Tissues and Organs; or how the Plant is built

5.1 Tissues

5.1.1 Epidermis and Parenchyma

Tissue is a union of cells which have common origin, function and similar morphology. Tissues belong to organs: **organ** is a union of different tissues which have common function(s) and origin. Plants have simple and complex tissues. The **simple tissues** are composed of the same type of cells; **complex tissues** are composed of more than one type of cell, these are unique to plants.

Parenchyma: are spherical, elongated cells with a thin primary cell wall. It is a main component of young plant organs. The basic functions of parenchyma are *photosynthesis and storage*. Parenchyma cells are widespread in plant body. They fill the leaf, frequent in stem cortex and pith and is a component of complex vascular tissues.

Epidermis covered with a **cuticle** which served a purpose similar to a plastic bag. For the really small (millimeters) plant it is enough because, in accordance to **surface / volume law**, they have high relative surface, and diffusion can serve for gas exchange. However, bigger plants also need to exchange gases, and they developed **stomata** which served as a regulated pore system. Contrary to parenchyma (which is a simple tissue), **epidermis** is a complex tissue composed of epidermal and stomata cells. Its main functions are *transpiration, gas exchange and defense*.

5.1.2 Supportive Tissues: Building Skyscrapers

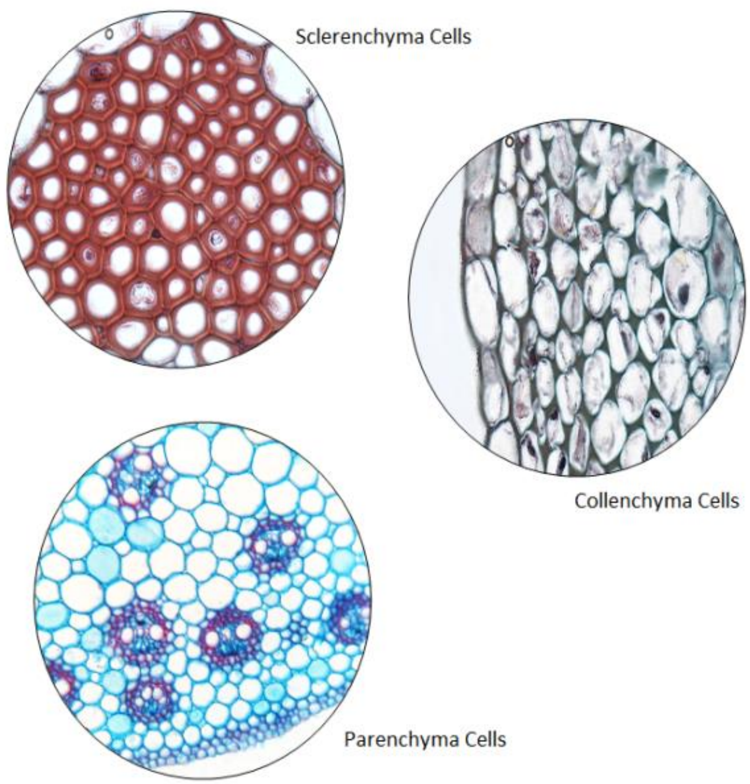
When more and more plants began to move from the water to the land, competition once again became a problem. To solve this, plants followed “Manhattan solution”: they grew vertically in order to be able to escape competition for the sunlight and therefore must develop **supportive tissues**.

Collenchyma is living supportive tissue that has elongated cells and a thick primary cell wall. Its main function is the mechanical support of young stems and leaves via turgor.

Sclerenchyma is a dead supportive tissue that consists of long fibers or short, crystal-like

cells. Each cell has a thick *secondary wall* that is rich in lignin. Its main function is a support of older plant organs, and also hardening different parts of plants (for example, make fruit inedible before ripeness so no one will take the fruit before seeds are ready to be distributed). Without sclerenchyma, if a plant isn't watered, the leaves will droop because the vacuoles will decrease in size which lowers the turgor. Fibers inside phloem are sometimes regarded as a separate
sclerenchyma.

Three times in their evolution plants found the new application for lignin or similar polymers: at first, similar chemicals covered the spore wall which was an adaptation to the spore distribution with wind. Then similar chemicals were used to make cuticle, "epidermal plastic bag" to prevent transpiration outside of stomata. Finally, with acquiring of sclerenchyma, plants found how to use dead cells with completely lignified cell walls.

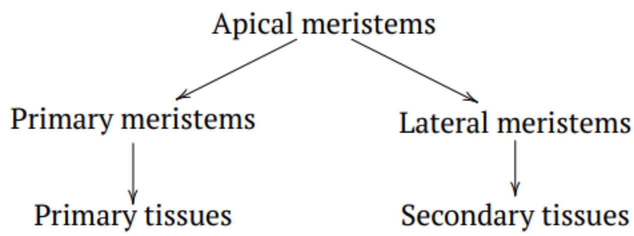


Cell types and tissues

"Parenchyma" and "sclerenchyma" terms are used in two ways: first, to name tissues (or even classes of tissues) which occur in multiple places of the plant body, and second, to name the cell types which are components of tissues. Therefore, it is possible to say "parenchyma of stem", "parenchyma of stem pith", "parenchyma of xylem" and even "leaf mesophyll is a parenchyma".

