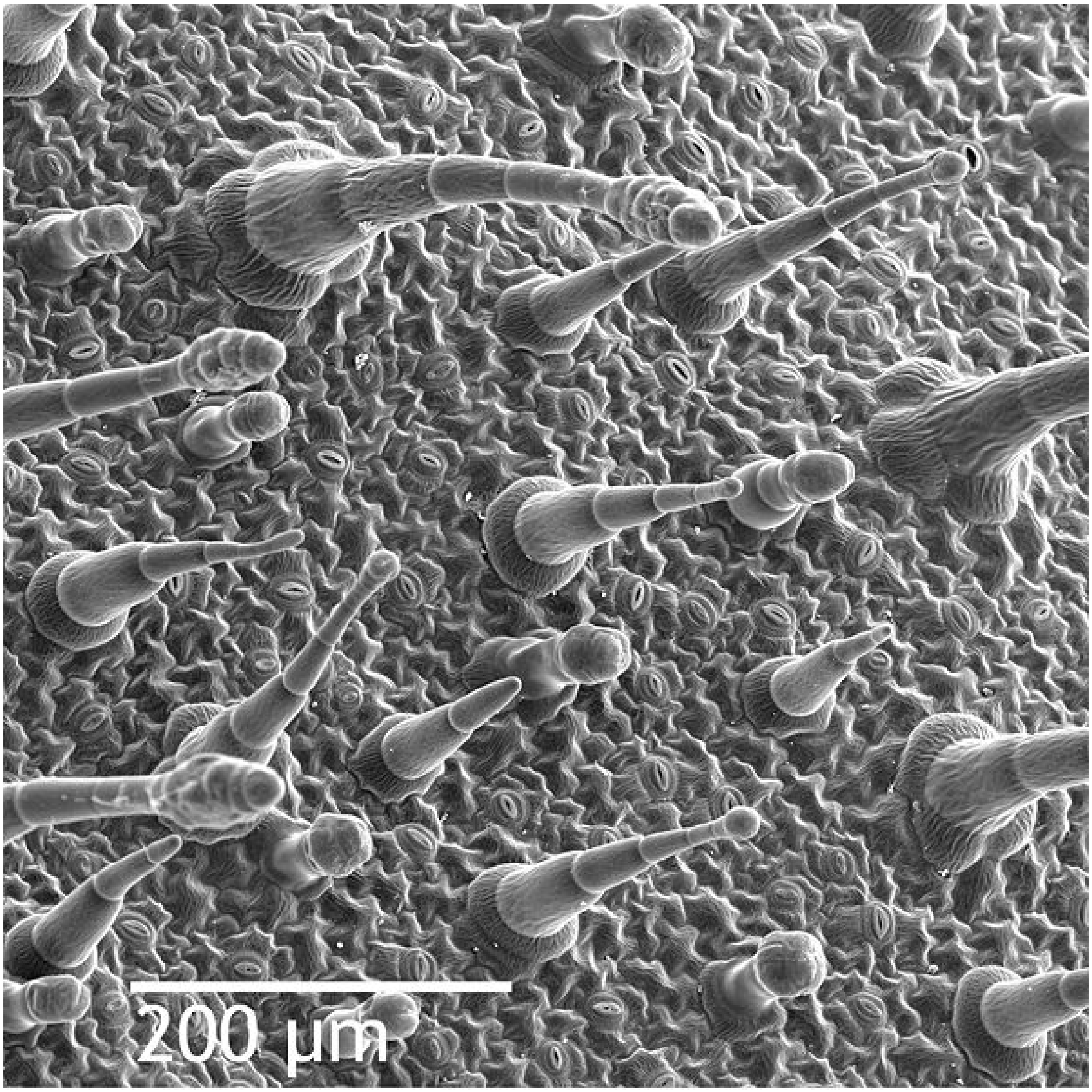
The leaf and stem epidermis is covered with pores called stomata (sing., stoma), part of a **stoma complex** consisting of a pore surrounded on each side by chloroplast-containing **guard cells**, and two to four **subsidiary cells** that lack chloroplasts. The stoma complex regulates the exchange of gases and water vapor between the outside air and the interior of the leaf. Typically, the stomata are more numerous over the abaxial (lower) epidermis of the leaf than the (adaxial) upper epidermis. An exception is floating leaves where most or all stomata are on the upper surface. Vertical leaves, such as those of many grasses, often have roughly equal numbers of stomata on both surfaces. The number of stomata varies from about 1,000 to over 100,000 per square centimeter of leaf surface.

The stoma is bounded by two guard cells. The guard cells differ from the epidermal cells in the following aspects:

- The guard cells are bean-shaped in surface view, while the epidermal cells are irregular in shape
- The guard cells contain chloroplasts, so they can manufacture food by photosynthesis (The epidermal cells do not contain chloroplasts)
- Guard Cells are the only epidermal cells that can make sugar. According to one theory, in sunlight the concentration of potassium ions (K+) increases in the guard cells. This, together with the sugars formed, lowers the water potential in the guard cells. As a result, water from other cells enter the guard cells by osmosis so they swell and become turgid. Because the guard cells have a thicker cellulose wall on one side of the cell, i.e. the side around the stomatal pore, the swollen guard cells become curved and pull the stomata open.

At night, the sugar is used up and water leaves the guard cells, so they become flaccid and the stomatal pore closes. In this way, they reduce the amount of water vapour escaping from the leaf.

Cell differentiation in the epidermis



Scanning electron microscope image of *Nicotiana alata* leaf's epidermis, showing trichomes (hair-like appendages) and stomata (eye-shaped slits, visible at full resolution)

The plant epidermis consists of three main cell types: pavement cells, guard cells and their subsidiary cells that surround the stomata and trichomes, otherwise known as leaf hairs. The epidermis of petals also form a variation of trichomes called conical cells. These cells all develop from the pavement cells, which make up the majority of the plants surface cells. In short, cellular differentiation of the epidermal cells is controlled by two major factors: genetics and environmental conditions.

Trichomes develop at a distinct phase during the actual leaf development, under the control of two major trichome specification genes: *TTG* and *GL1*. The process may be controlled by the plant hormones gibberellins, and even if not completely controlled, gibberellins certainly have an effect on the development of the leaf hairs. *GL1* causes endoreplication, the replication of DNA without subsequent cell division as well as cell expansion. *GL1* turns on the expression of a second gene for trichome formation, *GL2*, which controls the final stages of trichome formation causing the cellular outgrowth.

Arabidopsis thaliana uses the products of inhibitory genes to control the patterning of trichomes, such as *TTG* and *TRY*. The products of these genes will diffuse into the lateral cells, preventing them from forming trichomes and in the case of *TRY* promoting the formation of pavement cells.

As previously mentioned, conical cells are a form of trichome that occurs on the petals of flowers. Expression of the gene *MIXTA*, or its analogue in other species, later in the process of cellular differentiation will cause the formation of conical cells over trichomes. *MIXTA* is a transcription factor.

Stomatal pattering is a much more controlled process, as the stoma effect the plants water retention and respiration capabilities. As a consequence of these important functions, differentiation of cells to form stomata is also subject to environmental conditions to a much greater degree than other epidermal cell types.

Stomata are holes in the plant epidermis that are surrounded by two guard cells, which control the opening and closing of the aperture. These guard cells are in turn surrounded by subsidiary cells which provide a supporting role for the guard cells.

Stomata begin as stomatal meristemoids. The process varies between dicots and monocots. Spacing is thought to be essentially random in dicots though mutants do show it is under some form of genetic control, but it is more controlled in monocots, where stomata arise from specific asymmetric divisions of protodermal cells. The smaller of the two cells produced becomes the guard mother cells. Adjacent epidermal cells will also divide asymmetrically to form the subsidiary cells.

Because stomata play such an important role in the plants survival, collecting information of there differentiation if difficult by the traditional means of genetic manipulation, as stomatal mutants tend to be unable to survive. Thus the control of the process is not well understood. Some genes have been identified. *TMM* is thought to control the timing of stomatal initiation specification and *FLP* is thought to be involved in preventing further division of the guard cells once they are formed.

Environmental conditions affect the development of stomata, in particular their density on the leaf surface. It is thought that plant hormones, such as ethylene and cytokines, control the stomata’s developmental response to the environmental conditions. Accumulation of these hormones appears to cause increased stomatal density such as when the plants are kept in closed environments.

Stomatal cells only occur on the leaf epidermis, and it is thought that inhibitory signals must occur on other parts of the plants epidermis to prevent stomatal formation there.

These signals could be hormonal, or perhaps gene products transmitted from underlying tissues via the plasmodesmata.

Chapter 5

Fascicle (Botany) and Meristem

Fascicle (botany)

In botany, a **fascicle** (sometimes **short shoot**) is a bundle of leaves or flowers, or of the vascular tissues that supply these organs with nutrients. Vascular tissues may be in fascicles even when the organs supplied by them are not.

In pines

Fascicles of 5 needles in *Pinus flexilis*

Fascicles of 1 needle in *Pinus monophylla*

Leaf fascicles are present in all pines, and the number of adult leaves (needles) per fascicle is an important character for identification of pine species and genera. Most species have fascicles of 2 to 5 needles; only single species usually have fascicles of 1 or 6.

Variation is high between species, low within them. For example, *Pinus flexilis* (limber pine), has fascicles of 5 needles. This pine is a member of the white pine group, *Pinus* subgenus *Strobus*, section *Strobus*. In all members of the group the fascicles have five needles and the sheath at the base of the fascicle is deciduous.

The fascicle sheath is another character that is important for identification. Among North American pines the sheath is persistent in all so-called hard pines and deciduous in all so-called soft pines. Thus, the fascicle sheath and number of needles can be used to identify valuable timber pines in all seasons and many years before they are mature enough to produce cones. These two characters readily distinguish the major groups of pines.

Pinus durangensis (Durango pine) has fascicles of 6 needles, rarely 7, and is the only species in *Pinus* with so many needles per fascicle. *Pinus monophylla* has fascicles of one needle, rarely two. This is the only species of pine with just one needle per fascicle, and this rare and easily observed character is reflected in the specific epithet *monophylla* and common vernacular name single-leaf pinyon.

In flowering plants

Prunus fasciculata

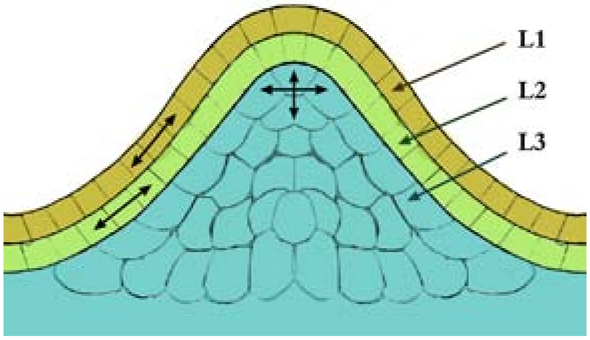
Fascicles are present in a small number of flowering plants. Both leaf and flower fascicles occur, but are rare. Consequently, when fascicles are present the specific epithet tends to refer to them. Examples include *Prunus fasciculata* and *Adenostoma fasciculatum*. Species with flowers in fascicles include *Aechmea biflora* and *Melicytus ramiflorus*, several species of *Malva*, and the entire genus *Flueggea*. Some species of the family Alseuosmiaceae have flowers in fascicles.

In *Opuntia* cacti, spines are produced in fascicle of a few long spines and many short spines.

In lower plants

Sphagnum has branches in fascicles.

Meristem



Tunica-Corpus model of the apical meristem (growing tip). The epidermal (L1) and subepidermal (L2) layers form the outer layers called the tunica. The inner L3 layer is called the corpus. Cells in the L1 and L2 layers divide in a sideways fashion, which keeps these layers distinct, whereas the L3 layer divides in a more random fashion.

A **meristem** is the tissue in most plants consisting of undifferentiated cells (**meristematic cells**), found in zones of the plant where growth can take place.

The term *meristem* was first used in 1858 by Karl Wilhelm von Nägeli (1817–1891) in his book *Beiträge zur Wissenschaftlichen Botanik*. It is derived from the Greek word *merizein* (μερίζειν), meaning to divide, in recognition of its inherent function.

Differentiated plant cells generally cannot divide or produce cells of a different type. Therefore, cell division in the meristem is required to provide new cells for expansion and differentiation of tissues and initiation of new organs, providing the basic structure of the plant body.

Meristematic cells are analogous in function to stem cells in animals, are incompletely or not at all differentiated, and are capable of continued cellular division (youthful). Furthermore, the cells are small and protoplasm fills the cell completely. The vacuoles are extremely small. The cytoplasm does not contain differentiated plastids (chloroplasts or chromoplasts), although they are present in rudimentary form (proplastids).

Meristematic cells are packed closely together without intercellular cavities. The cell wall is a very thin *primary cell wall*.

Maintenance of the cells requires a balance between two antagonistic processes: organ initiation and stem cell population renewal.

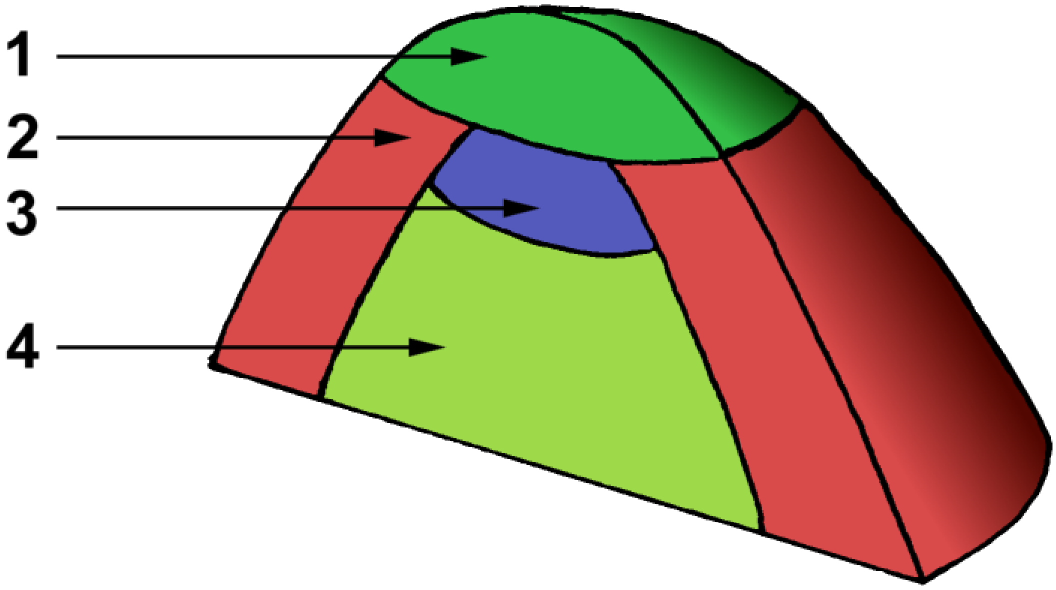
Meristematic zones

Apical meristems are the completely undifferentiated (indeterminate) meristems in a plant. These differentiate into three kinds of primary meristems. The primary meristems in turn produce the two secondary meristem types. These secondary meristems are also known as lateral meristems because they are involved in lateral growth.

At the meristem summit, there is a small group of slowly dividing cells, which is commonly called the central zone. Cells of this zone have a stem cell function and are essential for meristem maintenance. The proliferation and growth rates at the meristem summit usually differ considerably from those at the periphery.

Meristems also are induced in the roots of legumes such as soybean, *Lotus japonicus*, pea, and *Medicago truncatula* after infection with soil bacteria commonly called Rhizobium. Cells of the inner or outer cortex in the so-called "window of nodulation" just behind the developing root tip are induced to divide. The critical signal substance is the lipo-oligosaccharide Nod-factor, decorated with side groups to allow specificity of interaction. The Nod factor receptor proteins NFR1 and NFR5 were cloned from several legumes including *Lotus japonicus*, *Medicago truncatula* and soybean (Glycine max). Regulation of nodule meristems utilizes long distance regulation commonly called "Autoregulation of Nodulation" (AON). This process involves a leaf-vascular tissue located LRR receptor kinases (LjHAR1, GmNARK and MtSUNN), CLE peptide signalling , and KAPP interaction, similar to that seen in the CLV1,2,3 system. LjKLAVIER also exhibits a nodule regulation phenotype though it is not yet known how this relates to the other AON receptor kinases

Apical meristems



Organisation of an apical meristem (growing tip)
1 - Central zone
2 - Peripheral zone
3 - Medullary (i.e. central) meristem
4 - Medullary tissue

The **apical meristem**, or growing tip, is a completely undifferentiated meristematic tissue found in the buds and growing tips of roots in plants. Its main function is to begin growth of new cells in young seedlings at the tips of roots and shoots (forming buds, among other things). Specifically, an active apical meristem lays down a growing root or shoot behind itself, pushing itself forward. Apical meristems are very small, compared to the cylinder-shaped lateral meristems.

Apical meristems are composed of several layers. The number of layers varies according to plant type. In general the outermost layer is called the **tunica** while the innermost layers are the **corpus**. In monocots, the tunica determine the physical characteristics of the leaf edge and margin. In dicots, layer two of the corpus determine the characteristics of the edge of the leaf. The corpus and tunica play a critical part of the plant physical appearance as all plant cells are formed from the meristems. Apical meristems are found in two locations: the root and the stem. Some Arctic plants have an apical meristem in the lower/middle parts of the plant. It is thought that this kind of meristem evolved because it is advantageous in Arctic conditions.

Shoot apical meristems

The source of all above-ground organs. Cells at the shoot apical meristem summit serve as stem cells to the surrounding peripheral region, where they proliferate rapidly and are incorporated into differentiating leaf or flower primordia.

The shoot apical meristem is the site of most of the embryogenesis in flowering plants. Primordia of leaves, sepals, petals, stamens and ovaries are initiated here at the rate of one every time interval, called a plastochron. It is where the first indications that flower development has been evoked are manifested. One of these indications might be the loss of apical dominance and the release of otherwise dormant cells to develop as axillary shoot meristems, in some species in axils of primordia as close as two or three away from the apical dome. The shoot apical meristem consists of 4 distinct cell groups: -.

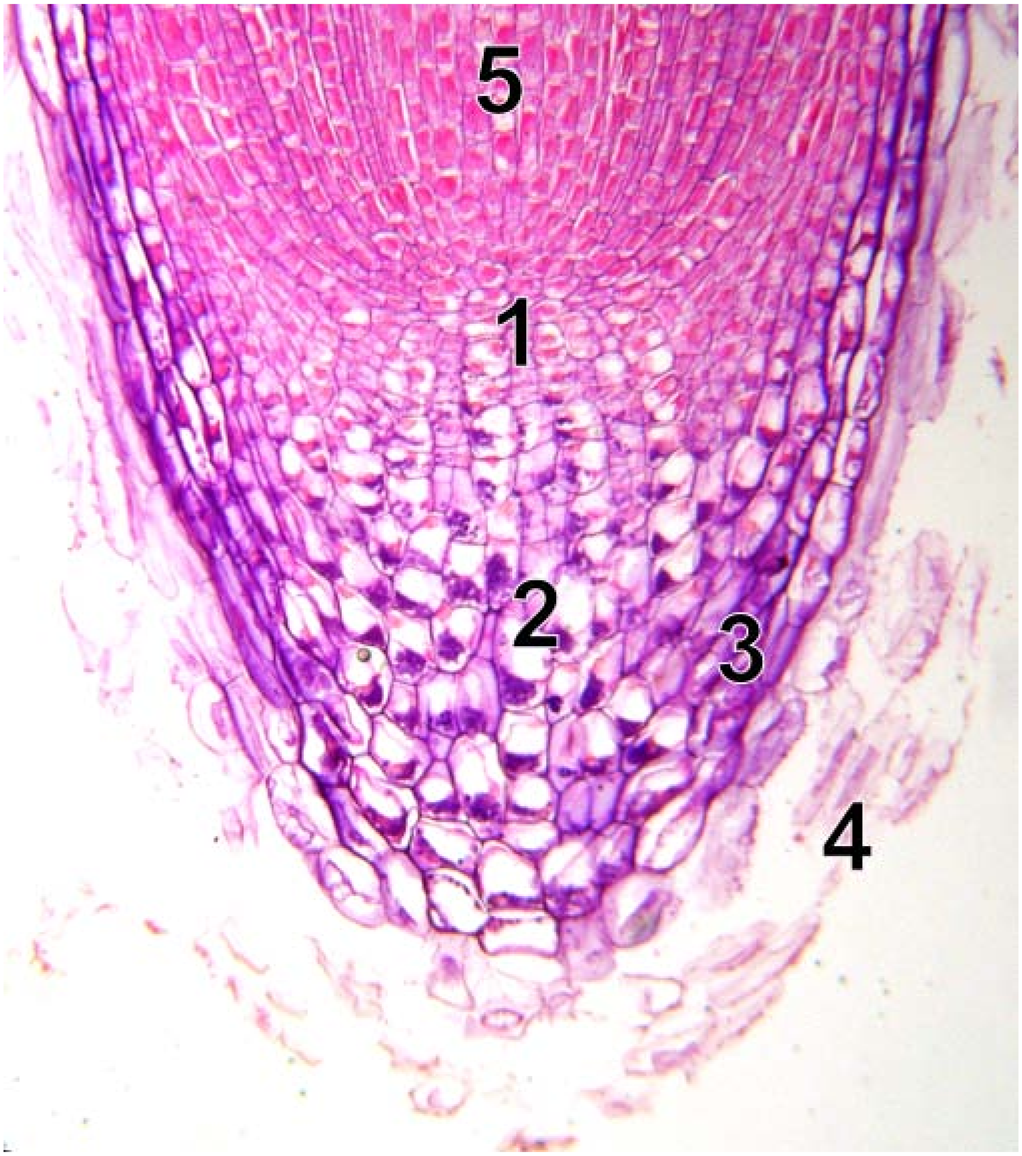
- Stem cells
- The immediate daughter cells of the stem cells
- A subjacent organising centre
- Founder cells for organ initiation in surrounding regions

The four distinct zones mentioned above are maintained by a complex signalling pathway. In *Arabidopsis thaliana* , 3 interacting *CLAVATA* genes are required to regulate the size of the stem cell reservoir in the shoot apical meristem by controlling the rate of cell division. CLV1 and CLV2 are predicted to form a receptor complex (of the LRR receptor like kinase family) to which CLV3 is a ligand. CLV3 shares some homology with the ESR proteins of maize, with a short 14 amino acid region being conserved between the proteins. Proteins that contain these conserved regions have been grouped into the CLE family of proteins.

CLV1 has been shown to interact with several cytoplasmic proteins that are most likely involved in downstream signalling. For example, the CLV complex has been found to be associated with Rho/Rac small GTPase-related proteins. These proteins may act as an intermediate between the CLV complex and a mitogen-activated protein kinase (MAPK), which is often involved in signalling cascades. KAPP is a kinase-associated protein phosphatase that has been shown to interact with CLV1. KAPP is thought to act as a negative regulator of CLV1 by dephosphorylating it.

Another important gene in plant meristem maintenance is *WUSCHEL* (shortened to *WUS*), which is a target of CLV signalling. *WUS* is expressed in the cells below the stem cells of the meristem and its presence prevents the differentiation of the stem cells. CLV1 acts to promote cellular differentiation by repressing *WUS* activity outside of the central zone containing the stem cells. *STM* also acts to prevent the differentiation of stem cells by repressing the expression of Myb genes that are involved in cellular differentiation.

Root apical meristems



10x microscope image of root tip with meristem
1 - quiescent center
2 - calyptrogen (live rootcap cells)
3 - rootcap
4 - sloughed off dead rootcap cells
5 - procambium

Unlike the shoot apical meristem, the root apical meristem produces cells in two dimensions. It is covered by the root cap, which protects the apical meristem from the rocks, dirt and pathogens. Cells are continuously sloughed off the outer surface of the root cap. The center of the root apical meristem is occupied by a quiescent center which has low mitotic activity. Evidence suggests the quiescent center does function as the zone of initials. Infrequent division of initial cells in the quiescent center is the source of cells for the root apical meristem. These initial cells and tissue patterns become established in the embryo in the case of the primary root, and in the new lateral meristems in the case of secondary roots.

Intercalary meristem

In angiosperms, intercalary meristems occur only in monocot (in particular, grass) stems at the base of nodes and leaf blades. Horsetails also exhibit intercalary growth. Intercalary meristems are capable of cell division and allow for rapid growth and regrowth of many monocots. Intercalary meristems at the nodes of bamboo allow for rapid stem elongation, while those at the base of most grass leaf blades allow damaged leaves to rapidly regrow. This leaf regrowth in grasses evolved in response to damage by grazing herbivores, but is more familiar to us in response to lawnmowers.

Floral meristem

When plants begin the developmental process known as flowering, the shoot apical meristem is transformed into an inflorescence meristem, which goes on to produce the floral meristem, which produces the familiar sepals, petals, stamens, and carpels of the flower.

In contrast to vegetative apical meristems and some exflorescence meristems, floral meristems are responsible for determinate growth, the limited growth of the flower to a particular size and form. The transition from shoot meristem to floral meristem requires floral meristem identity genes, that both specify the floral organs and cause the termination of the production of stem cells. *AGAMOUS* (*AG*) is a floral homeotic gene required for floral meristem termination and necessary for proper development of the stamens and carpels. *AG* is necessary to prevent the conversion of floral meristems to inflorescence shoot meristems, but is not involved in the transition from shoot to floral meristem. AG is turned on by the floral meristem identity gene *LEAFY* (*LFY*) and *WUS* and is restricted to the centre of the floral meristem or the inner two whorls. This way floral identity and region specificity is achieved. WUS activates AG by binding to a consensus sequence in the AG’s second intron and LFY binds to adjacent recognition sites. Once AG is activated it represses expression of WUS leading to the termination of the meristem.

Through the years, scientists have manipulated floral meristems for economics reasons. An example is the mutant tobacco plant "Maryland Mammoth." In 1936, the department of agriculture of Switzerland performed several scientific tests with this plant. "Maryland Mammoth" is peculiar in this sense that it grows much faster than other tobacco plants.

Apical dominance

Apical dominance is phenomenon where one meristem prevents or inhibits the growth of other meristems. As a result the plant will have one clearly defined main trunk. For example, in trees, the tip of the main trunk bears the dominant meristem. Therefore, the tip of the trunk grows rapidly and is not shadowed by branches. If the dominant meristem is cut off, one or more branch tips will assume dominance. The branch will start growing faster and the new growth will be vertical. Over the years, the branch may begin to look more and more like an extension of the main trunk. Often several branches will exhibit this behaviour after the removal of apical meristem, leading to a bushy growth.

The mechanism of apical dominance is based on the plant hormone auxin. It is produced in the apical meristem and transported towards the roots in the cambium. If apical dominance is complete, it prevents any branches from forming as long as apical meristem is active. If the dominance is incomplete, side branches will develop.

Recent investigations into apical dominance and the control of branching have revealed a new plant hormone family termed strigolactones. These compounds were previously known to be involved in seed germination and communication with mycorrhizal fungi and are now shown to be involved in inhibition of branching.

Primary meristems

Apical meristems may differentiate into three kinds of primary meristem:

- **Protoderm** - lies around the outside of the stem and develops into the epidermis.
- **Procambium** - lies just inside of the protoderm and develops into primary xylem and primary phloem. It also produces the vascular cambium, a secondary meristem.
- **Ground meristem** develops into the pith. It produces the cork cambium, another secondary meristem.

These meristems are responsible for primary growth, or an increase in length or height which were discovered by scientist Joseph D. Carr of North Carolina in 1943.

Secondary meristems

There are two types of secondary meristems, these are also called the *lateral meristems* because they surround the established stem of a plant and cause it to grow laterally (i.e., larger in diameter).

- Vascular cambium, which produces secondary xylem and secondary phloem. This is a process that may continue throughout the life of the plant. This is what gives rise to wood in plants. Such plants are called arborescent. This does not occur in plants that do not go through secondary growth (known as herbaceous plants).
- Cork cambium, which gives rise to the periderm, which replaces the epidermis.

Indeterminate growth of meristems

Though each plant grows according to a certain set of rules, each new root and shoot meristem can go on growing for as long as it is alive. In many plants meristematic growth is potentially **indeterminate**, making the overall shape of the plant not determinate in advance. This is the **primary growth**. Primary growth leads to lengthening of the plant body and organ formation. All plant organs arise ultimately from cell divisions in the apical meristems, followed by cell expansion and differentiation. Primary growth gives rise to the apical part of many plants.

The growth of nitrogen fixing nodules on legume plants such as soybean and pea is either determinate or indeterminate. Thus, soybean (or bean and Lotus japonicus) produce determinate nodules (spherical), with a branched vascular system surrounding the central infected zone. Often, Rhizobium infected cells have only small vacuoles. In contrast, nodules on pea, clovers, and Medicago truncatula are indeterminate; to maintain (at least for some time) an active meristem that yields new cells for Rhizobium infection. Thus zones of maturity exist in the nodule. Infected cells usually possess a large vacuole. The plant vascular system is branched and peripheral.

Cloning

Under appropriate conditions, each shoot meristem can develop into a complete new plant or clone. Such new plants can be grown from shoot cuttings that contain an apical meristem. Root apical meristems are not readily cloned, however. This cloning is called **asexual reproduction** or **vegetative reproduction** and is widely practiced in horticulture to mass-produce plants of a desirable genotype. This process is also known as mericloning.

Propagating through cuttings is another form of vegetative propogation that initiates root or shoot production from secondary meristematic cambial cells. This explains why basal 'wounding' of shoot-borne cuttings often aids root formation.