5.1.3 Meristems: the Construction Sites

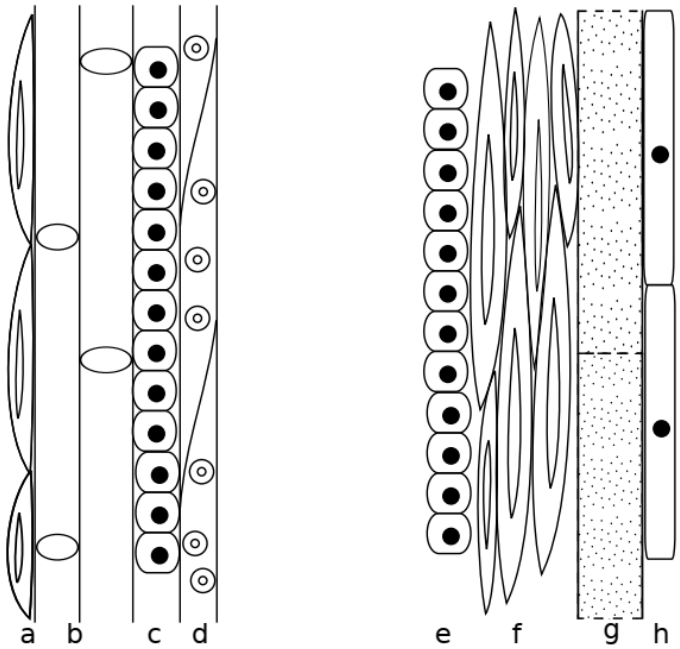
Plant growth requires centers of development which are **meristems**. **Apical meristems** are centers of plant development located on the very ends of roots (**RAM**) and stems (**SAM**). They produce intermediate meristems (like **procambium**) which form all **primary tissues**. The **lateral meristem** or **cambium** originates from the procambium which in turn originates from apical meristems. It usually arises between two vascular tissues and its main functions are thickening and producing **secondary vascular tissues**



Other meristems include: **intercalary** which elongate stems from the "middle", **marginal** which are responsible for leaf development and **repair** meristems arising around wounds, they also control vegetative reproduction.

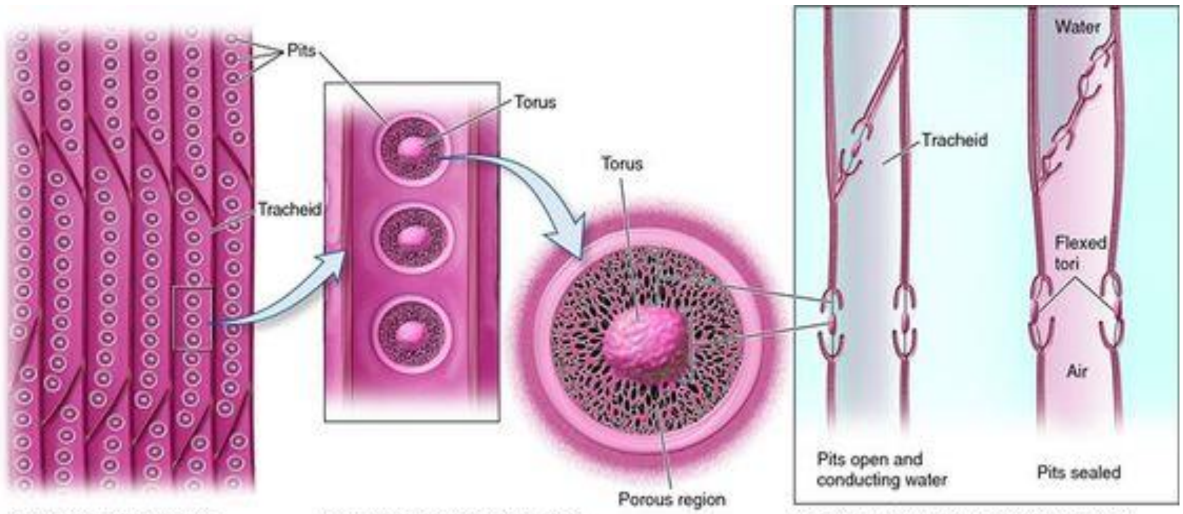
5.1.4 Vascular Tissues

Bigger plants escaped from competition and performed effective metabolism. However, with all the growth the plants went through, their size became too big for slow symplastic plasmodesmata connections. Another, filter paper-like apoplastic transport was also not powerful enough. The solution was to develop **vascular tissues**, xylem and phloem. The main functions of xylem are the transportation of water and mechanical support. The **xylem** may be found either in a vascular bundle or a vascular cylinder. The three types of xylem cells are **tracheary elements** (these include **tracheids** and **vessel members**), **fibers**, and **parenchyma**. Xylem elements, except for the parenchyma, are rich in lignin and are main components of wood. Tracheids are closed on both ends and connected with **pits** whereas vessel members are more or less open and connects via **perforations**. Tracheids, vessel members and fibers are dead cells. Xylem parenchyma, on the other hand, is alive.



Cells of xylem (left, a–d) and phloem (right, e–h): a. fibers, b. vessels with open perforations, c. parenchyma, d. tracheids with pits, e. parenchyma, f. fibers, g. sieve tubes, h.
companion cells.

Pits of tracheids consist of a pit membrane and the torus in a center, there are *no openings*. The presence of tracheids and/or vessel elements has evolutionary significance. Vessels (made of vessel members) are more effective; consequently, more "**primitive**" plants have **more tracheids** whereas more "**advanced**" have **more vessel members**. As an example, **gymnosperms** have **only tracheids** while most **flowering plants** have **tracheids and vessel** members. Individual development also mimics this evolutionary trend. Younger flowering plants have more tracheids whereas mature plants have more vessel members. **Primary xylem** mostly has **tracheids** and **vessels** with **scalariform perforations** whereas **secondary xylem** (which originates from cambium) consists **mostly of vessels** with **open perforations**. The common name for secondary xylem is **wood**.



(a) Columns of tracheids showing cell walls (b) Tracheid pits containing tori (c) Tracheid with open pits (left side) and tracheid with sealed pits (right side)

It is a mistake to think that tracheids are better than vessels. In fact, the main problem is frequently not too slow but too fast water transport. **Tracheids** have an **advanced connection system** (called **torus**) which has the ability to **close pore** if the **water pressure is too high** and therefore more controllable. Leaking would be less dangerous in tracheids. And in water-poor environments (like **taiga** in **winter**), plants with **tracheids** will have the **advantage**. Contrary, having **vessels** is like to have **race car** for ordinary life. Dead cells are useful but hard to control. However, if xylem transport needs to be decreased, there is a way. Xylem parenchyma cells will make **tyloses** (“stoppers”) which will grow into dead tracheary elements and stop water if needed. **Many broadleaved trees** use **tyloses** to **lower xylem transport before the winter**.

The **phloem** generally occurs adjacent, or right next to, the xylem, with the **xylem** facing the **inner** part of the plant and the **phloem** facing the **outer** part of the plant. The main functions of the phloem are the transportation of sugars and mechanical support. The four types of phloem cells are: **sieve tube cells**, **companion cells**, **fibers** (the only dead cells in phloem), and **parenchyma**.

Sieve tube cells of flowering plants **have cytoplasm flowing through perforations (sieve plates)** between cells but **do not contain nuclei**. **Companion cells** will **make proteins for them**.

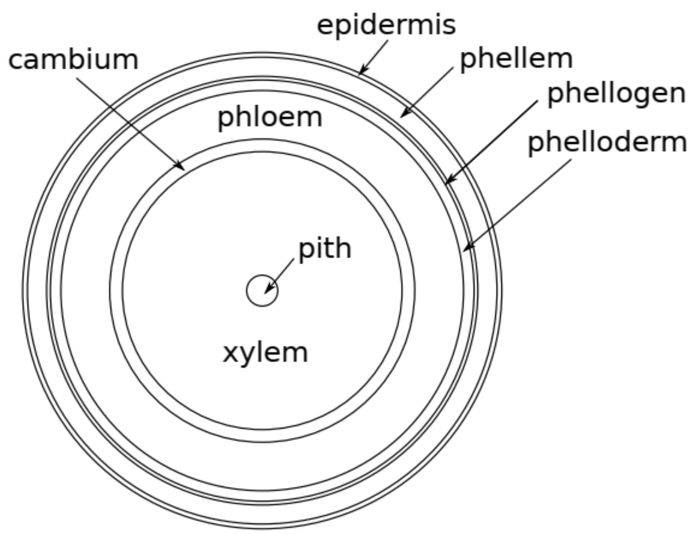
However, in **gymnosperms** and more "primitive" plants there are **no companion cells** at all, so **sieve tube** cells do **contain nuclei**. The **secondary phloem** generally has **more fibers** than the primary phloem.

5.1.5 Periderm

Periderm is a **secondary dermal** tissue which **arises inside the stem ground tissue**, closer to the surface. Like the other dermal tissue (epidermis), it is a complex tissue. It includes three layers (starting from surface): **phellem** (**cork**), **phellogen** (**cork cambium**) and **phelloderm**.

Phellem consists of **large dead cells** with secondary walls saturated with **suberin**, and is the main, **thickest** component of **periderm**.

Phellogen is a **lateral meristem**, like cambium; it often **arises fragmentarily** (and also **temporarily**) and does **not cover the whole stem** under-surface. But when phellem starts to grow, all peripheral tissues (like epidermis) will be separated from water transport and eventually die. Phellogen **makes phellem** towards the **surface**, and **phelloderm** towards the next layer (**phloem**). Phelloderm is a **minute tissue**, and does **not play significant** role in the periderm



In **older plants**, phellogen **arises deeper**, sometimes **inside phloem** and separates outer layers of phloem from vascular cylinder. All this mixture of tissues (phellogen, phellem, phelloderm, epidermis and upper layers of phloem) considered as a **bark**.

5.1.6 Absorption Tissues

Poikilohydric plants do not save water and they can survive even complete desiccation because their cells will hibernate (spend the winter in a dormant state). An example of a poikilohydric plants would be **mosses**.