Chapter 6

Leaf

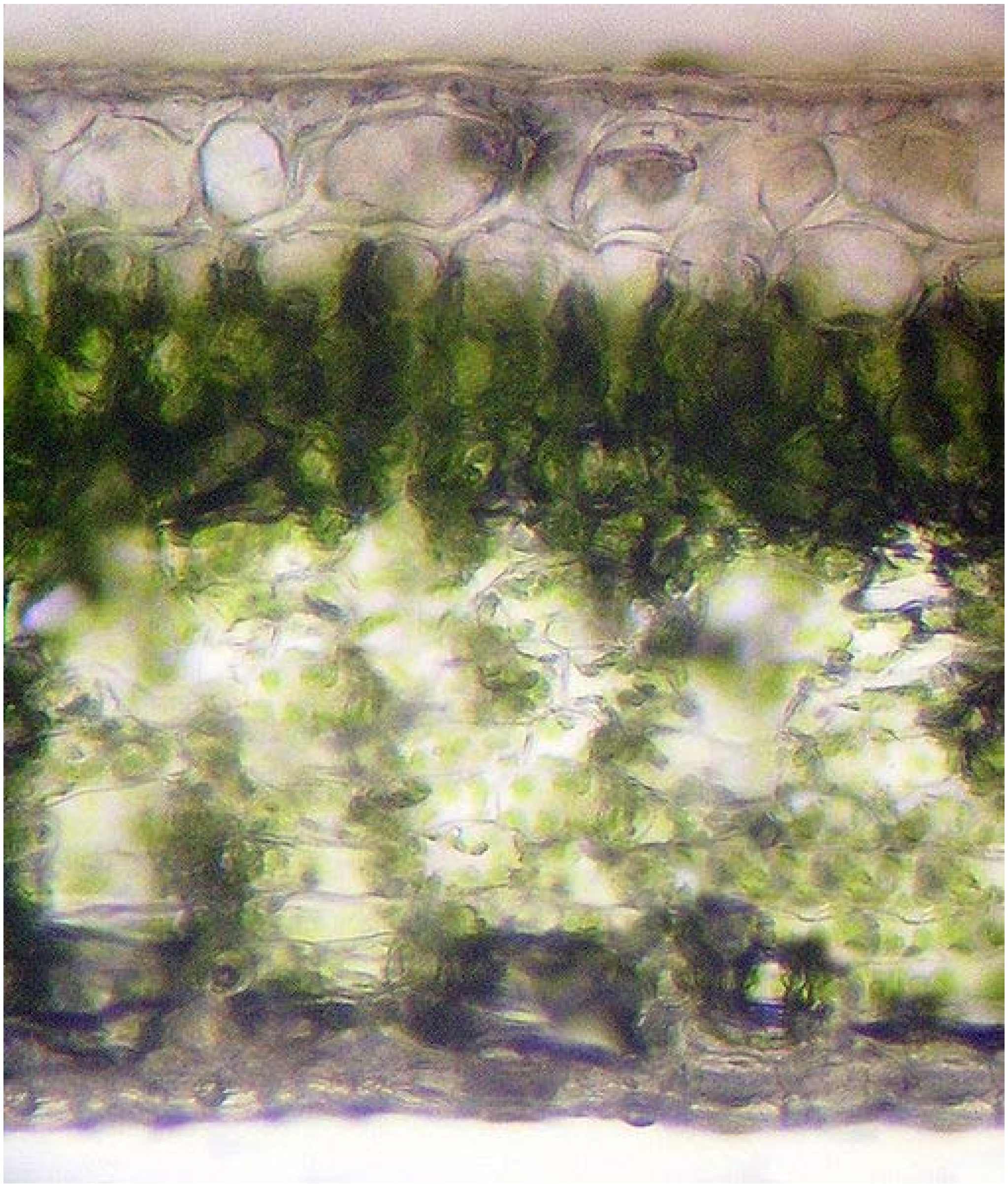
The leaves of a Beech tree

In botany, a **leaf** is an above-ground plant organ specialized for the process of photosynthesis. For this purpose, a leaf is typically flat (laminar) and thin. As an evolutionary trait, the flatness of leaves works to expose the chloroplasts to more light and to increase the absorption of carbon dioxide at the expense of water loss. In the Devonian period, when carbon dioxide concentration was at several times its present value, plants did not have leaves or flat stems. Many bryophytes have flat, photosynthetic organs, but these are not true leaves. Neither are the microphylls of lycophytes. The leaves of ferns, gymnosperms, and angiosperms are variously referred to as macrophyll, megaphylls, or euphylls.

Leaves are also the sites in most plants where transpiration and guttation take place. Leaves can store food and water, and are modified in some plants for other purposes. The comparable structures of ferns are correctly referred to as fronds. Furthermore, leaves are prominent in the human diet as leaf vegetables.

Anatomy

Leaf in autumn.

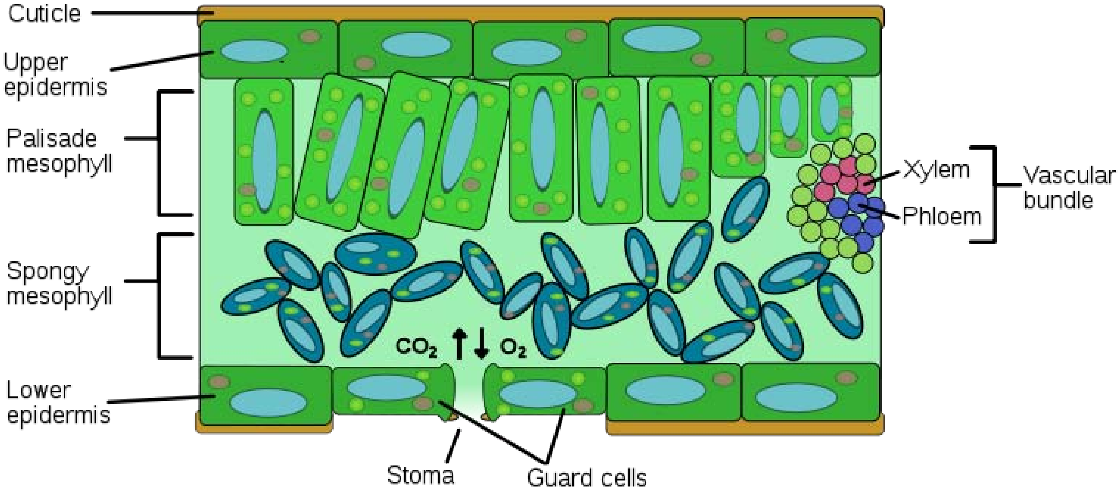


Cross section of a leaf

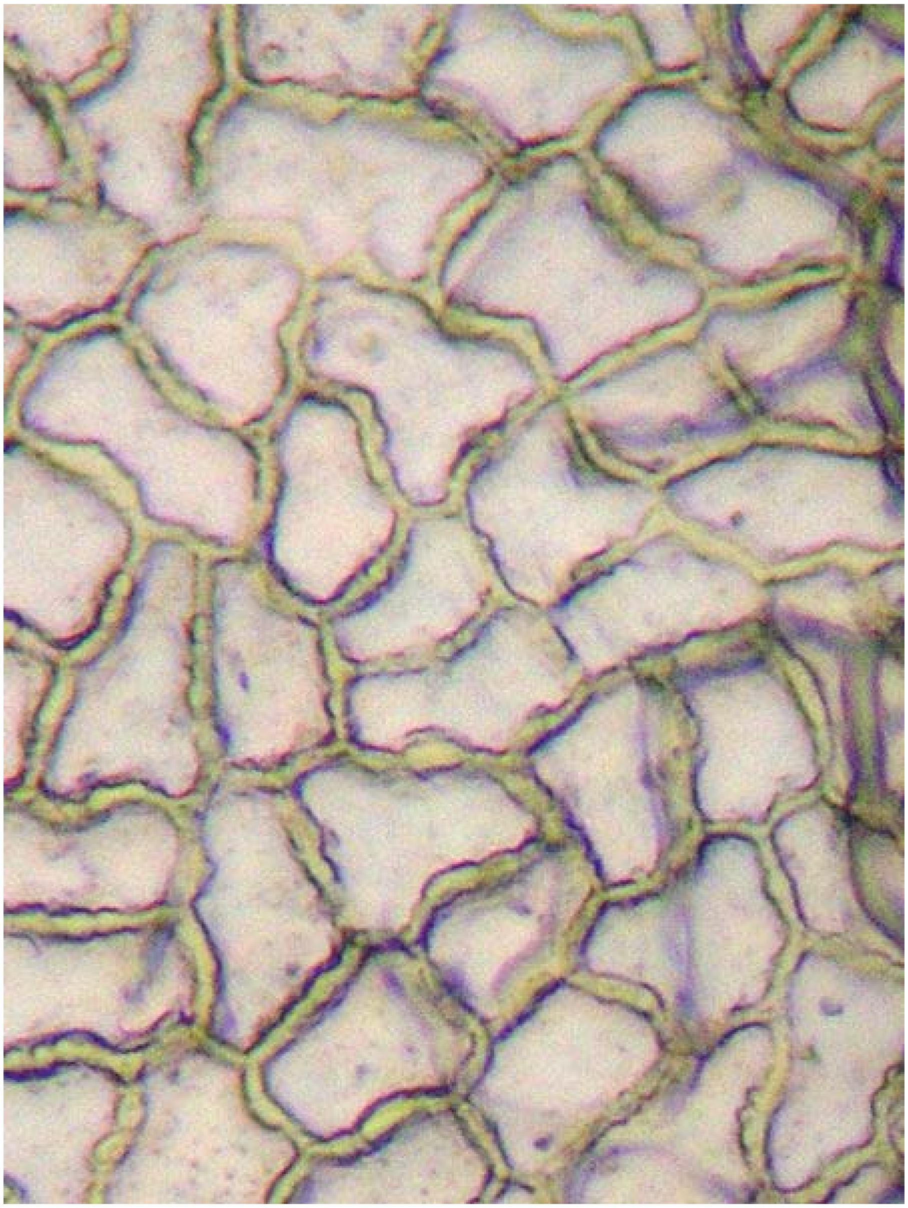
A structurally complete leaf of an angiosperm consists of a petiole (leaf stalk), a *lamina* (leaf blade), and stipules (small processes located to either side of the base of the petiole). The petiole attaches to the stem at a point called the "leaf axil." Not every species produces leaves with all of the aforementioned structural components. In certain species, paired stipules are not obvious or are absent altogether. A petiole may be absent, or the blade may not be laminar (flattened). The tremendous variety shown in leaf structure (anatomy) from species to species is presented in detail below under Leaf morphology. Periodically (*i.e.* seasonally, during the autumn), deciduous trees shed their leaves. These leaves then decompose into the soil.

A leaf is considered a plant organ and typically consists of the following tissues:

1. An **epidermis** that covers the upper and lower surfaces
2. An interior *chlorenchyma* called the **mesophyll**
3. An arrangement of **veins** (the vascular tissue)



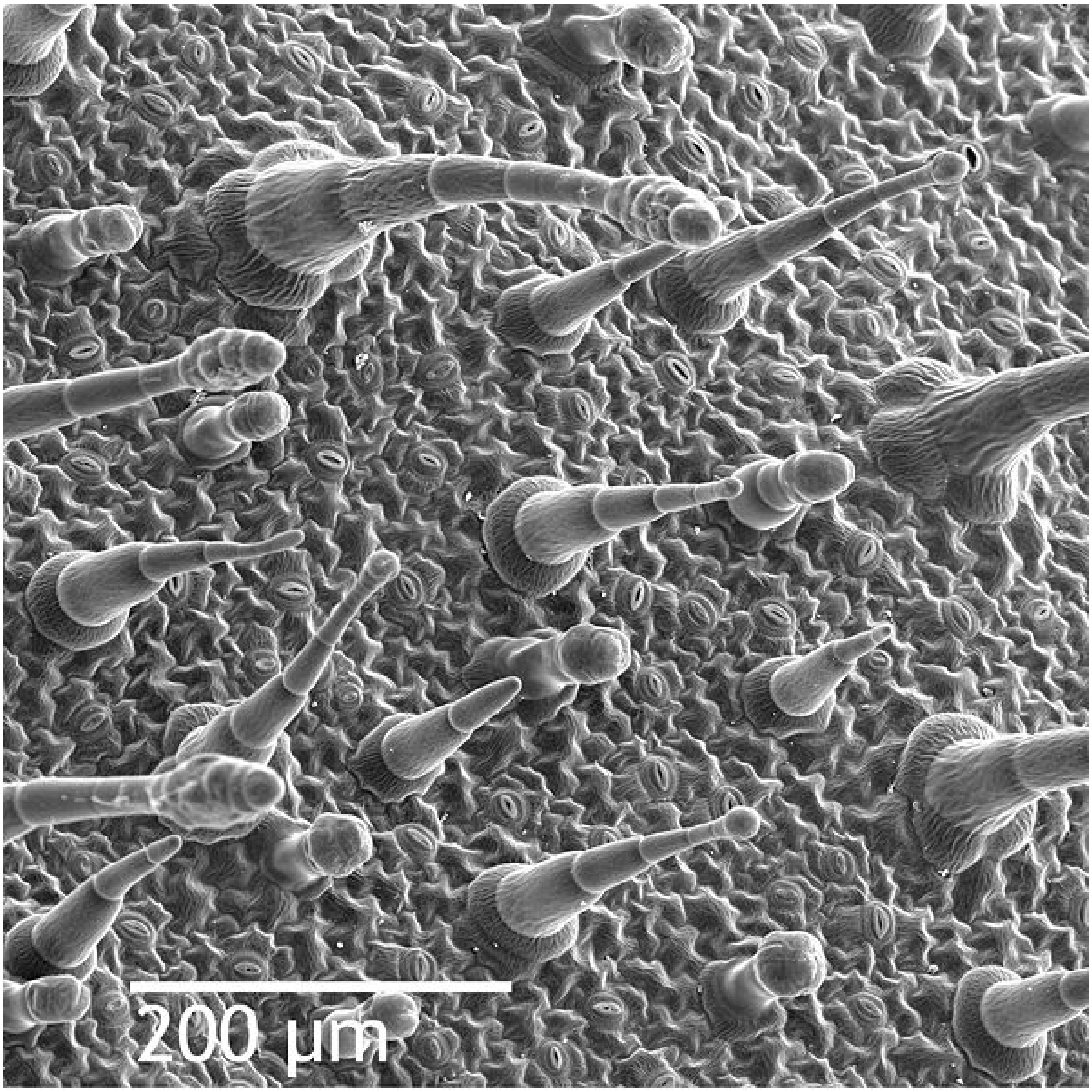
Epidermis



Epidermal cells

The epidermis is the outer layer of cells covering the leaf. It forms the boundary separating the plant's inner cells from the external world. The epidermis serves several functions: protection against water loss by way of transpiration, regulation of gas exchange, secretion of metabolic compounds, and (in some species) absorption of water. Most leaves show dorsoventral anatomy: the upper (adaxial) and lower (abaxial) surfaces have somewhat different construction and may serve different functions.

The epidermis is usually transparent (epidermal cells lack chloroplasts) and coated on the outer side with a waxy cuticle that prevents water loss. The cuticle is in some cases thinner on the lower epidermis than on the upper epidermis, and is thicker on leaves from dry climates as compared with those from wet climates.



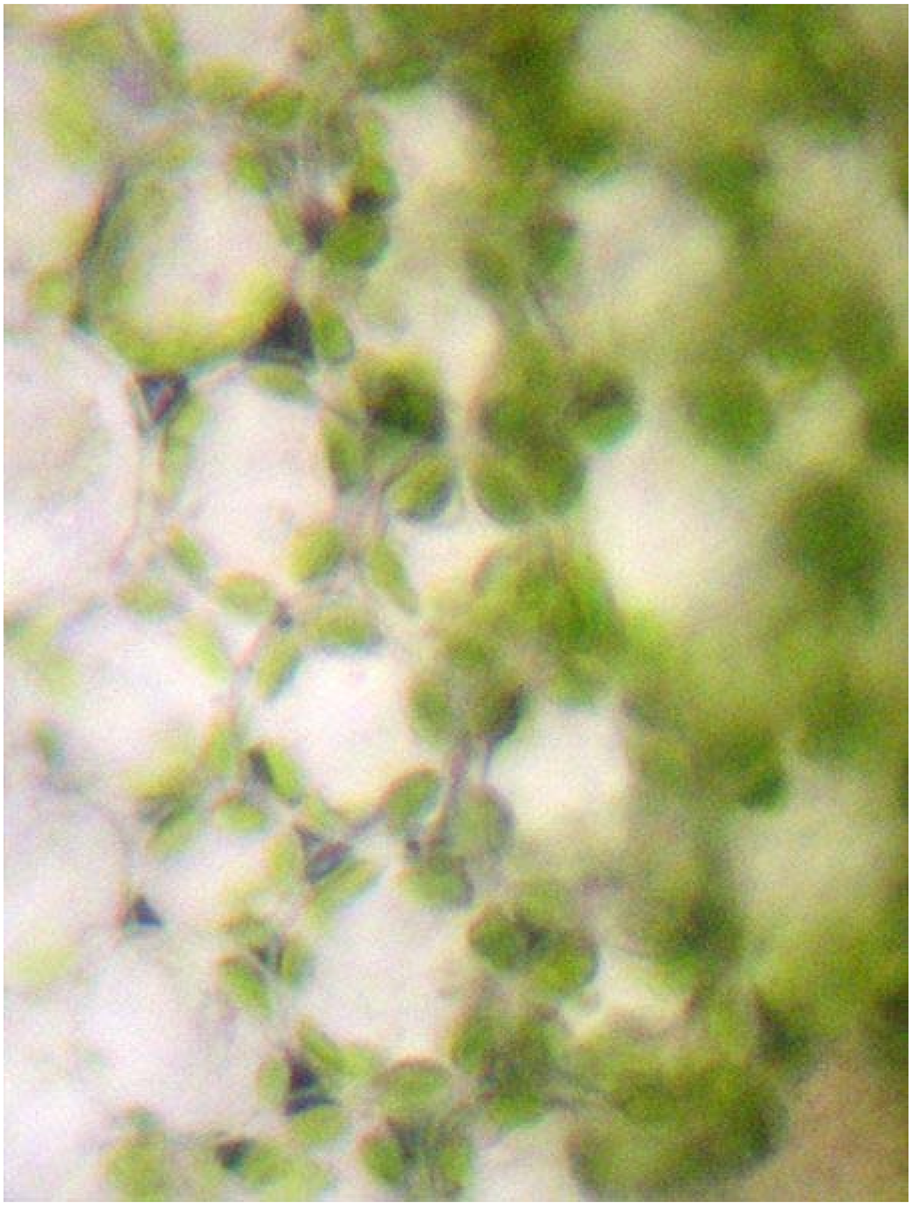
SEM image of *Nicotiana alata* leaf's epidermis, showing trichomes (hair-like appendages) and stomata (eye-shaped slits, visible at full resolution).

The epidermis tissue includes several differentiated cell types: epidermal cells, guard cells, subsidiary cells, and epidermal hairs (trichomes). The epidermal cells are the most numerous, largest, and least specialized. These are typically more elongated in the leaves of monocots than in those of dicots.

The epidermis is covered with pores called *stomata*, part of a stoma complex consisting of a pore surrounded on each side by chloroplast-containing guard cells, and two to four subsidiary cells that lack chloroplasts. The stoma complex regulates the exchange of gases and water vapor between the outside air and the interior of the leaf. Typically, the stomata are more numerous over the abaxial (lower) epidermis than the adaxial (upper) epidermis.

Mesophyll

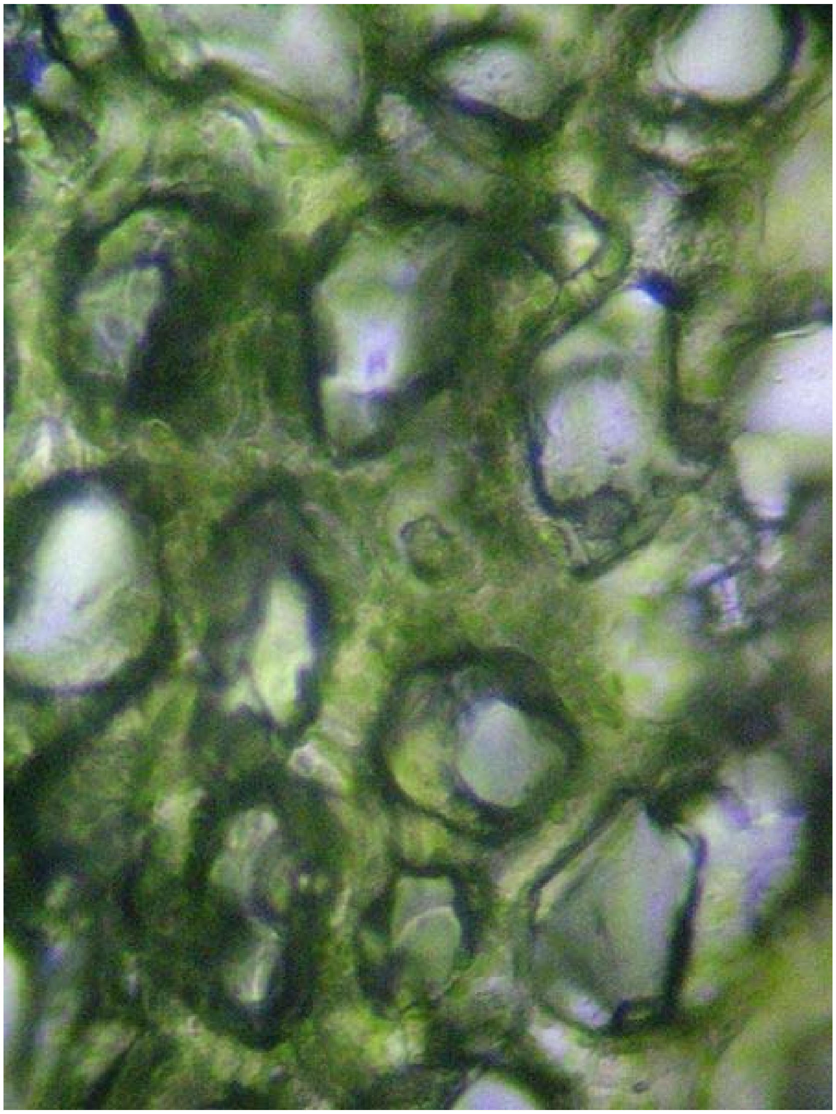
Most of the interior of the leaf between the upper and lower layers of epidermis is a *parenchyma* (ground tissue) or *chlorenchyma* tissue called the **mesophyll** (Greek for "middle leaf"). This assimilation tissue is the primary location of photosynthesis in the plant. The products of photosynthesis are called "assimilates".



Palisade cells

In ferns and most flowering plants the mesophyll is divided into two layers:

- An upper **palisade layer** of tightly packed, vertically elongated cells, one to two cells thick, directly beneath the adaxial epidermis. Its cells contain many more chloroplasts than the spongy layer. These long cylindrical cells are regularly arranged in one to five rows. Cylindrical cells, with the *chloroplasts* close to the walls of the cell, can take optimal advantage of light. The slight separation of the cells provides maximum absorption of carbon dioxide. This separation must be minimal to afford capillary action for water distribution. In order to adapt to their different environment (such as sun or shade), plants had to adapt this structure to obtain optimal result. Sun leaves have a multi-layered palisade layer, while shade leaves or older leaves closer to the soil, are single-layered.



Spongy cells

- Beneath the palisade layer is the **spongy layer**. The cells of the spongy layer are more rounded and not so tightly packed. There are large intercellular air spaces. These cells contain fewer chloroplasts than those of the palisade layer.

The pores or *stomata* of the epidermis open into substomatal chambers, connecting to air spaces between the spongy layer cells.

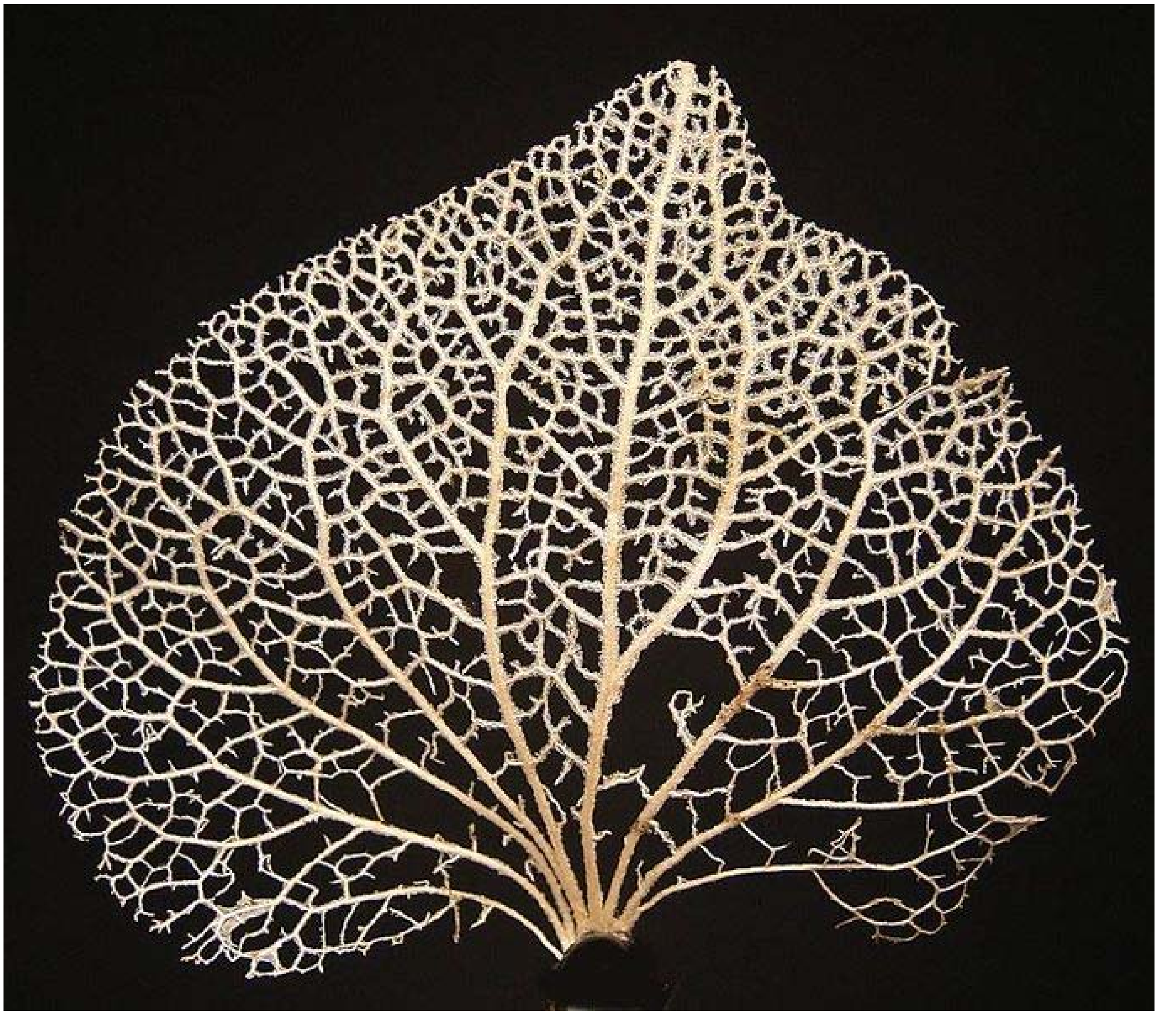
These two different layers of the mesophyll are absent in many aquatic and marsh plants. Even an epidermis and a mesophyll may be lacking. Instead for their gaseous exchanges they use a homogeneous **aerenchyma** (thin-walled cells separated by large gas-filled spaces). Their stomata are situated at the upper surface.

Leaves are normally green in color, which comes from chlorophyll found in plastids in the chlorenchyma cells. Plants that lack chlorophyll cannot photosynthesize.

Leaves shifting color in fall

Leaves in temperate, boreal, and seasonally dry zones may be seasonally deciduous (falling off or dying for the inclement season). This mechanism to shed leaves is called abscission. After the leaf is shed, a leaf scar develops on the twig. In cold autumns they sometimes change color, and turn yellow, bright orange or red as various accessory pigments (carotenoids and xanthophylls) are revealed when the tree responds to cold and reduced sunlight by curtailing chlorophyll production. Red anthocyanin pigments are now thought to be produced in the leaf as it dies, possibly to mask the yellow hue left when the chlorophyll is lost - yellow leaves appear to attract herbivores such as aphids.

Veins



Vein skeleton of a Hydrangea leaf

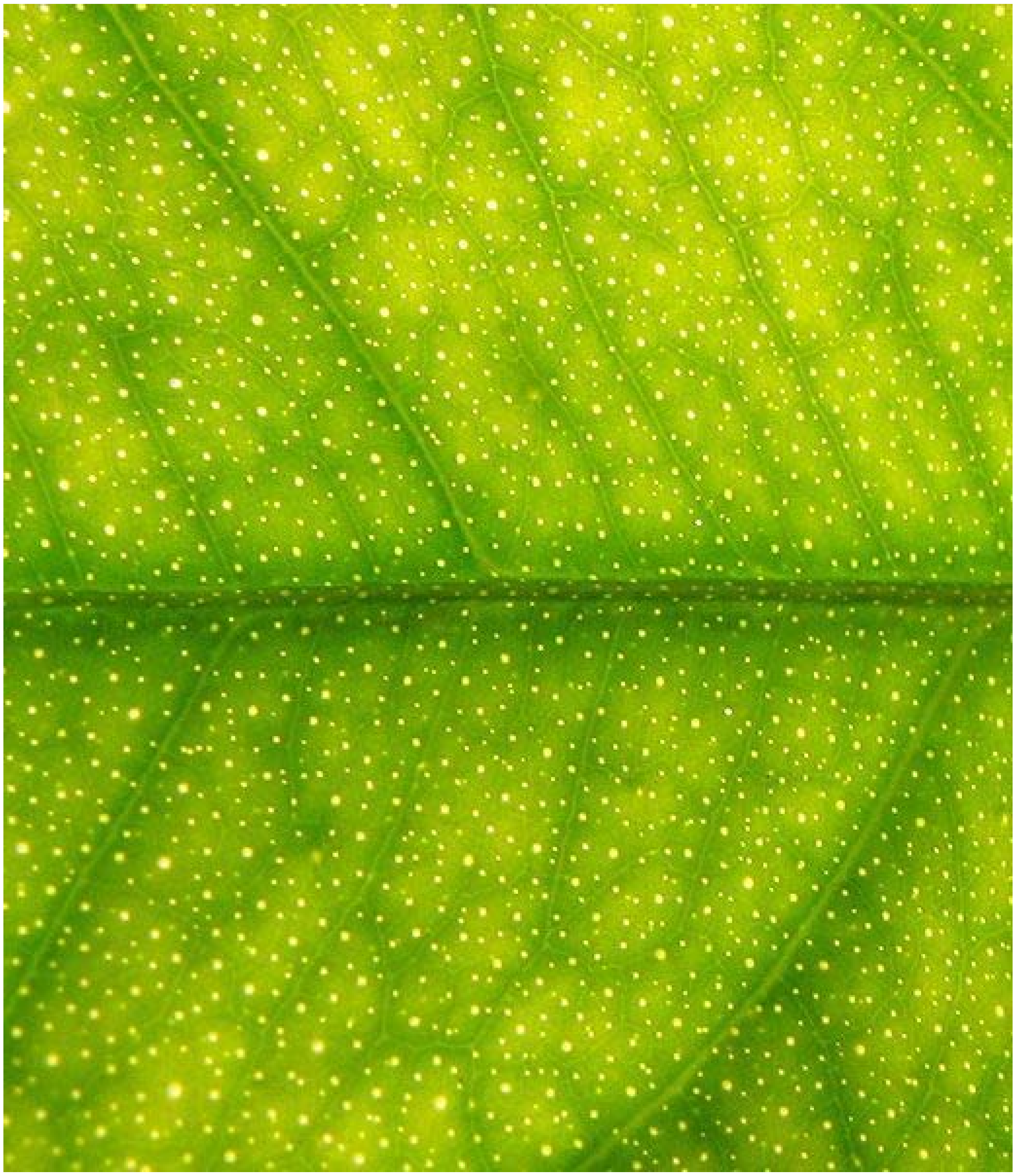
The **veins** are the vascular tissue of the leaf and are located in the spongy layer of the mesophyll. They are typical examples of pattern formation through ramification. The pattern of the veins is called venation.