Homoilohydric plants (which are majority of plants), however, do save water. They try to support the water content and do not survive complete desiccation. An example of a homoiohydric plant would be any "typical" plant, saying, corn.

Absorption tissues are always **simple, primary tissues**. Most important of them is **rhizodermis** (rhizoderm), or **root hairs**, which **originates** from **protoderm** (protoepidermis), but its lifespan is much shorter than of epidermis around 2 to 3 days. There are other absorption tissues, for example, **velamen**, which originates from the root cortex and consists of large, empty, easy to get wet dead cells. Velamen is a sponge-like tissue that can be found in epiphytic roots. Since these plants do not make direct contact with the soil, it aids in the absorption and storage of atmospheric moisture. In the case of the epiphytic orchids, their roots tend to grow upwards and they are totally independent of soil contact.

5.1.7 Other Tissues

Secretory tissues spread across the plant body, concentrating in **leaves** and **young stems**. These tissues may secrete **latex, volatile oils**, **mucus** and other chemicals. Its functions can be **attraction** or **dis-attraction**, **communication** or **defense**, and many others. In addition to tissues, plant body may contain **idioblasts**, cells which are quite dissimilar from surrounding cells. Idioblasts used for accumulation of unusual (and possibly dangerous) compounds like **myrosinase**, **protein splitting glucosinolates into sugars** and **toxic isothiocyanate** (**mustard oil**). We use mustard oil as a spice but for the plant, it works like a binary chemical **weapon against insect herbivores**: when myrosinase-containing idioblasts are damaged, mustard oil kills damaging insects.

Among plants, the whole order Brassicales from rosids is capable to produce myrosinase, examples are different cabbages (*Brassica* spp.), papaya (*Carica*), horseradish tree (*Moringa*) and many others.

5.2 Organs and Organ Systems

Vegetabilia (Any of various **photosynthetic**, **eukaryotic**, **multicellular** organisms of the **kingdom Plantae** characteristically containing **chloroplasts**, having **cell walls** made of cellulose, **producing embryos**, and **lacking the power of locomotion**) have three different types of body construction.

The most **primitive** plants have **thallus** body, more **advanced** is the **shoot** (**unipolar**) plant
body, and **most land plants** have the **bipolar** plant body.

*The **thallus** plant body is **flat, similar to leaf but do not differentiate into particular organs**.* Most **gametophytes** (**except true mosses**) have this type, and also **few sporophytes** (which mostly are reduced water plants).

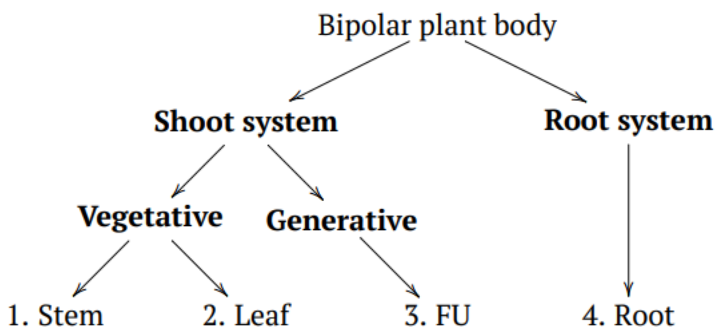
Shoot (unipolar) plant body consists only of branching shoots, **roots are absent**. This is typical to all **Bryophyta sporophytes**, **mosses** (Bryopsida) gametophytes, and also to sporophytes of Psilotopsida (whisk ferns).

Finally, **bipolar plant body** has **both shoots and roots**. Most bipolar plants have **shoots** consist of **stems and leaves**, but this is not an absolute requirement since young plant stems are normally green and can-do **photosynthesis**.

Typical organs of bipolar plant are **stems** (axial aerial organs with continuous growth), **leaves** (flat lateral organ with restricted growth), **roots** (axial soil organ modified for absorption) and **floral units (FU)** which are elements of the generative system (fructifications) such as a pine cone or any flower.
Buds, **fruits**, **seeds** and **specific to seedlings hypocotyl and epicotyl** are **non-organs** for different reasons: **buds** are just young shoos, **fruit** is the ripe flower, **hypocotyl** is a part of stem between first leaves of the seedling (cotyledons) and root (i.e., stem/root transition place), **epicotyl** is first internode of stem, and finally, **seed** is a chimeric structure with three genotypes so **it is impossible to call it "organ"**.
Root, stem, leaf and FU are *four basic plant organs* which in bipolar plant could be

grouped in root and shoot system; the latter is frequently split into ***generative shoot system*** (bearing FU), and ***vegetative shoot system*** (without FU).
Vegetative shoot system usually consists of **main** and **secondary shoots**; shoots contain terminal buds, axillary (lateral) buds, stem (nodes and internodes) and leaves. We will start from leaves.

5.3 The Leaf
The first and ultimate goal of every plant is photosythesis. If a plant is multicellular, it usually develops relatively large, flat structures which goal is to catch sun rays.

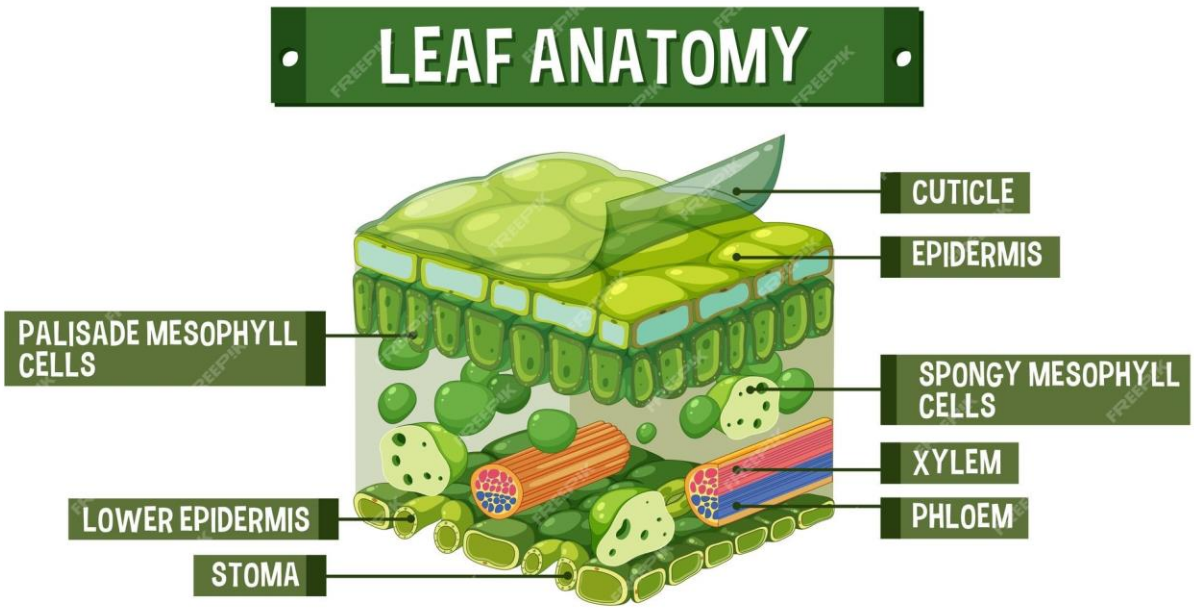


5.3.2 Anatomy of the Leaf
Anatomically, leaves consist of **epidermis** with **stomata**, **mesophyll** (kind of parenchyma) and **vascular bundles**, or veins. The mesophyll, in turn, has **palisade** and **spongy** variants.

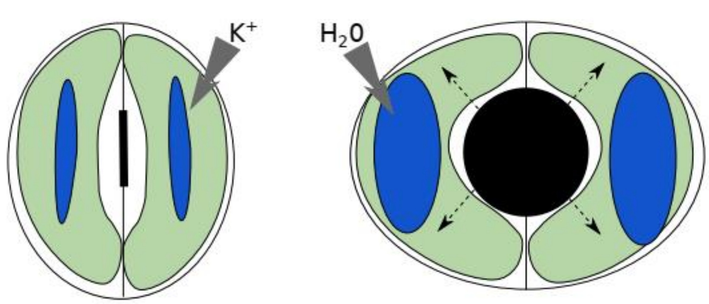
Palisade mesophyll is located in the **upper layer** and serves to **decrease the intensity of sunlight** for the spongy mesophyll, and also catches slanted sun rays. The **palisade mesophyll** consists of long, thin, tightly arranged cells with chloroplasts mostly along the sides.

The **spongy mesophyll** cells are roughly packed, they are rounded and have multiple chloroplasts.
When a typical stem vascular bundle (C3- plants) (which has xylem under phloem) enters the leaf, xylem usually faces upwards, whereas phloem faces downwards. Bundles of C4- plants have **additional bundle sheath** cells in their vascular bundles.
The epidermis includes **typical epidermal cells**, **stomata** surrounded with **guard cells**

(also optionally with **subsidiary cells**), and **trichomes**. Almost all epidermal cells are **covered with waterproof cuticle, rich of lignin and waxes**.



The stomata assist in **gas exchange**, **cooling** and **water transpiration**. There are two guard cells paired together on each side of the stoma. These guard cells are **kidney beans** shaped and have a **thicker cell wall** in the middle. The thicker cell wall on the inside makes use of the so-called "bacon effect" (when bacon slice curved on the frying pan) because thinner part of the cell wall is more flexible and therefore bends easier. The **opening** of the stoma starts from **K+ accumulation**, then **osmosis inflates guard cells**, and finally the uneven cell wall facilitates the opening of stoma. The **stoma closes** when the **potassium ions exit the cell** and **water amount decreases** in its vacuoles.



In **most cases**, the **lower epidermis contains more stomata than the upper epidermis** because the bottom of the leaf is cooler and transpiration there is safer. A similar logic is applicable to trichomes (hairs): they are also more frequent on the lower side of the leaf.

5.3.3 Ecological Forms of Plants

When plants adapt to the particular environment conditions, leaves usually respond first. Conversely, one can estimate the ecology of plant simply looking on its leaves. **In regards to water**, there are **four main types** of plants: **xerophytes**, **mesophytes**, **hygrophytes**, and **hydrophytes**.