The veins are made up of:

- Xylem: tubes that brings water and minerals from the roots into the leaf.
- Phloem: tubes that usually move sap, with dissolved sucrose, produced by photosynthesis in the leaf, out of the leaf.

The xylem typically lies over the phloem. Both are embedded in a dense parenchyma tissue, called "pith", with usually some structural collenchyma tissue present.

Morphology



The Citrus leaf is identified by the pores and pigments, as well as the margins.

External leaf characteristics (such as shape, margin, hairs, etc.) are important for identifying plant species, and botanists have developed a rich terminology for describing leaf characteristics. These structures are a part of what makes leaves determinant; they grow and achieve a specific pattern and shape, then stop. Other plant parts like stems or roots are non-determinant, and will usually continue to grow as long as they have the resources to do so.

Classification of leaves can occur through many different designative schema, and the type of leaf is usually characteristic of a species, although some species produce more than one type of leaf. The longest type of leaf is a leaf from palm trees, measuring at nine feet long.

Basic types

Leaves of the White Spruce (Picea glauca) are needle-shaped and their arrangement is spiral

- Ferns have fronds
- Conifer leaves are typically needle-, awl-, or scale-shaped
- Angiosperm (flowering plant) leaves: the standard form includes stipules, a petiole, and a lamina
- Lycophytes have microphyll leaves.
- Sheath leaves (type found in most grasses)

- Other specialized leaves (such as those of *Nepenthes*)

Arrangement on the stem

Different terms are usually used to describe leaf placement (phyllotaxis):

The leaves on this plant are arranged in pairs opposite one another, with successive pairs at right angles to each other ("decussate") along the red stem. Note developing buds in the axils of these leaves.

- **Alternate** — leaf attachments are singular at nodes, and leaves alternate direction, to a greater or lesser degree, along the stem.
- **Opposite** — Two structures, one on each opposite side of the stem, typically leaves, branches, or flower parts. Leaf attachments are paired at each node; decussate if, as typical, each successive pair is rotated 90° progressing along the stem; or **distichous** if not rotated, but two-ranked (in the same geometric flat-plane).
- **Whorled** — three or more leaves attach at each point or node on the stem. As with opposite leaves, successive whorls may or may not be decussate, rotated by half the angle between the leaves in the whorl (i.e., successive whorls of three rotated 60°, whorls of four rotated 45°, etc.). Opposite leaves may appear whorled near the tip of the stem.
- **Rosulate** — leaves form a rosette

As a *stem* grows, leaves tend to appear arranged around the stem in a way that optimizes yield of light. In essence, leaves form a helix pattern centred around the stem, either clockwise or counterclockwise, with (depending upon the species) the same angle of divergence. There is a regularity in these angles and they follow the numbers in a Fibonacci sequence: 1/2, 2/3, 3/5, 5/8, 8/13, 13/21, 21/34, 34/55, 55/89. This series tends to a limit close to 360° x 34/89 = 137.52 or 137° 30', an angle known mathematically as the golden angle. In the series, the numerator indicates the number of complete turns or "gyres" until a leaf arrives at the initial position. The denominator indicates the number of leaves in the arrangement. This can be demonstrated by the following:

- alternate leaves have an angle of 180° (or 1/2)
- 120° (or 1/3) : three leaves in one circle
- 144° (or 2/5) : five leaves in two gyres
- 135° (or 3/8) : eight leaves in three gyres.

Divisions of the blade

A leaf with laminar structure and pinnate venation

Two basic forms of leaves can be described considering the way the blade (lamina) is divided. A **simple leaf** has an undivided blade. However, the leaf shape may be formed of lobes, but the gaps between lobes do not reach to the main vein. A **compound leaf** has a fully subdivided blade, each leaflet of the blade separated along a main or secondary vein. Because each leaflet can appear to be a simple leaf, it is important to recognize where the petiole occurs to identify a compound leaf. Compound leaves are a characteristic of some families of higher plants, such as the Fabaceae. The middle vein of a compound leaf or a frond, when it is present, is called a rachis.

- *Palmately compound* leaves have the leaflets radiating from the end of the petiole, like fingers off the palm of a hand, e.g. *Cannabis* (hemp) and *Aesculus* (buckeyes).
- *Pinnately compound* leaves have the leaflets arranged along the main or mid-vein.
    - odd pinnate: with a terminal leaflet, e.g. *Fraxinus* (ash).
    - even pinnate: lacking a terminal leaflet, e.g. *Swietenia* (mahogany).
- *Bipinnately compound* leaves are twice divided: the leaflets are arranged along a secondary vein that is one of several branching off the rachis. Each leaflet is called a "pinnule". The pinnules on one secondary vein are called "pinna"; e.g. *Albizia* (silk tree).
- *trifoliate* (or *trifoliolate*): a pinnate leaf with just three leaflets, e.g. *Trifolium* (clover), *Laburnum* (laburnum).
- *pinnatifid*: pinnately dissected to the central vein, but with the leaflets not entirely separate, e.g. *Polypodium*, some *Sorbus* (whitebeams). In pinnately veined leaves the central vein in known as the *midrib*.

Characteristics of the petiole

The overgrown petioles of Rhubarb (*Rheum rhabarbarum*) are edible.

Petiolated leaves have a petiole (leaf stem). Sessile leaves do not: the blade attaches directly to the stem. In clasping or decurrent leaves, the blade partially or wholly surrounds the stem, often giving the impression that the shoot grows through the leaf. When this is actually the case, the leaves are called "perfoliate", such as in *Claytonia perfoliata*. In peltate leaves, the petiole attaches to the blade inside from the blade margin.

In some *Acacia* species, such as the Koa Tree (*Acacia koa*), the petioles are expanded or broadened and function like leaf blades; these are called phyllodes. There may or may not be normal pinnate leaves at the tip of the phyllode.

A stipule, present on the leaves of many dicotyledons, is an appendage on each side at the base of the petiole resembling a small leaf. Stipules may be lasting and not be shed (a stipulate leaf, such as in roses and beans), or be shed as the leaf expands, leaving a stipule scar on the twig (an exstipulate leaf).

- The situation, arrangement, and structure of the stipules is called the "stipulation".
    - free
    - adnate : fused to the petiole base
    - ochreate : provided with ochrea, or sheath-formed stipules, e.g. rhubarb,
    - encircling the petiole base
    - interpetiolar : between the petioles of two opposite leaves.
    - intrapetiolar : between the petiole and the subtending stem

Venation

Branching veins on underside of taro leaf

The venation within the bract of a Lime tree.

The lower epidermis of Tilia x europea

Palmate-veined leaf

There are two subtypes of venation, namely, *craspedodromous*, where the major veins stretch up to the margin of the leaf, and *camptodromous*, when major veins extend close to the margin, but bend before they intersect with the margin.

- Feather-veined, reticulate (also called pinnate-netted, penniribbed, penninerved, or penniveined) — the veins arise pinnately from a single mid-vein and subdivide into veinlets. These, in turn, form a complicated network. This type of venation is typical for (but by no means limited to) dicotyledons.
- Three main veins branch at the base of the lamina and run essentially parallel subsequently, as in *Ceanothus*. A similar pattern (with 3-7 veins) is especially conspicuous in Melastomataceae.
- Palmate-netted, palmate-veined, fan-veined; several main veins diverge from near the leaf base where the petiole attaches, and radiate toward the edge of the leaf; e.g. most *Acer* (maples).
- Parallel-veined, parallel-ribbed, parallel-nerved, penniparallel — veins run parallel for the length of the leaf, from the base to the apex. Commissural veins (small veins) connect the major parallel veins. Typical for most monocotyledons, such as grasses.
- Dichotomous — There are no dominant bundles, with the veins forking regularly by pairs; found in *Ginkgo* and some pteridophytes.

Note that although it is the more complex pattern, branching veins appear to be plesiomorphic and in some form were present in ancient seed plants as long as 250 million years ago. A pseudo-reticulate venation that is actually a highly modified penniparallel one is an autapomorphy of some Melanthiaceae which are monocots, e.g. *Paris quadrifolia* (True-lover's Knot).

Morphology changes within a single plant

- Homoblasty - Characteristic in which a plant has small changes in leaf size, shape, and growth habit between juvenile and adult stages.
- Heteroblasty - Characteristic in which a plant has marked changes in leaf size, shape, and growth habit between juvenile and adult stages.

Terminology

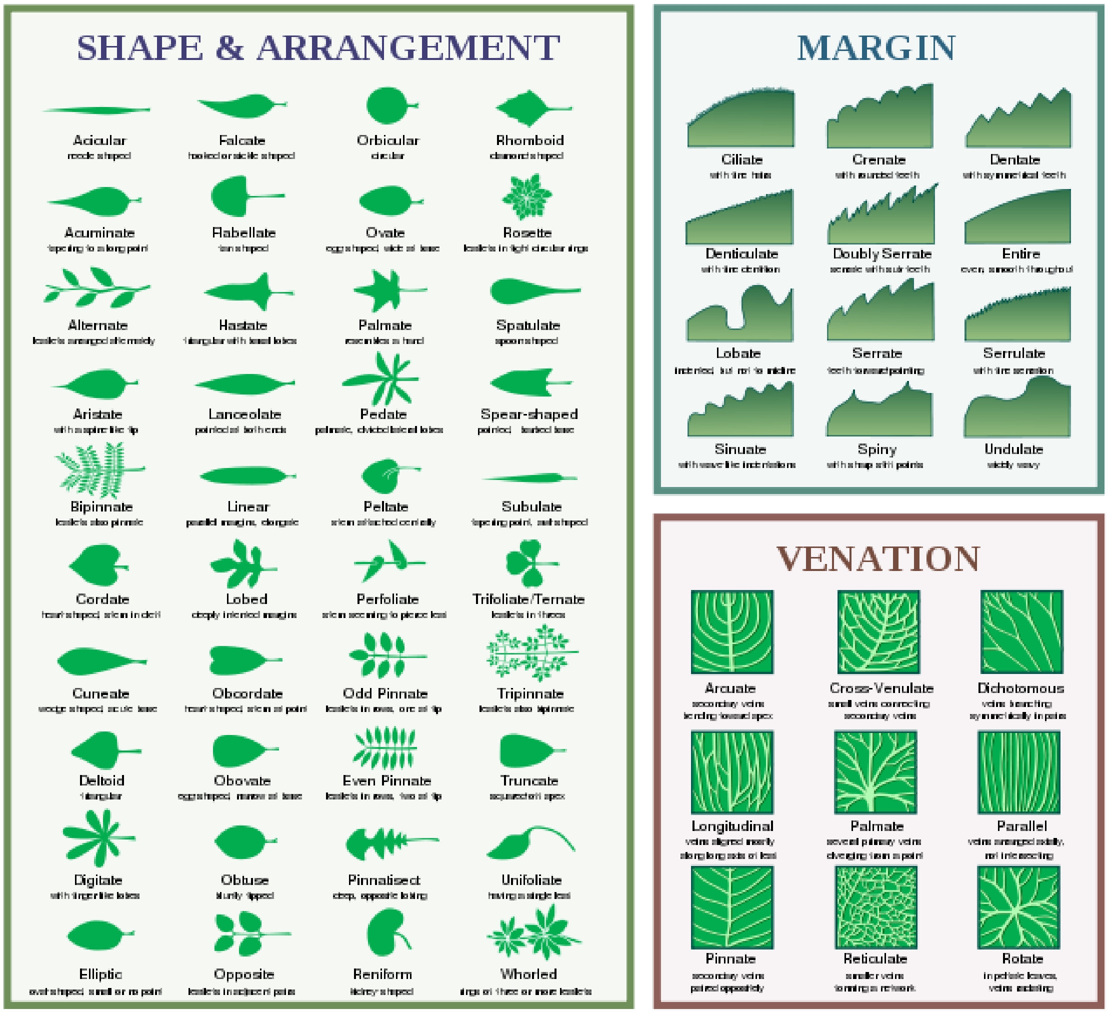


Chart illustrating some leaf morphology terms

A portion of a celery leaf

Shape

Edge (margin)

- ***ciliate:*** fringed with hairs
- ***crenate:*** wavy-toothed; dentate with rounded teeth, such as *Fagus* (beech)
- ***crenulate*** finely or shallowly crenate
- ***dentate:*** toothed, such as *Castanea* (chestnut)
    - ***coarse-toothed:*** with large teeth
    - ***glandular toothed:*** with teeth that bear glands.
- ***denticulate:*** finely toothed

- ***doubly toothed:*** each tooth bearing smaller teeth, such as *Ulmus* (elm)
- ***entire:*** even; with a smooth margin; without toothing
- ***lobate:*** indented, with the indentations not reaching to the center, such as many *Quercus* (oaks)
    - ***palmately lobed:*** indented with the indentations reaching to the center, such as *Humulus* (hop).
- ***serrate:*** saw-toothed with asymmetrical teeth pointing forward, such as *Urtica* (nettle)
- ***serrulate:*** finely serrate
- ***sinuate:*** with deep, wave-like indentations; coarsely crenate, such as many *Rumex* (docks)
- ***spiny*** or ***pungent:*** with stiff, sharp points, such as some *Ilex* (hollies) and *Cirsium* (thistles).

Tip

Leaves showing various morphologies. Clockwise from upper left: tripartite lobation, elliptic with serrulate margin, peltate with palmate venation, acuminate odd-pinnate (center), pinnatisect, lobed, elliptic with entire margin

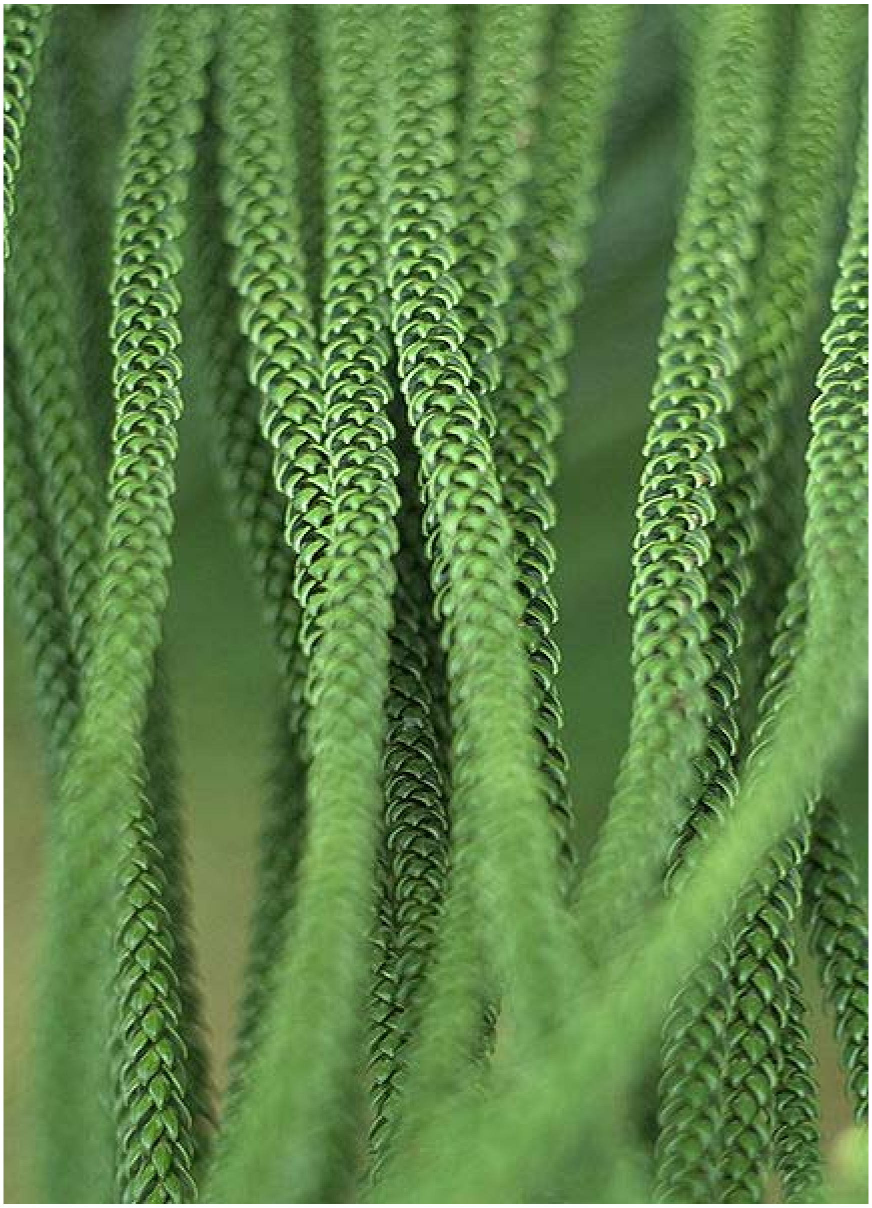
- ***acuminate:*** long-pointed, prolonged into a narrow, tapering point in a concave manner.
- ***acute:*** ending in a sharp, but not prolonged point
- ***cuspidate:*** with a sharp, elongated, rigid tip; tipped with a cusp.
- ***emarginate:*** indented, with a shallow notch at the tip.
- ***mucronate:*** abruptly tipped with a small short point, as a continuation of the midrib; tipped with a mucro.
- ***mucronulate:*** mucronate, but with a smaller spine.

- ***obcordate:*** inversely heart-shaped, deeply notched at the top.
- ***obtuse:*** rounded or blunt
- ***truncate:*** ending abruptly with a flat end, that looks cut off.

Base

- ***acuminate:*** coming to a sharp, narrow, prolonged point.
- ***acute:*** coming to a sharp, but not prolonged point.
- ***auriculate:*** ear-shaped.
- ***cordate:*** heart-shaped with the notch towards the stalk.
- ***cuneate:*** wedge-shaped.
- ***hastate:*** shaped like an halberd and with the basal lobes pointing outward.
- ***oblique:*** slanting.
- ***reniform:*** kidney-shaped but rounder and broader than long.
- ***rounded:*** curving shape.
- ***sagittate:*** shaped like an arrowhead and with the acute basal lobes pointing downward.
- ***truncate:*** ending abruptly with a flat end, that looks cut off.

Surface



Scale-shaped leaves of a Norfolk Island Pine, *Araucaria heterophylla*.

- ***farinose:*** bearing farina; mealy, covered with a waxy, whitish powder.
- ***glabrous:*** smooth, not hairy.
- ***glaucous:*** with a whitish bloom; covered with a very fine, bluish-white powder.
- ***glutinous:*** sticky, viscid.
- ***papillate***, or ***papillose:*** bearing papillae (minute, nipple-shaped protuberances).
- ***pubescent:*** covered with erect hairs (especially soft and short ones).
- ***punctate:*** marked with dots; dotted with depressions or with translucent glands or colored dots.
- ***rugose:*** deeply wrinkled; with veins clearly visible.
- ***scurfy:*** covered with tiny, broad scalelike particles.

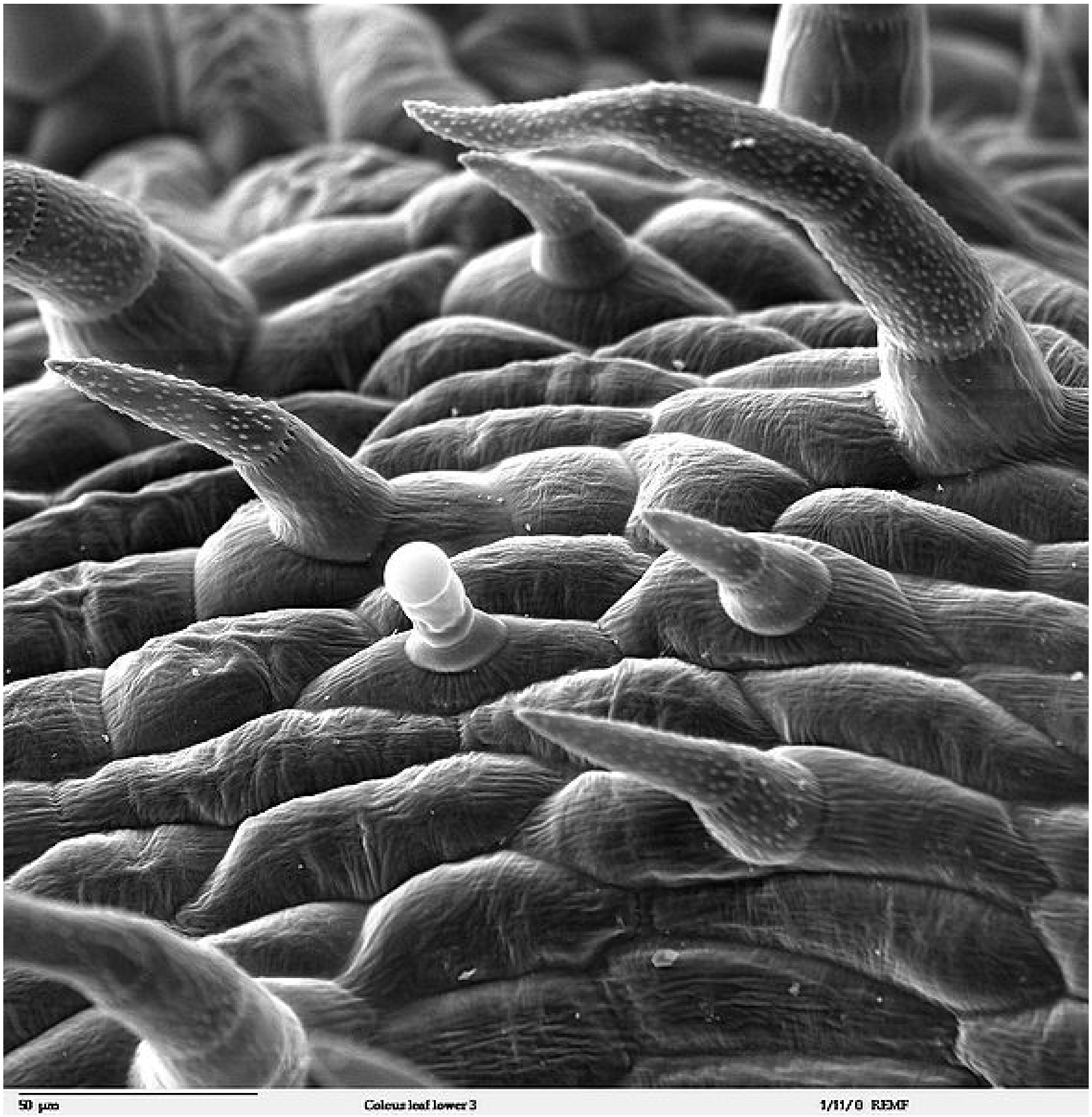
- ***tuberculate:*** covered with tubercles; covered with warty prominences.
- ***verrucose:*** warted, with warty outgrowths.
- ***viscid***, or ***viscous:*** covered with thick, sticky secretions.

The leaf surface is also host to a large variety of microorganisms; in this context it is referred to as the phyllosphere.

The parallel veins within an iris leaf.

Hairiness

Common Mullein (*Verbascum thapsus*) leaves are covered in dense, stellate trichomes.



Scanning electron microscope image of trichomes on the lower surface of a *Coleus blumei* (coleus) leaf.

"Hairs" on plants are properly called trichomes. Leaves can show several degrees of hairiness. The meaning of several of the following terms can overlap.

- ***arachnoid***, or ***arachnose:*** with many fine, entangled hairs giving a cobwebby appearance.
- ***barbellate:*** with finely barbed hairs (barbellae).
- ***bearded:*** with long, stiff hairs.
- ***bristly:*** with stiff hair-like prickles.
- ***canescent:*** hoary with dense grayish-white pubescence.
- ***ciliate:*** marginally fringed with short hairs (cilia).

- ***ciliolate:*** minutely ciliate.
- ***floccose:*** with flocks of soft, woolly hairs, which tend to rub off.
- ***glabrous:*** no hairs of any kind present.
- ***glandular:*** with a gland at the tip of the hair.
- ***hirsute:*** with rather rough or stiff hairs.
- ***hispid:*** with rigid, bristly hairs.
- ***hispidulous:*** minutely hispid.
- ***hoary:*** with a fine, close grayish-white pubescence.
- ***lanate***, or ***lanose:*** with woolly hairs.
- ***pilose:*** with soft, clearly separated hairs.
- ***puberulent***, or ***puberulous:*** with fine, minute hairs.
- ***pubescent:*** with soft, short and erect hairs.
- ***scabrous***, or ***scabrid:*** rough to the touch.
- ***sericeous:*** silky appearance through fine, straight and appressed (lying close and flat) hairs.
- ***silky:*** with adpressed, soft and straight pubescence.
- ***stellate***, or ***stelliform:*** with star-shaped hairs.
- ***strigose:*** with appressed, sharp, straight and stiff hairs.
- ***tomentose:*** densely pubescent with matted, soft white woolly hairs.
    - ***cano-tomentose:*** between canescent and tomentose.
    - ***felted-tomentose:*** woolly and matted with curly hairs.
- ***villous:*** with long and soft hairs, usually curved.
- ***woolly:'*** *with long, soft and tortuous or matted hairs.*

Adaptations

Poinsettia bracts are leaves which have evolved red pigmentation in order to attract insects and birds to the central flowers, an adaptive function normally served by petals (which are themselves leaves highly modified by evolution).

In the course of evolution, leaves have adapted to different environments in the following ways:

- A certain surface structure avoids moistening by rain and contamination.
- Sliced leaves reduce wind resistance.
- Hairs on the leaf surface trap humidity in dry climates and create a boundary layer reducing water loss.
- Waxy leaf surfaces reduce water loss.
- Large surface area provides large area for sunlight and shade for plant to minimize heating and reduce water loss.
- In more or less opaque or buried in the soil leaves, translucent windows filter the light before the photosynthesis takes place at the inner leaf surfaces (e.g. *Fenestraria*).
- Succulent leaves store water and organic acids for use in CAM photosynthesis.
- Aromatic oils, poisons or pheromones produced by leaf borne glands deter herbivores (e.g. eucalypts).

- Inclusions of crystalline minerals deter herbivores (e.g. silica phytoliths in grasses, raphides in Araceae).
- Petals attracts pollinators.
- Spines protect the plants (*e.g.* cacti).
- Insect traps feed the plants directly.
- Bulbs store food and water (*e.g.* onions).
- Tendrils allow the plant to climb (*e.g.* peas).
- Bracts and pseudanthia (*false flowers*) replace normal flower structures when the true flowers are greatly reduced (*e.g.* Spurges).

Interactions with other organisms

Some insects mimic leaves (*Kallima inachus* shown)

A girl playing with leaves

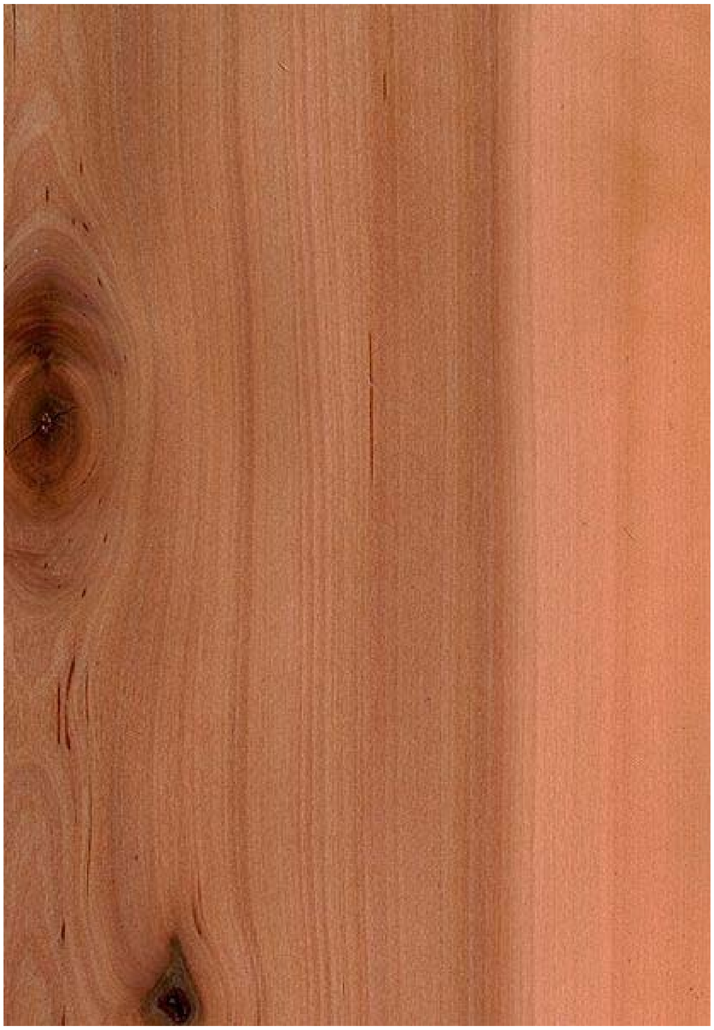
Leaf after being eaten by Caterpillar

Although not as nutritious as other organs such as fruit, leaves provide a food source for many organisms. Animals which eat leaves are known as folivores. The leaf is one of the most vital parts of the plant, and plants have evolved protection against folivores such as tannins, chemicals which hinder the digestion of proteins and have an unpleasant taste.