Xerophytes are adapted to the scarce water, they could be **sclerophytes** (usually with prickly and/or rich of sclerenchyma leaves) and **succulents** (with water-accumulating stems or leaves).

Mesophytes are typical plants which adapt to regular water.

Hygrophytes live in constantly wet environment, their leaves adapted to high transpiration and sometimes even to guttation (excretion of water drops).

Hydrophytes grow in water, their leaves are frequently highly dissected to access more gases dissolved in water, and their leaf petioles and stems have air canals to supply underwater organs with gases.

In regards to **light**, plants could be **sciophytes** or **heliophytes**.

Sciophytes prefer the shade to sunlight, their leaves contain **mostly spongy mesophyll**.

Heliophytes prefer the full sun and therefore have leaves filled with **palisade mesophyll**. The

Intermediate group are “partial shade” plants. Halophytes, nitrate halophytes, oxylophytes, and calciphytes are ecological groups adapted to the over-presence of particular chemicals.

Halophyte plants are frequent, they accumulate (and look similarly to succulents), excrete or avoid (which looks like sclerophyte) sodium chloride (NaCl). They grow in salty places: sea shores, salt deserts and solonets prairies.

Nitrate halophyte plants grow on soils rich in NaNO3.

Oxylophytes grow in acidic soils.

Calciphytes grow in basic, chalk soils rich in $CaCO_3$.

psammophytes (grow on sand): Leaves will reflect adaptations to the substrate,

Petrophytes (grow on rocks)

Rheophytes (grow in fast springs). They have serious simplifications in their body plan, their leaves and stems are often reduced to form a thallus-like body.

Parasitic plants could be classified into: **Mycoparasitic** plants feed on soil fungi, **phytoparasitic** plants are either plant **root parasites** or plant **stem parasites lacking chlorophyll and photosynthesis**.

Hemiparasitic plants are those which still **have chloroplasts** but take the significant part of water **and even organic compounds** from the host plant (like mistletoe, *Viscum*).

5.4 The Stem

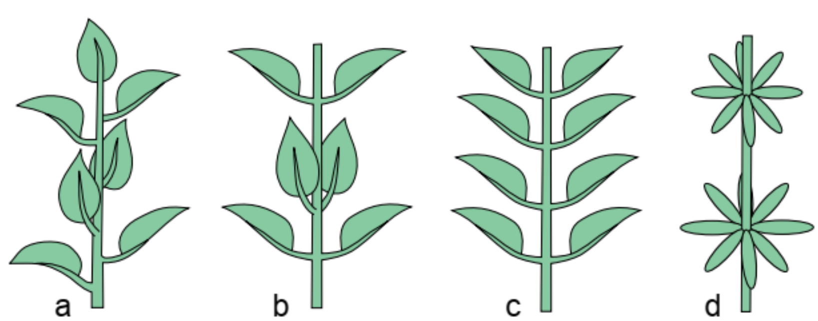
The **stem** is an *axial organ of shoot*. It has functions of support, transportation, photosynthesis, and storage. Stem has radial structure, no root hairs and grows continuously.

5.4.1 Morphology of the Stem

Stem morphology is simple. Its components are **nodes** (places where leaves are/were attached) and **internodes**, long or short (in the last case, plant sometimes appears to be stemless, rosette-like).

Stems are different by the type of **phyllotaxis**. The **phyllotaxis** refers to the **arrangement of leaves**. If there is **one leaf per node**, it is a **spiral** (**alternate**) arrangement.

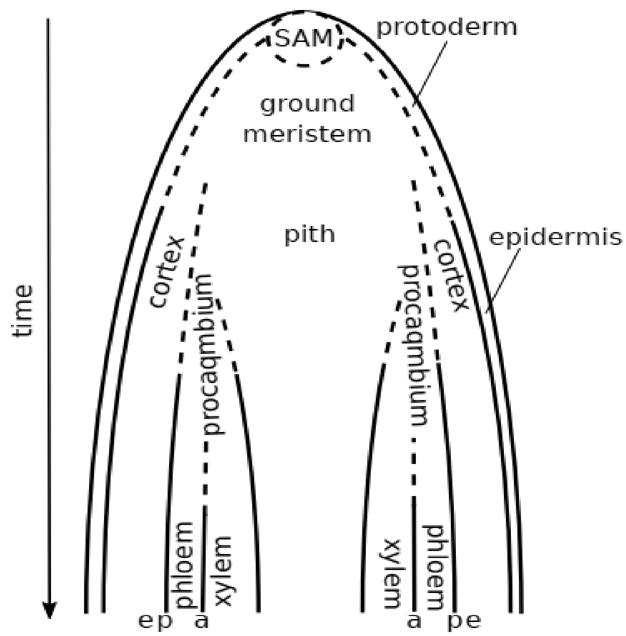
Two leaves per node means **opposite** arrangement. Opposite leaves can be all in the same plane or each pair can rotate at 90^0. If there are more than two leaves per node, it is a **whorled** arrangement, and each whorl can also rotate.



Types of phyllotaxis (leaf arrangement): a spiral (alternate), b and c opposite, d whorled.

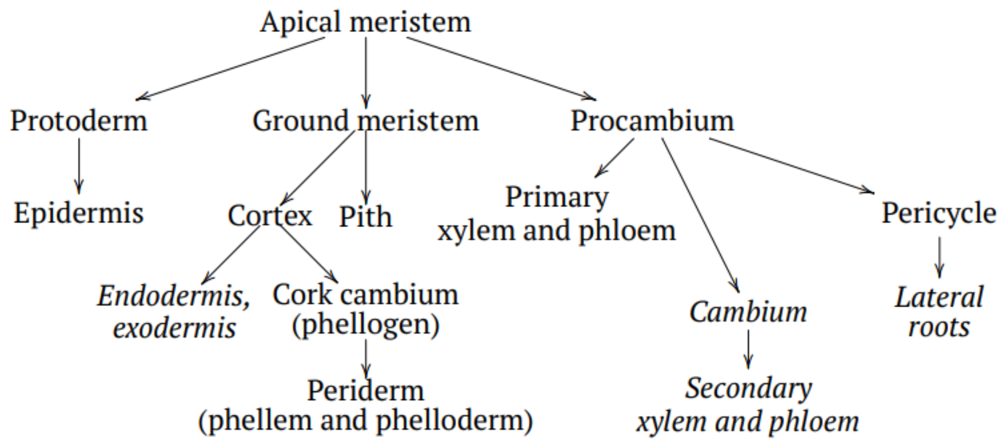
5.4.2 Anatomy of the Primary Stem

Plant evolution resulted first in the **primary stems** with no lateral meristems and secondary tissues. Only long after plants "learned" how to thicken their stems.



Developmental origin of stem tissues (simplified). Letters e, p, a show respectively where **e**ndoderm, **p**ericycle and v**a**scular c**a**mbium might appear.

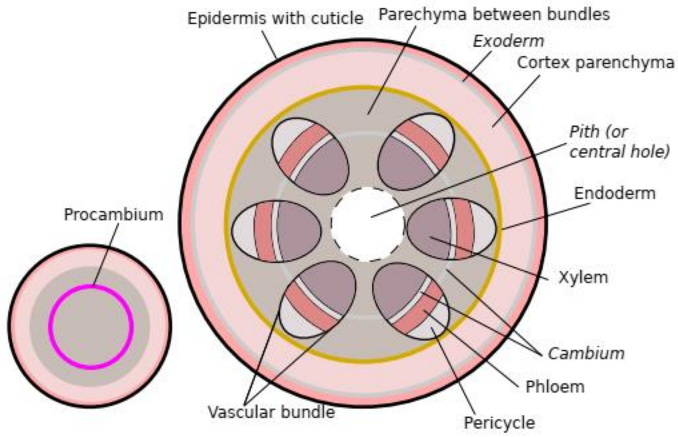
Development of stem starts from stem apical meristem (SAM) on the top of plant. The SAM produces three **primary meristems**: procambium, protoderm, and ground meristem. **Protoderm** cells differentiate into epidermal cells. The **ground meristem** differentiates into the **cortex** and **pith**. The **procambium** raises between the cortex and the pith. It forms **vascular bundles** or **vascular cylinder**.



Developmental origin of stem tissues (detailed). Root tissues have similar ways of development.

The **outer layers** of the procambium form the ***primary phloem***. The **inner layers** become the ***primary xylem***. The middle layer can be entirely spent or will make cambium for the secondary thickening. At times, the layers of the outside of the procambium can form a **pericycle**. Sometimes the innermost layer of the cortex can form an **endodermis** (endoderm), and outermost layer makes the **exodermis** (exoderm). All these layers are some kinds of the “border control” between functionally different layers of stem. Another frequent variant is the development of collenchyma in the cortex adjacent to epidermis.

Vascular bundles connect leaves and stems. In many plants, they form a ring on the cross-section of the stem. Parenchyma (ground tissue) between vascular bundles typically belongs to both cortex and pith. Another variant is a *vascular cylinder*, structure which fully encircles the stem. **Monocot** stems generally have **dispersed vascular bundles**. These three variants are **steles**, overall configurations of the primary vascular system of the plant stem. The most frequent kinds of steles are **eustele** (vascular bundles in a ring), **solenostele** (vascular cylinder) and **ataktostele** (dispersed vascular bundles).



Anatomy of the primary stem (right). *Slanted font* is used for “optional” tissues. Small image on the left is the young stem consisted of epidermis, cortex, procambium and pith.

5.5 The Root

Root is a latest evolutionary innovation in the vegetative plant anatomy. Many “primitive” plants (all mosses and even some ferns like *Psilotum*) do not have roots; some flowering water plants like the> rootless duckweed (*Wolffia*) or the coontail(*Ceratophyllum*) have also reduced their roots. However, large homoiohydric plants need the constant supply of water and minerals, and this evolutionary challenge was responded with appearance of the root system.

Root in *an axial organ of plant with geotropic growth*. One of root functions is to supply anchorage of the plant body in soil or on various surfaces. Other functions include water and mineral absorption and transport, food storage, and communication with other plants

There are two types of root systems. The first is a **fibrous root system** which has multiple big roots that branch and form a dense mass which does not have a visible primary root (“grass-like”).