Some animals have cryptic adaptations to avoid their own predators. For example, some caterpillars will create a small home in the leaf by folding it over themselves, while other herbivores and their prey mimic the appearance of the leaf. Some insects, such as the katydid, take this even further, moving from side to side much like a leaf does in the wind.

Chapter 7

Wood



Wood surface, showing several features

Wood is a hard, fibrous tissue found in many plants. It has been used for centuries for both fuel and as a construction material for several types of living areas such as houses. Construction with wood is known as carpentry. It is an organic material, a natural composite of cellulose fibers (which are strong in tension) embedded in a matrix of lignin which resists compression. In the strict sense wood is produced as secondary xylem in the stems of trees (and other woody plants). In a living tree it transfers water and nutrients to the leaves and other growing tissues, and has a support function, enabling woody plants to reach large sizes or to stand up for themselves. Wood may also refer to other plant materials with comparable properties, and to material engineered from wood, or wood chips or fiber.

People have used wood for millennia for many purposes, primarily as a fuel or as a construction material for making houses, tools, weapons, furniture, packaging, artworks, and paper. Wood can be dated by carbon dating and in some species by dendrochronology to make inferences about when a wooden object was created. The year-to-year variation in tree-ring widths and isotopic abundances gives clues to the prevailing climate at that time.

Formation

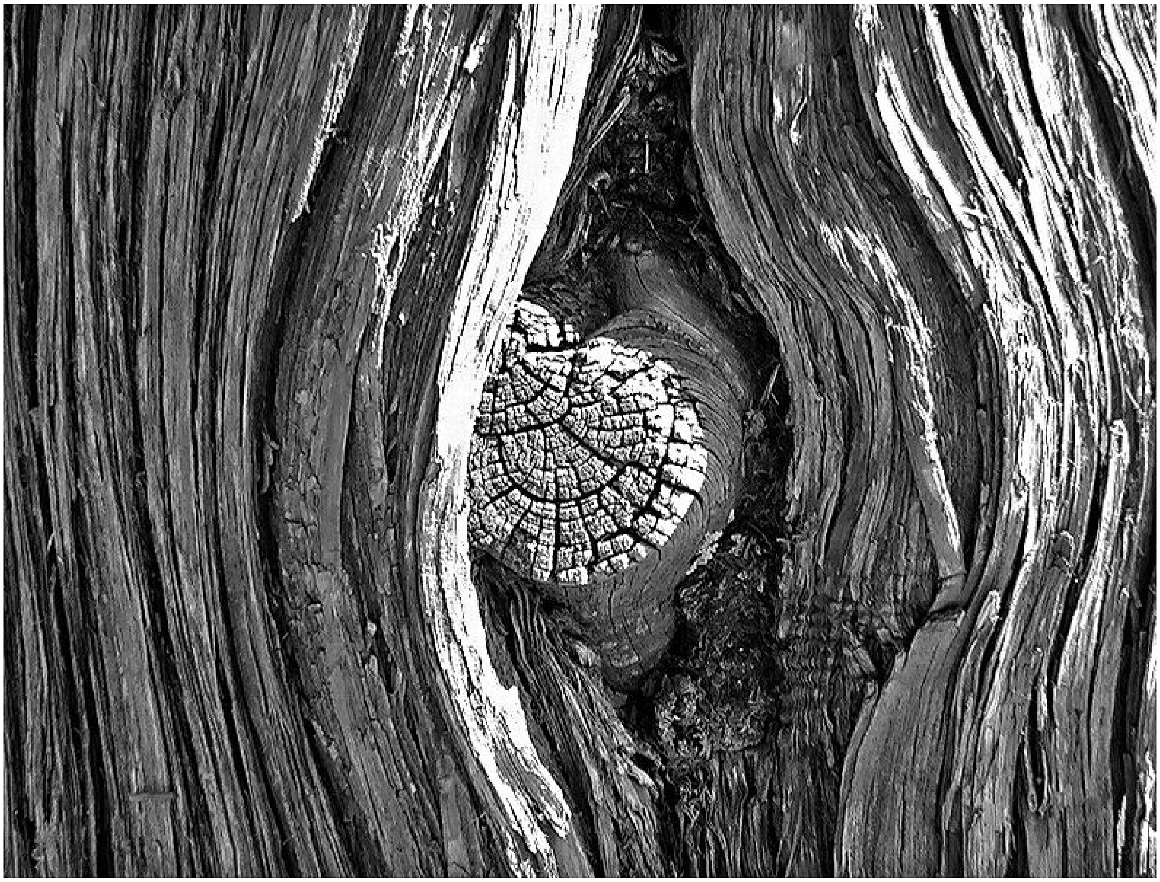
Wood, in the strict sense, is yielded by trees, which increase in diameter by the formation, between the existing wood and the inner bark, of new woody layers which envelop the entire stem, living branches, and roots. Technically this is known as secondary growth; it is the result of cell division in the vascular cambium, a lateral meristem, and subsequent expansion of the new cells.

Growth rings

Where there are clear seasons, growth can occur in a discrete annual or seasonal pattern, leading to growth rings; these can usually be most clearly seen on the end of a log, but are also visible on the other surfaces. If these seasons are annual these growth rings are referred to as annual rings. Where there is no seasonal difference growth rings are likely to be indistinct or absent.

If there are differences within a growth ring, then the part of a growth ring nearest the center of the tree, and formed early in the growing season when growth is rapid, is usually composed of wider elements. It is usually lighter in color than that near the outer portion of the ring, and is known as earlywood or springwood. The outer portion formed later in the season is then known as the latewood or summerwood. However, there are major differences, depending on the kind of wood (see below).

Knots



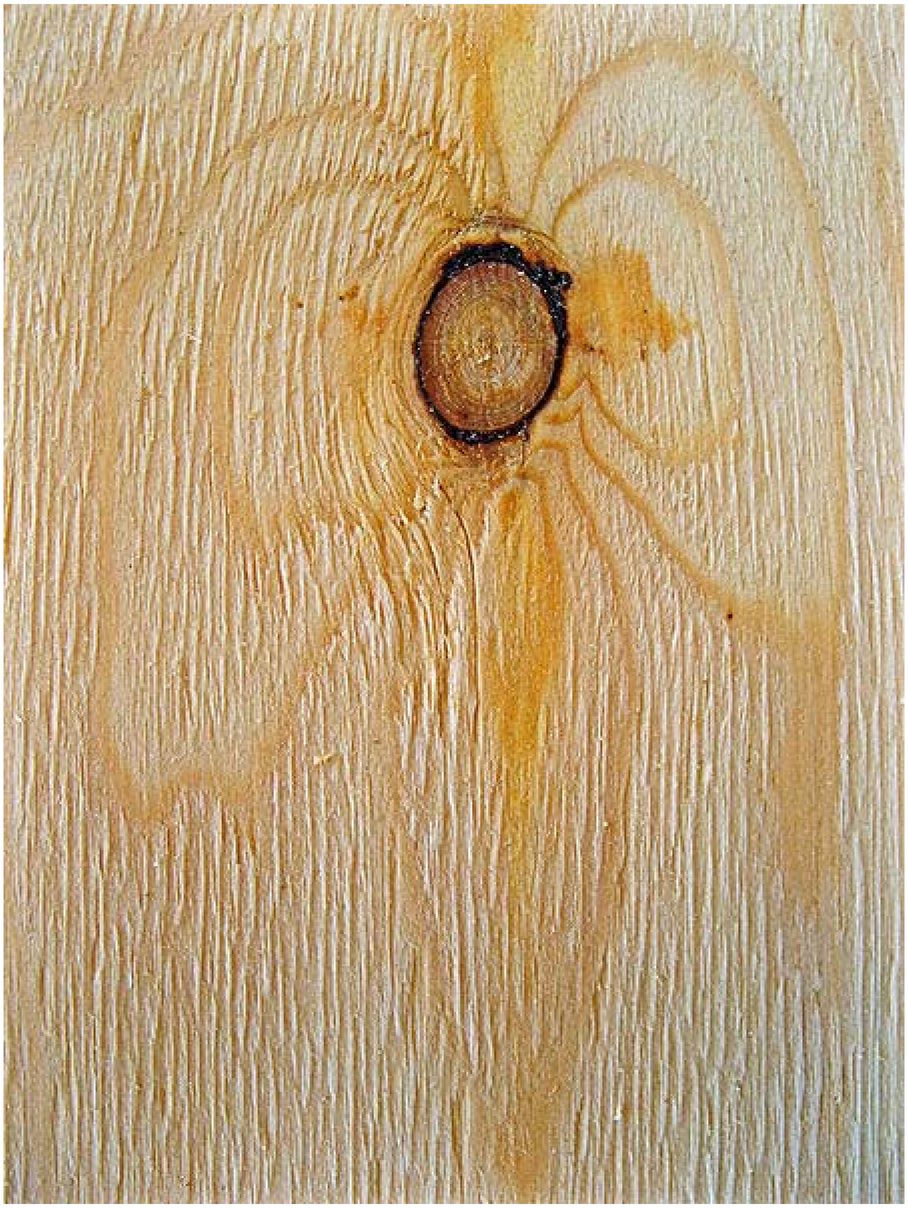
A knot on a tree at the Garden of the Gods public park in Colorado Springs, Colorado (October 2006)

A knot is a particular type of imperfection in a piece of wood; it will affect the technical properties of the wood, usually for the worse, but may be exploited for artistic effect. In a longitudinally sawn plank, a knot will appear as a roughly circular "solid" (usually darker) piece of wood around which the grain of the rest of the wood "flows" (parts and rejoins). Within a knot, the direction of the wood (grain direction) is up to 90 degrees different from the grain direction of the regular wood.

In the tree a knot is either the base of a side branch or a dormant bud. A knot (when the base of a side branch) is conical in shape (hence the roughly circular cross-section) with the tip at the point in stem diameter at which the plant's cambium was located when the branch formed as a bud.

During the development of a tree, the lower limbs often die, but may persist for a time, sometimes years. Subsequent layers of growth of the attaching stem are no longer intimately joined with the dead limb, but are grown around it. Hence, dead branches produce knots which are not attached, and likely to drop out after the tree has been sawn into boards.

In grading lumber and structural timber, knots are classified according to their form, size, soundness, and the firmness with which they are held in place. This firmness is affected by, among other factors, the length of time for which the branch was dead while the attaching stem continued to grow.



Wood Knot

Knots materially affect cracking (known in the US as checking, and the UK as shakes) and warping, ease in working, and cleavability of timber. They are defects which weaken timber and lower its value for structural purposes where strength is an important consideration. The weakening effect is much more serious when timber is subjected to forces perpendicular to the grain and/or tension than where under load along the grain and/or compression. The extent to which knots affect the strength of a beam depends upon their position, size, number, and condition. A knot on the upper side is compressed, while one on the lower side is subjected to tension. If there is a season check in the knot, as is often the case, it will offer little resistance to this tensile stress. Small knots, however, may be located along the neutral plane of a beam and increase the strength by preventing longitudinal shearing. Knots in a board or plank are least injurious when they extend through it at right angles to its broadest surface. Knots which occur near the ends of a beam do not weaken it. Sound knots which occur in the central portion one-fourth the height of the beam from either edge are not serious defects.

Knots do not necessarily influence the stiffness of structural timber, this will depend on the size and location. Stiffness and elastic strength are more dependent upon the sound wood than upon localised defects. The breaking strength is very susceptible to defects. Sound knots do not weaken wood when subject to compression parallel to the grain.

In some decorative applications, wood with knots may be desirable to add visual interest. In applications where wood is painted, such as skirting boards, fascia boards, door frames and furniture, resins present in the timber may continue to 'bleed' through to the surface of a knot for months or even years after manufacture and show as a yellow or brownish stain. A Knot Primer paint or solutuion, correctly applied during preparation, may do much to reduce this problem but it is difficult to control completely, especially when using mass-produced kiln-dried timber stocks.

Heartwood and sapwood

A section of a Yew branch showing 27 annual growth rings, pale sapwood and dark heartwood, and pith (centre dark spot). The dark radial lines are small knots.

Heartwood (or old xylem) is wood that, as a result of tylosis, has become more resistant to decay. Tylosis is the deposition of chemical substances (a genetically programmed process). Once heartwood formation is complete, the heartwood is dead. Some uncertainty still exists as to whether heartwood is truly dead, as it can still chemically react to decay organisms, but only once (Shigo 1986, 54).

Usually heartwood looks different; in that case it can be seen on a cross-section, usually following the growth rings in shape. Heartwood may (or may not) be much darker than living wood. It may (or may not) be sharply distinct from the sapwood. However, other processes, such as decay, can discolor wood, even in woody plants that do not form heartwood, with a similar color difference, which may lead to confusion.

Sapwood is the younger, outermost wood; in the growing tree it is living wood, and its principal functions are to conduct water from the roots to the leaves and to store up and give back according to the season the reserves prepared in the leaves. However, by the time they become competent to conduct water, all xylem tracheids and vessels have lost their cytoplasm and the cells are therefore functionally dead. All wood in a tree is first formed as sapwood. The more leaves a tree bears and the more vigorous its growth, the larger the volume of sapwood required. Hence trees making rapid growth in the open have thicker sapwood for their size than trees of the same species growing in dense forests. Sometimes trees (of species that do form heartwood) grown in the open may become of considerable size, 30 cm or more in diameter, before any heartwood begins to form, for example, in second-growth hickory, or open-grown pines.

The term *heartwood* derives solely from its position and not from any vital importance to the tree. This is evidenced by the fact that a tree can thrive with its heart completely decayed. Some species begin to form heartwood very early in life, so having only a thin layer of live sapwood, while in others the change comes slowly. Thin sapwood is characteristic of such species as chestnut, black locust, mulberry, osage-orange, and sassafras, while in maple, ash, hickory, hackberry, beech, and pine, thick sapwood is the rule. Others never form heartwood.

There is no definite relation between the annual rings of growth and the amount of sapwood. Within the same species the cross-sectional area of the sapwood is very roughly proportional to the size of the crown of the tree. If the rings are narrow, more of them are required than where they are wide. As the tree gets larger, the sapwood must necessarily become thinner or increase materially in volume. Sapwood is thicker in the upper portion of the trunk of a tree than near the base, because the age and the diameter of the upper sections are less.

When a tree is very young it is covered with limbs almost, if not entirely, to the ground, but as it grows older some or all of them will eventually die and are either broken off or fall off. Subsequent growth of wood may completely conceal the stubs which will however remain as knots. No matter how smooth and clear a log is on the outside, it is more or less knotty near the middle. Consequently the sapwood of an old tree, and particularly of a forest-grown tree, will be freer from knots than the inner heartwood.

Since in most uses of wood, knots are defects that weaken the timber and interfere with its ease of working and other properties, it follows that a given piece of sapwood, because of its position in the tree, may well be stronger than a piece of heartwood from the same tree.

It is remarkable that the inner heartwood of old trees remains as sound as it usually does, since in many cases it is hundreds, and in a few instances thousands, of years old. Every broken limb or root, or deep wound from fire, insects, or falling timber, may afford an entrance for decay, which, once started, may penetrate to all parts of the trunk. The larvae of many insects bore into the trees and their tunnels remain indefinitely as sources of weakness. Whatever advantages, however, that sapwood may have in this connection are due solely to its relative age and position.

If a tree grows all its life in the open and the conditions of soil and site remain unchanged, it will make its most rapid growth in youth, and gradually decline. The annual rings of growth are for many years quite wide, but later they become narrower and narrower. Since each succeeding ring is laid down on the outside of the wood previously formed, it follows that unless a tree materially increases its production of wood from year to year, the rings must necessarily become thinner as the trunk gets wider. As a tree reaches maturity its crown becomes more open and the annual wood production is lessened, thereby reducing still more the width of the growth rings. In the case of forest-grown trees so much depends upon the competition of the trees in their struggle for light and nourishment that periods of rapid and slow growth may alternate. Some trees, such as southern oaks, maintain the same width of ring for hundreds of years. Upon the whole, however, as a tree gets larger in diameter the width of the growth rings decreases.

Different pieces of wood cut from a large tree may differ decidedly, particularly if the tree is big and mature. In some trees, the wood laid on late in the life of a tree is softer, lighter, weaker, and more even-textured than that produced earlier, but in other trees, the reverse applies. This may or may not correspond to heartwood and sapwood. In a large log the sapwood, because of the time in the life of the tree when it was grown, may be inferior in hardness, strength, and toughness to equally sound heartwood from the same log. In a smaller tree, the reverse may be true.

Hard and soft woods

There is a strong relationship between the properties of wood and the properties of the particular tree that yielded it. For every tree species there is a range of density for the wood it yields. There is a rough correlation between density of a wood and its strength (mechanical properties). For example, while mahogany is a medium-dense hardwood which is excellent for fine furniture crafting, balsa is light, making it useful for model building. The densest wood may be black ironwood.

It is common to classify wood as either softwood or hardwood. The wood from conifers (e.g. pine) is called softwood, and the wood from dicotyledons (usually broad-leaved trees, e.g. oak) is called hardwood. These names are a bit misleading, as hardwoods are not necessarily hard, and softwoods are not necessarily soft. The well-known balsa (a hardwood) is actually softer than any commercial softwood. Conversely, some softwoods (e.g. yew) are harder than many hardwoods.

Engineered wood products have properties that usually differ from those of natural timbers. (see below)

Color

In species which show a distinct difference between heartwood and sapwood the natural color of heartwood is usually darker than that of the sapwood, and very frequently the contrast is conspicuous. This is produced by deposits in the heartwood of chemical substances, so that a dramatic color difference does not mean a dramatic difference in the mechanical properties of heartwood and sapwood, although there may be a dramatic chemical difference.

Some experiments on very resinous Longleaf Pine specimens indicate an increase in strength, due to the resin which increases the strength when dry. Such resin-saturated heartwood is called "fat lighter". Structures built of fat lighter are almost impervious to rot and termites; however they are very flammable. Stumps of old longleaf pines are often dug, split into small pieces and sold as kindling for fires. Stumps thus dug may actually remain a century or more since being cut. Spruce impregnated with crude resin and dried is also greatly increased in strength thereby.

The wood of Coast Redwood is distinctively red in color

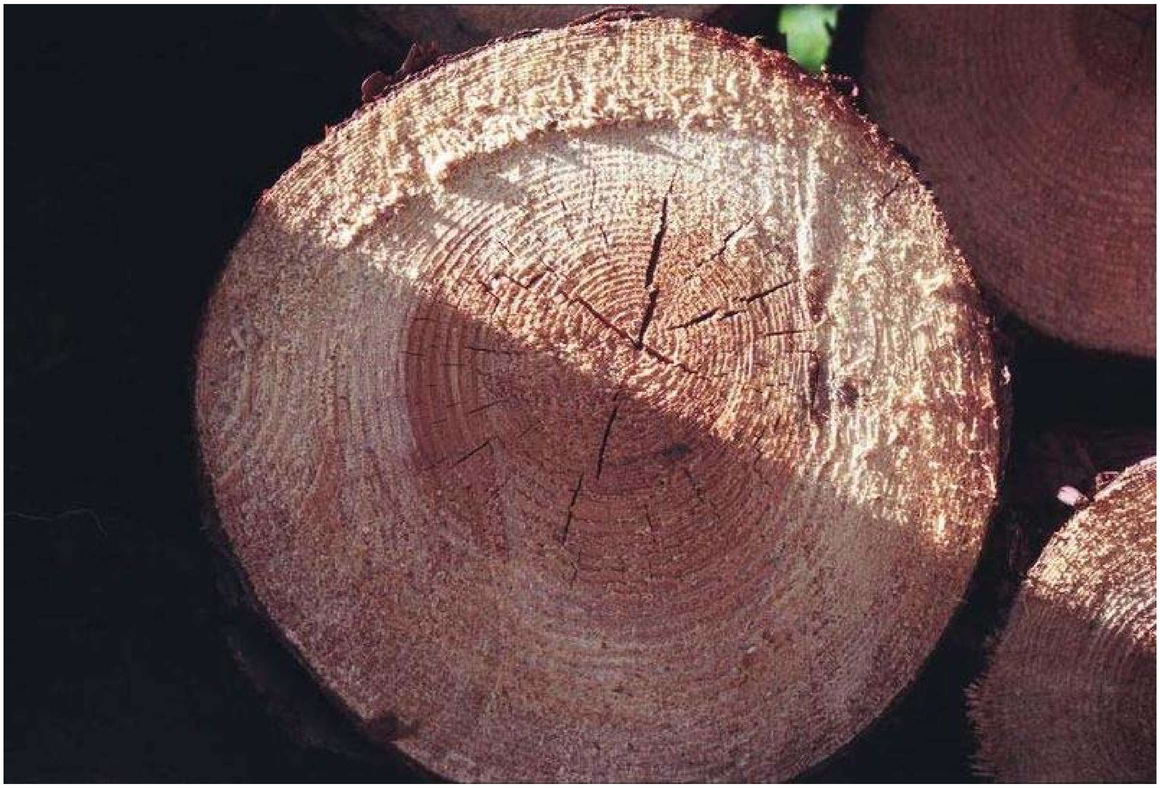
Since the latewood of a growth ring is usually darker in color than the earlywood, this fact may be used in judging the density, and therefore the hardness and strength of the material. This is particularly the case with coniferous woods. In ring-porous woods the vessels of the early wood not infrequently appear on a finished surface as darker than the denser latewood, though on cross sections of heartwood the reverse is commonly true. Except in the manner just stated the color of wood is no indication of strength.

Abnormal discoloration of wood often denotes a diseased condition, indicating unsoundness. The black check in western hemlock is the result of insect attacks. The reddish-brown streaks so common in hickory and certain other woods are mostly the result of injury by birds. The discoloration is merely an indication of an injury, and in all probability does not of itself affect the properties of the wood. Certain rot-producing fungi impart to wood characteristic colors which thus become symptomatic of weakness; however an attractive effect known as spalting produced by this process is often considered a desirable characteristic. Ordinary sap-staining is due to fungous growth, but does not necessarily produce a weakening effect.

Structure

Wood is a heterogeneous, hygroscopic, cellular and anisotropic material. It is composed of cells, and the cell walls are composed of micro-fibrils of cellulose (40% – 50%) and hemicellulose (15% – 25%) impregnated with lignin (15% – 30%).

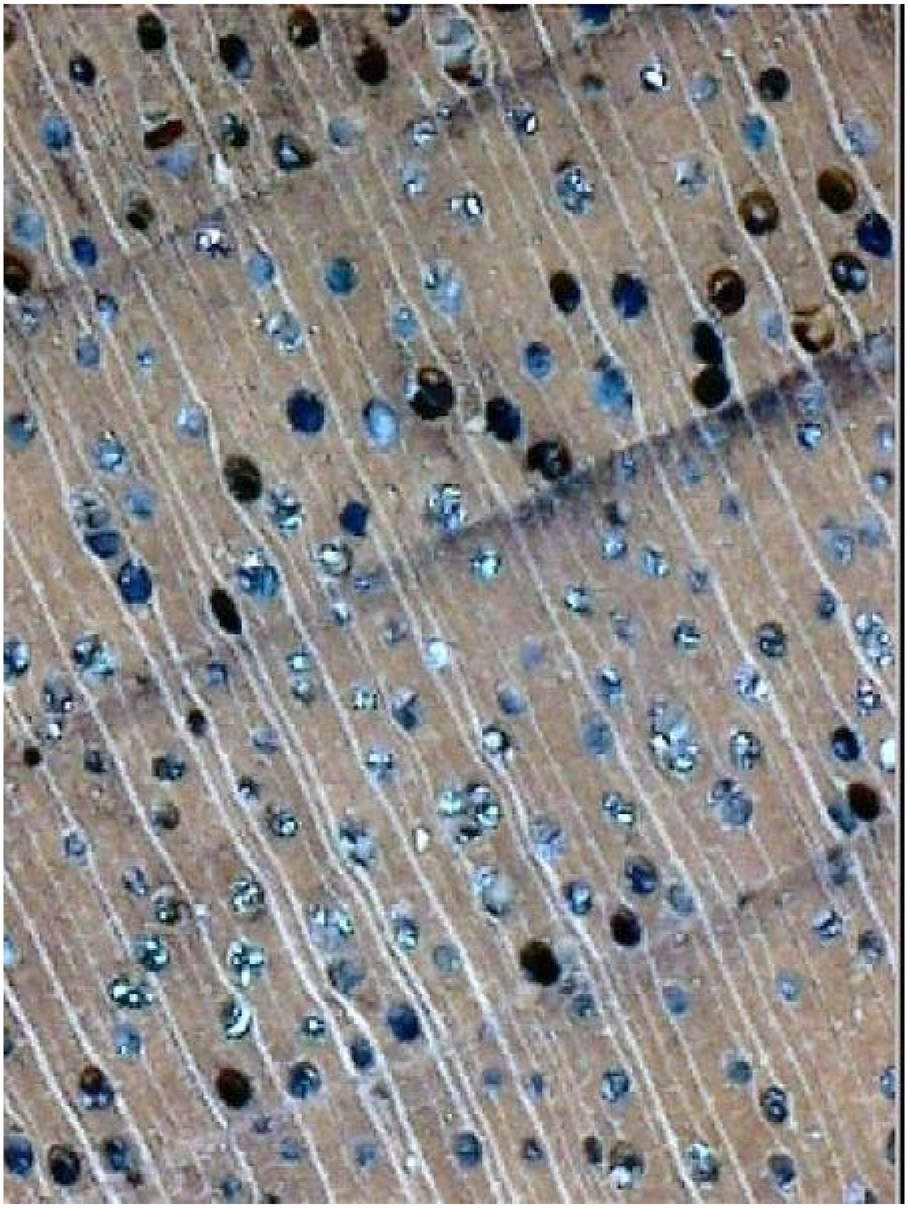
Sections of tree trunk



A tree trunk as found at the Veluwe, Netherlands

In coniferous or softwood species the wood cells are mostly of one kind, tracheids, and as a result the material is much more uniform in structure than that of most hardwoods. There are no vessels ("pores") in coniferous wood such as one sees so prominently in oak and ash, for example.

The structure of hardwoods is more complex. The water conducting capability is mostly taken care of by vessels: in some cases (oak, chestnut, ash) these are quite large and distinct, in others (buckeye, poplar, willow) too small to be seen without a hand lens. In discussing such woods it is customary to divide them into two large classes, *ring-porous* and *diffuse-porous*. In ring-porous species, such as ash, black locust, catalpa, chestnut, elm, hickory, mulberry, and oak, the larger vessels or pores (as cross sections of vessels are called) are localised in the part of the growth ring formed in spring, thus forming a region of more or less open and porous tissue. The rest of the ring, produced in summer, is made up of smaller vessels and a much greater proportion of wood fibers. These fiber are the elements which give strength and toughness to wood, while the vessels are a source of weakness.



Magnified cross-section of Black Walnut, showing the vessels, rays (white lines) and annual rings: this is intermediate between diffuse-porous and ring-porous, with vessel size declining gradually

In diffuse-porous woods the pores are evenly sized so that the water conducting capability is scattered throughout the growth ring instead of being collected in a band or row. Examples of this kind of wood are basswood, birch, buckeye, maple, poplar, and willow. Some species, such as walnut and cherry, are on the border between the two classes, forming an intermediate group.

Earlywood and latewood in softwood

earlywood and latewood in a softwood; radial view, growth rings closely spaced in a Pseudotsuga taxifolia

In temperate softwoods there often is a marked difference between latewood and earlywood. The latewood will be denser than that formed early in the season. When examined under a microscope the cells of dense latewood are seen to be very thick-walled and with very small cell cavities, while those formed first in the season have thin walls and large cell cavities. The strength is in the walls, not the cavities. Hence the greater the proportion of latewood the greater the density and strength. In choosing a piece of pine where strength or stiffness is the important consideration, the principal thing to observe is the comparative amounts of earlywood and latewood. The width of ring is not nearly so important as the proportion and nature of the latewood in the ring.

If a heavy piece of pine is compared with a lightweight piece it will be seen at once that the heavier one contains a larger proportion of latewood than the other, and is therefore showing more clearly demarcated growth rings. In white pines there is not much contrast between the different parts of the ring, and as a result the wood is very uniform in texture and is easy to work. In hard pines, on the other hand, the latewood is very dense and is deep-colored, presenting a very decided contrast to the soft, straw-colored earlywood.

It is not only the proportion of latewood, but also its quality, that counts. In specimens that show a very large proportion of latewood it may be noticeably more porous and weigh considerably less than the latewood in pieces that contain but little. One can judge comparative density, and therefore to some extent strength, by visual inspection.

The twisty branch of a Lilac tree

No satisfactory explanation can as yet be given for the exact mechanisms determining the formation of earlywood and latewood. Several factors may be involved. In conifers, at least, rate of growth alone does not determine the proportion of the two portions of the ring, for in some cases the wood of slow growth is very hard and heavy, while in others the opposite is true. The quality of the site where the tree grows undoubtedly affects the character of the wood formed, though it is not possible to formulate a rule governing it. In general, however, it may be said that where strength or ease of working is essential, woods of moderate to slow growth should be chosen.

Earlywood and latewood in ring-porous woods

Earlywood and latewood in a ring-porous wood (ash) in a Fraxinus excelsior ; tangential view, wide growth rings

In ring-porous woods each season's growth is always well defined, because the large pores formed early in the season abut on the denser tissue of the year before.

In the case of the ring-porous hardwoods there seems to exist a pretty definite relation between the rate of growth of timber and its properties. This may be briefly summed up in the general statement that the more rapid the growth or the wider the rings of growth, the heavier, harder, stronger, and stiffer the wood. This, it must be remembered, applies only to ring-porous woods such as oak, ash, hickory, and others of the same group, and is, of course, subject to some exceptions and limitations.

In ring-porous woods of good growth it is usually the latewood in which the thick-walled, strength-giving fibers are most abundant. As the breadth of ring diminishes, this latewood is reduced so that very slow growth produces comparatively light, porous wood composed of thin-walled vessels and wood parenchyma. In good oak these large vessels of the earlywood occupy from 6 to 10 per cent of the volume of the log, while in inferior material they may make up 25 per cent or more. The latewood of good oak is dark colored and firm, and consists mostly of thick-walled fibers which form one-half or more of the wood. In inferior oak, this latewood is much reduced both in quantity and quality. Such variation is very largely the result of rate of growth.