The other is the **tap root system** which has one main root that has branching into lateral roots (“carrot-like”). Along with having different systems, there are different types of roots: **primary root** originated from the root of the seedling, **secondary (lateral) roots** originate from the primary roots, and **adventitious roots** originate on stems (sometimes also on leaves), the example are prop roots of screw pine (*Pandanus*).

Roots employ many different modifications which help to protect, interact and storage. For example, roots of parasitic plants are modified into **haustoria** which sink themselves into the vascular tissue of a host plant and live off of the host plant's water and nutrients.
Roots of mangroves (plants growing in ocean coastal swamps) are frequently modified into *supportive aerial roots* ("legs"). Since these swamp plants need oxygen to allow cell respiration in underground parts, there are **pneumatophores**, specialized roots which grow upward (!) and passively catch the air via multiple pores.
Plants which grow on sand (psammophytes, see above) have another problem: their substrate constantly disappears. To avoid this, plants developed **contractile roots** which may shorten and pull plant body deeper into the sand.
Some orchid roots are green and photosynthetic. However, as a rule, root is the heterotrophic organ, because root cells have no access to the light.
Root nodules present on the roots of nitrogen-fixing plants, they contain bacteria capable to deoxidize athmospheric nitrogen into ammonia: NH_3. Root nodules contain also hemoglobin-like proteins which facilitate nitrogen fixation by keeping oxygen concentration low. Nitrogen-fixing plants are especially frequent among *faboid rosids*: legumes (Leguminosae family) and many other genera (like alder, *Alnus*, or *Shepherdia*, buffaloberry) have root nodules with bacteria. Some other plants (mosquito fern, *Azolla* and dinosaur plant, *Gunnera*) employ cyanobacteria for the same purpose.
Mycorrhiza is a root modification started when fungus penetrates root and makes it more efficient in mineral and water absorption: it will exchange these for organic compounds. In addition to mycorrhizal fungi, **endophytic fungi** inhabit other plant organs and tissues

5.5.2 Anatomy of the Root

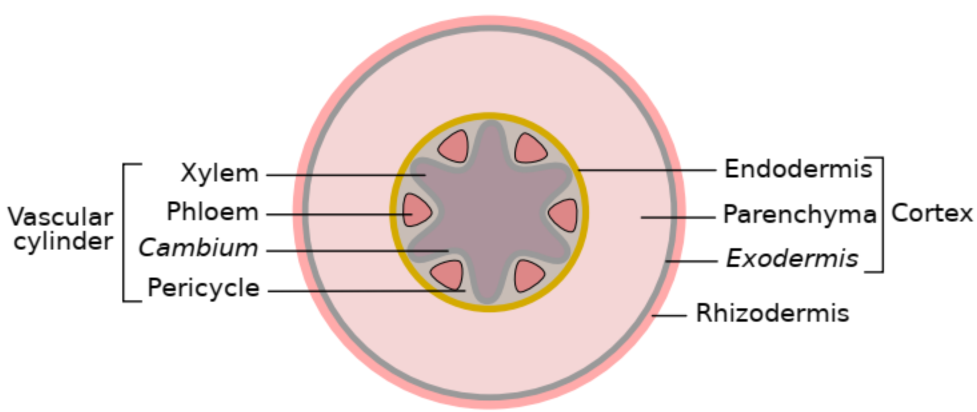
On the *longitudinal section* of young growing root, there are different horizontal layers, zones: root cap covering *division zone*, *elongation zone*, *absorption zone*, and *maturation zone*. The **root cap** protects the root apical meristem (RAM), which is a group of small regularly shaped cells. A small, centrally located part of the RAM is the **quiescent center** where initial cells divide and produce all other cells of root. Root cap is responsible for the geotropic growth, if the root tip comes into contact with a barrier, root cap will feel it and will grow on a different direction to go around it.

The **elongation zone** is where the cells start to elongate, giving it length. The **absorption zone** is where the rhizodermis tissue (root hairs) develops and where water and nutrients are absorbed and brought into the plant. Within the **maturation zone**, root hairs degrade, many cells start to acquire secondary walls and lateral roots develop.

On the *cross-section* of the root made within absorption zone, the first tissue is the rhizodermis, which is also known as the root epidermis, then cortex, which segregates external *exodermis* and internal *endodermis* one-cellular layers, and vascular cylinder. Typically, roots have no pith. In some cases (for example, in orchids), cortex may give multi-layered *velamen* (see above), another absorption tissue.

Vascular cylinder is located in the center of the root, it contains the pericycle which is made of mostly parenchyma and bordering endodermis. Pericycle cells may be used for storage, they contribute to the vascular cambium, and initiate the development of lateral roots (consequently, lateral roots are developing endogenously and break tissues located outside). Root phloem is arranged in several strands whereas xylem typically has a radial, sometimes star-shaped structure with few rays. In the last case, phloem strands are located between rays of xylem.

Root tissues develop in the way similar to stem, RAM gave rise to ground meristem, procambium, and the protoderm, which in turn make all primary tissues mentioned above. Later, pericycle develops into lateral roots or the vascular cambium which in turn produces into the secondary xylem and phloem. The secondary root is similar to secondary stem (see below)



Anatomy of root: cross-section through the maturation zone