Wide-ringed wood is often called "second-growth", because the growth of the young timber in open stands after the old trees have been removed is more rapid than in trees in a closed forest, and in the manufacture of articles where strength is an important consideration such "second-growth" hardwood material is preferred. This is particularly the case in the choice of hickory for handles and spokes. Here not only strength, but toughness and resilience are important. The results of a series of tests on hickory by the U.S. Forest Service show that:

"The work or shock-resisting ability is greatest in wide-ringed wood that has from 5 to 14 rings per inch (rings 1.8-5 mm thick), is fairly constant from 14 to 38 rings per inch (rings 0.7-1.8 mm thick), and decreases rapidly from 38 to 47 rings per inch (rings 0.5-0.7 mm thick). The strength at maximum load is not so great with the most rapid-growing wood; it is maximum with from 14 to 20 rings per inch (rings 1.3-1.8 mm thick), and again becomes less as the wood becomes more closely ringed. The natural deduction is that wood of first-class mechanical value shows from 5 to 20 rings per inch (rings 1.3-5 mm thick) and that slower growth yields poorer stock. Thus the inspector or buyer of hickory should discriminate against timber that has more than 20 rings per inch (rings less than 1.3 mm thick). Exceptions exist, however, in the case of normal growth upon dry situations, in which the slow-growing material may be strong and tough."

The effect of rate of growth on the qualities of chestnut wood is summarised by the same authority as follows:

"When the rings are wide, the transition from spring wood to summer wood is gradual, while in the narrow rings the spring wood passes into summer wood abruptly. The width of the spring wood changes but little with the width of the annual ring, so that the narrowing or broadening of the annual ring is always at the expense of the summer wood. The narrow vessels of the summer wood make it richer in wood substance than the spring wood composed of wide vessels. Therefore, rapid-growing specimens with wide rings have more wood substance than slow-growing trees with narrow rings. Since the more the wood substance the greater the weight, and the greater the weight the stronger the wood, chestnuts with wide rings must have stronger wood than chestnuts with narrow rings. This agrees with the accepted view that sprouts (which always have wide rings) yield better and stronger wood than seedling chestnuts, which grow more slowly in diameter."

Earlywood and latewood in diffuse-porous woods

In the diffuse-porous woods, the demarcation between rings is not always so clear and in some cases is almost (if not entirely) invisible to the unaided eye. Conversely, when there is a clear demarcation there may not be a noticeable difference in structure within the growth ring.

In diffuse-porous woods, as has been stated, the vessels or pores are even-sized, so that the water conducting capability is scattered throughout the ring instead of collected in the earlywood. The effect of rate of growth is, therefore, not the same as in the ring-porous woods, approaching more nearly the conditions in the conifers. In general it may be stated that such woods of medium growth afford stronger material than when very rapidly or very slowly grown. In many uses of wood, total strength is not the main consideration. If ease of working is prized, wood should be chosen with regard to its uniformity of texture and straightness of grain, which will in most cases occur when there is little contrast between the latewood of one season's growth and the earlywood of the next.

Monocot wood

Trunks of the Coconut palm, a monocot, in Java. From this perspective these look not much different from trunks of a dicot or conifer

Structural material that roughly (in its gross handling characteristics) resembles ordinary, "dicot" or conifer wood is produced by a number of monocot plants, and these also are colloquially called wood. Of these, bamboo, botanically a member of the grass family, has considerable economic importance, larger culms being widely used as a building and construction material in their own right and, these days, in the manufacture of engineered flooring, panels and veneer. Another major plant group that produce material that often is called wood are the palms. Of much less importance are plants such as *Pandanus, Dracaena* and *Cordyline.* With all this material, the structure and composition of the structural material is quite different from ordinary wood.

Water content

The churches of Kizhi, Russia are among a handful of World Heritage Sites built entirely of wood, without metal joints.

Water occurs in living wood in three conditions, namely: (1) in the cell walls, (2) in the protoplasmic contents of the cells, and (3) as free water in the cell cavities and spaces. In heartwood it occurs only in the first and last forms. Wood that is thoroughly air-dried retains from 8-16% of water in the cell walls, and none, or practically none, in the other forms. Even oven-dried wood retains a small percentage of moisture, but for all except chemical purposes, may be considered absolutely dry.

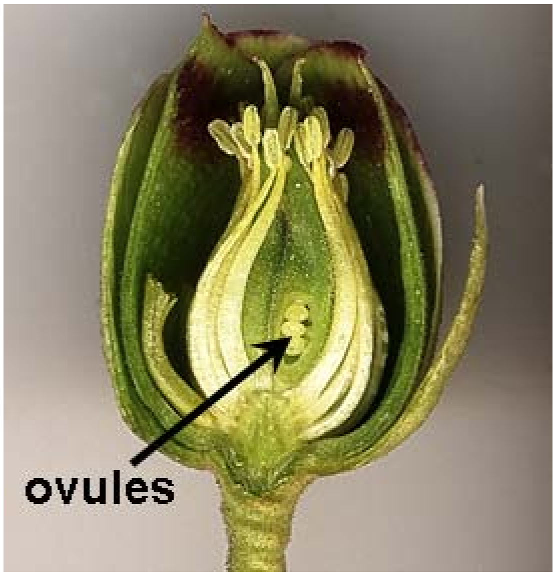
The general effect of the water content upon the wood substance is to render it softer and more pliable. A similar effect of common observation is in the softening action of water on paper or cloth. Within certain limits, the greater the water content, the greater its softening effect.

Drying produces a decided increase in the strength of wood, particularly in small specimens. An extreme example is the case of a completely dry spruce block 5 cm in section, which will sustain a permanent load four times as great as that which a green (undried) block of the same size will support.

The greatest increase due to drying is in the ultimate crushing strength, and strength at elastic limit in endwise compression; these are followed by the modulus of rupture, and stress at elastic limit in cross-bending, while the modulus of elasticity is least affected.

Chapter 8

Ovule



Location of ovules inside a *Helleborus foetidus* flower

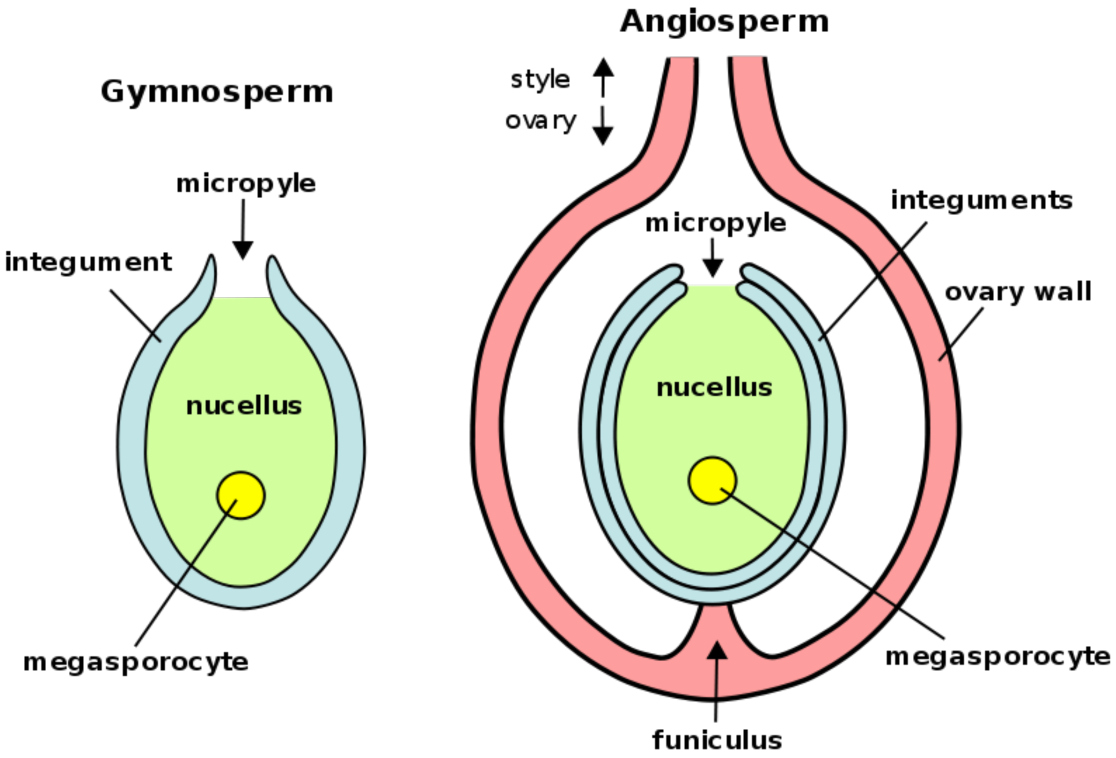
Ovule literally means "small egg." In seed plants, the ovule is the structure that gives rise to and contains the female reproductive cells. It consists of three parts: The **integuments** forming its outer layer, the **nucellus** (or megasporangium), and the megaspore-derived female gametophyte (or **megagametophyte**) in its center. The megagametophyte (also called **embryo sac** in flowering plants) produces the egg cell for fertilization. After fertilization, the ovule develops into a seed.

Location within the plant

In flowering plants, the ovule is located within the actual flower, the part of the carpel known as the ovary, which ultimately becomes the fruit. Depending on the plant, flowers may have one or multiple ovules per ovary. The ovules are attached to the placental wall of the ovary through a structure known as the funiculus, the plant equivalent of an umbilical cord. Different patterns of ovule attachment, or placentation, can be found among plants: In parietal placentation, the ovules are attached to the outer ovary wall, whereas in free central placentation, they are attached to a central column within the ovary. In axile placentation, they are attached to radial spokes within the ovary.

In gymnosperms such as conifers and similar plants, the ovules are borne unenclosed on the surface of an ovuliferous (ovule-bearing) scale, usually within an ovulate cone (also called megastrobilus).

Ovule parts and development



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

The ovule is composed of diploid maternal tissue that gives rise to the haploid tissue of the female gametophyte. The maternal tissues of the ovule include the integuments and the nucellus. The next "generation" formed within the ovule are the haploid megaspore and megagametophyte, or embryo sac. After fertilization of the egg cell and formation of a zygote, the ovule contains the embryo of the next sporophyte generation and, in flowering plants, the triploid endosperm.

Integuments, micropyle and chalaza

The integuments are the outer cell layers of the ovule enclosing the nucellus. Gymnosperms typically have one integument layer while angiosperms typically have two. The integuments develop into the seed coat when the ovule matures after fertilization.

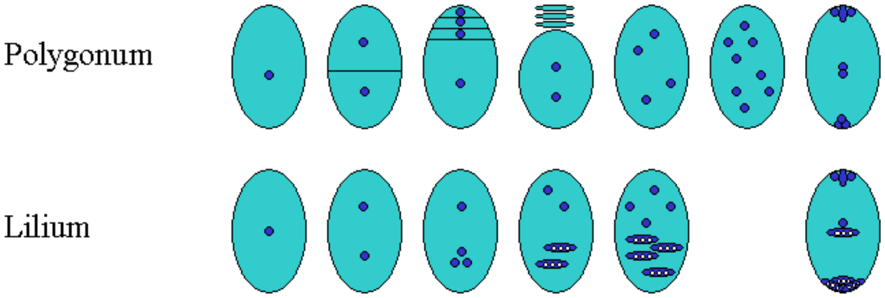
The integuments do not enclose the nucellus completely but leave an opening at its apex referred to as the **micropyle**. The micropyle opening allows the pollen tube to enter the ovule for fertilization. In gymnosperms (e.g. conifers), the pollen itself is drawn into the ovule and the micropyle opening closes after pollination. During germination, the seedling's radicle emerges through the micropyle.

Located opposite from the micropyle is the **chalaza** where the nucellus is joined to the integuments. Nutrients from the plant travel through the phloem of the vascular system to the funiculus and outer integument and from there apoplastically and symplastically through the chalaza to the nucellus inside the ovule. In chalazogamous plants, the pollen tubes enter the ovule through the chalaza instead of the micropyle opening.

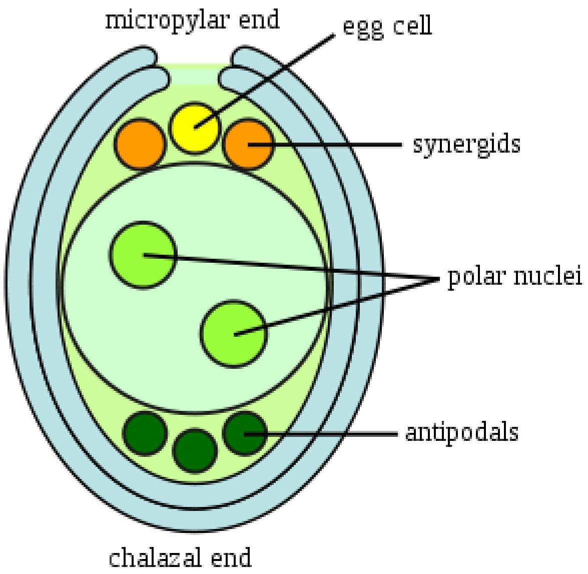
Nucellus, megaspore and perisperm

The **nucellus** (plural: nucelli) is the central portion of the ovule inside the integuments. It consists of diploid maternal tissue and has the function of a megasporangium. In immature ovules, it contains a megasporocyte (megaspore mother cell), which undergoes sporogenesis via meiosis. Three of the four haploid cells produced in meiosis degenerate, leaving one surviving megaspore inside the nucellus. After fertilization, the nucellus develops into the **perisperm** that feeds the embryo. In some plants, the diploid tissue of the nucellus can give rise to a seed through a mechanism of asexual reproduction called nucellar embryony.

Megagametophyte and embryo sac



Embryo sac formation of the genera *Polygonum* and *Lilium*. Triploid nuclei are shown as ellipses with three white dots. The first three columns show the meiosis of the megaspore, followed by 1-2 mitoses.



Ovule with embryo sac: egg cell (yellow), synergids (orange), central cell with two polar nuclei (bright green), and antipodals (dark green)

The haploid megaspore inside the nucellus gives rise to the female gametophyte (megagametophyte). In gymnosperms, the female gametophyte consists of around 2000 nuclei and forms archegonia which produce the egg cells for fertilization. In flowering plants, the megagametophyte, also referred to as **embryo sac**, is much smaller and typically consists of only seven cells and eight nuclei. The embryo sac develops from the megaspore through three rounds of mitotic divisions. The cell closest to the micropyle opening of the integuments differentiates into the egg cell, with two synergid cells by its side that may be involved in the production of signals that guide the pollen tube. Three antipodal cells form on the opposite (chalazal) end of ovule and later degenerate, serving no obvious function. The large central cell of the embryo sac contains two polar nuclei.

Zygote, embryo and endosperm

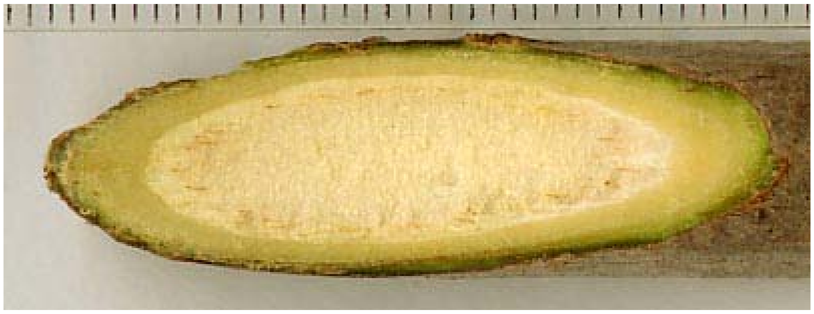
The pollen tube releases two sperm nuclei into the ovule. In gymnosperms, fertilization occurs within the archegonia produced by the female gametophyte. While it is possible that several egg cells are present and fertilized, typically only one zygote will develop into a mature embryo as the resources within the seed are limited.

In flowering plants, one sperm nucleus fuses with the egg cell into a zygote, the other fuses with the two polar nuclei of the central cell to give rise to the triploid endosperm. This double fertilization is unique to flowering plants. The plant stores nutrients such as starch, proteins and oils in the endosperm as a food source for the developing embryo and seedling, serving a similar function to the yolk of animal eggs. The endosperm is also called the albumen of the seed.

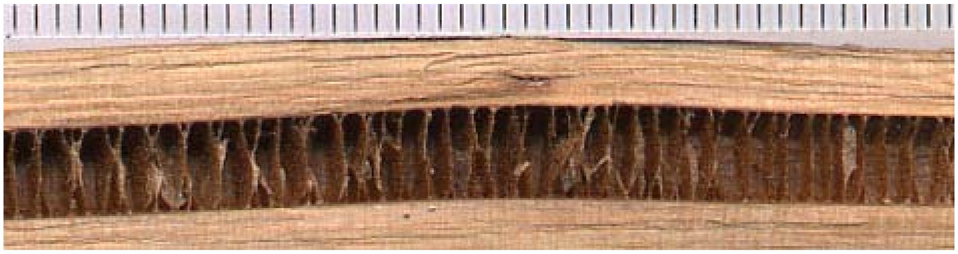
Chapter 9

Pith and Plant Cell

Pith



Elderberry shoot cut longitudinally to show the broad, solid pith (rough-textured, white) inside the wood (smooth, yellow-tinged). Scale in mm.



Walnut shoot cut longitudinally to show the chambered pith found in this genus. Scale in mm.

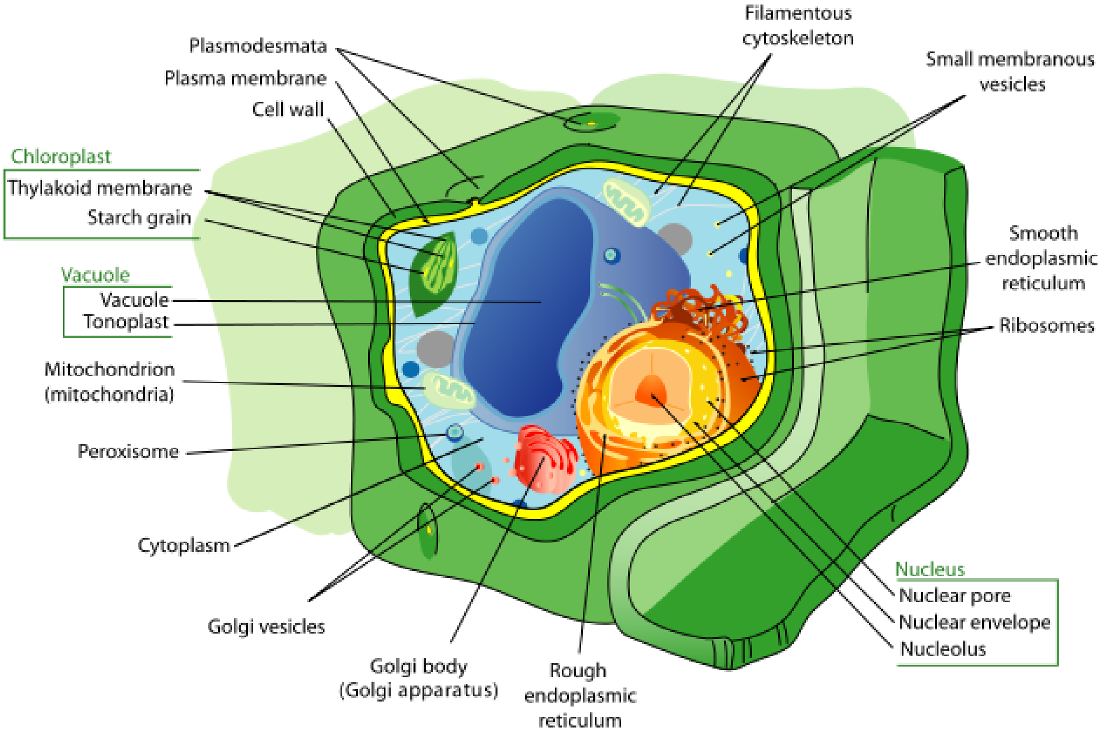
The tiny centre dark spot (about 1 mm diameter) in this yew wood is the pith

Pith - also called medulla - is a substance that is found in vascular plants. The two main functions of pith are nutrient storage and the transport of nutrients through the stem, branches, leaves, and roots of the plant. Pith is made up of soft, spongy parenchyma cells, and is located in the center of the stem in eudicots (both herbaceous and woody) and in the center of the roots in monocots. It is encircled by a ring of xylem (woody tissue), and outside that, a ring of phloem (bark tissue). In some plants the pith is solid, but for most it is soft.

While new pith growth is usually white or pale in color, as the tissue ages it commonly darkens to a deeper brown color. In trees pith is generally present in young growth, but in the trunk and older branches the pith often gets replaced - in great part - by xylem. In some plants, the pith in the middle of the stem may dry out and disintegrate, resulting in a hollow stem. A few plants, such as walnuts, have distinctive chambered pith with numerous short cavities. The cells in the peripheral parts of the pith may, in some plants, develop to be different from cells in the rest of the pith. This layer of cells is then called *the perimedullary region of the pithamus*. An example of this can be observed in *Hedera helix*, a species of ivy.

The term pith is also used to refer to the pale, spongy inner layer of the rind - more properly called mesocarp or albedo - of citrus fruits (such as oranges) and other hesperidia. The word comes from the Old English word *piþa*, meaning substance, akin to Middle Dutch *pitt*, meaning the pit of a fruit.

Plant cell



Plant cell structure

Plant cells are eukaryotic cells that differ in several key respects from the cells of other eukaryotic organisms. Their distinctive features include:

- A large central vacuole, a water-filled volume enclosed by a membrane known as the *tonoplast* maintains the cell's turgor, controls movement of molecules between the cytosol and sap, stores useful material and digests waste proteins and organelles.
- A cell wall composed of cellulose and hemicellulose, pectin and in many cases lignin, are secreted by the protoplast on the outside of the cell membrane. This contrasts with the cell walls of fungi (which are made of chitin), and of bacteria, which are made of peptidoglycan.

- Specialised cell-cell communication pathways known as plasmodesmata, pores in the primary cell wall through which the plasmalemma and endoplasmic reticulum of adjacent cells are continuous.

- Plastids, the notables one being the chloroplasts, which contain chlorophyll and the biochemical systems for light harvesting and photosynthesis, but also amyloplasts specialized for starch storage, elaioplasts specialized for fat storage, and chromoplasts specialized for synthesis and storage of pigments. As in mitochondria, which have a genome encoding 37 genes, plastids have their own genomes of about 100-120 unique genes and, it is presumed, arose as prokaryotic endosymbionts living in the cells of an early eukaryotic ancestor of the land plants and algae.

- Unlike animal cells, plant cells are stationary.

- Cell division by construction of a phragmoplast as a template for building a cell plate late in cytokinesis is characteristic of land plants and a few groups of algae, the notable one being the Charophytes and the Order Trentepohliales

- The sperm of bryophytes have flagellae similar to those in animals, but higher plants, (including Gymnosperms and flowering plants) lack the flagellae and centrioles that are present in animal cells.

Cell types

- Parenchyma cells are living cells that have diverse functions ranging from storage and support to photosynthesis and phloem loading (transfer cells). Apart from the xylem and phloem in its vascular bundles, leaves are composed mainly of parenchyma cells. Some parenchyma cells, as in the epidermis, are specialized for light penetration and focusing or regulation of gas exchange, but others are among the least specialized cells in plant tissue, and may remain totipotent, capable of dividing to produce new populations of undifferentiated cells, throughout their lives. Parenchyma cells have thin, permeable primary walls enabling the transport of small molecules between them, and their cytoplasm is responsible for a wide range of biochemical functions such as nectar secretion, or the manufacture of secondary products that discourage herbivory. Parenchyma cells that contain many chloroplasts and are concerned primarily with photosynthesis are called chlorenchyma cells. Others, such as the majority of the parenchyma cells in potato tubers and the seed cotyledons of legumes, have a storage function.

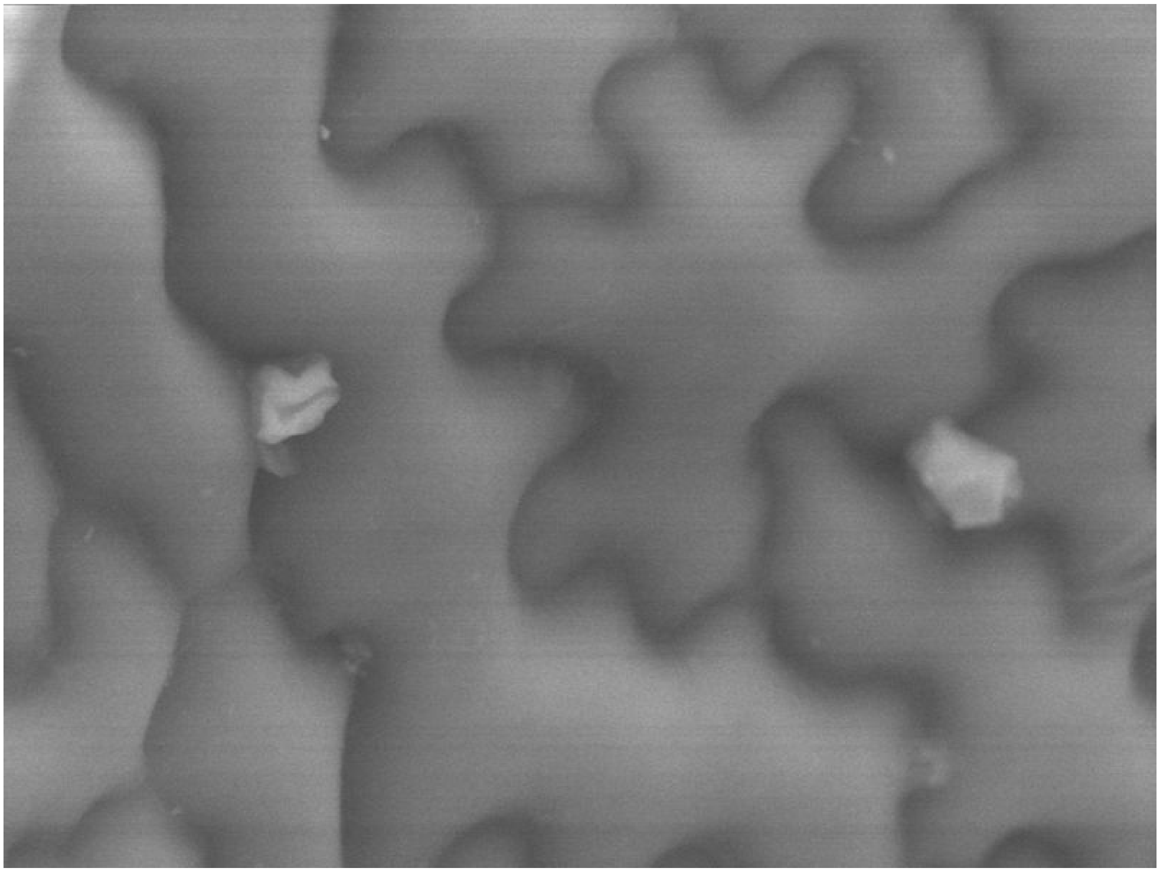
- Collenchyma cells - collenchyma cells are alive at maturity and have only a primary wall. These cells mature from meristem derivatives that initially resemble parenchyma, but differences quickly become apparent. Plastids do not develop, and the secretory apparatus (ER and Golgi) proliferates to secrete additional primary wall. The wall is most commonly thickest at the corners, where three or more cells come in contact, and thinnest where only two cells come in contact, though other arrangements of the wall thickening are possible.

Pectin and hemicellulose are the dominant constituents of collenchyma cell walls of dicotyledon angiosperms, which may contain as little as 20% of cellulose in *Petasites*. Collenchyma cells are typically quite elongated, and may divide transversely to give a septate appearance. The role of this cell type is to support the plant in axes still growing in length, and to confer flexibility and tensile strength on tissues. The primary wall lacks lignin that would make it tough and rigid, so this cell type provides what could be called plastic support - support that can hold a young stem or petiole into the air, but in cells that can be stretched as the cells around them elongate. Stretchable support (without elastic snap-back) is a good way to describe what collenchyma does. Parts of the strings in celery are collenchyma.

- Sclerenchyma cells - Sclerenchyma cells (from the Greek **skleros**, *hard*) are hard and tough cells with a function in mechanical support. They are of two broad types – sclereids or stone cells and fibres. The cells develop an extensive secondary cell wall that is laid down on the inside of the primary cell wall. The secondary wall is impregnated with lignin, making it hard and impermeable to water. Thus, these cells cannot survive for long' as they cannot exchange sufficient material to maintain active metabolism. Sclerenchyma cells are typically dead at functional maturity, and the cytoplasm is missing, leaving an empty central cavity.

Functions for sclereid cells (hard cells that give leaves or fruits a gritty texture) include discouraging herbivory, by damaging digestive passages in small insect larval stages, and physical protection (a solid tissue of hard sclereid cells form the pit wall in a peach and many other fruits). Functions of fibres include provision of load-bearing support and tensile strength to the leaves and stems of herbaceous plants. Sclerenchyma fibres are not involved in conduction, either of water and nutrients (as in the xylem) or of carbon compounds (as in the phloem), but it is likely that they may have evolved as modifications of xylem and phloem initials in early land plants.

Tissue types



cells of *Arabidopsis thaliana* epidermis

The major classes of cells differentiate from undifferentiated meristematic cells (analogous to the stem cells of animals) to form the tissue structures of roots, stems, leaves, flowers, and reproductive structures.

Xylem cells are elongated cells with lignified secondary thickening of the cell walls. Xylem cells are specialised for conduction of water, and first appeared in plants during their transition to land in the Silurian period more than 425 million years ago. The possession of xylem defines the vascular plants or Tracheophytes. Xylem tracheids are pointed, elongated xylem cells, the simplest of which have continuous primary cell walls and lignified secondary wall thickenings in the form of rings, hoops, or reticulate networks. More complex tracheids with valve-like perforations called bordered pits characterise the gymnosperms. The ferns and other pteridophytes and the gymnosperms have only xylem tracheids, while the angiosperms also have xylem vessels. Vessel members are hollow xylem cells aligned end-to-end, without end walls that are assembled into long continuous tubes. The bryophytes lack true xylem cells, but their sporophytes have a water-conducting tissue known as the hydrome that is composed of elongated cells of simpler construction.

Phloem is a specialised tissue for food conduction in higher plants. The conduction of food is a complex process that is carried in the plant with the help of special cell called phloem cells. These cells conduct inter- and intra-cellular fluid (food - proteins and other essential elements required by the plant for its metabolism) through the process of osmosis. This phenomenon is called ascent of sap in plants. Phloem consists of two cell types, the sieve tubes and the intimately-associated companion cells. The sieve tube elements lack nuclei and ribosomes, and their metabolism and functions are regulated by the adjacent nucleate companion cells. Sieve tubes are joined end-to-end with perforate end-plates between known as *sieve plates*, which allow transport of photosynthate between the sieve elements. The companion cells, connected to the sieve tubes via plasmodesmata, are responsible for loading the phloem with sugars. The bryophytes lack phloem, but moss sporophytes have a simpler tissue with analogous function known as the leptome.

Plant epidermal cells are specialised parenchyma cells covering the external surfaces of leaves, stems and roots. The epidermal cells of aerial organs arise from the superficial layer of cells known as the *tunica* (L1 and L2 layers) that covers the plant shoot apex, whereas the cortex and vascular tissues arise from innermost layer of the shoot apex known as the *corpus* (L3 layer). The epidermis of roots originates from the layer of cells immediately beneath the root cap.

The epidermis of all aerial organs, but not roots, is covered with a cuticle made of waxes and the polyester cutin. Several cell types may be present in the epidermis. Notable among these are the stomatal guard cells, glandular and clothing hairs or trichomes, and the root hairs of primary roots. In the shoot epidermis of most plants, only the guard cells have chloroplasts. The epidermal cells of the primary shoot are thought to be the only plant cells with the biochemical capacity to synthesize cutin.

Organelles

- Cell membrane
- Cell wall
- Nuclear membrane
- Plasmodesma
- Vacuole
- Plastids
- Chloroplast
- Leucoplast
- Chromoplast
- Golgi Bodies
- Ribosome
- Endoplasmic reticulum
- Mitochondrion
- Lysosome
- Cytoplasm
- Nucleus

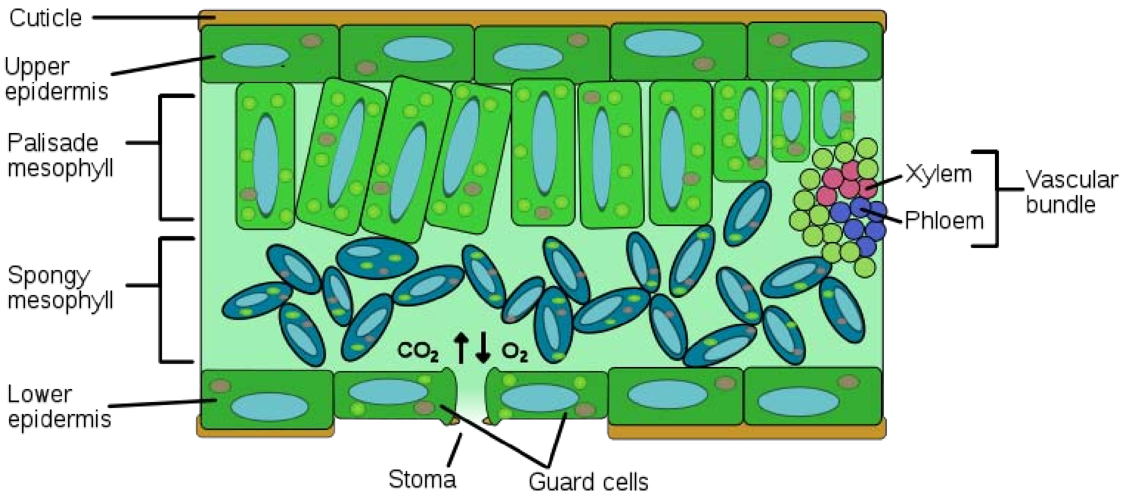
- DNA
- Chromatin
- RNA
- Cytoskeleton
- Nucleolus

Chapter 10

Plant Cuticle and Rhizome

Plant cuticle

Water beads on the waxy cuticle of kale leaves



Anatomy of a leaf

Plant cuticles are a protective waxy covering produced only by the epidermal cells of leaves, young shoots and all other aerial plant organs without periderm. The cuticle tends to be thicker on the top of the leaf, but is not always thicker in xerophytic plants living in dry climates than in mesophytic plants from wetter climates, despite a persistent myth to that effect.

The cuticle is composed of an insoluble cuticular membrane impregnated by and covered with soluble waxes. Cutin, a polyester polymer composed of inter-esterified omega hydroxy acids which are cross-linked by ester and epoxide bonds, is the best-known structural component of the cuticular membrane. The cuticle can also contain a non-saponifiable hydrocarbon polymer known as Cutan. The cuticular membrane is impregnated with cuticular waxes and covered with epicuticular waxes, which are mixtures of hydrophobic aliphatic compounds, hydrocarbons with chain lengths typically in the range C16 to C36.

The plant cuticle is one of a series of innovations, together with stomata, xylem and phloem and intercellular spaces in stem and later leaf mesophyll tissue, that plants evolved more than 450 million years ago during the transition between life in water and life on land. Together, these features enabled plant shoots exploring aerial environments to conserve water by internalising the gas exchange surfaces, enclosing them in a waterproof membrane and providing a variable-aperture control mechanism, the stomatal guard cells, which regulate the rates of transpiration and CO_2 exchange.

In addition to its function as a permeability barrier for water and other molecules, the micro and nano-structure of the cuticle confer specialised surface properties that prevent contamination of plant tissues with external water, dirt and microorganisms. Many plants, such as the leaves of the sacred lotus (*Nelumbo nucifera*) exhibit ultra-hydrophobic and self-cleaning properties that have been described by Barthlott and Neinhuis (1997). The lotus effect has potential uses in biomimetic technical materials.

"The waxy sheet of cuticle also functions in defense, forming a physical barrier that resists penetration by virus particles, bacterial cells, and the spores or growing filaments of fungi".

Rhizome

A harvested ginger rhizome

A Euphorbia plant sending out rhizomes

In botany and dendrology, a **rhizome** (from Ancient Greek: *rhízōma* "mass of roots", from *rhizóō* "cause to strike root") is a characteristically horizontal stem of a plant that is usually found underground, often sending out roots and shoots from its nodes. Rhizomes may also be referred to as **creeping rootstalks** or **rootstocks**.

If a rhizome is separated into pieces, each piece may be able to give rise to a new plant. This is a process known as vegetative reproduction and is used by farmers and gardeners to propagate certain plants. Examples of plants that are propagated this way include hops, asparagus, ginger, irises, Lily of the Valley, Cannas, and sympodial orchids.

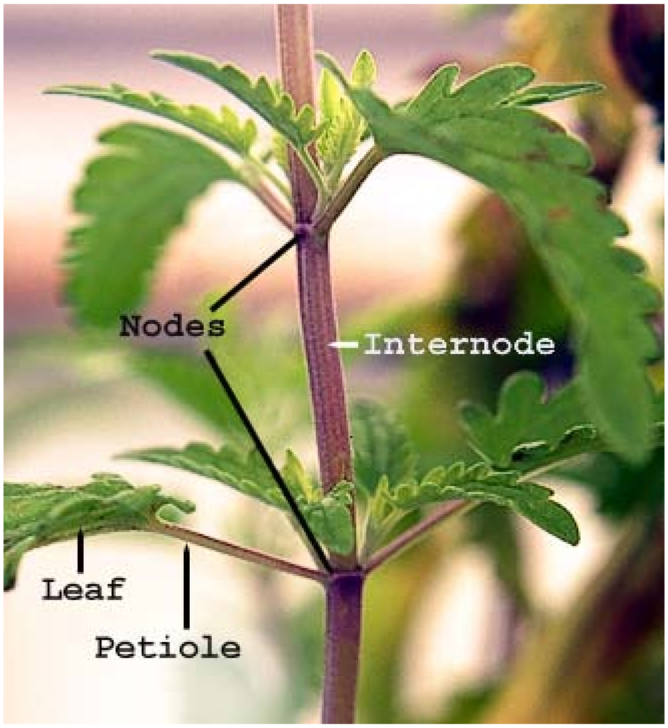
The Quaking Aspen (*Populus tremuloides*) is an example of a tree that propagates using a rhizome. Aspen clonal colonies in the American West, such as the large Pando colony in Utah, may have been living for over 1 million years. The rhizome of an aspen colony is the key to its longevity. Foragers, insects, fungus, and forest fires may destroy the above-ground portion of the tree, but the underground rhizome is somewhat protected against these threats.

A stolon is similar to a rhizome, but, unlike a rhizome, which is the main stem of the plant, a stolon sprouts from an existing stem, has long internodes, and generates new shoots at the end, such as in the strawberry plant. In general, rhizomes have short internodes; they send out roots from the bottom of the nodes and new upward-growing shoots from the top of the nodes. It is a method of reproduction for plants. A stem tuber is a thickened part of a rhizome or stolon that has been enlarged for use as a storage organ. In general, a tuber is high in starch, for example, the common potato, which is a modified stolon. The term tuber is often used imprecisely, and is sometimes applied to plants with rhizomes.

Some plants have rhizomes that grow above ground or that lie at the soil surface, including some *Iris* species, and ferns, whose spreading stems are rhizomes. Plants with underground rhizomes include gingers, bamboo, the Venus Flytrap, Chinese lantern, Western poison-oak, hops, and Alstroemeria, and the weeds Johnson grass, bermuda grass, and purple nut sedge. Rhizomes generally form a single layer, but in Giant Horsetails, can be multi-tiered.

Chapter 11

Plant Stem



Stem showing internode and nodes plus leaf petioles

A **stem** is one of two main structural axes of a vascular plant. The stem is normally divided into nodes and internodes, the nodes hold buds which grow into one or more leaves, inflorescence (flowers), cones or other stems etc. The internodes distance one node from another. The term shoots is often confused with stems; shoots generally refer to new fresh plant growth and does include stems but also to other structures like leaves or flowers. The other main structural axis of plants is the root. In most plants stems are located above the soil surface but some plants have underground stems. A stem develops buds and shoots and usually grows above the ground. Inside the stem, materials move up and down the tissues of the transport system.

Stems have four main functions which are:

- Support for and the elevation of leaves, flowers and fruits. The stems keep the leaves in the light and provide a place for the plant to keep its flowers and fruits.
- Transport of fluids between the roots and the shoots in the xylem and phloem.
- Storage of nutrients.
- The production of new living tissue. The normal life span of plant cells is one to three years. Stems have cells called meristems that annually generate new living tissue.

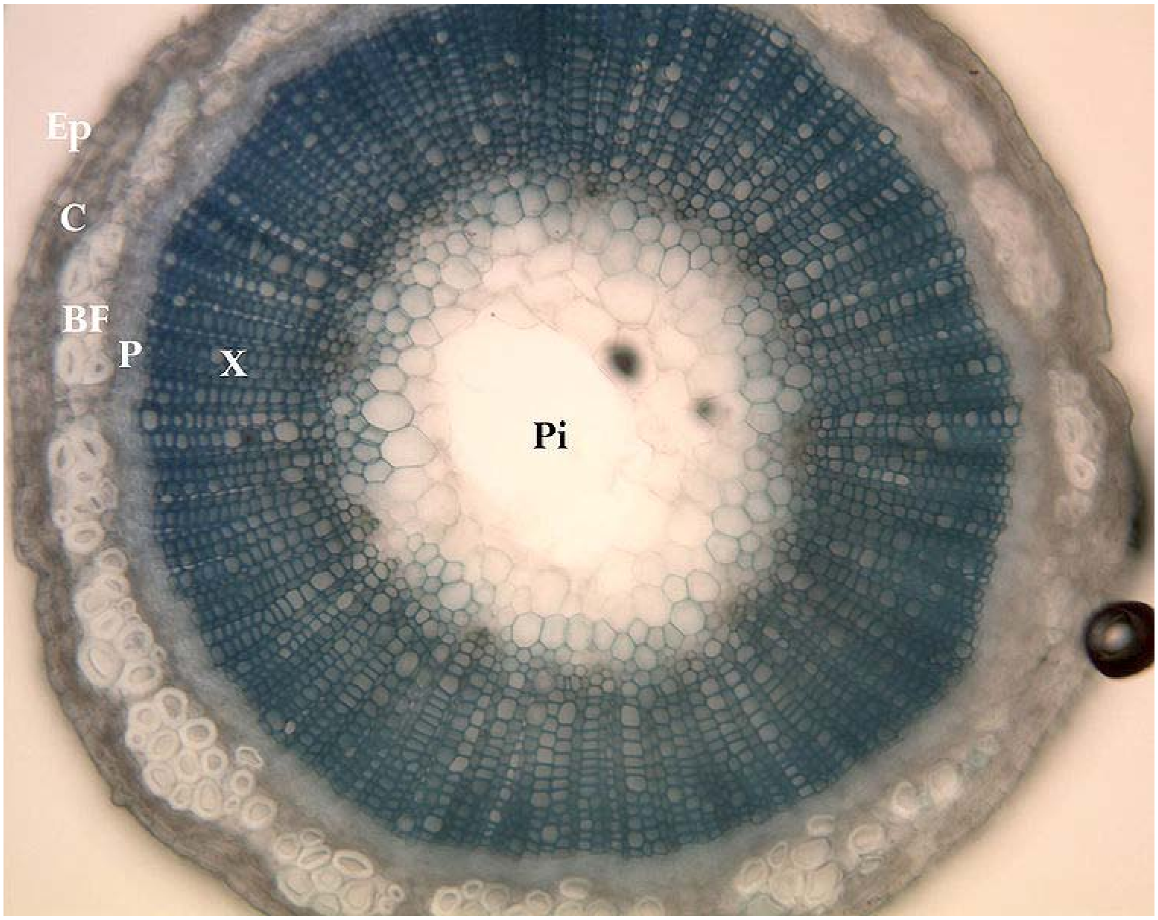
Specialized terms for stems

Stems are often specialized for storage, asexual reproduction, protection or photosynthesis, including the following:

- Acaulescent - used to describe stems in plants that appear to be stemless. Actually these stems are just extremely short, the leaves appearing to rise directly out of the ground, e.g. some *Viola* species.
- Arborescent - tree like with woody stems normally with a single trunk.
- Bud - an embryonic shoot with immature stem tip.
- Bulb - a short vertical underground stem with fleshy storage leaves attached, e.g. onion, daffodil, tulip. Bulbs often function in reproduction by splitting to form new bulbs or producing small new bulbs termed bulblets. Bulbs are a combination of stem and leaves so may better be considered as leaves because the leaves make up the greater part.
- Caespitose - when stems grow in a tangled mass or clump or in low growing mats.
- Cladophyll - a flattened stem that appears leaf like and is specialized for photosynthesis, e.g. asparagus, cactus pads.
- Climbing - stems that cling or wrap around other plants or structures.
- Corm - a short enlarged underground, storage stem, e.g. taro, crocus, gladiolus.
- Decumbent - stems that lie flat on the ground and turn upwards at the ends.
- Fruticose - stems that grow shrub like with woody like habit.
- Herbaceous - non woody, they die at the end of the growing season.
- Pseudostem - a false stem made of the rolled bases of leaves, which may be 2 or 3 m tall as in banana
- Rhizome - a horizontal underground stem that functions mainly in reproduction but also in storage, e.g. most ferns, iris
- Runner (plant part) - a type of stolon, horizontally growing on top of the ground and rooting at the nodes, aids in reproduction. e.g. strawberry, spider plant.
- Scape - a stem that holds flowers that comes out of the ground and has no normal leaves. Hosta, Lily, Iris.
- Stolon - a horizontal stem that produces rooted plantlets at its nodes and ends, forming near the surface of the ground.
- Spine - a modified leaf with a sharp point and rounded shape, used for protection against animals. e.g. honey locust, hawthorn.

- Thorn - a modified stem protruding from the axils of a plant. Used for protection against animals, though animals have adapted. (i.e. an animal will have a long tongue to reach past the thorns)
- Tree - a woody stem that is longer than 5 meters with a main trunk.
- Tuber - a swollen, underground storage stem adapted for storage and reproduction, e.g. potato.
- Woody - hard textured stems with secondary xylem.

Stem structure



Flax stem cross-section, showing locations of underlying tissues. Ep = epidermis; C = cortex; BF = bast fibres; P = phloem; X = xylem; Pi = pith

Stem usually consist of three tissues, dermal tissue, ground tissue and vascular tissue. The dermal tissue covers the outer surface of the stem and usually functions to waterproof, protect and control gas exchange. The ground tissue usually consists mainly of parenchyma cells and fills in around the vascular tissue. It sometimes functions in photosynthesis. Vascular tissue provides long distance transport and structural support. Most or all ground tissue may be lost in woody stems. The dermal tissue of aquatic plants stems may lack the waterproofing found in aerial stems. The arrangement of the vascular tissues varies widely among plant species.

Dicot stems

Dicot stem with primary growth have pith in the center, with vascular bundles forming a distinct ring visible when the stem is viewed in cross section. The outside of the stem is covered with an epidermis, which is covered by a waterproof cuticle. The epidermis also may contain stomata for gas exchange and multicellular stem hairs. A cortex consisting of Hypodermis (collenchyma cells) and Endodermis (starch containing cells)is present above the pericycle and vascular bundles.

Woody dicots and many nonwoody dicots have secondary growth originating from their lateral or secondary meristems: the vascular cambium and the cork cambium or phellogen. The vascular cambium forms between the xylem and phloem in the vascular bundles and connects to form a continuous cylinder. The vascular cambium cells divide to produce secondary xylem to the inside and secondary phloem to the outside. As the stem increases in diameter due to production of secondary xylem and secondary phloem, the cortex and epidermis are eventually destroyed. Before the cortex is destroyed, a cork cambium develops there. The cork cambium divides to produce waterproof cork cells externally and sometimes phelloderm cells internally. Those three tissues form the periderm, which replaces the epidermis in function. Areas of loosely packed cells in the periderm that function in gas exchange are called lenticels.

Secondary xylem is commercially important as wood. The seasonal variation in growth from the vascular cambium is what creates yearly tree rings in temperate climates. Tree rings are the basis of dendrochronology, which dates wooden objects and associated artifacts. Dendroclimatology is the use of tree rings as a record of past climates. The aerial stem of an adult tree is called a trunk. The dead, usually darker inner wood of a large diameter trunk is termed the heartwood and is the result of tylosis. The outer, living wood is termed the sapwood.

Monocot stems

Stems of two *Roystonea regia* palms showing characteristic bulge, leaf scars and fibrous roots, Kolkata, India

Vascular bundles are present throughout the monocot stem, although concentrated towards the outside. This differs from the dicot stem that has a ring of vascular bundles and often none in the center. The shoot apex in monocot stems is more elongated. Leaf sheathes grow up around it, protecting it. This is true to some extent of almost all monocots. Monocots rarely produce secondary growth and are therefore seldom woody, with Palms and Bamboo being notable exceptions. However, many monocot stems increase in diameter via anomalous secondary growth.

Gymnosperm stems

The trunk of this redwood tree is its stem.

Tasmanian tree fern

All gymnosperms are woody plants. Their stems are similar in structure to woody dicots except that most gymnosperms produce only tracheids in their xylem, not the vessels found in dicots. Gymnosperm wood also often contains resin ducts. Woody dicots are called hardwoods, e.g. oak, maple and walnut. In contrast, softwoods are gymnosperms, such as pine, spruce and fir.

Fern stems

Most ferns have rhizomes with no vertical stem. The exception is tree ferns, with vertical stems up to about 20 meters. The stem anatomy of ferns is more complicated than that of dicots because fern stems often have one or more leaf gaps in cross section. A leaf gap is where the vascular tissue branches off to a frond. In cross section, the vascular tissue does not form a complete cylinder where a leaf gap occurs. Fern stems may have solenosteles or dictyosteles or variations of them. Many fern stems have phloem tissue on both sides of the xylem in cross-section. .

Relation to xenobiotics

Foreign chemicals such as air pollutants, herbicides and pesticides can damage stem structures. In the case of herbicides many chemicals act by surficial effects, and other agents cause damage through uptake of the chemical herbicide, which is typically a complex organic chemical.

Economic importance

White and green asparagus - crispy stems are the edible parts of this vegetable

There are thousands of species whose stems have economic uses. Stems provide a few major staple crops such as potato and taro. Sugarcane stems are a major source of sugar. Maple sugar is obtained from trunks of maple trees. Vegetables from stems are asparagus, bamboo shoots, cactus pads or nopalitos, kohlrabi, and water chestnut. The spice, cinnamon is bark from a tree trunk. Cellulose from tree trunks is a food additive in bread, grated Parmesan cheese, and other processed foods. Gum arabic is an important food additive obtained from the trunks of *Acacia senegal* trees. Chicle, the main ingredient in chewing gum, is obtained from trunks of the chicle tree.

Medicines obtained from stems include quinine from the bark of cinchona trees, camphor distilled from wood of a tree in the same genus that provides cinnamon, and the muscle relaxant curare from the bark of tropical vines.

Wood is a used in thousands of ways, e.g. buildings, furniture, boats, airplanes, wagons, car parts, musical instruments, sports equipment, railroad ties, utility poles, fence posts, pilings, toothpicks, matches, plywood, coffins, shingles, barrel staves, toys, tool handles, picture frames, veneer, charcoal and firewood. Wood pulp is widely used to make paper, paperboard, cellulose sponges, cellophane and some important plastics and textiles, such as cellulose acetate and rayon. Bamboo stems also have hundreds of uses, including paper, buildings, furniture, boats, musical instruments, fishing poles, water pipes, plant stakes, and scaffolding. Trunks of palm trees and tree ferns are often used for building. Reed stems are also important building materials in some areas.

Tannins used for tanning leather are obtained from the wood of certain trees, such as quebracho. Cork is obtained from the bark of the cork oak. Rubber is obtained from the trunks of *Hevea brasiliensis.* Rattan, used for furniture and baskets, is made from the stems of tropical vining palms. Bast fibers for textiles and rope are obtained from stems include flax, hemp, jute and ramie. The earliest paper was obtained from the stems of papyrus by the ancient Egyptians.

Amber is fossilized sap from tree trunks; it is used for jewelry and may contain ancient animals. Resins from conifer wood are used to produce turpentine and rosin. Tree bark is often used as a mulch and in growing media for container plants. It also can become the natural habitat of lichens.

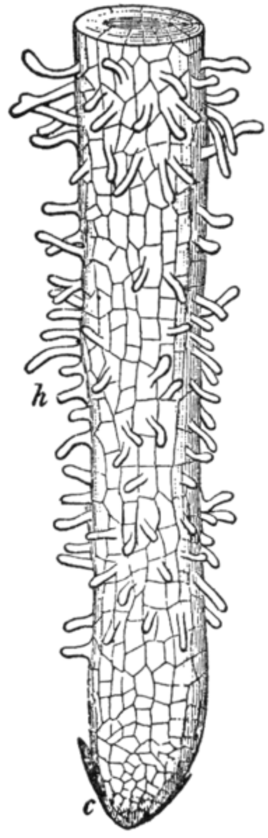
Some ornamental plants are grown mainly for their attractive stems, e.g.:

- White bark of paper birch
- Twisted branches of corkscrew willow and Harry Lauder's walking stick (*Corylus avellana* 'Contorta')
- Red, peeling bark of paperbark maple

Chapter 12

Root Hair and Sieve Tube Element

Root hair



Root-tip, showing young root-hairs

A **root hair**, the rhizoid of a vascular plant, is a tubular outgrowth of a trichoblast, a hair-forming cell on the epidermis of a plant root. That is, root hairs are lateral extensions of a single cell and only rarely branched, thus invisible to the naked eye. They are found only in the region of maturation of the root. Just prior to the root hair cell development, there is a point of elevated phosphorylase activity.

Formation

Root hairs are usually an outgrowth of a single epidermal cell. Root hair cells vary between 5 and 17 micrometres in diameter, and 80 to 1,500 micrometres in length (Dittmar, cited in Esau, 1965).

Importance

Root hairs form an important surface over which plants absorb most of their water and nutrients. They are also directly involved in the formation of root nodules in legume plants.

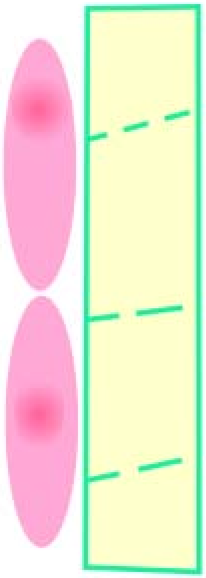
They have a large surface area, relative to the other cells, that helps them absorb water using osmosis and minerals more efficiently.

Survival

Root hair cells can survive for 2 to 3 weeks and then die off. At the same time new root hair cells are continually being formed at the top of the root. This way, the root hair coverage stays the same. When a new root hair cell grows, it excretes a poison so that the other cells in close proximity to it are unable to grow one of these hairs. This ensures equal and efficient distribution of the actual hairs on these cells.

It is, therefore, understandable that repotting must be done with care, because the root hair cells are pulled off for the most part. This is why planting-out leaves the plant withered for some time.

Sieve tube element



Proton gradient: Solid green: sieve tube; dashed green: sieve tube plates; light pink: companion cell; dark pink: nucleus; yellow: nutrients

Sieve tubes are mainly to transport sugars and nutrients up and down the plant. In plant anatomy, **sieve vascular tissue tube elements**, also called **sieve tube members**, are a type of elongated parenchyma cells in phloem tissue. At the ends these cells are connected with other sieve elements, and together they constitute the **sieve tube**. The main function of the sieve tube is transport of carbohydrates in the plant (e.g., from the leaves to the fruits and roots). Unlike vessel elements, which are elongated cells that transport water and minerals in the xylem/wood that are dead when mature, and represent another kind of vascular tissue in the plant, sieve elements are living cells. They are thick and circular and can be different colours. Sieve tubes are not known as 'Real Cells' as they lack a substantial amount of cytoplasm.

At the interface between two sieve tube members in angiosperms are **sieve plates**, pores in the plant cell walls that facilitate the movement of liquid. Neighbouring each of the sieve tube elements is a minimum of one companion cell, connected by plasmodesmata (channels between the cells). Sieve tube members have no cell nucleus, ribosomes, or a vacuole, the nucleus and ribosomes of its companion cell(s) compensate for this. In leaves, these cells help in moving the sugar produced by photosynthesis in the mesophyll tissue into the sieve tube elements.

Sieve cells are long, slender, conducting cells of the secondary phloem that do not form a constituent element of a sieve tube, but which are provided with relatively unspecialized sieve areas, especially in the tapering ends of the cells that overlap those of other sieve cells. They have a narrower diameter and are more elongated compared to sieve tube members, the other kind of sieve elements present in the phloem. Sieve cells are associated with albuminous cells, which lack starch, thus making it possible to differentiate them from phloem parenchyma.

The forest botanist Theodor Hartig was the first to discover and name these cells as *Siebfasern* (sieve fibres) and *Siebröhren* (sieve tubes) in 1837.

Chapter 13

Stele (Biology) and Suberin

Stele (biology)

In a vascular plant, the **stele** is the central part of the root or stem containing the tissues derived from the procambium. These include vascular tissue, in some cases ground tissue (pith) and a pericycle, which, if present, defines the outermost boundary of the stele. The endodermis is the innermost cell layer of the cortex.

The concept of the stele was developed in the late 19th century by French botanists P. E. L. van Tieghem and H. Doultion as a model for understanding the relationship between the shoot and root, and for discussing the evolution of vascular plant morphology. Now, at the beginning of the 21st century, plant molecular biologists are coming to understand the genetics and developmental pathways that govern tissue patterns in the stele.

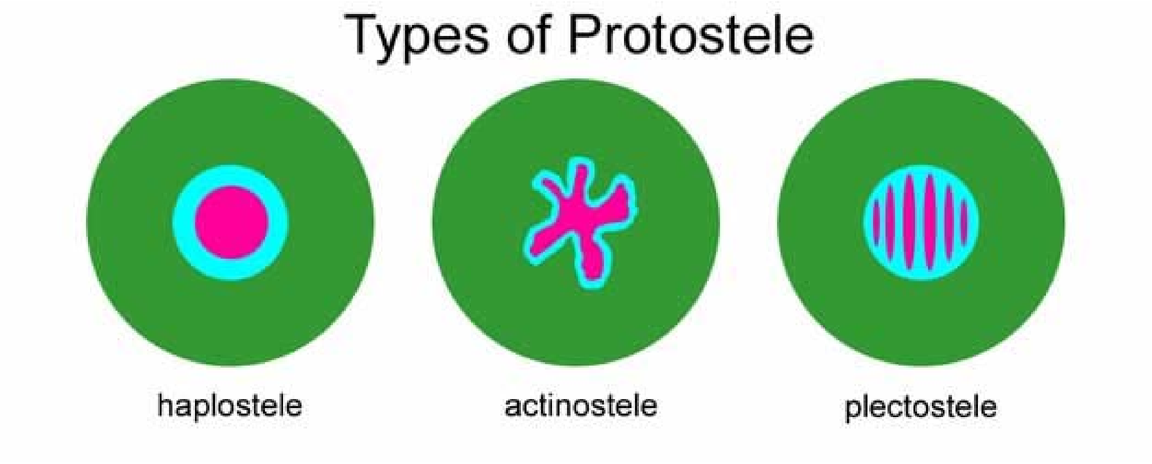
Protostele

The earliest vascular plants had stems with a central core of vascular tissue. This consisted of a cylindrical strand of xylem , surrounded by a region of phloem. Around the vascular tissue there might have been an endodermis that regulated the flow of water into and out of the vascular system. Such an arrangement is termed a **protostele**.

There are three basic types of protosteles:

- **haplostele** - consisting of a cylindrical core of xylem surrounded by a ring of phloem. An endodermis generally surrounds the stele. A centrarch (protoxylem in the center of a metaxylem cylinder) haplostele is prevalent in members of the rhyniophyte grade, such as *Rhynia*.
- **actinostele** - a variation of the protostele in which the core is lobed or fluted. This stele is found in many species of club moss (*Lycopodium* and related genera). Actinosteles are typically exarch (protoxylem external to the metaxylem) and consist of several to many patches of protoxylem at the tips of the lobes of the metaxylem. Exarch protosteles are a defining characteristic of the lycophyte lineage.
- **plectostele** - a protostele in which plate-like regions of xylem appear in transverse section surrounded by phloem tissue. In fact, these discrete plates are

interconnected in longitudinal section. Some modern club mosses have plectosteles in their stems. The plectostele may be derived from the actinostele.



Siphonostele

Siphonosteles have a region of ground tissue called the pith internal to xylem. The vascular strand comprises a cylinder surrounding the pith. Siphonosteles often have interruptions in the vascular strand where leaves (typically megaphylls) originate (called leaf gaps).

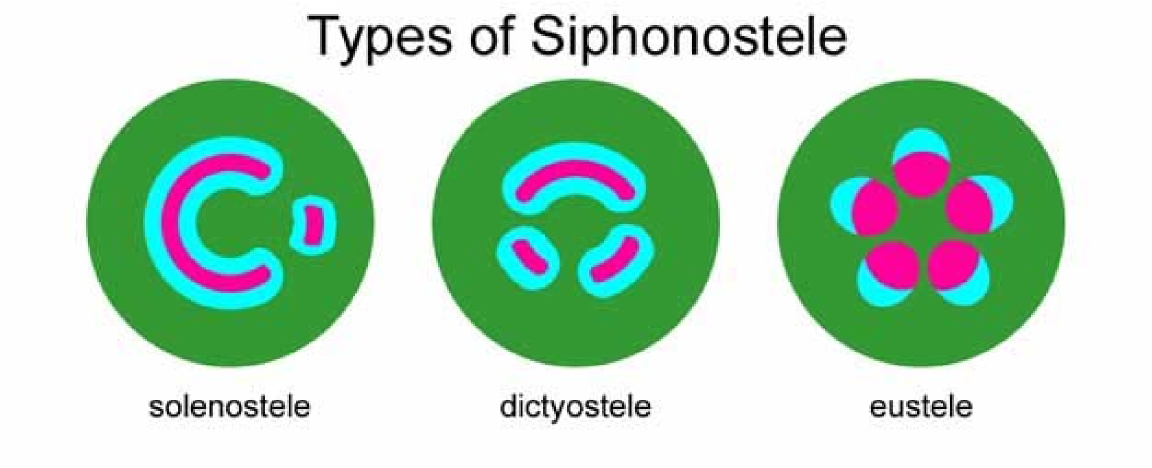
Siphonosteles can be ectophloic (phloem present only external to the xylem) or they can be amphiphloic (with phloem both external and internal to the xylem. Among living plants, many ferns and some Asterid flowering plants have an amphiphloic stele.

An amphiphloic siphonostele can be called a:

- **solenostele** - if the cylinder of vascular tissue contains no more than one leaf gap in any transverse section (i.e. has non-overlapping leaf gaps). This type of stele is primarily found in fern stems today.
- **dictyostele** - if multiple gaps in the vascular cylinder exist in any one transverse section. The numerous leaf gaps and leaf traces give a dictyostele the appearance of many isolated islands of xylem surrounded by phloem. Each of the apparently isolated units of a dictyostele can be called a meristele. Among living plants, this type of stele is found only in the stems of ferns.

Most seed plant stems possess a vascular arrangement which has been interpreted as a derived siphonostele, and is called a

- **eustele** - in this arrangement, the primary vascular tissue consists of vascular bundles, usually in one or two rings around the pith. In addition to being found in stems, the eustele appears in the roots of monocot flowering plants. The vascular bundles in a eustele can be collateral (with the phloem on only one side of the xylem) or bicollateral (with phloem on both sides of the xylem, as in some Solanaceae).



There is also a variant on the **eustele** found in monocots like maize and rye. The variation has numerous scattered bundles in the stem and is called an **atactostele**. However, it is really just a variant of the eustele.

Suberin

Suberin is a waxy substance found in higher plants. Suberin is a main constituent of cork, and is named after the Cork Oak, *Quercus suber*.

Anatomy and physiology

Suberin is highly hydrophobic and a somewhat, 'rubbery' material. Its main function is to prevent water from penetrating the tissue. In roots suberin is deposited in the radial and transverse cell walls of the endodermal cells. This structure is known as the Casparian strip or Casparian band. Its function is to prevent water and nutrients taken up by the root from entering the stele via the neoplastic. Instead, water must traverse the endodermis through the symplast. This allows the plant to select the solutes that pass further into the plant. It thus forms an important barrier to harmful solutes. Mangroves use suberin to minimize salt intake from their littoral habitat, for example.

Suberin is found in the phellem layer of the periderm (or cork). This is outermost layer of the bark. The cells in this layer are dead and abundant in suberin, preventing water loss from the tissues below. Suberin can also be found in various other plant structures. For example, the net structure in the rind of a netted melon is suberin.

Structure and biosynthesis

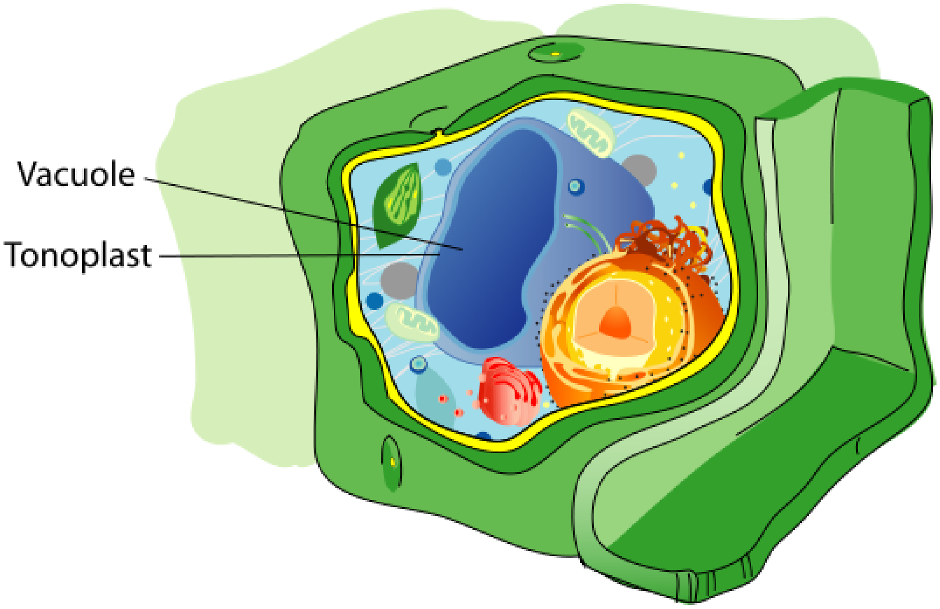
Suberin consists of two domains, a polyaromatic and a polyaliphatic domain. The polyaromatics are predominantly located within the primary cell wall, and the polyaliphatics are located between the primary cell wall and the plasmalemma. The two domains are supposed to be cross-linked. The exact qualitative and quantitative composition of suberin monomers varies in different species. Some common aliphatic monomers include α-hydroxyacids (mainly 18-hydroxyoctadec-9-enoic acid) and α,ω-diacids (mainly octadec-9-ene-1,18-dioic acid). The monomers of the polyaromatics are hydroxycinnamic acids and derivatives, such as feruloyltyramine.

In addition to the aromatics and aliphatics components, glycerol has been reported a major suberin component in some species. The role of glycerol is proposed to interlink aliphatic monomers, and possibly also to link polyaliphatics to polyaromatics, during suberin polymer assembly. The polymerization step of aromatic monomers has been shown to involve a peroxidase reaction.

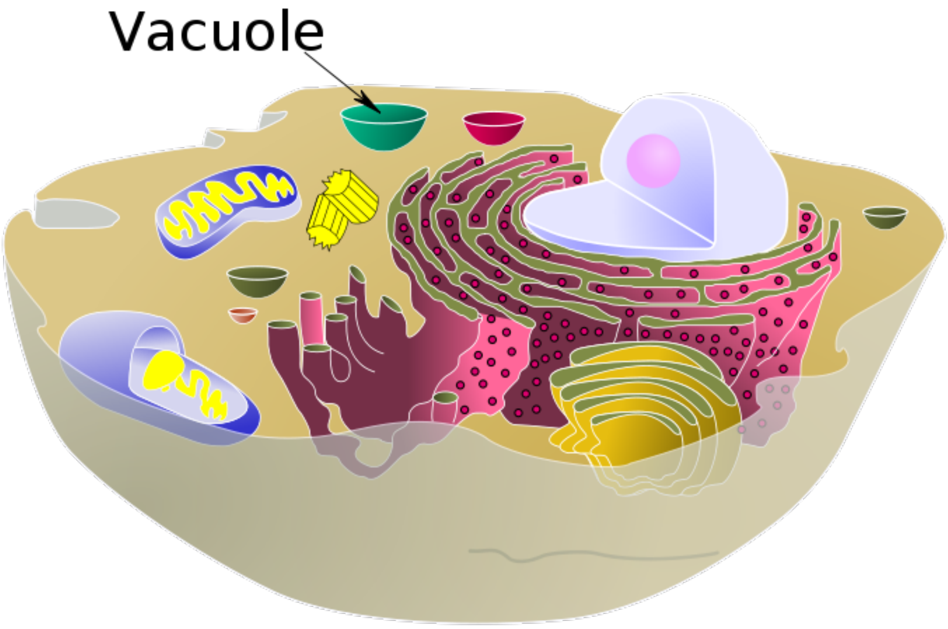
The biosynthesis of the aliphatic monomers shares the same upstream reactions with cutin biosynthesis, and the biosynthesis of aromatics shares the same upstream reactions with lignin biosynthesis. Lignin and suberin are the only known biological polymers that are irregular.

Chapter 14

Vacuole



Plant cell structure



Animal cell structure

A **vacuole** is a membrane-bound organelle which is present in all plant and fungal cells and some protist, animal and bacterial cells. Vacuoles are essentially enclosed compartments which are filled with water containing inorganic and organic molecules including enzymes in solution, though in certain cases they may contain solids which have been engulfed. Vacuoles are formed by the fusion of multiple membrane vesicles and are effectively just larger forms of these. The organelle has no basic shape or size, its structure varies according to the needs of the cell.

The function and importance of vacuoles varies greatly according to the type of cell in which they are present, having much greater prominence in the cells of plants, fungi and certain protists than those of animals and bacteria. In general, the functions of the vacuole include:

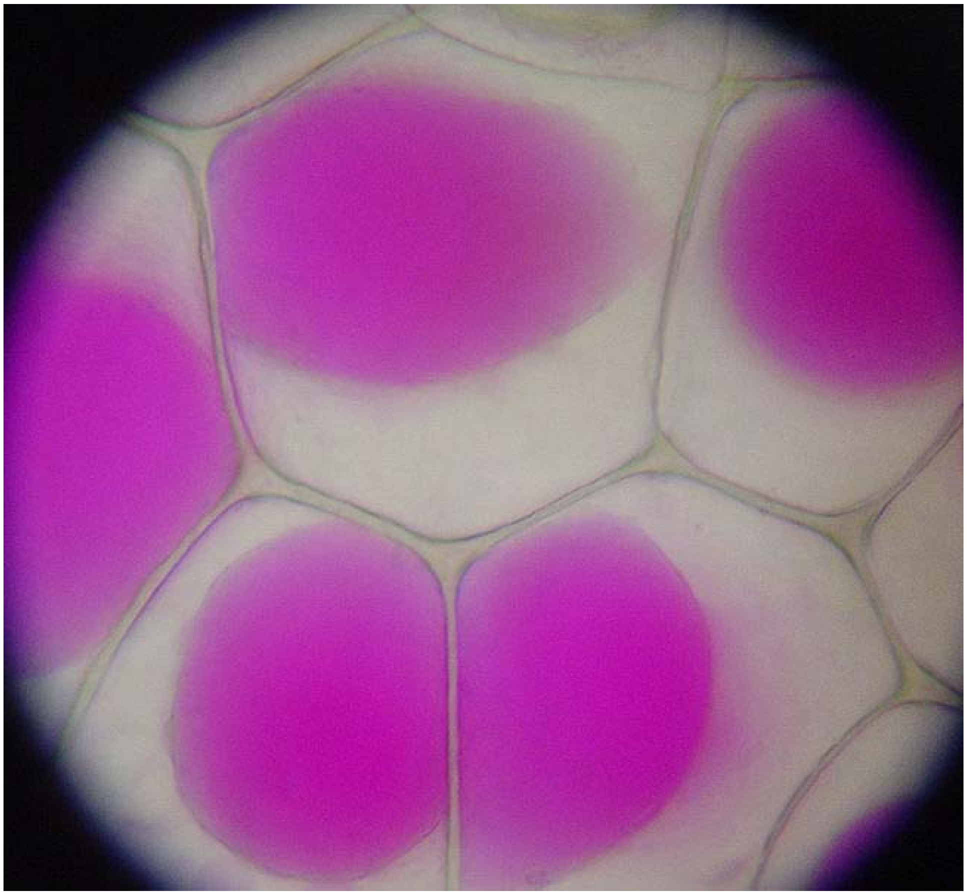
- Isolating materials that might be harmful or a threat to the cell
- Containing waste products
- Containing water in plant cells
- Maintaining internal hydrostatic pressure or turgor within the cell
- Maintaining an acidic internal pH
- Containing small molecules
- Exporting unwanted substances from the cell
- Allows plants to support structures such as leaves and flowers due to the pressure of the central vacuole
- In seeds, stored proteins needed for germination are kept in 'protein bodies', which are modified vacuoles.

Vacuoles also play a major role in autophagy, maintaining a balance between biogenesis (production) and degradation (or turnover), of many substances and cell structures in certain organisms. They also aid in the lysis and recycling of misfolded proteins that have begun to build up within the cell. Thomas Boller and others proposed that the vacuole participates in the destruction of invading bacteria and Robert B Mellor proposed organ-specific forms have a role in 'housing' symbiotic bacteria. In protists, vacuoles have the additional function of storing food which has been absorbed by the organism and assisting in the digestive and waste management process for the cell.

Bacteria

Large vacuoles are found in three genera of filamentous sulfur bacteria, the *Thioploca*, *Beggiatoa* and *Thiomargarita*. The cytosol is extremely reduced in these genera and the vacuole can occupy between 40-98% of the cell. The vacuole contains high concentrations of nitrate ions and is therefore thought to be a storage organelle.

Plants



The anthocyanin-storing vacuoles of *Rhoeo spathacea*, a spiderwort, in cells that have plasmolyzed

Most mature plant cells have one large central vacuole that typically occupies more than 30% of the cell's volume, and that can occupy as much as 80% of the volume for certain cell types and conditions. Strands of cytoplasm often run through the vacuole.

A vacuole is surrounded by a membrane called the **tonoplast** (word origin: Gk tón(os) + -o-, meaning “stretching”, “tension”, “tone” + comb. form repr. Gk plastós formed, molded). Also called the **vacuolar membrane**, the tonoplast is the cytoplasmic membrane surrounding a vacuole, separating the vacuolar contents from the cell's cytoplasm. As a membrane, it is mainly involved in regulating the movements of ions around the cell, and isolating materials that might be harmful or a threat to the cell.

Transport of protons from the cytosol to the vacuole stabilises cytoplasmic pH, while making the vacuolar interior more acidic creating a proton motive force which the cell can use to transport nutrients into or out of the vacuole. The low pH of the vacuole also allows degradative enzymes to act. Although single large central vacuoles are most common, the size and number of vacuoles may vary in different tissues and stages of development. For example, developing cells in the meristems contain small provacuoles and cells of the vascular cambium have many small vacuoles in the winter and one large one in the summer.

Aside from storage, the main role of the central vacuole is to maintain turgor pressure against the cell wall. Proteins found in the tonoplast (aquaporins) control the flow of water into and out of the vacuole through active transport, pumping potassium (K^+) ions into and out of the vacuolar interior. Due to osmosis, water will diffuse into the vacuole, placing pressure on the cell wall. If water loss leads to a significant decline in turgor pressure, the cell will plasmolyse. Turgor pressure exerted by vacuoles is also required for cellular elongation: as the cell wall is partially degraded by the action of expansins, the less rigid wall is expanded by the pressure coming from within the vacuole. Turgor pressure exerted by the vacuole is also essential in supporting plants in an upright position. Another function of a central vacuole is that it pushes all contents of the cell's cytoplasm against the cellular membrane, and thus keeps the chloroplasts closer to light.

Most plants store chemicals in the vacuole that react with chemicals in the cytosol. If the cell is broken, for example by a herbivore, then the two chemicals can react forming toxic chemicals. In garlic, alliin and the enzyme alliinase are normally separated but form allicin if the vacuole is broken. A similar reaction is responsible for the production of syn-propanethial-S-oxide when onions are cut.

Fungi

Vacuoles in fungal cells perform similar functions to those in plants and there can be more than one vacuole per cell. In yeast cells the vacuole is a dynamic structure that can rapidly modify its morphology. They are involved in many processes including the homeostasis of cell pH and the concentration of ions, osmoregulation, storing amino acids and polyphosphate and degradative processes. Toxic ions, such as strontium (Sr^{2+}), cobalt(II) (Co^{2+}), and lead(II) (Pb^{2+}) are transported into the vacuole to isolate them from the rest of the cell.

Animals

In animal cells, vacuoles perform mostly subordinate roles, assisting in larger processes of exocytosis and endocytosis.

Animal vacuoles are relatively smaller that their vegetable counterparts but also usually greater in number. There are also animal cells that do not have any vacuoles.

Exocytosis is the extrusion process of proteins and lipids from the cell. These materials are absorbed into secretory granules within the Golgi apparatus before being transported to the cell membrane and secreted into the extracellular environment. In this capacity, vacuoles are simply storage vesicles which allow for the containment, transport and disposal of selected proteins and lipids to the extracellular environment.

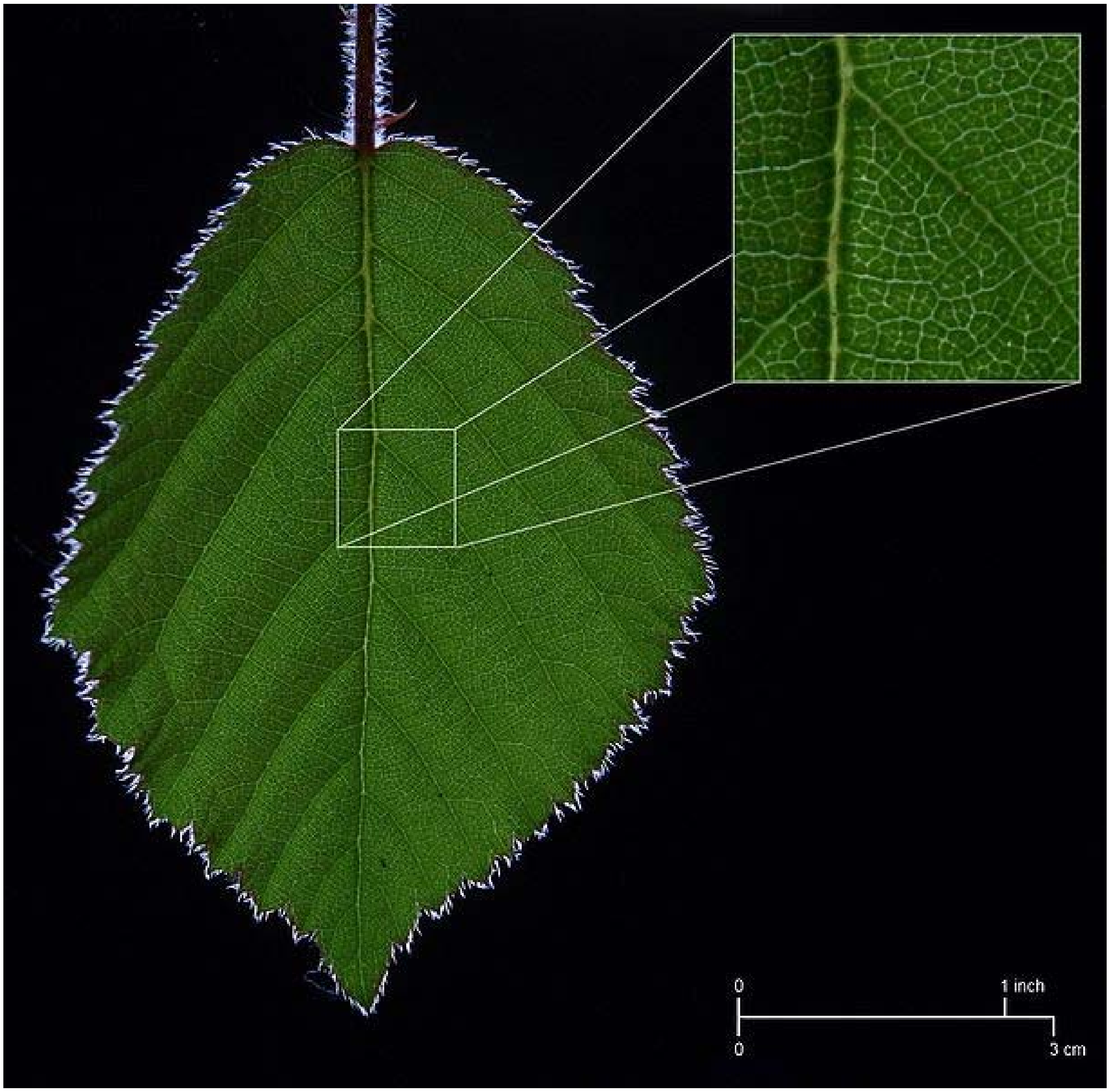
Endocytosis is the reverse of exocytosis and can occur in a variety of forms. Phagocytosis ("cell eating") is the process by which bacteria, dead tissue, or other bits of material visible under the microscope are engulfed by cells. The material makes contact with the cell membrane, which then invaginates. The invagination is pinched off, leaving the engulfed material in the membrane-enclosed vacuole and the cell membrane intact. Pinocytosis ("cell drinking") is essentially the same process, the difference being that the substances ingested are in solution and not visible under the microscope. Phagocytosis and Pinocytosis are both undertaken in association with lysosomes which complete the breakdown of the material which has been engulfed.

Chapter 15

Vascular Tissue and Vessel Element

Vascular tissue

Cross section of celery stalk, showing vascular bundles, which include both phloem and xylem.



Detail of the vasculature of a bramble leaf.

Vascular tissue is a complex conducting tissue, formed of more than one cell type, found in vascular plants. The primary components of vascular tissue are the xylem and phloem. These two tissues transport fluid and nutrients internally. There are also two meristems associated with vascular tissue: the vascular cambium and the cork cambium. All the vascular tissues within a particular plant together constitute the **vascular tissue system** of that plant.

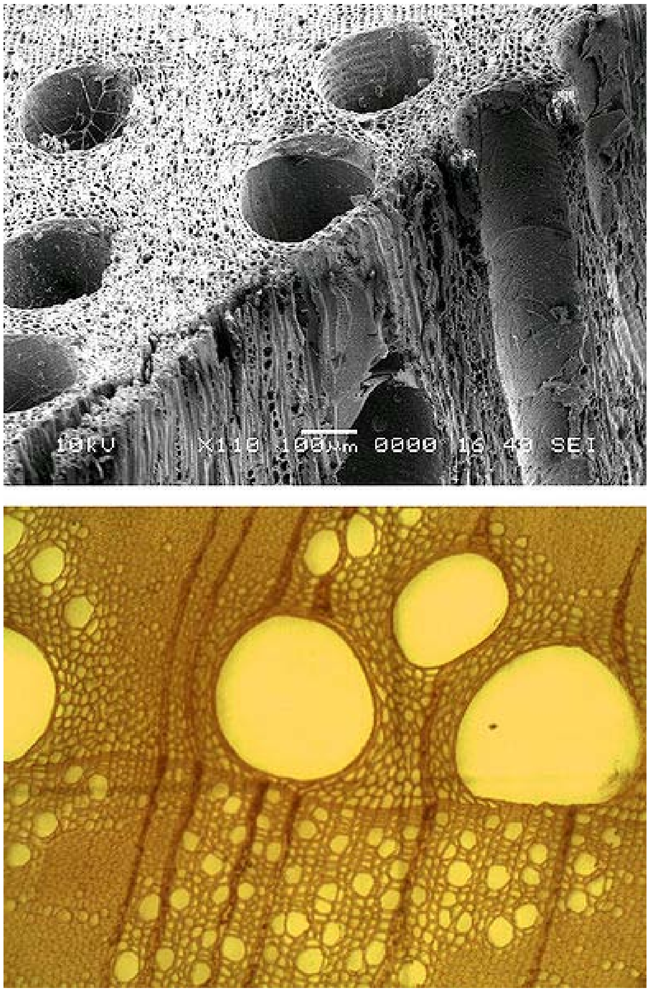
The cells in differentiated vascular tissue are typically long and slender. Since the xylem and phloem function in the conduction of water, minerals, and nutrients throughout the plant, it is not surprising that their form should be similar to pipes. The individual cells of phloem are connected end-to-end, just as the sections of a pipe might be. As the plant grows, new vascular tissue differentiates in the growing tips of the plant. The new tissue is aligned with existing vascular tissue, maintaining its connection throughout the plant.

The vascular tissue in plants is arranged in long, discrete strands called vascular bundles. These bundles include both xylem and phloem, as well as supporting and protective cells. In stems and roots, the xylem typically lies closer to the interior of the stem with phloem towards the exterior of the stem. In the stems of some Asteriidae dicots, there may be phloem located inwardly from the xylem as well.

Between the xylem and phloem is a meristem called the vascular cambium. This tissue divides off cells that will be become additional xylem and phloem. This growth increases the girth of the plant, rather than its length. As long as the vascular cambium continues to produce new cells, the plant will continue to grow more stout. In trees and other plants that develop wood, the vascular cambium allows the expansion of vascular tissue that produces woody growth. Because this growth ruptures the epidermis of the stem, woody plants also have a cork cambium that develops among the phloem. The cork cambium gives rise to thickened cork cells to protect the surface of the plant and reduce water loss. Both the production of wood and the production of cork are forms of secondary growth.

In leaves, the vascular bundles are located among the spongy mesophyll. The xylem is oriented toward the adaxial surface of the leaf (usually the upper side), and phloem is oriented toward the abaxial surface of the leaf. This is why aphids are typically found on the underside of the leaves rather than on the top, since the phloem transports sugars manufactured by the plant and they are closer to the lower surface.

Vessel element



SEM image (top) and Transmission Light Microscope image (bottom) of vessel elements in Oak

A **vessel element** is one of the cell types found in xylem, the water conducting tissue of plants. Vessel elements are typically found in the angiosperms but absent from most gymnosperms such as the conifers.

Vessel elements are the building blocks of vessels, which constitute the major part of the water transporting system in the plants where they occur. Vessels form an efficient system for transporting water (including necessary minerals) from the root to the leaves and other parts of the plant.

In secondary xylem, a vessel element originates from a fusiform initial in the cambium, at maturity the protoplast dies and disappears, but the lignified cell walls persist. It may be seen as a dead cell, which still has a function, and is still being protected by surrounding living cells.

The cell wall is strongly lignified. At both ends there are openings that connect the individual vessel elements. These are called perforations or perforation plates. These perforations may have a variety of shapes: the most common are the simple perforation (a simple opening) and the scalariform perforation (several elongated openings on top of each other in a ladder-like design). Other types include the foraminate perforation plate (several round openings) and reticulate perforation plate (net-like pattern, with many openings). The side walls will have pits, and may have spiral thickenings.

The presence of vessels in xylem has been considered to be one of the key innovations that led to the success of the flowering plants. It was once thought that vessel elements were an evolutionary innovation of flowering plants, but their absence from some basal angiosperms and presence in some members of the Gnetales suggest that this hypothesis must be re-examined; vessel elements in Gnetales may not be homologous with those of angiosperms, or vessel elements may have originated in a precursor to the angiosperms and were subsequently lost in some archaic or "basal" lineages (e.g., Amborellaceae, Tetracentraceae, Trochodendraceae, and Winteraceae), described by Arthur Cronquist as "primitively vesselless". Cronquist considered the vessels of *Gnetum* to be convergent with those of angiosperms.

Vessel-like cells have also been found in the xylem of *Equisetum* (horsetails), *Selaginella* (spike-mosses), *Pteridium aquilinum* (bracken fern), *Marsilea* and *Regnellidium* (aquatic ferns), and the enigmatic fossil group Gigantopteridales. In these cases, it is generally agreed that the vessels evolved independently. It is therefore not a stretch to believe that vessels may have appeared more than once among the angiosperms as well.

Chapter 16

Biosequestration

Flowering Corymbia ficifolia, Austins Ferry, Tasmania, Australia.

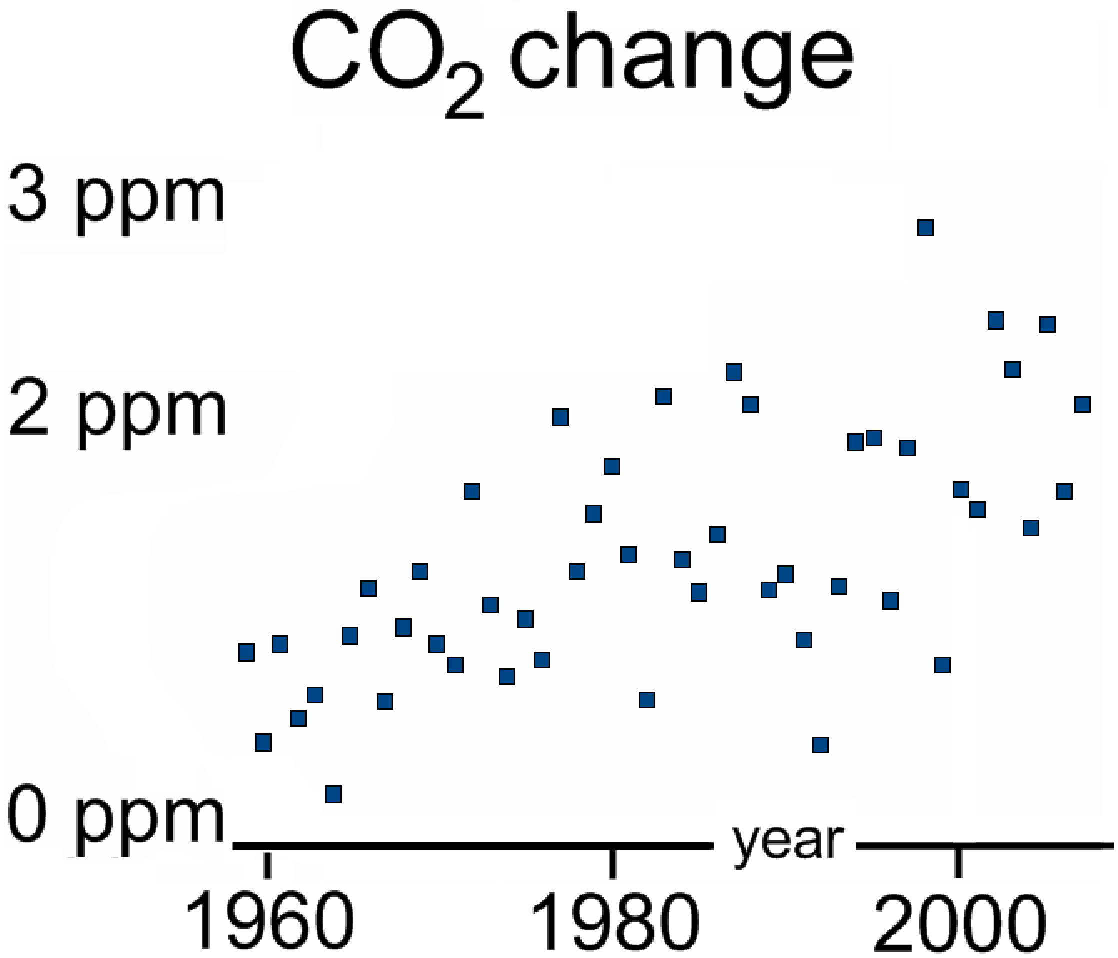
Biosequestration is the capture and storage of the atmospheric greenhouse gas carbon dioxide by biological processes.

This may be by increased photosynthesis (through practices such as reforestation / preventing deforestation and genetic engineering); by enhanced soil carbon trapping in agriculture; or by the use of algal bio sequestration to absorb the carbon dioxide emissions from coal, oil or gas-fired electricity generation.

Biosequestration as a natural process has occurred in the past, and was responsible for the formation of the extensive coal and oil deposists which we are now burning. It is a key policy concept in the climate change mitigation debate. It does not generally refer to the sequestering of carbon dioxide in oceans or rock formations, depleted oil or gas reservoirs, deep saline aquifers, or deep coal seams or through the use of industrial chemical carbon dioxide scrubbing.

The importance of plants in storing atmospheric carbon dioxide

Kew Gardens Waterlily House. David Iliff, 2008



Recent year-to-year increase of atmospheric CO_2

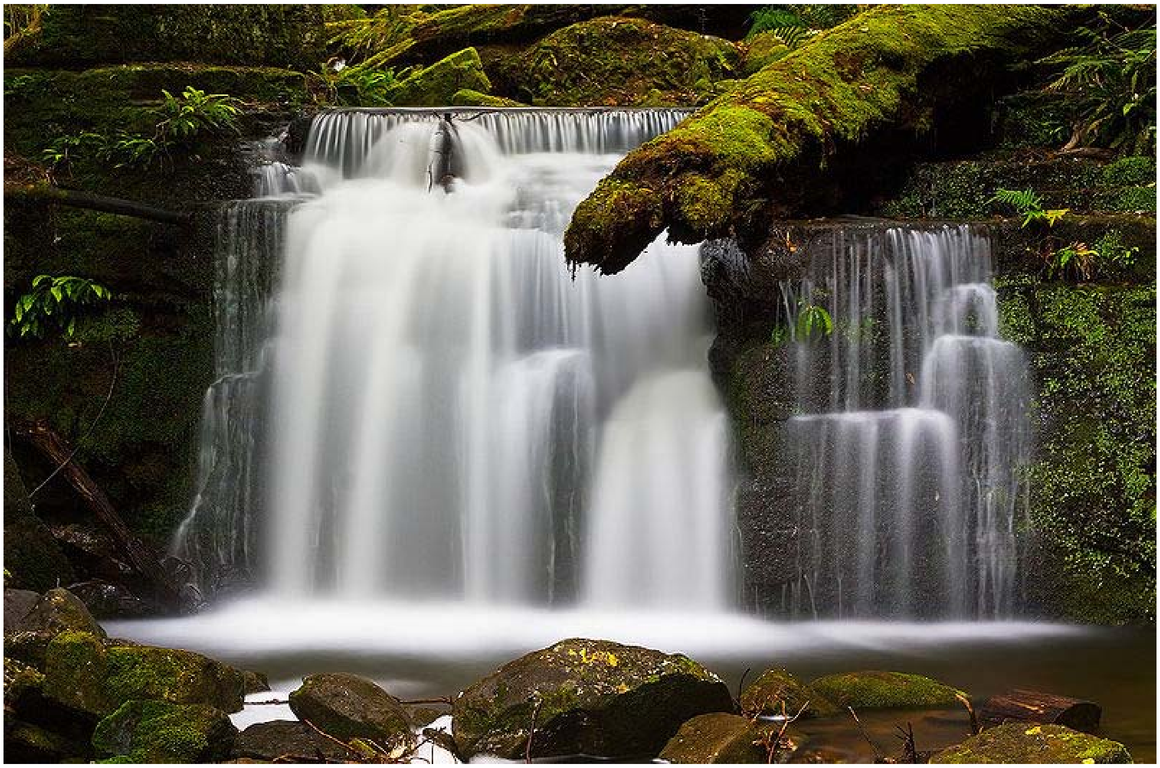
After water vapour (concentrations of which humans have limited capacity to influence) carbon dioxide is the most abundant and stable greenhouse gas in the atmosphere (methane rapidly reacts to form water vapour and carbon dioxide). Atmospheric carbon dioxide has increased from about 280 ppm in 1750 to 383 ppm in 2007 and is increasing at an average rate of 2 ppm pr year. The world's oceans have previously played an important role in sequestering atmospheric carbon dioxide through solubility and the action of phytoplankton. This, and the likely adverse consequences for humans and the biosphere of associated global warming, increases the significance of investigating policy mechanisms for encouraging biosequestration.

Reforestation, Avoided Deforestation and LULUCF

Reforestation and reducing deforestation can increase biosequestration in four ways. Pandani (Richea pandanifolia) near Lake Dobson, Mount Field National Park, Tasmania, Australia

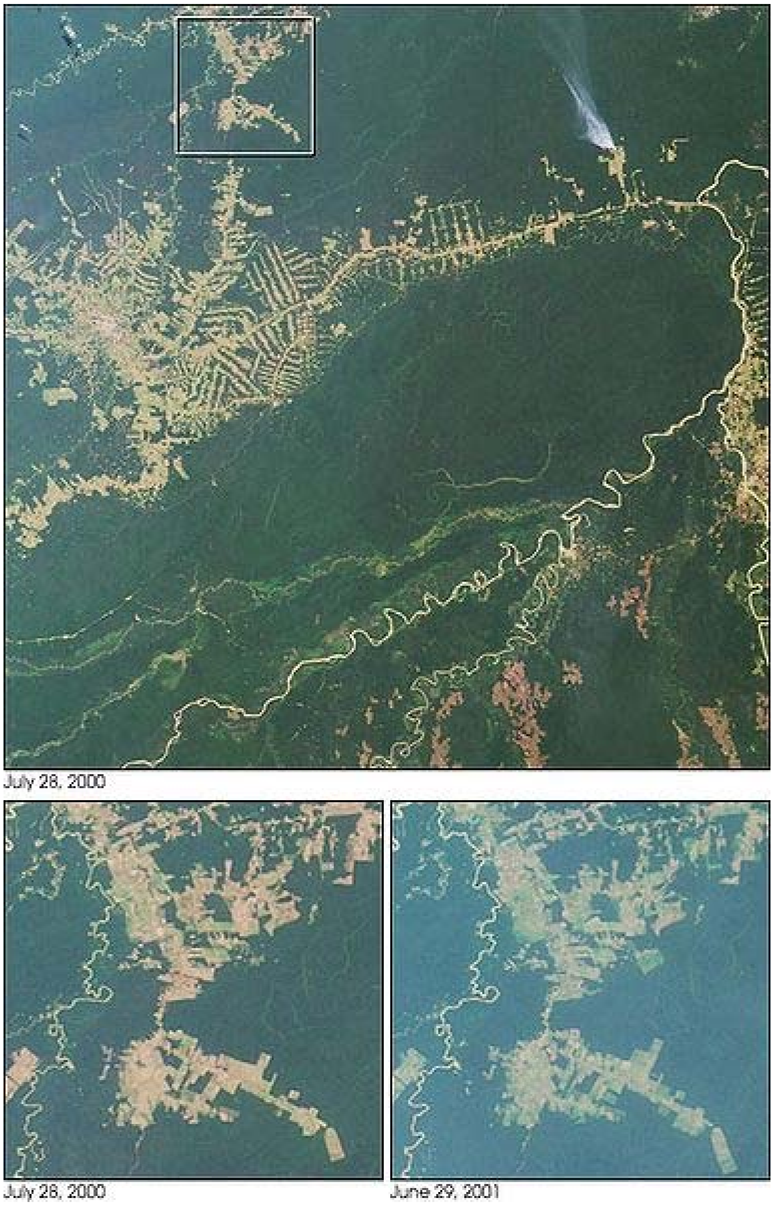
The Intergovernmental Panel on Climate Change (IPCC) estimates that the cutting down of forests is now contributing close to 20 per cent of the overall greenhouse gases entering the atmosphere. Candell and Raupach argue that there are four primary ways in which reforestation and reducing deforestation can increase biosequestration. First, by increasing the volume of existing forest. Second, by increasing the carbon density of existing forests at a stand and landscape scale. Third, by expanding the use of forest products that will sustainably replace fossil-fuel emissions. Fourth, by reducing carbon emissions that are caused from deforestation and degradation.

A recent report by the Australian CSIRO found that forestry and forest-related options are the most significant and most easily achieved carbon sink making up 105 Mt per year CO_2-e or about 75 per cent of the total figure attainable for the Australian state of Queensland from 2010-2050. Among the forestry options, the CSIRO report announced, forestry with the primary aim of carbon storage (called carbon forestry) clearly has the highest attainable carbon storage capacity (77 Mt CO_2-e/yr) and is one of the easiest options to implement compared with biodiversity plantings, pre-1990 eucalypts, post 1990 plantations and managed regrowth. Legal strategies to encourage this form of biosequestration include permanent protection of forests in National Parks or on the World Heritage List, properly funded management and bans on use of rainforest timbers and inefficient uses such as woodchipping old growth forest.



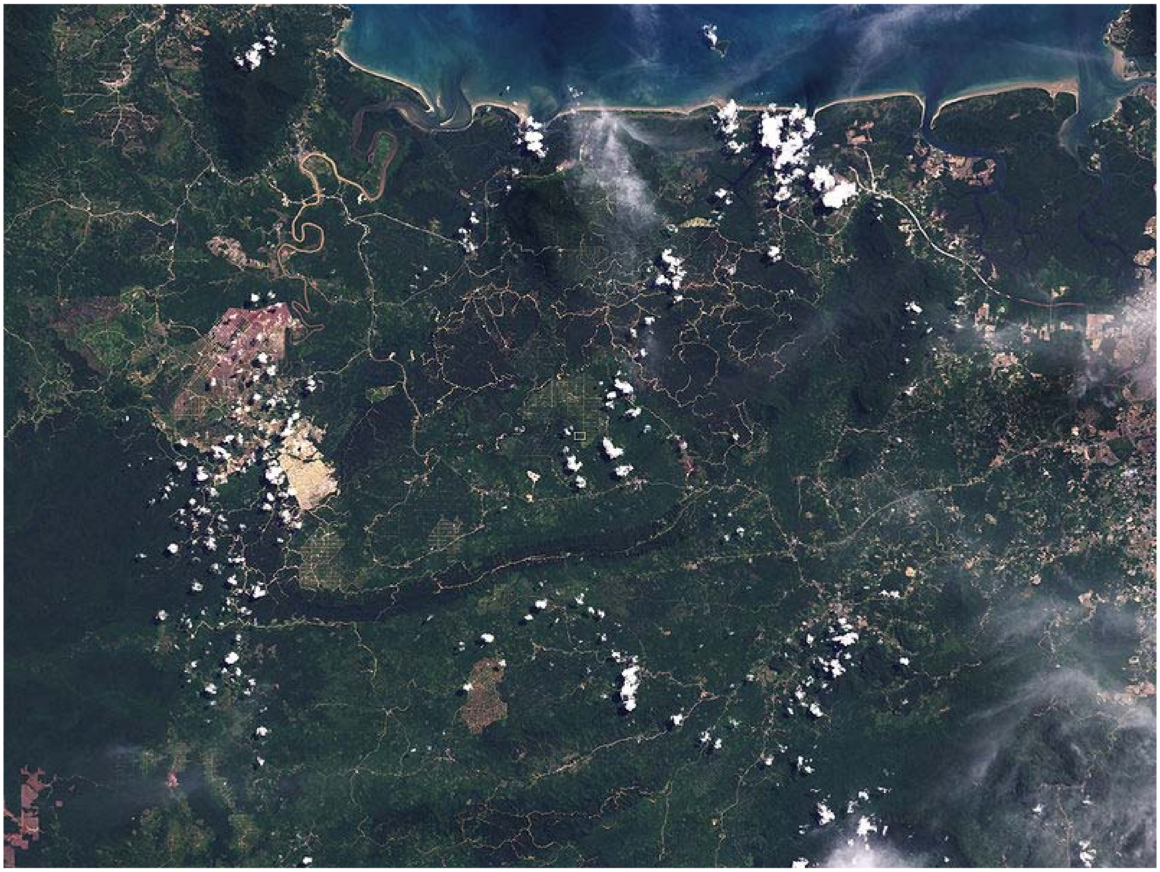
Strickland Falls, Tasmania, Australia.

As a result of lobbying by the developing country caucus (or Group of 77) in the United Nations (associated with the United Nations Conference on Environment and Development (UNCED) in Rio de Janeiro, the non-legally binding Forest Principles were established in 1992. These linked the problem of deforestation to third world debt and inadequate technology transfer and stated that the "agreed full incremental cost of achieving benefits associated with forest conservation...should be equitably shared by the international community" (para1(b)). Subsequently the Group of 77 argued in the 1995 *Intergovernmental Panel on Forests* (IPF) and then the 2001 *Intergovernmental Forum on Forests* (IFF), for affordable access to environmentally sound technologies without the stringency of intellectual property rights; while developed states there rejected demands for a forests fund. The expert group crated under the United Nations Forum on Forests (UNFF) reported in 2004, but in 2007 developed nations again vetoed language in the principles of the final text which might confirm their legal responsibility under international law to supply finance and environmentally sound technologies to the developing world.



Settlement and deforestation surrounding the Brazilian town of Rio Branco are seen here in the striking "herring bone" deforestation patterns that cut through the rainforest. NASA, 2008.

In December 2007, after a two year debate on a proposal from Papua New Guinea and Costa Rica, state parties to the United Nations Framework Convention on Climate Change (FCCC) agreed to explore ways of reducing emissions from deforestation and to enhance forest carbon stocks in developing nations. The underlying idea is that developing nations should be financially compensated if they succeed in reducing their levels of deforestation (through valuing the carbon that is stored in forests); a concept termed 'avoided deforestaion (AD) or, REDD if broadened to include reducing forest degradation. Under the free market model advocated by the countries who have formed the *Coalition of Rainforest Nations*, developing nations with rainforests would sell carbon sink credits under a free market system to Kyoto Protocol Annex I states who have exceeded their emissions allowance. Brazil (the state with the largest area of tropical rainforest) however, opposes including avoided deforestation in a carbon trading mechanism and instead favors creation of a multilateral development assistance fund created from donations by developed states. For REDD to be successful science and regulatory infrastructure related to forests will need to increase so nations may inventory all their forest carbon, show that they can control land use at the local level and prove that their emissions are declining.



NASA Earth Observatory, 2009. Deforestation in Malaysian Borneo.

The United Nations Framework Convention on Climate Change (UNFCCC) Article 4(1)(a) requires all Parties to "develop, periodically update, publish and make available to the Conference of the Parties" as well as "national inventories of anthropogenic emissions by sources" "removals by sinks of all greenhouse gases not controlled by the Montreal Protocol." Under the UNFCCC reporting guidelines, human-induced greenhouse emissions must be reported in six sectors: energy (including stationary energy and transport); industrial processes; solvent and other product use; agriculture; waste; and *land use, land use change and forestry* (LULUCF). The rules governing accounting and reporting of greenhouse gas emissions from LULUCF under the Kyoto Protocol are contained in several decisions of the Conference of Parties under the UNFCCC and LULUCF has been the subject of two major reports by the Intergovernmental Panel on

Climate Change (IPCC). The Kyoto Protocol article 3.3 thus requires mandatory LULUCF accounting for afforestation (no forest for last 50 years), reforestation (no forest on 31 December 1989) and deforestation, as well as (in the first commitment period) under article 3.4 voluntary accounting for cropland management, grazing land management, revegetation and forest management (if not already accounted under article 3.3).

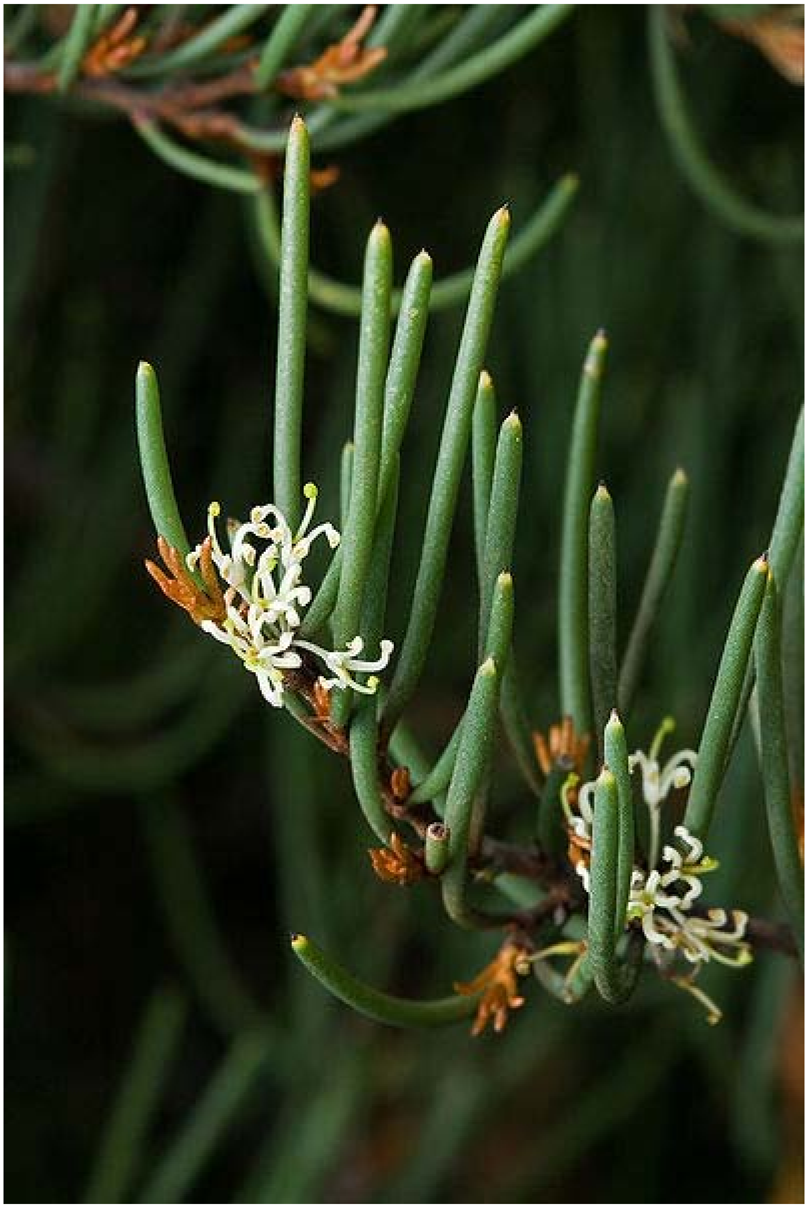
Continent of Australia from space. Australia is a major producer of fossil fuels and has significant problems with deforestation.

Deforestation in Haiti. NASA, 2008.

As an example, the *Australian National Greenhouse Gas Inventory* (NGGI) prepared in compliance with these requirements indicates that the energy sector accounts for 69 per cent of Australia's emissions, agriculture 16 per cent and LULUCF six per cent. Since 1990, however, emissions from the energy sector have increased 35 per cent (stationary energy up 43% and transport up 23%). By comparison, emissions from LULUCF have fallen by 73%. However, questions have been raised by Andrew Macintosh about the veracity of the estimates of emissions from the LULUCF sector because of discrepancies between the Australian Federal and Queensland Governments' land clearing data. Data published by the *Statewide Landcover and Trees Study* (SLATS) in Queensland, for example, show that the total amount of land clearing in Queensland identified under SLATS between 1989/90 and 2000/01 is approximately 50 per cent higher than the amount estimated by the Australian Federal Government's *National Carbon Accounting System* (NCAS) between 1990 and 2001. Satellite imaging has become crucial in obtaining data on levels of deforestation and reforestation. Landsat satellite data, for example, has been used to map tropical deforestation as part of NASA's Landsat *Pathfinder Humid Tropical Deforestation Project*, a collaborative effort among scientists from the University of Maryland, the University of New Hampshire, and NASA's Goddard Space Flight Center. The project yielded deforestation maps for the Amazon Basin, Central Africa, and Southeast Asia for three periods in the 1970s, 1980s, and 1990s.

Enhanced photosynthesis

Sprekelia formosissima in Tasmania, Australia.



Hakea epiglottis, Cape Raoul, Tasman Peninsula, Tasmania, Australia.

Biosequestration may be enhanced by improving photosynthetic efficiency by modifying RuBisCO genes in plants to increase the catalytic and/or oxygenation activity of that enzyme.

One such research area involves increasing the Earth's proportion of C4 carbon fixation photosynthetic plants. C4 plants represent about 5% of Earth's plant biomass and 1% of its known plant species, but account for around 30% of terrestrial carbon fixation. In leaves of C3 plants, captured photons of solar energy undergo photosynthesis which assimilates carbon into carbohydrates (triosephosphates) in the chloroplasts of the mesophyll cells. The primary CO_2 fixation step is catalysed by ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) which reacts with O2 leading to photorespiration that protects photosynthesis from photoinhibition but wastes 50% of potentially fixed carbon. The C4 photosynthetic pathway, however, concentrates CO_2 at the site of the reaction of Rubisco, thereby reducing the biosequestration-inhibiting photorespiration. A new frontier in crop science consists of attempts to genetically engineer C3 staple food crops (such as wheat, barley, soybeans, potatoes and rice) with the "turbo-charged" photosynthetic apparatus of C4 plants.

Biochar

Biochar (charcoal created by pyrolysis of biomass) is a potent form of longterm (thousands of years) biosequestration of atmosphereic CO_2 derived from investigation of the extremely fertile Terra preta soils of the Amazon Basin. Placing biochar in soils also improves water quality, increases soil fertility, raises agricultural productivity and reduce pressure on old growth forests. As a method of generating bio-energy with carbon storage Rob Flanagan and the EPRIDA biochar company have developed low-tech cooking stoves for developing nations that can burn agricultural wastes such as rice husks and produce 15% by weight of biochar; while BEST Energies in NSW Australia have spent a decade developing an Agrichar technology that can combust 96 tonnes of dry biomass each day, generating 30-40 tonnes of biochar. A parametric study of biosequestration by Malcolm Fowles at the Open University, indicated that to mitigate global warming, policies should encourage displacement of coal with biomass as a power source for baseload electricity generation if the latter’s conversion efficiency rose over 30%, otherwise *biosequestering* carbon from biomass as a cheaper mitigation option than geosequestration by CO_2 capture and storage.

Improved agricultural and farming practices

Panicum virgatum switchgrass, valuable in biofuel production, soil conservation and biosequestration

Zero-till farming practices occur where there is much mulching but ploughing is not used, so that the carbon-rich organic matter in soil is not exposed to atmospheric oxygen, or to the leaching and erosion effects of rainfall. Over grazing is reduced by moving cattle and sheep away from grazed areas for several months. Ceasing ploughing has been alleged to encourage more ants to become predators of wood-eating (and CO_2 generating) termites, allows weeds to regenerate soils and helps slow water flows over the land.
Dedicated biofuel and biosequestration crops, such as switchgrass (panicum virgatum), are also being developed. It requires from 0.97 to 1.34 GJ fossil energy to produce 1 tonne of switchgrass, compared with 1.99 to 2.66 GJ to produce 1 tonne of corn. Given that switchgrass contains approximately 18.8 GJ/ODT of biomass, the energy output-to-input ratio for the crop can be up to 20:1.

Biosequestration can also be enhanced by farmers choosing crops species that produce large numbers of phytoliths. Phytoliths are microscopic spherical shells of silicon that can store carbon for thousands of years.

Biosequestration and climate change policy

Biosequestration could be critical to climate change mitigation till cleaner forms of power generation are established. The Nesjavellir Geothermal Power Plant in Þingvellir, Iceland

Windmills D4 (nearest) to D1 on the Thornton Bank

Industries with large amounts of CO_2 emissions (such as the coal industry) are interested in biosequestration as a means of offsetting their greenhouse gas production. In Australia, university researchers are engineering algae to produce biofuels (hydrogen and biodiesel oils) and investigating whether this process can be used to *biosequester* carbon. Algae naturally capture sunlight and use its energy to split water into hydrogen, oxygen and oil which can be extracted. Such clean energy production also can be coupled with desalination using salt-tolerant marine algae to generate fresh water and electricity.

Many new bioenergy (biofuel) technologies, including cellulosic ethanol biorefineries (using stems and branches of most plants including crop residues such as corn stalks, wheat straw and rice straw) are being promoted because they have the added advantage of biosequestration of CO_2. The Garnaut Climate Change Review recommends that a carbon price in a carbon emission trading scheme could include a financial incentive for biosequestration processes. Garnaut recommends the use of algal biosequestration to absorb the constant stream of carbon dioxide emissions from coal-fired electricity generation and metal smelting until renewable forms of energy, such as solar and wind power, become more established contributors to the grid. Garnaut, for example, states: "Some algal biosequestration processes could absorb emissions from coal-fired electricity generation and metals smelting." The United Nations Collaborative Programme on Reducing Emissions from Deforestation and Forest Degradation in Developing Countries (UN-REDD Programme) is a collaboration between FAO, UNDP and UNEP under which a trust fund established in July 2008 allows donors to pool resources to generate the requisite transfer flow of resources to significantly reduce global emissions from deforestation and forest degradation. The UK government's Stern Review on the economics of climate change argued that curbing deforestation was a "highly cost-effective way of reducing greenhouse gas emissions".

James E. Hansen argues that, "An effective way to achieve drawdown [of carbon dioxide] would be to burn biofuels in power plants and capture the CO_2, with the biofuels derived from agricultural or urban wastes or grown on degraded lands using little or no fossil fuel inputs."

Under a 2009 agreement, Loy Yang Power and MBD Energy Ltd will build a pilot Fossil fuel power plant at the Latrobe Valley power station in Australia using biosequestration technology in the form of an algal synthesiser system. Captured CO_2 from the waste exhaust flue gases will be injected into circulating waste water to grow oil-rich algae where sunlight and nutrients will produce heavy oil-laden slurry that can make high grade oil for energy, or stock feed. Other commercial demonstration projects involving biosequestration of CO_2 at point of emission have begun in Australia.

Philosophical basis of biosequestration

The arguments for biosequestration are often shaped in terms of economic theory, yet there is a well-recognised quality of life dimension to this debate. Biosequestration assists human beings to increase their collective and individual contributions to the essential resources of the biosphere. The policy case for biosequestration overlaps with principles of ecology, sustainability and sustainable development, as well as biosphere, biodiversity and ecosystem protection, environmental ethics, climate ethics and natural conservation.

Barriers to increased global biosequestration

Russell Falls, Mount Field National Park, Tasmania, Australia.

Lassen National Park, Kings Creek, USA.

The Garnaut Climate Change Review notes many barriers to increased global biosequestration. "There must be changes in the accounting regimes for greenhouse gases. Investments are required in research, development and commercialisation of superior approaches to biosequestration. Adjustments are required in the regulation of land use. New institutions will need to be developed to coordinate the interests in utilisation of biosequestration opportunities across small business in rural communities. Special efforts will be required to unlock potential in rural communities in developing countries." Saddler and King have argued that biosequestration and agricultural greenhouse gas emissions should not be handled within a global emissions trading scheme because of difficulties with measuring such emissions, problems in controlling them and the burden that would be placed on numerous small-scale farming operations. Collett likewise maintains that REDD credits (post-facto payments to developing countries for reducing their deforestation rates below an historical or projected reference rate), simply create a complex market approach to this global public health problem that reduces transparency and accountability when targets are not met and will not be as effective as developed nations voluntarily funding countries to keep their rainforests.

The World Rainforest Movement has argued that poor developing countries could be pressured to accept reforestation projects under the Kyoto Protocol's Clean Development Mechanism in order to earn foreign exchange simply to pay off the interest on debt to the World Bank. Tensions also exist over forest management between the sovereignty claims of nations states, arguments about common heritage of mankind and the rights of indigenous peoples and local communities; the Forest Peoples Programme (FPP) arguing the anti-deforestation programs could merely allow financial benefits to flow to national treasuries, privilege would-be corporate forest degraders who manipulate the system by periodically threatening forests, rather than local communities who conserve them. The success of such projects will also depend on the accuracy of the baseline data and the number of countries involved. Further, it has been argued that if biosequestration is to play a significant role in mitigating anthropogenic climate change then coordinated policies should set a goal of achieving global forest cover to its extent prior to the industrial revolution in the 1800s. It has also been argued that the United Nations mechanism for Reducing Emissions from Deforestation and Forest Degradation (REDD) may increase pressure to convert or modify other ecosystems, especially savannahs and wetlands, for food or biofuel, even though those ecosystems also have high carbon sequestration potential. Globally, for example, peatlands cover only 3% of the land surface but store twice the amount of carbon as all the world's forests, whilst mangrove forests and saltmarshes are examples of relatively low-biomass ecosystems with high levels of productivity and carbon sequestration. Other researchers have argued that REDD is a critical component of an effective global biosequestration strategy that could provide significant benefits, such as the conservation of biodiversity, particularly if it moves away from focusing on protecting forests that are most cost-effective for reducing carbon emissions (such as those in Brazil where agricultural opportunity costs are relatively low, unlike Asia, which has sizeable revenues from oil palm, rubber, rice, and maize). They argue REDD could be varied to allow funding of programs to slow peat degradation in Indonesia and target protection of biodiversity in “hot spot”—areas with high species richness and relatively little remaining forest. Some purchasers, they maintain, of REDD carbon credits, such as multinational corporations or nations, might pay a premium to save imperiled eco-systems or areas with high-profile species.